

THE THEORY OF THE FOVEA

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(With Ten Text-figures)

INTRODUCTION

There is ordinarily in the retina of vertebrates with good diurnal vision a region where the density of cones is higher than elsewhere. To this region the name *area* (or less appropriately *area centralis*) has been applied. In anthropoid anatomy, it is more often referred to as the *macula* or yellow spot, because the region of high cone-density is more or less coextensive with the distribution of a yellow pigment which is conspicuous on ophthalmoscopic inspection of the retina. This *area*, because of the high cone-density and because it is usually situated near the optic axis where the effect of aberration is least, is believed to be a region of high resolving power.

Within the *area* there is very frequently a *fovea*, so called because it appears as a depression or pit when the retina is viewed from the pupil side. Histologically the *fovea* is a region of higher cone-density than the rest of the *area* and the density rises to a maximum at its centre. Moreover, it is established that a one-to-one relation exists between the cones of the *fovea* and the ganglion cells, i.e. each cone is individually represented by a fibre in the optic nerve. It is quite probable, however, that this one-to-one correspondence extends well out into the *area* if not over the whole of it.

Both *area* and *fovea* are clearly part of the equipment of the eye for daylight vision. Rods are scarce in the *area* and invariably absent from the *fovea*, except in one or two scattered groups of animals in which nocturnality is evidently a relatively recent secondary acquisition (owls, *Sphenodon*) and the *fovea* appears degenerate.

The depression on the inner aspect of the retina from which the *fovea* takes its name is caused by the displacement radially from its centre of the cells of the neural layers of the retina, leaving a cavity filled by the vitreous humour. And *foveae* are divisible into two fairly distinct classes on the basis of the form of this depression. In one class the depression is relatively shallow and saucer-shaped; in the other it is deep and funnel- or whirlpool-shaped. The shallow class includes the *fovea* of anthropoids, and also the temporal *fovea* of some birds. The *foveae* of fish, reptiles and birds (with the exception mentioned) belong to the deep class which Walls has labelled convexiclvate (Fig. 1).

Within the classes there is a considerable variation of form and the anthropoid type is often rather irregular in outline. But it is a consistent feature of the latter that the central floor of the *fovea* (apposed to the region of highest cone-density) is relatively flat with a low curvature; whereas in the convexiclvate type the curvature

at the centre is relatively very high. Consequently, if any functional significance attaches to the *shape* of the fovea, it is rather improbable that it will be the same for the two classes.

Walls (1937) appears to have been the first to attempt a specific functional interpretation of the shape of the convexiclivate fovea. It had previously been supposed that the 'purpose' of the radial displacement of the neural layers away from the centre was simply to clear the optical path between pupil and cones at the point where the cones were densest and visual acuity was potentially highest. Walls correctly pointed out that the neural retina in life was optically homogeneous and its transparency not measurably different from that of the vitreous, so that the advantage to be gained by substituting one for the other over a few per cent of the total optical path between pupil and cones was vanishingly small. The extreme regularity of the profile of the convexiclivate fovea suggested to him a lens-like

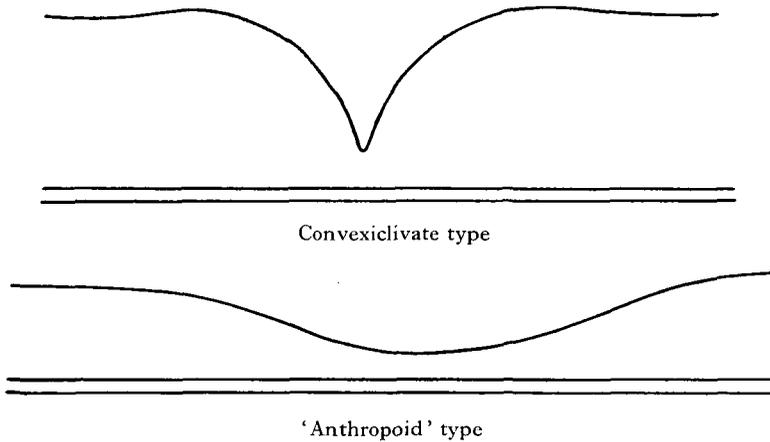


Fig. 1.

function. Refraction must occur at the vitreo-retinal boundary if the refractive indices of vitreous and retina are not identical; and that they are not can be inferred from the fact that the fovea can be seen by ophthalmoscopic inspection in the living retina. Walls (1940) later resuscitated measurements of the refractive indices of vitreous and retina by Valentin showing that the refractive index of the retina was the higher in the ratio of about 1.006. And on this basis he computed by a graphical method the 'magnifying effect' of the fovea. From this result, he arrived at an estimate of the extent to which 'visual acuity' was improved by foveal refraction. Later (1942, p. 662) he states that '*foveally* the visual acuity of some hawks and eagles reaches a value at least eight times that of man'.

Walls is entitled to great credit for seeing that a problem existed and for his courageous attack upon it. But his analysis, especially in its neglect of aberration, is incomplete and his later conclusions are in error. It is the purpose of this paper to attempt a more thorough assessment of the effect of foveal refraction and to suggest a probable function for the convexiclivate fovea.

REFRACTION BY THE FOVEA

The central fovea of Falconiform birds is typically convexiclivate and of great regularity and symmetry. Walls based his analysis on the central fovea of a buzzard. The following treatment is based on Polyak's (1941) figure of the central fovea of the golden eagle (*Aquila chrysaëtus*) which is very closely similar in contour. In Walls's figure of the buzzard's fovea the external limiting membrane is appreciably curved. In the eagle this membrane (which may be taken to be the locus of the seen image) is very nearly plane over the whole foveal area. And this fact somewhat simplifies the geometry of the problem.

Fig. 2 is a reproduction of Polyak's figure. And it can be seen that, except very near to the centre where the curvature changes sign, the profile can be represented by quadrants of circles which are tangent and whose centres lie in the external limiting

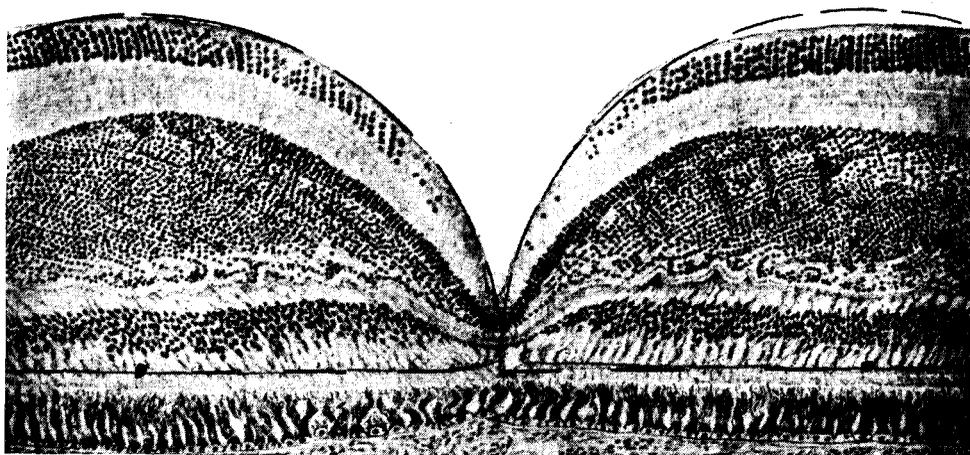


Fig. 2. Reproduction of section across the centre of the central fovea of *Aquila* from Polyak (1941). Superimposed are a dashed line in the plane of the external limiting membrane, and circles centred on this line (see text).

membrane. The slight divergences are probably attributable to unequal post-mortem shrinkage which may also be responsible for the small tear in the external limiting membrane near the centre. In Walls's figure of the *Buteo* fovea the coincidence with circles is even more exact, so it is reasonably safe to assume that such a profile represents with considerable accuracy the *in vivo* configuration of the fovea in Falconiform birds. As to the geometrical form at the centre it is evident by inspection that a paraboloid of revolution about the axis of symmetry is a reasonable approximation. It will be seen that no more explicit assumption is necessary.

This relatively simple geometrical form makes it possible to compute the effect of refraction with substantially greater accuracy than is possible by graphical methods. And it will be possible to show that in certain respects it is the 'best' form.

For the calculations which follow, radial symmetry is assumed and dimensions as indicated in Fig. 3. It is also assumed, following Valentin, that the ratio of refractive indices of retina and vitreous is 1.0063.

Now consider the path of single ray PQ normal to the plane of the photoreceptor cells until refracted at Q to intersect this plane at S . Let x be the distance between PQ and OY , the axis of symmetry of the fovea, and let X be the distance OS . The effect of refraction is evidently to displace the point of intersection with the image plane radially from the axis of the fovea by a distance $(X - x)$.

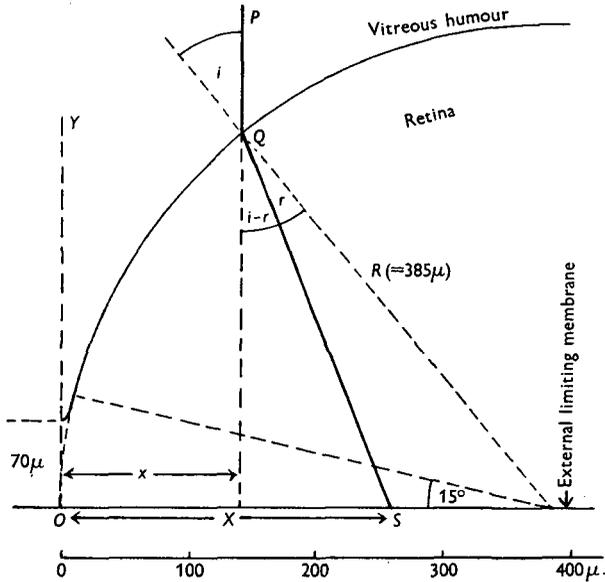


Fig. 3.

Suppose the ray PQ to trace out a cylinder of radius x about the foveal axis OY . Then the locus of the intersection of the ray with the image plane will be a circle, radius X , whereas, but for refraction, it would have been a circle, radius x ; and the circumferences of these circles will also be in the ratio X/x . Hence, a magnification factor in the tangential direction can be defined, say

$$M_t = \frac{X}{x}.$$

Similarly, a radial magnification factor M_r can be defined. Evidently

$$M_r = \frac{dX}{dx}.$$

The physical meaning of these factors can be seen by considering the set of narrow pencils of rays which, without refraction, would form in the image plane a small circle of diameter δ and centre distant x from OY ($\delta \ll x$). Refraction will cause the set to intersect the image plane in an ellipse, whose centre is distant by $M_t x$ from OY and whose axes are in the tangential and radial directions (with respect to the centre of the fovea) and are equal to $M_t \delta$ and $M_r \delta$ respectively.

The values of these factors can be readily evaluated for values of x between 10 and 385μ . Let i be the angle of incidence, r the angle of refraction, R the radius of curvature, and μ the ratio of refractive indices of neural retina and vitreous humour, then

$$\sin i = \mu \sin r,$$

and from Fig. 3

$$x = R(1 - \sin i),$$

$$X = x + R \cos i \tan(i - r).$$

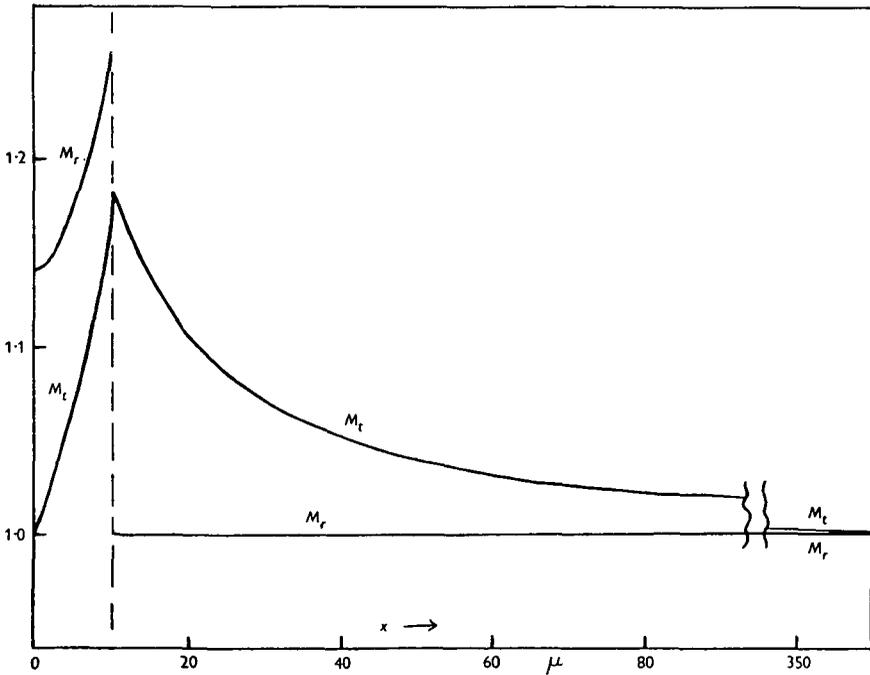


Fig. 4.

Hence
$$M_i = \frac{X}{x} = 1 + \frac{\cos i}{1 - \sin i} \tan(i - r),$$

and
$$M_r = \frac{dX}{dx} = 1 + \tan i \tan(i - r) - [\sec^2(i - r)] \left[1 - \frac{\cos i}{\mu \cos r} \right]$$

$$\doteq \tan i \tan(i - r) + \frac{\cos i}{\mu \cos r}.$$

The resulting values for M_i and M_r are plotted in Fig. 4, to the right of the dashed line which corresponds to the value of x where the curvature changes at an angle of incidence of 75° . As x decreases, M_i rises from unity to about 1.2. M_r is practically unity for all values of x . It rises from $0.994 (= 1/\mu)$ at the periphery to 1.000 in the immediate vicinity of the point of inflexion.

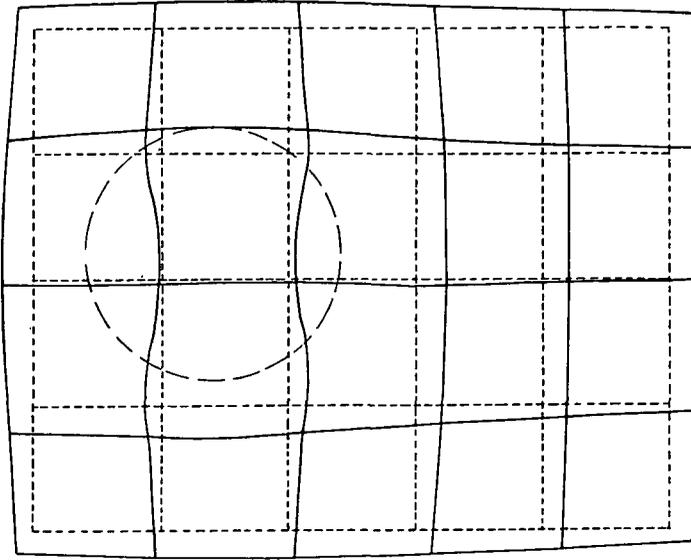


Fig. 5. The solid lines represent the effect of foveal refraction on an image which would otherwise have the form shown dotted. The circle indicates the centre of the fovea, its radius is 10μ .

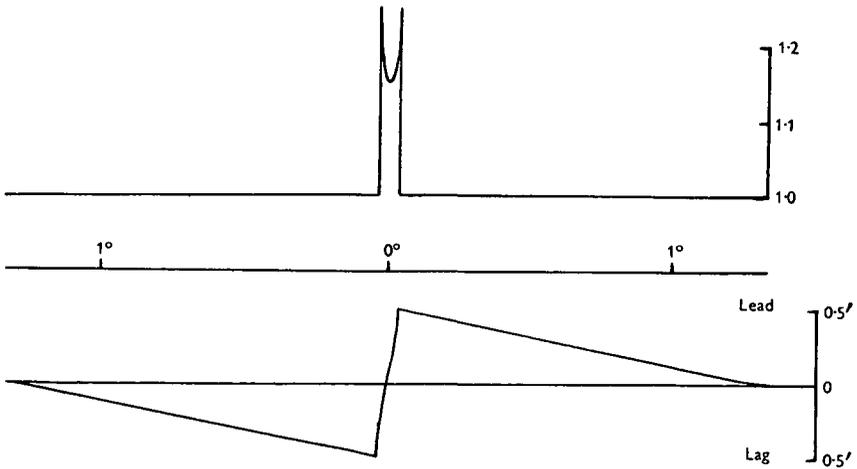


Fig. 6. The upper curve shows the ratio of the angular velocities of image (M, θ) and of object (θ). The lower shows the angular displacement of the image from its 'true' position. The horizontal co-ordinate expresses the angle between object and axis of symmetry of the fovea (focal length of eye assumed to be 17 mm.).

It is now necessary to consider the effect of the change of curvature in the centre of the fovea. It is assumed that the profile is here a parabola, $y = ax^2 + c$, say. Then, using the same notation as previously,

$$\sin i = \mu \sin r, \quad x = \frac{\tan i}{2a}, \quad X = x + y \tan(i - r),$$

$$M_t = \frac{X}{x} = 1 + \left(\frac{1}{2} \tan i + 2ac \cot i\right) \tan(i - r),$$

$$M_r = \frac{dX}{dx} = 1 + \tan i \tan(i - r) + \left(\frac{1}{2} \sin^2 i + 2ac \cos^2 i\right) [\sec^2(i - r)] \left[1 - \frac{\cos i}{\mu \cos r}\right].$$

From Fig. 3, $y = c = 70\mu$ when $x = 0$, and a can be found if the parabola is assumed to be tangent to the circle at the point where the curvature changes ($i = 75^\circ$, $x = 10\mu$). Evaluating M_t and M_r for $x < 10\mu$ we find the values shown in Fig. 4 to the left of the dashed line. They are uncertain to the extent that the exact form of the central depression is uncertain. But there is no uncertainty about the existence of an abrupt change of slope in the curve for M_t and of an abrupt change in the magnitude of M_r where the curvature changes sign.

The effect of the changes in these factors with distance from the centre of the fovea will perhaps be clearer from a consideration of Fig. 5 which shows the effect which foveal refraction would have on a rectilinear pattern (aberration and diffraction being neglected). Another way of regarding the effect is to imagine a point object moving across the visual field in such a way that its image traverses the centre of the fovea. If the angular velocity of the object is θ the angular velocity of the image is $M_r\theta$; and the image will lag behind the object till the centre is reached and thereafter lead it (see Fig. 6).

ABERRATION AND DIFFRACTION

So far attention has been limited to single rays and narrow pencils and it has been assumed that point images can exist. But, in fact, a convergent beam of fairly wide angle is required to form from a point source an image in which the central bright zone is not large compared with the area of a single cone. And this is evidently a necessary condition if full use is to be made of the high cone-density of the fovea in the resolution of detail in the visual field. The angle can be calculated directly from a knowledge of the cone-density or rather less directly from a comparison of the relative sizes of human and avian foveal cones and a knowledge of the pupil width below which diffraction limits the acuity of the human eye.

The cone-density at the centre of the fovea of a buzzard is stated by Rochon-Duvigneaud (quoted by Walls, 1942) to be $10^6/\text{mm}^2$ so that the area of a single cone is approximately $1\mu^2$. For two point images to be resolvable by Rayleigh's criterion the angular width of the convergent pencils forming them must be greater than ϕ , where

$$\tan \frac{1}{2}\phi = \frac{0.61 \lambda}{\mu r},$$

and λ = wave-length *in vacuo*, μ = refractive index of the medium, and r = distance between the centres of the images.

If we suppose the cones to be packed as a regular honeycomb, the distance between the centres of adjacent cones will be 1.07 , and the least distance between the centres of cones which do not touch will be 1.86μ . It is probable that for two images to be just recognizably separate, their distance apart will be between these values; hence r is put at 1.5μ . The wave-length of light of maximum photopic luminosity is 5.6×10^{-5} cm. and the mean refractive index of the ocular media is about 1.33 .

$$\text{Hence} \quad \tan \frac{1}{2}\phi = 0.17, \quad \phi \doteq 19^\circ.$$

Alternatively, accepting that diffraction limits the acuity of the human eye for pupil widths less than 2.3 mm. (Schlaer, Smith & Chase, 1941), taking the cone-density at the centre of the human fovea to be $200,000$ per mm^2 (one-fifth of the avian density, Walls 1942) and assuming a similar focal length for the avian and human eyes (which is probably true for the larger hawks)

$$\phi_{\text{avian}} = \sqrt{5} \phi_{\text{human}} \doteq \sqrt{5} \tan^{-1} \left[\frac{2.3 \text{ mm.}}{\text{posterior nodal distance (17 mm.)}} \right] \doteq 17^\circ.$$

The agreement is fair, but to be on the safe side the value $\phi = 15^\circ$ will be assumed.

Now it can be seen from inspection of Fig. 7 that a pencil of rays which, in the absence of the fovea, would converge to a point in the image plane at an angle of 15° , will include part of the zone of inflexion if its axis is less than 20μ from the axis of the fovea. And if any part of this zone is included aberration is severe. For simplicity, consider the special case of a 15° pencil coaxial with the fovea. The peripheral rays of this pencil encounter the retina at an angle of incidence approximately 81° and will consequently be refracted outwards about 2° . The effect of foveal refraction is, therefore, to replace the point image in the plane of the external limiting membrane by a circle of confusion embracing over thirty cones.

This degree of aberration could be reduced by a reduction of pupil width, but only at the cost of increasing the extent of the diffraction pattern. By no compromise could the bird utilize the high cone-density at the centre of the fovea to improve its acuity as compared with man.

On the other hand, outside the zone of severe aberration (radius 20μ about the axis) the magnification by the fovea is small and, as we have seen, in the tangential direction only; in the radial direction images

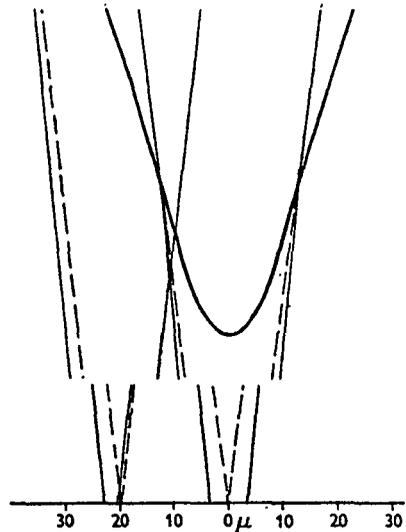


Fig. 7. The effect of refraction on two 15° pencils of rays centred 20μ from the axis and on the axis respectively. The heavy line represents the profile of the vitreo-retinal boundary. The light continuous lines represent the course of peripheral rays of the pencils and the dashed lines their course if there had been no refraction. The discontinuity indicates the omission of 40μ in the vertical direction.

are actually very slightly reduced. It is not evident that such a characteristic could aid in increasing acuity, though perhaps it does little to diminish it.

DISCUSSION

In accepting the idea that, so far from increasing acuity, foveal refraction has little effect at the periphery and very substantially diminishes the potential acuity in the centre we are forced to look for an alternative function which makes the sacrifice worth while.

The convexiclivate fovea is just such a device as one would choose to aid in the exact alignment of an optical system, for it has the remarkable property of transforming a radially symmetrical image into an asymmetrical one except when there is exact coincidence between the axes of symmetry of the fovea and of the object. (This is evident from Fig. 5.) This strongly suggests that the convexiclivate fovea is concerned with two cognate functions, the maintenance of accurate fixation and the sensitive appreciation of angular movements of a fixated object.

In assessing the correctness of this conclusion it is important to realize that the efficiency of such a device for detecting and correcting misalignment does not (like acuity) depend on the completest possible resolution of detail in the image. When a diatom is examined under a high power of the microscope the symmetry or lack of symmetry in the sculptured pattern is often *more* evident if the full aperture is not used or if the diatom is slightly out of focus. The condition for its best appreciation is not that in which the image most exactly represents the object, but that in which the effects of diffraction and aberration combine to give maximum contrast between one element of the image and another. If the object approaches the size of a single point, its image, viewed through an ordinary microscope, will be radially symmetrical for all combinations of lack of focus and small aperture. But with an ocular having the attributes of the convexiclivate fovea, there will only be radial symmetry for the images of points lying on its axis. Obviously the asymmetry in the image of a point not quite on the axis will be most readily perceived if the image is large enough for its form to be appreciated and does not itself approach a point, i.e. if it is aberrated or out of focus or the aperture is so small that the diffraction pattern is readily seen.

This argument has been emphasized for two reasons. In the first place, it makes clear that though in a large measure the optical structure conducing to high acuity is identical with that conducing to a high capacity for fixating objects in the visual field, yet there is a level of refinement at which acuity must gain at the expense of accuracy of fixation and of movement sensitivity or vice versa. In the second place, the argument casts doubt on the validity of acuity estimates based on the optomotor reaction; for it clearly does not follow, as has been frequently assumed, that because an animal has responded to a moving visual field its eye has resolved the field as a microscope under optimal conditions resolves the detail of *Pleurosigma*. All that can be legitimately inferred is that the visual field has somewhere in the photosensitive zone produced a gradient of light intensity which is above the differential threshold of the photosensitive elements. For example, an interferometer can be used to register changes in the distribution of light in a field with

extraordinary accuracy but it does not 'resolve' it, i.e. there is no simple point-to-point correspondence between the field and what is seen in the interferometer.

The convexiclivate fovea then is an appropriate device for emphasizing angular displacements; and the same properties make it suitable for increasing the animal's awareness of angular movements. Both phenomena depend on an important and almost wholly mysterious property of the vertebrate optical system, its extreme sensitivity to trifling irregularities in an otherwise regular pattern. This property lies at the root of a number of well-known optical illusions and also of the extraordinary Vernier acuity of the human eye. If two lines are parallel and placed end to end (like the lines of a Vernier scale) they can be seen to be misaligned when their angular separation is very much less than the angular separation of two just resolvable points.

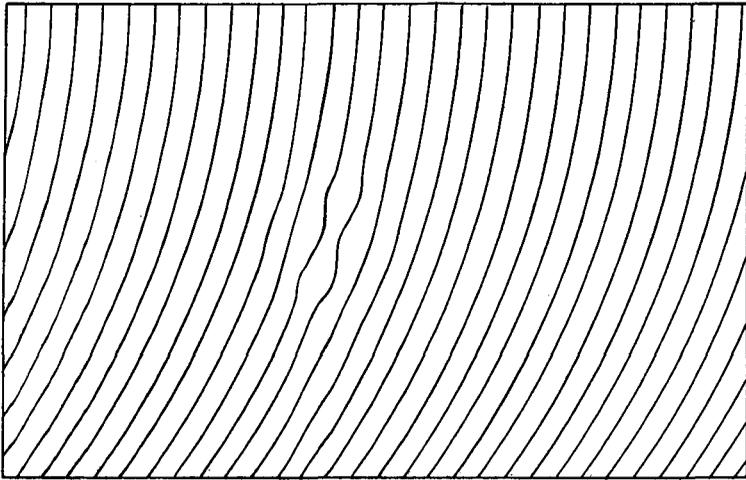


Fig. 8. Distortion by the fovea. The lines represent the successive images at equal time intervals of the boundary of a regular object when the object moves steadily across the visual field. If this picture is viewed at 7 m., the area of irregularity subtends an angle about equal to the angle subtended by the central part of the hawk fovea. It will be found that the irregularity is very evident to the human eye at this distance though the lines are resolvable with difficulty.

The eye, therefore, cannot be resolving the discontinuity at the junction of the lines; and what is seen as misalignment must be the lack of straightness in the single line which the two lines combine to form. Vernier acuity is in fact a particular example of sensitivity to regularity and irregularity of form and pattern. It has nothing to do with acuity in its ordinary sense, though, of course, acuity must be adequate to resolve the general structure of the pattern. If the lines, in the example quoted, could barely be distinguished from the background, obviously their misalignment could not be so well appreciated.

Vernier acuity has not been directly demonstrated in animals, but birds have been shown by ingenious methods to be subject to optical illusions similar to those of man and it is reasonable to assume that they have a basically similar visual sensitivity for patterns.

The effect of the convexitivate fovea of the hawks on the image of a regular object passing across it is to introduce momentarily the kind of irregularity which we might expect to be most conspicuous, namely a small and fluctuating irregularity in an otherwise regular image. The essential point here would seem to be the emphasis given to the distortion by its juxtaposition to almost undistorted parts of the image (Fig. 7) and for this the abrupt discontinuity in the refraction of the central and peripheral parts of the fovea is important. Outside the central zone of aberration, the distortion is very small, no image point being displaced from its 'true' position by more than $2\frac{1}{2}$ cone diameters. And the central zone contains only about 1000 out of the total of roughly 500,000 cones in the fovea. Over more than 95% of the area of the fovea, therefore, almost the full potential acuity can be realized.

It will have been noted that the conditions for optimal fixation of a limitingly small object and for optimal detection of angular movement of a larger one, though similar, are not quite identical. For the former it is only necessary that misalignment shall be associated with distortion of an aberrated image. There is not the same requirement for freedom from distortion in the immediately surrounding area.

It seems probable that fixation of objects and appreciation of angular movement were primitive functions of the optical system, and that the power of resolving detail, at first a useful accessory, grew in relative importance as central functions, such as recognition of and memory for visual patterns, emerged. Consequently, it is not surprising that the most primitive foveae (in fish) are of moderately convexitivate form. Ultimately, as we have seen, there must be rivalry between acuity and movement sensitivity, especially for limitingly small objects; and two directions of development are possible. The first is to specialize the centre of the fovea as an alignment device relying for acuity on the periphery of the fovea and the parafoveal area. The second is to sacrifice the higher development of the alignment function and devote the centre of the fovea to the optimal resolution of an undistorted image.

The reflexion of these developments on the geometry of the fovea is possibly indicated by such a scheme as in Fig. 9.

The scheme is not to be regarded as strictly geneological, but merely illustrative of possible lines of functional development. The central fovea of the hawks represents the highest development of the fovea as a fixation device which is consistent with the realization of nearly maximal acuity and movement sensitivity. The kingfisher has sacrificed acuity and movement sensitivity to fixation, for aberration at the centre is greater, the zone of aberration is more extensive and the transition to the zone of negligible distortion is less abrupt than in the hawks (see Fig. 10). Another possible development is illustrated by the fovea of the flamingo, shearwater, herring gull, curlew, snowgoose, cormorant, birds in which, according to Wood's (1917) figures, both area and fovea are more or less elongated along the horizontal equator of the eye. Such a design appears suited to fixation of the horizon and to effecting a preferential increase in sensitivity to vertical movements of objects in relation to the horizon (Pumphrey, 1948). All these birds frequent open spaces of land or water.

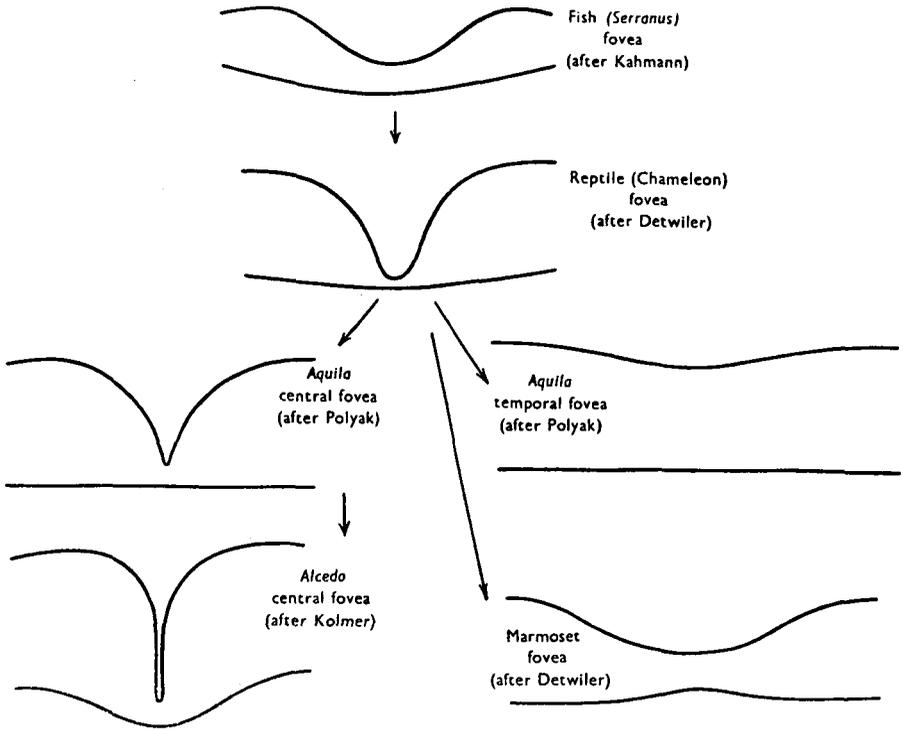


Fig. 9.

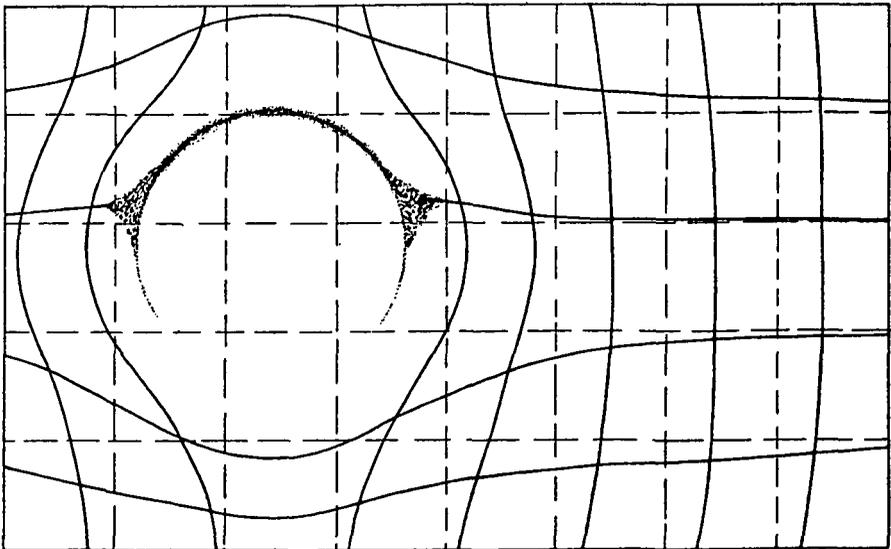


Fig. 10. Distortion of a rectangular pattern by the central fovea of the kingfisher for comparison with Fig. 5. As Kolmer gives no scale it has been assumed that the fovea is about one-half the size of the eagle's. The dashed squares have a side of about 5μ .

It seems very significant that the shallow 'anthropoid' type of fovea is found *only* where the eyes are used for binocular vision, and where central superposition or fusion of the left and right foveal images must be presumed to occur. It may well be that in these circumstances the optical errors inseparable from a steep foveal clivus cannot be tolerated. Distinct central (monocular) and temporal (binocular) foveae occur in the retinae in many distantly related birds (mostly predators) which are capable of occasional binocularity. It cannot yet be said with certainty that in these the temporal fovea is always more 'anthropoid' than the central, but it is evidently the case for the eagle, and Kolmer (1924) states that the temporal fovea of the kingfisher is more open than the central, though he does not figure it.

Birds, as a rule (even those with well-developed binocular vision), appear to scrutinize distant objects monocularly using the central fovea if they have one. We have seen reason to believe that no exceptionally high acuity is associated with the central fovea, but it is, nevertheless, alleged that birds have exceptionally 'acute' vision as compared with man. On the basis of cone-density alone it is possible that some birds have an acuity from two to three times that of man. To realize even this figure needs a large eye with a very wide aperture and consequently a corresponding degree of chromatic aberration in the dioptric system (quite apart from the foveal contribution). And no trick can wholly overcome this disability except at the sacrifice of colour vision which contributes to the resolving power actually attainable in the field.

But there is, in fact, no evidence of very high acuity in birds which cannot be interpreted either as an exceptional sensitivity to movement of an object scrutinized, or to an exceptional ability to 'hold on' to an object once seen. And these faculties, as we have seen, are just those which a convexiclivate fovea might be expected to aid substantially. Man, with his flat fovea, finds it extremely hard to continue to hold in sight an object which is approaching the limit of visibility, and, of course, once lost the chances of finding it again are small. It is likely that a device which would keep the object accurately centred would effect an astonishing increase in the range to which a bird or an aircraft could be visually followed by a human observer.

SUMMARY

The structure and distribution of the two principal types of fovea are briefly described. Using the convexiclivate central fovea of the eagle as a type the effect of refraction at the boundary of retina and vitreous humour on the foveal image is computed. It is shown that, when aberration and diffraction are taken into account, no improvement in acuity can result from refraction at the fovea. On the contrary, the results strongly suggest that the convexiclivate fovea is a device for achieving improved fixation and improved sensitivity to movement of objects in the visual field at some sacrifice of acuity.

The application of these results to other variants of fovea is discussed, and a scheme indicating possible relations between function and geometrical form is proposed.

REFERENCES

- DETWILER, S. R. (1943). *Vertebrate Photoreceptors*. New York.
- KAHMANN, H. (1934). Über das Vorkommen einer Fovea centralis im Knochenfischeauge. *Zool. Anz.* **106**, 49-55.
- KOLMER, W. (1924). Über das Auge des Eisvogels. *Pflüg. Arch. ges. Physiol.* **204**, 266-74.
- POLYAK, S. L. (1941). *The Retina*. Univ. of Chicago Press.
- PUMPHREY, R. J. (1948). The sense organs of birds. *Ibis*, **90**, 171-99.
- ROCHON-DUVIGNEAUD, A. (1919). Quelques données sur la fovea des oiseaux. *Ann. Oculist., Paris*, **157**, 673.
- SHLAER, S., SMITH, E. L. & CHASE, A. H. (1941). Visual acuity and illumination in different spectral regions. *J. Gen. Physiol.* **25**, 326-33.
- WALLS, G. L. (1937). Significance of the foveal depression. *Arch. Ophthal., N. Y.*, **18**, 912-19.
- WALLS, G. L. (1940). Postscript on image expansion by the foveal clivus. *Arch. Ophthal., N. Y.*, **23**, 831-2.
- WALLS, G. L. (1942). *The Vertebrate Eye*. Michigan: Cranbrook Inst. of Science.
- WOOD, C. A. (1917). *The Fundus oculi of Birds*. Chicago: Lakeside Press.