Directional sensitivity of the foveal and parafoveal retina

Jay M. Enoch and G. M. Hope*

Photopic directional sensitivity was measured at the fovea and at 2°, 3.75°, and 10° from fixation (referred to the center of the entrance pupil of the eye; nonfoveal tests were conducted in the nasal field projected onto temporal retina). These data confirm and extend an earlier experiment performed by Westheimer. The central fovea exhibited significantly less directionality than parafoveal test points. Differences in directionality between the three parafoveal test loci were not significant. Possible factors giving rise to the foveal-parafoveal difference in directionality are reviewed. Evidence corroborating our earlier observations that receptors across the retina are aligned with the point approximating the center of the exit pupil of the eye is also presented.

Key words: retina, photoreceptors, retinal receptor orientation, Stiles-Crawford effect, directional sensitivity of the retina, center of convergence of orientation and directional sensitivity, test of central fixation.

No current approach to directional sensitivity of the retina satisfactorily integrates the available psychophysical, morphological, physical, and other relevant data. We have begun a systematic analysis of factors contributory to retinal directional sensitivity and, as a part of such an analysis, it seemed prudent to verify an important observation reported by Westheimer. Westheimer's data indicated that the directional sensitivity of parafoveal cones was greater than that of foveal cones. In the brief analysis presented here, we have taken advantage of technical improvements in Stiles-Crawford measures and extensive subject training in order to overcome difficulties of high intersubject variability and qualitative data analysis which were present in the earlier work.

We used a Stiles-Crawford technique similar to that employed by Westheimer. In addition, through the use of an infrared image converter unit, we could observe the entrance pupil of the test subject and could continuously maintain centration of the pupil on a reference reticule. We determined the Stiles-Crawford functions through the peak of directivity in the pupil based on a two-dimensional analysis at
Fig. 1. These are log just detectable luminance (ΔB) thresholds plotted against log background adaptation luminance (B) levels at the test points used to measure the Stiles-Crawford functions in the three subjects.

each retinal test locus, and we extended the test to additional retinal points. Increment threshold curves were obtained at each retinal test point. The fact that the resultant slopes were parallel allowed comparison of Stiles-Crawford functions obtained at different retinal points. Data were analyzed by using a least squares fit to Stiles' function for photopic directional sensitivity data. This allowed tests of significance to be performed.

Method

Apparatus. The apparatus employed in this research has been described in detail by Enoch and Hope. The apparatus consists of a two channel Maxwellian view system with auxiliary viewing channels for the operator. It allows the position of entry of either beam path to be varied in the entrance pupil in two dimensions. The position of entry for both paths, the entrance pupil of the eye, and an orienting and positioning reticule and caliper system may be monitored continuously by an infrared image converter. Three dimensional controls for subject eye position allow correction for eye movements during data collection, while variable positioning of fixation lights allows the testing of Stiles-Crawford functions for retinal positions corresponding to points over 60° of field along the horizontal meridian.

The stimulus array consisted of a large adaptation field (4° 24') of circular configuration surrounding a superimposed small (12') flashing (139 msec. of every 500 msec.) test spot*. The configuration and size of both the test and background fields were determined by field stops in the two beam paths and the sharpness of the retinal image could be optimized by their functioning as Badel optometers. The entry position of either of the two beams could be adjusted optically by translating the position of an aperture early in the system, with small corrections to the centration of the two fields being made at the plane of the field stops. These corrections are made necessary as a result of retinal image shifts accompanying translation of the point of entry and due to aberrations in the optical components of the eye.

The luminance of the test flash was controlled via a circular, variable, neutral density filter. Adapting field luminance was set at 3.76 log millilamberts. Light for both channels was supplied by the same ribbon filament tungsten lamp and was passed through a Wratten No. 23A (orange-red) filter. The beam of the adapting field was transversed across the entrance pupil during directional sensitivity determinations. The increment threshold of the test beam (which remained centered in the pupil) was the dependent variable. The adapting field was always centered on the test field.

Experimental subjects. The left eyes of three college age normal emmetropic subjects were studied. All subjects were given extensive training in executing the requirements of the experimental procedures prior to data collection. During the training period ΔB/B curves were determined for each retinal position tested (Fig. 1). It is necessary in determining and comparing Stiles-Crawford functions through the use of an incremental stimulus that the data be taken at luminance levels of the adaptation field which insure that

*Note, the test-field diameter is much smaller than that used in reference 2.
the Weber fraction is a constant (see Appendix 2 in Enoch and Hope). If this condition is met, the slope of the Weber functions at each retinal position tested must be equal and approximate +1.0 on a log log plot. In Fig 1 it can be seen that the slopes of the Weber functions for the three subjects at the retinal positions tested were essentially equal for each subject, with the possible exception of the 10° function for the subject KC. We assumed the departure from the slope of +1.0 in that case was artifactual (the subject was not available for further testing). Only the Weber portions of the \( \Delta B/B \) functions are shown in the figure since all data were taken within this range of luminance.

This experiment required very consistent performance on the part of the subjects. Changes in threshold criterion within a transverse across the entrance pupil could result in alterations to the form of the Stiles-Crawford curve. In order to stabilize the criteria within the traverse at each retinal locus, subjects were allowed to compare their end-point determinations at each of several points of entry. By this means, each subject evolved his own consistent end-point criterion within the traverse at each retinal test locus.

**Procedure.** For general procedure, see Enoch and Hope, except as noted here. Prior to data collection, the pupil was dilated with Euphthalmine (5 per cent) and the subject dark adapted for 20 minutes. In a given test run, the stimulus array was located either at the point of fixation (foveal test) or at positions 3.75°, 10.0° or, for two subjects 2° nasally in the visual field from the point of fixation. The angle was measured externally to the eye about the center of the entrance pupil. In previous analyses, this angle was termed \( \theta \).

Positioning of the subject's eye in the instrument for this experiment differed from the usual procedure in that the entrance pupil was shifted vertically until the horizontal meridian of the instrument and, therefore, the horizontal path to be traversed by the image of the aperture of the background field in the entrance pupil, was coincident with the centroid or maximum of the previously determined vertical Stiles-Crawford curve for that fixation condition. The Badal optometers were then set to minimize blur and data collection was initiated. A transverse across the pupil was initiated at the periphery and "laced" back and forth to the center of the entrance pupil in 1 mm. increments at either half or whole millimeter points. This was usually followed by a second similar traverse at the complimentary set of points.

The subject was asked to signal when the test flash just appeared or disappeared as its luminance was adjusted in 0.02 log unit increments by the experimenter. A minimum of 8 determinations were made at each point of entry and an average taken. Several complete sets of data were taken at each fixation point and, in turn, these were averaged in order to provide basic data for additional analysis.

**Data reduction and analysis.** In order to reduce the mass of data to a summary form, the data for each point of entry for each retinal test locus were averaged for each subject. Each collection of such points, defining a Stiles-Crawford curve, was subjected to a computerized mathematical curve fitting analysis which provided the parameters of the curve fitting the data with the least-squared error (least-squares analysis). A generalized form of Stiles' exponential formula was used (this differs from Crawford's relationship only in base). In simplified form, this may be written

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\frac{\Delta B}{B} = 10^{-\rho(\Delta L)}
\]

where \( \Delta B \) refers to the luminance of the test field, \( B \) to the luminance of the adapting field, \( \Delta L \) indicates position of the adapting field in the entrance pupil (as written, \( \Delta L \) is measured from the maximum of sensitivity). Note, we actually computed and plotted \( \rho \) relative to the geometric center of the pupil. Rho (\( \rho \)) is an index of the magnitude of the Stiles-Crawford effect. The greater \( \rho \), the greater the directional sensitivity. It is this value which is of interest in this experiment. Displacement of the peak was suitably accounted for in the least-squares analysis. All data points were equally biased, although this may not be quite valid. That is, it is possible that points located at different distances from the peak of sensitivity should have more or less weight in determining the shape of the function and the locus of the peak (e.g., as in a probit analysis). The advantage of an iterative least-squares fit was that it eliminated experimenter bias and provided a precise numeric analysis. The latter was valuable because variance could be determined and significance of differences could be tested at retinal points employed. While one may debate the relative merits of one or another function in fitting Stiles-Crawford data, this one is simple to apply, provides an adequate fit for this application and allows ready comparison with Stiles-Crawford data collected over the past several decades.

Rho values and each of the other parameters (position of peak, etc.) from each of the mathematical functions were averaged across subjects at each retinal test locus, then, separately, the individual data points for each retinal locus were

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Fig. 2A. This is a set of single Stiles-Crawford function traverses for one subject. The empirical data points have been fit to a least-squared error criterion (solid line). Empirical data points are indicated by open and closed circles alternated for adjacent curves. The curves have been arbitrarily shifted along the vertical axis in order to avoid overlap. The angle defining the retinal test locus and the values of $p$ for the fitted mathematical functions are indicated beside each curve. Note that no curve is presented at $2^\circ$ in this part of the figure. This subject was unavailable for testing at that point.

Fig. 2B. These curves are similar to those in A except that the empirical data points are the means across all subjects and the mathematical functions are the composites for the averaged parameters (see text). Symbols and notations are as for A. Note that the $2^\circ$ curve is included in this part of the figure.

Results

A set of single traverses at the three primary retinal test loci for one subject* are also averaged across subjects. The averaged parameters were then fed back into the computer and sets of points defining group mean functions were generated. Thus, a mean mathematical function and a separate set of mean empirical data points at each retinal test locus were produced for comparison. The $p$ values for the subjects were subjected to an analysis of variance (one-way, repeated measures\(^{17}\)). Since the major effect was anticipated from Westheimer’s\(^1\) earlier work, an a priori comparison among means\(^{17}\) was planned in order to elaborate upon it. In addition, other possible effects were investigated in detail via post hoc comparison.\(^{17}\)

*No data are shown at $2^\circ$ for this subject as she had left St. Louis. The decision to test the $2^\circ$ locus was made after she became unavailable. She was chosen for presentation as the most conservative one, representing the other end of the continuum from the group data presented in Fig. 2B.

The results of the averaging procedures are provided in Fig. 2B. In both parts of this figure, it is apparent that directional sensitivity ($p$) increases rather dramatically and sharply from the fovea to the parafovea. The computer-generated smooth curves, best fitting under the least-squared error criterion, provide a good approximation to the empirical data points (open and closed circles for alternate curves).

Fig. 3 plots the $p$ values for the mean data for each individual subject and across subjects against $\theta_i$ ($\theta_i$ is angular position of the test field in the nasal visual field measured relative to center of the entrance pupil of the eye). Note, when $\theta_i = 0$, this corresponds to foveal fixation. It is clear from this plot that $p$ increased sharply in the parafovea and changed little between

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2° and 10°. Statistical analysis supported these observations, with the main effect in the analysis of variance (essentially a test of the curve in Fig. 3) being significant \((p<0.05)\). This indicates that \(p\) changed significantly across retinal test loci. Individual comparisons among means further indicated that the significant over-all effect was primarily due to the sharp increase between the foveal and 2° test loci. The difference between the rho values at the foveal position and those in the parafoveal positions was highly significant \((p < 0.01)\), whereas there was no significant difference between data obtained at 2° from the point of fixation and the other two parafoveal test loci \((p > 0.25)\). Thus, regardless of the level of data reduction or type of data analysis, the results are clear, \(p\) changed rapidly between the foveal and 2° test loci and remained essentially stable out to 10°.

The rather large time investment required on the part of the subject and experimenter made it necessary to restrict the size of the subject sample. Thus, it is desirable to present accessory data which corroborates earlier observations and improves their generality. It has been previously reported that the receptors transretinally are oriented such that they are aligned with the approximate center of the exit pupil of the eye.²,⁶ Fig. 4 presents the two-dimensional peaks of directional sensitivity (determined in the entrance pupil), intrinsic

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**Fig. 3.** This figure plots the \(p\) values for each subject and the mean across subjects (filled circles) against retinal test locus. Mean values have been connected by a line for clarity.

**Fig. 4.** The figure is similar to Fig. 10 in reference 2. Each point designated by a number is the combined mean Stiles-Crawford function peak value for both horizontal and vertical sweeps of the image of the aperture of the background field beam in the entrance pupil for a given retinal test point. Each number corresponds to the specific retinal test point tested in the horizontal meridian. Stated another way, the number is the entrance pupil intercept of the projection of the Stiles-Crawford maximum of sensitivity for a given retinal test point. (I. MacLeod uses the excellent simplifying term "pupil intercept." Here the term is modified in order to differentiate entrance pupil from pupillary aperture from the exit pupil.) Values \(\theta_i\) are appended to allow comparison of these data with those presented in Reference 2. Values of \(\theta_i\) given on this figure in Column A are for this paper. Here \(\theta_i = 0°\) corresponds to the point of fixation. In Reference 2, \(\theta_i = 0°\) corresponds to the pupillary axis of the eye and the point of fixation was located at approximately \(\theta_i = 5°\) (see Column B values). In both cases \(\theta_i\) was measured with the apex of the angle located at the center of the entrance pupil of the eye. All values used here are for the fovea and the nasal visual field or temporal retina. At bottom right, the combined means of the individual points are presented as well as the total combined mean (point 0). The latter may be compared with point 0, Fig. 11, Reference 2.
in the data of the present experiment, for these three subjects. Though the range of retinal test loci employed here was not as extensive as in the earlier work, the results corroborate the earlier observations. The mean centers of directional sensitivity and orientation correspond closely to those seen previously for different subjects.

Discussion

The data unequivocally support the findings presented earlier by Westheimer. However, it is evident that the transition from the "flatter" or less directional central foveal psychophysical function to that present in the parafovea is rather sharp. This apparent step-like change is hard to define in terms of any single mechanism. Several factors differ between the fovea and parafovea.

1. Cone ellipsoid taper, taper length, inner segment length, diameter, and outer segment length (and diameter slightly) vary from the center of the fovea outward. Cone density per unit area decreases with increasing eccentricity from the fovea. Changes occurring in these parameters in the central area of the squirrel monkey were tabulated by Enoch. The latter data (means) did not reveal any sharp transition at the bound of the fovea. Ellipsoid taper angle and receptor inner-segment diameter were the most rapidly changing factors in the critical region.

2. In the central fovea the inner retina thins, bipolar and ganglion cells are displaced, and the Henle fiber layer is found. Ohzu, Enoch, and O'Hair and Ohzu and Enoch showed that less light is scattered within the retina in this region. Since scatter would broaden rather than narrow the Stiles-Crawford distribution, this factor cannot be responsible for the difference in central foveal directivity reported here and by Westheimer.

3. The central foveal pit forms a diverging lens because of its concave shape. Millidot has reviewed data on the index of refraction of the retina proper. Based on these fragmentary data, a figure of 1.36 seems reasonable for human retina; Fortin shows several excellent sections through the central fovea. However, no determinations of the shape of unfixed foveal pits are available (e.g., is the bottom of the foveal pit relatively flat or curved?) and hence it is difficult to assess this factor properly, although it could have influenced the results seen here.

4. Neural connections change and receptive field dimensions increase from the central fovea outward. While we did not alter test and background field dimensions, the fact that AB functions remained parallel (with one exception) probably means this is not a major factor in the analysis when Stiles-Crawford data are plotted on a semi-log plot.

5. Distribution of cone pigments and macula pigment change with retinal point tested in the central retinal area. Since red-orange test and background fields were employed in this study, one assumes that blue receptors and the blue absorbing macula pigment had little influence upon the result described here.

6. Refractive error is generally only corrected for the fovea and changes when other retinal points are tested. This factor was corrected for each retinal locus tested in this experiment.

7. The tight receptor packing and increased outer segment length present in the central fovea bring corresponding portions of neighboring photoreceptors into close proximity for a greater length of fiber. This could lead to somewhat increased optical interaction (frustrated total reflection) between neighboring elements. The very fine-limiting visual resolution present in the central fovea precludes this as being a major contributory factor in vision. However, this does not rule out the presence of some interaction effects.

Several of the above-mentioned factors could have contributed to these results. Clearly, the directionality of any given group of receptors in a given sampling area is dependent upon the directionality of the individual cells and the distribution of
orientation about a mean. As suggested by Westheimer, the morphologic changes occurring in cones in the central fovea may be a major factor. Similarly, the shape of the foveal pit may be contributory. We have no reason to believe that receptor orientation in the tightly packed fovea is less orderly than that present in the peripheral retina. Any theory describing the Stiles-Crawford effect must account for the change in directional sensitivity between the fovea and parafovea.

Although the technique employed here is not readily adaptable to clinical application, it is useful to point out that the central foveal-parafoveal difference in directivity can be used as a test of central fixation in individuals having essentially normal receptor orientations. Since rho may vary with criterion and training, care must be applied in drawing conclusions when using a patient population unfamiliar with the test.

REFERENCES