THE VISUAL ACUITY OF THE BEE AND ITS RELATION TO ILLUMINATION

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1. Two reasons prompted us to investigate the relation between visual acuity and illumination in the bee. We wished to know, first, whether the variation of visual acuity with illumination as it exists in the human eye[1] is to be found in so differently constructed an organ as the insect eye; and second, whether the explanation suggested by one of us[2] for this relation in the human eye is of sufficiently general significance so as to be adequate for the bee's eye as well.

In the human eye visual acuity is poor at low illuminations; as the intensity increases, visual acuity increases with it at first rapidly and then slowly; and finally at high illuminations further increases in intensity produce no change in acuity. Visual acuity, since it represents the resolving power of the retina, depends on the distance which separates the receiving elements in the retina. In order to make this distance vary with illumination it has been assumed that the minimum illumination necessary to stimulate the individual cones and rods—their threshold, in short—is distributed in the usual probability or statistical manner of populations. When expressed quantitatively these ideas describe in detail the data of human visual acuity.

It is proposed to see whether these facts and ideas have any general validity in the physiology of the visual process. In order to do so we had to develop a method for the investigation of the vision of animals other than man. Starting with the common observation that animals with eyes respond to a sudden movement in their visual field, we converted it, in terms of the following considerations, into a method of measuring visual acuity. If the visual field of a sensitive animal is made up of a pattern of dark and illuminated bars of equal size, the animal will respond to a displacement of this field only when it can distinguish the components of the pattern. In case the animal cannot resolve the black and white bars, the field will appear uniformly illuminated and displacement of the pattern will elicit no response. If visual acuity varies with illumination, then the capacity to respond to these movements in the visual field will depend on the illumination and on the size of the pattern.

The bee is sensitive to changes in its visual field, and responds by a reflex, sidewise movement of the head and thorax. If the bee is crawling on an inclined, transparent surface, below which is the luminous visual pattern, the response to a movement of this pattern becomes evident by a sudden change in the direction of its progression, which is opposite in sign to the movement of the pattern. We prepared a series of plates composed of equally wide opaque and translucent bars, each plate having a different size of bar. The experiments then consisted in determining for each size of pattern the minimum illumination at which a bee will just respond to a movement of that pattern. The reciprocal of the visual angle subtended by each size of bar is then the visual acuity of the eye at the corresponding illumination.

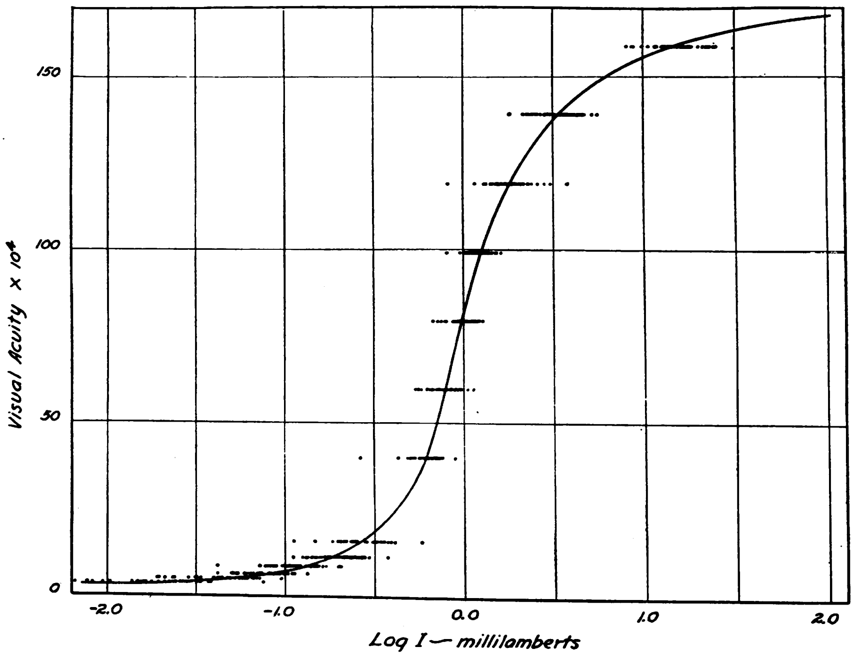

FIGURE 1

Relation between visual acuity and illumination. An effort has been made to represent with a dot each measurement made with each bee. Since this is obviously impossible when the measurements come close together, the plot shows the general distribution of the data.

2. We made measurements with 91 normal, worker bees. The data are given in figure 1, where visual acuity is plotted against the logarithm of the illumination. Each dot represents, as well as is graphically possible, a single determination with a single bee. It is at once apparent that visual acuity in the bee's eye varies with the illumination in much the same way as in the human eye.

Certain comparisons may be made between the two. The disposition of the data in figure 1 indicates that the experiments cover the whole range of visual acuity of which the bee is capable. The maximum lies between 0.016 and 0.017. This is below the visual acuity of the human eye at the lowest perceptible illuminations. Our maximum visual acuity is about 1.5; our minimum is about 0.03. Incredible as it may seem, the bee's greatest capacity for the optical resolution of its environment is never better than ours is at our worst.

The disparity in the visual acuity of our eyes and those of the bee is even greater than this and is brought out by considering the visual acuities at the same illuminations. The maximum visual acuity in both cases occurs at very nearly the same intensities of illuminations and corresponds to a brightness of between 50 and 100 millilamberts. Our maximum here is about 1.5; the bee's maximum is 0.017. We can therefore resolve the environment about 100 times better than a bee can. That this low value is no laboratory product is borne out by the experiments of Baumgärtner[3] in which bees on the wing in the field were shown to have a similar, almost negligible, form discrimination.

3. Differences in resolving power mean differences in the distances which separate the centers of the receiving elements. The data of figure 1 would then require that the ommatidia be separated by a variable distance which depends on the intensity. Since this cannot be true structurally the results must be interpreted in such a way as to secure a functionally variable separation of ommatidia which are structurally fixed.

Let it therefore be supposed that the receptor elements in the ocular mosaic do not all possess the same threshold, but that the threshold varies among the ommatidia as does any other characteristic in a population. At low illuminations then, only a few ommatidia are functional. Since these are distributed at random, they will be far apart and will give the same result functionally as if there were no receiving structures between them. As the illumination increases more and more ommatidia become functional; the distance between functional elements becomes smaller, and the resolving power becomes greater. This continues until an illumination is reached when all the elements are functional, and no further increase in visual acuity can take place. Such an explanation obviously describes the data. But before it can be formulated quantitatively it is necessary to examine the structure of the eye in some detail.

4. In these experiments the relation of the creeping bee to the visual field is such that the pattern is registered across the long axis of the eye. At an illumination when all the elements are functional, the maximum visual acuity will then occur when a horizontal row of elements receives light, and an adjacent row receives no light, and so on. The size of the smallest perceptible pattern will correspond to the visual angle which separates the centers of two adjacent elements.

If the elements were all the same angular size the maximum visual acuity could be registered all over the eye. But since the elements in the bee's eye are not uniform in angular dimension, the maximum visual acuity can be obtained only at that position on the eye where the angular separation is a minimum. In our measurements the visual acuity corresponding to any illumination is always the maximum visual acuity at that intensity. Therefore, at any illumination, no matter how many functional elements it represents, visual acuity is determined at that area on the eye where the angular separation between functional elements is at a minimum.

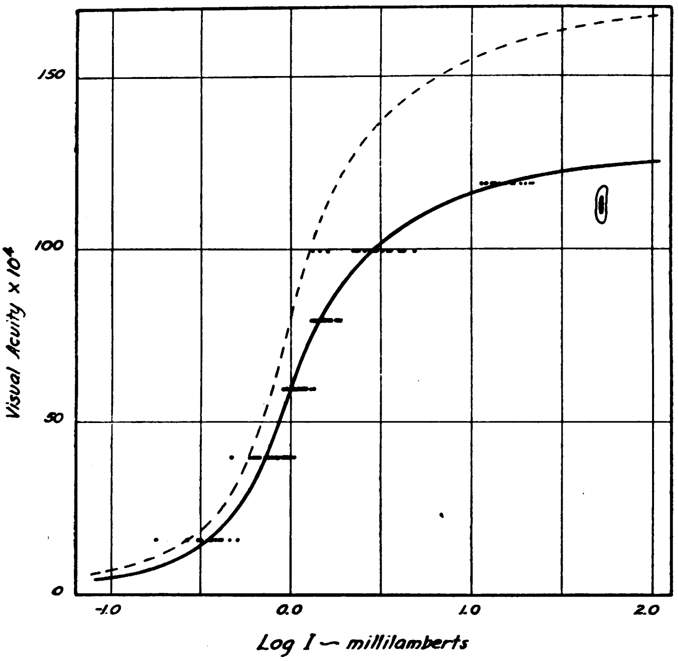

FIGURE 2

Relation between visual acuity and illumination for bees with the central part of the eye painted out as shown in the figure. The points are individual measurements. The broken curve is the normal relation taken from figure 1. The full curve is made from the normal curve by multiplying its ordinates by 0.75.

This concept is so important for understanding the vision of the bee that we tested it in several ways. The measurements as plotted in figure 1 show that the maximum visual acuity of which the bee is capable at the highest illuminations is about 0.017. This corresponds to a visual angle of between 0.9° and 1.0°. Since at these illuminations all the ommatidia are functional, this experimentally determined, minimal, angular separation should correspond to the smallest vertical separation between adjacent ommatidia as determined anatomically. Baumgärtner[8] has recently measured the angular separation of adjacent ommatidia in the bee's eye. In vertical section the smallest separation is near the middle, in the lower half of the eye; it includes about 20 elements and its value lies between 0.9° and 1.0°.

The evidence is even better if one examines the structure of the eye in detail. In vertical section, according to Baumgärtner, the angular separation of adjacent ommatidia increases from about 1° at the center to about 4° at the periphery. The increase is gradual, the middle half of the eye constituting a region of small angular separation in comparison with the rest of the eye—a sort of fovea. If visual acuity is always mediated by the region of minimum angular separation, then the elimination of this central foveal area should depress the visual acuity function to the level of the remaining peripheral ommatidia. We measured the relation between visual acuity and illumination in 21 bees with a spot

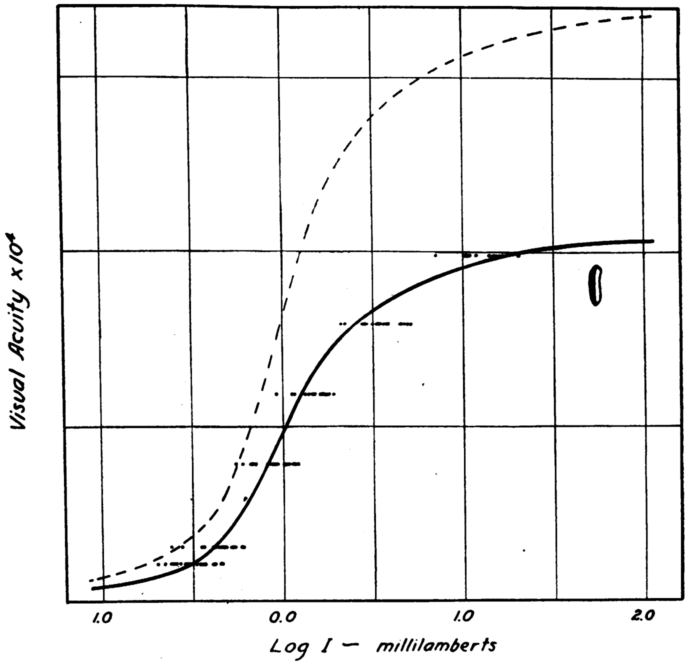

FIGURE 3

Relation between visual acuity and illumination for bees with the anterior half of the eyes painted out. The points are individual measurements. The broken curve is the normal curve of Fig. 1. The full curve is constructed from the normal by multiplying its ordinates by 0.62.

of opaque black paint placed in the center of each eye. Such a spot of paint covers about one quarter of the area of the eye, and renders non-functional all ommatidia whose angular separation is less than about 1.3°. Such bees should give a visual acuity of about three-fourths of normal. The data secured with these animals are given in figure 2. The broken line is the normal visual acuity; the continuous line is drawn so that its ordinates are 0.75 of the normal. It obviously describes the data, and supports the idea that visual acuity determination is a regional function, and depends on the utilization of the part of the bee's eye which structurally permits the maximal resolution.

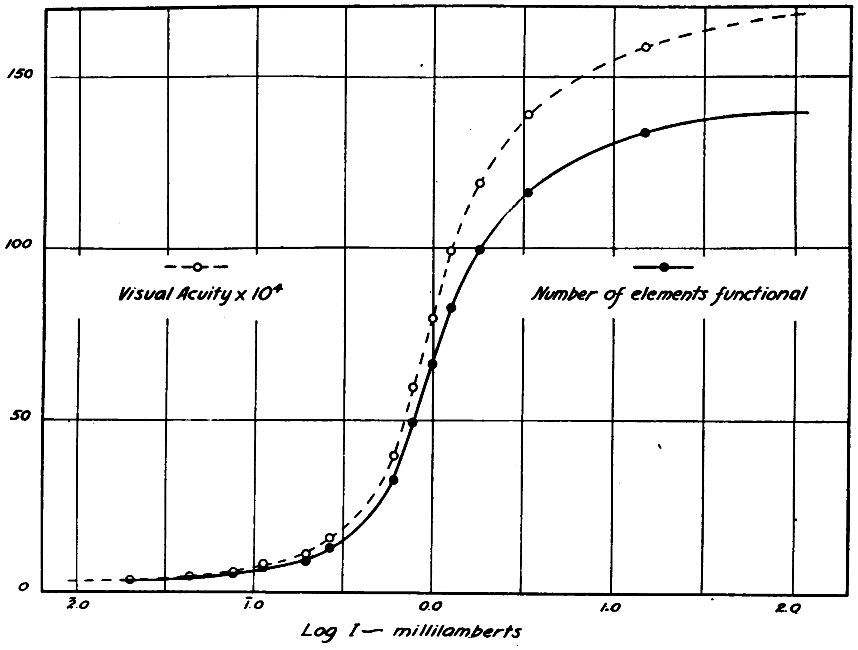

FIGURE 4

Comparison between visual acuity and number of ommatidia functional in a given angular distance in their relation to the logarithm of the illumination. The relation between the number functional and log I is in the nature of an integral probability or distribution curve.

This resolution occurs on the long axis of the eye, because the pattern is received as a series of horizontal dark and luminous bars across the eye. For the eye to perceive the pattern as a series of bars, each bar must stimulate at least two functional ommatidia; and since the eye is very nearly symmetrical these ommatidia are most likely distributed on either side of the eye. If one side were rendered non-functional this would reduce the number of functional ommatidia to half, and in order to have the same number of elements determine a bar as before, the width of the bar would have to be increased about twice, and the visual acuity function would be depressed to about half. We made measurements with 19 bees in which the anterior half of each eye was painted out. The results are given in figure 3, where each measurement is given as before. Through the points there is drawn a continuous curve whose ordinates are 0.62 of the values for the normal, unpainted eye.

The longitudinal use of the bee's eye is not fortuitous. As shown in figures 2 and 3, the eye is about four times as long as it is wide. Furthermore the angular separation between adjacent ommatidia is more than three times as great in the horizontal meridian as in the vertical meridian. Both these facts would tend to make the bee's eye an organ which functions essentially as a linear receptor. This we found to be true experimentally because we were unable to get any responses to a pattern arranged to register on the eye as bars parallel to its long axis. This confirms Baumgärtner's findings that bees in the field are very astigmatic, and resolve their environment vertically with much greater accuracy than horizontally.

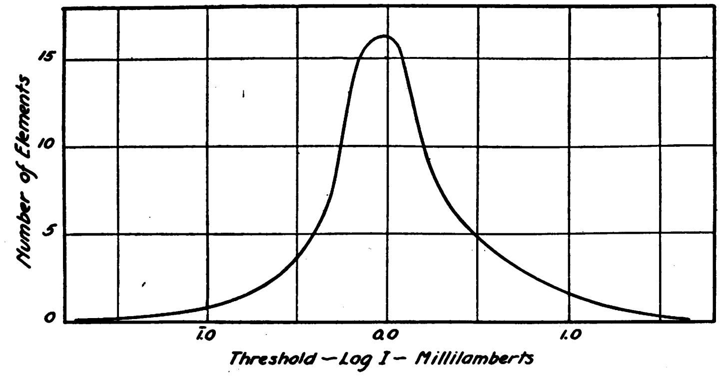

FIGURE 5

Distribution of thresholds of the ommatidia in the bee's eye. The curve is the first differential of the number curve in figure 4, and is a differential probability or distribution curve.

5. We have interpreted the shape of the curve in figure 1 as meaning that the number of elements functional varies with the illumination. If the ocular mosaic were uniform, it would follow that since visual acuity is determined by the vertical distance between elements in the region of maximum ommatidial density, the curve in figure 1 represents the number of functional elements in the vertical axis of the fovea corresponding to any illumination. But the angular separation between adjacent ommatidia is not constant. The precise way in which it varies must therefore

be considered in the conversion of visual acuity data into the number of ommatidia functional in the eye.

Fortunately this is possible because of Baumgärtner's anatomical study. By remembering that visual acuity is always determined in the region of the eye where the angular separation of ommatidia is a minimum, one can determine the actual number of ommatidia which are included in vertical section in any given visual angle. There are only about 70 ommatidia in vertical section in the lower half of the eye, and one can lay off the angle occupied by each ommatidium on a linear scale and compute the actual number of ommatidia in vertical projection which must be functional in order to give a definite visual acuity. The results of this computation are to be found in figure 4, where the number of elements in vertical section required to produce a given visual acuity are given. The ordinates of the number curve have been arbitrarily multiplied by 3.5 to make the two curves comparable.

The number curve in figure 4 resembles the usual integral distribution curves of the statisticians, even as its first differential, the threshold curve, in figure 5 resembles the more commonly encountered differential distribution curves. Therefore, we may make our hypothesis of the relation of visual acuity and illumination quantitatively specific by stating it as follows. Taking the structural relations of the ocular mosaic as given by Baumgärtner, our data relating visual acuity and illumination may be described with complete fidelity by assuming a distribution of the thresholds of the various ommatidia corresponding to the population curve of figure 5.

This distribution curve may be interpreted in two ways. Assuming that a given threshold is a permanent characteristic of a given element, the curve in figure 5 then represents the distribution of this characteristic in the population of ocular elements. However, one may conceive this situation purely in terms of probability. Assume that the threshold of a given element is not fixed, but can vary over the whole range included in figure 5. Then the probable number of elements which have the same threshold at the same time is given by the curve in figure 5. This may therefore be used as the basis for visual acuity in precisely the same way as before.

The full details of these experiments are to appear in the *Journal of General Physiology.*

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[3] Baumgärtner, H., *Zeit. vergl. Physiol.*, vii, 56, 1928.