THE VISUAL ACUITY AND INTENSITY DISCRIMINATION OF DROSOPHILA*

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I

Problem and General Method

The visual functions of many animals vary with the prevailing light intensity to which they are subjected. In general the visual capacities are poor at low illuminations and become increasingly better as the intensity rises (Aubert, 1865; Koenig and Brodhun, 1889; Koenig, 1897; Hecht, 1924; and Hecht and Wolf, 1929). In recent years certain ideas have been proposed which offer an explanation of this capacity for variation in the visual system and which link this capacity with other apparently unrelated properties of photoreception (Hecht, 1931). Given a photosensory organ composed of a number of discrete receptor elements, each containing a particular photochemical system, then the various data of vision may as a first approximation be described in terms of commonly accepted properties of photochemical and chemical reactions and in terms of the distribution with respect to their sensibility to intensity of similar elements in a population.

Up to the present, the human eye has been the visual system for which most data have been available. However, a distinct difficulty in the quantitative derivations and comparisons of the various sets of data for the human eye is that even when they have been secured with the same eye the conditions of measurement have not been the same, so that both the similarities and the differences have often had to be discounted and their meaning obscured. The various measurements with *Mya* and similar animals, though fairly extensive (Hecht,

* A preliminary report of these measurements was presented at the XIV International Physiological Congress in Rome in September, 1932.

1931), do not involve functions such as visual acuity which are particularly interesting in this connection. We therefore determined to measure some of these functions in another animal whose vision is significantly different from our own so as to furnish the basis for an independent description of its underlying physiological structure. In this paper we record such measurements of visual acuity and of intensity discrimination as they are influenced by the intensity.

A previous success in the measurement of visual acuity with the bee (Hecht and Wolf, 1929) led us to use the common fruit-fly, *Drosophila melanogaster*, which in addition to the genetic uniformity also possessed by the bee, has the advantages of ease of culture and year-round availability. Obviously the use of such an animal demands the development of a special procedure for measuring visual response. This has already been accomplished for the bee and can be used with modifications for the fly. The method depends on the reflex response given by an animal to a movement in its visual surroundings. Presented with a visual field composed of a definite pattern, an animal can obviously respond to a movement of this pattern only when it is able to resolve the essential elements of the pattern. The composition of the pattern may then be varied to obtain a measurement of either visual acuity or of intensity discrimination.

The simplest pattern is a series of stripes. For visual acuity the stripes may be varied in width and the intensity determined at which they are just resolved. For intensity discrimination the relative intensities of the alternating stripes may be varied and the minimum difference in intensity determined which, for a given stripe width, will just elicit a response at a series of selected intensities. We arranged our apparatus so that both measurements could be made on a single fly in the same set-up and under identical conditions.

II

Nature of the Reflex Response

The response of the fly presents several interesting aspects. A fly is allowed to creep freely along the horizontal length of a narrow glass cell placed parallel to an illuminated, vertically striped plate constituting its entire visual field. With the striped plate at rest the fly

usually creeps back and forth from one end of the 7 cm. cell to the other. If now the striped plate is moved in the direction in which the fly is creeping, the fly stops, creeps backward for a few millimeters, turns around, and rapidly runs off in the opposite direction. This behavior is almost diagrammatic. By moving the plate repeatedly back and forth, it is possible to keep the fly revolving about any point in the cell.

It is simple to show that the behavior of the fly is not acquired during its first essays at motion. We allowed several pupae to emerge in complete darkness, each in an experimental cell. The response of the flies during their very first exposures to light was just as characteristic and clear as that of older flies raised in the light. A measurement of the threshold for a response to a given stripe made with one of these flies gave a value of 1.8×10^{-2} millilamberts; the measurement occupied 3 minutes during only a small fraction of which the fly was actually illuminated. 8 days later its threshold was 1.5×10^{-2} millilamberts, an agreement well within the daily variability of the animals. Between these two measurements the fly had been exposed daily to the light from an open window. Evidently the response of *Drosophila* to moving patterns is an inherited, complicated reflex.

Almost all animals with eyes perform such directed reactions when presented with a movement in their visual environment (Lyon, 1904; Garrey, 1905; Hadley, 1906; Demoll, 1909; Doflein, 1910; Loeb, 1918; Schlieper, 1927; Hecht and Wolf, 1929; Grundfest, 1931; Schulz, 1931). The response is either *with* the direction of the environmental displacement, or *against* the displacement. Thus fish under certain conditions follow a moving pattern (Grundfest) as do certain arthropods (Schlieper), whereas bees (Hecht and Wolf) and *Drosophila* move against the background motion.

The animals which move with the motion of the background are fish, aquatic insects, crabs, and hovering insects, which maintain relatively stationary positions for some time even in a moving medium. Very likely they accomplish this by optically fixating some portion of their visual field and adhering to it even if they have to swim or fly against the current. On the contrary, the animals which move against the displacement in their visual field are bees and flies which move in a relatively stationary environment. When they fly or creep, their visual environment usually passes by them. Their response when

their visual field suddenly begins to overtake them is then concerned with so orienting themselves that the visual environment assumes its characteristic motion past them.

It is to the point that the one animal which has been studied under both conditions may go with or against a movement in its visual field depending on whether the animal itself is fixed or free to move. The honey bee when it creeps freely always goes against any movement of its visual environment. Confronted with a series of moving stripes, the change in direction of creeping of the bee results from the bending of the head and thorax in the new direction opposite to the stripe movement. On the other hand when the bee is fixed in position and confronted by a similar movement of stripes, the head and thorax characteristically follow the movement (Schlieper).

The main significance of these responses for us is that they may be used as a tool in the quantitative study of the visual capacities of animals. In the present experiments, the response of the fly was used merely to indicate that the fly resolved the particular pattern presented to it under the given conditions. The response is so vigorous and clear-cut that even at threshold conditions it is unmistakable. Actually at these threshold conditions the fly does not leap backward and turn about; rather it stops when the stripes are moved in the direction in which it is creeping, and starts again when the stripes are moved in the opposite direction. This was the constant response used as end-point in all the measurements to be described.

We made no special effort to control precisely the speed of the plate movement used in evoking the reaction. However, this motion was always sufficiently slow so that any complication by fusion of the stripes is out of the question.[1] To obtain a sharp response it is not

[1] This is the difficulty with the work of Graham and Hunter (1931) who in using this method for measuring the visual acuity of humans found that a moving pattern yielded markedly different results from a stationary pattern. One of us (G. W.) with the help of Dr. Harry Grundfest repeated enough of Graham and Hunter's measurements to be certain that such discrepancies disappear when the plates are moved with the velocity which we habitually use in these experiments. This was confirmed personally by Dr. Graham, who saw these measurements. It emerged that in the work of Graham and Hunter the pattern had been moved very much more quickly,—so quickly indeed that fusion occurred. This high rate of motion of the pattern completely accounts for the aberrant results obtained by these authors.

necessary to move the striped plate more than just perceptibly faster than the movement of the fly itself.

III

Apparatus and Procedure

The relation which visual acuity and intensity discrimination both bear to the prevailing intensity may be measured in two ways. One may set a given intensity and determine by trial with the animal what the visual acuity or the intensity discrimination corresponding to it is; or one may choose a pattern corresponding to a given visual acuity or select a given intensity difference and by trial with the

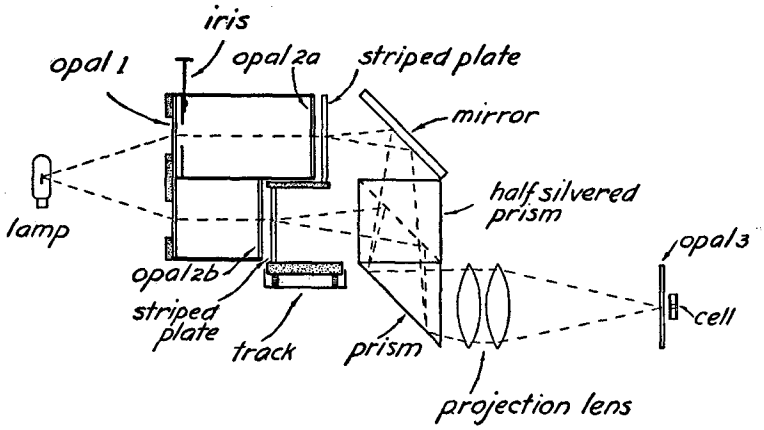

FIG. 1. First apparatus for measuring intensity discrimination

animal determine the intensity at which the resolution of the pattern takes place or the intensity difference is recognized. With intensity discrimination we used both methods; with visual acuity only the latter.

The apparatus used for the first method of measuring intensity discrimination consists essentially of a movable set of vertical stripes separated by interspaces of the same width, the whole being so arranged that the illumination of the stripes and of the interspaces may be controlled independently. It may be understood by reference to Fig. 1.

The light from a 500 watt concentrated-filament Mazda lamp falls on two separated, and light-insulated portions of an opal plate (opal 1), thus forming two secondary sources of illumination, an upper and a lower. The lamp is kept in one dark room, the rest of the apparatus in another; the wall between the two contains two openings for the light to reach the two portions of opal 1, which is in immediate contact with the openings in the wall. The intensity falling on opal 1

is varied by placing the lamp at different fixed distances from the openings. At a given position of the lamp, the intensity of the lower secondary source remains fixed, and illuminates an opal plate (opal 2*b*) immediately in front of which is a series of opaque vertical bars separated by equal sized transparent spaces. The upper secondary source similarly illuminates an opal plate (opal 2*a*) in front of which is a duplicate bar and space arrangement. The intensity falling on opal 2*a* can be varied by means of an accurate iris diaphragm immediately in front of the upper secondary source which controls its radiating area. A fixed diaphragm in front of the lower secondary source so adjusts its radiating area that with the iris wide open the illumination on opal 2*a* is just perceptibly greater than on opal 2*b*, even though the latter is nearer opal 1.

The light from the two series of bars and spaces, after reflection by a mirror and prism, is focussed with a projection lens on a third opal screen. The optical paths of the light from the two sets of stripes to the screen are of identical length and composition; hence the two are projected in simultaneous focus. The two sets of stripes are mounted on the same heavy brass carriage which moves on roller bearings along a track perpendicular to the plane of the drawing in Fig. 1. The relative positions of the two sets of stripes are so adjusted that in the projection on the final opal screen (opal 3) the image of the bars of one falls exactly in the clear spaces of the other. The result on the final screen is a movable series of alternating, illuminated stripes whose relative intensities may be controlled by the iris diaphragm at the upper secondary source. When the iris diaphragm is slightly closed, the two sets of stripes are of equal brightness and the field is uniform. When the iris diaphragm is completely closed, every other stripe is at zero illumination and the field is a series of black bars separated by equally wide, illuminated interspaces. At any intermediate position of the iris, the bars may take on any intensity value between zero and that of the interspaces. As already indicated, the intensity of the interspaces may be set at any desired value by regulating the position of the Mazda source. The width of each stripe on the final pattern occupies a visual angle of 85°; as will be apparent later, this is well above the largest visual angle required for the lowest visual acuity of the fly.

The fly is placed in a rectangular glass cell in front of the final opal screen on which the moving pattern is projected. The interior of the cell is about 2 mm. high, 3 mm. wide, and 70 mm. long. The fly, which is broader than it is tall, always walks upright or inverted in the cell, never on the sides. The fly thus always turns one eye full toward the pattern. The fly is observed through a cylindrical reading lens mounted parallel to the cell.

The measurements are made as follows. A fly is put into the apparatus and allowed to walk freely when the light is on. By means of the iris diaphragm, the intensities of the two sets of stripes are equated. Motion of this uniform field produces, of course, no response. The brightness of the variable stripes is now progressively decreased by decreasing the iris diaphragm, and the animal subjected to the moving pattern with each small diminution. A point is soon reached

when the animal responds to the movement, indicating that it can distinguish between the intensities of the alternating stripes.

The apparatus for the second method of measuring intensity discrimination is much simpler than for the first method. Here the animal is presented with a plate so constructed that its alternating stripes transmit a fixed ratio of intensities, and the prevailing intensity is adjusted until the fly responds to a movement of the plate. Fig. 2 makes the arrangements clear. Light from a 500 watt concentrated-filament Mazda lamp in one dark room falls on an opal glass plate (opal 1) which covers an opening in a rectangular box mounted on the wall of the dark room. The opposite end of the box opens against a hole in the wall leading into an adjoining dark room. Immediately against the hole is another opal glass (opal 2) which forms one wall of a second rectangular box of which the opposite wall is a third opal glass plate (opal 3). The intensity of the light falling on opal plate 3 is controlled

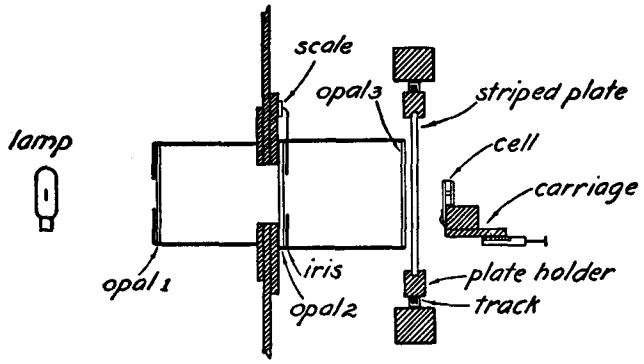

FIG. 2. Second apparatus for measuring intensity discrimination. This set-up also serves to measure visual acuity.

(*a*) discontinuously by placing the lamp at three selected distances from opal 1, and by removing opal 1, and (*b*) continuously for the intervening steps by means of the accurate iris diaphragm in front of opal plate 2. The illumination on opal plate 3 can be accurately and continuously varied over a range of 6 logarithmic units of intensity.

Immediately in front of opal 3 is the striped plate, mounted in a carriage which slides easily along brass tracks. A plate is composed of translucent bars and equally wide, clear interspaces. For all the plates the width of the bars and spaces is the same, and the clear interspaces are the same. The plates differ in the density of the bars, so that each plate represents a pattern of stripes whose alternating elements have a fixed ratio of light transmissions. The plates were prepared by photographically enlarging on Eastman Process plates a striped pattern accurately engraved by Max Levy and Company of Philadelphia. The Levy plate consists of equally wide, alternating opaque and clear stripes, such as

were employed in the visual acuity work with the bees (Hecht and Wolf). By varying the time of exposure and keeping all conditions of lighting and development constant, a graded series of stripe densities were obtained. The six plates which we used were calibrated for the transmissions of the stripes and the clear spaces with a Koenig-Martens spectrophotometer using light of 500 mμ.

The measurements are made by setting for each plate an intensity at which motion of the plate produces no response. The intensity is then gradually raised by small steps until the characteristic threshold reaction of the animal is elicited. Knowing the intensity of the clear spaces and the relative transmissions of the bars and clear spaces, we have a measure of the difference in intensity required at a given intensity for the fly to respond to the stripes.

We began with the first apparatus, but soon abandoned it for the second, which we adopted because of its greater simplicity, and because we could also use it for measuring visual acuity. All that is required for determining visual acuity with the second apparatus are plates of proper density and size of stripe. We prepared photographically a series of striped plates, using Eastman Process plates and Eastman special hydroquinone developer. They were all enlargements of the accurately made Levy plate previously mentioned. The size of the stripes was varied, but the exposures were complete. In this way we secured plates with stripes of a very high degree of opacity, transmitting certainly less than 1/10,000 of the incident light, and with interspaces which were almost perfectly clear. The transmissions of the clear spaces were nevertheless measured and an appropriate correction applied to the intensity.

The procedure for making the visual acuity measurements is similar to that for intensity discrimination. For each plate an intensity is set at which a motion of the plate evokes no response. The intensity is then gradually raised and the fly tested until an intensity is found at which it just gives its characteristic response. Knowing the distance of the fly from the plate and the width of the stripe, the visual acuity is merely the reciprocal of the visual angle in minutes. The distance of the fly from the plate was kept constant for each series of measurements, though it was not the same for all the series. It is of the order of 15 mm. and is measured from the center of the eye.

The flies used in all the measurements here recorded were selected from a homozygous wild-type stock and were grown in the cornmeal-agar-molasses medium, seeded with yeast, used by Morgan and his coworkers. In our final measurements only females were used, because they crawled more slowly and steadily than the males. Each female was usually supplied with a male, and the pairs were quartered in individual vials containing 2 per cent agar in Pasteur's medium seeded with yeast. In this way a fly could be kept active for 3 weeks and longer.

IV

RESULTS

1. Intensity Discrimination.—With the first apparatus we made measurements of the intensity discrimination of seven flies during

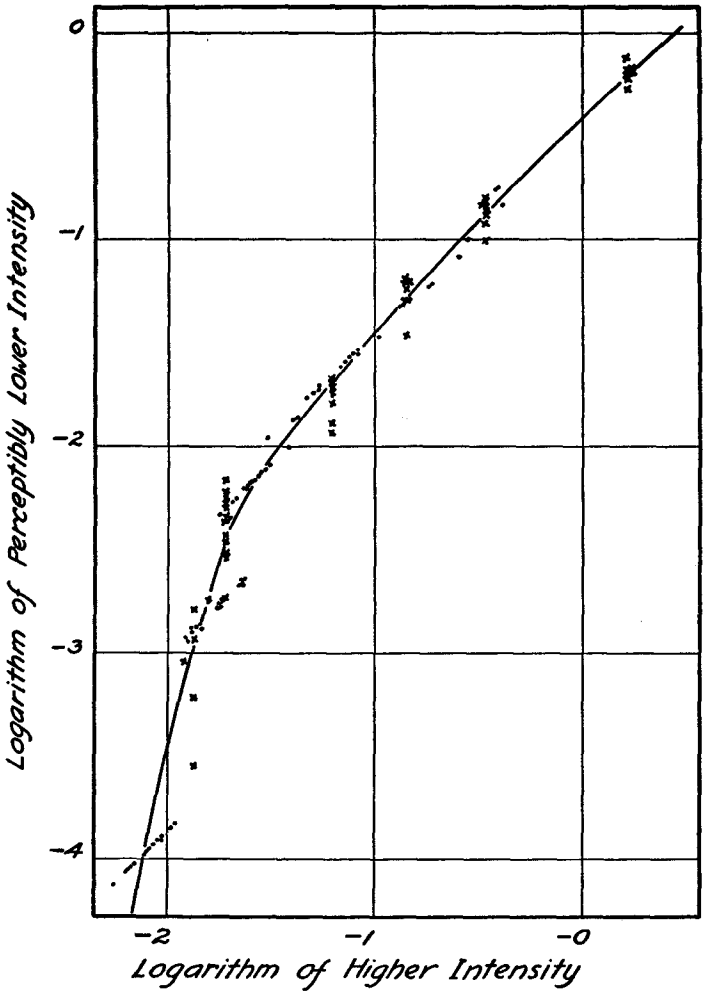

FIG. 3. Intensity discrimination of *Drosophila*. Each measurement with 24 flies is recorded. The crosses were secured with the first apparatus; the dots with the second apparatus.

October and November of 1930; with the second apparatus we measured seventeen flies between February and June of 1931. Each measurement with each fly is shown in Fig. 3, where those made with the first apparatus are crosses and those with the second apparatus are dots. It is apparent that the results from the two sources are the same, and that the data are homogeneous. The 113 measurements have been combined in the obvious groups into which they fall in the plot in Fig. 3, and have been averaged. These averages are given in Table I. The curve drawn through the data in Fig. 3 is made to pass

TABLE I

Intensity Discrimination of Drosophila

No. of readings	Higher intensity ($I + \Delta I$)	Lower intensity (I)	Perceptible difference (ΔI)	$\frac{\Delta I}{I}$	$\frac{\Delta I}{I + \Delta I}$
	millilamberts	*millilamberts*	*millilamberts*		
16	0.00773	0.000104	0.00763	73.33	0.987
12	0.0137	0.00109	0.0126	11.57	0.920
24	0.0186	0.00300	0.0156	5.20	0.839
12	0.0269	0.00706	0.0198	2.81	0.736
13	0.0533	0.0165	0.0368	2.33	0.690
6	0.0753	0.0269	0.0484	1.80	0.643
9	0.139	0.0532	0.0858	1.61	0.617
14	0.333	0.132	0.201	1.52	0.604
7	1.62	0.647	0.973	1.50	0.601

through these average points, and it is plain that the averaged data are a real representation of the individual measurements.

The data show that at the lowest intensities, for the fly to recognize the pattern, the higher intensity has to be about 100 times as strong as the lower. As the intensity increases, the just perceptibly lower intensity increases at first much more rapidly than the higher, then the two increase at about the same rate until the ratio of higher to the just perceptibly lower intensity becomes about 2.50, which value is maintained up to the highest intensities. This is shown by the fact that the plot in Fig. 3 rapidly approaches a straight line with a slope of 45°.

In order to be certain that the ratio of the two perceptibly different intensities undergoes no further change as the intensity increases, we

tested flies at intensities up to 1000 millilamberts. Our first apparatus varies the ratio continuously, but unfortunately cannot achieve high intensities. The second apparatus can reach high intensities, but gives ratios in discrete steps only. Using the second apparatus we therefore tested flies at three intensities to each of three plates whose stripes transmit light in the ratios of 1.84, 2.17, and 2.77 respectively. The data for Fly 10c are given in Fig. 4. The measurements made in the usual way are marked with circles. The responses of the fly to the highest three intensities are shown by a minus sign when it failed to respond, by a plus sign when it responded clearly, and by a combination of the two when its behavior was doubtful.

Fig. 3 and Fig. 4 show that intensity discrimination in *Drosophila* begins to be effective at a prevailing brightness of 0.008 millilamberts. At this value, intensity discrimination is extremely poor; but in the short space of half a logarithmic unit the intensity discrimination improves at a tremendous rate so that it reaches very nearly its maximum value, which then remains constant for 4.5 log units up to the highest intensities obtainable in the measurements.

It should be pointed out that even these high intensities are not really high for *Drosophila*. We give the intensities in millilamberts, which are brightness units for our eyes. Our photometric measurements represent the effectiveness of light in terms of the efficiency of the spectrum, which for our eyes with a 500 watt lamp is maximal between 560 and 570 mμ. The maximum effectiveness of the spectrum for *Drosophila* is at 360 mμ at which point the light is easily 100 times more effective than at 560 mμ (Bertholf, 1932). Considering the comparatively trifling amount of light of 360 mμ which a 500 watt lamp emits, and the trifling amount which the various opal glasses transmit, a brightness of 1000 millilamberts thus secured must be a fairly low intensity for *Drosophila*. It will therefore be important to extend these measurements of intensity discrimination using ultra-violet light.

A practical consequence of this situation for our present measurements is that a photometric reproduction of a given brightness in the present apparatus as made with visible light and with our eyes need not necessarily represent a similar amount of effective energy for *Drosophila* in the ultra-violet. Indeed we often did find variations in threshold which are very likely due to this factor. In combining

the measurements of many animals as in Fig. 3 and also later in Fig. 7, we compensated for these occasional changes in threshold by shifting the data equally along both intensity axes to bring them into con-

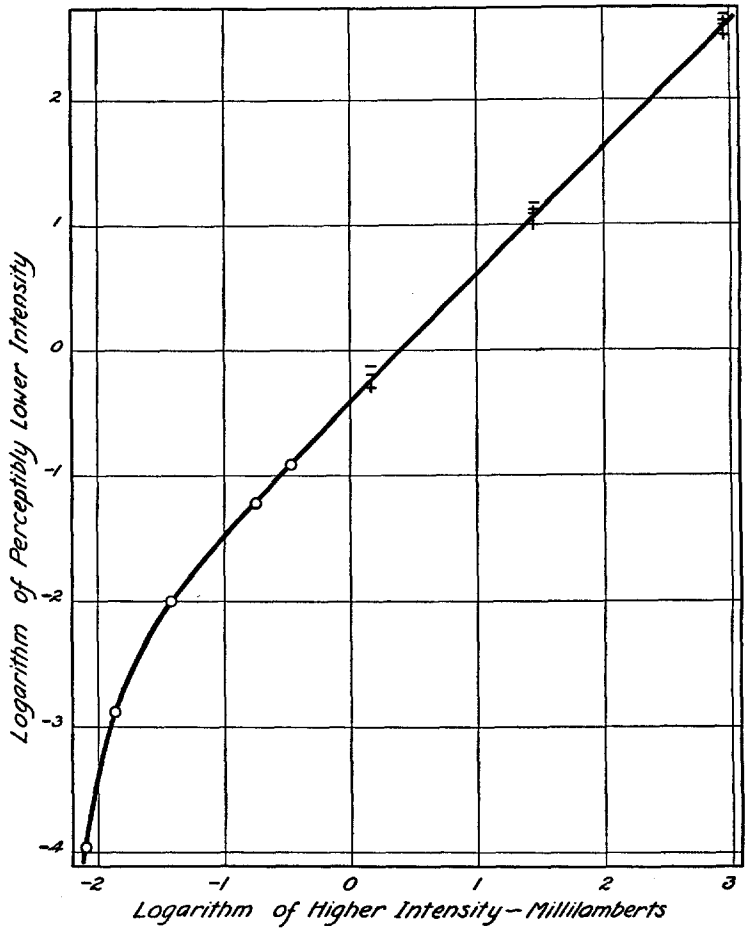

FIG. 4. Intensity discrimination of Fly 10 c to show that even at the highest illuminations intensity discrimination remains at its maximum and does not deteriorate.

formity. Since the intensity is plotted logarithmically, the procedure is simple and introduces no difficulties.

In Table I and in Figs. 3 and 4 the measurements are given in their

simplest and most direct form; namely as the two intensities which when placed side by side in stripes are just discriminated by the flies as indicated by their response to the movement of the pattern formed by these intensities. Following common procedure one may call the lower intensity I and the higher $I + \Delta I$, the difference between them being ΔI. We have computed $\Delta I/I$, and have plotted its values

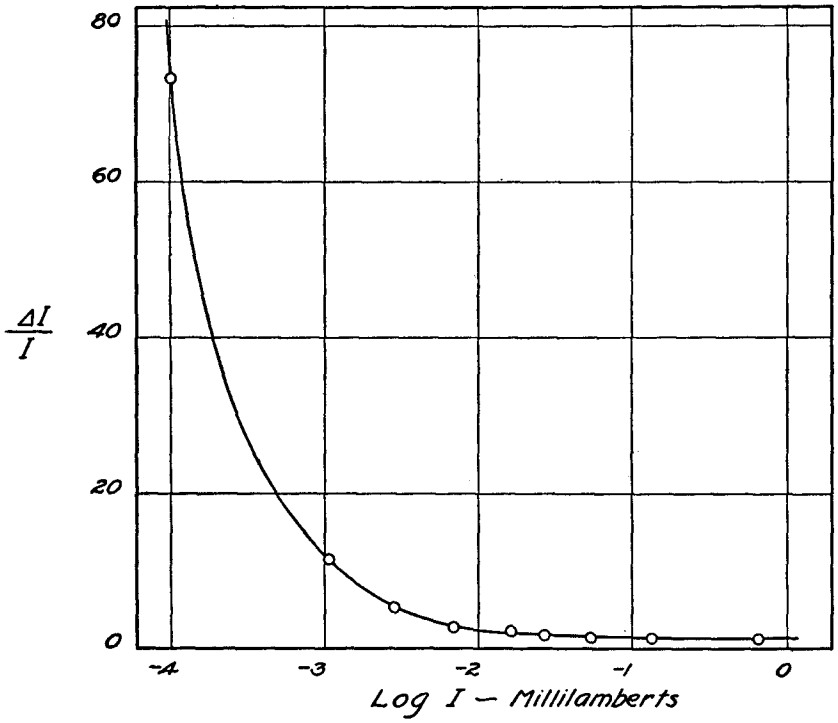

FIG. 5. The average data of intensity discrimination plotted as $\Delta I/I$ against log I. The fraction $\Delta I/I$ remains minimal at the highest illuminations.

against log I in Fig. 5. In the present instance, this method of describing intensity discrimination overemphasizes the events at the very lowest intensities. A value of ΔI which is 80 times as large as I itself tells only that I is probably below or very near the threshold of visibility. In particular, the plot of $\Delta I/I$ against log I fails to bring out what is apparent from the direct data themselves (Figs. 3 and 4), that there is a sharp change in intensity discrimination at about log

$(I + \Delta I) = -1.7$ and that below log $(I + \Delta I) = -2.1$ intensity discrimination is practically non-existent.

A method adopted by many workers in photometric practice is to plot $\Delta I/(I + \Delta I)$ against log $(I + \Delta I)$. In the human eye where the difference between I and $(I + \Delta I)$ is very small, it makes little difference which of the two methods is used. But in the fly the difference is tremendous. Fig. 6 shows the data of Table I in this form, and indicates that this function is much more expressive of the real way in which the data behave. From Fig. 6 it is clear that below a value of

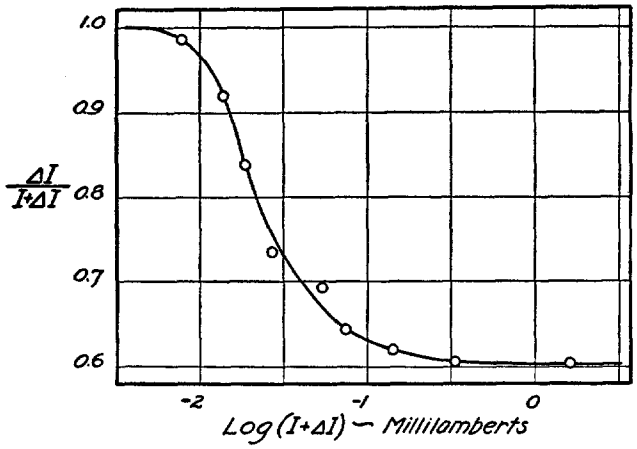

FIG. 6. The average data of intensity discrimination plotted as $\Delta I/(I + \Delta I)$ against log $(I + \Delta I)$. The function begins at about -2.1 and continues to improve steadily, showing no decline.

log $(I + \Delta I) = -2.1$ for an intensity to be discriminated by the fly as lower than the prevailing intensity, it practically has to be extinguished,—which is the fact.

Whichever of the three ways one records the measurements, the fact remains that intensity discrimination for *Drosophila* changes first very rapidly and then more slowly over a small range of intensities above the threshold, and then reaches a constant value which is maintained as the intensity continues to increase. A similar condition holds for the bee's intensity discrimination as recently measured by Wolf (1933). The measurements of Koenig and Brodhun (1889) supported more recently by Lowry (1931), and by Houstoun and Shearer (1930), for

the human eye show no constant value for the higher intensities; instead the intensity discrimination increases, and then decreases as the intensity rises. The same is apparently true for the clam (Hecht, 1924). The older data of Aubert on the human eye do not show this fall, and unpublished measurements by Mr. Jacinto Steinhardt of our Laboratory indicate that this fall at high intensities disappears under proper conditions of measurement.

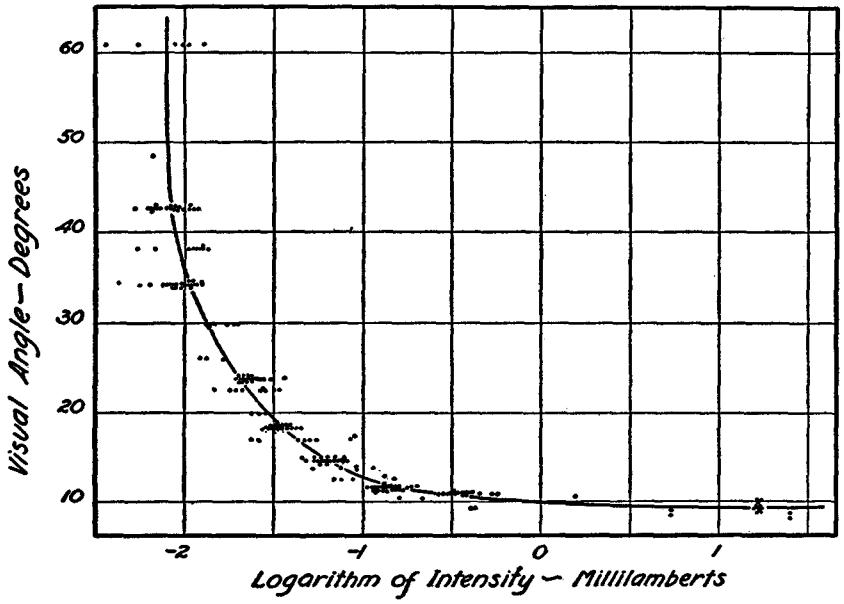

FIG. 7. The relation between intensity and the angular distance occupied by the stripes to which the fly can just respond. Each measurement with 32 flies is recorded.

2. Visual Acuity.—We measured the relation of visual acuity to illumination in twenty-four flies in November, 1929, and in eight more flies between March and August of 1931. Each measurement for each fly is given in Fig. 7. The ordinates are the actual visual angle subtended by the just visible stripe. The averages of the 220 measurements are recorded in Table II, and the curve in Fig. 7 passes through these average values. It is apparent that the measurements for the various animals form a consistent description of the phenomenon.

Graphically the data are best represented as visual acuity against the logarithm of the illumination, following the usual practice of defining visual acuity as the reciprocal of the just resolvable visual angle measured in minutes of arc. Fig. 8 shows the averaged data of Table II plotted in this way. There are several points to be made with regard to the data. Of these the most obvious is that visual acuity increases with the logarithm of the illumination in a sigmoid manner, already familiar from the data on the human eye, and on the bee eye. At the lowest intensities the visual acuity of *Drosophila* does not decrease continuously with the decrease in intensity, but instead stops

TABLE II

Visual Acuity of Drosophila

No. of readings	Intensity	Visual angle	Visual acuity $\times 10^4$
	millilamberts	*degrees*	
6	0.00794	61.08	2.73
20	0.00800	42.90	3.89
30	0.00966	35.33	4.72
10	0.0142	28.54	5.84
32	0.0234	23.30	7.15
24	0.0343	18.24	9.14
10	0.0511	16.58	10.05
20	0.0627	14.45	11.53
10	0.0908	13.19	12.64
25	0.141	11.69	14.27
20	0.378	10.73	15.53
13	14.6	9.28	17.95

quite sharply at an intensity corresponding to a brightness of 0.008 millilamberts. No matter how large the stripes are, the animals do not respond to them until this intensity is reached. This is made evident in Fig. 8 by the vertical line at this intensity, and was apparent in every animal which we tested for this purpose. This is related to the fact, obvious from Fig. 3 and Fig. 6, that at this intensity for another intensity to be recognized as perceptibly lower it must be practically extinguished.

The maximum visual acuity achieved by *Drosophila* is 0.0018, a value about 1/1000 that of the human eye, and 1/10 that of the bee's eye. This maximal value had to be obtained by a modification of the

usual method as already described. The response of a fly to stripes depends on the size of the stripes, the distance of the fly from the stripes, and the intensity of the light. The usual method fixes the distance of the fly, presents it with a series of plates having each a fixed size of stripe, and measures the intensity required for the fly to respond to each stripe. To determine the maximum visual acuity in this manner

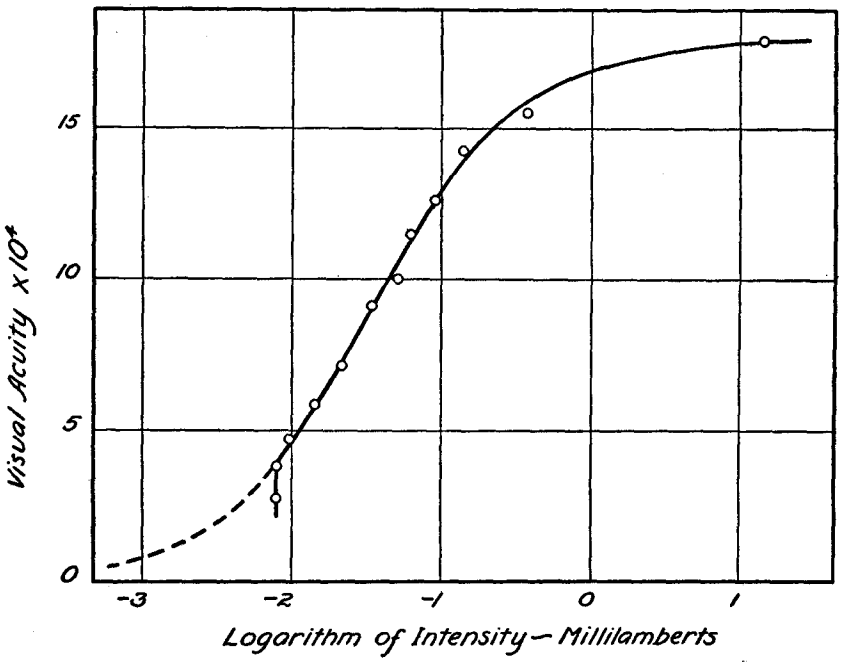

FIG. 8. The averaged data of Fig. 7 plotted as visual acuity against the logarithm of the intensity. The function starts abruptly at −2.1, below which the flies do not respond to stripes no matter how large they are.

requires the size of the stripe to be continuously variable—a difficult thing to achieve in practice. We therefore adopted the procedure of choosing a stripe of approximately the correct size, fixing a high intensity, and measuring the distance at which the fly must be in order just to respond to the movement of the stripes.

The procedure of varying the distance of the fly from the test object may influence visual acuity by changing the brightness, and may com-

plicate matters in the same way as the curious but unexplained effect of distance on human visual acuity first found by Aubert and Foerster (Aubert, 1865) and recently emphasized by Freeman (1932). Neither of these can be very serious for our measurements because the distances involved are 2 or 3 mm. Nevertheless we made special measurements to determine whether any such effects are present, varying the distance about 20 mm. Taking two plates with stripes 6.3 mm. and 1.27 mm. wide, we placed them 25.8 mm. and 5.21 mm. from the fly respectively. These both correspond to a visual acuity of 0.0012. Then we measured the threshold intensities of sixteen flies to a movement of these stripes, and secured as averages 4.36 and 4.07 respectively for the two plates. Similarly two plates having stripes 6.3 mm. and 2.84 mm. wide and at 21.5 mm. and 9.69 mm. from the fly (visual acuity = 0.0010) gave average intensity thresholds for the same sixteen flies as 1.66 and 1.86 respectively for the two plates. The differences between the two plates in each case are obviously negligible, and are opposite in direction in the two cases. The units of intensity here given do not correspond with the others previously given because we used a violet monochromatic filter in these measurements; according to Koenig (1897) the distance effect in the human eye is most prominent in the blue and violet, and we wished to make the test extreme. Therefore the determination of the maximum visual acuity by the distance method introduces no new variables, and the value 0.00180 for this maximum for *Drosophila* is the real value.

The maximum visual acuity of the human eye and the bee's eye is associated with the size of the structural units of the receiving elements (Müller, 1826; Ramon y Cajal, 1894; Exner, 1891; Best, 1911). In man the maximum value approximates the distance between foveal cones, though under special conditions it seems possible to increase the maximum performance (Hartridge, 1922; Anderson and Weymouth, 1923). In the bee the minimum perceptible visual angle (0.9°–1.0°) as determined physiologically (Hecht and Wolf) corresponds with the smallest angles (also 0.9°–1.0°) subtended by the ommatidia in the central portion of the eye as measured anatomically (Baumgärtner, 1928).

The ommatidial angles in the eye of *Drosophila* have not been adequately measured (Johannsen, 1924). We therefore prepared for

this purpose many sections of eyes using essentially Baumgärtner's technique. This consists of rapidly fixing the heads in hot water, carefully running them through the alcohols, staining with eosin, imbedding in celloidin, preparing sections 20μ thick with a sliding microtome, clearing the sections with cedar oil, and mounting them in Canada balsam. We made photomicrographs of some of our best preparations, and on the mounted pictures we measured the angles between adjacent ommatidia. A thread stretched between two needles was passed through the axis of each ommatidium. The needle

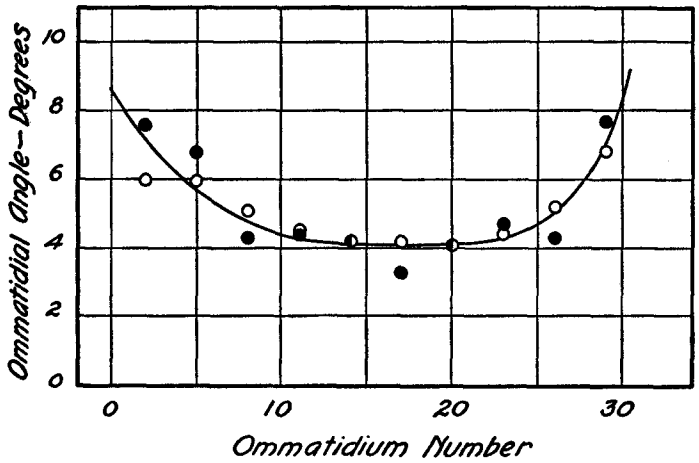

FIG. 9. The distribution of ommatidial angles in the left (open circles) and right (solid circles) eyes of *Drosophila* (Animal Iiii). The angles were measured for groups of three ommatidia, and the average ommatidial angle for each group is assigned to the middle ommatidium of the group.

pricks were connected with a line and the angle between adjacent axis-lines measured.

The results are fairly irregular but, as Fig. 9 shows, quite adequate for the purpose. The largest section of the eye contains 31 ommatidia. The middle 16–18 of these show a constant angular separation of about 4.2°. At both ends the angular separation rises sharply to about 8°; measurements at the ends are uncertain due to the pronounced curvature of the ommatidia in these regions. The central region of the eye with its ommatidial separation of 4.2° is thus the

place of sharpest vision, much as in the bee's eye. The average maximum visual acuity which we found experimentally for *Drosophila* corresponds to an angle of 9.28°, which therefore includes about two ommatidia instead of one.

This difference between the physiologically achieved and anatomically expected resolving power may mean that the neural paths of the ommatidia are interconnected, and that they therefore cannot act as individuals but as connected groups. However, we are inclined to ascribe it to another cause, namely the small number of ommatidia present in the eye as a whole. To distinguish a pattern, a certain minimal number of elements must be stimulated. This number is apparently a small fraction of the total population of retinal elements in the eye of man or of the bee. In the fly where the total number of elements is much smaller than in the human eye or in the bee eye, it probably represents a considerable proportion of the retinal population, and the group of units called into play to register a single stripe thus transcends the boundaries of a single line of elements. This idea is supported to a certain extent by the observation that homozygous bar-eye females, the eyes of which contain only 4–5 elements in the widest horizontal section, do not respond to the motion of the stripes at all.

Perhaps the best support for this idea comes from the experiments with the bee's eye in which parts of the eye were painted out. In the bee's eye it was found (Hecht and Wolf) that the maximum visual acuity coincided very well with the minimum angular separation between ommatidia, which shows that the individual elements act independently. Yet in an experiment in which the anterior half of each eye was painted out, the visual acuity at all intensities dropped to about 0.6 of its normal value, even at the maximum. Since the unpainted residue of the eye still contained elements having the original minimum angular separation, the drop in maximum visual acuity must be due to the decrease in the total number of elements acting in the eye.

V

Comparisons

A comparison between the two visual functions studied in *Drosophila* brings out the significant fact that the two functions begin and end at

about the same intensities. As Fig. 8 shows, visual acuity begins to increase at an intensity whose logarithm is -2 and accomplishes most of its change in about 2 log units; the maximum visual acuity is not reached for about 1 log unit more, but this final change is very slow and not very large. Essentially the same thing is true of intensity discrimination. Fig. 3 and Fig. 6 show quite clearly that this function, after beginning at an intensity whose logarithm is -2, accomplishes most of its change in about 2 log units. Its maximum capacity is reached in about 1 log unit more, and this final change is slow and not very large.

The recently published measurements of the intensity discrimination of the bee by Wolf show that a similar relation exists between visual acuity and intensity discrimination for the bee. Visual acuity in the bee (Hecht and Wolf) begins to increase perceptibly with intensity at an intensity corresponding to $\log I = -1.0$, and accomplishes nearly all of its range at $\log I = 1.0$, though the small increase to the maximum visual acuity continues till after $\log I = 2.0$. The same range is covered by intensity discrimination. According to Wolf's data, $\Delta I/I$ begins to vary effectively at about $\log I = -1.5$ and accomplishes most of its range at about $\log I = 1.0$; its lowest value is reached after about one more log unit.

It would be well if a similar comparison of the two functions could be made for the human eye, but the existing measurements were made under such different conditions that it is not possible to do so with any certainty. Koenig's visual acuity data (Koenig, 1897) cover about the same range as his intensity discrimination data (Koenig and Brodhun, 1889), that is, between 8 and 9 log units; but the precise way in which the two functions vary has been called into doubt by Lythgoe's measurements of visual acuity (Lythgoe, 1932), and by unpublished measurements of intensity discrimination by Mr. Jacinto Steinhardt in our own Laboratory. For the present, therefore, it is well to omit discussion of them.

A comparison of the maximum values for intensity discrimination and visual acuity in the three species is of interest. The minimum value of $\Delta I/I$ for *Drosophila* is 1.5; for the bee it is 0.25 (Wolf); and for man the minimum recorded is 0.006 (Helmholtz, 1866; Aubert, 1865). Taking the reciprocal of the minimum $\Delta I/I$ as a measure of maximum

intensity discrimination, and putting *Drosophila* at 1, the ratios *Drosophila*/bee/man are 1/60/249 for maximum intensity discrimination, and 1/9.4/1110 for maximum visual acuity. A rough parallelism is apparent in these functions. Possibly some other, more theoretically defensible measure of maximum intensity discrimination might show a better parallelism to maximum visual acuity.

VI

Interpretation of Data

1. Visual Acuity.—Drosophila is the fourth organism whose visual acuity has been found to vary with illumination,—the other three being man (Koenig), the bee (Hecht and Wolf), and the fiddler crab (Clark, 1932). In each case the visual acuity is low at low intensities and increases with log I in a characteristically sigmoid manner. The only quantitative interpretation at present available for this property of visual acuity (Hecht, 1926, 1928) depends on the recognition of visual acuity as a measure of the resolving power of the retinal surface. The resolving power of a surface composed of independently functioning elements depends on the number of elements per unit area, or more specifically on the distance between the centers of the sensitive elements. To account for the required variation in number of elements at different intensities, it is assumed that the thresholds of the retinal elements vary in the retinal population much as any other characteristic of biological population. Curves have been drawn to show the threshold distribution required to account quantitatively for the data of the human eye (Hecht, 1928), and for so differently constructed an organ as the bee's eye (Hecht and Wolf, 1929). The present data with *Drosophila* (Fig. 8) show the same type of sigmoid relationship, and there is no reason to suppose that the same explanation is not available for *Drosophila.*

Fig. 10 shows the differential $\Delta v.a./\Delta \log I$. It is made from the smooth curve in Fig. 8 by finding the difference in visual acuity ($\Delta v.a.$) for points 0.2 log units apart ($\Delta \log I$) and plotting this difference against the value of log I midway between them. The resulting curve has the appearance of an ordinary, symmetrical, biological distribution. A quantitative explanation of the visual acuity data of *Drosophila* then depends on the assumption that the visual acuity is inversely

proportional to the angular distance between functional ommatidia, and that the thresholds of the ommatidia along the horizontal axis of the eye are distributed according to the curve in Fig. 10.

Criticism of the ideas on which such an explanation is based has been made by Freeman (1930), by Best (1930), by Wilcox (1932), and by Wilcox and Purdy (1933). Freeman argues that since visual acuity may be varied by factors other than intensity, its variation with

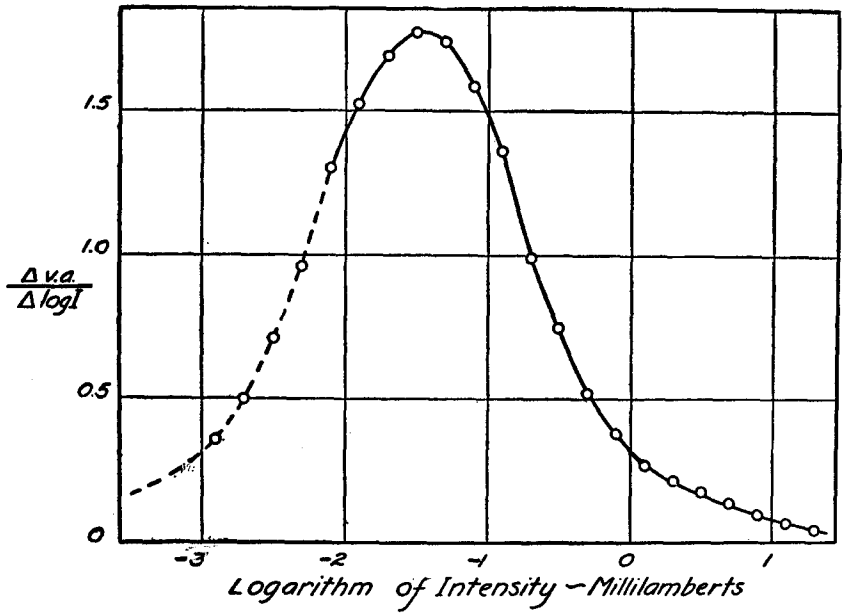

FIG. 10. Differential of the visual acuity curve of Fig. 8. The differences in visual acuity ($\Delta v.a.$) between points 0.2 log units apart ($\Delta \log I$) in Fig. 8 are plotted against the value of the logarithm of the intensity midway between them.

intensity cannot depend only on the number of elements functional. Wilcox and Purdy's criticism is an elaborate form of this standpoint. They state that our ideas are "inconsistent with the fact that acuity may vary within wide limits even though illumination remains constant." Moreover, the ideas fail "to take into account the concrete perceptual situation involved in the recognition of detail,"—which apparently means that we have offered no mechanism to explain how visual resolution takes place at all.

It is hard to see the force of these arguments, since the idea of how visual acuity varies with intensity is quite independent of the particular mechanism which controls the magnitude of visual acuity at a given intensity. No matter what that mechanism may be, nor how complex or simple it may be, it must rest on the fact that the ultimate resolving surface is composed of units which are independent functionally. The variation of visual acuity with intensity then follows very obviously in terms of the probable distribution of thresholds. Best (1930) is worried because the necessary range of distribution of thresholds is large. However, even when the apparent range, as in the human eye, appears quite large, about 90 per cent of the variation occurs in less than 2 log units (Hecht, 1930). In the case of the bee and *Drosophila* this range is even smaller. But even if the range were very large indeed, the difficulty disappears when it is recalled that different portions of the human retina actually do possess thresholds which differ by just such large magnitudes.

Differing from these criticisms are those of Wilcox, who found that under certain conditions visual acuity does not rise steadily with log I as measured by Koenig and everyone since, but actually becomes worse at high illuminations. He then concludes that the increase in number of functional elements which presumably takes place at these high intensities cannot account for the decrease in visual acuity, and therefore the whole conception is not valid.

Wilcox used a novel procedure in his measurements. Two tiny, illuminated vertical bars each subtending 2.4 by 20 *minutes* of visual angle are viewed against an absolutely black background, and the distance is determined by which the bars must be separated for them to be recognized as two bars. It would seem almost too elementary, but apparently quite necessary, to point out that the term retinal illumination refers to the general level of illumination of the retina as a whole, or of a goodly portion of it. In Wilcox's measurements the retina as a whole is completely dark, and only the very tiny test objects are illuminated. What Wilcox measured is a glare phenomenon, and may require a new name; but it is not the relation of visual acuity to the illumination prevailing on the retina. That this criticism of his method is valid becomes clear when the reverse of this procedure is used, that is, when the test bars are black and are viewed

against an evenly illuminated background. The results which Wilcox secured in this manner are in agreement with the classic data of Koenig and others, and are obviously open to the same explanation.

Wilcox himself proposes an explanation of his particular findings and in general of the relation between visual acuity and illumination, which depends on two sets of measurements made with the method already described. One set records the distance by which the two bars must be separated so that between them there appears a space which is just perceptible to the eye. The other set records the distance by which the bars must be separated so that the space between them appears of the same size as one bar. The first set Wilcox calls measurements of visual acuity; the second set, measurements of irradiation. It then appears that at different intensities the first set of measurements equals the second set of measurements multiplied by a factor. Wilcox then concludes that irradiation is the explanation of the visual acuity variation. The reverse would be equally true.

These criticisms therefore leave the original explanation of the relation between visual acuity and illumination—as due to a population distribution of thresholds of the sensitive elements—as valid as when it was proposed. This does not mean that it is the correct explanation; it is merely the only explanation which describes the data quantitatively. That is its main virtue, plus the fact that its basis is not inherently improbable, and rests on concrete assumptions with regard to the structure of the visual mechanism.

The only other explanation worth mentioning is the one given by Hoffman (Best, 1930) for the human eye. It supposes that the diffusion circles produced by two points have to be separated differently at different intensities in order to produce a recognizably lower intensity between them. This assumes that the eye can discriminate intensities absolutely—which we know it does only relatively. Even so, this explanation has never been put into quantitative form and therefore cannot be tested.

It is worth noting that the visual acuity data of *Drosophila* as given in Table II and Fig. 8 may be described with excellent precision by the stationary state equation $KI = x/(a - x)$ representing a reversible photochemical system in which the light and the dark reactions are both monomolecular. The numerical equation is $22I = (x - 2)/$

$(18 - x)$ where x equals the visual acuity multiplied by 10,000. The shape of the stationary state curve is specific with regard to the power to which x is raised in the numerator (Hecht, 1928). The human visual acuity curve (Koenig) conforms to a second power equation. The visual acuity of *Drosophila* is described by a first power equation. The visual acuity curve of the bee (Hecht and Wolf) may be described with a fair degree of approximation by a first order equation of the form $KI^2 = x/(a - x)$ in which the intensity enters as the square. The numerical form is $0.95\ I^2 = (x - 3)/(160 - x)$ where x is the visual acuity multiplied by 1,000. The values are direct and are not corrected for varying ommatidial angle—a correction which is useful at the very low visual acuities only.

2. Intensity Discrimination.—Intensity discrimination has been described theoretically (Pütter, 1918; Hecht, 1924, 1926) on the assumption that in the action of light on the photosensory system, intensities which are just recognized as different produce effects which differ by a constant increment. These increments may be recorded as changes in the frequency of discharge of the individual sensory elements, or as changes in the number of elements functional, or as both. The work on visual acuity and illumination (Hecht, 1928) favors the number idea but does not exclude frequency. The work on single end-organs (Adrian and Zotterman, 1926; Hartline and Graham, 1932) favors frequency but does not exclude number.

The quantitatively developed idea (Hecht, 1926, 1928) that the influence of intensity on visual acuity and on intensity discrimination may be described in terms of the number of elements functional has been adopted by Houstoun (Houstoun and Shearer, 1930; Houstoun, 1932) without recognizing the theoretical difficulties involved. The original supposition was that whereas visual acuity increases with the total number of active elements, each step in intensity perception corresponds only to the differential increment in the number of active elements. If the relations between visual acuity and intensity discrimination were as simple as this, the intensity at which visual acuity alters most rapidly with $\log I$ should represent the most rapid rate of entrance of functional elements, and should therefore correspond to the place where intensity discrimination is best. Moreover, at high intensities when visual acuity practically ceases to increase because

nearly all the elements are already functional and very few new ones enter, intensity discrimination should be poorest—in fact almost non-existent.

Yet neither of these things is true for *Drosophila* and for the bee, and probably also for the human eye. Fig. 8 and Fig. 10 show that the maximum rate of increase in visual acuity occurs at an intensity whose logarithm is very near -1.5, whereas Figs. 3 and 6 show that at this point intensity discrimination is by no means maximal. Moreover at the highest intensities, when visual acuity has reached its top value, intensity discrimination instead of being at its worst is actually at its best. Exactly the same is true for the bee, where the maximum rate of increase in visual acuity comes very nearly at $\log I = 0$ (Hecht and Wolf) at a point where intensity discrimination is certainly not at its best (Wolf, 1933). Moreover when visual acuity has reached its maximum at $\log I = 2.0$, and intensity discrimination should be worst, it is nevertheless also at its best in the bee and shows no sign of falling off at the highest intensities.

These failures in the correspondence of the two functions are very important, and cannot be due to any chance shift in the intensities for the two functions. We are certain that for *Drosophila* the intensities for visual acuity and intensity discrimination are exactly comparable, because both functions for many of the animals were measured within a very short time of each other with the same piece of apparatus. Similarly for the bee, the two functions were measured with practically identical apparatus using the identical striped plates, and the measurements were made by the same person (Wolf). But even if the intensities were not exactly comparable, the fact that at the highest intensities both functions are maximal is adequate evidence against the interpretation.

Thus in *Drosophila* and in the bee, intensity discrimination does not depend on the rate at which elements become functional, but apparently rather on the total number of elements functional, as in visual acuity. It is possible that though both are functions of the total number of elements active in a given unit of sensory surface, the specific relation is different for each. For visual acuity the situation is simple, but for intensity discrimination it means a revision of ideas held up to now. One possibility is that intensity discrimination is

similar and constant for all the sensory elements, but that the thresholds have a probability distribution. Then increasing the total number of elements decreases the sensory contribution each has to make to produce a constant increment in total sensory effect, and therefore the fraction $\Delta I/I$ becomes smaller as the total number of elements increases. Other possibilities are also available, but a discussion of them is unfruitful at the present stage of our knowledge.

SUMMARY

Drosophila possesses an inherited reflex response to a moving visual pattern which can be used to measure its capacity for intensity discrimination and its visual acuity at different illuminations. It is found that these two properties of vision run approximately parallel courses as functions of the prevailing intensity.

Visual acuity varies with the logarithm of the intensity in much the same sigmoid way as in man, the bee, and the fiddler crab. The resolving power is very poor at low illuminations and increases at high illuminations. The maximum visual acuity is 0.0018, which is 1/1000 of the maximum of the human eye and 1/10 that of the bee.

The intensity discrimination of *Drosophila* is also extremely poor, even at its best. At low illuminations for two intensities to be recognized as different, the higher must be nearly 100 times the lower. This ratio decreases as the intensity increases, and reaches a minimum of 2.5 which is maintained at the highest intensities. The minimum value of $\Delta I/I$ for *Drosophila* is 1.5, which is to be compared with 0.25 for the bee and 0.006 for man.

An explanation of the variation of visual acuity with illumination is given in terms of the variation in number of elements functional in the retinal mosaic at different intensities, this being dependent on the general statistical distribution of thresholds in the ommatidial population. Visual acuity is thus determined by the integral form of this distribution and corresponds to the total number of elements functional. The idea that intensity discrimination is determined by the differential form of this distribution—that is, that it depends on the rate of entrance of functional elements with intensity—is shown to be untenable in the light of the correspondence of the two visual functions. It is suggested that, like visual acuity, intensity discrimina-

tion may also have to be considered as a function of the total number of elements active at a given intensity.

BIBLIOGRAPHY

Adrian, E. D., and Zotterman, Y., The impulses produced by sensory nerve endings. Part 3. Impulses set up by touch and pressure, *J. Physiol.*, 1926, **61**, 465.

Anderson, E. E., and Weymouth, F. W., Visual perception and the retinal mosaic I. Retinal mean local sign—an explanation of the fineness of binocular perception of distance, *Am. J. Physiol.*, 1923, **64**, 561.

Aubert, H., Physiologie der Netzhaut, Breslau, E. Morgenstern, 1865.

Baumgärtner, H., Der Formensinn und die Sehschärfe der Bienen, *Z. vergleich. Physiol.*, 1928, **7**, 56.

Bertholf, L. M., The extent of the spectrum for *Drosophila* and the distribution of stimulative efficiency in it, *Z. vergleich. Physiol.*, 1932, **18**, 32.

Best, F., Die Sehleistung des Facettenauges, *Arch. Augenheilk.*, 1911, **68**, 221.

Best, F., Kritische Bemerkungen zu Hechts Theorie der Sehschärfe, *Naturwissensch.*, 1930, **18**, 236.

Cajal, Ramon y, Nouvelles idées sur la structure du systeme nerveux chez l'homme et chez les vertébrés, Paris, C. Reinwald, 2nd edition, 1895.

Clark, L. B., Visual acuity of the fiddler crab, *Uca pugnax*, *Anat. Rec.*, 1932, **54**, suppl., 35.

Demoll, R., Ueber die Augen und Augenstielreflexe von *Squilla mantis*, *Zool. Jahrb., Abt. Anat. u. Ontog. Tiere*, 1909, **27**, 171.

Doflein, F., Lebensgewohnheiten und Anpassungen bei dekapoden Krebsen, in Festschrift zum 60. Geburtstage R. Hertwigs, Jena, Gustav Fischer, 1910, **3**, 215.

Exner, S., Die Physiologie der facettirten Augen von Krebsen und Insecten, Leipsic and Vienna, Franz Deuticke, 1891.

Freeman, E., Anomalies of visual acuity in relation to intensity of illumination, *Am. J. Psychol.*, 1930, **42**, 287.

Freeman, E., Anomalies of visual acuity in relation to stimulus-distance, *J. Opt. Soc. America*, 1932, **22**, 285.

Garrey, W. E., A sight reflex shown by sticklebacks, *Biol. Bull.*, 1905, **7**, 79.

Graham, C. H., and Hunter, W. S., Thresholds of illumination for the visual discrimination of direction of movement and for the discrimination of discreteness, *J. Gen. Psychol.*, 1931, **5**, 178.

Griffith, R. O., and McKeown, A., Photo-processes in gaseous and liquid systems, London, Longmans, Green and Co., 1929.

Grundfest, H., The relative effectiveness of spectral radiation for the vision of the sun-fish, *Lepomis*, *Proc. Nat. Acad. Sc.*, 1931, **17**, 359.

Hadley, P. B., The relation of optical stimuli to rheotaxis in the American lobster, *Homarus americanus*, *Am. J. Physiol.*, 1906, **17**, 326.

Hartline, H. K., and Graham, C. H., Nerve impulses from single receptors in the eye, *J. Cellular and Comp. Physiol.*, 1932, **1**, 277.

Hartridge, H., Visual acuity and the resolving power of the eye, *J. Physiol.*, 1922, **57**, 52.

Hecht, S., Intensity discrimination and the stationary state, *J. Gen. Physiol.*, 1924, **6**, 355.

Hecht, S., The visual discrimination of intensity and the Weber-Fechner Law, *J. Gen. Physiol.*, 1924, **7**, 235.

Hecht, S., A quantitative basis for visual acuity and intensity discrimination, *Skand. Arch. Physiol.*, 1926, **49**, 146.

Hecht, S., The relation between visual acuity and illumination, *J. Gen. Physiol.*, 1928, **11**, 255.

Hecht, S., Eine Grundlage für die Beziehung zwischen Sehschärfe und Beleuchtung, *Naturwissensch.*, 1930, **18**, 233.

Hecht, S., Die physikalische Chemie und die Physiologie des Sehaktes, *Ergebn. Physiol.*, 1931, **32**, 243.

Hecht, S., and Wolf, E., The visual acuity of the honey bee, *J. Gen. Physiol.*, 1929, **12**, 727.

Helmholtz, H., Handbuch der physiologischen Optik, Hamburg and Leipsic, L. Voss, 1867.

Houstoun, R. A., New observations on the Weber-Fechner law, in Report of a joint discussion on vision, Physical Society of London, Cambridge, The University Press, 1932, 167.

Houstoun, R. A., and Shearer, J. F., Weber's law and visual acuity, *Phil. Mag.*, 1930, **10**, 433.

Johannsen, O. A., Eye structure in normal and eye-mutant drosophilas, *J. Morphol. and Physiol.*, 1924, **39**, 337.

Koenig, A., Die Abhängigkeit der Sehschärfe von der Beleuchtungsintensität, *Sitzungsber. Akad. Wissensch. Berlin*, 1897, 559.

Koenig, A., and Brodhun, E., Experimentelle Untersuchungen über die psychophysische Fundamentalformel in Bezug auf den Gesichtssinn, *Sitzungsber. Akad. Wissensch. Berlin*, 1889, 641.

Loeb, J., Forced movements, tropisms, and animal conduct, Philadelphia, J. B. Lippincott Company, 1918.

Lowry, E. M., The photometric sensibility of the eye and the precision of photometric observations, *J. Opt. Soc. America*, 1931, **21**, 132.

Lyon, E. P., On rheotropism. I. Rheotropism in fishes, *Am. J. Physiol.*, 1904, **12**, 149.

Lythgoe, R. J., The measurement of visual acuity, *Great Britain Med. Research Council, Special Rep. Series, No. 173*, 1932.

Müller, J., Zur vergleichenden Physiologie des Gesichtssinnes, Leipsic, Cnobloch, 1826.

Pütter, A., Studien zur Theorie der Reizvorgänge, *Arch. ges. Physiol.*, 1918, **171**, 201.

Schlieper, C., Farbensinn der Tiere und optomotorische Reaktionen, *Z. vergleich. Physiol.*, 1927, **6**, 453.

Schulz, W., Die Orientierung des Rückenschwimmers zum Licht und zur Strömung, *Z. vergleich. Physiol.*, 1931, **14**, 392.

Wilcox, W. W., The basis of the dependence of visual acuity on illumination, *Proc. Nat. Acad. Sc.*, 1932, **18**, 47.

Wilcox, W. W., and Purdy, D. M., Visual acuity and its physiological basis, *Brit. J. Psychol.*, 1933, **23**, 233.

Wolf, E., The visual intensity discrimination of the honey bee, *J. Gen. Physiol.*, 1933, **16**, 407.