THE VISUAL ACUITY OF THE PIGEON FOR DISTANT TARGETS¹

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The acuity of six pigeons was measured in an apparatus that required the birds to make visual discriminations at a distance of 28.75 in. (73 cm) from the stimulus targets. The stimuli were black and white gratings of varying stripe width. A forced choice procedure was used, and both the Method of Constant Stimuli and a descending series technique determined the order of stimulus presentation. Thresholds, obtained by interpolating at the 25% error point on the psychometric functions, ranged from 1.16 to 4.0 min of arc. Thresholds measured in the same apparatus for two human observers were 0.79 and 0.82 min of arc. The descending series design produced lower per cent error rates at the widest stripe value, but otherwise there appeared to be no difference between psychophysical methods. Position preferences occurred in most of the birds; differential per cent error functions and differential latency functions to the two keys illustrate these. Retinal histology revealed shallow, centrally located foveae in the three pigeon breeds used.

Birds are known for their well-developed ability to discriminate visual detail. Various aspects of eye structure differ among the different avian species, however, and related differences in visual acuity should be expected. The process of domestication may produce some retinal deterioration (Wood, 1917), for example, so that acuity in pigeons and other domestic species may be less than that of their wild relatives. Despite the popularity of pigeons as subjects for animal research, there have been surprisingly few behavioral studies of their visual acuity.

The literature abounds with anatomical descriptions of the pigeon's eye (*e.g.*, Walls, 1963; Chard and Gundlach, 1938; Wylie, 1962; Bingeli and Paule, 1969; Galifret, 1968). In common with other bird species, the pigeon eye has several structural characteristics that may suggest its adaptation for good acuity. Included among these features are the relatively large size of the eyeball, the thick, cone-rich

retina, the presence of colored oil droplets, and the relatively wide range of accommodation.

An important difference between pigeons and other avian species concerns the fovea. The pigeon fovea is relatively shallow, and it tends to be variable among birds in its shape and extent (Slonaker, 1898; Walls, 1963; Galifret, 1968). Its approximately central location suggests its role in lateral, monocular vision. Granting an important role to the fovea in visual acuity, one would predict that pigeons would have better acuity for lateral than for frontal targets, but that their acuity would be poorer than that of many other bird species.

Among the few behavioral studies of pigeons acuity are several done with two-choice techniques. Gundlach (1933) used a two-alley maze and required the bird to choose between alleys at a distance of 15 ft from a striped test field. According to his data tables, discrimination learning was very poor, and there appeared to be little or no relation between performance and stripe width. The "threshold" values of 23 to 28 sec of arc that he reported are based on a sequential statistic, and the relation of these values to the more conventionally defined thresholds is unclear.

Two studies used jumping stands to study acuity as a function of distance from a striped test field. Hamilton and Goldstein (1933) reported acuity figures ranging from 2.7 to 3.1

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min of arc at an unspecified brightness; their data appear to be based on relatively few (four to eight) trials, however, and on a rather casual criterion of threshold performance. In a more detailed paper, Chard (1939) shows psychometric functions (per cent correct plotted against visual angle) for different target distances. Interpolation at the 75% correct point on the curve for the 23.5 in. (60 cm) target distance reveals thresholds ranging from about 3.5 to 5.0 min of arc. Illuminance at the stimulus targets was 3.1 foot-candles. From the effect of target distance on performance, he concluded that the near point of accommodation was in the neighborhood of 15.5 in. (40 cm).

A recent study of the pigeon acuity (Nye, 1968) reported modulation transfer functions, *i.e.*, curves describing the minimum contrast at which the birds could detect varying spatial frequencies of a sinusoidal bar pattern. This research used a key-pecking response; the large stimulus field had a luminance of 0.02 log foot-lamberts, and it fell in the bird's binocular field within 3.5 in. (8 cm) of its beak. Nye concluded that peak sensitivity occurs at a slightly lower spatial frequency for the pigeon than it does for humans.

The present research had several aims. The principal goal was to obtain visual acuity data at a specified brightness from the White Carneaux and White King breeds that are currently popular subjects for animal research; it sought also to compare the performance of these birds with a group of homers bred for racing. The experiment was designed to maximize discrimination performance by forcing the bird to respond to stimuli located well beyond its near-point of accommodation (Chard, 1939), and by continuing daily sessions over many months in order to reduce learning effects. A second goal was to compare the acuity functions derived from two psychophysical methods, a modified descending series and a Method of Constant Stimuli. A final aim was to seek related histological information by examining retinas of pigeon breeds used in this research.

METHOD

Apparatus

In order to run three birds simultaneously, three similar experimental boxes were mounted one above the other in a dark-

ened room. Figure 1 depicts a single experimental chamber.

Fig. 1. Diagram of the experimental chamber. A partition divides the chamber into two alleys, entrances to which are marked by hurdles mounted 2 in. (5 cm) above the floor. Photocells, illuminated by a white 28-v, 0.1-ampere lamp, record entrances into the alleys. The plastic observing key and the glass stimulus keys are 1 in. (2.5 cm) in diameter and mounted approximately 10 in. (25 cm) above the floor. The observing key is illuminated from behind by white light, the stimulus keys, by the optical system described in the text. A section removed from the bottom of the central partition permits access to the food magazine.

Mounted at the rear of each chamber was an optical system designed to illuminate the two response keys. The source was an 18 ampere, 6-v GE Microscope-Illuminator lamp. Lenses focused the light on a relay operated shutter, which, when opened, allowed light to fall on two 17.8 cm diameter Plexiglas discs mounted 0.6 cm behind the response keys. The stimulus patterns were mounted around these discs.

The stimuli were photographic negatives of a striped pattern in which the black and white stripes were of equal width. Negatives of varying stripe width were produced by enlarging or reducing the original photograph; thus, the total amount of light transmitted by the various negatives was approximately constant. The contrast between the light and dark stripes as measured by a microdensitometer was at least two logarithmic units; contrast ratios thus exceeded 98% for all stimulus patterns. Stepping motors turned the discs bearing the stimulus patterns, allowing the different stimuli to fall behind the key. For striped stimulus fields, the stimuli were mounted on the subject's side of the disc, so that light passing through the disc and then through the negative produced a striped field just behind the key. For a blank field equal in color and luminance to the stripes, one of the finely striped negatives, covered by a piece of glass, was mounted on the rear of the disc, so that light through the negative was diffused by the disc before reaching the key. Densitometer measurements confirmed the absence of sys-

tematic luminance differences among the various striped patterns.

The inside of the box was light gray, and it was illuminated by the small lamp that provided excitation to the photocells. Luminance measurements were made in various parts of the box with an SEI photometer. Stimulus field luminance was 1.1 log millilamberts; luminance values in the rear portion of the box's interior ranged from 1.8 log millilamberts in the corners to 1.8 log millilamberts on the lighted observing key. Human data (Craik, 1939) suggest that adaptation to luminances in this range would have little effect on acuity for the stimulus fields described here.

A LINC computer (Clark and Molnar, 1964) and associated relay equipment controlled the experiment and recorded data, which it stored on magnetic tape. The computer also analyzed the data and printed out the results.

Subjects

Six male pigeons served. Birds WC1 and WC2 were White Carneaux, 2 to 3 yr of age; Bird WK, a White King 7 to 8 yr of age; and H1, H2, and H3 were homers 1 to 2 yr of age. The white birds came from the Palmetto Pigeon Plant; the homers were the gift of a local donor, who raised pigeons for racing. All but one of the birds were experimentally naive at the beginning of this research; WC1 had been used in a demonstration of response differentiation. The birds were maintained at 70 to 80 % of their free-feeding weights.

Procedure

The basic procedure followed a forced choice, trial-by-trial organization. The pigeon's first task on each trial was to peck three times at the lighted observing key mounted on the rear wall of the experimental chamber. Completion of the ratio turned off the observing keylight and illuminated the two stimulus keys, one striped, one blank, on the front panel. The bird then entered one of the two alleys, recording a response either to the right or to the left side as it crossed the photocell beam. If the bird chose the alley leading to the blank key, the stimulus lights went out and the intertrial interval began; if it entered the alley leading to the striped key, the stimulus lights remained on until the bird pecked three times on that key. Completion of this ratio was required to turn off the stimulus lights, and,

on half the correct trials it led to reinforcement (1.5 sec access to grain for WC1; 2 sec for the other birds). The intertrial interval then began.

During the intertrial interval all three keys were dark, and responses on any of the keys or to the photocell had no effect. The photocell light remained on during this period to maintain light adaptation. Both stepping motors operated following every correct trial whether or not a new stimulus array was to be set up; thus, vibratory and auditory cues produced by these motors were not related to the plan of the next trial. The intertrial interval lasted 20 sec and ended when the observing keylight went on.

A randomized block procedure determined the stimulus array and the reinforcement schedule. On eight trials in a block of 16, the striped key was on the right and the blank on the left; the striped key was on the left for the other eight trials. Reinforcement was set up on eight trials in each block, but its occurrence was independent of the position of the striped key. Within the limitations of this procedure, the plan of each trial was determined randomly. A correction procedure helped prevent the development of position habits; that is, following an incorrect response, the same stimulus array reappeared on succeeding trials until a correct response occurred. These correction trials did not count among the trials in the randomized block; however, a reinforcement set up for the original trial was delivered when the correct response was finally made.

In order to improve stimulus control, the method included some features intended to discourage rapid choices between alleys. One of these was the insertion of the hurdles at the alley entrances (Fig. 1). The other was a 1.5-sec delay requirement between the completion of the observing key ratio and the breaking of a photocell beam. Photocell responses that had a shorter latency turned off the stimulus lights, started the intertrial interval, and set up the same stimulus array on the next trial. Such short latency responses were not recorded; observations suggested that they occurred infrequently.

Altogether, there were 11 stimulus values, ranging in spatial frequency from 0.03 to 0.64 cycles per minute of arc subtended at the photocell beam. Not all stimulus values were used in all phases of the experiment; the

graphs indicate where various combinations were used.

The procedure employed two methods of stimulus presentation. One of these was a type of descending series in which each stimulus value was presented for two consecutive sessions, and the presentations were in order of increasing spatial frequency (decreasing stripe width). These sessions continued until the bird's performance reached chance level. The second procedure was a Method of Constant Stimuli, in which eight stimulus values appeared within a single session. The randomized block procedure described above determined the order of presentation; each of the eight stimulus values occurred twice within a 16-trial block, once on the right and once on the left key. A group of sessions using either method began with a series of practice sessions at the lowest spatial frequency. These practice sessions continued until the birds' error rate on the second of the two consecutive sessions failed to drop by more than two percentage points from the first day's score. In the case of the constant stimulus method, the remaining stimulus values were introduced one at a time in descending order, with two sessions allotted for the introduction of each new value.

In order to work effectively at this task, the birds required several weeks of training. This procedure started with shaping and a few days on a variable-interval schedule in a single-key apparatus. Discrimination training began in the two-key situation with no observing or photocell response required and no partition between the keys. The observing response was then shaped, and the photocells were then introduced at gradually increasing distances from the stimulus keys. When training was complete, the birds worked for nine or more months on both the descending series and the constant stimulus versions of the problem as apparatus and scheduling modifications proceeded. Daily sessions, each composed of 128 trials, then provided the final data; groups of sessions comprising a descending series alternated with groups using the Method of Constant Stimuli.

Two human subjects, both corrected for 20/20 vision, made a series of judgements using the same apparatus. The subject sat behind the rear panel of the box and viewed the stimulus keys with both eyes through a rectangular opening. The four narrowest stripe

patterns were presented in random order, and the subjects stated whether the stripes appeared on the right or the left side. Values from a random number table determined the side on which the stripes appeared, as well as the order of stimulus presentation. Each subject made 30 judgements for each stimulus value; of the 120 total trials, the striped field appeared on the right half the time, and on the left, the other half.

Histology

Five pigeons, a White Carneaux, two White Kings, and two homers were sacrificed and enucleated. The eyes were fixed in Heidenhain's Susa fluid with Picric acid added and embedded in Low Viscosity Nitrocellulose. Ten-micron sections were stained with Cason's Mallory Heidenhain and examined and photographed under a light microscope.

RESULTS

Behavioral Data

The psychometric functions that follow express the behavioral results in terms of a measure of per cent error at each stimulus value. The spatial frequency values on the ordinates may be converted by the following formula to determine the angle subtended by a single stripe at the photocell:

$$\text{Visual angle (min of arc)} = \frac{0.5}{\text{spatial frequency (cycles per min arc)}}$$

These data do not include the "correction" trials; that is, they omit the non-randomized trials that followed incorrect responses.

Fig. 2 shows psychometric functions for each of the six birds. These data are based on two successive descending series, run when learning effects seemed to have reached a minimum. Plotted as *z* scores, the data in most cases appeared linear, so a straight line seemed an appropriate fit. This figure does not include data from the tails of the distributions; that is, it omits points at the lower spatial frequencies where stripe width did not appear to affect performance.

The acuity thresholds indicated in Fig. 2 are the spatial frequency values at which the functions cross the 25% error score ($z=0.67$); thus, threshold was defined in terms of the performance that fell midway between chance and

Fig. 2. Psychometric functions for the three white birds and the three homers. The values on the ordinate are z transformations of the per cent error scores. On the abscissa is a logarithmic plot of a spatial frequency. Straight lines were fitted by the method of least squares (Lewis, 1960). Points are based on an N ranging from 400 to 500 trials. Arrows indicate points at which each function crosses the z value of -0.67 (corresponding to 25% error).

perfect levels. In terms of visual angle, these values were 1.72, 3.62, and 1.40 min of arc for Birds WC1, WC2, and WK respectively. For the homers HO1, HO2, and HO3, the respective threshold values were 1.94, 4.00, and 3.58 min of arc.

Human thresholds determined by a similar procedure were 0.61 and 0.63 cycles per min arc for subjects L.A. and P.B. respectively. In terms of visual angle, these values would be 0.82 and 0.79 min of arc subtended by a single stripe at the rear of the box. These values agree well with other data at similar luminances (e.g., Patel, 1966, Schlaer, 1937).

The variability among threshold values makes it difficult to compare pigeon breeds. Clearly, the mean threshold for the homers is at a somewhat lower spatial frequency than that for the white birds; however, there is too much overlap in the distributions to justify a conclusion based on this difference. It does seem clear, on the other hand, that the human thresholds are at a slightly higher spatial frequency than the pigeons'.

In the remaining figures, per cent error rather than z appears on the ordinates. Figure 3 shows for each bird, functions obtained using the constant stimulus and descending series techniques. For Birds WK, HO1, and HO3, the curves for the two methods are remarkably

similar. Using the Method of Constant Stimuli, one would find a threshold at a higher spatial frequency for WC2; for the other birds, the 25% error points are very close for the two methods. One effect does occur consistently, however; error rates for the lowest spatial frequency were always lower when the descending series technique was used.

Figures 4 and 5 deal with response biases in terms of position preference. Measured by false alarms, that is, responses to a given side when its key is blank, consistent position preferences seemed to be the rule for all birds except HO2. These preferences were greater at the higher spatial frequencies where, presumably, the stimulus itself exerted less control over the choice behavior. A second measure of position bias, differential response latency to the two sides, shows related effects. Birds WC1, WK, HO1, and HO3 tended to respond more quickly to the preferred side, although the enhancement of this effect at the lower spatial frequencies was not so clear. There appears to be a rough correlation between extent of bias as measured by the false alarm and the latency criteria.

Observational data, taken during the course of the same descending series described in Fig. 4 and 5, revealed that, when the shutter opened, the birds tended to look first at the

Fig. 3. Psychometric functions plotted as per cent error *versus* spatial frequency from two psychophysical methods. The descending series data are based on two series, one taken before and one after the constant stimulus sessions. Each point represents an N of between 256 and 512 trials.

stimulus target on the preferred side. According to these observations, made over a period of 20 consecutive trials, Birds WC1, WK, HO1, and HO3 all looked first at the preferred key 70 to 100% of the time. Bird WC2 was an exception in that it looked first at the non-preferred key most often on this set of trials.

For all the white birds and for HO2 there appears to be a fairly regular positive relation between latency and spatial frequency. This

relationship is not as pronounced as that between spatial frequency and per cent error. Because of that fact and because the relation between latency and spatial frequency appears almost absent for the other two homers, latency would seem to be a poorer index of sensitivity than is the error measure. The fact that latencies did tend to be greater at the more difficult discriminations, however, suggests some other behavior was going on between the times the

Fig. 4. Comparison of responses to the right and left alleys. Per cent error is the measure on the left set of graphs, median latency, on the right. Data are for white birds and are based on a single descending series. Each point represents an N of approximately 128 trials.

shutter opened and the choice occurred. Informal observation revealed that during sessions with high spatial frequencies, the birds often looked back and forth between the stimulus targets several times before entering an alley.

Retinal Histology

Histological examination revealed shallow foveae in three pigeon eyes, one belonging to a White Carneux, one to a White King, and one to a homer. In two of the remaining eyes,

the portion containing the fovea was probably missed during cutting, and in the third there appeared to be an area centralis, but no foveal depression. The photomicrographs in Fig. 6 show a White King and a homer fovea. The area centralis surrounding the fovea is marked by increased thickness of all cell layers except, in the case of the White King, the layer of receptor nuclei. At the depression there is only a slight decrease in density in the cells of the inner nuclear layer and the ganglion cell layer;

Fig. 5. Data for the homers corresponding to the functions in Fig. 4.

the receptor layer appears to be free of rods when examined under higher power. The location of the fovea is close to the vertical meridian of the retina. It is somewhat ventral to the horizontal meridian and about 2 to 3 mm superior and 1 to 2 mm nasal to the optic disc, which has an even more ventral location. Thus, the fovea appears to serve a superior portion of the lateral visual field.

DISCUSSION

It is difficult to compare the results of the present research with data from other pigeon

acuity studies because of the many differences in procedure, illumination conditions, and threshold criteria. The corresponding threshold values from the Chard study (1939), ranging from about 3.5 to 5 min of arc tend to be higher, but this difference could be attributable to an apparently lower luminance level. The extent of agreement between the present data and Chard's findings is quite remarkable in view of the large differences in apparatus and procedure.

Comparing this research with the recent Nye study (1968) is also difficult because of pro-

Fig. 6. Photomicrographs of the fovea of a White King pigeon (A) and of a homing pigeon (B). Magnification is about 80X. Optic nerve fibers form the top layers in each photograph; layers of ganglion cell nuclei (GC), cells of the inner nuclear layer (INL), and the receptor nuclei or outer nuclear layer (ONL) are indicated. The receptors themselves make up the layer below their nuclei, separated from them by the outer limiting membrane, which appears as a thin black line. A black layer of pigment lies below and, below it, the choroid coat of the eyeball.

cedural differences and the fact that Nye used lower luminance and contrast levels. Extrapolation of his data suggests a threshold of about 0.4 cycles per minute arc at a 100% contrast level, but this value is speculative in view of irregularities in the overall function. Both studies agree in the finding that human acuity is slightly better than that of the pigeon.

With regard to the comparison between the human and pigeon acuity data, it should be noted that these results apply to relatively unrestricted viewing conditions. Thus, for example, the lower human thresholds could result partly from the binocular nature of the human judgements (the pigeons' tended to be monocular), as well as from structural factors.

Better stimulus control in the case of the human subjects may also have contributed to this effect.

Acuity and Structure

Pigeons are commonly observed to look at nearby stimuli (*e.g.*, food) with frontal, binocular regard, and distant stimuli with lateral, monocular regard. The manner in which the birds viewed the stimulus fields in the present study was ascertained by frequent observations made throughout the experiment by several observers. The birds' tendency to orient themselves sidewise to the alleys was so pronounced that they often turned all the way around after viewing one target in order to achieve a lateral orientation to the other. Since stimuli in the lateral field fall on the central retina, it seems probable that foveal vision determined the acuity data presented here.

The pigeon foveae shown in Fig. 6 are similar in appearance to those shown by Slonaker (1898), Chard and Gundlach (1938), and Galifret (1968). Their position on the retina also conforms to other descriptions (Chard and Gundlach, 1938; Galifret, 1968). Although the shape looks somewhat like other birds foveae, the depressions are relatively shallow. The fovea of the starling (Tansley, 1965), for example, appears to be almost completely free of ganglion cells and fibers, and at the center of the depression the inner nuclear layer is reduced to a small fraction of its parafoveal thickness. In many ways, however, the pigeon retina is like that of other birds; especially notable is the relative thickness of the inner nuclear layer and the absence of blood vessels on the retina's surface.

The role of retinal structure in visual acuity is not yet clear. Birds, such as hawks, with deep foveae are reputed to have very acute vision. As yet, however, we do not know how such species would compare with the pigeon in a laboratory study.

Methodological Considerations

The problem of response bias, such as the position preferences seen here, is prevalent in animal psychophysics. In a study of psychophysical methods in pigeons, Mentzer (1966) reported strong position habits, especially during difficult discrimination. Recent studies of auditory discrimination in rats (Terman, 1970; Irwin and Terman, 1970) also describe

position preferences that tended to be greater at lower signal strengths, and the latter paper puts forth a rationale based on reinforcement contingencies. In the present experiment, such habits may also have arisen from very slight brightness differences between keys or from the fact that the birds tended to view the two keys with different eyes, which may have had different acuities.

The Terman study also describes differential latency effects, such as the ones shown above in Fig. 4 and 5. Terman believes his effect may have resulted from the rat's tendency to approach the preferred key and to switch sides only when it was about to make its response. This behavior pattern seems analagous to the tendency of the pigeons to look at the preferred side first once the shutter had opened.

The fact that two methods yielded comparable acuity functions suggests that the psychometric functions shown here reflect chiefly the sensory capacities of the subjects. However, compensating features might have obscured some methodological effects. At an intuitive level, the Method of Constant Stimuli would seem to have an advantage in that the subject does not work for long periods on difficult discriminations. This advantage may have been overcome in this experiment by the relative complexity of the constant stimulus task. An absence of methodological effects is reported by Stebbins (1970), who used the Method of Limits, the Method of Constant Stimuli, and a tracking procedure to measure auditory thresholds in monkeys. The results of the present comparison led to the decision to use the descending series technique to obtain the final threshold data, because that method yielded a greater range of per cent error values.

A note about the nature of the task required of the birds in this experiment seems in order. The desirability of spatial proximity between stimulus and response manipulandum is generally accepted (Woodworth and Schlosberg, 1954). Thus, most visual discrimination experiments with pigeons require the bird to peck directly at the stimulus, and this was also the case in the present procedure. The measured response in this experiment, however, was the crossing of the photocell beam, and it was perhaps this spatial separation between choice point and the stimulus field that introduced some instability into the response measure. Such instability was reflected in the lengthy

training required and in disrupted performances produced by slight apparatus modifications or the passage of an unusual amount of time between sessions. The error rate to the easy discrimination was also somewhat higher in the final procedure than it had been early in training when the measured response was the peck at the stimulus target. Because of the nature of the acuity problem, however, it seemed worthwhile to have the stimuli at a distance, keeping them well beyond the near-point and allowing the bird to work under a slightly relaxed condition of accommodation.

In summary, this research produced a measure of the pigeon's visual acuity, perhaps confounded to some extent by non-stimulus factors. Thus, one must view with caution the evidence presented here that the pigeon's acuity, while good, is poorer than the human's. Certainly, however, this species does not live up to the reputation of those birds whose acuity is thought to exceed man's. The histological findings, revealing the poorly developed nature of the pigeon fovea, support the behavioral data. While these domesticated birds make fine subjects for studies of visual discrimination, one must take care not to overestimate their ability to resolve visual detail.

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