

A displaced Stiles-Crawford effect associated with an eccentric pupil

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Receptors tend to be oriented toward a point near the center of the pupil in the normal eye. We report psychophysical studies of receptor orientation and directional sensitivity in a subject whose right pupil is displaced nearly 3 mm nasally as a result of injury sustained 25 years ago. The Stiles-Crawford effect was measured for foveal cones and for parafoveal cones and rods. Greatest sensitivity was found in all cases at a point close to the center of the natural pupil, indicating that the receptors in this eye are trained toward the abnormally situated pupil. At large angles of incidence, foveal cones exhibited a clear asymptote of sensitivity 0.83 log units below the sensitivity for axially incident light. Parafoveal cones were more directionally sensitive, with a suggestion of an asymptote for oblique incidence about 1.2 log units below the sensitivity for axial incidence. Rods showed a sensitivity pattern decentered like that of the cones, with a greatest observed sensitivity loss of 0.28 log units. Best acuity for cones was observed for entrance pupils close to the optical axis of the eye, remote from the pupillary region for best sensitivity.

Key words: receptor orientation, Stiles-Crawford effect, tropism, rods, cones

Typically, the alignment of retinal receptors is not perpendicular to the eyeball surface as one might tend to assume, but rather toward a point near the pupil center,¹ an arrangement which makes for optimal visual sensitivity and resolution. This has led to speculation that receptor orientation may be influenced by a corrective mechanism, guided perhaps by the direction of incident radiation^{2, 3}; however, evidence for or against such an alignment mechanism is sparse. Enoch et al.³ reported in a case of retinal detachment that receptor orientation (as in-

dictated by the Stiles-Crawford effect), initially disrupted following scleral buckling surgery, recovered to a normal pattern over the following months. Although this supports the conjecture that an active mechanism may exist, it does not establish whether light may itself provide a guiding function. This report concerns an individual in whom one pupil has been displaced as a result of injury in early childhood. Preliminary observations,⁴ using the Stiles-Crawford effect (variation of visual sensitivity across the pupil) as an index of receptor orientation, suggested that the receptors in this eye are trained approximately toward the center of the displaced pupil. The more precise and comprehensive experiments reported here have verified this for both foveal and parafoveal retinal areas. In addition, the deviant orientation of these receptors has allowed an investigation of photopic and scotopic sensitivity to obliquely incident light using larger angles of incidence than is usually possible.

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Background

The subject of this investigation is the first author who, at the age of 4, suffered a penetration of the right eye in a locus centered vertically on the midline and approximately 1 mm nasal from the medial limbus. After surgery it was evident that part of the iris in that location had been drawn into the wound, resulting in an adhesion that fixed the nasal margin of the pupil. Compensatory growth of the iris has resulted in a pupil displaced nasally which is smaller than that of the left (normal) pupil under normal conditions of illumination (see Fig. 2, *a*). Pupil size in the right eye does not vary greatly with changing illumination. The outline indicated in Fig. 2, *a* would be appropriate for a bright interior or moderate daylight and will be termed the "ecological" pupil.

A recent ophthalmological examination has revealed the retina to be free of obvious injury or defect. The only internal evidence of the penetration is a rupture of the ciliary bodies over about 30° on the nasal edge of the lens; this limits accommodation to about 2 diopters. Present acuity is 20/200; with best correction (+3.00 D.S. -2.75 D.C. × 130°) using the ecological pupil it is 20/40. Direct examination with a visuoscope showed fixation to be foveal and steady.

Methods

Apparatus. A standard Maxwellian view apparatus provided three beams of light, each of which formed a compact image in the subject's dilated pupil. The sizes of the filament images were for the test beam, 0.3(H) × 1.2(V) mm, and for the reference beam and surround, 0.8(H) × 2.2(V) mm. All the beams were derived from a single 6v, 90w ribbon filament lamp. The reference and surround beams always entered the pupil at a fixed location, centered about 0.5 mm nasal and 2 mm above the axis of symmetry. The entry locus of the test beam was varied with the use of a mirror pivoted on orthogonal axes, which was mounted in the beam path just behind the aperture that defined the retinal image.

Results were obtained by means of silent substitution, with the subject adjusting a wedge in the test beam path to produce no change discernible to the subject upon substitution of the test and

reference beams which were presented alternately with shutters (1.25 sec and 0.75 sec on-time, respectively). Only a barely noticeable color shift, either of hue or saturation, due to the Stiles-Crawford effect of the second kind would be expected from the red test light which was used.

Because of the poor optics in the eye, movement of the test field when the test beam entered peripherally posed a serious difficulty which was circumvented by means of the following configuration. Both the test and reference beams illuminated a rectangular patch subtending 3.5° × 5°. Upon this was superimposed a surround field with outer limits of 10° × 10° and a small central "hole" 1.5° wide × 2.5° high. The illuminances of the beams were then adjusted so that the test and reference patches were masked by the surround and yet were still clearly visible in the "hole." With the effective test area being delimited by the boundaries of the "hole" in the surround, this allowed up to 1° displacement of the test field in any direction without evident effect on the test locus. Larger displacements were not encountered. For testing cones, the surround was 3.47 log photopic td (white) and the reference beam (against which the test beam was matched) was set at 2.12 log photopic td. Both the test and reference beams shared an RG610 (red, transmitting above 610 nm) filter. The rod effect was measured with the RG610 in the surround, producing 0.77 log photopic td, with the reference level fixed at -1.5 log photopic td or -0.6 log scotopic td, a value well below cone threshold. In this case, the test and reference beams shared a 500 nm interference filter.

Technique. The subject's head position was fixed with a dental bite mounted on a compound vise. Best optical correction was used for each eye. The eye under test was kept dilated with a combination of 1% Mydracyl (tropicamide) and 10% Neo-Synephrine (phenylephrine hydrochloride). To ensure precise location of the points of entry of the beams within the pupil, eye position was monitored with an infrared-sensitive television camera. Calibrated movements of the test beam brought it onto the iris where its reflection was easily observed on the television screen. Tracings from the screen, showing the iris reflecting a Maxwellian filament image suitably displaced horizontally or vertically, were taken regularly as a record of the relation between the pupil and the coordinate system used for positioning the test beam. The measurements were sufficient to locate the entry point with an uncertainty of 0.2 mm. To

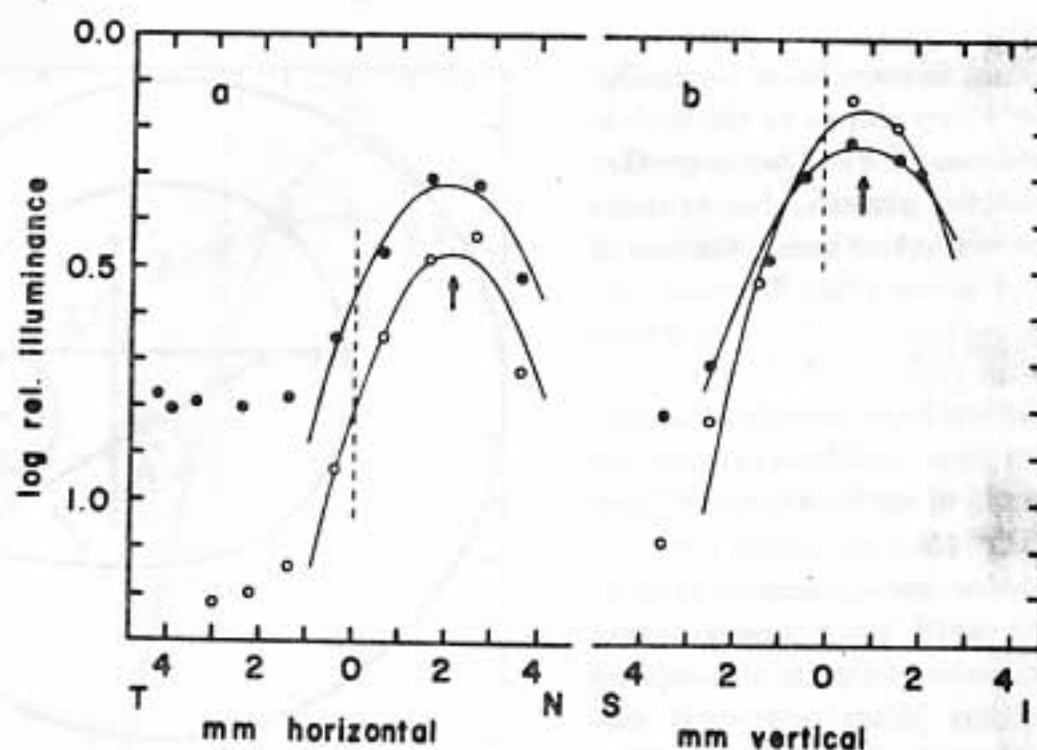


Fig. 1. Photopic Stiles-Crawford functions. Test illuminance at a match vs. beam entry displacement from optical axis. In this and all other plots of the photopic Stiles-Crawford function, illuminance is referenced to the minimum value at a match (i.e., maximum sensitivity) found in the eye. Filled circles, foveal fixation; open circles, 4.5° temporal retina. Arrows indicate maxima of functions. Except for the scotopic measurement, the standard error of the mean for all points is smaller than the symbol size. *a*, Horizontal traverse; *b*, vertical traverse. Smooth curves represent the function $\log \text{illum} = \rho(r - r_m)^2$. For the horizontal traverse, $\rho = 0.062$ (fovea) and $\rho = 0.079$ (4.5°); for the vertical traverse, $\rho = 0.051$ (fovea) and $\rho = 0.081$ (4.5°).

correct for distortion of the coordinate system caused by the cylindrical spectacle lens, the viewing system was itself calibrated by using it to observe, with all correcting lenses in place, a rectangular grid of known dimensions held in the plane usually occupied by the pupil.

As is customary, eccentricities are measured in the "apparent" or "entrance" pupil; that is, they represent the horizontal and vertical coordinates of the beams at the cornea, with no allowance for refraction by the cornea. Eccentricities in the actual pupillary aperture will be less by about 13%.

The axis of symmetry of the optical elements of the right eye was determined as a reference point to gauge the absolute displacement of the Stiles-Crawford sensitivity peak and as a check that the lens was properly centered relative to the cornea and limbus. With the subject fixating a point source at optical infinity, his direction of gaze was guided by the experimenter so as to superimpose the first, third, and fourth Purkinje images, which were viewed ophthalmoscopically. When this was done, the collimated beam was directed (and reflected) normal to the cornea at the optical axis, where the approximately coincident Purkinje images appeared. The optical axis was seen to be

centered vertically in the pupil plane but was approximately 0.5 mm nasal relative to the "center" of the limbus (extrapolated as a circle using the uninjured region).

Results

Photopic effect. The Stiles-Crawford effect was measured for both foveal and 4.5° temporal retina under the photopic conditions of illumination described above. The reference beam, always entering at a fixed location, provided an illumination standard for comparison with the test beam, which was placed at 1 mm intervals along some chosen meridian. The test and standard beams alternately illuminated the same retinal region (see Methods). The subject's task was to match the test beam to the standard by varying the illuminance of the test beam, using a graded neutral density filter. Each point from each session was the mean of at least four such matches. Symbol sizes in the figures represent approximately ± 1 standard error of the mean. The small scatter attests to the steady-

ness of fixation; had fixation been unsteady, variability on the steep slopes of the Stiles-Crawford function would have been greater than that found on the plateaus due to shifts in the entry point of the test beam. Curves of the form

$$\log \text{illum} = \rho(r - r_m)^2$$

as suggested by Stiles⁵ have been fitted to the parabolic portion (i.e., without regard to peripheral plateaus) of each data set by the method of least squares.

With foveal fixation, measurements (Fig. 1; filled circles) averaged from two sessions showed both horizontal and vertical functions which had sensitivity peaks noticeably displaced from the optical axis of the eye. The peak of the horizontal traverse was located about 2.1 mm nasal (or about 2.6 mm nasal from the center of the limbus), and that of the vertical was 0.6 mm inferior. Although the horizontal function (Fig. 1, *a*) was displaced, the slope on either side of the peak seemed reasonably symmetric. The total range of the effect was 0.5 log units. However, the peak sensitivity along the horizontal meridian was 0.3 log units less than the best seen in the eye. On the temporal side the reduction of sensitivity was limited by a plateau extending at least 2.75 mm with a sensitivity change of no more than 0.04 log units. The vertical function (Fig. 1, *b*; filled circles) showed a total effect of 0.6 log units, primarily because it approached more closely the point of peak sensitivity. Although it descended to the value of sensitivity shared by the plateau of the horizontal traverse, the clear leveling-off of sensitivity indicated at large horizontal eccentricities could not be seen here owing to occlusion by the iris.

Similar measurements were made on the left (normal) eye. The peak for the horizontal traverse was 1.2 mm nasal from the center of the pupil. A slightly nasal sensitivity peak is typical of normal eyes,^{6,7} and the eccentricity of the peak for the left eye, though greater than average, lies well within the normal range. The peak for the vertical traverse was found to be exactly centered within the pupil, making the total displacement of the

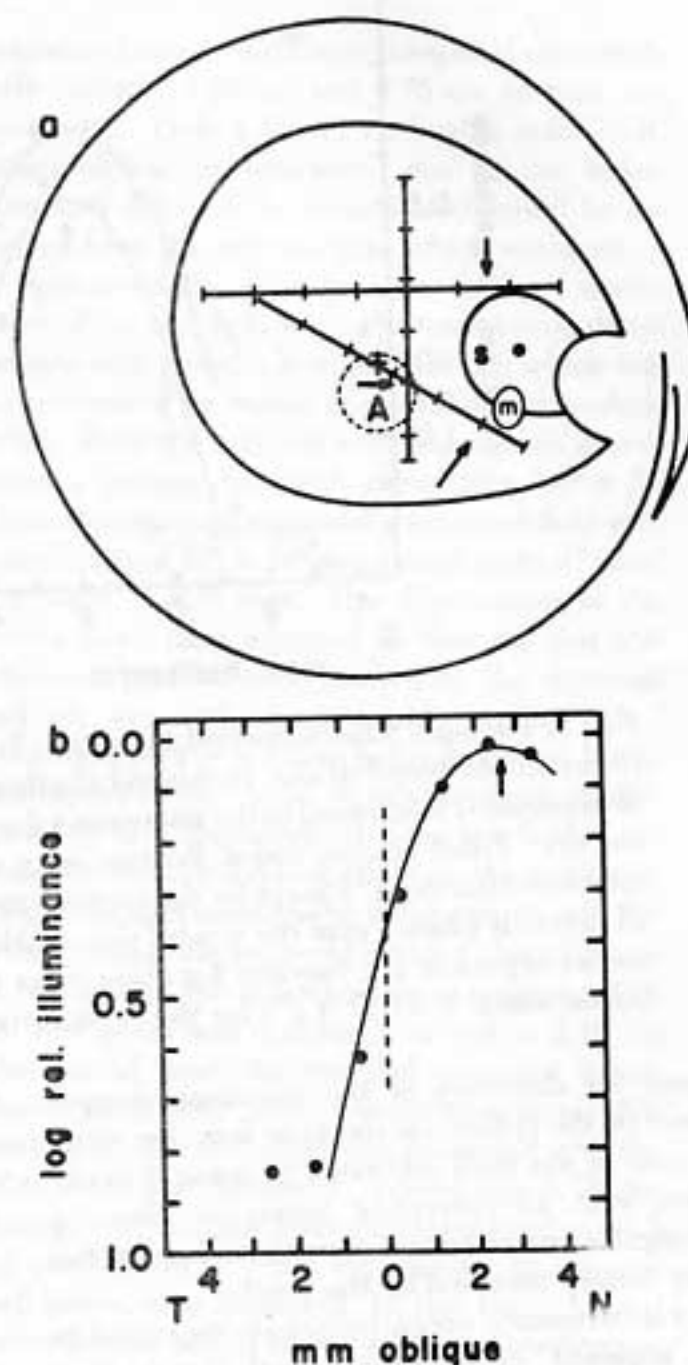


Fig. 2. *a*, Schematic representation of the eye and test entry loci (for foveal fixation) in the dilated pupil. Each cross (separated by 1 mm increments) on the horizontal and vertical traverses represents a test entry point for which the sensitivity is shown in Fig. 1. The sensitivity function for the oblique traverse is presented below. The approximately circular contour is the limbus, and the outline of the dilated pupil is shown within it. The smaller bounded area *s* represents the natural pupil under photopic viewing conditions; its center is indicated by the dot. *A* represents the entry region for best acuity, and *m* the entry region for maximum sensitivity. The cross within region *A* near the oblique traverse is the optical axis of the cornea and lens. *b*, Photopic Stiles-Crawford function for oblique traverse, foveal fixation, plotted as in Fig. 1. Note the peak sensitivity is nearly the maximum seen in the eye ($\rho = 0.056$).

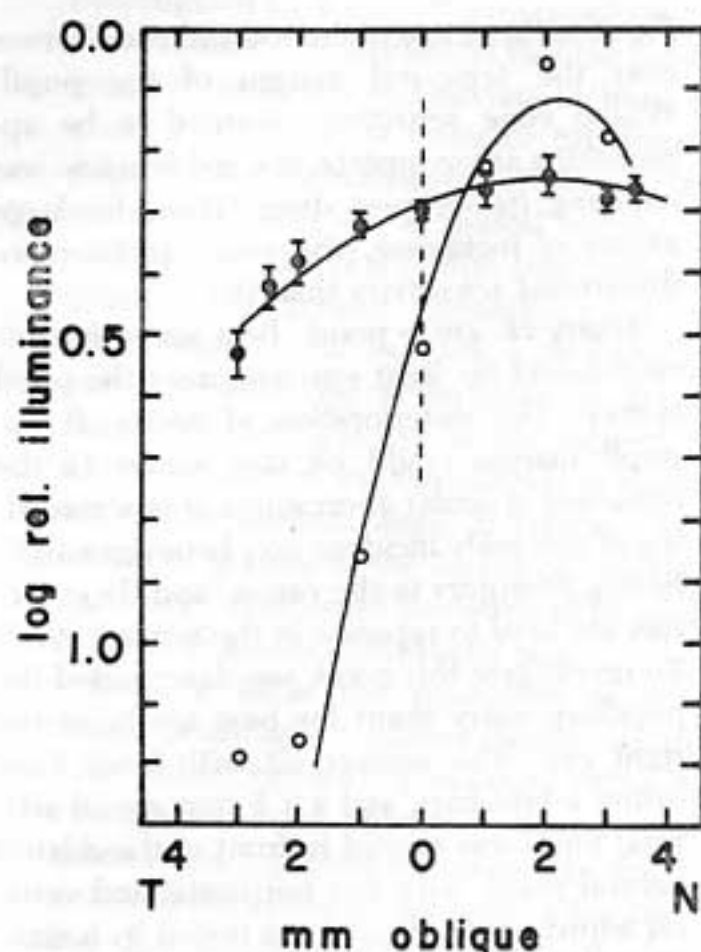


Fig. 3. Open circles, photopic Stiles-Crawford function for oblique traverse, 4.5° temporal retina, plotted as in Fig. 1; $\rho = 0.076$. Filled circles, scotopic Stiles-Crawford function along same entry paths and with same fixation; $\rho = 0.0098$. Illuminance reference is arbitrary. Bars denote ± 1 standard error.

Stiles-Crawford maximum from the center of the pupil or of the limbus 1.2 mm as compared with 2.7 mm for the right eye.

Right eye measurements were repeated for a parafoveal (4.5° temporal) region of the retina (Fig. 1; open circles) and showed Stiles-Crawford patterns which paralleled the foveal results when plotted (as they are in Fig. 1) in terms of entry point relative to the optic axis in the plane of the pupillary aperture. Both the horizontal and vertical traverses showed a somewhat steeper slope, resulting in larger total ranges of 0.81 and 0.97 log units, respectively. Previous investigators have also noticed this sharper directional tuning of parafoveal cones,^{8,9} and it has an obvious morphological basis, discussed below. On the horizontal traverse the two most temporal entry points suggested the beginnings of a leveling-off of sensitivity similar to that seen under foveal fixation, but attempts to

follow this further were frustrated by iris occlusion.

It was obvious that neither of the orthogonal traverses intersected the probable region of best sensitivity, so an oblique traverse was made. Results using foveal fixation are shown in Fig. 2, *b*, together with a map of the pupil (Fig. 2, *a*) showing the horizontal, vertical, and oblique traverse paths. For the oblique traverse, the sensitivity peak was found to be about 2 to 2.5 mm nasal and downward from the optical axis, and its eccentricity was correspondingly greater when referred to the center of the limbus. Total range of the effect for the oblique traverse using foveal fixation was 0.83 log units, again limited by a leveling-off near the temporal border of the pupil.

As a final check on whether the region of entry for peak sensitivity had been found, the subject manipulated the entrance point of the test beam for maximum subjective brightness. For these determinations the test beam was fixed in illuminance and was presented alternately with a suitably chosen fixed illuminance from the reference beam. Six such trials were performed; at each final position chosen by the subject, four sensitivity measurements were made in the usual way. This yielded a cluster of points (within the area *m* in Fig. 2, *a*), all of which had a sensitivity varying no greater than 0.02 log units. The mean of these maximal sensitivities was used for normalization of the data presented in Figs. 1, 2, and 3.

The area *m* of maximum sensitivity was horizontally centered on the ecological pupil and about 0.5 mm below its center of gravity. If the sensitivity peak is an indicator of the axial attitude of the receptors, these measurements demonstrate that they are much more closely aligned with the actual pupil than with the innately programmed pupil position.

An oblique traverse was also made at 4.5° in the temporal retina (Fig. 3; open circles). The peak was again located close to the ecological pupil center, and as in the orthogonal traverses for this fixation, the slope was steeper ($\rho = 0.076$) than in the fovea ($\rho = 0.056$), yielding a total effect of 1.14 log units.

An approach to an asymptote is suggested by the two most temporal points. The photopic Stiles-Crawford curve of Fig. 3 is unusually narrow and steep. This steepness is presumably due to the use of red light (which minimizes self-screening) and parafoveal vision. MacLeod⁴ found similarly steep curves for another observer under conditions similar to these.

Scotopic effect. The large variation of photopic sensitivity found for the traverse just described prompted us to test for a Stiles-Crawford effect under scotopic conditions. Although the spatial arrangement of the testing method was the same as that used above, different color filters were used, and the illuminances were reduced as described in the Methods section. The results for an oblique traverse using the 4.5° temporal retina are shown in Fig. 3 as filled circles. Although the uncertainty of the settings was somewhat greater than for photopic measurements, there was a clear reduction in sensitivity amounting to 0.28 log units as the test beam approached the temporal margin of the pupil.

Like the cone curve (open circles), the rod curve of Fig. 3 was clearly displaced with respect to the optical axis. The rod sensitivity peak was displaced toward the ecological pupil to at least some extent. Although the remarkable flatness of the rod curve for moderate angles of incidence made it impossible to determine the precise location of the peak, it is plausible that both the rod and cone peaks coincide.

Although the raw data are fitted reasonably well by a parabola ($p = 0.0098$), we do not believe this to be an accurate representation of the rod Stiles-Crawford function. When corrected for the slight effects of variation in lens transmission (with the use of the data of Mellerio,¹⁰ his Figs. 3 and 5), rod sensitivity was constant to within 0.03 log units ($\pm 7\%$) for entry points within 3 mm of the optimal location. Yet, 5 mm from the optimal location, sensitivity has fallen by more than 0.7 log units, a reduction of over 50%. This distribution of rod sensitivity across the pupil is in general agreement with previous observations.^{11, 12} A particularly interesting feature of

Fig. 3 is the shape of the rod and cone curves near the temporal margin of the pupil. Where cone sensitivity seemed to be approaching an asymptote, the rod function was enjoying its steepest drop. Thus, for large angles of incidence, the rods exhibit more directional sensitivity than the cones.

Acuity vs. entry point. Best acuity is typically found for light entering near the pupil center. The deterioration of acuity at the pupil margin could be due either to the influence of ocular aberrations or to a spreading of obliquely incident rays between neighboring receptors in the retina, and these factors are hard to separate in the normal eye.¹³ To investigate this point, we determined the pupillary entry point for best acuity in the right eye. The subject sat with head fixed (using a bite bar), and a 1.5 mm round artificial pupil was moved in front of the dilated natural pupil, with fine horizontal and vertical adjustments. Acuity was tested by a standard Snellen chart. With appropriate spherical and cylindrical correction, best acuity (approaching 20/20) was found in the region marked A in Fig. 2, *a*. This was horizontally aligned with the optical axis and 0.5 mm below it. In the region of greatest flicker-photometric sensitivity (*m* in Fig. 2, *a*), acuity ranged from 20/40 to 20/50. Measurements at other entry points suggested a variation of acuity roughly symmetric about the optic axis rather than about the region toward which the receptors were aligned. We conclude from this that, with appropriate correction, the optics of the eye are not severely disrupted and that the acuity advantage accruing from axial illumination of the receptors is small relative to the adverse effects of aberrations due to peripheral entry of light. It is important to note, however, that the optical quality of this eye is imperfect; receptor orientation could well prove more influential upon acuity in eyes with superior optics.

Discussion

Our primary finding is that sensitivity was greatest for light entering at a point near the center of the abnormally situated pupil. Could this be a coincidence? Normal varia-

bility in the Stiles-Crawford pattern has been investigated by Enoch,¹⁴ who concluded that there is only a 1% likelihood that the point for greatest sensitivity will deviate by more than about 1 mm (2.6° of receptor tilt) from the pupil center. Dunnewold⁶ studied a larger number of eyes (in a clinical setting, and without the use of a dental bite) and found considerably greater variability, but even Dunnewold's data indicate a probability of only about 1% for a deviation as great as shown by the right eye of our subject. The deviation shown by the normal left eye is within the normal range. If referred to the center of gravity of the ecological pupil, the right eye's downward deviation of its peak of 0.5 mm is also not unusually large.

Leaving aside the possibility of coincidence (although it cannot really be ruled out), there remains a chance, difficult to evaluate, that the abnormal receptor orientation in the right eye was caused by shearing forces in the retina at the time of the trauma and has simply persisted without change since then. We can find no evidence or persuasive argument for or against that possibility, but it is worth noting that the interposition of the optic disc would tend to protect the retinal regions investigated here from shearing forces due to traction at the site of injury. A reasonable alternative hypothesis is the existence of a phototropic mechanism guiding receptor alignment. Independent support for this comes from a congenitally colobomatous eye studied by Dunnewold,⁶ which showed greatest sensitivity at a point corresponding roughly to the location of the displaced pupil (though not, in this case, clearly outside normal limits).

Despite their statistical significance the results presented here should obviously not be regarded as establishing at all definitely the idea that receptors are phototropic. They should, however, encourage serious consideration of the tropism hypothesis as well as encourage further experimental tests of it. The reports that adult trends in receptor orientation can be observed prenatally (and presumably before exposure to light)¹³ is by no means inconsistent with the hypothesis,

since a light-guided corrective mechanism might still be useful in fine-tuning or maintaining an innately present alignment.

The investigation of directional sensitivity at large angles of incidence, made possible by the large tilt of the receptors in the abnormal eye, showed interesting differences between the foveal and parafoveal cones that are well expressed by the differences between their asymptotic sensitivity levels. For foveal cones sensitivity for red light fell to an asymptote at between 1/6 and 1/7 of the sensitivity for axial incidence; for parafoveal cones, to about 1/16. The foveal value is in fair agreement with the value of about 1/5 obtained at the red end of the spectrum by Wijngaard and van Kruysbergen,¹⁵ who also noted a clear asymptote at large angles of incidence in an observer with a displaced Stiles-Crawford effect. These authors suggested that the asymptotic sensitivity is due to unguided light passing across the outer segments whereas the peaked part of the Stiles-Crawford pattern is due to light funneled down the inner segment and concentrated (mainly) within the outer segment by internal reflection. On this view, the asymptotic sensitivity for obliquely incident light may perhaps be simply related to receptor morphology in the following way. It is a reasonable assumption that light passing obliquely across the outer segment layer will not be concentrated heavily either within or between the outer segments but will be distributed more or less uniformly within the illuminated region. Axially incident light, on the other hand, once trapped by an inner segment, is funneled, with perhaps little loss, into the outer segment. The average flux within an outer segment is thus increased for axially incident light by the ratio of the cross-sectional areas of the inner and outer segments, and visual sensitivity would be increased in proportion. Although this crude model avoids the complexity obviously needed for an exact treatment, the prediction seems consistent with the observed foveal asymptotic sensitivities, since the outer segments of foveal cones are roughly 40% as wide as their inner segments.¹⁶

This simple, idealized model can also account for the lower asymptotic sensitivity of parafoveal cones, which have a more pronounced taper from the inner to the outer segment.⁸

Note added in proof. Records from preliminary measurements of the Stiles-Crawford effect in this eye⁴ show a similar deviation of the entry point for best sensitivity in yet another retinal locus. The test region was 6° above the line of sight, and on the horizontal meridian greatest sensitivity was found nearly 3 mm nasal from the center of the limbus. This decreases the likelihood that the deviation of the Stiles-Crawford effect is coincidental.

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