VISUAL ACUITY AND THE CONE CELL DISTRIBUTION OF THE RETINA*

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BOTH Polyak (1941) and Ludvigh (1941) have discussed the acuity gradient of the visual field and its relation, among other matters, with the structure of the retina. In general, for photopic vision, the relevant structural characteristics of the retina include the regional variations of (i) the size and the separating interval of the cones, and (ii) the ratio of the number of cones to that of the optic nerve fibres (Polyak, 1936) referred to as the convergence ratio. Polyak and Ludvigh have compared the acuity gradient of the visual field with the gradient of the cone-cell intervals in the retina, and have shown that to some extent they are closely similar. In this paper some details are discussed which arise as a result of their work.

THE WORK OF POLYAK AND LUDVIGH

The curves 1*a* and 1*b* of Fig. 1 (opposite), including the ordinate scale shown on the left, are reproduced from Polyak's comprehensive monograph on the retina (1941, Fig. 99). These curves have since appeared in the writings of Ruch (1946) and Adler (1950), and are now widely known. The curve 1*a* shows the angular intervals between adjacent cones, whilst curve 1*b* represents the visual acuity, both of which are plotted against the angular displacement from the centre of the fovea and of the visual field. With reference to these curves Polyak (1941, p. 436) writes that the cone intervals '... form a curve similar to the visual acuity curve of Wertheim and others', and quotes Emsley (1936) as the source of visual acuity data. Emsley specifically acknowledges Wertheim (1894) as the source of his quantitative data.

In Fig. 2, the curve 2*a* is reproduced from the results of Wertheim's experiments in which wire gratings were used; it shows the variation of the mean of the nasal and temporal values acuity in the horizontal meridian of the visual field. Wertheim recorded his results as relative values of acuity, the centre of the field having a maximum value of unity, and the peripheral zones having smaller values which ultimately reach zero.

If one now compares the curves 1*b* and 2*a*, it will be seen that they are almost identical, and that in fact the curve 2*a* has been directly superimposed upon Fig. 1. The ordinate scale of Fig. 2 has been drawn on the right hand side of Fig. 1 to facilitate this comparison. If a graphical comparison of Wertheim's acuity values in Fig. 2 (ranging from unity in the centre of the field to zero at the extreme periphery) is to be made with the cone intervals in Fig. 1 (ranging from 24" in the centre of the fovea to approximately 3' 40" at the ora serrata), it is essential first to transform one of these sets of values so that it can be inserted in the co-ordinate system of the other. It would appear that Polyak has overlooked the necessity for allowing for the dissimilarity in the co-ordinate systems of Figs 1 and 2.

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FIG. 1.—Curve 1a indicates the variation of the cone cell intervals with angular displacement from the centre of the fovea (Polyak). Curve 1b shows the variation of the visual acuity with angular displacement from the centre of the visual field in the horizontal meridian; the right-hand ordinate scale is only for comparison with the curve 2a in Fig. 2 as described in the text. Curve 1c is Wertheim's acuity curve in terms of the left-hand ordinate scale.

FIG. 2.—Curve 2a shows the variation of the visual acuity (Wertheim), and is the mean of the nasal and temporal values in the horizontal meridian of the visual field. Curve 2b is the variation of the cone cell intervals (Polyak) in terms of this ordinate scale.

In the central fovea, the smallest cones are separated by intervals almost as small as 1μ between their centres; Polyak estimates this as equivalent to $12''$ – $15''$, and occasionally more specifically as $12''$, corresponding to a first focal length of 17.2 mm. for distant vision. In a central area 100μ in diameter, there are some 2,000 cones which have an average interval between centres of 2μ , or $24''$ (Polyak, 1941, p. 425). The value of $24''$ is therefore used as the average cone interval for 0° displacement in curve 1a. Thus, if a unity value of acuity is to correspond with a central foveal cone interval of $24''$, then each relative value of acuity must be first divided into $24''$ before inserting it in Fig. 1. In other words, if any of Wertheim's acuity values is denoted by w , it must be first altered to $24''/w$, before transposing it from Fig. 2 to Fig. 1. As a result of this transformation we obtain the curve 1c, and it is in this form, not as in curve 1b, that Wertheim's acuity values should be contrasted with the cone intervals of curve 1a. Or, alternatively, if Polyak's cone intervals are denoted by p seconds of arc, they can be inserted in Fig. 2 by first transforming them to $24''/p$. Curve 2b then follows as a result, and the two curves 2a and 2b provide an alternative comparison of acuity and cone intervals within the co-ordinate system of Fig. 2.

The curves in Fig. 2 now resemble to some extent the results obtained by Ludvigh (Fig. 3, overleaf). The curve 3a is the variation of the acuity, out to a maximum displacement of 10° , as determined by Ludvigh using selected Snellen letters. It is moderately similar to Wertheim's results shown in curve 2a. Curve

FIG. 3.—Curve 3a shows the variation of the visual acuity (Ludvig). Curve 3b gives the variation of the cone cell intervals (Østerberg).

possible that Fig. 2 is more reliable than Fig. 3.

The fact that a point of intersection occurs is the surprising feature of Figs 2 and 3. Polyak (1941, p. 426) explains the difference between curves 1a and 1b as due to an increase in the size of the functional cone unit in the extra-foveal zones of the retina, *i.e.* the cones become linked with increasing multiple synaptic relations and as a result they tend to function in groups rather than as individuals. But if, more correctly, we now use the curves 1a and 1c (similarly, 2a and 2b, and 3a and 3b), this explanation can only hold for displacements greater than the point of intersection. For displacements less than the point of intersection, the curves would seem to suggest that the details resolved in the visual field have angular dimensions smaller than the cone intervals. Cone cells respond *in toto* to a light stimulus (Polyak, 1941, p. 423), and it is highly unlikely that they possess a structural subdivision permitting the resolution of detail more fine than that of the cone cell intervals. One would therefore expect to find that the acuity curve lies either on or beneath the cone interval curve, and that a point of intersection can occur nowhere. The problem is therefore to find how the curves have been wrongly contrasted.

When discussing visual acuity, it is first necessary to distinguish between the minimum perceptible (minimum perceptibile) visual angle and the minimum resolvable (minimum separabile) visual angle. Various experiments have shown that objects are visible even when they subtend extremely small angles.

3b shows the variation of the cone intervals calculated from the cone densities per unit area determined by Østerberg (1935). From Østerberg's results the average cone interval in the centre of the fovea is 2.6μ , or $31''$, which is close to Polyak's average value of $24''$.

DISCUSSION

Figs 2 and 3 are similar, in that the acuity and cone interval curves have a point of intersection; 2a and 2b intersect at a point of 12° displacement, and 3a and 3b intersect at a point of 2° displacement. The curves have steep gradients in the region of small displacements, and relatively small discrepancies will therefore produce large differences in the position of this point of intersection. Polyak's work on the size and distribution of the cones in the retina is later and more detailed than that of Østerberg, and for this reason it is

For example, Hecht and Mintz (1939, 1947) have shown that wires having diameters subtending $0.5''$ to $0.6''$ of arc can be perceived. This is not surprising when we remember that Arcturus (α Bootis) and Betelgeuse (α Orionis), the fifth and twelfth brightest stars in the sky, have angular diameters as small as $0.047''$ and $0.022''$, respectively. Objects subtending such small angles as these appear as diffraction patterns upon the retina; for a point source of light the centre of the diffraction pattern consists of a disc, receiving 84 per cent of the radiant energy entering the pupil, and having a diameter of approximately $\theta = 2.44 \lambda/d$, where d is the diameter of the pupil. White light has an effective wavelength of 556μ , and if $d = 3$ mm., then $\theta = 1.55'$. However small the object, the diffraction image will remain unchanged in size, and the minimum perceptible visual angle is only limited by the light intensity of the source and the brightness of the background.

The acuity curves 2a and 3a, however, are derived from the minimum resolvable visual angle. Raleigh's criterion for the minimum angle of resolution is $\theta = 1.22 \lambda/d$, and using the previous values, we have that $\theta = 46''$. Unfortunately, Wertheim does not record the resolutions corresponding to his relative values of acuity, but if we suppose that $46''$ corresponds to his unity value of acuity for the centre of the visual field, the error should not be large. Using the relation $p = 46''/w$, we obtain the curve 4a in Fig. 4, which is Wertheim's experimental result now expressed in terms of the minimum resolvable visual angle. Curve 4b is Polyak's cone interval curve 1a, and it can now be seen that there is no point of intersection between the two curves. Finally, curve 4c gives the ratio of the resolution to the cone intervals, in terms of the right-hand ordinate scale.

For displacements greater than 3° , the ratio of the resolution to the cone intervals progressively increases, and possibly has some close relation with the convergence ratio of the cone cells to the optic nerve fibres. For displacements of less than 3° , the ratio is again larger than unity, rising to a value of 1.9° for zero displacement. Polyak (1941, p. 221) describes the foveal photoreceptors as having monosynaptic relations with the conducting neurons, and states (p.

FIG. 4.—Curve 4a is the visual acuity (Wertheim) assuming that a unity value corresponds to a minimum resolvable visual angle of $46''$. Curve 4b shows the variation of the cone cell intervals (Polyak). Curve 4c is the ratio of the minimum resolvable visual angle to the cone cell intervals.

425) that each cone is an almost independent functional unit. The increase in the ratio in this region must therefore have a different explanation from that which accounts for large displacements.

One possibility is that Wertheim was unable in his experiments to resolve the finest detail in the centre of the visual field. This would seem to be the most likely explanation, for, *a priori*, one can see no reason for the centre of the retina possessing a degree of refinement in its cone structure, equal to or better than that shown in 4b, unless it is for the purpose of resolving discriminate detail in the visual field. Wertheim extrapolated his results from $\pm 2.5^\circ$ to 0° displacement; Weymouth and others (1928) and Jones and Higgins (1947), however, have made measurements within this range and have found relative values of acuity having a gradient approximately the same as Wertheim's. In one case, Weymouth and others found that the minimum resolved angle was $40''$. Shlaer (1937) determined experimentally the relation between visual acuity and illumination, and for a maximum illumination found that the minimum resolved angle was $28''$. This would correspond to a ratio of 1.13 in curve 4c for zero displacement. Using Lagrange's law, with a value of 1.337 for the refractive index of the vitreous humour and a magnification of 0.923 between the entrance and exit pupils of the unaccommodated eye (Hardy and Perrin, 1932), we obtain $\alpha' = \alpha 1.235$ where α and α' are the angles subtended in the object and image spaces respectively. Thus Shlaer's value of $28''$ becomes $22.7''$ in the image space of the eye, corresponding to a zero-displacement ratio of 0.95 for curve 4c.

A cone interval of $12''$ is equivalent to $14.8''$ in the visual field, and it remains to be seen whether more refined techniques in visual acuity experiments are capable of yielding minimum resolvable visual angles approaching this value, in spite of eye movements, dioptric aberrations, and the diffraction effect produced on the retina.

Summary

Polyak and Ludvigh have compared graphically the acuity gradient of the visual field with the gradient of the cone separating intervals in the retina; some details arising from their results are discussed.

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