NEAR-FIELD VISUAL ACUITY OF PIGEONS: EFFECTS OF HEAD LOCATION AND STIMULUS LUMINANCE¹

WILLIAM HODOS, ROSALIND W. LEIBOWITZ, AND
JAMES C. BONBRIGHT, JR.

UNIVERSITY OF MARYLAND AND WALTER REED ARMY INSTITUTE OF RESEARCH

Two pigeons were trained to discriminate a grating stimulus from a blank stimulus of equivalent luminance in a three-key chamber. The stimuli and blanks were presented behind a transparent center key. The procedure was a conditional discrimination in which pecks on the left key were reinforced if the blank had been present behind the center key and pecks on the right key were reinforced if the grating had been present behind the center key. The spatial frequency of the stimuli was varied in each session from four to 29.5 lines per millimeter in accordance with a variation of the method of constant stimuli. The number of lines per millimeter that the subjects could discriminate at threshold was determined from psychometric functions. Data were collected at five values of stimulus luminance ranging from -0.07 to $3.29 \log \text{ cd/m}^2$. The distance from the stimulus to the anterior nodal point of the eye, which was determined from measurements taken from high-speed motion-picture photographs of three additional pigeons and published intra-ocular measurements, was 62.0 mm. This distance and the grating detection thresholds were used to calculate the visual acuity of the birds at each level of luminance. Acuity improved with increasing luminance to a peak value of 0.52, which corresponds to a visual angle of 1.92 min, at a luminance of $2.33 \log \text{ cd/m}^2$. Further increase in luminance produced a small decline in acuity.

Key words: visual acuity, key pecking, accommodation, luminance, vision, pigeons

The past decade has seen a resurgence of interest in the visual acuity of pigeons (Blough, 1971, 1973; Catania, 1964; Chard, 1939; Donner, 1951; Hamilton and Goldstein, 1933; Nye, 1968). These studies suggested that pigeons have different mechanisms for viewing objects that are distant and those that are relatively near. For viewing objects at a distance, pigeons appear to use the lateral visual fields, which are also the monocular visual fields. For viewing objects that are relatively close to the end of the beak, these birds appear to use the anterior visual fields, which include the binocular field of view. The optics of the pigeon eye have refractive differences in the regions corresponding to the anterior and lateral visual fields (Millodot and Blough, 1971; Nye, 1973). In addition, the retina of pigeons contains specialized regions on which images viewed in the anterior and lateral visual fields fall. These

regions contain the highest densities of receptors and ganglion cells (Bingelli and Paule, 1969; Galifret, 1966, 1968).

A well-known phenomenon in studies of human vision is the increase in the detectability of a visual stimulus as its luminosity increases (Schlaer, 1937). Because of this relationship, measurement of visual acuity at a single level of stimulus luminance would be of limited value. Therefore, a major purpose of the present investigation was to determine the visual acuity of pigeons over a wide range of luminance levels. We varied the stimulus luminance over a range of approximately 3.5 log units and observed an acuity-luminance relationship similar to that reported for humans (Lythgoe, 1932). Since the stimuli were located immediately behind a transparent pecking key, the situation was comparable to the conditions of viewing stimuli in conventional operant-conditioning experiments.

In calculating the visual acuity of a subject, the distance from the stimulus to the anterior nodal point of the eye must be known with reasonable precision. A special problem in investigating the visual acuity of stimuli that are fairly close to the eye is that relatively small

¹Reprints may be obtained from William Hodos, Department of Psychology, University of Maryland, College Park, Maryland 20742. The authors thank Patricia M. Blough, Katherine V. Fite, J. Levinson, and Patrick W. Nye for their valuable comments and suggestions and Janice Wildberger who prepared the manuscript for publication.

differences in the location of the head can produce sizeable changes in the visual angle subtended by the retinal image of the stimulus. Head location is not a serious problem in far-field determinations of acuity, in which such differences would constitute a trivial proportion of the total viewing distance. However, head location is a major problem in determination of the subject's visual acuity for objects that are relatively close to the eye. To estimate the viewing distance for near-field vision, we measured the eye-to-key distance in high-speed motion-picture photographs of pigeons pecking keys. These measurements were used in calculating the estimated near-field visual acuity of the pigeons. In addition, the measurements provided an estimate of the pigeons' near point of accommodation.

METHOD

Subjects

Five White Carneaux pigeons, obtained from Palmetto Pigeon Plant, Sumter, S.C., ranged in age from 5 to 7 yr at the start of the study. The birds were maintained at 75 to 80% of their free-feeding weights during the experiment. One bird, C-412, had served in a previous study of visual acuity; the other four were experimentally naive.

Apparatus

The rear wall of a three-key Lehigh Valley Electronics pigeon chamber was modified to permit the light from an externally located slide projector to fall on the center key. The center key was fabricated from a transparent, 1.0 mm thick, glass microscope slide, which is much more resistant to the development of optical defects as a result of pecking than is the conventional Plexiglas pigeon key. The side keys were constructed from Polacoat rear-projection screen. A 75- by 100-mm sheet of rear-projection screen (Edmund Scientific Co., Barrington, N.J.) was mounted 15 cm behind the key and served to diffuse and attenuate the light from the projector. The glass center key was made opaque, except for a 1.5 cm diameter circular region in the center of the key, by applying a sheet of thin, black-painted stainless steel to the rear of the key.

The stimuli were a series of diagonal square-wave gratings (Ronchi rulings obtained from Max Levy and Co., Philadelphia, Pa.) that

ranged in spatial frequency from 4 to 29.5 lines per millimeter (nominal). The line widths and spaces between the lines were equal, but decreased from 0.252 mm to 0.017 mm as the spatial frequency increased. The bar and space widths were measured using a Zeiss stereomicroscope with ocular and stage micrometers. Table 1 presents the nominal values of the spatial frequencies of the gratings and the empirical bar and space widths.

The contrast of the gratings was measured using a Zeiss microdensitometer with the measuring area diameter set at 0.005 mm. The luminance of the dark and light bars was measured and the percentage of contrast calculated from the following formula:

$$\%C = \frac{L_L - L_D}{L_L + L_D} \times 100$$

in which %C = percentage contrast, L_D = the luminance of the dark bars, and L_L = the luminance of the light bars. The resulting calculations indicated that the contrast was 98.9% for the coarsest gratings and 92% for the finest grating. The contrast of each grating is presented in Table 1.

Each grating was paired with a Bausch and Lomb glass neutral density filter of nominal density of 0.3, referred to hereafter as the "blank stimulus". Microscope cover glasses, ranging in optical density from 0.04 to 0.07 were added to either the gratings or the neutral density filters to match the average luminance within each stimulus pair. Luminance differences within pairs were less than 0.025 log unit. Hodos and Bonbright (1972) reported that the average luminance difference threshold for successively presented stimuli is approximately 0.10 log unit. The average luminance difference between stimulus pairs was less than 0.04 log unit. All key luminances were measured with a Photovolt Model 520-M photometer calibrated against a certified luminance

Table 1
Grating Stimuli

<i>Spatial Frequency</i> (lines/mm)	<i>Bar-Space Width</i> (mm)	<i>Per Cent</i> <i>Contrast</i>
4	0.126	98.9
8	0.066	98.9
12	0.042	96.8
20	0.026	94.9
24	0.018	93.7
29.5	0.017	92.0

standard traceable to the U. S. Bureau of Standards. The sensing head of the photometer was in a clamp. A metal tube extended from the sensing head to the surface of the key and served to exclude ambient light.

The gratings and neutral density filters were mounted in a 37.5 cm diameter, aluminum filter wheel mounted between the diffusing screen and the center key. The distance from the front surface of the key to the front surface of the grating was 7.0 mm. The wheel was driven by a Geneva movement and powered through a gear train by a reversible ac motor. A solenoid-operated shutter was mounted between the wheel and the center key. This shutter was closed between trials so the subjects could not see whether the wheel was changing position or not. The wheel contained two complete sets of gratings and matched neutral density filters. Before each session, the stimuli were carefully cleaned with an air stream and a camel's-hair brush to remove dust particles, feather fragments, and lint that could serve as extraneous stimuli.

The light source for the center key was a Sylvania CBA projection lamp housed in a Kodak Ektagraphic Slide Projector. The lamp was powered through a Superior Electric 3016 Voltage Regulator and was continuously maintained at 3.5 A. A series of Kodak #96 Wratten neutral density filters, placed in the path of the light beam, was used to reduce the luminance of the stimulus field. Following are the density values of the filters used. The nominal density is followed by the empirical density in parentheses. 1.0 (0.97), 2.0 (1.83), 3.0 (2.60), and 3.5 (3.37). A 0.2 neutral density filter was permanently mounted in the beam path. With only the 0.2 neutral density filter in the light path, the luminance of the center key was 1943.3 cd/m². The side keys were each illuminated by a Tung-Sol No. 1819 lamp powered from a regulated 28-v dc power supply. The left-key luminance was 109.6 cd/m² and the right-key luminance was 69.8 cd/m², a difference of approximately 0.2 log units.

The interior of the subject's chamber, which had been painted flat white, was illuminated by two ceiling-mounted General Electric F6T5-CW-HH daylight fluorescent lamps. The light from the lamps was diffused by a sheet of white, translucent Plexiglas.

The overall chamber illumination was 171.0 lx as measured with an SEI photometer and a

Leeds and Northrop calibrated test plate. The luminance of the walls varied from 44.8 to 84.7 cd/m². The ceiling luminance varied from 996.6 cd/m² directly below the lamps to 26.4 cd/m² in the darkest corner.

Procedure

The procedure was the same as that used by Hodos and Bonbright (1972) to study visual intensity difference thresholds and by Krasnegor and Hodos (1974) to study acoustical intensity difference thresholds. Subjects were trained to eat from the grain dispenser before the preliminary key-peck training procedure was introduced. The preliminary training procedure was as follows: a single peck on an illuminated side key resulted in access to mixed grain for 3 to 5 sec. After the birds learned to alternate pecks between the right- and left-side keys, the center key was illuminated. The grating patterns were not presented during pre-training. Instead, the blank stimulus was present behind the center key. A single peck on the center key closed the shutter and illuminated one or the other of the side keys. When this sequence was satisfactorily executed, the response requirement on the center key was gradually raised to 10 pecks. The pretraining procedure required two to three sessions to complete. The four lines per millimeter stimulus pattern was then presented alternately with its matched blank stimulus. The birds were trained to perform a conditional discrimination procedure in which a single peck on the right-side key produced reinforcement if the center key had displayed a grating pattern and a single peck on the left-side key produced reinforcement if the center key displayed the blank stimulus. In order to increase the number of trials per session, the following reinforcement contingency was in effect. Every correct response was followed by illumination of the feeder light, but only a random 50% of these responses were accompanied by the delivery of grain.

When the preliminary training was completed, a series of psychophysical sessions was started. Each session began with a block of 20 trials of the four lines per millimeter grating *versus* the blank stimulus. The first 20 trials served as a "warm-up" period and the data were discarded. This was followed by an "assessment" block of 20 trials in which the same stimulus pair was repeated. The purpose of

the assessment was to determine whether the subjects' performance level was high enough to permit psychophysical testing or whether additional training on the basic discrimination (four lines per millimeter *versus* blank) was needed. If the bird achieved less than 90% correct (*i.e.*, more than two errors) during the assessment block, the stimuli remained the same for the remainder of the session and the session was recorded as a training session. If the bird performed at 90% or better in the assessment block, the psychophysical testing was continued and the data collected during this period was used as the first determination of performance at four lines per millimeter. The sequence of 20 trials blocks of stimulus-pairs (grating *versus* blank) following the assessment block was carried out in ascending order of spatial frequency (*i.e.*, progressively finer gratings). Within each pair, the order of stimulus presentation was determined by a quasi-random sequence. After completing the series of gratings and blanks, the entire sequence was then repeated, including the warm-up block. Introduction of the warm-up block between the first and second series of stimuli eliminated extreme response biases that sometimes developed during the most difficult discriminations at the end of the sequence and otherwise carried over into the first block of the second sequence, resulting in a performance decrement. The second warm-up block resulted in a marked increase in consistency between the data of the first and second series. The assessment contingency was not in effect during the second series because the decision had already been made that the session was to be a psychophysical testing session, rather than a training session. The total number of trials for training or testing sessions, including both warm-up blocks, was 336.

In both the training and psychophysical testing sessions, pecks on the incorrect key (*i.e.*, errors) resulted in 4.5 sec of timeout, in which the keys were dark. Pecks on dark keys were ineffective. The chamber illumination did not change during the timeout period so as not to alter the birds' state of light adaptation. Following an error, a correction procedure was used in which the previous stimulus would be repeated until the correct response was eventually emitted. Correction responses were followed by the feeder light, but were never accompanied by the delivery of grain. The in-

troduction of this procedure reduced the birds' tendencies to use the "win-stay-lose-shift" response strategy and improved discrimination performance. As a check on the influence of extraneous stimuli, such as vibrations from the motor, *etc.* that might contaminate the data, the 29.5 lines per millimeter gratings were occasionally removed and 0.3 neutral density filters put in their place. The performance of the subjects in these "blank *versus* blank" blocks of trials was always in the range of 45 to 60% correct, which indicated that performance was probably not influenced by extraneous stimuli. The presentation of stimuli, collection of data, and other aspects of the procedure were controlled by a system of solid-state, digital logic modules.

The luminance level of the center key was constant during each session. In the first psychophysical session, only the permanent 0.2 neutral density filter was in the beam path. On each successive session, a filter of progressively greater optical density was placed in the beam path so that by the fifth session, the pigeon had been tested at each of five luminance levels. During the next five sessions, the sequence of center-key luminances was reversed. During the final five sessions, the sequence was reversed once again. At the end of the fifteenth session, the birds had been tested three times at each luminance level. This arrangement of progressively increasing and decreasing the center-key luminances permitted the data to be collected with no more than one log unit difference in center-key luminance from one session to the next. The chamber illumination and the side-key luminances remained unchanged throughout the experiment. A psychometric function was calculated for each session. The grating-detection threshold was regarded as that spatial frequency of the gratings at which performance was 75% correct.

To calculate the visual acuity of the pigeons, data were required on the distance from the surface of the gratings to the anterior nodal point of the eye. High-speed (1000 frames per second) cinematography was used to measure the viewing distance of three pigeons trained to discriminate the presence or absence of the gratings in the experimental chamber. To accomplish this task, the birds were adapted to perform with a clear sheet of Plexiglas substituted for the standard chamber door. In addition, the chamber was illuminated by a pho-

tographic flood light. After several sessions, the birds performed readily under these conditions. They seemed undisturbed by the presence of the camera or the photographers.

At 1000 frames per second, a 30.5-m roll of 16-mm film will be exposed in approximately 4 sec. Therefore, we were usually not able to photograph a complete sequence of center-key pecks on a single roll of film. After each session of photographing a bird, a millimeter scale was placed in the chamber and photographed with the high-speed camera. The alignment of the scale was such that it permitted subsequent measurement of the distance from the anterior surface of the cornea to the surface of the key in the projected images of the birds pecking.

After the films were developed, they were edited to eliminate segments of inactivity. Those segments showing activity were spliced together to form a single reel for analysis. The measurements were obtained by first projecting the image of the millimeter scale on a large sheet of white paper with a single-frame motion-picture projector. The scale was drawn on the paper. The images of the birds pecking were then projected on the drawing of the scale without moving the projector. A frame-by-frame examination was made of each segment of film to determine the point in the pecking sequence at which the anterior surface of the cornea was closest to the grating. This distance was recorded. Also recorded were the distance at which the bird's eyelid was half closed and the distance at which the peck was initiated. A total of 84 peck sequences were measured and recorded in this manner. The measurements thus obtained were used to estimate the visual angle subtended by the retinal images of the gratings.

To obtain some data on human performance in this apparatus, which could be compared to the pigeons' performance, two human subjects were tested. Each subject viewed the gratings through a 5-mm hole in the rear wall of the pigeon chamber. Their heads were maintained in position by a chin and forehead support frame. Push buttons were substituted for the keys and the feeder light provided feedback for correct responses. Each subject was tested for one full session at $2.33 \log \text{ cd/m}^2$, which was the peak of the pigeons' acuity-luminance function. The distance from the grating to the anterior nodal point was 360 mm for Subject WH and 497 mm for Subject MW.

The visual acuity of each subject was calculated from their psychometric function in the same way as for the pigeons.

RESULTS

Eye-position Measurements

Figure 1 shows representative frames from the high-speed motion pictures of the pigeons pecking the center key. Each vertical column of photographs represents a peck sequence from a single pigeon. Segments of a peck sequence of each of the three pigeons are shown. In each column, the top frame shows the bird at the initiation of the peck sequence. This position will be referred to as the "far distance". The middle frame shows the position of the pigeon's eye when the eyelid is approximately half closed. This will be referred to as the "mid-distance". The bottom frame of each column indicates the position of the eye when the beak is against the key and the key is maximally depressed. This will be referred to as the "near distance". In this position, the eyelid is closed in nearly every such frame. Occasionally, the eyelid does not close completely, as may be seen in the frame at the bottom left of the figure. The black bar at the bottom of the figure indicates 10 mm.

Eighty-four peck sequences of the three birds were examined. The measurements of the near, mid-, and far distances were averaged for all three birds. No significant differences between the individual mean distances of the birds were found. The means, standard deviations, standard errors of the means, 95% confidence intervals, and errors of estimate are presented in Table 2.

The table indicates the mean near distance was 32.8 mm, the mean mid-distance was 39.7 mm, and the mean far distance was 51.5 mm. Since the birds' eyes are closed at the near point, this distance is probably meaningless as an estimate of visual acuity. Some experimenters may prefer the mid-distance, since the lid is half opened and presumably the bird is capable of viewing the stimulus. We prefer the far distance because our observations of the peck sequence on the greatly expanded time scale that results from 1000 frame per second photography suggested strongly that most of the inspection of the center key occurred from the far distance before the first peck was emitted. Therefore, the estimates of visual acuity to be

Fig. 1. High-speed (1000 frames per second) motion-picture photographs of three pigeons pecking the center key. Each vertical column represents a sequence within a single peck of a different pigeon. The top photograph of each column shows the location of the head when the peck was initiated. The middle photograph shows the location of the head when the lid was half closed. The bottom photograph shows the location of the head when the beak is against the key and the key is maximally depressed. The bar at the bottom of the figure indicates 10 mm. Note the closed eyelids in the three bottom photographs.

presented are based on the far-distance measurements. If the mid-distance were taken as the more appropriate, the result would be to increase the estimate of the visual angle by 23%.

Table 2 also provides information about the reliability of the eye-position measurements. The 95% confidence intervals (± 1.96 standard errors) indicate the range in which 95% of the population values fall. The percentage error of estimate indicates the percentage of error in estimating the visual angle if the actual distance on a given trial deviated from the mean value by as much as 1.96 standard error.

Additional distances that must be included in the estimation of the visual angle are the

distance from the surface of the key to the surface of the grating, and the distance from the anterior surface of the cornea to the anterior nodal point of the eye. The key-to-grating distance was 7.0 mm. The cornea-to-nodal point distance was 3.46 mm (Marshall, Mellerio, and Palmer, 1973). Thus, the total distances from the grating surface to the anterior nodal point were: near distance = 43.3 mm, mid-distance = 51.2 mm, and far distance = 62.0 mm. The latter distance was used in our estimates of the near-field visual acuity.

Psychometric Results

Figure 2 presents psychometric functions for two pigeons at each level of stimulus lumi-

Table 2
Eye-Position Measurements for Three Pigeons

	Near Distance	Mid- Distance	Far Distance
Number of Observations	84	84	84
Mean	32.8 mm	39.7 mm	51.5 mm
Standard Deviation	4.05 mm	3.78 mm	4.58 mm
Error of the Mean	0.44 mm	0.41 mm	0.50 mm
95% Con- fidence Interval	31.9-33.7 mm	38.9-40.5 mm	50.5-52.5 mm
Percentage Error of Estimate	2.7	2.0	1.9

nance. The curves are plots of the mean percentage of correct responses as a function of the spatial frequency of the stimulus grating. Each data point represents the mean of 144 trials averaged over three sessions. The point of subjective equality between the grating and the blank stimulus was determined by the spatial frequency of the stimulus continuum at the point at which the psychometric function crossed the 75% correct line, which is halfway between chance discrimination and perfect discrimination. For each bird, the psychometric functions of the two lower luminance values remained generally flat after crossing the 75% correct line. However, the three higher luminance curves reached the lowest performance levels at the frequencies of 20 to 24 lines per millimeter and thereafter showed moderate improvements in performance. These improvements did not elevate the functions above 75%, but they did differ from the generally monotonic form that psychometric functions characteristically have.

The visual angle subtense of the bar width at each point of subjective equality was determined using the far-distance estimate of 62.0 mm from the surface of the grating to the anterior nodal point of the pigeon's eye. Figure 3 presents the decimal visual acuity ($1/\text{visual angle}$) of each pigeon as a function of the luminance of the stimulus. The curves show a progressive increase in acuity as a function of luminance to a peak at $2.33 \log \text{cd/m}^2$. At luminances below $-0.07 \log \text{cd/m}^2$, the pigeons ceased pecking the center key. Presumably, at

Fig. 2. Psychometric functions for each pigeon. Mean percentage of correct responses has been plotted as a function of the spatial frequency of the stimulus. The number after each function indicates the stimulus luminance in $\log \text{cd/m}^2$.

these luminances the center key appeared dark to the light-adapted birds. At luminances above $3.29 \log \text{cd/m}^2$, the pigeons also ceased pecking the center key. Included in the figure are determinations of pigeon visual acuity at specified values of stimulus luminance from the literature (Blough, 1971; Chard, 1939).

The visual acuity of the two human subjects at $2.33 \log \text{cd/m}^2$ was considerably better than that of the pigeons. The acuity of Subject WH was 3.12, corresponding to a visual angle of 0.32 min . The acuity of Subject MN was 2.43, corresponding to a visual angle of 0.41 min .

The psychometric data were also subjected to a signal-detection analysis (Green and Swets, 1966; McNicol, 1972). Table 3 presents the results of this analysis: the data are shown for each spatial frequency of the stimulus and each level of stimulus luminance. The mean "hit" values are the percentage of correct responses when the grating was present averaged

Fig. 3. Visual acuity ($1/\text{visual angle}$) plotted as a function of stimulus luminance for each subject. Also shown are estimates from the literature of far-field visual acuity at specified luminances (Blough, 1971; Chard, 1939).

across the three sessions at that luminance. The mean "false-alarm" values are one minus the percentage of correct responses when the blank stimulus was present averaged across the three sessions at that luminance. The value A' is a nonparametric index of stimulus detectability that is free from response bias (Pollack and Norman, 1964). A' varies from 1.00 (perfect detection) to 0.50 (no detection). The value per cent bias is a nonparametric index of response bias (Hodos, 1970). Per cent bias varies from +100% (strong preference for the right-side key, very conservative observer, high criterion) through 0% (no preference for either key, unbiased observer) to -100% (strong preference for the left-side key, very liberal observer, low criterion).

The table indicates that as grating frequency increased, the mean proportion of hits tended to decrease and the mean proportion of false alarms tended to increase. In some cases, the relationship of the hit rate and the false-alarm rate was such that the value of A' was less than 0.50. The point falling at the intersection of these hit and false-alarm rates would fall below the main diagonal of the unit square of signal-detection analysis (Green and Swets, 1966; McNicol, 1972). Points located subadjacent to the main diagonal indicate no detection of the stimulus and perhaps a

response strategy based on discrimination reversal. Since such points are difficult to interpret in the context of signal-detection analysis, they have been omitted from the detectability and response-bias analysis. The hit and false-alarm rates upon which such points are based are given in the table, however.

The detectability analysis is shown graphically in Figure 4. The figure shows A' plotted as a function of the spatial frequency of the gratings with luminance as a parameter. The figure indicates that the detectability of the coarsest grating, four lines per millimeter, was unaffected by all but the most extreme decrease in luminance. Even there, the detectability was excellent. However, as the grating frequency increased, the effect of diminished luminance on detectability increased. The figure also indicates that the improvements in performance seen with the finest gratings at high luminances in Figure 2 were not due solely to changes in response bias, but represent an increase in the detectability of those gratings.

Figure 5 is a graphic presentation of the response-bias data. Neither pigeon showed any

Fig. 4. The signal-detection index of detectability, A' , has been plotted as a function of the spatial frequency of the stimulus. Values of A' less than 0.5 have not been plotted (see Table 3 and text). The number after each function indicates the luminance of the stimulus in log cd/m^2 .

Table 3
Signal-Detection Analysis

Grating Frequency (lines/mm)	Luminance ($\log \text{cd/m}^2$)																									
	3.29					2.33					1.40					0.42					-0.07					
	Mean Hit	Mean False Alarm	% Bias	A'		Mean Hit	Mean False Alarm	% Bias	A'		Mean Hit	Mean False Alarm	% Bias	A'		Mean Hit	Mean False Alarm	% Bias	A'		Mean Hit	Mean False Alarm	% Bias	A'		
PIGEON C-412																										
4	0.98	0.03	0.99	-48		1.00	0.02	0.99	100		1.00	0.03	0.99	100		0.98	0.02	0.99	0		0.92	0.08	0.96			
8	0.92	0.02	0.97	73		1.00	0.13	0.97	100		0.95	0.18	0.94	-68		0.32	0.15	0.68	41		0.30	0.35	*			
12	0.87	0.15	0.92	-13		0.87	0.20	0.90	-29		0.70	0.27	0.80	6		0.45	0.45	0.50	0		0.35	0.20	0.65			
20	0.45	0.53	*	*		0.43	0.33	0.60	10		0.37	0.27	0.60	15		0.35	0.42	*	*		0.45	0.20	0.72			
24	0.65	0.50	0.63	-8		0.45	0.47	*	*		0.63	0.33	0.73	5		0.38	0.42	*	*		0.27	0.23	0.55			
29.5	0.63	0.38	0.70	-1		0.83	0.52	0.57	-43		0.82	0.45	0.78	-40		0.30	0.42	*	*		0.27	0.32	*			
PIGEON D-27																										
4	1.00	0.03	0.99	100		1.00	0.00	1.00	100		1.00	0.00	1.00	100		0.97	0.03	0.98	0		0.97	0.13	0.96			-74
8	0.78	0.08	0.91	57		1.00	0.02	0.99	100		0.97	0.07	0.97	-55		0.37	0.15	0.71	45		0.13	0.27	*			*
12	0.70	0.12	0.87	50		0.82	0.07	0.93	56		0.62	0.15	0.83	46		0.38	0.15	0.72	46		0.23	0.23	0.50			0
20	0.45	0.28	0.65	19		0.37	0.37	0.50	0		0.28	0.18	0.62	27		0.25	0.10	0.69	52		0.33	0.32	0.51			2
24	0.57	0.53	0.54	-2		0.62	0.35	0.71	3		0.43	0.48	*	*		0.22	0.20	0.53	7		0.23	0.23	0.50			0
29.5	0.67	0.60	0.57	-8		0.63	0.38	0.70	-1		0.65	0.32	0.75	4		0.27	0.23	0.55	10		0.12	0.28	*			*

*The intersection of the hit and false-alarm coordinates was below the main diagonal of the unit square.

Fig. 5. Per cent Bias plotted as a function of the spatial frequency of the stimulus. Per cent Bias values associated with A' values of less than 0.5 have not been plotted (see Table 3 and text). The number after each function indicates the luminance of the stimulus in $\log \text{cd/m}^2$.

consistent relationship between response bias and luminance with the coarse gratings. However, as the grating frequency increased, D-27 showed a progressive shift towards zero bias. Pigeon C-412 followed a somewhat similar course, although this bird's performance was not so consistent.

DISCUSSION

The result of the high-speed cinematographic analysis of the head locations of the pigeons pecking the center key during the discrimination of gratings from the blanks indicated that location of head and eyes was fairly constant both within and between three randomly selected White Carneaux pigeons. Our observation that the pigeons close their eyes when they peck supports Smith's (1974) report of this phenomenon. Therefore, the near distance, while surely the most conservative estimate of the stimulus-to-nodal-point distance, is also not meaningful for purposes of a visual acuity study. The far distance seemed to us to be the most reasonable, although one could, with some justification, use the mid-distance as the estimate of the inspection distance. However, at the far distance, and especially

just before a run of responses on the center key, the pigeons appeared to viewers of the high-speed films to be inspecting the center key.

The location of the near point of accommodation of pigeons has been a subject of much discussion (Blough, 1971, 1973; Catania, 1964; Chard, 1939; Donner, 1951; Hamilton and Goldstein, 1933; Nye, 1973). Most of this discussion has centered on the near point of accommodation of the lateral visual fields, which are used for viewing distant stimuli. These workers are in general agreement that the near point of accommodation for the lateral fields is located roughly at 400 mm. Nye (1973) calculated from ray-tracing studies based on measurements from frozen specimens that the near point of accommodation for stimuli in the anterior fields should be about 20 to 30 mm. However, the accommodative state of these eyes at the time of measurement was unknown. This degree of myopia seems unreasonable because the distance from the anterior surface of the cornea to the end of the beak is roughly 40 mm. If one is willing to assume that in the present experiment the pigeons positioned their heads in such a way as to be as close to the stimulus as possible while maintaining the stimulus in focus, then the estimates of the viewing distance also may be used as estimates of the near point of accommodation for the anterior fields. This distance was 62.0 mm from the anterior nodal point of the eye or 58.5 mm from the anterior surface of the cornea.

The psychometric functions indicated that discrimination of the coarsest gratings (four lines per millimeter) from the blanks was quite good over the full range of luminances. With increasing grating frequency, however, discrimination fell progressively as the stimulus luminosity declined. Several points should be considered when interpreting this decline in acuity at low target luminances. First, the chamber illumination remained high and the birds were therefore well light-adapted. Second, the lowest stimulus luminance used in this study, $-0.07 \log \text{cd/m}^2$, is approximately 2.5 log units above the "rod-cone break" of the pigeon's adaptation function (D. S. Blough, 1956). Therefore, the decline in acuity probably does not represent a shift from cone vision to rod vision. A possible artifact that could have produced some decline in stimulus

visibility was the fact that at the lowest luminance levels, the luminance of the stimulus was less than the luminance of the walls. Thus, reflections from the glass key could have impaired the birds' view of the stimulus.

At the highest spatial frequencies, a modest improvement in discrimination performance was observed at the higher luminances. The signal-detection analysis confirmed these observations. Although systematic changes in response bias toward zero bias were observed, which had the effect of increasing the percentage of correct responses, the index of detectability (A') indicated that the increase in discrimination performance was also due to increased detectability of the stimuli. What factors can account for this effect? Several studies suggest that pigeons are somewhat myopic in the anterior visual field, which is used for viewing stimuli located ahead of the bird and relatively close to the end of the beak (Catania, 1964; Millodot and Blough, 1971; Nye, 1973). Defocussed optical systems take on certain peculiar properties when periodic stimuli, such as gratings, are viewed through them (O'Neill, 1963). One of these properties is "spurious resolution", in which gratings of certain frequencies, which are not resolved because of the defocussing, appear after further defocussing of the lens. These images have greatly reduced contrast and are shifted in position by one bar width. The effect can be readily demonstrated by placing a grating in a slide projector, focussing sharply, and then slowly defocussing the lens. The image of the grating will disappear and then reappear with reduced contrast and shifted in position by one bar width. The suggestion is that the spurious resolution effect may occasionally have produced a low contrast image dependent upon small variations in the viewing distance, or perhaps an instability of accommodation.

The acuity-luminosity function (Figure 3) indicated that acuity improved continuously with increasing stimulus luminosity. The data are in good agreement with data from other laboratories (Blough, 1971; Chard, 1939) on far-field acuity at specified values of stimulus luminance. The peak of the function was at $2.33 \log \text{cd/m}^2$. The two human subjects tested at this luminance level had visual acuities roughly comparable to the values reported by Lythgoe (1932) and Schlaer (1937) for humans with high-luminance targets.

At $3.29 \log \text{cd/m}^2$, acuity declined slightly for both subjects. This small decrement in acuity at high luminance has been described for humans (Lythgoe, 1932) viewing targets within a dark surround, an arrangement comparable to that of the present experiment.

We were unable to train the pigeons to perform at stimulus luminances of 0.5 log unit or more in excess of $3.29 \log \text{cd/m}^2$. At these luminances, the birds would look at the center key and then turn away from it. Human observers found these luminances to be rather aversive.

The density of retinal receptor elements is a factor often discussed in studies of visual acuity, although as Riggs (1965) pointed out in his review of this topic, the retinal grain seems to be less important in determining the limits of resolution than are other factors, such as the optics of the eye and the organization of the retina. Galifret (1966) estimated the density of receptor elements in various regions of the pigeon retina. Using his value of 175 receptors/ $2500 \mu\text{m}^2$ for the region of the posterior temporal quadrant in which the retinal images of frontally viewed objects would fall, we calculated that a receptor element would have a diameter of approximately $3.78 \mu\text{m}$, which would have an angular subtense of 1.65 min. Nye (1968) estimated that the diameter of the receptor elements from unspecified retinal regions was $3.3 \mu\text{m}$, with an angular subtense of 1.43 min. However, Nye's figures were not corrected for shrinkage, which he estimated to be about 10%. Using Nye's shrinkage estimate (which is probably too conservative) to correct his figures, we obtained an estimate of the receptor diameter of $3.63 \mu\text{m}$, with an angular subtense of 1.58 min. The angular subtense of one bar at the peak of the acuity-luminosity function reported here was 1.92 min, which corresponds to a retinal width of $4.42 \mu\text{m}$. Thus, the estimate of the peak spatial frequency of the retinal image seems to be a reasonable approximation of the estimate of the retinal grain. Similar results were reported by Donner (1951) for seven species of passerine birds.

The angular subtense of the stimulus field is another factor that can affect acuity (Pokorny, 1968). The stimulus field in the present experiment was 13.86 degrees. Blough (1971) used a 12-min stimulus field. In her 1973 paper, Blough used a 7.9 degree field under some conditions of the experiment and reported an im-

provement in grating discrimination. This would suggest that Blough's (1971) estimate of far-field visual acuity might have been higher had she used large stimulus fields. Further support for this suggestion comes from Nye's (1968) study of the modulation transfer function of pigeons. Extrapolating Nye's functions to 100% contrast yields visual acuity estimates of acuity of 0.8, corresponding to 1.25 min at a luminance of 0.56 log cd/m². However, the angular subtense of Nye's stimulus field was 58 degrees. Thus, a large stimulus field may improve acuity for high-contrast stimuli, even under conditions of low stimulus luminosity. However, this point should be investigated systematically. On the other hand, Nye's exceptionally high estimate of the acuity of pigeons may be a consequence of the unconventionally low criterion that he employed to determine the point of subjective equality in his psychometric functions. The point of subjective equality is conventionally taken as that value of the stimulus that is associated with a performance halfway between chance and perfect discrimination (Engen, 1971). In difference threshold experiments, this performance level is 75% correct. While this is in many respects an arbitrary convention, the use of lower percentages of correct performance to determine the point of subjective equality will result in lower thresholds. Nye (1968) used criteria that were in the vicinity of 60% correct to determine the point of subjective equality. Had he used the more conventional 75% criterion, his data would be in accord with those in Figure 3.

Another factor that may have affected the measurements of visual acuity in the present experiment was the oblique orientation of the gratings. Campbell, Kulikowski, and Levinson (1966) reported that oblique gratings are not as visible to human observers as vertical or horizontal gratings. At high contrast, comparable to that used in the present study, the loss of acuity due to the oblique effect was approximately 0.15 min, which represents a loss of roughly 10%. At present, no direct investigation of the oblique effect on visual acuity has been carried out in pigeons. However, Zeigler and Schmerler (1965) reported no deterioration of discrimination performance of oblique rectangles as compared to vertical or horizontal rectangles.

An additional factor that should be consid-

ered in interpreting the measurements of visual acuity in the present study involves the contrast of the gratings. As indicated in Table 1, the contrast of the gratings decreased slightly as the spatial frequency of the gratings increased. The data of Campbell and Robson (1968) on the contrast sensitivity of humans indicated that relatively small changes in contrast can have sizeable effects on the detectability of fine gratings. However, Nye's (1968) data on the contrast sensitivity of pigeons indicate that pigeons are not nearly as sensitive to the effects of contrast at high spatial frequencies as are humans. Therefore, we conclude that the effects of the contrast differences in the present study were negligible.

Some practical implications of the data reported here, and of other visual acuity studies of animals and humans for optimal performance in animal visual discrimination experiments are: (1) The luminosity of the stimulus should be fairly high (2.0 to 3.0 log cd/m²) if fine detail is to be discriminated. If the stimuli contain only coarse details, lower luminosity (0.0 to 1.0 log cd/m²) will not result in a serious loss of discrimination. (2) The size of the stimulus field should be large. A standard pigeon key, 25 mm in diameter, subtends a visual angle of approximately 26 degrees, assuming a distance of 58.5 mm between the anterior nodal point and the surface of the key. The human data (Porkorny, 1968) suggest that when the contrast of the stimulus is high (50 to 100%), acuity does not improve with increasing stimulus size beyond about 10 degrees. But with lower percentages of contrast, stimuli as large as 50 degrees may be necessary to achieve maximal acuity. The pigeon data discussed above are generally consistent with the human data in this respect. (3) The contrast of the stimuli should be high; *i.e.*, the percentage difference between the luminosity of the brightest region and the luminosity of the darkest region should be as close to 100% as possible and not less than 50%.

REFERENCES

- Binggeli, R. L. and Paule, W. J. The pigeon retina: quantitative aspects of the optic nerve and ganglion cell layer. *Journal of Comparative Neurology*, 1969, 137, 1-18.
- Blough, D. S. Dark adaptation in the pigeon. *Journal of Comparative and Physiological Psychology*, 1956, 49, 425-430.

- Blough, P. M. The visual acuity of the pigeon for distant targets. *Journal of the Experimental Analysis of Behavior*, 1971, 15, 57-68.
- Blough, P. M. Visual acuity in the pigeon. II. Effects of target distance and retinal lesions. *Journal of the Experimental Analysis of Behavior*, 1973, 20, 333-343.
- Campbell, F. W., Kulikowski, J. J., and Levinson, J. The effect of orientation on the visual resolution of gratings. *Journal of Physiology*, 1966, 187, 427-436.
- Campbell, F. W. and Robson, J. G. Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, 1968, 197, 553-568.
- Catania, A. C. On the visual acuity of the pigeon. *Journal of the Experimental Analysis of Behavior*, 1964, 7, 361-366.
- Chard, R. D. Visual acuity in the pigeon. *Journal of Experimental Psychology*, 1939, 24, 588-608.
- Donner, K. O. The visual acuity of some passerine birds. *Acta Zoologica Fennica*, 1951, 66, 4-40.
- Engen, T. Psychophysics. I. Discrimination and detection. In J. W. Kling and L. A. Riggs (Eds.), *Woodworth and Schlosberg's experimental psychology*. New York: Holt, Rinehart & Winston, 1971. Pp. 11-46.
- Galifret, Y. *Le système visuel du pigeon: Anatomie et physiologie corrélations psychophysiologiques*. Doctoral Thesis, Faculty of Sciences, University of Paris, 1966.
- Galifret, Y. Les diverses aires fonctionnelles de la rétine du pigeon. *Zeitschrift für Zellforschung*, 1968, 86, 535-545.
- Green, D. M. and Swets, J. A. *Signal detection theory and psychophysics*. New York: Wiley, 1966.
- Hamilton, W. F. and Goldstein, J. L. Visual acuity and accommodation in the pigeon. *Journal of Comparative Psychology*, 1933, 15, 193-197.
- Hodos, W. Nonparametric index of response bias for use in detection and recognition experiments. *Psychological Bulletin*, 1970, 74, 351-354.
- Hodos, W. and Bonbright, J. C. Jr. The detection of visual intensity differences by pigeons. *Journal of the Experimental Analysis of Behavior*, 1972, 18, 471-479.
- Krasnegor, N. A. and Hodos, W. The evaluation and control of acoustical standing waves. *Journal of the Experimental Analysis of Behavior*, 1974, 22, 243-249.
- Lythgoe, R. J. *The measurement of visual acuity. Special Report Series. No. 173*. London: Medical Research Council, 1932.
- Marshall, J., Mellerio, J., and Palmer, D. A. A schematic eye for the pigeon. *Vision Research*, 1973, 18, 2449-2453.
- McNicol, D. A. *Primer of signal detection theory*. London: Allen and Unwin, 1972.
- Millodot, M. and Blough, P. The refractive state of the pigeon eye. *Vision Research*, 1971, 11, 1019-1022.
- Nye, P. W. The binocular acuity of the pigeon measured in terms of the modulation transfer function. *Vision Research*, 1968, 8, 1041-1053.
- Nye, P. W. On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research*, 1973, 13, 559-574.
- O'Neill, E. *Introduction to statistical optics*. Reading, Massachusetts: Addison-Wesley, 1963.
- Pokorny, J. The effect of target area on grating acuity. *Vision Research*, 1968, 8, 543-554.
- Pollack, I. and Norman, D. A. A non-parametric analysis of recognition experiments. *Psychonomic Science*, 1964, 1, 125-126.
- Riggs, L. A. Visual acuity. In C. H. Graham, (Ed.), *Vision and visual perception*, New York: Wiley, 1965. Pp. 575-588.
- Shlaer, S. The relation between visual acuity and illumination. *Journal of General Physiology*, 1937, 21, 165-188.
- Smith, R. F. Topography of the food-reinforced key peck and the source of 30-millisecond interresponse times. *Journal of the Experimental Analysis of Behavior*, 1974, 21, 541-551.
- Zeigler, H. P. and Schmerla, S. Visual discrimination of orientation by pigeons. *Animal Behaviour*, 1965, 13, 475-477.

Received 5 March 1975.

(Final Acceptance 17 October 1975.)