An analysis of retinal receptor orientation
III. Results of initial psychophysical tests

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Retinal receptors are directionally sensitive for light entering different parts of the eye pupil. The central tendency of photoreceptor orientation at any retinal point can be inferred by carefully determining the position of the peak of the photopic Stiles-Crawford (S-C) function relative to the center of the entrance pupil of the eye. Transretinal orientation can be deduced by making such determinations at a number of points across the retina, and considering the collective distribution of the resultant peaks of the S-C functions in the entrance pupil. A new Stiles-Crawford apparatus was employed, and data were analyzed in terms of experimental models previously defined by Enoch and Laties. Laties’ earlier histologic finding of anterior pointing and graded differential orientation of retinal receptors has been confirmed psychophysically in vivo, and has been extended to the human. The anterior point toward which the receptors are carefully aligned was found to be most probably the center of the exit pupil of the eye. This finding has important implications in terms of the efficiency of utilization of the relevant visual stimulus by the receptor and provides us with considerable insight relative to the role of retinal receptor optics in vision.

Key words: retina, photoreceptors, retinal receptor orientation, Stiles-Crawford effect, directional sensitivity of the retina, graded differential orientation, entrance and exist pupils of the eye, anterior pointing tendency, center of convergence of orientation and directional sensitivity, sighting intersect.

The research presented here constituted tests of hypotheses derived by Enoch and Laties as a part of a theoretical discussion of retinal receptor orientation. The basic argument has been expanded by Enoch. While the hypotheses tested and the rationale behind this work will be generally and briefly summarized below, the reader is urged to refer to the previous papers—not only for the detailed derivation of the hypotheses, but for the discussion of the significance of receptor orientation as a basic organizing factor in vision.

This study was inspired by the careful histologic investigations of retinal receptor orientation conducted by Laties. In a number of species, he found that photoreceptor orientation varied systematically across the retina and the receptors tended...
Fig. 1. If all receptors point toward an anterior point in the eye, D, their orientation relative to the retinal sphere (having its center at point O) must continually vary in a gradual manner. That is, at (or near) the posterior pole of the eye, the receptors would be perpendicular to the pigment epithelium. The more peripheral the retinal point, the more the axis of the receptor would depart from the perpendicular to the pigment epithelium. Thus, collectively the photoreceptors would have a g.d.o. across the retina.

to point toward an (as yet undefined) anterior point in the eye. He concluded that the individual cells have a transretinal* graded differential orientation (g.d.o.) (Fig. 1). Three largely theoretical works by Laties, Liebman, and Campbell, Laties and Enoch, and Enoch and Laties have subsequently elaborated on Laties' initial histologic results. The g.d.o. has been demonstrated in additional species, including some having histologically nearly pure-rod retinas (Gecko gecko, albino rabbit, and albino rat) and near pure-cone retinas (chicken). It has been shown that g.d.o. is present before birth in the rhesus monkey and before hatching in the chick. Webb has demonstrated anterior pointing in the frog by x-ray diffraction techniques. The initial findings have been buttressed by unpublished, preliminary findings of Enoch, Laties, and Thorpe that the anterior pointing receptors in certain elasmobranch fish are oriented perpendicular to the tapetal plates (and pigment cells) which, in turn, have a graded differential orientation across the retina. Enoch has discussed the significance of having the receptors, which are known to function as fiber optics elements (waveguides), oriented in a manner such that they are essentially coaxial with the light rays constituting the relevant visual stimulus. The preliminary results of the study reported here also were incorporated into the same paper.

This study provides an independent psychophysical test of the histologic findings described by Laties. It also allows us to determine whether anterior pointing is present in the human. Further, the technique allows assessment in vivo of this receptor property. The precision of the method is such that an estimate of the anterior point toward which the receptors are directed is made.

The psychophysical technique employed utilized the photopic Stiles-Crawford effect. Stiles and Crawford demonstrated that retinal cones were more sensitive to light passing through the center of the pupil than to light passing peripherally through the pupil (which, after refraction, strikes the retina somewhat obliquely). Today it is generally accepted that the Stiles-Crawford effect has origin largely in the retina and it is associated with the optical properties of the retinal receptors and associated structures. In this paper, we assume that the peak of the measured photopic Stiles-Crawford function reflects the central orientational tendency of the population of directional sensitive photoreceptors contained within the test area. By assessing the position of the transretinal peaks of directional sensitivity relative to the center of the entrance pupil of the eye, it is possible to infer the nature of transretinal receptor orientation.

It is important to recognize the sensitivity of the Stiles-Crawford (S-C) phenom-
Enon. A change in the peak position of the S-C function in the entrance pupil of the eye by 1 mm. implies an orientational shift of only 2.5°. With care, determinations of the locus of the maximum of sensitivity can be made with a precision of less than 1° (e.g., note the range of test-retest determinations in the Results section).

In order to be able to adequately distinguish between the various orientational possibilities, Enoch and Laties\textsuperscript{1} and Enoch\textsuperscript{2} developed three working hypotheses describing retinal receptor alignment. It was assumed that one orientational "law" held for the entire retina. The three working hypotheses employed were: 1. All receptors point toward the center of the retinal sphere. This scheme would require the receptors to be perpendicular to the pigment epithelium at all retinal points. This was termed the center-of-the-retinal-sphere-pointing hypothesis (CPH). 2. All receptors are parallel to those lying on the pupillary axis (or fovea). While this hypothesis is clearly inconsistent with anatomic observations with respect to the retinal periphery (it would require the receptors beyond the equator to be doubled back upon themselves), it has been suggested as obtaining in the posterior region of the eye.\textsuperscript{10,11} This hypothesis is termed the parallel-pointing hypothesis (PPH). 3. All receptors are oriented toward the center of the exit pupil of the eye. Alignment with this point would provide the most efficient utilization of the relevant visual stimulus by receptors. This is assumed to be the anterior point suggested by the anatomic data of Laties.\textsuperscript{2} This hypothesis was termed the anterior-pointing hypothesis (APH).

\textbf{[NOTE:} (1) Enoch and Laties\textsuperscript{1} did not rule out the possibility of limited local variations existing within an over-all scheme, nor the possibility of an area such as the fovea having somewhat special properties.

(2) Because the fovea lies temporalward to both the effective optic and pupillary axes and because the pupillary axis has been used as the reference in the theoretical development,\textsuperscript{1,2} the latter has been used as the zero or reference axis in the present experiment.]

For any given retinal locus (except the one falling on the pupillary axis), the center, or the sensitivity maximum of the S-C curve would be expected to correspond to a different point of entry in the entrance pupil for each of the hypotheses. Thus, if tests were conducted at more and more peripheral retinal loci, the S-C centroids would remain centered in the entrance pupil under the APH, move more peripherally in the pupil in one direction under the CPH, and in the other direction under the PPH. These relationships are presented schematically in Fig. 2. \(\theta_1\) is the angle between the direction of the test line of sight and the pupillary axis. As angle \(\theta_1\) increases, the resultant test locus (\(P_n\)) on the retina moves more peripherally. Because of refraction, angle \(\theta_3\) is not equal to angle \(\theta_1\). Positions in the entrance pupil are denoted by \(a_k\) and are expressed in millimeters from the center of the entrance pupil. Positive values of \(a_k\) have been arbitrarily defined as those on the same side of the entrance pupil as the direction of angle \(\theta_3\), and negative values as those in the opposite direction (Fig. 2).

Point O is the center of the retinal sphere, E and D are the centers of the entrance and exit pupils of the eye, respectively. The mutual relationships among points E, D, and O and angles \(\theta_1\) and \(\theta_3\) have been discussed at length by Laties and Enoch\textsuperscript{5}, and Enoch and Laties\textsuperscript{1} (also see Appendix 1). The projection of the long receptor axes for each of the hypothesized receptor orientations at \(P_a\) is indicated (Fig. 2, right) by a broken line for the CPH and PPH and by the center, unbroken line for the APH. Schematic photopic S-C curves have been drawn with their centroids on these projections to depict the direction of the shift predicted by each hypothesis.\textsuperscript{1,2} Thus, for the case in which the receptors are aligned with the center of the retinal sphere (CPH), the centra of the S-C curves would
The figure (left) defines the test angle $\theta_i$ measured at the center of the entrance pupil of the eye. $\theta_i = 0^\circ$ falls on the pupillary axis of the eye (defined by determining the angle kappa, the angle between the pupillary axis and the principal line of sight). Since the pupillary and optic axis do not coincide, the projection of the pupillary axis in the eye suffers refraction (not shown). The projection of the pupillary axis generally intersects the retina near the posterior pole of the eye between the fovea and the optic nerve head. In this figure, $E$ is the center of the entrance pupil, $D$ is the center of the exit pupil, $O$ is the center of the retinal sphere, $F$ is the fovea, $P_n$ is the test locus, $\theta_i$ is the test angle, $\theta_3$ is the refracted test angle. See Appendix 1 and Reference 1. The right-hand figure shows a parallel bundle of rays incident at the left eye at an angle $\theta_i$, and being refracted without aberrations to test locus $P_n$. If the receptors at the test locus are oriented such that their central tendency is to point at the center of the exit pupil of the eye ($D$), then the resultant S-C function (parabolic dashed curve) will have its peak in the center of the entrance pupil ($E$). This is predicted by the APH. If the photoreceptors point at the center of the retinal sphere, $O$ (the CPH), then the peak of the S-C function will shift in the same direction as angle $\theta_i$ in the entrance pupil (displacement $a_3$, nasally in this example). Displacement of this sort has been arbitrarily termed $+a_3$. If all receptors are parallel to the refracted pupillary axis, then the S-C function would suffer displacement to the opposite side, in the direction opposite to angle $\theta_i$ of the pupil (predicted PPH) and this S-C centrum displacement will be considered negative ($-a_3$).

If the parallel pointing hypothesis obtained, the centra would be translated in the direction of negative $a_3$.

Enoch and Laties\(^1\) and Enoch\(^2\) have calculated predictor curves for progressive displacements of the S-C centra for progressively greater values of $\theta_i$ (Fig. 3). These curves indicate that under either the CPH or the PPH, the S-C centrum will move completely out of a 9 mm. entrance pupil for $\theta_i > 16^\circ$. Thus, by determining S-C functions for human observers for angles $\theta_i$ between $0^\circ$ and $25^\circ$, then plotting the centra against $\theta_i$, it was possible to determine which of the alternative hypotheses was most consistent with the data. The collective trend of the individual points is of significance, as well as the positions of the several S-C maxima. In this study, S-C peaks have been determined in two pupillary meridians (horizontal and vertical) for a number of retinal loci lying on the horizontal retinal meridian.

**Method**

**Apparatus.** As usually defined, an S-C apparatus requires two controlled Maxwellian view-light paths; with one beam passing through the center of (or some fixed point in) the entrance pupil of the eye and another beam being subject to displacement in the entrance pupil. Because small head and eye movements and other factors can alter measured functions markedly, the quality of data obtained is dependent upon careful control of the visual stimuli and the ability of the experimenter to relate observer position to the stimulus array very precisely. The current instrument (Fig. 4) incorporates some of the better features of earlier designs and adds certain additional control features. This instrument provides the following:

1. Ability to introduce an auxiliary source.
2. Constant monitoring of output of the light source.
3. Provision for translation of the source so that the area of the filament (beam) used for testing may be controlled.
4. Remote positioning of the background field aperture stop.
5. Capacity to vary both test and background apertures and field stops continuously in the z-y plane.
6. Field stop design such that they function as Badal optometers. By using stigmatoscopy\(^1\)2

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Fig. 2. The figure (left) defines the test angle $\theta_i$ measured at the center of the entrance pupil of the eye. $\theta_i = 0^\circ$ falls on the pupillary axis of the eye (defined by determining the angle kappa, the angle between the pupillary axis and the principal line of sight). Since the pupillary and optic axis do not coincide, the projection of the pupillary axis in the eye suffers refraction (not shown). The projection of the pupillary axis generally intersects the retina near the posterior pole of the eye between the fovea and the optic nerve head. In this figure, $E$ is the center of the entrance pupil, $D$ is the center of the exit pupil, $O$ is the center of the retinal sphere, $F$ is the fovea, $P_n$ is the test locus, $\theta_i$ is the test angle, $\theta_3$ is the refracted test angle. See Appendix 1 and Reference 1. The right-hand figure shows a parallel bundle of rays incident at the left eye at an angle $\theta_i$, and being refracted without aberrations to test locus $P_n$. If the receptors at the test locus are oriented such that their central tendency is to point at the center of the exit pupil of the eye ($D$), then the resultant S-C function (parabolic dashed curve) will have its peak in the center of the entrance pupil ($E$). This is predicted by the APH. If the photoreceptors point at the center of the retinal sphere, $O$ (the CPH), then the peak of the S-C function will shift in the same direction as angle $\theta_i$ in the entrance pupil (displacement $a_3$, nasally in this example). Displacement of this sort has been arbitrarily termed $+a_3$. If all receptors are parallel to the refracted pupillary axis, then the S-C function would suffer displacement to the opposite side, in the direction opposite to angle $\theta_i$ of the pupil (predicted PPH) and this S-C centrum displacement will be considered negative ($-a_3$).
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Fig. 3. On the basis of the models proposed by Enoch and Laties, the position of the centrum of the S-C curve can be predicted for varying angles \( \theta_i \). The APH requires that the centrum measured at several retinal loci stay centered in the entrance pupil. The predictor curve is line \( D \) at \( \theta = 0 \). For the CPH, the predictor is the curve designated \( O \) and for the parallel pointing hypothesis, the anticipated curve is marked \( || \). Note how quickly the peak of the S-C function would move out of the entrance pupil of the eye for the latter two possibilities. The dashed lines indicate the bounds of a 9.0 mm entrance pupil. Thus, the hypotheses may be tested within a very few degrees of \( \theta = 0^\circ \).

(8) An optical trick (which is believed to have origin with Professor H. Ripps) providing images of the increment and background apertures (as displayed in the entrance pupil of the eye) superimposed on the reticle display. Hence entrance pupil, corneal reflexes, and aperture images are continually subject to observation and control.

(9) Remote controls allowing the experimenter to locate the subject in \( x, y, \) and \( z \) directions. Additional adjustments provide rotations. A bite bar and head rest assembly is provided.

(10) Capacity for rotation of the observer's fixation about the center of the entrance pupil, using two collimated fixation devices with vernier settings of angle \( \theta_i \).

(11) An interferometric retinal resolution measuring device modeled after an instrument designed by Green and Cohen incorporated into the primary instrument.

(12) A special Burke and James f/1 copy camera with lateral magnification of \(-1.0X\) allowing recording of the display seen on the infrared image converter phosphor. An increment threshold-type display was employed, with the test field subtending a smaller angle than the background field. In a reversal of usual technique, the image of the test (increment) field aperture was held fixed in the entrance pupil and the projection of the aperture of the background field in the entrance pupil was translated during S-C function determinations (see Appendix 2). The background field was always recentered on the test field prior to determinations (after aperture translations), and its radiance was held constant throughout. A neutral density wedge located in the increment field path (controllable by either subject or investigator) allowed determination of the increment threshold.

This approach was utilized in order to minimize positional and other errors. That is, we sought to limit testing to the group of retinal receptors located at a specific retinal locus defined by angle \( \theta_i \). Ocular aberrations and refractive errors associated with aperture translation serve to displace the retinal image of the field stop when the aperture is translated in the entrance pupil. The field may be recentered by making an \( x-y \) field-stop adjustment. In addition, blur alters the boundary configuration of that field whose aperture is displaced. By using a large background field (the aperture of which was translated) which could be recentered, a small superimposed incremental field and an independent fixation source, it could be assumed that small recentering errors and/or changes in border configuration (remaining in spite of correction) of the translated background would be negligible.

The instrument is presented schematically in Fig. 4. Lens \( L_s \) collimates light from the primary source. This allows insertion of interference filters
Fig. 4. This is a schematic drawing of the instrument employed in this experiment. A tungsten ribbon filament lamp was employed as the source. Horizontal ribbon filaments were used for determinations of the S-C function in the horizontal meridian and vertical ribbon filament lamps were used for vertical meridian determinations. The filament was successively imaged in aperture stop and entrance pupil (Eₚ) planes. The field stops were imaged on the observer’s retina. S, light source; H, heat filter; L, lens; IF, interference or other wavelength control filter; ND, neutral density filter; M, CS, mirror, cover slip; M, FS, mirror, front surface; P.M., photomultiplier; F, focal point; M₁, M₂, motors; FS, field stop; SH, shutter; D, paired diffusers; θᵢ, an angle having origin at the center of the entrance pupil and measuring the angular subtense between the chief ray of the fixation unit and test (increment) field beam (angle kappa is added to the measured value for record purposes); IR, infrared image converter unit; and M, mirror.

NOTE: There are two collimated fixation units, and two infrared source units—only one of each is shown on this schematic drawing.

and/or the introduction of collimated light from an auxiliary source (or laser source used for alignment). Lenses Lₐ and L₂ₐ focus the ribbon filament on the two aperture stops. All lenses employed are achromats. Lateral magnification in this first stage of the instrument was -4.0X. Lenses L₂ₐ, L₃ₐ, L₄ₐ, L₅ₐ, and L₆ₐ all had the same focal length. Hence, magnification in the second stage of the device was -1.0X. The aperture stops were collimated by lenses L₈ and L₉ₐ. After recombination of the two beams at a beam splitter, the two apertures were imaged in the plane of the entrance pupil of the eye, Eₚ, by lens L₅ₐ. The light falling on the front surface mirror at F₅ₖ was redirected back toward the reticule plane. The display imaged at F₅ₖ is imaged with unit magnification after passing through L₅ₐ and L₆ₐ. By this means, the duplicate of the aperture display imaged in the entrance pupil is presented to the experimenter (in the reticle plane) for fine observation and control.

All beams passing the beam splitter located be-
Table I

<table>
<thead>
<tr>
<th>Subject</th>
<th>Sex</th>
<th>Age</th>
<th>Refraction</th>
<th>Snellen acuity (Without correction)</th>
<th>Horizontal angle kappa (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. B.L.</td>
<td>F</td>
<td>42</td>
<td>Plano</td>
<td>20/20-2</td>
<td>4.5</td>
</tr>
<tr>
<td>2. H.E.</td>
<td>M</td>
<td>16</td>
<td>+0.50 = +0.25 x 150°</td>
<td>20/15-1</td>
<td>6.0</td>
</tr>
<tr>
<td>3. S.H.</td>
<td>M</td>
<td>14</td>
<td>+0.25 x 95°</td>
<td>20/15-1</td>
<td>6.0</td>
</tr>
<tr>
<td>4. J.C.</td>
<td>F</td>
<td>19</td>
<td>-0.25 = +0.25 x 80°</td>
<td>20/15-1</td>
<td>5.5</td>
</tr>
</tbody>
</table>

Between shutters SH1 and SH2 are collimated. Lens L5 acts as the objective for an observation telescope, L6 serves a role similar to an erector and the IR image converter and Lens L4 act as an eyepiece. Actually, L3 is introduced in order to provide a means of making the measuring and control reticule visible. Lens L3 was made moveable in order to allow fine focus on the corneal light reflexes which are not imaged in the entrance pupil plane. In most instances these small images were readily identified without having to adjust the focus of this element.

Since the focal plane of lens L4 falls in the entrance pupil, the field stops of both light paths could be treated as classical Badal optometers. As is well known, increment threshold determinations are quite sensitive to the effects of blur.14 Of course, since the projection images of the apertures are small, there is relatively greater depth of field.

Because of the nature of the experiment proposed,1,2 it was necessary to rotate the fixation target and eye about the center of the entrance pupil rather than the sighting intersect of the eye. An approximate relationship between rotations of fixation about these two reference points is developed in Appendix 1.

The interferometric device coupled to the S-C instrument is described in a recent paper by Enoch and Hope.16 Since the publication of that paper, a major simplification suggested by Prof. Hans Goldmann has been introduced. The Ronchi grating and spatial filter similar to that of the Green and Cohen13 device have been eliminated, although point Flme is still imaged in the plane of Flme. Variable doubling is accomplished by translating a Wollaston prism over a path lying between lenses L4 and L5. Two polarizers oriented 45° to the doubling plane, one in front of and one behind the Wollaston prism, are necessary in order to obtain satisfactory interference. This modification provides an extended range of separations and therefore, fringes, eliminates the necessity for sensitive and artifact-inducing spatial-filter adjustments and readily allows testing for any fringe orientation.

Shutter SH3 is inserted in order to allow the experimenter to see the corneal reflexes induced by the stimulus pattern. The corneal reflexes caused by the IR sources were always visible when the entrance pupil was viewed. Shutter SH3 can be placed in the system when necessary adjustments are being made.

In this experiment, a Kodak Wratten filter (No. 23A) was employed. It was placed after L5 and provided an orange-red test and background field which favored photopic vision. Because it is a broad-band red filter, the aperture stop images formed in the entrance pupil (really located at Flme) and observed corneal reflexes were readily visible when observing or photographing the infrared image converter display (even at relatively low stimulus levels).

The background field was present continuously while the increment field was presented for 138 msec. of every 500 msec. The luminance of the fixed background field (centered on the entrance pupil of a normal observer) was 3.76 log milli-lamberts (ml.) (6V 18A General Electric tungsten ribbon filament source with filter in place). The rate of change of luminance of the incremental test field was set at 0.1 log unit per second. The projection of the round background aperture in the plane of the entrance pupil was 0.0804 mm.2 and the projection of the increment field aperture in the plane of the pupil was 0.0780 mm. The round background field subtended 4° 24’ at the center of the entrance pupil of the emmetropic eye and the increment field subtended 44’.

Experimental subjects. The left eyes of four essentially emmetropic observers were studied in this experiment (Table I).

None had a history of eye disease. Fundi and ocular media were normal. None had flat anterior chambers. Increment threshold data obtained at several test points for these subjects are presented in Fig. 5. The entry of the flashing test beam was central in the entrance pupil, while entry of the background beam was through the point of maximum sensitivity along the horizontal dimension. These data represent means collected over a period of weeks. The near identity of response suggests the presence of normal retinal function at the points tested.

Procedure. In this experiment, the center of the entrance pupil and the pupillary axis were used as primary references.2 Ordinarily there are arguments for the use of the corneal reflex, but the
Fig. 5. These increment threshold data were obtained from the four near emmetropic test subjects used in this experiment. NOTE: The values plotted at \( \theta_i = 0^\circ \) do not project down to the same point on the abscissa. The angle between the pupillary axis and the principal line of sight (angle kappa) varied for the different subjects. For simplification, angle kappa is always considered as \( 5^\circ \) for construction of subsequent figures, but data were taken at the true value of angle kappa. Those values are shown in the table giving the refraction of the subjects.

Differences in luminance due to the translation of the aperture of the background field in the entrance pupil (during measures of the S-C effect) did not exceed one log unit, the \( a \) priori condition of remaining on the linear portion of the increment threshold curve was met (Fig. 6). This same statement may be made for all angles \( \theta_i \) employed and for all four subjects.

Since all subjects were naive—both with respect to the task as well as to psychophysical procedures in general—extensive training was provided prior to actual data collection. Subjects' eyes were dilated prior to and during data collection sessions through the application of Euphthalmine (5 per cent).

A typical session consisted of, first, placing the subject in the forehead rest and dental impression. The subject was asked to view the fixation target, which was set at the test angle \( \theta_i \). The subject was then given approximately five minutes to adapt to the background field (centered in the entrance pupil). During this adaptation period (and throughout the test), the eye of the subject was carefully positioned through the use of the infrared viewing system and the \( x, y, \) and \( z \) controls. The eye position was manipulated until the pupil was sharply focused and positioned symmetrically around the center of the reticule upon which it was imaged. Initial positioning of the entrance pupil, therefore, utilized the pupillary boundary and the reticule markings; but monitoring and
corrections during a data collection run utilized a number of available criteria. Corneal reflexes from the infrared sources could be maintained in a constant position on the reticule. In addition, two pairs of adjustable calipers were symmetrically placed around the center of the reticule in both the vertical and the horizontal meridians. The relationships of the reference corneal reflexes were noted. The two infrared-source corneal reflexes proved to be excellent reference points for detecting and correcting horizontal movements, whereas the vertically placed calipers provided more sensitive control in that dimension. Reflections of the IR sources from the cornea proved to be poor reference points at larger angles \( \theta \), but horizontally positioned calipers provided quite adequate control under these conditions. Eye position was found to be easily controlled within approximately 0.1 mm. utilizing these various criteria.

When the subject’s eye was adequately positioned and the subject adapted, the Badal optometers were set at the best position to minimize blur. A data collection run was then initiated. A typical run consisted of determining the subject’s threshold for detecting the test flash using a modified ascending and descending method of limits. The average or mean value of a series of pairs (usually 4 or more pairs) of such determinations was taken as the subject’s threshold for a given test condition. A shutter was then placed before the subject’s eye, the image of the background aperture was translated in the entrance pupil and the procedure repeated, after recentering the background field stop and readapting the subject. The initial point of entry in a run was taken sometimes at the center of the pupil with subsequent translations being “laced” from side to side to the pupillary periphery and in the reverse order at other times. The test flash intensity was manipulated by depressing a key. An entire S-C curve was determined with a single seating of the subject. Test and retest data were collected in separate sessions on different days.

The retinal image of the background field was displaced slightly with translations of the image of its aperture in the entrance pupil. These displacements were corrected by x-y adjustments of the field stop. Thus, the test flash was always centered on the background field. When fixation was at or near the fovea, this correction required a simple judgment of centration on the part of the subject. For larger angles \( \theta \), the task was more difficult, as the subject was sometimes unable to judge whether or not the test flash was centered in the background. Under these conditions, the field stop was adjusted until the test flash was clearly out of the background on first one side, then the other, and the center point of these two positions was taken as the subjective center for the subject.

When testing more peripheral \( \theta \), it was found that frequent blinking on the part of the subject served to avoid local adaptation of the background field. Subjects were instructed to synchronize such blinking with changes in the test stimulus. The IR viewing system proved helpful in this regard, allowing the experimenter to aid in the synchronization. If there was evidence of change in the subject’s response criterion (infrequent), or unsteadiness on the part of the observer during a test run, data were rejected and the entire test run was repeated. Individual data points were rejected if an eye movement occurred either immediately preceding or at the time the subject activated the response key. Complete sets of test-retest data were collected for both horizontal and vertical scans of the entrance pupil at the several angles \( \theta \), lying in the horizontal retinal meridian.

**Data analysis.** The hypotheses tested in this research concerned predictions of the movement of the peak or centrum of the S-C functions for progressively greater \( \theta \)'s. Because of the special nature of these hypotheses, it was necessary to determine the position of the peak or centrum of the S-C function in the entrance pupil for each traverse at each angle \( \theta \). In order to accomplish this, the mean threshold for each point of entry in the entrance pupil was determined for each data run. The series of means obtained in a single run were fit by Stiles’ or Crawford’s equivalent exponential functions (differing only in base). Expressed in the nomenclature of this paper, these equations are,

\[
\Delta B = \Delta B_{max} 10^{-\rho (a + C^2)} = \Delta B_{max} e^{-\alpha (a + C)}
\]

where \( C \) is the point of maximum sensitivity in the entrance pupil. Since pupil extremes were avoided in testing, these simple relationships provided an adequate fit to the data. The peak or centrum of the best fitting S-C curve served as the individual datum point used below. Because the portion of the curve near the peak provides a less sensitive indication of the exact peak, curve fitting emphasized the “legs” of the curves, 1 to 3 mm. from the apex.

There is a temptation to reap a second harvest, i.e., to compare \( \rho \) or \( \alpha \) values for transretinal points. Overlooking the special features of the functions used to fit these data, it was felt best to deal with comparisons between the shapes of S-C curves at different retinal points only when the test is conducted at each retinal point by passing the variable aperture in the entrance pupil through the peak of the S-C function previously determined in two meridians (as performed in this experiment). Only by this means can subtle artifacts be eliminated. We hope to present such data in the near future.

*Also see Appendix 2.*
Fig. 7. This is a series of individual data sets (observer, B. L.). The background aperture was translated horizontally. Alternate data sets are indicated by open and filled circles. These data have been fit by Stiles' formula. The parameter $p$ provided by the best fitting curve is indicated to the right. The peak or centrum of each curve is indicated by a short vertical line.

*Data for the setting of $\theta_i = 25^\circ$ are translated upward on the graph by 0.2 log units to prevent overlap. **Similarly, data for $\theta_i = 0^\circ$ (pupillary axis) are displaced downward by 0.6 log units to prevent overlap. ***To minimize confusion, when plotting S-C maxima against $\theta_i$, angle kappa is always assumed to be 5°, although actual determinations may have differed slightly from this value. For example, for this observer, the measured angle kappa was 4.5°.

Results

Sample single sets of data (for subject B. L.) are illustrated in Fig. 7. S-C centra were determined for traverses of the background aperture horizontally across the entrance pupil. The data for the different test angles $\theta_i$ have been fitted by theoretical S-C functions varying only in the value of $p$ as indicated to the right of each curve. The vertical slash mark centered on each theoretical curve indicates the mathematically defined peak and centrum of the theoretical function. Great care was taken in fitting the theoretical curves to the data. A series of templates, varying in $p$, was used and the best fitting curve was selected.

It is quite clear in Fig. 7 that the centra of the curves did not change markedly with angle $\theta_i$. It was possible, through the use of finely gridded paper, to determine the $a_k$...
coordinate of each centrum with great accuracy. Comparable determinations were made for each of the four subjects at each test angle $\theta_i$, with the results seen in Fig. 8, A. In this figure the $a_k$ coordinates are plotted against angles $\theta_i$, with the format and scale being identical to those in Fig. 3. Fig. 8, B presents the same data but averaged over all four subjects. These data, either for individual subjects or the average, were clearly inconsistent with either the center-pointing hypothesis or the parallel-pointing hypothesis (CHP and PPH, predictor lines O and ||, respectively, in Fig. 3) but were consistent with the anterior-pointing hypothesis (APH—predictor line D).

The hypothetical derivations of predictor curves in Enoch and Laties\textsuperscript{1} and Enoch\textsuperscript{2} only considered one meridian. For angles $\theta_i$ in the horizontal meridian, the predictor curves are for the horizontal meridian. However, the direction of maximum sensitivity with reference to the entrance pupil of the eye can be defined for both the horizontal and vertical meridian. Brief consideration of the three models will show that for all three, for the points $P_n$ chosen along the horizontal meridian, one might expect the S-C peak to stay centered in the entrance pupil in the vertical meridian. This assumes that angle kappa in the vertical meridian is zero and that the S-C peak is not displaced so much that the basic nature of the function is altered. Thus, testing on the vertical pupillary meridian for horizontal retinal reference points does not differentiate between the proposed models. Rather, it allows one to determine if yet another model is required.

The experiment was repeated on the three available subjects, only this time the aperture of the background field was varied in the vertical meridian. The same angles $\theta_i$ and corresponding reference retinal points $P_n$ along the horizontal retinal meridian were tested. Data for the vertical traverses are presented in Fig. 9. The individual records (Fig. 9, A) did not show any systematic tendency to depart from

![Fig. 8, A. Data taken from the left eyes of four subjects are displayed in this figure. The $a_k$ coordinates of the centra of the individual S-C curves are plotted here. The $a_k$ values have been determined for a number of different retinal points ($P_n$) in the horizontal retinal meridian. The mean value is plotted at each point as well as the total range of values obtained on a test-retest basis. Angle $\theta_i$ is measured from the pupillary axis of the eye, rather than from the fovea. Data for Point 1 in Fig. 10 are not shown here, but appear below.](image-url)

![Fig. 8, B. The mean across subjects whose individual mean data is plotted in Fig. 8, A is displayed in this figure. The total range of the raw values obtained from the four emmetropic subjects is also indicated. It is clear that the lines linking the mean values are essentially parallel to the predictor curve (line D, Fig. 3). Predictor line D corresponds to the anterior pointing hypothesis as defined in Enoch and Laties.\textsuperscript{1}](image-url)
Fig. 9, A. Data obtained by traversing the aperture of the background field in the vertical meridian of the pupil. The same retinal points (Ps as defined by angles $\Theta_1$) along the horizontal retinal meridian were tested. The maxima of the S-C functions of three of our four subjects are indicated. The points are mean values, the vertical bars indicate total range of test-retest values of S-C peaks. Subject J. C. was not available for this series of tests. Since the entrance pupil designation of $\alpha$ in the horizontal meridian carried a specific sign convention which was not defined for the vertical meridian, it has been replaced by "mm, up or down" on the ordinate in this figure.

Fig. 9, B. These are the means across subjects whose individual mean values are shown in Fig. 9, A. The vertical bars indicate the total range of raw data (distribution of S-C peaks) for the three subjects available for these tests. The line connecting the mean values essentially parallels the predictor line D.

the approximate center of the entrance pupil. If anything, the data indicated that there was less intersubject disparity in receptor orientation at more peripheral $\Theta$s, as evidenced by the tendency of the individual records to converge with increasing $\Theta$s (right, Fig. 9, A). The convergence was notably toward the vertical center of the entrance pupil. For the average over-all subjects (Fig. 9, B), the vertical centra were quite close to the center of the entrance pupil for all $\Theta$s. It seems doubtful that another working hypothesis would be required.

Combining the data from the vertical traverses (Fig. 9, A) with those presented...
Retinal receptor orientation

earlier for the horizontal traverses (Fig. 8, A) allowed us to determine the two dimensional centrum of the S-C functions for each angle $\theta_j$. The two dimensional plots for the individual subjects (Fig. 10) indicated that the S-C peaks were clustered within a small area of the pupil, regardless of $\theta_j$. These areas were about 1 mm.\(^2\) (though slightly larger for subject H. E.). No mean of the seven points for any subject was more than one millimeter from the center of the entrance pupil.

These data have been replotted in Fig. 11 on a 9 mm. entrance pupil. The mean across all $\theta_j$s and subjects fell very close to the geometric center of the dilated entrance pupil. The areas of the three smallest circles which would contain all points for each of the three subjects were calculated. None of the areas comprised more than 2.8 per cent of the total area of a 9 mm. pupil.

The data presented above included one angle $\theta_j$ not presented in the primary data in the horizontal meridian. $\theta_j = -5^\circ$ was investigated following Laties'\(^2\) observation that the systematic orientational scheme was sometimes disrupted in the region immediately surrounding the optic papilla. $\theta_j = -5^\circ$ was near the edge of the blind spot. There did not appear to be a great deal of difference in the position of the centra of the S-C curves for this position (points "1", Fig. 10) except horizontally for subject B. L. In this case, point 1 was separated from the remainder of the cluster by about 0.75 mm., which was hardly more than the spread of points along the vertical meridian. However, in no case did point 1 fall near the individual mean value (point 0).

This may reflect the possibility that, in life, there may be special pressures exerted in the region of the optic papilla.

Discussion

There are several criteria which may be used to judge the match of the data pre-
Fig. 11. An arbitrary dilated 9 mm. entrance pupil is indicated. The small cross indicates the center of the pupil and corresponds to Point E in Fig. 2. The data points are values 1 through 7 for each observer taken from Fig. 10. A grand mean across three observers, 0, has been plotted and fell quite close to the pupil center.

The evidence presented in Figs. 8-11 with the individual working hypotheses. First, one may ask how well do the individual S-C maxima center in the entrance pupil? Second, when joining the individual maxima, as in Figs. 8, A or B, one may ask which predictor curve (Fig. 3) do the joined points seem to follow? Third, one may ask if there is some apparent systematic (1) shift or (2) clustering of points in the entrance pupil of the eye. No matter which criterion one chooses, it is apparent that the APH most closely predicts the results reported in this study. Further, the evidence presented, although based on a small subject sample (but a massive data set), indicates that, for a normal population the point toward which the receptors are aligned transretinally is most probably the center of the exit pupil of the eye, D. Thus, we believe we have defined the anterior point suggested by Laties’ work. We have presented clear evidence for careful transretinal orientation of retinal receptors. Clearly, from these results, there must be a g.d.o. (Fig. 1) of cone receptors in the intact human eye. In previous histologic studies and x-ray diffraction experiments, it is clear that receptors in rod-dominated retinas exhibit the same trait in this regard as cones in cone-dominated retinas. Similarly, in well-mixed retinas, rods show the same directional properties as their neighboring cones. One would expect then, if adequate tests were available, to see psychophysical evidence of g.d.o. of rods in the intact human eye.

Such precision of alignment with a remote point, across more than 30° of retina, probably cannot occur by chance (Fig. 1). The demonstrated orientation of central tendencies of populations of receptors is not random, and would be difficult to explain as the effect of simple receptor packing. As pointed out in the introduction, the approximate arrangement has been shown
to be present prior to birth or hatching.\textsuperscript{2} The definition of factors establishing, contributing to, and maintaining the alignment of photoreceptors is clearly the most pressing and challenging problem in this line of investigation.\textsuperscript{2} The study of receptor mal-orientation as a form of pathology is another aspect of this general problem. Research intended to clarify some of these issues is currently underway.

There are small disparities in the mean of all test points relative to the center of the entrance pupil for each subject. Two possible hypotheses explaining the discrepancies might be considered: (1) The dilated entrance pupil of the eye may not be concentric with the normal or constricted pupil. Data pertaining to this question will be reported shortly by Enoch and Hope.\textsuperscript{21} (2) The angle kappa has a small (as yet unconnected) vertical component possibly altering defined reference points.

A limited nasal bias in three of the four subjects can be seen in Fig. 8, A. Thus, the combined mean (Fig. 9, B) shows a displacement from the center of the entrance pupil of a bit less than 0.5 mm. The relationship (based on ray trace) between displacement in the entrance pupil and angular orientation is 1 mm. = 2.5°. The mean angular displacement here is only about 1.0°! The question which must be emphasized is how such precision of alignment, relative to a remote reference point, is achieved by the receptors?

One might wish that additional data existed similar to that described in this paper. As pointed out previously, Aguilar and Plaza's study, while pertinent, allowed no clear cut conclusions to be drawn relative to the hypotheses developed by Enoch and Laties.\textsuperscript{3} Crawford\textsuperscript{18} presents data which seem to support the findings presented here, although his data at 0° and 5° for subject B. H. C. are somewhat inconsistent.\textsuperscript{8}

The fact that the photoreceptors trans-retinally are aligned essentially coaxially with the center of the exit pupil (which is imaged in the center of the entrance pupil) has considerable meaning for the visual system. This question has been treated in depth by Enoch.\textsuperscript{2} This property implies that the optical system-detector system of the eye has evolved in such a manner that it makes optimum use of the relevant visual stimulus passing through the pupil. It suggests that the receptor, acting as a fiber optics element (waveguide) serves to select, collect, and guide light, having origin in the environment and passing through the pupil of the eye, to the oriented photolabile pigment. The fact that all fiber optics elements have a limiting aperture serves to help the receptor reject the everpresent stray light from the integrating-sphere-like eye. It is aided in this role by the sheathing dark pigment contained in the microfibrils and cell bodies of the pigment epithelium.

In conjunction, the orientation of receptors trans-retinally, the directional transmissivity and sensitivity of the receptors, and the screening effect of the surrounding pigment necessarily constitute a most basic and precise organizing orientation and directional sensitivity factor in vision. The center of convergence of directionality and sensitivity defined by these influences (estimated by the individual point 0 values in Fig. 10) is also the effective center of the aperture for the retina. Most efficient function depends on coincidence of this aperture with the center of the exit pupil.\textsuperscript{1}

REFERENCES


Appendix 1

Ordinarily in experiments where angle of fixation is varied over a substantial range, one uses the sighting intersect\(^{22, 23}\) as the reference for measuring the angle of eccentricity of fixation. The sighting intersect is that point in space where lines corresponding to the various directions of the primary line of sight cross at a common point. Actually, the definition of this approximate point is complex. The reader is referred to Reference 22 for a discussion of the problem. It becomes desirable to define a relationship between rotation about the sighting intersect versus the center of the entrance pupil of the eye, because the latter was used in this study.

In order to greatly simplify the argument, it will be assumed that point \(O\), which is the center of the retinal sphere (Fig. 12, A), corresponds to the sighting intersect and the center of rotation of the eye. Also it will be assumed that the fovea lies on the optic and pupillary axis, and the Gullstrand schematic eye is emmetropic. These assumptions allow us to use the model presented in Fig. 1 of Enoch and Laties\(^1\) for the analysis (reproduced here in Fig. 12, A). Here we seek to define a relationship between \(\theta_1\) and \(\phi\) in that model. Let \(r\) equal the radius of the retinal sphere and \(d\) equal the distance between the center of the exit pupil and the center of the retinal sphere (point \(O\)). Representative values are \(r = 11.4\) mm. and \(d = 9.312\) mm. \(\theta_1\) is the angle between the chief ray leaving the center of the exit pupil and the optic-pupillary axis. \(\phi\) is the angle between the optic-pupillary axis and the line connecting the center of the retinal sphere and the retinal test point \(P_2\). \(\theta_1\) is the angle between the chief ray incident at the center of the entrance pupil (and destined to intersect the retina at point \(P_2\)) and the optic-pupillary-fixation axis.

\[
\theta_1 = \phi - \theta_3
\]

\[
\frac{d}{\sin (\phi - \theta_3)} = \frac{r}{\sin \theta_3}
\]

\[
\phi = \theta_3 + \arcsin \frac{d}{r \sin \theta_3}
\]

From Enoch and Laties’ Formula 1 (derived by ray trace), valid only for small angles,\(^2\)

\[
\theta_1 = \theta_3 (1.2144).
\]

Substituting for \(\theta_1\) and \(d\) and \(r\),

\[
\phi = (0.8235) \theta_3 + \arcsin (0.8169) \sin (0.8235) \theta_3.
\]
Solving this equation reveals an essentially linear relationship for small angles of $\theta_i$. This is readily understood if one glances at Fig. 12, B. Here point $P_n$ approaches $F'$ (focal point and fovea). In this case, consider the model as simply a pair of right triangles. In Fig. 12, B,

$$\theta_i = \frac{P_n F'}{d + r}$$

and

$$\phi = \frac{(d + r)}{r} \theta_i^*.$$

Again inserting the relationship for $\theta_i$ (from above) and substituting the appropriate values,

$$\phi = 1.496 \theta_i.$$

Thus when $\theta_i = 0^\circ$, $\phi = 0^\circ$; when $\theta_i = 5^\circ$, $\phi = 7.48^\circ$; when $\theta_i = 12^\circ$, $\phi = 17.95^\circ$; etc. Obviously, this simple relationship tends to break down at larger angles and the more precise function (also subject to limitations) derived above must be substituted.

### Appendix 2

In this study, our intent was that all data, taken at a given angle $\theta_i$, were obtained from the same retinal locus. To achieve this goal, not only was the observer's position constantly monitored, but changes were made in the standard S-C test procedure in order to minimize induced positional artifacts. However, when using the technique outlined in this paper, a significant artifact may be encountered.

Let Fig. 13 represent a single mechanism, photopic increment threshold curve. In the region of the curve defined by luminance levels $B_3$ and $B_4$, the Weber fraction, $\frac{\Delta B}{B}$ = Constant. Below the straight line, “Weber”, portion of the function, $\frac{\Delta B}{B}$ becomes variable, finally reaching asymptote at $\Delta B$ = Constant at low levels of background luminance $B$.

Let us also assume that the hypothetical observer whose data is shown in Fig. 13 has a normal S-C function, and that it peaks in the center of the entrance pupil. When the aperture of the background field is translated in the entrance pupil, while radiance remains constant, perceived brightness of the background field varies because luminous efficiency changes because of the S-C effect. Thus, the background, having luminance $B_4$, when its trace in the entrance pupil is centered, has a lower luminance $B_3$ for peripheral aperture location in the pupil. A change in luminance from $B_4$ to $B_3$ results in a reduction in the increment threshold from $\Delta B_1$ to $\Delta B_2$ with...
Fig. 13. This is a hypothetical single mechanism, increment threshold curve. It relates the just detectable light flash luminance $\Delta B$ to background luminance $B$.

\[
\frac{\Delta B_1}{B_1} = \frac{\Delta B_2}{B_2} = \frac{\Delta B_3}{B_3} = \frac{\Delta B_4}{B_4}
\]

Let us now consider the case where the initial adaptation level is reduced such that the luminance of the background field (aperture centered in entrance pupil) falls at $B_2$. Repeating the test, although

\[
B_2 - B_1 = B_4 - B_3
\]

$\Delta B_1 - \Delta B_1$ is not equal to $\Delta B_3 - \Delta B_3$, and $\Delta B_2 - \Delta B_2$ is not equal to $\Delta B_4 - \Delta B_4$. Thus, although the underlying directional sensitivity mechanism may be identical for the two test situations, the resultant increment threshold curve would vary markedly and a family of quite different apparent Stiles-Crawford functions would be plotted at different adaptation levels. At the lower background adaptation levels, the resultant increment threshold curve would be quite a bit flatter, although the peak would not be translated.

Clearly, the shape of a S-C function taken (using the method outlined) is quite dependent upon the portion of the increment threshold curve used for determinations. The nature of the flattening effect, the point of onset of relative flattening as a function of pupil displacement and the degree of flattening are strictly dependent upon the initial adaptation level. In this study, all data were obtained with the total range of measurement falling on the “Weber portion” of the increment threshold curve—such curves being plotted at each test angle $\Theta_1$. Only when all data fall on the Weber portion of the curve and only when differences in the Weber fraction constant are considered, can S-C curves taken at different wavelengths or test loci be compared.