

VISUAL ACUITY IN THE PIGEON II: EFFECTS OF TARGET DISTANCE AND RETINAL LESIONS¹

PATRICIA M. BLOUGH

BROWN UNIVERSITY

Visual acuity thresholds for grating targets were determined for three pigeons at target distances ranging from 13 to 73 cm. These measurements were made both while the birds were wearing goggles restricting vision to the frontal field of view and when vision was unrestricted. Using a slightly different method, performance was also compared for target distances of 6 and 13 cm while the goggles were in place. For a second group of three pigeons, acuity data were obtained before and after laser lesions of the retina's foveal region. The findings suggested that acuity was relatively poor for targets at the intermediate distances and that it improved as distance both increased and decreased from these intermediate values. The acuity improvement with increasing distance did not occur, however, when the birds were wearing frontal goggles. The data appear to be consistent with Catania's 1964 suggestion that the pigeon has separate frontal and lateral visual systems that differ in their refractive characteristics. Foveal lesions did not appear to affect acuity for distant targets, and it was concluded that, while the fovea serves the lateral field of view, its presence is not necessary to the static acuity characteristics of this system.

Various pieces of evidence combine to suggest that the pigeon has separate systems for frontal and lateral vision. The eye of this species has a well-defined, if somewhat shallow fovea that serves the lateral field of view. Recent anatomical data (Galifret, 1968; Binggeli and Paule, 1969) suggest the presence of an additional area of specialization in the superior temporal quadrant of the retina, which would serve the lower portion of the frontal field of view. Although this area does not contain a foveal depression, it is characterized by a pronounced increase in the density of the retinal cells. Catania (1964) cited a variety of evidence to suggest that the pigeon is hypermetropic for targets in the lateral field, while the frontal field of view is myopic.

Catania's hypothesis has been evaluated through refraction by retinoscopy and by analysis of optical data. Millodot and Blough (1971) reported retinoscopic and anatomical

data that suggested non-uniformity of the pigeon eye with respect to its refraction characteristics, although their data were not clear enough to confirm or reject Catania's hypothesis. Nye (1973) reported optical data based on ray tracing computations. These findings indicate that the near point for objects in the center of the visual field is at a slightly greater distance than are near points for objects in the anterior or posterior visual fields. Although this result is generally consistent with Catania's conclusion, Nye's figures indicate that differences between the various portions of the visual field are too small to account for the observations described in the Catania paper.

The myopic subject is relatively poor at resolving distant targets, while in hypermetropia, resolving power is poor for targets at close range. Thus, behavioral studies of the acuity-distance relation should help to describe the eye's refractive characteristics. Two such studies are available in the earlier literature: Hamilton and Goldstein (1933) and Chard (1939) reported that acuity became poorer for target distances less than 31 to 66 cm. Although these studies did not separate frontal from lateral vision, they do suggest that the pigeon is hypermetropic relative to the human subject. The Catania hypothesis suggests, however, that at short target distances the myopic area

¹This research was supported by Grant No. MH-02456 from the National Institute of Mental Health. Donald Blough's suggestions and criticisms were helpful through all phases of the study. Katherine Fite and Mitchell Glickstein helped with the production and assessment of the laser lesions. Reprints may be obtained from the author, Walter S. Hunter Laboratory of Psychology, Brown University, Providence, Rhode Island 02912.

of the retina would take over and be the determiner of visual acuity.

Because it serves the lateral but not the frontal field of view, the role of the pigeon fovea is relevant to this problem. It is well known that acuity is best for many primate subjects when the target is viewed foveally. If this were the case for the pigeon, we might expect a well-focussed target falling on the fovea to be resolved better than one focussed on the temporal retina, which is characterized by increased cell density but not by a foveal depression. Two lesion studies suggest, however, that the pigeon fovea may not have special significance in visual performance. Yarczower (1964) found that foveal lesions did not affect the birds' ability to resolve a Landolt Ring target at a distance of 20 cm; Goodson (1969) reported that foveal lesions did not affect the optokinetic response to a 36-cm distant stimulus field. If indeed pigeons use lateral vision only for distant objects, the effects of foveal lesions may be most evident at still greater target distances.

The purpose of the present experiments was to examine further the ways in which the structural characteristics of the pigeon eye relate to its visual acuity. One experiment studied acuity thresholds at various target distances both in a free-viewing condition and in a condition that restricted vision to the frontal field. The second experiment considered the effect on distant acuity of lesions in the retina's foveal region.

EXPERIMENT I: EFFECTS OF TARGET DISTANCE

Subjects

The three pigeons used in this experiment were one White Carneau (002), one White King (144), and one homing pigeon (194). These birds had extensive experience with the present apparatus and procedure. Earlier acuity data for them were reported by Blough (1971), where their designations were WC1, WK, and HO1 respectively.

Apparatus

Except for a modification to allow for variations in target distance, the apparatus was identical to that described by Blough (1971). The box was divided into two sections. A front portion contained two glass response

keys with dark and light grating stimuli mounted just behind them. A back portion included an observing key mounted on the rear panel and two photocells mounted on the side panels 36 cm in front of the rear panel. A length-wise partition divided the front portion of the chamber into two alleys, one leading to each target key. The partition extended from the front panel to a position just opposite the photocells. A small lamp mounted on the partition illuminated both photocells simultaneously. The front and back sections of the box fitted together in a telescopic fashion, so that the back portion could move toward or away from the target keys. Thus, the length of the central partition and the distance of the photocell beams from the target keys could be varied while the relative positions of the observing key and the photocells remained unchanged.

As in the previous study, target luminance was approximately 41 cd/m², and contrast between the dark and light bars of the stimulus pattern, at least 98%. The visual angle subtended by the diameter of the circular target keys was maintained at a constant value of 12 min of arc for all target distances. The experiment was controlled by a LINC computer (Clark and Molner, 1964) and associated relay equipment.

Procedure

The procedure was similar to that described by Blough (1971). A session consisted of 128 trials, each beginning with the onset of the observing keylight at the rear of the box. A single peck on this key turned off its light, turned on the photocell light, and operated a shutter to illuminate the two target keys. One key was striped and the other blank, according to a program based on a randomized block design. If the bird crossed the photocell beam leading to the blank key, the shutter closed, the photocell light turned off, and a 20-sec inter-trial interval began. This contingency also occurred if the bird crossed either photocell beam within 0.5 sec of shutter operation. If the bird paused for 0.5 sec or more and then crossed the photocell beam corresponding to the striped target, the shutter remained open until a peck on the target key occurred. This peck closed the shutter, turned off the photocell light and, with a probability of 0.5, operated the food magazine.

For each trial, the response recorded was the one that broke the photocell beam, and this response was designated correct if the beam broken led to the striped target key. A correction procedure was used so that the stimulus array remained unchanged on trials following errors (crossing the beam leading to the blank key). Since these "correction" trials were not random, photocell responses following an error were not recorded until after a correct choice occurred. Also not recorded were photocell responses that occurred during the 0.5-sec delay following the response to the observing key.

Spatial frequencies used in this study ranged from 0.02 to 0.61 cycles per minute arc subtended at the photocell beam. For any given condition, a set was chosen so that there was at least one value at which the birds' error rates were less than 10% and so that additional values yielded, when possible, a range of error rates between 10% and 40%. There were two blank stimuli differing from each other slightly in luminance. A random program determined which blank stimulus would occur on each trial. Although all striped and blank stimuli were approximately equal in luminance, slight differences did occasionally occur. The two blank stimuli were used to confound luminance effects.

Each daily session tested at a single spatial frequency; across sessions, the various stimulus values occurred in descending order of visual angle (increasing order of spatial frequency). At the beginning of each descending series, there was an initial training period at the highest visual angle; the birds were maintained at this value until their error rate was 12% or less and until performance over two daily sessions did not improve by more than two percentage points. Then, sessions occurred at each new stimulus value, and the series ended when error rates reached or exceeded 40%. Final data for each condition were based on at least two such descending series (512 trials per point). If the birds' performance appeared to improve from the first to the second series, the series continued, and final data were based on successive series that did not show systematic differences from each other.

Psychophysical functions were determined at varying target distances, first under conditions restricting vision to the frontal field and then under free-viewing conditions. To restrict

the field of view, the birds were fitted with frontal goggles (Catania, 1963) that were held in place with dental acrylic (Mello, 1967). The goggles permitted vision through a 15-mm diameter circular opening in front.

There were four target distances: 73, 53, 26, and 13 cm. Table I summarizes the order in which testing conditions occurred. For Bird 194, attempts to obtain data at target distances shorter than 73 cm were unsuccessful while the goggles were in place, since no spatial frequency associated with an error rate of 12% or less could be found. With the goggles removed, efforts to obtain acuity data at progressively increasing target distances failed until the 73 cm distance was reached. Because the bird seemed to be performing so well at this distance, it was again tested without goggles, as Table I indicates.

Table 1

Summary of conditions to show order in which target distances occurred. Figures indicate distances in cm. They are enclosed in parentheses when the constant stimulus method was in effect.

Condition	Birds		
	002	144	194
With goggles	73	73	73
	53	53	-
	26	13	-
	13	26	-
	(13)	(13)	(13)
	(6)	(6)	(6)
Without goggles			(13)
	13	26	73
	26	13	53
	53	26	26
	73	53	13
	73		

Because Bird 144, while wearing goggles, showed an improvement in acuity at the 13-cm distance relative to that at 26 cm, some data were taken at even shorter distances. The method was somewhat different for this portion of the study, which was conducted before the goggles were removed. Error rate was measured for four stimuli having spatial frequency values of 0.01, 0.02, 0.04, and 0.06 cycles per minute of arc, and the birds were tested at the 13-cm distance and at a distance of approximately 6 cm. In the latter condition, the choice response was the key peck itself, not the crossing of the photocell beam. Thus, the bird's dis-

tance from the target was controlled by its head position and the length of its beak; the 6-cm figure is an estimated average based on observation and measurements of the distance between the tip of the beak and the cornea. A larger target was used in this portion of the experiment, since two of the birds had relatively high thresholds at the 13-cm distance under the conditions described earlier. The target in this part of the experiment had a diameter that subtended a visual angle of 7 deg 54 min of arc. This portion of the experiment was also different in that a method of constant stimuli was used to determine order of stimulus presentation. Thus, all four spatial frequencies, after being introduced during pre-

liminary sessions in descending order of visual angle, were presented in a randomized block design within each session. At the 13-cm distance and again at the 6-cm distance, each value was presented a total of 256 times. Details of this procedure are like the constant stimulus procedure described in Blough (1971). Since the performance of Bird 194 clearly improved when tested at the 6-cm distance, the procedure for the 13-cm distance was repeated and the data found to be consistent with the previous results.

RESULTS

Table II summarizes the raw data. The principal psychophysical functions are shown in

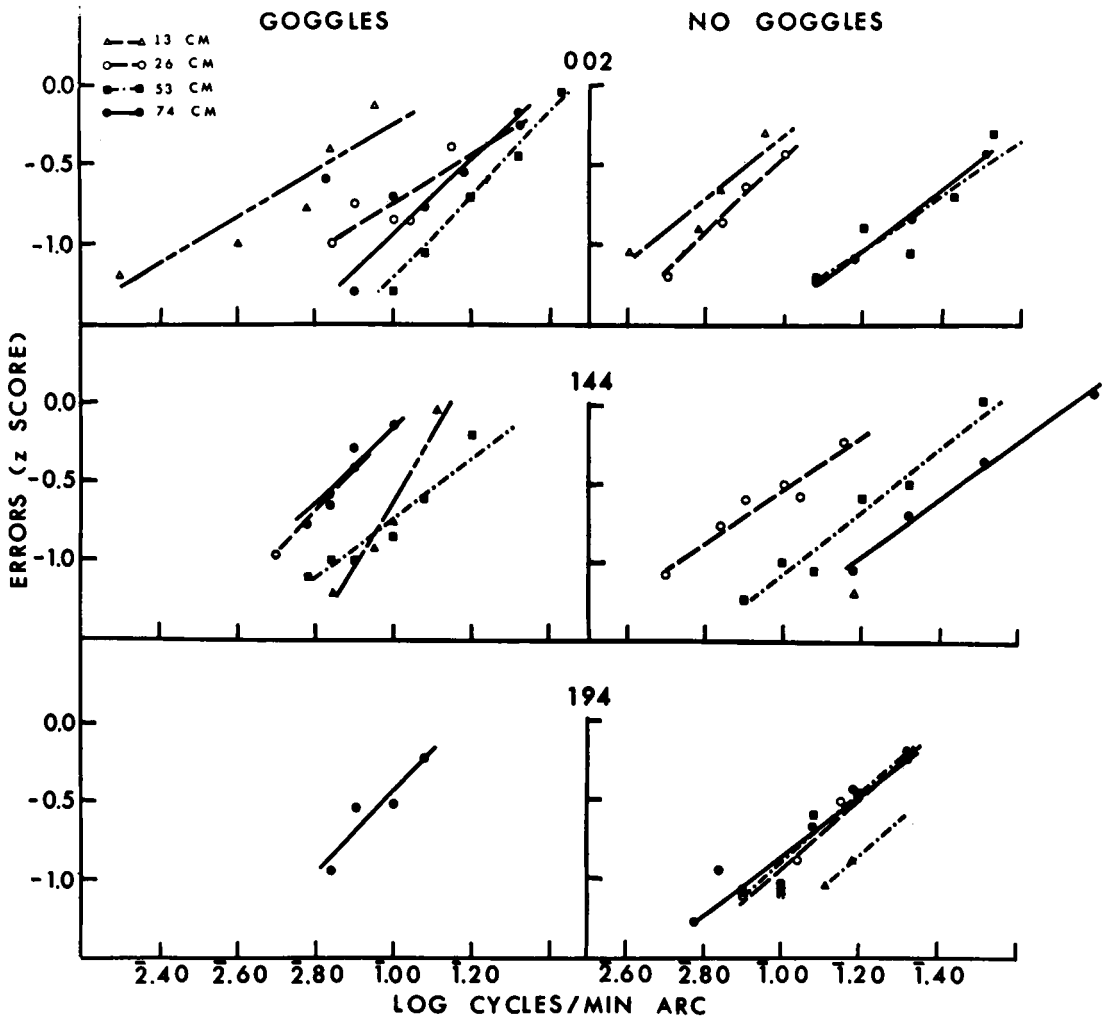


Fig. 1. Psychophysical functions at varying target distances for conditions where frontal goggles were worn and where field of view was unrestricted (no goggles). Data points include only those representing error rates of 10% or greater. Straight lines were fit by the Method of Least Squares (Lewis, 1960).

Figure 1. To facilitate interpolation, these functions are presented as cumulative normal-log transformations in which z scores are plotted against log spatial frequency. Since error rates less than 10% tended not to be linear with the rest of the data when plotted in this fashion, the plotted data include only points corresponding to error rates of 10% or greater.

It is difficult to apply conventional measures of variability to these data, since each point represents only four determinations of error rate. However, since the birds were tested at each spatial frequency for two successive days, the difference in error rate for each of these

sets of days helps to indicate the reliability of the data. Thus, for Bird 002, the difference between performance on the first and second day of testing averaged 2.6 percentage points for the 53-cm distance without goggles. This value is based on the five stimuli indicated in the appropriate functions in Figure 1 and includes differences between the first and second day of testing for both sets of descending series. The corresponding figures for Bird 144 was 4.8 percentage points and, for Bird 194, it was 4.4 percentage points.

Because of the possibility of order effects, psychophysical functions were checked in two instances following testing at new distances. As

Table 2

Per cent error scores as a function of spatial frequency for each bird at four target distances. Goggle and no-goggle conditions are shown separately.

Target Distance (cm)	Stimulus (Cycles/min arc)	Goggles			No Goggles		
		002	144	194 002	144	194	
13	0.02	11.5	2.8	-	3.1	-	-
	0.04	15.6	3.9	-	15.4	-	-
	0.06	22.4	5.9	-	18.1	-	-
	0.07	34.4	12.2	-	24.6	2.3	-
	0.09	45.0	18.3	-	38.3	2.9	-
	0.10	-	23.1	-	-	5.2	4.8
	0.13	-	49.0	-	-	8.4	15.2
	0.15	-	-	-	-	12.1	19.1
26	0.04	6.0	8.8	-	7.0	6.8	8.2
	0.05	8.6	17.6	-	12.5	13.8	-
	0.07	16.2	27.8	-	19.8	22.1	-
	0.08	23.0	34.0	-	26.4	26.6	13.7
	0.10	20.4	-	-	32.9	29.9	13.6
	0.11	20.5	-	-	-	28.2	19.4
	0.14	34.7	-	-	-	41.3	29.9
	0.21	40.4	-	-	-	45.0	41.2
53	0.04	1.2	5.7	-	-	4.4	6.2
	0.06	1.8	14.2	-	-	-	-
	0.07	4.3	16.2	-	-	-	-
	0.08	9.6	15.8	-	-	11.3	14.5
	0.10	10.0	19.6	-	8.0	16.3	14.4
	0.12	14.8	26.8	-	11.6	15.1	27.8
	0.16	23.8	42.2	-	18.8	27.5	33.4
	0.21	33.0	-	-	14.6	31.1	42.5
	0.27	47.5	-	-	24.0	-	-
	0.34	-	-	-	38.1	51.4	-
73	0.04	1.8	2.9	6.8	-	-	3.2
	0.06	4.8	21.5	7.5	-	-	10.2
	0.07	1.8	26.4	17.2	-	-	16.6
	0.08	10.3	39.0	29.4	-	-	14.2
	0.10	23.8	41.0	29.5	4.9	-	15.4
	0.12	22.2	-	40.7	10.9	8.8	25.0
	0.15	28.7	-	-	13.9	15.2	32.6
	0.21	42.8	-	-	20.5	23.6	43.1
	0.32	-	-	-	33.8	35.8	-
	0.61	-	-	-	56.3	53.3	-

mentioned above, Bird 194 was re-tested at 13 cm following testing at 6 cm. In another case, Bird 144 was re-tested at 26 cm following testing at 13 cm (bottom half of Table I). For both these cases, the data were reasonably well replicated, indicating that the improvement in acuity at the shorter distances was not merely a training effect.

The functions in Figure 1 indicate that (1) an effect of target distance on performance was present, but it differed among birds; (2) error rates were greater when the birds wore goggles. A complete set of data for Birds 144 and 194 at the 13-cm distance is unavailable because of the necessity for using very fine lines to test under that condition. The finest grating contained 208 lines per inch; it did not seem advisable to use anything finer because of the possibility that diffraction-induced contrast changes would contaminate the data. However, the available data indicate that both these birds had better acuity at 13 cm than at the greater distances.

Data for psychophysical functions were not collected unless there was a spatial frequency at which the bird's error rate was less than 12%. Thus, there is only one function for Bird 194 for the frontal goggle condition. Despite many hours of training, this bird failed to meet the 12% criterion at the shorter target distances.

Figure 2 summarizes the acuity-distance relationship with acuity thresholds defined as the spatial frequency that yielded an error rate of 25% (z score of -0.67). Here, the reduction in acuity under the restricted viewing conditions is clear; and for Birds 002 and 144, it appears that this effect is greater at the greater target distances. Under free-viewing conditions, two of the birds (002 and 144) showed an improvement in acuity as target distance increased beyond 26 cm. For Birds 144 and 194, there was improvement in acuity as distance decreased from 26 to 13 cm. Figure 1 must be consulted for this information with regard to Bird 144 because those data are inadequate for

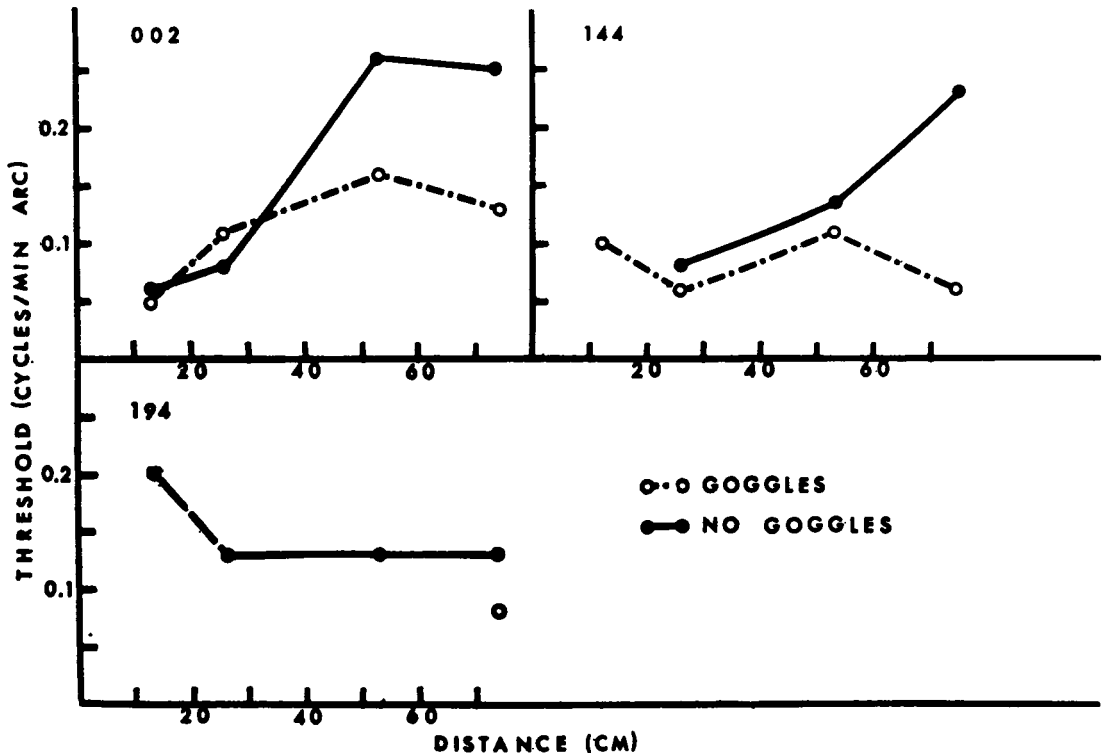


Fig. 2. Acuity threshold plotted against target distance for both the goggle and no-goggle conditions. (For Bird 194, only one threshold was obtainable when the goggles were in place.) Threshold values were determined in most cases by interpolation at the 25% error point (z score of -0.67) on the psychophysical functions shown in Figure 1. For Bird 194, the threshold at 13 cm was determined by extrapolation, and a dashed line is used to connect this point with the rest of the function.

threshold specification. The improvement at the 13-cm distance was also evident for this bird when it was wearing goggles.

Error rates dropped markedly for Birds 002 and 194 when target size was enlarged and the method of constant stimuli introduced to compare acuity at short distances. The data from this experiment are not shown graphically because at both distances, Birds 002 and 144 had error rates of less than 10% to all four stimulus values. Bird 194 showed similar low error rates at the 6-cm distance, but acuity was notably poorer at the 13-cm distance. The effect is illustrated by the fact that, for the 0.06 cycles per minute arc pattern, Bird 194's error rate was 11.3% at the 6-cm distance, while it was 23.8% at the 13-cm distance. Error rate to the 0.04 cycles per minute arc pattern were 6.6% at 6 cm and 21.9% at 13 cm. The difference in the response requirement for these two conditions may have contributed to the effect.

The drop in error rate following enlargement of target size may be illustrated by the following examples: for Bird 002, error rate to the 0.06 cycles per minute arc stimulus was 22.4% for the smaller target diameter and dropped to 4.3% for the larger target. In the case of Bird 194, error rate was 32.4% to the 0.02 cycles per minute arc stimulus when the target was small, and for the larger target, error rate to this stimulus dropped to 15.8%. There was little or no training effect for this bird; results for the smaller target were replicated following the experiments with the larger field. Bird 144, whose error rates were low at the 13-cm distance even when the target was small, did not show the target size effect. When the effect did occur, it was probably unrelated to the difference in method of stimulus presentation. Earlier data (Blough, 1971) indicated little difference in acuity data generated by the descending series and constant stimulus methods. The improvement in acuity for the larger target areas may have contributed to the apparent difference in thresholds obtained by Blough (1971) and Nye (1968). In the Nye study, target size was relatively large, and thresholds appeared to be lower.

EXPERIMENT II: EFFECTS OF RETINAL LESIONS

Subjects

The three pigeons used in this experiment were one White Carneau (626) and two hom-

ing pigeons (668 and 670). These subjects had extensive experience in the apparatus; their performances on a binocular acuity task have been described in a previous paper (Blough, 1971), where their designations were WC2, HO2, and HO3 respectively.

Apparatus

The apparatus is described in Experiment I. Target distance for this study was 73 cm and its overall angle of subtense, 12 min of arc.

Procedure

The plan of this study was to obtain acuity data for each eye individually and to compare findings obtained before and after the production by laser of retinal lesions. Goggles like those described in Experiment I were used to occlude vision. Each bird was to wear a single goggle, its opening covered with black cardboard and its base attached to the feathers with collodion. Although this procedure worked well with Birds 626 and 668, Bird 670's goggle would not remain in place, and tests in its case were binocular.

The procedure was similar to that described in Blough (1971). It differed from the procedure described in Experiment I in that the photocell light remained on continuously and only one blank stimulus was used. Stimulus presentations occurred in descending order of visual angle with two daily sessions (total of 256 trials) allowed for each stimulus value. Initial training was in the presence of the stimulus having the largest visual angle and continued until the birds' performances reached a level of 10% error or better, and then until the error level failed to drop by more than two percentage points over two consecutive sessions. Birds 626 and 668 were tested on this procedure first with the left eye and then with the right eye covered. For these subjects, data were based on one descending series for each condition (256 trials per data point). Data for Bird 670 were binocular and were based on two descending series (512 trials per point).

Lesions were made with a ruby-laser photo-coagulator. An attached ophthalmoscope permitted observation of the eye's fundus and directing of the laser beam to the fovea. To increase the probability of destroying the fovea, seven lesions, all aimed at the fovea, were made in each eye. The lesions were later exam-

ined ophthalmoscopically and, at the end of the experiment, by post-mortem histology.

Several weeks after the lesions were made, acuity testing resumed according to the pre-lesion procedure. When there appeared to be a lesion effect on the first data set, data for a second psychophysical function were collected.

RESULTS

Figure 3 summarizes the findings for this experiment. The fundus diagrams are based on examination by light microscopy of the

stained retinal sections. They indicate the approximate location and size of the lesions, which in most cases appeared to have affected all layers of retinal cells. An exception was the right eye of Bird 626, where the ganglion cell fibers appeared undamaged. Except in this case, microscopy revealed no evidence of a fovea outside of the lesioned area in any of the eyes. (In unlesioned eyes, the fovea is ordinarily found without difficulty by its position just nasal and superior to the optic disc.) Earlier ophthalmoscopic examination also indicated

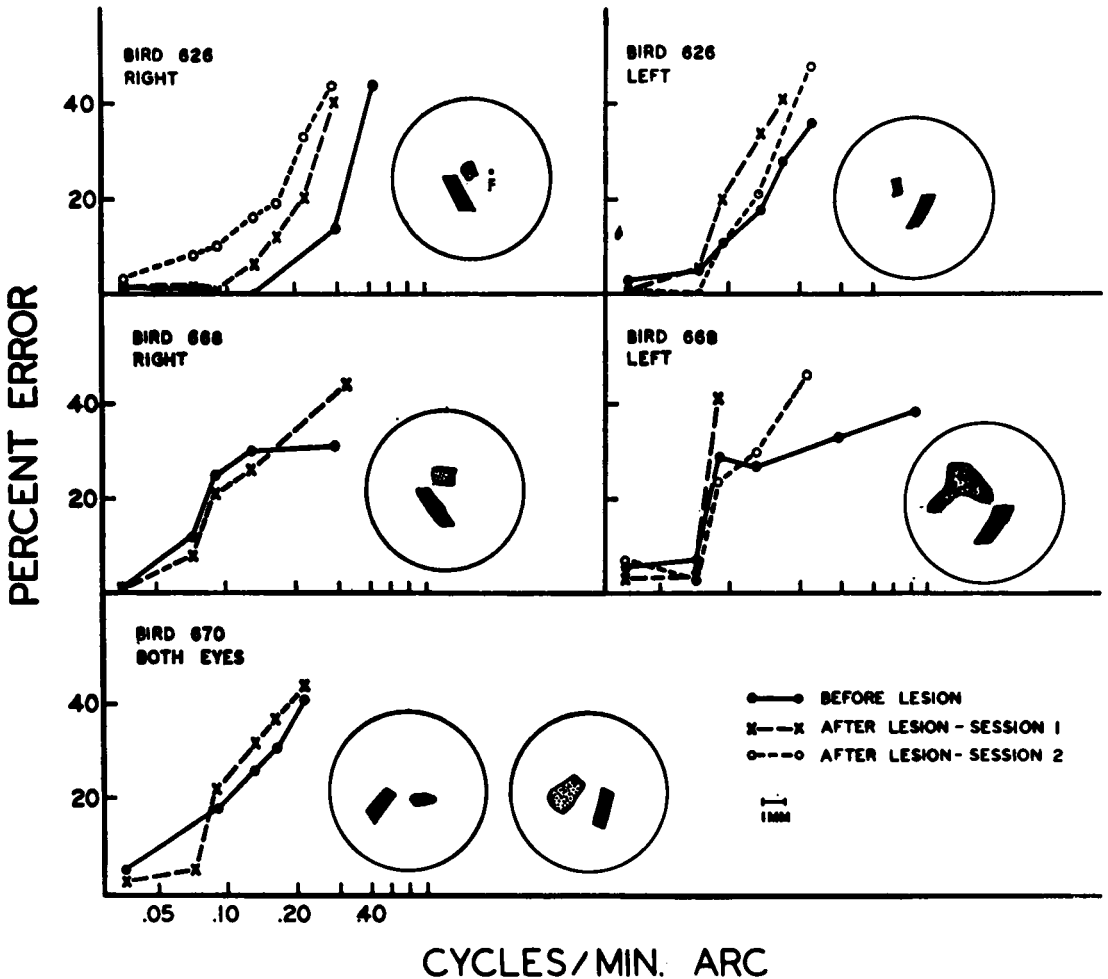


Fig. 3. This figure includes psychophysical functions obtained for each eye before and after production of laser lesions and diagrams to indicate the location and size of the lesions. Note that the functions are in terms of per cent error (not the z score transformations) and that the abscissa is scaled logarithmically. The diagrams to the right of each set of functions represent schematically a portion of the fundus of the corresponding eye, showing the location of the optic disc, the lesion, and, when it was found, the fovea. In these diagrams, the optic disc is the approximately rectangular solid area. The lesion is indicated as an irregular stippled area, to the right of (nasal to) the optic disc for the right eyes, and to the left (also nasal) for the left eyes. For Bird 670, the left-hand diagram is for the right eye and the right diagram for the left eye. Orientation of the eyes is not precise, but the superior point on the fundus is approximately at the top of the diagram.

that the lesions were in the region of the fovea; thus, it appears that both foveas of Bird 668 and 670 and the fovea of the left eye of Bird 626 were destroyed. The fovea of the right eye of Bird 626 was intact, and the lesion was located between it and the optic disc.

The psychophysical data, shown in Figure 3, indicate a clear effect of the lesions only in the case of the right eye of Bird 626. The initial effect in the case of this bird's left eye nearly disappeared on re-testing, possibly due to practice. The separation between the pre-lesion and post-lesion functions for the left eye of Bird 668 occurs beyond the region of conventional threshold definition (25% error). The flattening out of the pre-lesion curve suggests poor stimulus control, and it is possible that here some other variable, such as slight luminance differences, may have affected the data.

It is surprising that the only clearcut lesion effect was in the eye where the fovea remained intact and where the damage appeared not to reach all cell layers. It is possible that this particular lesion produced a distorting effect that reduced acuity; however, there are not enough data here to justify further speculation. Goodson (1969) found that certain non-foveal lesions in pigeons appeared to enhance the optokinetic response.

DISCUSSION

The optics of the pigeon eye have not been fully described, but there is good evidence that it is non-uniform with respect to its refractive characteristics (Millodot and Blough, 1971; Nye, 1973). Myopia and hypermetropia are defined by the manner in which the unaccommodated eye focusses distant objects. These conditions cannot be specified completely on the basis of the present data, since accommodation was uncontrolled. However, since defocussing is associated with a drop in acuity, the present findings probably bear on the eye's refractive condition. Where acuity begins to improve with increasing target distance, it is reasonable to conclude that the target is crossing the eye's near point of accommodation and the target is coming into focus; if acuity drops with increasing target distance, we may conclude that the distant objects are out of focus. The latter condition indicates myopia, since the normal, emmetropic eye focusses targets of in-

finite distance. For an eye containing two refractive systems, such systems might fail to overlap completely, such that there would be distances at which neither system could achieve perfect focus; such distances might be within the near point of accommodation for a hypermetropic system and beyond the far point for a myopic system. Under these conditions, one would expect the acuity *versus* distance function to fall and then to rise again as target distance increased. If vision were limited to the myopic system (as attempted here with frontal goggles), acuity should be relatively poor for distant targets.

Although these predictions appear to receive partial support from the present data, individual differences cloud the picture. Because the individual psychometric functions are regular, the variability of the findings appears to be based on real between-subject differences. That such differences exist is not surprising; certainly they would occur in human data, since people differ widely with respect to the refractive characteristics of their eyes. Thus, the data shown in Figure 2 may reflect basic pigeon acuity-distance functions confounded by individual differences in refractive condition.

For the free-viewing condition, the improvement in acuity with increasing distance for Birds 002 and 144 is consistent with the data of Chard (1939), although his data suffered from day-to-day variability. Chard concluded that the near point of accommodation is between 40 and 60 cm, but he did not investigate distances shorter than 30 cm. In the present data, the improvement in acuity is not as clear in the data for Birds 002 and 144 when their field of view was restricted. At the greater distances, then, the availability of the lateral field of view may contribute to the improvement in acuity. This notion is consistent with informal observations (Blough, 1971) indicating that pigeons view distant objects laterally. The flatness of Bird 194's function range beyond 26 cm may be attributable to a wider range of accommodation or, perhaps, to a more distant far point, which would have been revealed if measurements had been made at even greater target distances.

For Birds 144 and 194, acuity also appeared to improve as distance decreased from 26 cm. This rise in acuity at very close distances is suggested by the psychophysical functions for

Bird 144 shown in Figure 1, by the solid function for Bird 194 shown in Figure 2, and by the results for this latter subject when acuity was compared between the 13- and the 6-cm distances. The effect was seen both when the birds were wearing goggles and when the field of view was unrestricted. Together with informal observations that the birds viewed near objects frontally, these findings suggest that the improvement in acuity for very close targets does not depend on the availability of the lateral field of view. It is possible that acuity would have improved with shorter distances for Bird 002, but apparatus limitations prevented us from making the appropriate measurements.

The present findings are partially, but not entirely, consistent with optical data reported by Nye (1973). Nye's ray-tracing computations indicated that objects in the lateral field would be in best focus at a distance of about 4 to 5 cm from the pupil, while objects lying in parts of the anterior and posterior fields would achieve maximum focus at a 2 to 3 cm distance. These data were based on frozen sections of eyes whose accommodative states were apparently unknown, and the report indicates that there may have been other sources of error. It seems unlikely that the pigeon is as extremely myopic as the Nye figures suggest. Its ability to focus at much greater distances is indicated by the present data, those of Chard (1939), and the fact that this bird presumably uses distant visual cues while in flight. However, the relationship described by Nye between points of best focus for frontal and lateral fields is consistent with the present findings and the notion of Catania. These relationships are important for operant research, because they indicate that some viewing distances and target orientations may be less appropriate for visual stimuli than others.

The improvement in acuity for distant targets under free-viewing conditions could be attributable to the use of the centrally located fovea as well as to better focussing. However, the lesion experiments described here suggest that the pigeon fovea is relatively unimportant to acuity, and these findings are consistent with those of Goodson (1969) and Yarczower (1964)².

²The exact location of the lesions was not specified in the Yarczower paper. However, a personal communication from a collaborator, M. Wolbarsht, states that the foveas were destroyed.

The substantial effect of stimulus field size is also consistent with the hypothesis that static acuity is not primarily determined by a small restricted area on the retina. Lesions of the primate fovea, on the other hand, have a pronounced effect on acuity (*e.g.*, Yarczower, Wolbarsht, Galloway, Fligsten, and Malcolm, 1966); the fovea's relative importance in these species is probably due to its great anatomical specialization. The thick, cone-rich retina of the pigeon may be functionally more homogeneous; the fovea is shallow and variable compared to that of many other bird species, and it has the convexiculate form that Pumphrey (1948) has suggested is adapted to motion detection rather than static acuity.

The superior portion of the temporal retina in the pigeon is characterized, like the fovea, by a pronounced increase in cell density (Galfret, 1968). It does not, however, contain an actual foveal depression. This area probably serves at least the lower portion of the frontal field of view. Comparisons of static and dynamic acuity for well-focussed images falling on these two areas of specialization might help further to clarify the role of the foveal depression. The present data are not adequate to indicate how the two retinal areas compare in resolving power, but their existence adds to the indirect evidence for the presence of two visual systems in the pigeon. The physiological basis for the refractive differences might have to do with a peculiar lens shape or possibly with differing distances between lens and various portions of the retina (Millodot and Blough, 1971).

In summary, it may be concluded that target distance is an important factor in pigeon visual acuity and that this bird may have separate systems to deal with near and far visual stimuli. The exact effect of target distance may differ for different birds. The present findings agree with others to the effect that the fovea does not have an important role in some visual tasks, but there is evidence that the foveal region is a part of the system that is used for distant vision.

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, P. M. The visual acuity of the pigeon for

- distant targets. *Journal of the Experimental Analysis of Behavior*, 1971, 15, 57-67.
- Catania, A. C. Techniques for the control of monocular and binocular viewing in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1963, 6, 627-629.
- 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.
- Clark, W. A. and Molner, C. E. The LINC: a description of the Laboratory Instrument Computer. *Annals of the New York Academy of Science*, 1964, 115, Art. 2, 653-668.
- Galifret, Y. Les diverse aires fonctionelles de la rétine du Pigeon. *Zeitschrift für Zellforschung*, 1968, 86, 535-545.
- Goodson, J. E. *Optokinetic responses in the pigeon*. Unpublished doctoral dissertation, George Washington University, 1969.
- Hamilton, W. F. and Goldstein, J. L. Visual acuity and accommodation in the pigeon. *Journal of Comparative Psychology*, 1933, 15, 193-197.
- Lewis, D. *Quantitative methods in psychology*. New York: McGraw-Hill, 1960.
- Mello, N. K. A method for restricting stimuli to the frontal or lateral visual field of each eye separately in pigeon. *Psychonomic Science*, 1967, 8, 15-16.
- Millodot, M. and Blough, P. The refractive condition 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.
- Pumphrey, R. J. The theory of the fovea. *Journal of Experimental Biology*, 1948, 25, 299-312.
- Yarczower, M. *The development of a behavioral system to evaluate visual performance in animals*. Report for Institute of Behavioral Research, August, 1964.
- Yarczower, M., Wolbarsht, M. L., Galloway, W. D., Fligsten, K. E., and Malcolm, R. Visual acuity in a stump-tail macaque. *Science*, 1966, 152, 1392-1393.

Received 19 February 1973.

(Final Acceptance 5 July 1973.)