
Visual consequences of the foveal pit

David R. Williams

When viewing a uniform field through a small aperture moved circularly before the pupil of the eye, many observers report a diffuse dim spot subtending roughly 1° visual angle, which rolls around the fixation point in synchrony with the motion of the aperture. Measurements of the Stiles-Crawford maximum for different locations within the fovea confirm that small but systematic shifts in foveal directional sensitivity are responsible for this entoptic effect. A quantitative model is developed which accounts for the directional sensitivity shifts on the basis of refraction of light at the sloping sides of the foveal pit. Supporting evidence for the model is provided by a second entoptic phenomenon: fundal scatter from the image of a glare source on the eccentric retina is reflected by the foveal pit in such a way as to render it visible. Estimates of the slope of the foveal pit from this effect agree well with that predicted from the observed shifts in directional sensitivity.

Key words: Stiles-Crawford effect, fovea, entoptic effects, directional sensitivity, receptor orientation, fundal scatter

Since the first report of Stiles and Crawford,¹ a large body of histological and psychophysical evidence has accumulated to show that cones in different retinal regions are directionally sensitive, having peak sensitivities clustered about a common point in the exit pupil of the eye.^{2, 3} In addition to this general directional tendency, psychophysical evidence shows that small local variations in the directional sensitivity of the normal retina do exist. O'Brien and Miller⁴ (see also Enoch⁵) demonstrated these local variations by rapidly changing the entry point of light in the pupil while continuously adjusting its intensity to compensate for the Stiles-Crawford effect. Observers reported light and dark patches in the visual field which did not change with the entry point of light in the pupil. O'Brien and Miller interpreted these

patches to be a result of small differences in photoreceptor orientation in different retinal locations.

The subject of this investigation is an entoptic effect which implies a systematic variation in the directional sensitivity of cones within the fovea. If a small aperture is moved in a circular fashion close to the eye while the observer views a dim uniform surface, the retinal vasculature can be seen as a fine branching pattern surrounding the foveal avascular area. Within this avascular area, many observers report a gray patch roughly 1° in diameter which moves within the central 2° of the fovea, depending on the entry point of light in the pupil. Circular motion of the aperture causes this dim spot to revolve around the line of sight in phase with the aperture, appearing on the same side of fixation as the light is entering in the pupil. There is often a less conspicuous brightening which revolves in diametrical opposition to the dark spot. Like the entoptic retinal blood vessels, this phenomenon disappears quickly when the aperture motion is stopped.

The appearance of the dim patch on the

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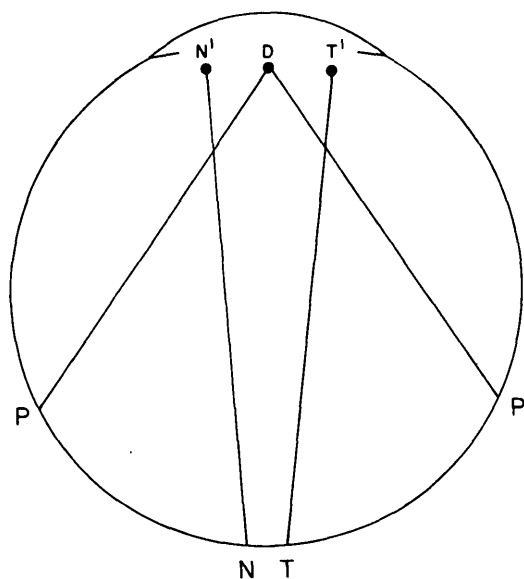


Fig. 1. Hypothesized directional sensitivity of cones on opposite sides of fixation which would account for the entoptic dim patch seen in the fovea when the pupillary entry point is changed.

same side of fixation as the light is entering in the pupil suggests that cones at slightly eccentric positions within the fovea are less sensitive to light entering from the opposite side of the pupil than they are to light entering from the same side. In Fig. 1 the lines within the eye connect cones in various retinal locations with the respective points in the pupil at which they are most sensitive. Extrafoveal cones (labeled *P*) obey the anterior pointing hypothesis⁶; they are maximally sensitive to rays passing through the center of the exit pupil, *D*. However, suppose that for some reason cones in the nasal fovea (*N*) are maximally sensitive to light entering in the nasal pupil (*N'*) whereas temporal cones (*T*) prefer light from the temporal pupil (*T'*) (and similarly for cones in the superior and inferior retina). Then a light entering, say, in the temporal pupil will be relatively ineffective in stimulating nasal cones; the diminished signal from these cones could be responsible for the entoptic gray patch.

Although it seems reasonably clear that the entoptic effect implies local variations in directional sensitivity within the fovea, the actual cause of these variations is less certain.

Koppenberg* has described the entoptic effect, attributing it to the hillock formed by the elongated cones in the central fovea.⁸ He assumes that rays entering through one side of the pupil are less effective in stimulating cones on the far side of the hillock than those on the near side. Unfortunately, there is no obvious physical justification for this assumption. Heath and Walraven⁹ briefly report a similar effect, i.e., uniform fields briefly imaged within the fovea have a gradient of brightness across the field, dependent on the peripheral entry point of light in the pupil. On the basis of Stiles-Crawford measurements for 1° fields within the fovea, Heath and Walraven⁹ conclude that foveal cones are oriented nearly parallel to each other rather than pointing toward a common location in the pupil.

This paper argues that small local variations in directional sensitivity may not always reflect differences in *photoreceptor orientation*; a quantitative model is developed which shows that the entoptic effect can be explained by *refraction* at the sloping sides of the foveal pit rather than by some perturbation in the orientation of the cones themselves.

Local variation in directional sensitivity within the fovea

In order to find out about small variations in the Stiles-Crawford effect across the fovea, a technique was developed which provided an accurate measure of directional sensitivity in the pupil for small retinal locations.

Apparatus. The Maxwellian view system shown in Fig. 2 consisted of a test channel, a fixation

*The phenomenon exhibits significant individual differences, but Koppenberg⁷ reported that with his apparatus nearly everyone he examined could eventually see the effect. Relatively crude observations were made in this laboratory by having observers view a dim white surface through a 2 mm aperture jiggled by hand in front of the pupil. The effect was visible in only about 40% of the 62 eyes tested. The remaining observations consisted of a bewildering variety of foveal percepts including flickering but motionless gray patches of various shapes and sizes. Two observers even reported a light spot instead of a dark spot which moved in phase with the aperture.

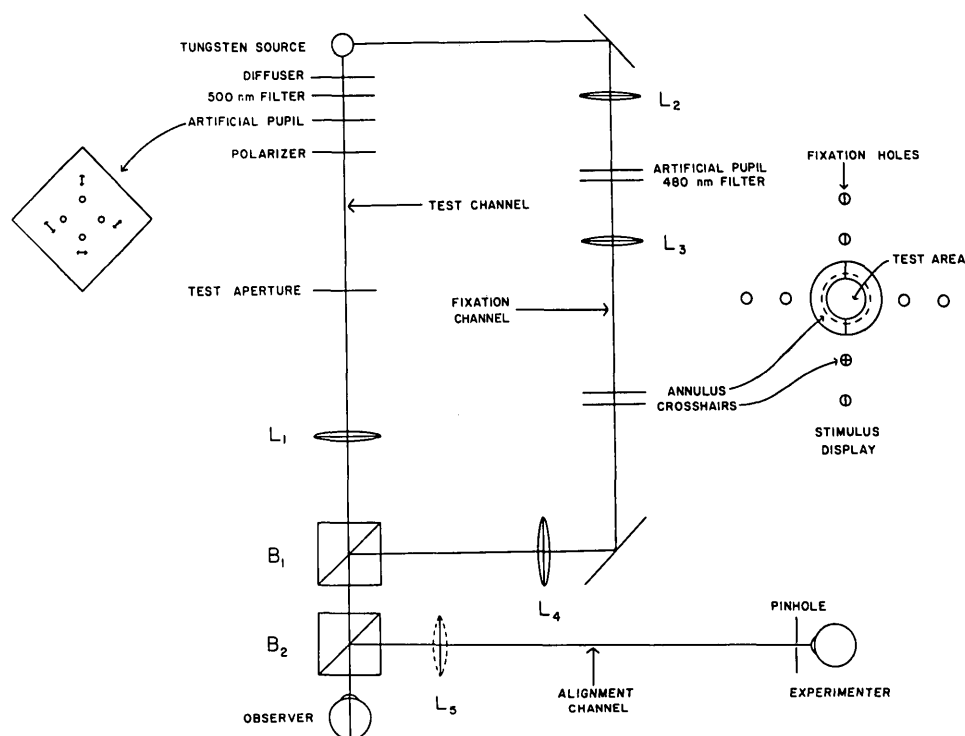


Fig. 2. Apparatus used to measure foveal directional sensitivity.

channel, and an alignment channel. The test and fixation channels were combined by beamsplitter B_1 , which was in turn combined with the alignment channel by beamsplitter B_2 . The source was a tungsten lamp (GE 200 watt, 120 V Quartzline lamp). A piece of frosted glass between the lamp and the artificial pupil in the test channel provided uniform illumination of the aperture defining the artificial pupil. This aperture was imaged at slightly less than unit magnification by lens L_1 in the plane of the observer's pupil. A test aperture at roughly one focal length from L_1 formed a small circular test field on the observer's retina. The retinal illuminance of the 500 nm test field was 460 trolands.

The artificial pupil in the test channel consisted of a metal plate in which four small holes were drilled, forming a diamond-shaped array as shown in Fig. 2. Thus light entered the eye through four spots in the plane of the pupil, each spot measuring 0.75 mm in diameter, with spots opposite each other spaced 4 mm apart from outer edge to outer edge. Each of the holes in the aperture had a small piece of linear polarizer over it whose transmission axis was oriented as shown by the arrows in Fig. 2. A circular polarizer with its linearly polarizing face toward the artificial pupil aperture rotated in the

test channel at 4 to 5 Hz, sinusoidally modulating light from each hole in the artificial pupil aperture at 8 to 10 Hz.

This arrangement had the effect of changing the entry point of light in the observer's pupil in a circular fashion at 8 to 10 Hz while keeping the total flux entering the eye constant over time. This was verified by placing a photodiode in the image plane and noting that the output did not change by more than 2.8% with the orientation of the circular polarizer. The photodiode output was also independent of the position of the test aperture (which was moved to different locations in a plane orthogonal to the optical axis during the experiment), establishing that the test aperture did not selectively vignette any of the four spots in the image plane at the pupil.

The position of the artificial pupil aperture and hence of the image in the pupil could be controlled by the observer with horizontal and vertical micrometer adjustments. His task was to find a position of the array in the pupil for which flicker in the test field was minimized. If the four spots were either vertically or horizontally off-center with respect to the Stiles-Crawford maximum for the retinal location under test, then the cones would be more sensitive to light from one of the

spots than from the others, resulting in flicker. However, when the image in the pupil was centered around the Stiles-Crawford maximum, the cones in the test area were equally sensitive to light from each of the four entry points in the pupil, and flicker was minimized.* By finding the minimum flicker setting for different retinal locations, one should be able to determine how directional sensitivity varies across the fovea.

The eye was maintained in a fixed position relative to the apparatus by holding the observer's head steady with a sturdy bite bar and having him fixate a set of crosshairs in the fixation channel which were never moved throughout the experiment. The fixation channel also imaged a bright annulus (486 nm, 1470 trolands), shown in Fig. 1, onto the observer's retina which surrounded and slightly overlapped the test field. Since the test field was formed from light which passed through four different parts of the pupil, optical imperfections in the observer's eye often caused distortion at the edge of the field. The annulus masked the contour of the test field, preventing motion there from influencing the minimum flicker judgment, a technique adapted from Bonds and MacLeod.¹¹ The inner diameter of the annulus, which fixed the effective area of the test field, was 30 min arc, whereas the outer diameter was 54 min arc.

Alignment. The observer's pupil was dilated with 2 drops of 0.5% tropicamide (Mydracyl) about 30 min before each experimental session. The crosshairs and the aperture defining the annulus lay in a collimated beam between L_3 and L_4 and could be shifted along the optical axis to provide optimum focus without changing the visual angle subtended by the display. The test aperture in the test channel was also slid fore and aft to provide the best possible image of the test field.

The corneal reflex was used as a landmark to ensure that the position of the eye relative to the apparatus did not change during the experiment. The pinhole in the alignment channel (less lens L_5) was aligned by the observer to coincide visually with the fixation crosshairs. This arrangement allowed the experimenter to peer through the pinhole, looking precisely down the visual axis of the observer as he fixated the crosshairs. By ap-

propriate adjustment of the array imaged in the observer's pupil, the experimenter could find four well-defined positions where a corneal reflex could be seen through the pinhole. The four positions, one for each spot imaged in the pupil, corresponded to a single location where the visual axis is normal to the surface of the cornea. This location could be checked at the beginning and end of the session to verify that the relative positions of the eye and apparatus had not changed.

By placing lens L_5 in the alignment channel at one focal length from the observer's pupil, the experimenter could obtain a magnified view of the pupil. This was of limited usefulness in monitoring the position of the image in the pupil because of inadequate light. However, it was possible to determine in one observer (M. M. H.) by direct observation that the dilated iris never occluded any of the diamond-shaped array during the experiment. Subjective observations of the position of the array in the pupil which occluded each of the four images separately confirmed that iris occlusion was not a difficulty. The minimum flicker settings never fell beyond a small region about 1.2 mm in diameter near the corneal reflex. The array was only 4 mm across, falling within fully dilated (about 8 mm) pupils.

Four observers were tested; D. I. A. M., A. N., and M. M. H. had normal uncorrected acuity, whereas D. R. W. was 1.0 diopter myopic (which was corrected in the experiment). The fundi of D. I. A. M., M. M. H., and D. R. W. were carefully examined ophthalmoscopically and appeared normal, showing healthy foveal reflexes.

Procedure. For all observers except A. N., a total of 16 retinal locations within the fovea were tested: four locations at each of four retinal eccentricities (15, 27, 45, and 75 min arc). The four locations at each eccentricity were symmetrically arranged around the line of sight, lying in the horizontal and vertical retinal meridians. For A. N. only three retinal eccentricities were tested: 15, 45, and 75 min arc.

The test location could be changed by moving the aperture defining the annulus with respect to the immobile crosshairs and then moving the aperture defining the test field accordingly, so that the annulus once again masked the edges of the test field. For the 15 and 27 min eccentricities, the crosshairs fell at the inner and outer edges of the annulus, respectively. For the 45 and 75 min eccentricities, "satellite" holes about 10 min arc in diameter were drilled in the plate defining the annulus (see Fig. 2). Each of these holes could be

*The technique as described above, similar to one described by Enoch,¹⁰ rests on the assumption that the Stiles-Crawford function is radially symmetrical over a central range of 4 mm, the width of the array in the pupil. However, the technique provides a valuable index of directional tendency, though not the Stiles-Crawford peak, even if the symmetry assumption is not met.

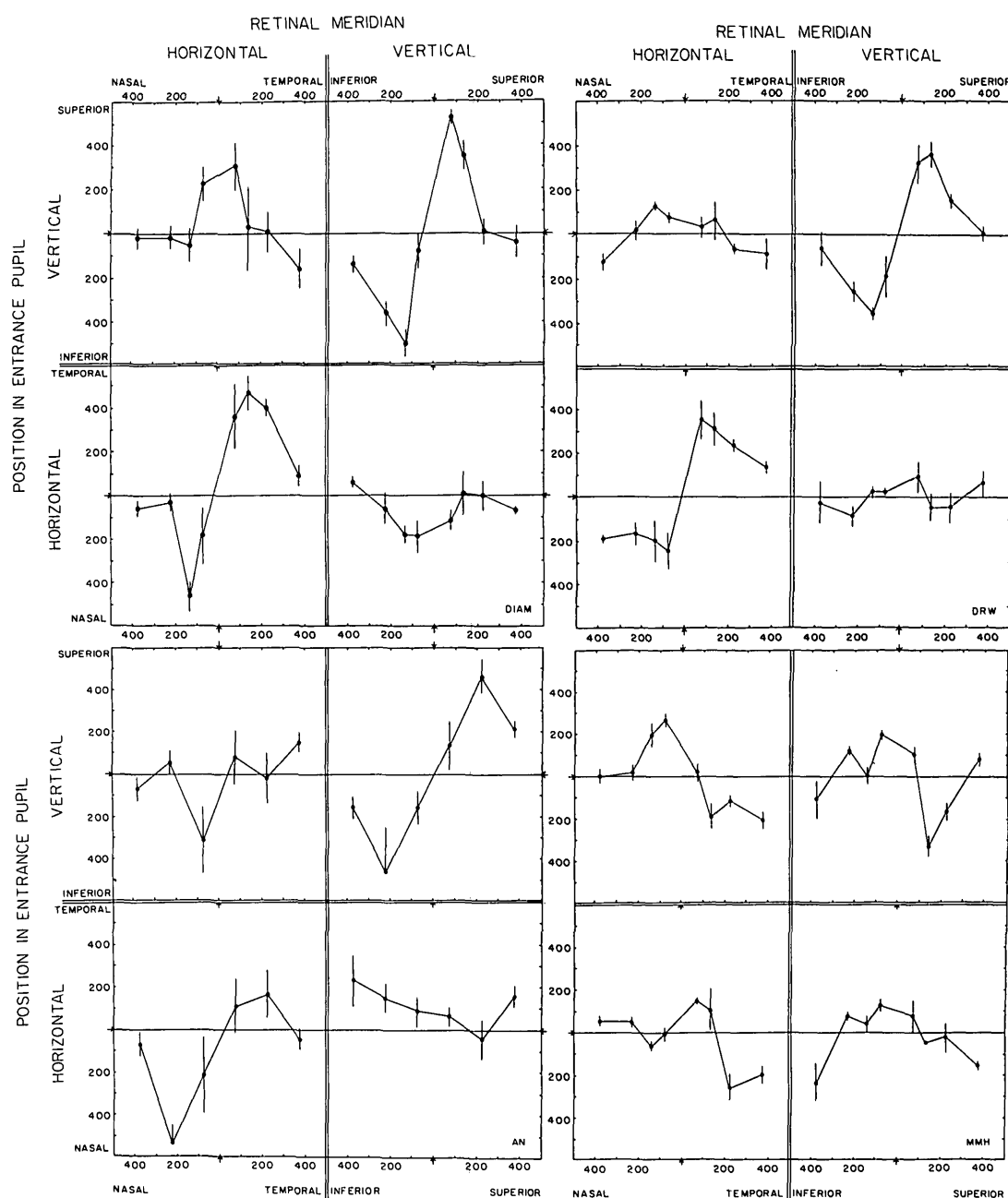


Fig. 3. Individual data for each of the four observers showing the horizontal and vertical position of the Stiles-Crawford maximum in the entrance pupil as a function of retinal location in the fovea.

centered around the crosshairs, providing the appropriate location for the test field.

Locations in the horizontal retinal meridian were tested first, proceeding from the smallest eccentricity to the largest with succeeding locations alternating from one side of fixation to the other.

The same procedure was then repeated for the vertical retinal meridian. Three or more settings were made at each location by adjusting the horizontal and vertical position of the image in the pupil until flicker was minimized. At the end of the session, several locations were briefly re-

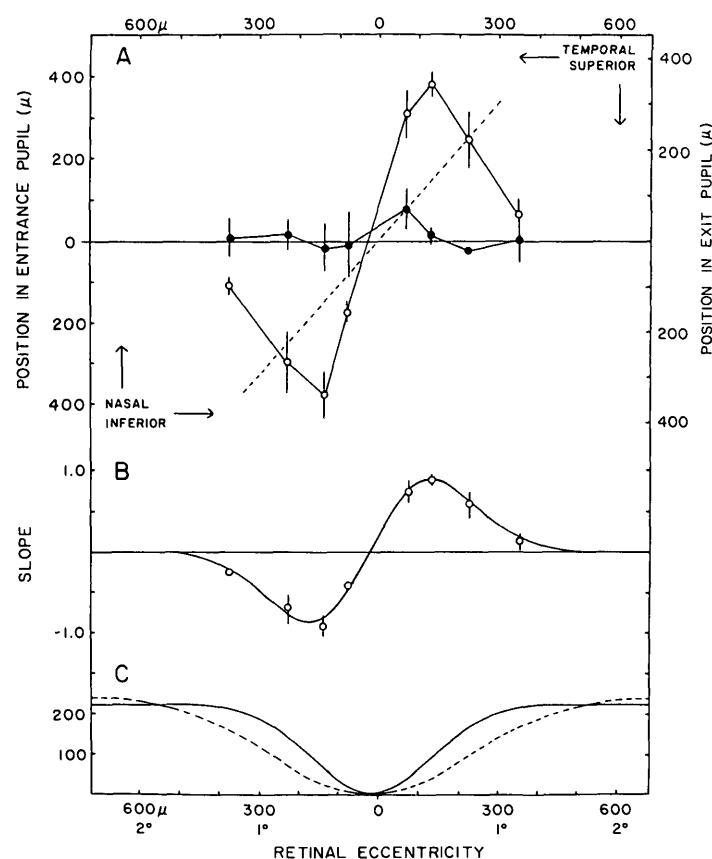


Fig. 4. A, Foveal Stiles-Crawford maxima averaged across Observers D. I. A. M., D. R. W., and A. N. and across horizontal and vertical retinal meridians. The ordinate on the left plots the maxima in the entrance pupil, and the ordinate on the right plots them in the exit pupil, where the exit pupil is 0.9094 times the size of the entrance pupil.⁶ B, Slope of the foveal pit required to account for the observed shifts in foveal directional sensitivity (unfilled symbols from A). C, Solid curve is the shape of the foveal pit required to account for the directional sensitivity shifts compared with Polyak's pit⁸ (dotted curve).

peated as a check to supplement the corneal reflex measure that the eye had not moved relative to the apparatus. D. I. A. M. and D. R. W. were tested in three separate sessions; M. M. H. and A. N. had single sessions only.

Results and discussion. All four observers found it possible to make minimum flicker settings which were consistent for a given retinal location. Observers occasionally reported that no residual flicker remained at the minimum flicker setting, but more often a faint impression of flicker persisted. Accuracy was remarkably good: the average S.E.M. based on variability within sessions ranged from 40 μ m (M. M. H.) to 90 μ m (A. N.).

Fig. 3 shows the individual results for each of the four observers plotted in four panel graphs. The left two panels show data from the horizontal retinal meridian with eccentricity plotted in micrometers along the abscissae, whereas the right two panels show data from the vertical retinal meridian. The upper panels for each observer plot the vertical position of the Stiles-Crawford maximum in the entrance pupil along the ordinate in micrometers. The lower panels plot the horizontal position of the Stiles-Crawford maximum in the entrance pupil. The origin for the coordinate system in the entrance pupil was the mean of all minimum flicker settings for all retinal locations tested for that observer.

This location was chosen because it facilitated comparison of data from different observers; the corneal reflex was not used because its displacement from the mean Stiles-Crawford maximum varied from observer to observer.* If foveal cones had Stiles-Crawford maxima at a common location in the pupil, then the data for all retinal eccentricities should hover closely around the mean pupil position in each panel.

Error bars for D. I. A. M. and D. R. W. represent ± 1 S.E.M. based on variability *between* the three sessions. Those for A. N. and M. M. H. represent ± 1 S.E.M. based on variability *within* the single session in which they were run.

Observers D. I. A. M., D. R. W., and A. N. saw the entoptic effect quite clearly; M. M. H. on the other hand did not see the typical effect. The results for the three observers who did see the entoptic effect showed a similarity: the functions representing the horizontal position of the Stiles-Crawford maximum in the pupil for locations in the horizontal retinal meridian (lower left panel for each observer) and the functions for vertical position in the pupil for the vertical retinal meridian (upper right panels) were all diphasic in shape. In these panels, the largest retinal eccentricity tested, $375\ \mu\text{m}$ or $75\ \text{min}$, typically showed a relatively small deviation in the Stiles-Crawford maximum away from the mean, consistent with the anterior-pointing hypothesis.⁶ Smaller eccentricities, however, tend to show larger deviations from the mean which are in opposite directions on opposite sides of fixation. Specifically, cones in the nasal fovea had Stiles-Crawford maxima displaced nasally in the pupil, cones in the superior fovea had maxima displaced superiorly in the pupil, etc. This pattern was

*With respect to the corneal reflex, the mean Stiles-Crawford maximum was located 1.4 mm superior, 1.3 temporal; 1.0 superior, 0.8 nasal; 0.65 superior, 1.5 nasal; 0.5 superior, 0.95 nasal for Observers D. I. A. M., D. R. W., A. N., and M. M. H. respectively. The mean Stiles-Crawford maximum was 1.3 mm nasal, 0.4 superior; 0.4 temporal, 1.4 superior to the geometric center of the pupil for Observers M. M. H. and D. I. A. M. respectively.

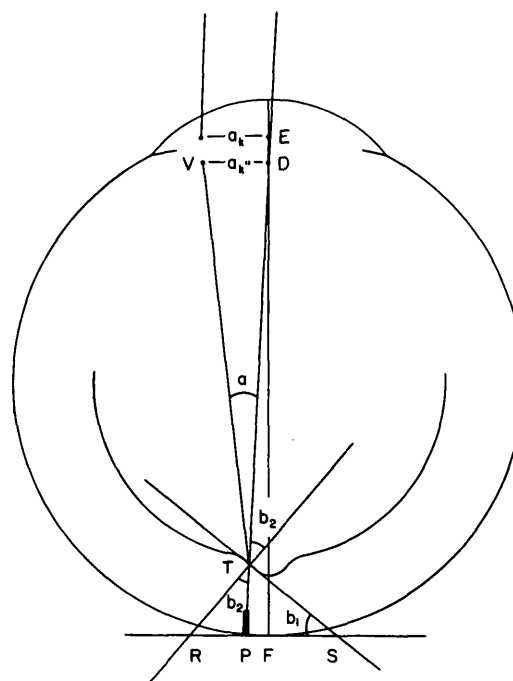


Fig. 5. Schematic eye, demonstrating how refraction of light rays at the foveal pit could alter directional sensitivity of the underlying cones. The eye is also used in Appendix 1 to estimate the slope of the foveal pit required to account for the directional sensitivity shifts measured with the minimum flicker technique.

consistently obtained in both retinal meridians of all three observers who see the entoptic effect.

The upper left and lower right panels show no consistent trends, with the data clustering more or less randomly around the mean. This means that for these observers foveal cones in the horizontal meridian did not have Stiles-Crawford maxima systematically displaced vertically in the pupil nor did cones in the vertical meridian have maxima systematically displaced horizontally in the pupil.

The data from the minimum flicker technique confirmed the description of directional sensitivity deduced from the entoptic effect: for cones at a given eccentricity within the central 2° of the fovea, the locus of Stiles-Crawford maxima in the pupil is a ring rather than a single point. The data from M. M. H., who did not see the entoptic effect,

provided additional confirmation of the correspondance between the entoptic effect and the Stiles-Crawford measurements. After repeated attempts to view the entoptic effect, this practiced observer reported instead a mottled appearance of the avascular region with no consistent distinguishing features. The Stiles-Crawford data for M. M. H. showed significant differences in directional sensitivity for different foveal locations, but they were unsystematic.

Fig. 4, A, shows the data for the three observers who reported the entoptic effect averaged across observers and retinal meridians. The filled symbols represent the average of the upper left and lower right panels of Fig. 3 for all three observers. As expected, the points lay very close to the mean pupil position at each eccentricity. The unfilled symbols show the mean diphasic function (lower left and upper right panels) for the three observers. Error bars represent the S.E.M. based on variability between the three observers and the two retinal meridians ($n = 6$).

The average diphasic function peaked at 27 min arc ($135 \mu\text{m}$) where the Stiles-Crawford maxima deviated from the mean by 0.38 mm. Assume for the moment that this effect is caused entirely by differences in cone orientation within the fovea, neglecting the retinal refraction effects to be discussed later. By the rule of thumb that a deviation of 1 mm in the entrance pupil corresponds to a change in angle of 2.5° at the retina,³ foveal cones at an eccentricity of about 0.5° deviate from pointing toward a common location in the pupil by about 1° . The dotted line in Fig. 4, A shows the prediction if cones in the central fovea were oriented parallel to one another; that is, if cones at a given distance and direction from fixation on the retina had Stiles-Crawford maxima at the same distance and direction from the average Stiles-Crawford maximum in the exit pupil. For the observers tested here, the Stiles-Crawford maxima for the 15 and 27 min retinal eccentricities (75 and $135 \mu\text{m}$, respectively) deviated farther from the mean Stiles-Crawford maximum than pre-

dicted by the parallelism hypothesis proposed by Heath and Walraven⁹ for foveal cones. If photoreceptor orientation is the basis for the variation in directional sensitivity within the fovea, then the central foveal cones are actually slightly splayed apart, rather than parallel or pointing toward a common location in the pupil.

An alternative to the receptor orientation explanation is that foveal cones do point toward a common location in the pupil and are not physically disrupted in orientation but that their directional sensitivity is shifted in the pupil by refraction at the foveal pit. Fig. 5 illustrates this alternative. The cone at P is trained toward the center of the exit pupil at D as predicted by the anterior pointing hypothesis. Let T represent the intersection of the cone's long axis PD , with the sloping side of the foveal pit where ST represents the tangent and RT the normal to the vitreous-retinal interface at T . Now if the index of refraction of the retina is higher than that of the vitreous, then rays striking the foveal pit at T will be refracted toward the normal. The light ray which maximally stimulates the cone at P will not be that which passes through the center of the entrance (E) and exit (D) pupils; because of refraction at T , the ray which maximally stimulates the cone must originate from an eccentric point in the exit pupil at V . Thus refraction at the internal limiting membrane might shift the Stiles-Crawford maximum away from the center of the pupil for cones beneath the sloping sides of the foveal pit, just as if these cones were physically splayed apart.*

According to Snell's law, the amount of refraction that occurs at an interface depends on the ratio of the refractive indices of the two media and the obliquity of incidence of light. Thus the expected shift in the Stiles-Crawford maximum depends on the refrac-

*The main effect of refraction at the foveal pit would be a shift in the Stiles-Crawford maximum in the pupil, though in theory refraction also slightly skews and broadens the shape of the Stiles-Crawford function. Calculations show that these effects are negligibly small.

tive indices of the retina and vitreous and the slope of the foveal pit. The higher the refractive index of the retina relative to the vitreous or the steeper the slope of the foveal pit, the larger the outward shift of the Stiles-Crawford maximum in the pupil. Under the assumption that the directional sensitivity shifts measured here are due entirely to refraction at the foveal pit, and with reasonable estimates of the refractive indices of the retina and vitreous, it is possible to estimate the slope of the foveal pit at each retinal eccentricity tested. The details of this analysis are given in Appendix 1.

The viability of a refraction model to account for the observed shifts in foveal directional sensitivity hinges on the assumption that the retina has a higher refractive index than the vitreous. The refractive index of the vitreous is usually taken as 1.336.¹² The old German literature on the subject, reviewed by Guggenheim and Franceschetti,¹³ suggests values close (± 0.002) to this. More recently, Pauflique et al.¹⁴ report an average value of 1.3358. The refractive index of the inhomogeneous retina is less certain. Nordenson¹⁵ measured the refractive index of the human retina, assigning it a value of 1.363. Ajo¹⁶ assigned values of 1.361, 1.357, and 1.361 to the retinas of cows, pigs, and horses, respectively. This agrees well with the refractive index of the rod myoid (1.36) which is considered to be the equivalent of ordinary cell cytoplasm.¹⁷ Valentin¹⁸ reported substantially lower refractive indices for the retina, but his measurements are suspect according to Millodot.¹⁹ The weight of the available evidence thus suggests that the retinal refractive index, n_r , is indeed higher (by about 2%) than that of the vitreous, n_v . The values adopted for this analysis are $n_r = 1.36$ and $n_v = 1.336$.

The results of the analysis are shown in Fig. 4, B. The slope of the foveal pit required to account for the observed shifts in the Stiles-Crawford maximum (from Fig. 4, A) is plotted as a function of retinal eccentricity. The curve fitted by eye to the data is the first derivative of a gaussian. This theoretical

function is convenient since its integral describes a gaussian approximation to the shape of the average foveal pit of these observers. The first derivative has the form:

$$\frac{dy}{dx} = h(x/\sigma^2) e^{-x^2/2\sigma^2} \quad (1)$$

whose integral is

$$y = h(1 - e^{-x^2/2\sigma^2}) \quad (2)$$

where x specifies the retinal location, y the distance above the floor of the pit, h the total depth of the pit, and σ the standard deviation. The values of the parameters which provide the excellent fit of equation 1 to the slope predicted from the Stiles-Crawford data are $d = 220 \mu\text{m}$ and $\sigma = 150 \mu\text{m}$. (The function has also been shifted $20 \mu\text{m}$ to the left to improve the fit.) The slope of the predicted foveal pit is largest at 0.5° ($150 \mu\text{m}$) where it is nearly 1.0 (43°). The slope passes through zero near the center of fixation and approaches zero again at relatively large eccentricities.

The solid curve in Fig. 4, C shows the shape of the foveal pit given by equation 2 with the appropriate parameter values. Unfortunately, quantitative information about the true shape of the foveal pit in the living eye for comparison with the shape predicted here is lacking. The dashed curve in Fig. 4, C is Polyak's estimate of the shape of the foveal pit from an excised retina⁸; the amount of distortion in this shape caused by excision, sectioning, and fixation is not known. Polyak's curve reaches a maximum slope of about 30° at an eccentricity of $250 \mu\text{m}$, i.e., shallower and larger than the pit predicted from the Stiles-Crawford data. The depths of the pits agree well: 240 and $220 \mu\text{m}$ for Polyak's and the predicted pit, respectively.

Estimation of the foveal pit slope: the entoptic fovea visualized with fundal scatter

An independent measure of the slope of the foveal pit in vivo would be valuable in its own right and could help in evaluating the refraction model proposed to explain the sys-

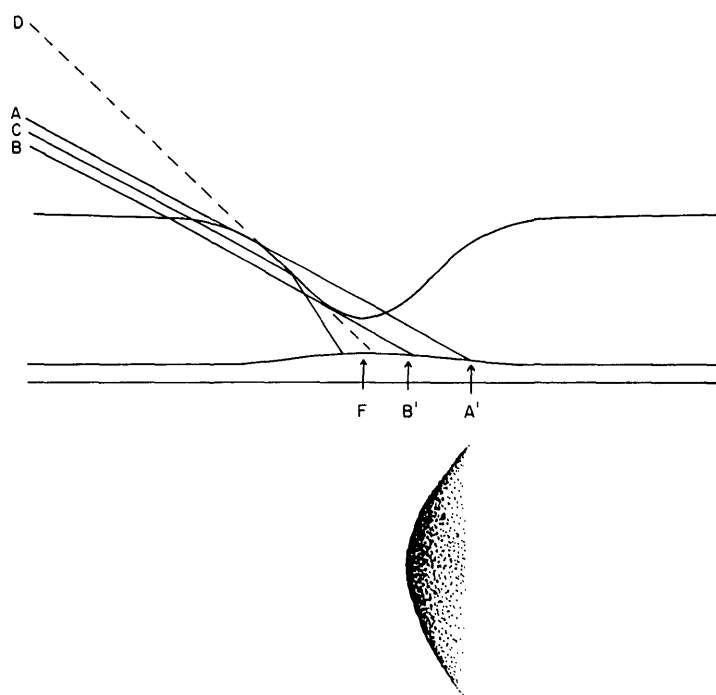


Fig. 6. Diagram showing how total internal reflection could account for the entoptic foveal pit seen with fundal scatter. The dotted line labeled *D* represents the angle of incidence of scattered light at which the entoptic effect will extinguish. Below the diagram is a rendering of the appearance of the entoptic effect for retinal eccentricities of the glare source around 30° .

tematic variations in foveal directional sensitivity. Burow²⁰ and later Müller²¹ described a foveal entoptic effect distinct from the phenomenon described above, which can be adapted to provide an estimate of the slope of the foveal pit. If an intense orange point source in an otherwise dark room is imaged on the eccentric retina, scatter from the fundus illuminates a large portion of the retina, casting impressive shadows of the retinal blood vessels.* These shadows are particularly striking if the position of the glare source is rapidly changed. For a range of eccentricities of the glare source, it is also possible to see a distinct crescent-shaped dark region within the foveal avascular area opposite the fixation point from the eccentric glare source.

*Some of the light illuminating the retina originates from scatter in the anterior media, reducing the contrast of the entoptic effects visualized from fundal scatter. The use of long wavelength light, which is more strongly reflected by the fundus,²² improves their visibility.

Müller²¹ proposed that the darkening was a shadow created by absorption of light at the edge of the foveal pit, but this is unlikely since the retina is highly transparent, particularly in the long wavelengths used to view the phenomenon. Fig. 6 shows a more reasonable, new interpretation. The orange glare source is imaged on the fundus off the diagram to the left, scattering rays *A*, *B*, and *C* toward the foveal pit. Ray *A* just misses the left rim of the foveal pit, striking its right slope where it is slightly refracted, and is finally absorbed in photoreceptors at *A'*. Ray *B* intersects the retina to the left of the foveal pit, is refracted downward slightly, grazes the bottom edge of the foveal pit, and is finally absorbed by photoreceptors at *B'*. Now rays between *A* and *B*, represented by ray *C*, pass into the retina and then meet the internal limiting membrane once again, striking the left side of the foveal pit from inside the retina. If the internal membrane has a high refractive index relative to the vitreous

and providing these rays strike the membrane obliquely enough, total internal reflection will occur, preventing the rays from stimulating receptors between B' and A' . Instead, they will be reflected downward toward points to the left of B' , leaving a dark region between the intersections of the limiting rays, A and B , with the photoreceptive layer.

Several qualitative experimental observations are consistent with this interpretation. First, the distance of the darkening from the fixation point decreases with increasing eccentricities of the glare source; at eccentricities of 40° or more the darkening overlaps the fixation point whereas at an eccentricity of 10° the near edge of the shadow at B' is perhaps 1.5° from fixation. Furthermore, the near edge of the darkening shows slightly less parallax than the nearby retinal blood vessels, indicating that it is defined by a structure closer to the receptors than the blood vessels. The far edge of the darkening at A' , on the other hand, shows more parallax than the blood vessels, suggesting that it is limited by a structure further than the blood vessels from the receptors. This is what would be expected if the rim and floor of the foveal pit were responsible for defining the far and near edges of the entoptic foveal darkening, respectively. In addition, it is sometimes possible to see a brightening along the near edge of the darkening which may be caused by the totally internally reflected light rays striking the photoreceptive layer to the left of the darkening.

A ray tracing analysis of light impinging on the foveal pit shape estimated from the Stiles-Crawford data predicts that total internal reflection will occur over the entire surface struck from inside the retina for glare source eccentricities greater than about 30° , so that the region between A' and B' is completely protected from fundal scatter. For smaller eccentricities rays striking the steepest slope of the pit penetrate back into the vitreous, eventually striking photoreceptors between B' and A' , though total internal reflection still occurs at the shallower slopes of the pit. This analysis is based on the con-

servative assumption that the critical angle for total internal reflection depends on the refractive indices of the retina and vitreous assumed for the refraction model of directional sensitivity proposed here. If the refractive index of the inner limiting membrane is higher than that of the retina, then the critical angle could be reduced, allowing total internal reflection to occur over the entire surface of the foveal pit for small eccentricities.

If the retinal eccentricity of the glare source is gradually increased, the crescent-shaped dark region becomes thinner and thinner as the limiting rays A and B move closer and closer together. Finally, at some critical eccentricity, rays scattered from the image of the glare source will impinge on the foveal pit parallel to its steepest slope (shown as a dotted line, D , in Fig. 6), and the darkening will entirely disappear. By measuring this critical eccentricity, it is possible to estimate the angle of incidence of the scattered rays at the foveal pit which are parallel to its steepest slope and hence to estimate that slope. If the refraction model proposed above to account for the observed shifts in foveal directional sensitivity is correct, then this independent estimate of the steepest slope of the foveal pit should agree with the steepest slope predicted from the Stiles-Crawford data.

Method. The observer's eye was positioned a few centimeters from a small first-surface mirror which could be rotated by the observer about a vertical axis. The observer fixated a small red light 8 m directly in front of him in an otherwise dark room. The glare source was a slide projector (750 watt, 120 V tungsten lamp) 2.5 m from the observer whose optical axis was orthogonal to the observer's line of sight as he gazed at the fixation light. The source was attenuated by heat-absorbing glass and a Wratten 23A orange filter and subtended a visual angle of 54 min arc. A linear polarizer whose transmission axis was oriented vertically was placed between the glare source and the mirror since it increased the contrast of the entoptic phenomenon. Light from the glare source was reflected into the observer's eye by the mirror, small rotations of which changed the source's retinal eccentricity. A protractor mounted around the vertical axis of the mirror provided a measure

of the mirror's orientation and the retinal eccentricity of the source. With this arrangement, a given change in the angle of the mirror resulted in twice the angular change in the retinal eccentricity of the glare source.*

By making small amplitude flicks with the mirror, the observer could maintain a reasonably steady view of the retinal vasculature and the entoptic foveal pit. His task was to adjust the position of the mirror to the critical angle at which the crescent-shaped darkening extinguished. The four observers tested in the Stiles-Crawford experiment served again in this study, using the same eyes that were tested previously. Each observer made 10 settings.

Results. With practice, all observers could make consistent settings at which the entoptic darkening rather abruptly extinguished. In each case, the observers claimed that the darkening disappeared independently of changes in the appearance of the surrounding blood vessels, indicating that the disappearance cannot be attributed to the simple loss of scattered light to the foveal region. The determination was easier when the source was imaged in the hemifield opposite that containing the blind spot since the optic disc often disrupted the otherwise homogenous fundal scatter onto the fovea. However, it was shown for one observer, D. R. W., that the critical eccentricity at which the darkening extinguished did not depend on whether the nasal or temporal hemifield contained the image of the glare source. This suggests that the nasal and temporal slopes of the foveal pit are about the same steepness.

Appendix 2 describes a model for estimating the steepest slope of the foveal pit from the critical eccentricity at which the entoptic effect extinguishes. The critical eccentricities were 53°, 45°, 56°, and 40° for Observers D. I. A. M., D. R. W., A. N., and M. M. H., respectively, corresponding to maximum foveal pit slopes of 39°, 33°, 41°, and 29°. The standard error of the mean based on variability

within the 10 settings averaged about 1.2°.

Discussion. The maximum slope of the foveal pit estimated with scattered light from the fundus agrees reasonably well with the corresponding figure predicted from the directional sensitivity data for Observers D. I. A. M., D. R. W., and A. N. Their average maximum slope is 38° when measured with fundal scatter, intermediate between the 43° maximum slope estimated from directional sensitivity shifts and the 30° slope of Polyak's sectioned retina.⁸ This provides independent support for the refraction model described above since the small discrepancy between the maximum slopes estimated from the two psychophysical techniques could be reconciled if the ratio of the refractive indices of the retina and vitreous used in the refraction model was underestimated by as little as 0.3%.

M. M. H., who showed no systematic variation in directional sensitivity and who did not see the entoptic dim patch by changing the entry point of light in the pupil, also had the shallowest foveal pit estimated from the fundal scatter technique. However, the refraction model predicts that the slope estimated from fundal scatter for this observer is still sufficiently steep to produce a small but measurable shift in directional sensitivity, reaching a maximum deviation of 200 μ m from the mean foveal directional tendency. Also the estimated pit slope for M. M. H. (29°) is nearly as steep as that estimated in one of the observers (D. R. W., 33°) who saw the original entoptic effect and showed a relatively small but clear systematic shift in directional sensitivity. This does not show that foveal pit refraction is insignificant, since its effects are calculable under fairly secure assumptions. Rather it suggests that M. M. H. has local variations in foveal receptor orientation superimposed on and obscuring the reduced refraction effects of the relatively shallow foveal pit. This is consistent with the mottled and nonuniform appearance of the entoptic avascular region reported by M. M. H. when viewing a uniform surface through a pinhole moved around the pupil.

*Because the eye is slightly displaced from the center of rotation of the mirror, this is not precisely true. However, calculations revealed that this factor did not alter the measured retinal eccentricity by more than 15 min arc.

On the face of it, the foveal directional sensitivity shifts reported here seem inconsistent with the failure to find directionally selective adaptation in the fovea.²³⁻²⁷ However, the systematic shifts measured with the minimum flicker technique are very small (never larger than 400 μm in the entrance pupil). Furthermore, as MacLeod²⁶ has pointed out, the increased breadth of the foveal Stiles-Crawford function relative to that of the periphery^{3, 27} could reduce the effects of directional adaptation.

Originally Walls,²⁸ and more recently Snyder and Miller,²⁹ suggested that refraction by the foveal pit may serve to magnify the image available to the avian fovea, increasing its resolving power. Though refraction effects are probably not large enough to cause substantial image magnification in the human fovea, they are large enough to cause small but measurable shifts in the directional sensitivity of foveal cones provided the refractive index measures of the retina and vitreous are roughly correct. The directional sensitivity measurements reported here do not by themselves distinguish between the hypotheses that foveal cones are splayed apart, that their directional sensitivity is altered by foveal pit refraction, or some combination of both. However, the estimate of the foveal pit slope with fundal scatter taken together with the refraction model show that the foveal pit is sufficiently steep to account for nearly all of the measured shift in foveal directional sensitivity. Local variations in foveal receptor orientation may exist as well, as in the case of M. M. H., introducing differences in directional sensitivity in addition to the systematic shifts produced by refraction at the foveal pit.

Recent evidence suggests that photoreceptors may have the remarkable capacity to realign themselves toward the pupil after retinal detachment³⁰ or displacement of the pupil.¹¹ If receptor orientation is guided by light, foveal cones might be tilted to achieve proper optical alignment with the pupil center despite the refraction at the foveal pit. The correlation reported here between foveal pit slope and cone directional sensitivity indicates that if such a phototropic response

exists, it fails to compensate for foveal pit refraction.

Appendix 1

Fig. 5 shows the model eye adapted from the emmetropized Gullstrand schematic eye described by Enoch and Laties.⁶ The reader is referred to their paper regarding the basic assumptions of the model. The photoreceptor at *P* obeys the anterior pointing hypothesis in the sense that it physically points toward the center of the exit pupil *D*. However, the cone is maximally sensitive to a ray leaving the exit pupil at *V* which is displaced some distance a_k'' from *D*, owing to an angular displacement, *a*, of the Stiles-Crawford maximum due entirely to refraction by the foveal pit at *T*. The value of *a* for a given displacement, a_k , of the Stiles-Crawford maximum in the entrance pupil is given by the expression³:

$$a = 2.5 a_k \quad (3)$$

where *a* is given in deg and a_k is in mm.

The angle b_1 represents the slope of the foveal pit at *T* measured relative to the tangent *RS* at the center of fixation *F*. *RT* represents the normal to the foveal pit at *T* and is orthogonal to *ST*. According to Snell's law, if the ratio of the refractive indices of retina and vitreous is $\frac{n_r}{n_v}$, then

$$\frac{n_r}{n_v} = \frac{\sin(a + b_2)}{\sin b_2} \quad (4)$$

For the small retinal eccentricities used in this experiment (less than or equal to 75 min arc), angle *TPS* is approximately 90° and *P*, *F*, *S* are co-linear. This allows the simplification that b_1 , the slope of the foveal pit at *T*, is equal to b_2 , the angle of refraction. (A more sophisticated model which takes the retinal eccentricity of *P* into account predicts the same foveal pit slope as the simplified model described here to within less than a degree.) Substituting the estimates of the refractive indices and exchanging b_1 for b_2 in equation 4 we have:

$$\frac{1.36}{1.336} = 1.018 = \frac{\sin(a + b_1)}{\sin b_1} \quad (5)$$

Expanding $\sin(a + b_1)$ and solving for $\tan b_1$ we have:

$$\tan b_1 = \frac{\sin a}{1.018 - \cos a} \quad (6)$$

Since *a* can easily be estimated with equation 3,

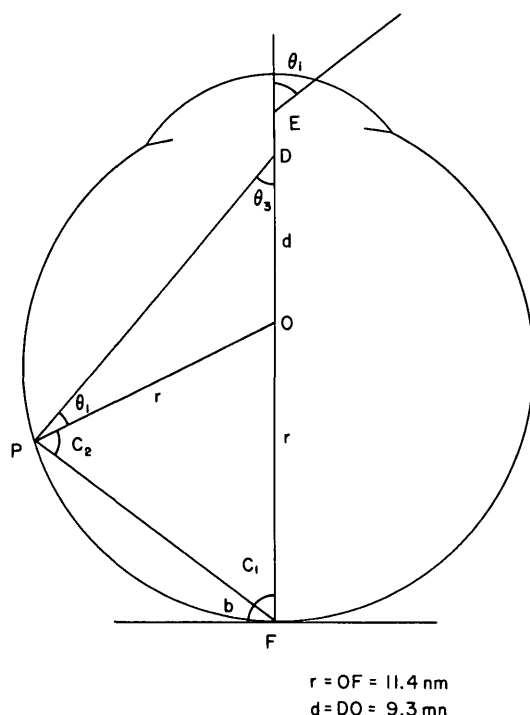


Fig. 7. Model eye used to estimate the slope of the foveal pit from fundal scatter. (Adapted from Enoch and Laties.⁶)

equation 6 provides a means of estimating the foveal pit slope, $\tan b_1$, which accounts for the observed shifts in directional sensitivity at each retinal eccentricity.

Appendix 2

Fig. 7 shows the model eye adapted from that described by Enoch and Laties⁶ used to estimate the maximum slope of the foveal pit from fundal scatter. The chief ray from the glare source intersects the center of the entrance pupil *E* at an angle θ_1 (which defines the retinal eccentricity) and leaves the center of the exit pupil *D* at an angle θ_3 . The ray strikes the diffusely reflecting fundus at *P* and is scattered in many directions. The scattered ray which is pertinent for this analysis is *PF*, the ray scattered toward the foveal pit. In the interest of simplicity, we assume that the image of the glare source at *P* can be considered a point source. Furthermore, we neglect the small differences in angle for rays from *P* which impinge on different areas of the fovea, tantamount to assuming that the fundal point source is infinitely distant from the fovea. The angle formed by a scattered ray *PF* relative to the tangent to the retinal sphere at *F* is designated *b*. The derivation of an equation which

expresses *b* as a function of θ_1 , retinal eccentricity, goes as follows.

First, as described by Enoch and Laties⁶ in their equation 1:

$$\theta_3 = \frac{\theta_1}{1.2144} \quad (7)$$

Also, the angles C_1 and C_2 are equal angles of isosceles triangle *OPF* with sides of length, *r*, so that the sum of the angles of triangle *DPF* can be expressed as:

$$\theta_3 + \theta_1 + 2 C_1 = 180 \quad (8)$$

Since *EF* is orthogonal to the tangent to the retinal sphere at *F*, then $C_1 = 90 - b$. Substituting this into equation 8 and solving for *b* we have:

$$b = \frac{\theta_3 + \theta_1}{2} \quad (9)$$

Equation 4 from Enoch and Laties⁶ tells us that:

$$\frac{d}{\sin \theta_1} = \frac{r}{\sin \theta_3} \quad (10)$$

Solving for θ_1 and substituting into equation 9 we have

$$b = \frac{\theta_3 + [\arcsin(dr^{-1} \sin \theta_3)]}{2} \quad (11)$$

Substituting equation 7 into equation 11 we obtain:

$$b = \frac{\theta_1/1.2144 + \arcsin[dr^{-1} \sin (\theta_1/1.2144)]}{2} \quad (12)$$

When θ_1 is such that the entoptic foveal pit is just extinguished, the ray *PF* will be parallel with the maximum slope of the foveal pit and the angle *b* will estimate that slope.

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