JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1975, 25, 143-156 NUMBER 2 (MARCH)

DETECTION OF THE VELOCITY OF MOVEMENT OF VISUAL STIMULI BY PIGEONS[1]

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Nine pigeons were trained to discriminate a moving stimulus from a stationary stimulus. In one experiment, the stimulus was a rotating disc with radial stripes. In a second experiment, the stimulus was a vertically moving film strip with horizontal bars. Several psychophysical procedures were used to determine the minimal detectable velocity of movement. The detection thresholds for most of the pigeons fell in the range of 4.4 to 6.5 millimeters per second, corresponding to a retinal velocity of 4.1 to 6.01 degrees per second. A signal-detection analysis of the psychophysical data indicated systematic changes in response bias that were related to the ordinal position of the stimulus velocity in the sequence.

Key words: movement discrimination, movement detection, movement threshold, animal psychophysics, signal detection, stimulus velocity, key peck, pigeons

Movement is one of the fundamental properties of visual stimuli. The detection of absolute and relative rates of movement of stimuli is crucial for the survival of all organisms that are capable of detecting patterned light. Such basic survival mechanisms as predation, avoidance of predators, food gathering in nonpredators, and locomotion through the habitat are all highly dependent upon motion detection. The importance of movement discrimination to survival in human civilizations does not require description here. Physiologists have recognized the importance of motion detection and have made extensive use of moving stimuli in their explorations of the visual system (Barlow and Hill, 1963; Finkelstein and Grüsser, 1965; Maturana and Frenk, 1963; Straschill and Taghavy, 1967). Psychologists studying human vision have also devoted considerable effort to investigating perception of visual movement (Gibson, 1968; Graham, 1968). In contrast, animal psychologists have devoted relatively little effort to this important aspect of visual functioning. Since Kennedy's (1936) review of the early literature on motion perception in animals, little additional information has been added to the literature. Indeed, the past three decades have seen virtually no systematic investigations of the minimal detectability of moving stimuli by animals.

Our initial attempts to use moving stimuli consisted of requiring pigeons to discriminate between two radially striped discs, one of which was stationary and the other rotating at one revolution per minute (rpm). In spite of all of the various discrimination training techniques employed, the performance of the pigeons remained at chance. Finally, we changed the rotation rate of the moving disc to 10 rpm. All subjects immediately showed dramatic improvement in performance and rapidly satisfied our criterion of discrimination. This preliminary study suggested that the minimal detectable velocity was somewhere between 1 rpm and 10 rpm of the stimulus disc. We therefore embarked upon a series of psychophysical investigations to determine the minimal detectable velocity of a moving stimulus.

EXPERIMENT I: DETECTION OF ROTARY MOVEMENT

METHOD

Subjects

Five White Carneaux Pigeons (*Columba livia*), obtained from Palmetto Pigeon Plant, Sumter, S.C., were 4 to 5 yr of age at the start of the experiment. They were maintained at approximately 75% of free-feeding weights throughout the experiment.

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[1] Reprints may be obtained from Dr. William Hodos, Department of Psychology, University of Maryland, College Park, Maryland 20742. Portions of this research were supported by Grant No. EY-00735 from the National Eye Institute. The manuscript was prepared for publication by Janice Wildberger.

Apparatus

The experimental chamber was a Plexiglas compartment 30 cm long, 23 cm wide, and 30 cm high. The interior walls were flat black. Three holes, each 21 mm in diameter, were drilled in one wall at a height of 22 cm. The holes were spaced 7 cm apart. A Lehigh Valley Electronics pigeon key was mounted behind each hole. The key behind the center hole was transparent and the two side keys were translucent. A square opening below the center key provided access to a Lehigh Valley Electronics grain dispenser. A diagram of the chamber is shown in Figure 1. A disc of translucent Plexiglas, 68 mm in diameter was positioned 17 mm behind the center key. The surface of the disc that was visible through the transparent center key had radially arranged black stripes, 2.0 mm wide. A small sector of the disc, bearing three or four stripes was visible through the center key at all times (see Figure 1). The disc was mounted on the shaft of a variable-speed ac motor (R.M.S. Motor Co., Binghampton, N.Y.). The motor speed was controlled by supplying the appropriate resistor to the speed-control circuit of the motor. The disc speed was calibrated by a sector disc mounted on the shaft of the motor. Light passing through the sector disc was detected by a photocell. Voltage changes in the photocell were recorded on an oscilloscope.[2] The speed of the disc was determined from the outermost point of the radial stripes that was visible through the center key, since this point would travel the greatest distance per revolution and hence would have the highest velocity. The velocity range of the disc was from 15.7 to 2.3 mm/sec. The velocity of the outer tip of the second hand (13.3 cm in length) of an office clock (29 cm diameter) is 13.9 mm/sec.

To minimize the likelihood of the pigeons discriminating extraneous vibratory cues from the motor, which would be correlated with motor speed, the following precautions were taken. First, the motor was shock-mounted to minimize the transfer of vibratory cues to the pigeon's compartment. Second, a small exhaust blower with worn bearings and in need of oil was loosely mounted on the outer wall of the pigeon's compartment to provide a masking vibration. Third, a loudspeaker mounted inside the pigeon's compartment delivered white noise (85 dBA) to mask any auditory cues that might be present. As a check on the effectiveness of these procedures, after each pigeon had completed training on the basic velocity discrimination, the disc was disengaged from the motor shaft, so that it would remain stationary irrespective of the speed of the motor. The pigeon was then given a full session in which the motor ran or was stationary according to the discrimination sequence, but in which the disc was always stationary. All subjects performed in the range of 40 to 60% correct during this test; at no time was there any evidence to suggest that vibratory or acoustical cues were controlling the subjects' behavior.

The disc and side keys were each trans-illuminated by a General Electric 1812 lamp powered through a regulated 28-V dc power supply. The interior of the pigeons, compartment was illuminated by the same type of lamp. Photometric determinations of ambient illumination and key luminances were not taken during Experiment I. However, since the same illumination sources were used in Experiment II, with the exception of the center key, the illumination and key luminances in Experiment I can be assumed to be roughly the same as those in Experiment II.

Stimulus sequences, collection of data, delivery of reinforcers, and other contingencies were controlled by a system of timers, switches, and relays.

Procedure

The subjects were first trained to peck the illuminated side keys. Pecks on either key were

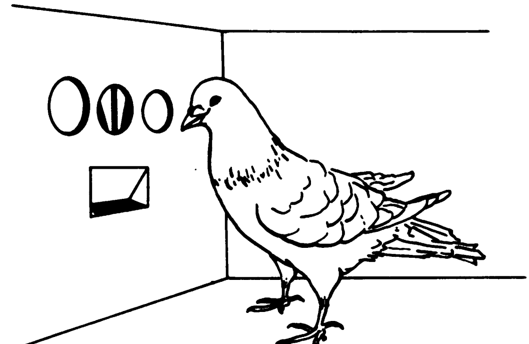

Fig. 1. The testing chamber and stimulus used in Experiment I.

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[2] We wish to express our gratitude to Maurice E. T. Swinnen and Lee Fallon of the Biomedical Instrumentation of the Walter Reed Army Institute for Research for designing and constructing the remote speed-selection circuit and the calibration system.

reinforced with 2- to 5-sec access to the grain dispenser. While grain was available, the keys were darkened and a magazine light was turned on. Subsequently, pecks on the illuminated center key were reinforced by illumination of the side keys. The center key was darkened when side keys were illuminated. The subjects were gradually trained to complete 30 pecks on the center key before the side keys were illuminated. Generally, the 30 pecks were emitted in about 10 to 12 sec. Following this preliminary training, the disc was positioned behind the center key and subjects were trained to discriminate between the moving and the stationary stimulus. On trials in which the stationary disc had been presented, a peck on the left-side key was reinforced. A peck on the right-side key was reinforced when a moving disc had been shown. Correct responses were reinforced on a 50% random probability basis. The moving and stationary conditions of the motor were presented in a quasi-random discrimination sequence. On trials with stimulus movement, the velocity of the disc was 15.7 mm/sec. Pecks on incorrect side keys were followed by 5 sec of darkness. Pecks on the keys were ineffective during the reinforcement and "blackout" periods. Following an error, a noncorrection procedure was used, *i.e.*, a new trial was immediately started following the period of darkness for an incorrect response. Each session was terminated after 180 trials. The criterion of discrimination was satisfied when errors were 10% or less of the total trials for three successive sessions.

When each subject had met the criterion, psychophysical testing was started. The test phase consisted of a series of alternate training and testing sessions. On days following training on the basic discrimination, the subjects were tested using a modified method of constant stimuli in which the velocity of the disc was decreased in successive blocks of 10 trials. In each block, five moving and five stationary trials were scheduled in a quasi-random sequence. The first block of trials began with the velocity that had been in effect during training (15.7 mm/sec). On each subsequent block, the velocity of the disc was reduced. In the ninth and last block, the velocity of the disc was 2.3 mm/sec. Following is a list of the block numbers (in parentheses) and respective stimulus velocities (mm/sec): (1) 15.7; (2) 12.2; (3) 10.5; (4) 8.8; (5) 7.3; (6) 5.5; (7) 4.3; (8) 2.7; (9) 2.3. After the ninth block, the entire descending series repeated. Thus, each testing session consisted of 20 trials at each of the nine velocities, totalling 180 trials for the session. The reinforcement contingencies were the same as in the training sessions.

The percentage of correct responses at each velocity during the testing sessions was plotted to form a psychometric function. The velocity that corresponded to 75% correct (half way between chance performance and perfect detection) on the psychometric function was taken to represent the point of subjective equality. Since the standard had a velocity of zero, the point of subjective equality is equivalent to the movement-detection threshold.

Testing was continued until the criterion of threshold stability was satisfied. The criterion was that the range of thresholds obtained in five successive testing sessions should not exceed ±25% of the mean of those five sessions. For example, if the mean threshold for five successive sessions were 4.0 mm/sec, this mean would be regarded as stable only if the five individual thresholds fell within the range of 3.0 to 5.0 mm/sec. On several occasions, the psychometric function crossed the 75% correct line twice. Such sessions were discarded to avoid the ambiguities of interpretation that such data provide.

RESULTS

Figure 2 summarizes the results of the preliminary training on the coarse motion discrimination task of 15.7 mm/sec *versus* a stationary stimulus. All five subjects required an unusually large number of sessions to acquire this discrimination. Pigeon C-102 acquired the discrimination in 29 sessions, the smallest number for any subject. Pigeon C-166 reached the criterion of discrimination in 57 sessions. Pigeons C-117 and C-094 each performed at chance for long periods, followed by a sudden improvement in performance. C-102 and C-152 each had long periods of chance performance followed by a gradual improvement in discrimination. C-166 showed an erratic performance during preliminary training.

Figure 3 presents mean psychometric functions of two subjects, C-102, which had the lowest threshold, and C-152, which had the

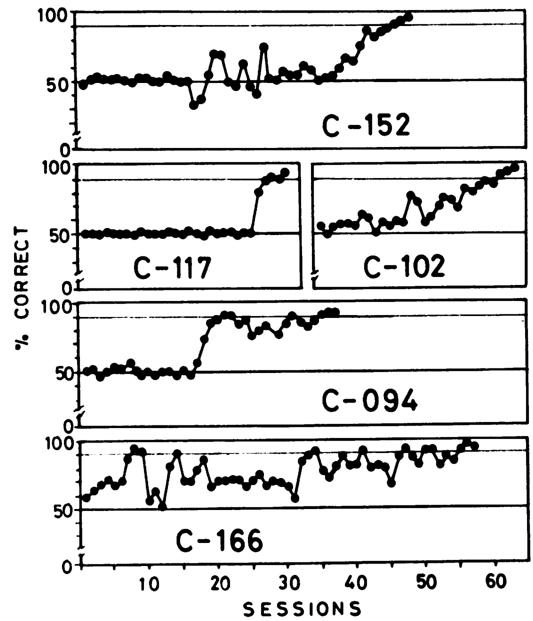

Fig. 2. Acquisition of the discrimination of rotary movement of 15.7 mm/sec from a stationary stimulus.

highest. The stimulus velocity at which each psychometric function crossed the 75% correct line was taken as the point of subjective equality. Since the standard stimulus had a velocity of zero, the point of subjective equality was equal to the threshold. These mean psychometric functions were calculated from the data of the five successive sessions of stable thresholds. Each data point represents the mean of 100 trials.

Figure 4 depicts the development of stable thresholds in each subject. Each point represents the movement-detection threshold in each successive session. Broken lines indicate sessions in which the entire psychometric function was below 75% correct and therefore no threshold could be calculated. The open circle at the end of each graph represents the mean of the five stable sessions and the vertical bar represents the ±25% range. In general, the birds tended to stabilize rather rapidly and did not show much improvement in threshold beyond their initial sessions of psychophysical testing.

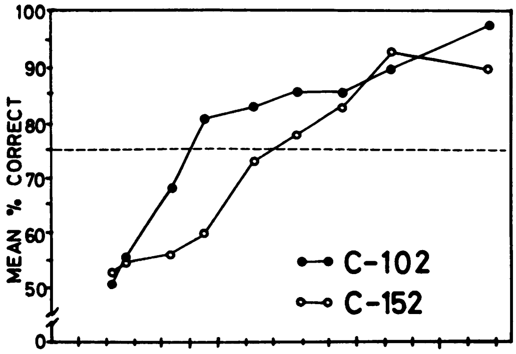

Fig. 3. Mean stable psychometric functions of the pigeons with the highest (C-152) and lowest (C-102) detection thresholds for rotary movement.

In addition to a conventional psychophysical analysis of the data, a signal-detection analysis (Green and Swets, 1966) was carried out. Table 1 presents the results of this analysis; data are presented separately for each stimulus velocity. The data were calculated from the five stable sessions. The "hit" values are the percentage of correct responses when the stimulus was moving. The "false-alarm" values are one minus the percentage correct when the stimulus was stationary. The value A′ is a nonparametric index of detectability that is free from response bias (Pollack and Norman, 1964). A′ is comparable in some ways to the detectability index d′ (Green and Swets, 1966), but does not make such strong assump-

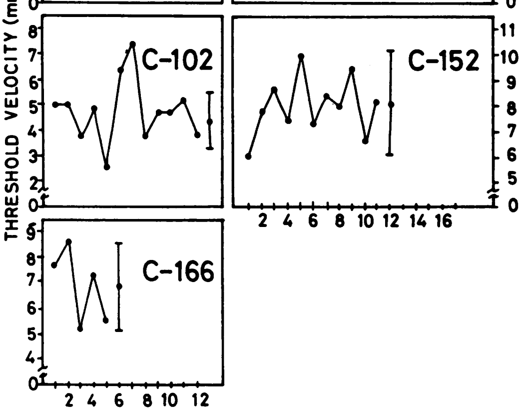

Fig. 4. Successive thresholds of rotary movement detection. The open circle at the end of each graph indicates the mean of the last five sessions. The vertical bar represents the ±25% stability range.

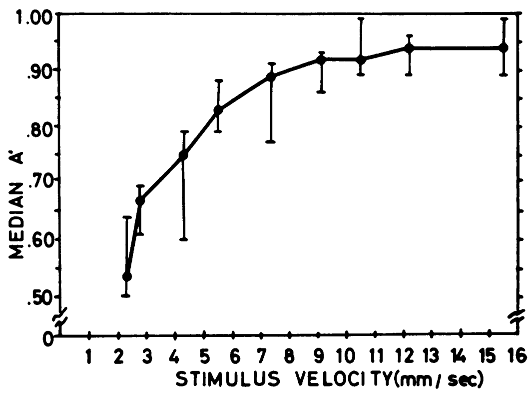

Fig. 5. The index of detectability, A′, plotted as a function of stimulus velocity. Each point represents the median A′ of all subjects during the five stable sessions. The vertical bars represent the range of individual values of each median.

tions about the statistical properties of the underlying distributions of nervous system events that are present during the occurrence of the signal and noise conditions. A′ varies from 1.00 (perfect detection) to 0.50 (no detection). The value %B is a nonparametric index of response bias that is related to A′ (Hodos, 1970). %B varies from +100 (strong preference for the right-side key, strong preference for the moving stimulus, very conservative observer, high criterion) through 0% (no preference for either key, no preference for either stimulus, unbiased observer) to −100% (strong preference for the left key, strong preference for the stationary stimulus, very liberal observer, low criterion). In general, the data indicate that as stimulus velocity decreased, "hits" declined, but "false alarms" tended to remain rather constant.

Figure 5 summarizes the signal-detection analysis. The median value of A′ has been plotted as a function of stimulus velocity. The vertical bars indicate the range of A′ values from which the median was determined.

Figure 6 is a graphic representation of the response bias data. Two patterns of response bias as a function of stimulus velocity are indicated in the figure. The upper panel, which presents the data of Pigeons C-102 and C-152, shows that at the highest velocity, the birds had a strong positive bias: *i.e.*, a preference for the side key associated with the moving stimulus. At the second highest velocity, the birds showed a negative bias or preference for the key associated with the stationary stimulus. This was followed by a return to a positive and relatively constant bias at the remaining lower velocities. The lower panel, which presents the data of Pigeons C-117, C-094, and C-166, shows a negative (stationary) bias at the highest velocity, followed by a progressive shift to a positive (moving) bias as stimulus velocity declined and no bias at the lowest velocity.

DISCUSSION

The results of the preliminary training experiment confirmed the results of our earlier pilot study, which suggested that pigeons do not discriminate low velocities of movement and that they are very difficult to train to discriminate between moving and stationary stimuli. The large numbers of successive sessions at chance performance and the large numbers of sessions required to reach criterion in a discrimination task in which the difference between the discriminanda was immediately obvious to human observers were surprising in view of the otherwise excellent vision of these

Table 1

Signal-Detection Analysis of Experiment I

	C-094		*C-102*		*C-117*		*C-152*		*C-166*	
Stimulus Velocity (mm/sec)	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*
15.7	0.98	0.10	0.98	0.00	0.86	0.18	0.88	0.08	0.98	0.38
12.2	0.88	0.12	0.92	0.12	0.78	0.02	0.94	0.08	0.90	0.28
10.5	0.92	0.10	0.84	0.12	0.96	0.00	0.74	0.08	0.92	0.30
8.8	0.84	0.10	0.84	0.12	0.90	0.04	0.68	0.12	0.78	0.22
7.3	0.74	0.06	0.82	0.16	0.64	0.04	0.60	0.14	0.47	0.38
5.5	0.50	0.06	0.80	0.18	0.38	0.02	0.34	0.14	0.58	0.18
4.3	0.26	0.06	0.48	0.12	0.24	0.02	0.18	0.06	0.42	0.32
2.7	0.18	0.08	0.24	0.12	0.12	0.04	0.16	0.06	0.46	0.34
2.3	0.22	0.22	0.20	0.18	0.08	0.08	0.12	0.06	0.46	0.42

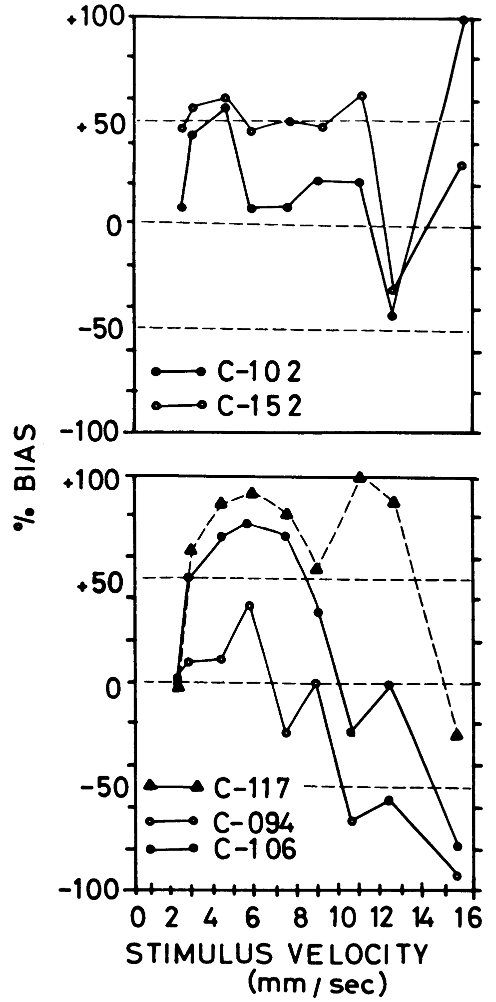

Fig. 6. Response bias plotted as a function of stimulus velocity.

birds (Blough, 1971, 1973; Hodos and Bonbright, 1972; Hodos, Leibowitz, and Bonbright, 1976). Equally unexpected, following this tortuous acquisition, was the rapid stabilization of the psychophysical performance.

Pigeon C-102 had the lowest thresholds of any in this experiment during the first two psychophysical sessions, and eventually stabilized at a much higher threshold. In view of the number of sessions in which this bird's thresholds were below the lower limit of the ±25% stability range, we must seriously question whether stability, as defined for purposes of this experiment, is really descriptive of this bird's ultimate capability to detect movement or whether continued testing might not have resulted in a lower stabilization point.

The signal-detection analysis indicated that the index of detectability was systematically related to stimulus velocity in each subject. The lowest velocities generally had detectabilities in the vicinity of $A' = 0.50$, which indicates that these velocities were virtually undetectable to the pigeons. A notable exception was Pigeon C-152. This bird had a value of $A' = 0.64$ at a velocity of 2.3 mm/sec. This indicates that this velocity was more detectable to it than it was to the other birds. Thus, according to the signal-detection analysis, C-152 was the most sensitive pigeon. However, according to the threshold analysis, C-152 was the least sensitive subject because it had the highest threshold. Furthermore, this bird's A' values were below the group median at most of the other velocities. Moreover, an examination of the data of the five individual sessions that were averaged to produce the mean hit and false-alarm scores suggested that the higher value of A' at 2.3 mm/sec was mainly due to one exceptionally good session, in which $A' = 0.77$. The mean hit and false-alarm rates of the remaining four values resulted in a value of A' of 0.50. Therefore, we conclude that the seemingly greater sensitivity of C-152 is an artifact of averaging.

The systematic changes in response bias as a function of stimulus velocity are suggestive of sharp changes in response criterion by the subjects as the session progressed. Unfortunately, we have no data from an ascending series of velocities and therefore are unable to determine from the data of this experiment, whether these changes in response bias are related to the velocity of the stimulus *per se* or merely its ordinal position in the series. The extreme negative response biases that are associated with the highest velocities were accompanied by very high detectability scores. Thus, they are generally not the result of very high false-alarm rates, as would be the case with stimuli of moderate or low detectability. Indeed, as Table 2 indicates, the false-alarm rates tended to be rather low and constant irrespective of stimulus velocity. Thus, the sharp changes in criterion were mainly expressed by changes in the hit rate.

To relate the psychophysical data to events in the central nervous system, one must know the velocity of the retinal image of the stimulus. To calculate the retinal image velocity in degrees of visual angle per second, the distance from the stimulus to the anterior nodal point of the eye must be known. We have no accurate measurements of the distance from which the pigeons inspected the stimuli in this experiment. However, Hodos *et al.* (1976) measured the inspection distance through the use of high-speed photography (1000 frames per second) in a study of visual acuity in a similar apparatus. These films indicated that when the pigeons were closest to the stimulus (*i.e.,* when the beak was against the key and the key was maximally depressed) the eyelids were closed. Therefore, this most conservative estimate of the inspection distance is also the least meaningful. They also reported the distance from the stimulus to the eye at which the peck was initiated, which they concluded was the inspection distance, and an intermediate distance at which the lid was half-opened. These near, mid, and far points were 43.3 mm, 51.2 mm, and 62.0 mm, respectively. These values include 3.46 mm from the external surface of the cornea to the anterior nodal point of the eye (Marshall, Mellerio, and Palmer, 1973). Using these estimates, threshold retinal image velocities were calculated for each subject and are presented in Table 2. The table indicates that the mean stimulus velocity at threshold, 6.10 mm/sec, corresponds to near, mid, and far retinal image velocities of 8.11, 6.78, and 5.64 deg/sec. The last of these is probably the most meaningful.

Table 2

Movement-Detection Thresholds in Experiment I

Pigeon	*Stimulus Velocity at Threshold (mm/sec)*	*Retinal Image Velocity at Threshold (deg/sec)*		
		Near	*Mid*	*Far*
C-094	4.58	6.06	5.13	4.23
C-102	4.44	5.91	4.97	4.10
C-117	6.50	8.64	7.28	6.01
C-152	8.14	10.82	9.12	7.52
C-166	6.86	9.12	7.39	6.34
Mean	6.10	8.11	6.78	5.64
Median	6.50	8.64	7.28	6.01

EXPERIMENT II: DETECTION OF LINEAR MOVEMENT

Subjects

Four White Carneaux pigeons, from the same source and in the same age range as the subjects in Experiment I, were maintained at about 75% of free-feeding weights.

Apparatus

In view of the unusually protracted acquisition phase of Experiment I, a number of changes were made in both the stimulus and the procedure in the hope of improving performance. The stimulus was changed from the rotary motion of radial stripes to the linear motion of horizontal stripes. This was accomplished by fixing 12.5-mm wide strips of black tape 28.5 mm apart on a continuous loop of transparent 35-mm film. The motor used in Experiment I was used to drive a system of gears and pulleys that smoothly advanced the film strip through a set of plastic guides mounted behind the center key. The dimensions of the center key were 40 by 30 mm. This system provided a range of velocities similar to those used in Experiment I. The velocity range in Experiment II was from 13.6 mm/sec to 3.0 mm/sec. The following list indicates velocities (in mm/sec) used in each block of the procedure in Experiment II: (1) 13.6; (2) 9.0; (3) 7.0; (4) 5.8; (5) 4.7; (6) 3.0. For one pigeon, the velocity range had to be reduced to obtain velocities less than 3.0 mm/sec. This was accomplished by replacing one of the drive pulleys with a smaller pulley, which resulted in a velocity range from 7.4 mm/sec to 1.7 mm/sec. The range of velocities obtained with the small pulley is referred to as the "low range" and is presented the following list: (1) 7.4; (2) 5.2; (3) 3.9; (4) 3.1; (5) 2.4; (6) 1.7.

The light source for the center key was an optical and illumination system salvaged from a film-strip projector of unknown manufacture. The lamp was a Radiant 100W CDX projection lamp powered through a Sorenson voltage regulator. The light from this optical system was projected on a translucent Plexiglas diffusing screen mounted between the light source and the film strip. This was intended to provide a high-luminance, diffuse background for the black stripes. A solenoid-operated shutter was mounted between the light source and the diffusion screen. In all other respects, the apparatus was the same as that used in Experiment I. The key luminances were measured with an SEI photometer. The ambient chamber illumination was determined by measuring the luminance of a

Leeds and Northrup test plate of calibrated reflectance. The luminance of the center key, in the region between the black bars was 70.0 cd/m^2. The left and right side-key luminances were 9.6 and 18.9 cd/m^2, respectively. The chamber illumination, with the center key illuminated was 13.7 lx, with the side keys illuminated 15.1 lx, and with the feeder illuminated was 19.0 lx. A diagram of the chamber is shown in Figure 7.

Procedure

During Experiment I, a number of other procedures were developed in other psychophysical studies in our laboratory (Hodos and Bonbright, 1972; Hodos *et al.*, 1976; Krasnegor and Hodos, 1974) that were more efficient than the procedure used in Experiment I. We decided to incorporate some of these procedures into the method of Experiment II. The procedural changes were as follows: (1) A "warm-up" period, consisting of the largest difference in velocity (13.6 mm/sec *versus* a stationary stimulus) was presented for 20 trials. The data from this warm-up period were discarded. (2) The warm-up was followed by a block of 20 trials with the same stimuli, which was called the "assessment" block. If the bird's performance during the assessment block was less than 90% correct, the program did not advance into the other blocks and the session was a training session. However, if performance in the assessment block was 90% correct or better, then the program advanced through the additional blocks of slower stimulus movements and the session was a psychophysical testing session. After the final stimulus block, the program returned to the first stimulus block and after another "warm-up" block (data discarded), a second descending series was begun. Since the decision had already been made that the session was to be a testing session, no assessment contingency was in effect on the second descending series of velocities. (3) Only six velocities were used, instead of nine as in Experiment I. Thus, each psychophysical testing session consisted of 240 testing trials plus 40 warm-up trials. A training session consisted of 240 trials on the first velocity (13.6 mm/sec) plus 20 warm-up trials. (4) A correction procedure was used in which the stimulus did not advance following an error until the correct response was made. Following a correction response, the feeder light was illuminated, but grain was not available. In all other respects, the procedure was the same as in Experiment I.

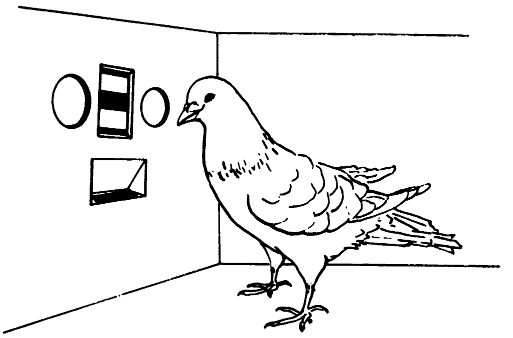

Fig. 7. The testing chamber and stimulus used in Experiment II.

RESULTS

The acquisition curves for the preliminary discrimination of 13.6 mm/sec *versus* a stationary stimulus are shown in Figure 8. These curves indicate performance in each session until the first session in which the birds satisfied the assessment requirement of 90% correct or better in the first stimulus block following the warm-up. Subsequent failures of assessment (*i.e.*, training sessions) are not shown. Pigeons C-460 and C-470 showed chance performance initially followed by a gradual, progressive improvement in discrimination. Pigeons C-312 and C-235 each exceeded the 90% correct point in their fourth session. However, their subsequent performance tended to oscillate between good and poor discrimination. In spite of their early high performance on the training task, these pigeons did not satisfy the assessment requirement any more rapidly than did C-460 and C-470.

Figure 9 presents psychometric functions that represent the extremes of psychophysical performance observed in Experiment II. These data were collected during the five stable sessions. Each data point represents the mean of 200 trials. Pigeon C-470 had a stable threshold of 5.62 mm/sec, which was the highest threshold of any of the four pigeons in this experiment. Pigeon C-235 had a threshold of 4.4 mm/sec, which was the lowest threshold of the group. However, in several of the stable sessions, C-235 scored 75% correct at the lowest stimulus velocity, which was 3.0 mm/sec. Therefore, we assessed the motion-detection ability of this bird in a lower velocity range; *i.e.*, 7.4 mm/sec to 1.7 mm/sec. This psycho-

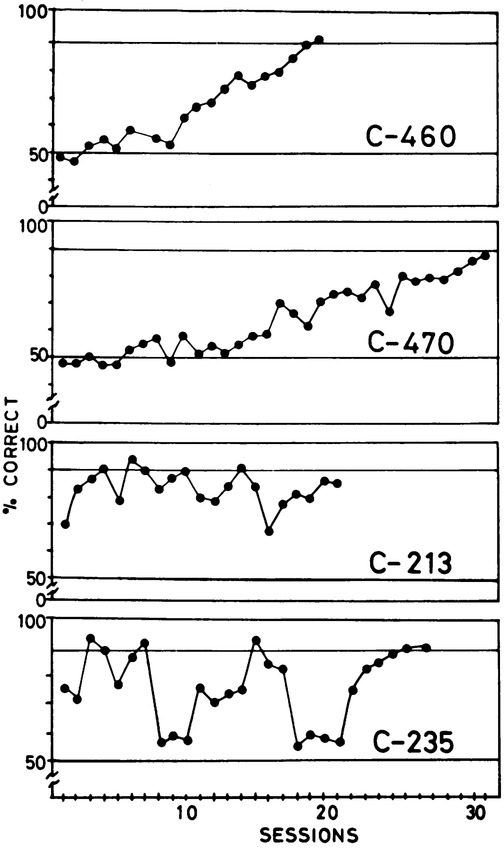

Fig. 8. Acquisition of the discrimination of vertical movement of 13.6 mm/sec from a stationary stimulus.

metric function is also presented in Figure 9. The movement-detection threshold of C-235 in this range of velocities was 2.74 mm/sec.

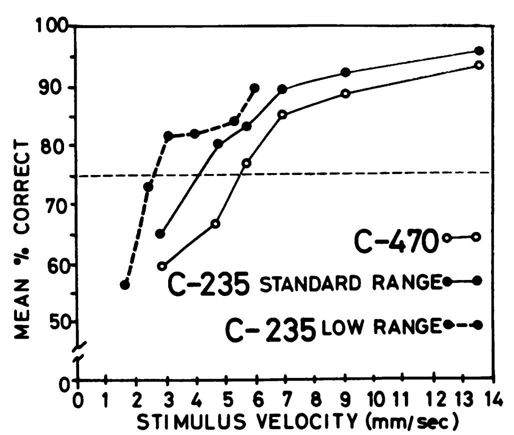

Fig. 9. Mean stable psychometric functions of the pigeons with the highest (C-470) and lowest (C-235) detection thresholds for vertical movement. Data are shown for Pigeon C-235 for both the standard and low velocity ranges.

The development of threshold stability is shown in Figure 10. The open circle and vertical bar at the end of each graph indicate the mean of the five stable sessions and the ±25% range. Three of the four birds, C-235, C-470, and C-460 gave evidence of a progressive decrease in threshold as psychophysical testing progressed. Pigeon C-213 remained at approximately the same average threshold throughout psychophysical testing. In all cases, failures to satisfy the assessment requirement were frequent. For example, of a total of 119 sessions following the first psychophysical session for C-470, only in 43 sessions was the assessment requirement satisfied. The total number of sessions to achieve stability is indicated for each bird. Although the psychophysical performance curves are shown as continuous lines, adjacent points were frequently separated by several training sessions resulting from failures to satisfy the assessment requirement. The high number of assessment failures in C-470 prompted us to extend the stability period to eight sessions to increase confidence that this bird's performance had indeed stabilized.

A signal-detection analysis was performed on the data of the five stable sessions for each

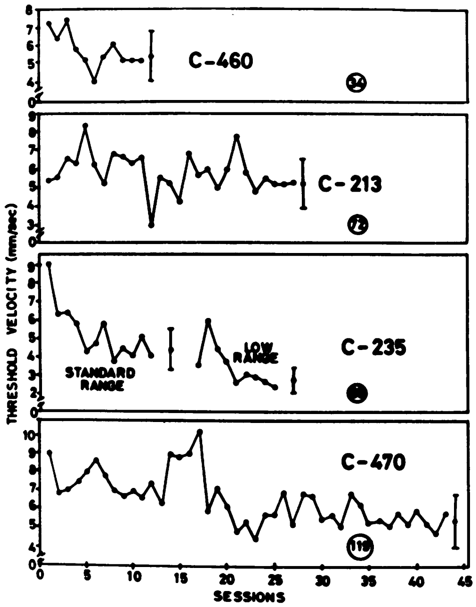

Fig. 10. Successive thresholds of vertical movement detection. The open circle at the end of each graph indicates the mean of the last five sessions. The vertical bar represents the ±25% stability range. The encircled number in each panel indicates the total number of sessions following acquisition of the discrimination of 13.6 mm/sec *versus* a stationary stimulus.

subject in Experiment II; Table 3 presents the results. The table indicates that as stimulus velocity decreased, "hits" declined, but "false alarms" tended to remain constant. The median detectability (A′) of each velocity for all subjects is graphically depicted in Figure 11. The vertical bars represent the range of values for each median A′. This curve includes the data of Pigeon C-235 that were obtained using the standard range of velocities. The open circles indicate this bird's performance using the low range of velocities. In the case of Pigeon C-235, the data are shown separately for the velocities produced by the standard pulley and the lower range produced by the small pulley. In each case, the index of detectability, A′, varied monotonically with decreasing stimulus velocity. However, the detectability index of the lowest velocity, 3.0 mm/sec, ranged from 0.68 to 0.74, which indicates that these velocities are quite detectable, even though they are "below threshold". The velocity of the lower range that was closest to the lowest velocity of the standard range was 3.1 mm/sec. Pigeon C-235 had a detectability index of A′ = 0.89 for the 3.1 mm/sec stimulus, which indicates that this velocity was highly detectable. The lowest velocity of the small pulley range was 1.7 mm/sec. Pigeon C-235 had a detectability index of A′ = 0.60 for this stimulus, which indicates that the movement was still detectable to the subject, even though this velocity was "below threshold" according to the traditional psychometric function.

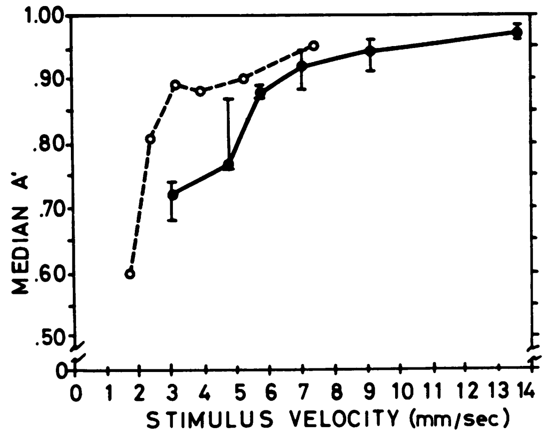

Fig. 11. The index of detectability, A′, plotted as a function of stimulus velocity. The filled circles represent the median A′ of all subjects during the five stable sessions. The vertical bars represent the range of individual values of each median. These medians include the performance of C-235 in the standard velocity range. The open circles indicate A′ as a function of stimulus velocity in the low range for C-235.

The analysis of response bias indicated a systematic relationship between stimulus velocity and response bias in every subject. The response bias data are presented in Figure 12. The response bias curves have the general form of an inverted U-curve with a negative bias at the highest velocities, a moderate to strong positive bias at the intermediate velocities, and a decline toward zero bias at the lowest velocities. Pigeon C-235 had this type of bias curve for its performance in both the standard and low-velocity ranges.

Table 3

Signal-Detection Analysis of Experiment II

	C-235			*C-213*		*C-460*		*C-470*	
	Stimulus Velocity (mm/sec)	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*	*Mean Hit*	*Mean False Alarm*
Standard Range									
	13.6	0.99	0.08	0.97	0.10	0.94	0.08	0.97	0.10
	9.1	0.89	0.05	0.84	0.15	0.84	0.10	0.83	0.05
	7.0	0.88	0.09	0.83	0.21	0.82	0.10	0.80	0.08
	5.8	0.81	0.16	0.73	0.13	0.76	0.15	0.61	0.07
	4.7	0.78	0.14	0.66	0.29	0.59	0.23	0.52	0.19
	3.0	0.52	0.22	0.59	0.30	0.49	0.26	0.39	0.20
Low Range									
	7.4	0.98	0.19						
	5.2	0.84	0.16						
	3.9	0.77	0.16						
	3.1	0.76	0.13						
	2.4	0.68	0.23						
	1.7	0.51	0.40						

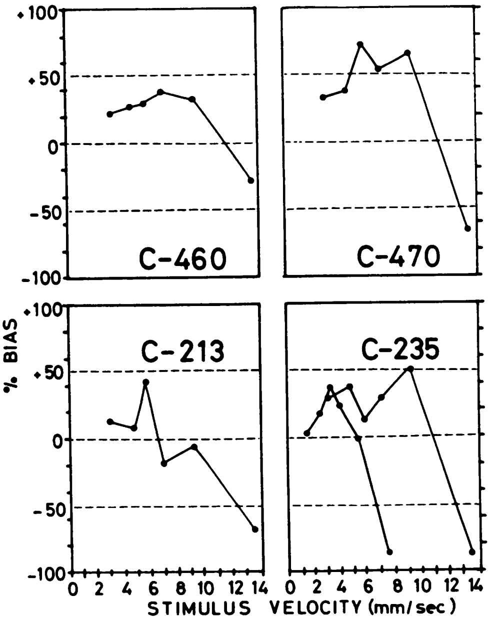

Fig. 12. Response bias plotted as a function of stimulus velocity. The filled circles represent data collected using the standard range of velocities. The open circles represent data from Pigeon C-235 collected using the low range of velocities.

Discussion

The results of preliminary training of the pigeons to discriminate the highest velocity of movement confirm our earlier results that movement detection is a difficult task for pigeons. The slow rate of acquisition of several of the birds, and the oscillations between high and low discrimination performance suggest some instability of the movement-detection mechanism. This instability cannot be attributed to variability in the stimulus system, since this was repeatedly checked during the study using the calibration device described in Experiment I. Only trivial differences were found from measurement to measurement. A further indication of the difficulty of the discrimination was seen in the frequent failures to satisfy the assessment requirement at the beginning of the session. Over the course of the psychophysical sessions, the birds generally showed progressive declines in threshold until stability was achieved. In all cases, the range of stable thresholds was well within the ±25% limit for five successive sessions. Pigeon C-235 continued to show progressive declines in threshold even after being transferred to the lower range of stimulus velocities. There is some suggestion in this bird's performance curve that continued training may have resulted in additional improvements in performance.

The signal-detection analysis indicated that the slowest velocities in the standard range were quite detectable to the subjects. Moreover, even the 1.7 mm/sec velocity, the lowest of the low range, had a detectability index of $A' = 0.60$. The sharp discrepancy between the traditional psychophysical approach and the signal-detection analysis is most likely accounted for by the systematic changes in response bias reported in Figure 12. The effects of the response bias changes were to depress the psychometric functions at the intermediate velocities, resulting in a higher threshold determination. A comparison of the response bias curves of Pigeon C-235 for the standard and low-velocity ranges is most instructive, since the curves are very similar in the two conditions. Thus, we have some evidence to suggest that the systematic bias changes are not associated with specific stimulus velocities, but are related to the ordinal positions of the stimuli in the descending series. This observation tends to rule out an interpretation of the initial negative bias as due to a motion aftereffect of the higher velocities.

To estimate the retinal image velocity, we carried out the same type of calculations of visual angle per second based on near, mid, and far inspection points as in Experiment I. Using the same values as in Experiment I for the near, mid, and far inspection distances, the retinal image velocities were estimated for each subject and are given in Table 4. The far estimate, which is probably the most meaningful, indicates that the retinal velocities of three of the four pigeons fell within the range

Table 4

Movement-Detection Thresholds in Experiment II

Pigeon	*Stimulus Velocity at Threshold (mm/sec)*	*Retinal Image Velocity at Threshold (deg/sec)*		
		Near	*Mid*	*Far*
C-213	5.20	6.92	5.82	4.80
C-235	2.74*	3.64	3.07	2.53
C-460	5.47	7.28	6.13	5.05
C-470	5.62	7.47	6.29	5.19
Mean	4.76	6.32	5.33	4.39
Median	5.39	7.10	5.98	4.93

*Determined in the low-velocity range.

of 4.80 to 5.05 deg/sec. The remaining pigeon, C-235, had an estimated retinal image velocity of 2.53 deg/sec.

GENERAL DISCUSSION

The results of Experiments I and II were generally consistent, in that both experiments indicated that pigeons have great difficulty in acquiring discriminations based on stimulus movement. Moreover, velocities that are either undetectable or poorly detectable to the pigeons were reported as quite obviously moving by human observers after only a brief glance at the stimulus. The performance of the birds in Experiment II was somewhat better than in Experiment I. In addition to increased detectability of the stimuli, we also observed a marked reduction of intersubject variability in Experiment II. This difference can be seen by comparing Figures 5 and 11. We cannot draw any firm conclusions about whether the improvement was due to the difference in the stimuli (stripes or bars, vertical or rotary movement) or the changes in the behavioral procedures, such as the warm-up, assessment, and correction contingencies. However, our speculation, based on experience with other psychophysical procedures, is that most of the improvement is due to the behavioral changes.

Although an improvement in the minimal detectable velocity was found in Experiment II, the best performance of the most sensitive subject, C-235, was still far in excess of what human observers characterize as slow movement, which according to Graham (1968) is about 3 min/sec. The lowest velocity of the low range, 1.7 mm/sec, which was somewhat detectable to C-235, had a retinal velocity of 1.57 deg/sec. This is a relatively high velocity and leads to the conclusion that pigeons detect movement poorly, at least under the conditions of these experiments.

A factor that must be considered in the interpretation of these data is that the estimates of retinal velocity are based on a hypothetical eye, which is immobile with respect to the movement of the stimulus. The pigeons in these studies were free to move their eyes and heads in tracking the movement of the stimuli. This could result in a retinal velocity considerably lower than the estimated value. Nye (1969) reported that pigeons are capable of precise eye movements in response to stimulus movement, although over a more restricted range than humans. He reported that eye-movement drifts, which are initiated by stimulus motion, occur at velocities of about 1 to 5 deg/sec. However, he does not report eye movement as a function of stimulus velocity. Therefore, we cannot state the possible role of eye movements in reducing the retinal velocity. Head movement probably does not contribute much to the tracking ability of the bird because of the relatively small distance that the stimulus traverses and the relatively short inspection distance. This too is a speculative conclusion, since we have no information about head movements as a function of stimulus velocity. However, even if the *retinal* velocity is considerably lower than our estimates, we are still confronted with the fact that the least detectable *stimulus* velocities for the pigeons are so surprisingly high and so readily detectable by humans. Indeed, we must consider the question of whether the absolute retinal velocity of the stimulus is critical to movement detection at all. Gibson (1968) pointed out the movement of an image across the retina is not sufficient to produce the perception of motion. For example, each time the eye scans a stationary scene the retinal image of the objects in that scene sweeps across the retina, yet the scene is perceived as stationary. Gibson argues that the perception of motion is based on a complex interaction between the relative motion of the stimulus, and the motion of the eyes, head and body of the observer and various perceptual cues to motion, such as the leading edge of an object progressively appearing or disappearing from behind another object.

The signal-detection analysis clearly indicated that the pigeons systematically altered their response criterion as stimulus velocity diminished during the session. The data obtained from C-235 in the low velocity range indicates that these systematic shifts in criterion were related to the position of the stimulus in the sequence, not to its absolute velocity. The factors that can affect response criterion are the probability of the occurrence of the signal, the probability of reinforcement of correct responses and the cost of incorrect responses (Green and Swets, 1966; McNicol, 1972). In Experiments I and II, the probability of the occurrence of a moving stimulus was 0.50. The pay-off matrix was symmetrical; *i.e.,* the probability of reinforcement was the same for "hits" and "correct rejections" and the cost of an error was the same for "misses" and "false alarms". In a symmetrical pay-off matrix, departures from zero bias result in a decline of the percentage of correct responses and, hence, the empirical probability of reinforcement falls. However, a subject's choice performance is based on its perception of the empirical probability; *i.e.*, "subjective" probability. Therefore, any explanation of the changes in response bias must depend upon the subject's failure to discriminate accurately the probability of the occurrence of a moving stimulus, the probability of reinforcement, or the reinforcement cost of an error. A number of features of the design of these experiments could contribute to differences in the objective and "subjective" probabilities. For example, in Experiment II the number of correction trials was not included in the determination of the probabilities of signal and noise. However, they may have influenced the subjects' choice behavior. Likewise, the presence of a correction procedure may have affected the "subjective" probability of reinforcement. However, neither of these were present in Experiment I, in which essentially the same effects were observed.

Another observation common to both experiments is that in general, each subject tended to maintain its false-alarm rate within a relatively constant band. Tables 1 and 3 indicate that the difference between the highest and lowest false-alarm rates did not exceed 0.24, and for the most subjects was less than 0.20. Indeed, many of the systematic changes in response bias can be accounted for by the constancy of the false-alarm rate, which systematically cuts across first the negative and then the positive isobias contours (Hodos, 1970). Unfortunately, we can no better account for the constancy of the false-alarm rate than we could the systematic bias changes. However, these two effects seem to be two sides of the same coin.

Comparison of these results with those obtained from other species is difficult, due to the considerable differences in methodology employed. J. F. Brown (1931) studied the movement-detection thresholds of humans and found that the minimal detection velocity was in the range of 11 to 30 mm/sec, which corresponds to 2 to 6 min/sec of retinal velocity. R. H. Brown and Conklin (1954) reported that under their conditions, the minimal detectable velocity was in the range of 6.70 to 12.53 min/sec. Carpenter and Carpenter (1958) compared the movement-detection abilities of two human children and two young chimpanzees. They found that the range of detection thresholds of these four primates was 37 min/sec to 1.7 deg/sec. Hawley and Munn (1933) investigated the ability of rats to detect the horizontal movement of vertical black and white stripes. They reported that the detection threshold was in the range of 33 to 100 mm/sec, which corresponds to a retinal velocity of approximately 3.2 to 9.7 deg/sec. Kennedy and Smith (1935) studied rotary movement in cats and reported that the minimal detectable velocity was in the range of 4 to 24 mm/sec, corresponding to a retinal velocity of 2.6 to 14.6 deg/sec. Three of their four subjects performed in the range of 2.6 to 5.5 deg/sec. Although these values are roughly in the range of those reported here in Experiments I and II, the detection threshold can be affected by such variables as the size of the target, the luminance, *etc.*, (Graham, 1965, 1968), and therefore the testing may not have been done under anything even approximating comparable conditions. Moreover, the technology of animal psychophysics has improved considerably in the past 40 yr and contemporary behavioral methods might have resulted in considerable improvement in performance using the same stimulus displays as Hawley and Munn and Kennedy and Smith used.

Why is stimulus movement so difficult for pigeons to detect? One factor may be retinal image "slippage" (Graham, 1968), which is related to the cues to stimulus movement described by Gibson (1968). Retinal image slippage is the displacement between a point on the retinal image of the moving stimulus and a corresponding point on the retina during visual pursuit of the stimulus. In an animal such as a pigeon, with a relatively limited extent of eye movement (Nye, 1969), and with head movements limited by the relatively small excursion of the stimulus, the appropriate feedback from proprioceptive mechanisms may be insufficient to permit detection of small velocities of movement. Perhaps stimuli that moved at the same velocity, but through a larger excursion would be more detectable, since they would permit a greater range of head movement during visual pursuit and hence would provide greater proprioceptive feedback.[3]

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Received 5 March 1975.
(Final Acceptance 5 December 1975.)

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[3] W. M. Schleidt has suggested to us that the Columbiformes may have developed their method of feeding the young "crop-milk" rather than catching insects, worms, *etc.* to feed them as do other orders of birds because they do not detect the rather low rates of movement of such "prey".