THE SIZE OF OMMATIDIA IN APPOSITION EYES

By H. B. BARLOW

Physiological Laboratory, University of Cambridge

(*Received* 19 *May* 1952)

(With Three Text-figures)

INTRODUCTION

The vertebrate eye appears to have an acuity that closely approaches a theoretical limit set by the size of the pupil. The optimum resolving power obtainable with a lens of diameter δ is given by the formula

$$\theta = 1 \cdot 22\ \lambda/\delta,$$

where λ is the wave-length of light and θ is the angle (radians) subtended by two point sources which can just be detected as double. In the case of the human eye, for example, the diameter of the pupil in bright daylight is about 0·3 cm., and the light to which it is most sensitive has a wave-length $5 \cdot 6 \times 10^{-5}$ cm. This gives an optimum resolving power of 47 sec., whereas the best observed two-point acuity in the human eye is just under 1 min. The figure was known empirically before it was realized that it approached a theoretical limit set by the physical properties of light, but it is interesting to realize in retrospect that the limit deduced from the pupil diameter would have been a good guide to the actual performance.

It is usually supposed that the resolving power of a compound eye is limited simply by the angle between neighbouring ommatidia, but it is possible that the small diameter of each ommatidium compared with the wave-length of light is really the limiting factor. If it were, then it would be most inefficient simply to scale up a small compound eye to suit a large insect; in this paper the optimum relation between the size of the eye and the size of the ommatidium is deduced and eyes of varying size have been measured to see if the relationship holds.

Johannes Müller (1826—quoted by Exner, 1891) suggested that each ommatidium of a compound eye of the apposition type was only sensitive to light coming from a point lying on, or close to, the axis of the ommatidium. This was not accepted immediately, because it was thought that each single ommatidium might have some ability to discriminate the direction of the light falling on it. Exner's examination of the anatomy and optics of compound eyes made the alternatives to Müller's suggestion unlikely, and Hecht & Wolf (1929) have shown that the optimum resolving power of the bee's eye corresponds to the smallest inter-ommatidial angle. Hassenstein has recently provided convincing evidence that the ommatidia behave as functionally independent units in an eye of the apposition type.

Model compound apposition eye

Müller's suggestion seems to be well established, and the potentialities of this type of eye are most easily discussed in terms of a model. The model is not supposed to correspond accurately to the anatomical details of any particular eye, but it is supposed to imitate the optical arrangement. It consists of a number of directionally sensitive elements with a small angle between each of them, and together covering the required field of view. The acuity of such a model eye would depend on the angle between neighbouring elements, and at first sight it might be thought that the acuity could be improved indefinitely simply by reducing this angle and increasing the number of elements. This would only increase the acuity up to a certain point; beyond this point the acuity would be limited by the resolving power of each ommatidium, for it can easily be seen that acuity would no longer be improved when neighbouring ommatidia were set at such a narrow angle that overlapping occurred in the regions of the field from which they received light.

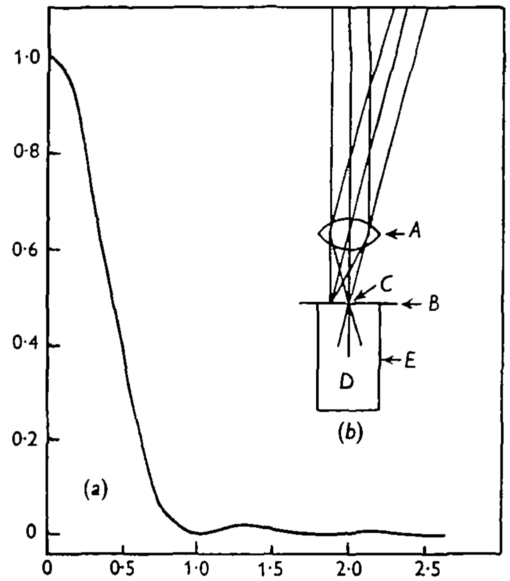

Fig. 1. (*a*) Relative effectiveness of light entering the ommatidium at increasing angles to its axis. Ordinates: effectiveness relative to effectiveness on main axis; abscissae: angle with main axis as multiple of minimum resolvable angle (θ). (*b*) Model of ommatidium. *A*, lens (cornea and crystalline cone); *B*, black screen (primary iris pigment); *C*, pinhole (point of contact of rhabdome and crystalline cone); *D*, photosensitive pigment; *E*, secondary iris pigment.

The usually accepted criterion for the resolving power of a telescope is the angle subtended by two point sources when the peak of the Airy disk of one falls at the first minimum of the other. In the case of an ommatidium functioning optimally, this corresponds to the smallest angle between two point sources such that one stimulates it to the greatest possible extent, and the other not at all. The resolving power according to this criterion is then given by the ordinary formula for a telescope:

$$\theta = 1{\cdot}22\ \lambda/\delta,$$

θ = resolving power, λ = wave-length of light, δ = diameter of ommatidium.

Fig. 1 (*a*) shows how the amount of light absorbed by such an ommatidium would vary with the angle the incident light made with the main axis of the ommatidium.

(*b*) shows a possible structure for achieving this resolution, and the actual anatomy appears to correspond to this proposed model. One would suppose that improvements in acuity would have survival value for many classes of insect; let us therefore suppose that this theoretical limit is achieved, and see what generalizations about the structure and performance of compound eyes follow.

First consider what happens if ommatidia of resolving power θ are set at different angles ϕ to each other. Two point sources will be resolved if they can each stimulate an ommatidium, leaving an unstimulated one in between. Fig. 2 shows the amount of light reaching the central ommatidium as a fraction of the light reaching each of the outer ommatidia, as ϕ, the angle of separation of the ommatidia, is reduced; it is supposed that the two point sources lie on the main axes of the two flanking ommatidia.

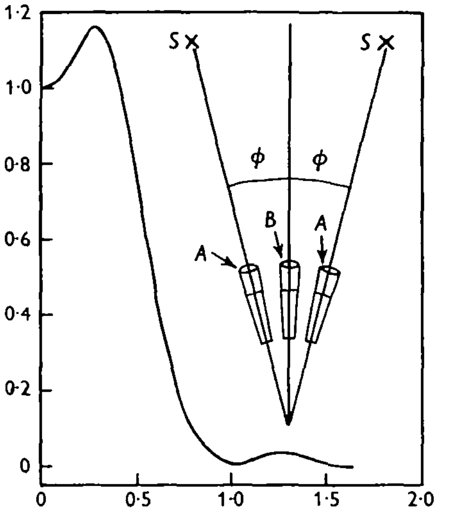

Fig. 2. Three ommatidia (A, B, A), of limiting resolving power θ, are set at an angle ϕ, and illuminated by two sources (*SS*) on the axes of *AA*. The graph shows illumination of *B* relative to *A* (ordinates) as ϕ/θ (abscissae) is increased.

It will be seen that when $\phi \geqslant \theta$ the two point sources excite the central ommatidium little or not at all. In a compound eye in which the angular separation of the ommatidia is equal to, or greater than, the angular resolving power of each ommatidium, there should be no difficulty in resolving points separated by twice this angle. On the other hand, when $\phi = 0{\cdot}4\theta$, the central ommatidium is actually receiving more light than the flanking ommatidia, and the two points would not be resolved. One would therefore suppose that such an eye, in which the angular separation of the ommatidia was less than 0·4 of the angular resolving power of the ommatidia, would fail to resolve points separated by twice the inter-ommatidial angle; there would seem to be no point in constructing an eye like this.

The first conclusion reached is, therefore, that ϕ should be greater than $0{\cdot}4\theta$ in a compound eye in which ϕ is the angular separation of the ommatidia, and θ is the angular resolving power of each ommatidium. If the assumption that the theoretical resolving power is closely approached is granted, one would expect $0{\cdot}4\theta < \phi < \theta$ in those types of insects in which acuity has survival value.

Imagine the problems concerned in designing an eye for an insect. It must obviously be of limited size, and it must presumably cover a wide field of view. The first question would be 'how large should the ommatidia be?' If they are too small, each one will have a poor resolving power, and the acuity of the whole eye could be improved by having fewer, larger, ommatidia. If they are too big, the angle between them must be large, and the acuity could be improved by having more, smaller, ones and reducing the angle between them. For an eye of good acuity the actual size should be smaller than the size which would make acuity be limited by inter-ommatidial angle, and larger than the size which would make acuity be limited by the resolution of each ommatidium. These two limits can be worked out as follows:

δ = Diameter of a single ommatidium (cm.).
ϕ = Angle between axes of ommatidia (radians).
n = Number of ommatidia in a row.
d = Length of a row (cm.).
a = Angular field of view of a row (radians).
θ = Resolving power of an ommatidium (radians).
λ = Wave-length of light (cm.).

From $n\phi = a$ and $n\delta = d$,

$$\phi = \frac{a\delta}{d}.$$

From the formula for the resolving power of telescope

$$\theta = \frac{1{\cdot}22\lambda}{\delta}.$$

Upper limit, $\phi = \theta$,

$$\delta = \sqrt{\frac{1{\cdot}22\lambda d}{a}}.$$

Lower limit, $\phi = 0{\cdot}4\theta$,

$$\delta = \sqrt{\frac{0{\cdot}49\lambda d}{a}}.$$

Real compound eyes

There are now two points which can be checked against the actual anatomy of a compound eye. First, in any eye, one can see if the relationships between inter-ommatidial angle, ommatidial size, and total size of eye, fall within the limits suggested. Secondly, one can see if ommatidial size varies in the predicted way in a range of eyes of different size. The first point can be decided by measuring the diagrams in Baumgärtner's (1928) paper on the vision of bees. The ommatidia were taken in groups of six or four from his figs. 31 and 32, and their breadth measured at right angles to their long axis at the level of the cornea. His figures for inter-ommatidial angle were used.

In the centre of the eye, where the inter-ommatidial angle is least, the ommatidia have a mean diameter of $21{\cdot}6\mu$. Taking $\lambda = 5 \times 10^{-5}$ cm. (Sander 1933), $\theta = 1{\cdot}6^\circ$. The smallest inter-ommatidial angles in the bee occur in this region, and have a mean value of 0·97° over the region measured. This corresponds to $\phi = 0{\cdot}61\theta$. The largest angles, measured in a vertical plane, occur at the tops of the eye, and have a mean value of 1·84°. Over this region the mean diameter of the ommatidia is reduced to $16{\cdot}9\mu$, so that their resolving power is $\theta = 2{\cdot}07°$, and $\phi = 0{\cdot}89\theta$. In the lowest region of the eye ϕ is increased to 1·74°, but θ remains at 1·6°. The bee's eye is highly 'astigmatic' in the sense that the angle between ommatidia measured in a horizontal plane is greater than any of the figures given above. In the central region it averages 2·8°; the mean diameter of the ommatidia measured in this direction is $20{\cdot}9\mu$, so that $\phi = 2{\cdot}8° = 1{\cdot}67\theta$. At the edges the inter-ommatidial angles get bigger than 4°, so that $\phi > 2{\cdot}5\theta$.

The conclusion reached from these measurements was that the bee's eye is constructed in accordance with the principles that were put forward, but only in those regions where the acuity is greatest. Elsewhere the ommatidia are too large (or the inter-ommatidial angle too large) to give the eye optimum acuity for the space covered.

Before it was realized how much the inter-ommatidial angle varied in different parts of the same eye, the eyes of an assortment of museum specimens of insects were examined. A plane, usually vertical, was found in which the eye appeared, by inspection, to cover 180°. The overall 'height' of the eye in this plane was then measured. It was assumed that a section of the eye in this plane would be nearly semicircular, and that the distance measured would be the diameter of the semicircle. These observations and measurements gave an estimate of d and a. From these the limiting values of δ, the diameter of an ommatidium, for optimum resolution were calculated. The actual diameters of the ommatidia were measured for comparison. All these observations and measurements were made with a micrometer eyepiece in a dissecting microscope.

The agreement between the observed and the calculated sizes of ommatidia was only moderately good, and the plot of height of eye against diameter of ommatidium failed to show the expected square-root relationship; a straight line would have fitted equally well. It was clear, however, that this disappointing result did not simply represent deviation from optimal design. The eyes were of very different shapes; some, like the dragonfly's, were almost exactly hemispherical protuberances, whereas others, like the eye of the praying mantis, were moulded to the contour of the head. The spectral sensitivity curves of insect eyes are not necessarily alike, and the optimal ommatidial size might vary accordingly. It is also possible that insects living where the light is feeble might sacrifice acuity for sensitivity by having large ommatidia.

To reduce variation from these causes the eyes of twenty-seven Hymenoptera were examined. They were all diurnal species, and were chosen to cover as wide a range of eye size as possible, the largest being a tropical bee 60 mm. long with a 5 mm. eye, and the smallest a Chalcid less than 1 mm. long with an eye of 0·2 mm. A list of these insects is given at the end of this paper in order of increasing eye size. The external shape of the eyes was remarkably similar throughout the group, except for a tendency to be more globular in some of the smaller ones; these species are placed in brackets in the list.

Fig. 3 shows the diameters of the ommatidia plotted against the square root of the heights of the eyes. The point for the bee's eye is indicated by a cross. If all the eyes were the same shape, had the same distribution of acuity in the visual field, and the same ratio of ϕ/θ, then the points should lie on a straight line through the cross and the origin. There is a tendency for the small eyes to have rather bigger ommatidia than expected. This might be because small ommatidia can only collect little light, which would limit contrast sensitivity and necessitate a higher value of ϕ/θ, but, considering that no allowance has been made for factors such as the thickness of ommatidial walls, the deviations are small.

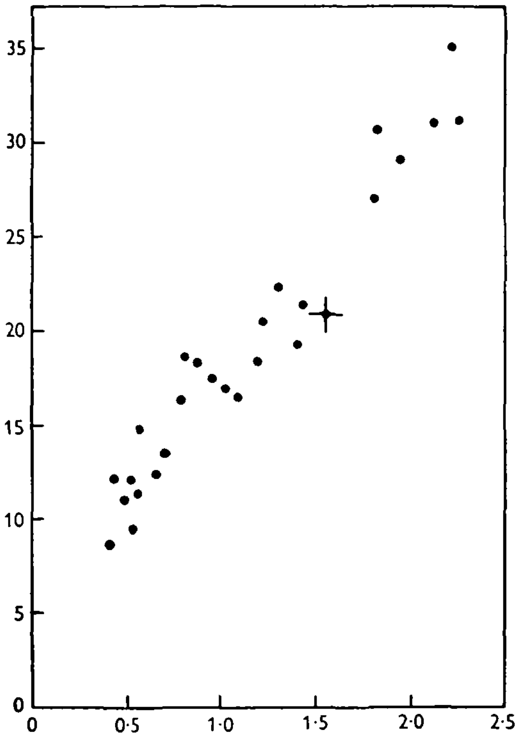

Fig. 3. Diameter of ommatidia in twenty-seven Hymenoptera. Ordinates: diameter in μ; abscissae: square root of height of eye in mm.

This result supports the suggestion that the resolving power of the compound eye is limited by the diameter of the ommatidium in relation to the wave-length of the visible light. In any given eye, of course, the resolution is also limited by inter-ommatidial angle, but the way in which ommatidial size and inter-ommatidial angle are adjusted in eyes of different size suggests strongly that the wave structure of light is the limiting factor in the design of the compound eye.

DISCUSSION

The rather theoretical approach which has been presented gives a satisfactory explanation of the size of the ommatidia in eyes of different sizes, and one is tempted to make further generalizations about compound eyes. It was shown that the lower limit to the useful size of an ommatidium in an eye of length d and field a was given by

$$\delta=\sqrt{\frac{0{\cdot}49\lambda d}{a}}.$$

The minimum resolvable angle of the eye will be twice the inter-ommatidial angle ϕ, and this angle will be smallest when the ommatidia are smallest if the other dimensions of the eye are fixed. The minimum resolvable angle r of the compound eye will therefore be given by

$$r=2\phi=2\sqrt{\frac{0{\cdot}49\lambda a}{d}}.$$

In the case of a simple eye the minimum resolvable angle is inversely proportional to the pupil diameter. It is difficult to compare the merits of the two types of eye, because pupil diameter, in a simple eye, is obviously not a measure of the 'size' comparable with the length of a row of ommatidia d in a compound eye. Nevertheless, one can say that an increase of size allows greater improvement of acuity in simple eyes than in compound eyes.

Oddly enough one comes to the same conclusion in considering sensitivity. This must depend on many factors outside the scope of this paper, such as the quantity of photosensitive pigment, the percentage of incident light it absorbs, and its stability, but the actual amount of light admitted by the optical system is clearly one of the most important factors. The human eye admits less than 1000 quanta per second from a point source which is just visible. The bee's eye would admit one quantum about every 3 min. from such a source, and to be constantly visible the light would certainly have to be increased in intensity more than a thousand times. Since in a compound eye of optimum acuity the area of an ommatidium is proportional to the length of the eye, the sensitivity might also be expected to increase directly in proportion to the length. In the simple eye, on the other hand, the area of the pupil increases as the square of its diameter, and an increase of size can bring a correspondingly greater improvement in sensitivity.

At first sight one is inclined to judge that the compound eye is an inefficient contraption compared with the simple eye of vertebrates. But it is not, relatively, so inefficient for small eyes, and the insect may perhaps have other tricks to humble the critical theorizing biologist; the bee's visible spectrum extends into the ultraviolet (Bertholf, 1931; Wigglesworth, 1950), and there is also evidence for a mechanism sensitive to the plane and intensity of polarization of light (von Frisch, 1950; Autrum & Stumpf, 1950). The additional information so obtained might easily compensate for the poor acuity of this type of eye, and where sensitivity is required the apposition eye has been elegantly modified to the superposition type.

List of insects measured in order of increasing eye size

Aphelinus tibialis; Dacnusa areolaris; (*Aphidius ulmi*); *Dacnusa stramneipes; Tetrastichius brevicornis;* (*Praon lepelleyi*); (*Aphidius ervi*); (*Paxylomma buccata*); (*Polemochartus liparae;* (*Macrocentus thoracicus*); *Macrocentus marginator;* (*Dufourea halictula*); *Chelostoma campanularum; Prosopis hyalinata; Heriades truncorum; Symmorphus sinustissimus; Stelis phaeoptera; Stelis punctatissima; Eumenes coarctata; Ancistrocerus callosus; Apis mellifera; Vespula germanica; Bombus terrestis; Scolia speciosa; Vespa crabro; Scolia procer; Salius sycophanta.*

Those placed in brackets had eyes of an unusual, more globular, shape.

SUMMARY

1. In a compound apposition eye the acuity may be limited by the inter-ommatidial angle or by the optical performance of each ommatidium. In the honeybee the performance of the ommatidia must approach the theoretical limit set by diffraction if the whole eye resolves points separated by twice the inter-ommatidial angle.

2. The eyes of twenty-seven other species of Hymenoptera were measured, and the results show that in eyes of different sizes the number of ommatidia is adjusted so that inter-ommatidial angle is just below the limiting resolving power of the ommatidia; this is the condition for optimum acuity in a compound apposition eye.

3. When this condition is fulfilled the minimum resolvable angle is inversely proportional to the square root of the linear dimensions of the eye. Acuity increases with size more rapidly in the simple type of eye.

I am very grateful to Mr John Smart for allowing me to use specimens in the collections of the University Museum of Zoology, and for helping me in the selection of suitable species.

REFERENCES

AUTRUM, H. & STUMPF, H. (1950). Das Bienenauge als Analysator für polarisiertes Licht. *Z. Naturforschung*, 5*b*/2, 116–22.

BAUMGÄRTNER, H. (1928). Der Formensinn und die Sehschärfe der Bienen. *Z. vergl. Physiol.* 7, 56–143.

BERTHOLF, L. (1931) The distribution of stimulative efficiency in the ultra-violet spectrum for the honey bee. *J. Agric. Res.* 43, 703–713.

EXNER, S. (1891). *Die Physiologie der Facettirten Augen.* Franz Deuticke.

VON FRISCH, K. (1950). *Bees; their Vision, Chemical Senses, and Language.* New York: Cornell University Press.

HASSENSTEIN, B. (1951). Ommatidienraster und afferente Bewegungsintegration. *Z. vergl. Physiol.* 33, 301–26.

HECHT, S. & WOLF, E. (1929). The visual acuity of the honey-bee. *J. Gen. Physiol.* 12, 727–60.

MÜLLER, J. (1826). *Zur vergleichenden Physiologie des Gesichtssinnes.* Leipzig.

SANDER, W. (1933). Phototaktische Reaktionen der Bienen auf Lichten verchiedener Wellenlänge. *Z. vergl. Physiol.* 20, 267–86.

WIGGLESWORTH, V. B. (1950). *The Principles of Insect Physiology.* London: Methuen.