Active Alignment of Vertebrate Cone and Rod Photoreceptor Waveguides: Might This Serve As A Useful Fiber-Optics Model?

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ABSTRACT

Some years ago, the speaker demonstrated that vertebrate retinal photoreceptors are fiber optics elements and waveguides, and he succeeded in defining many of their properties. For a summary of much of this research, please see the reference to Enoch and Tobey listed below (Reference 4). Included are studies of photo-receptor alignments and maintenance of receptor alignments across the retina in normal and abnormal human eyes. With very rare exceptions, rod and cone photoreceptors across the retina align remarkably and precisely with the center-of-the-exit-pupil-of-the-optics-of-the-eye throughout the lifetime of the individual! And within a modest period of time (a day or a bit more), it proved possible to alter that photoreceptor alignment by physically displacing the pupillary aperture; and with recentration of the eye pupil, these alignments recovered their original state.

Here, the author asks, "*Might advantage be gained by developing alignment sensitive, photo-activated, waveguide/fiber optic units? That is, might comparable mechanisms be adapted in a useful manner to non-biological fiber-optics applications? Since such characteristic responses have been clearly of great value for biological species; might similar designs serve other important roles?*"

Key Words: Fiber Optics, Retinal Photoreceptors, Function of..; Retinal Receptor Waveguide Modal Patterns and Fiber Optics Properties; Evolutionary Mechanisms; Active Alignment of Photoreceptors with the Exit Pupil of the Eye (and Rare Failures of That Mechanism).

Current Developments in Lens Design and Optical Engineering X, edited by Pantazis Z. Mouroulis, R. Barry Johnson,
Virendra N. Mahajan, Proc. of SPIE Vol. 7428, 74280F · © 2009 SPIE · CCC code: 0277-786X/09/$18
doi: 10.1117/12.828470

HERE, LET US CONSIDER SOME SALIENT FEATURES OF PHOTO-RECEPTORS AS FIBER OPTICS ELEMENTS AND WAVEGUIDES:

The writer will consider a number of examples of bio-mechanisms encountered in vertebrate eyes of animals and of humans. Emphasis will be upon how photo-receptor waveguides/fiber-optics elements function.

The Discovery of a Vertebrate-Type Photoreceptor Outer-Segment in a Brain Area Serving the Circadian Rhythm in an Ancient Aquatic Worm!

Today, we may be on a threshold leading to an understanding of the critical transition which occurred among visual-detectors in the development of animal species. Invertebrate species pre-dated vertebrates for a long period of time. Simply stated, invertebrate visual systems and photoreceptors are quite different from those found in vertebrates, but many similar functions have evolved. Thus, critical questions arise: how did vertebrates emerge, and how did invertebrate eyes evolve into vertebrate forms?

Today, there still exist very ancient and primitive aquatic annelid worms. Not surprising, they have invertebrate-types of eyes. Recently, there were found apparent vertebrate-type photoreceptor-outer-segments (!) located within the brain area serving circadian-rhythms of these worms! See: Detlev Arendt, K. Tessmar-Raible, H. Snyman, A.W. Dorresteijn, T. Wittbrodt. Science Oct.29, 2004, 306(5697): pp. 869-871,[1] and for a discussion in the same issue, turn to pp. 796-797 in that issue of Science. For a brief review of this work, please see Jay M. Enoch: A Remarkable and Historic Find: The Earliest Evidence to Date of a Vertebrate Retinal Photoreceptor in an Invertebrate Brain! “Hindsight” (J. Optometry History Society) Vol. 36 (#2, April): pp. 36/9-36/10, 2005.[2]

An Important Brief Discussion by J.J. Gibson in His Book, "The Senses Considered As Perceptual Systems" (Houghton-Mifflin, Boston, 1966, pp. 163-165).[3]

In this book[3] Gibson sought to describe and to differentiate simply the nature of the visual system of the invertebrate eye from that structure and form which evolved in the vertebrate eye. He distinguished between (a) the acceptance of light rays by a convex compound eye of the type commonly found in invertebrates, that is, in such eyes, the individual receptor units "embrace a converging sheaf of "pencils" of light and register the differences in excitation incident in the several directions sampled", and (b) the acceptance of light rays by a concave vertebrate-type eye. In the latter case, the eye accepts a converging sheaf of (chief) light-rays, but "the receptors register differences in individual directions by utilizing an inverted image formed by the lens system of the eye".[3] See Fig. 1, which duplicates the figure shown in Gibson's book; the same figure is also to be found in Ref. 4, p. 129.[4]

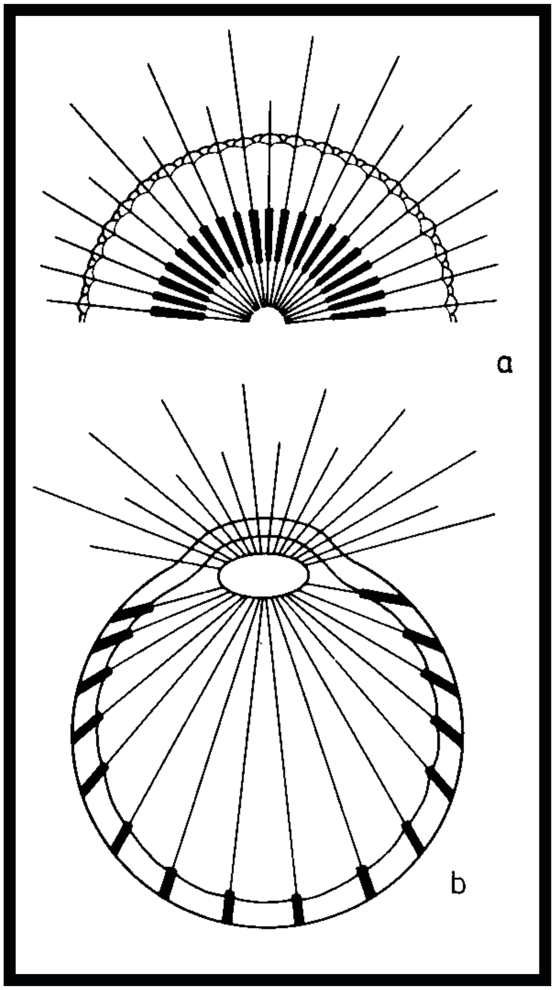


Fig. 1 (Courtesy of J.J. Gibson and Houghton-Mifflin Co.)

Prof. J.J. Gibson died quite a number of years ago. Shortly before his death, JME met him at a meeting held at the Waldorf-Astoria Hotel in New York City. He asked Gibson how he came up with this model, including the orientations of photoreceptors in vertebrate and invertebrate eyes? Gibson replied that he really didn't know, but added, this model simply made good sense to him. Let us consider some associated underlying and related concepts and assumptions:

1. Located in physical space about "an animal observer" is an array of primary and secondary light sources which serve as stimuli for his/her visual system. The animal needs to know *both* where an object-of-regard is located in that space within the observer's (the animal's) visual field, and where he/she is located relative to such objects? The observer also must consider if that object is moving, and towards where it is heading, and whether he/she (the observer) is also moving, and where he/she is going (heading)? Thus, the animal needs to detect and locate those stimuli falling within its field of view, and to relate those detected objects of regard to its own perceived position in space, and subsequently to use that information to define it's future course of actions (e.g., ignore, acquire, remember, fight, flee/flight, etc.).

2. For simplicity, assume there is a fixed relationship between an observed sense of direction and the retinal locus stimulated. Implied here is that the animal is able to differentiate different directions in space in an orderly manner, and that it can interpret where it is in space relative to other objects.

3. This ability implies that the pertinent signal exciting the retina at a given point is identifiable, and a trace of it is retained for central data processing. Furthermore, directionally-sensitive rod and cone photoreceptor waveguides function most efficiently if they are axially aligned with the aperture of the eye.

4. Thus, it becomes necessary to relate that aperture and the alignment of the photoreceptor waveguide/fiber-optics-element relative to the center of the iris aperture. It is important to think of the retinal receptor-pupillary system: (a) as a functional unit designed for optimization of light capture of quanta (the luminous signal) having origin at a given locus in physical space, and (b) that this unit also efficiently/effectively rejects stray-light noise (e.g., within the integrating-sphere-like eye).

Please consider the very substantial development required in order for these two rather separate eye forms and visual systems to evolve!

THE PRECISE ALIGNMENT OF RETINAL RECEPTORS IS THE RESULT OF AN ACTIVE SYSTEM FOR ORIENTATION!

Here we will consider the nature of photoreceptor alignments, as well as the maintenance of the alignment of retinal photoreceptors in the vertebrate eye with emphasis upon the human eye. Based upon such diverse data, one can infer that there is an active feedback system for alignment of these photoreceptors. Note, except for the initial presentation of histological evidence, there is no particular order to aspects of the problem-set considered in this section of this paper.

1. Alignments of photoreceptors across the vertebrate retina (Histology)

The model drawn by J.J. Gibson[1] rather well characterizes the existing scheme which has evolved (Fig.1, and Refs 3,4). Please compare natural photoreceptor alignments in the retina at the *posterior pole of the eye* (the top parts of Figs. 2-4), and in the far peripheral portions of the same retina (the bottom portions of Figs. 2-4) in three different species of vertebrates presented. They are: Fig. 2, a monkey retina (this monkey retina was chosen, in part, because it is rather similar to the human retina); Fig. 3, a cold-blooded vertebrate animal (*gecko gecko*), which is a form of lizard; and, Fig. 4, a highly rod-dominant mammalian retina (the albino rabbit). These fine micrographs of quick frozen and thinly sliced retinal sections were kindly provided by Prof. A. Laties, M.D., Department of Ophthalmology, U. of Pennsylvania College of Medicine, and were given to Enoch by him for publication in Enoch's research papers.[e.g.,4] Laties further verified this basic design feature by assembling large photo-montages of such retinal receptors all about a given retina in each of these and other species. Enoch and co-workers, using psychophysical techniques, further pursued this set of issues in detail (with similar results), but those efforts are not the subject of this paper. That work is discussed in Ref. 4, Chapters 3-5 (the main argument considered here is to be found in Chaps. 3,4), etc.

Also in this regard, and also of special interest, is an added-design-feature found in a number of animals exhibiting a *tapetum lucidum* (i.e., back-reflective surfaces, e.g., as in a cat's eye) located behind the photoreceptor outer-segments. Many tapetal "plates" or layers are also aligned in order to optimize their reflective properties. Tapeta make possible more efficient back-reflectance of the radiant stimulus energy through the photoreceptors (for simplicity, think of a plane mirror), and *this serves to enhance detection of the signal (as a second pass of this radiant energy back through the detector fiber optics/waveguide cells)*. Laties demonstrated this added feature ably in the "dogfish" (a marine animal in the shark family), and revealed additional associated dynamic features which accompany this phenomenon at high and low light levels (Ref. 4, pp. 142-144)..

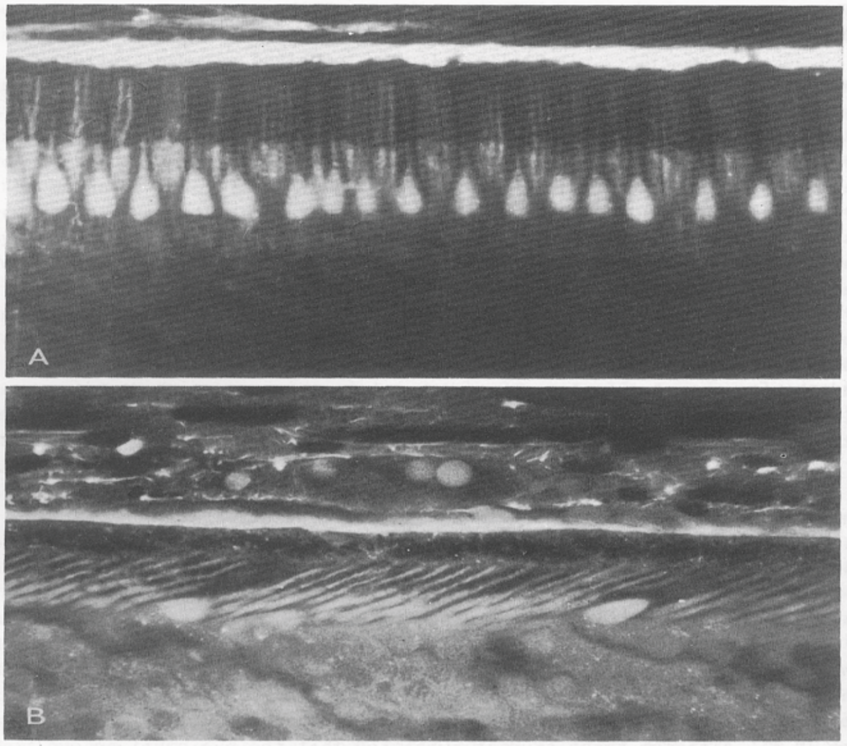


Fig.4.2a,b. Fluorescence micrographs of monkey retinas. (a) Receptors near the posterior pole of the eye. Cones can be readily distinguished from rods and are more plentiful in this part of the retina than in the periphery. In this retinal area the receptors are nearly perpendicular to the pigment epithelial layer. (b) In the periphery the receptors are aligned with an anterior ocular point, most probably the pupillary aperture. Note the relative dimensions of inner and outer segments of rods. Light would pass from below. (Courtesy of A. Laties, University of Pennsylvania, Philadelphia, and the Polytechnic Institute of New York, NY)

Fig. 2

Fig.4.3a,b. An example of differential orientation of photoreceptors at two points along the same meridian of a Gekko *gekko* retina as shown by fluorescence microscopy. (a) Posterior pole. (b) Peripheral area. Light would strike the receptors from below. (Courtesy of A. Laties, University of Pennsylvania, Philadelphia, and C.V. Mosby Co., St. Louis, MO)

Fig. 3

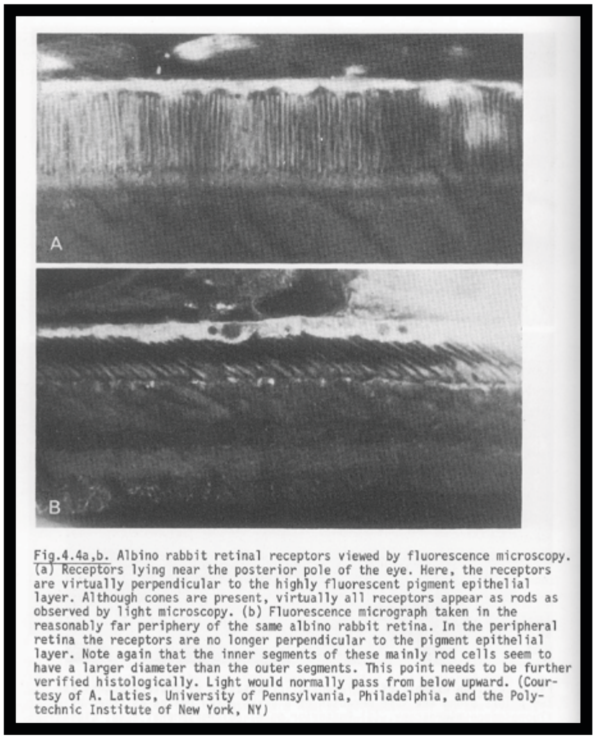


Fig.4.4a,b. Albino rabbit retinal receptors viewed by fluorescence microscopy. (a) Receptors lying near the posterior pole of the eye. Here, the receptors are virtually perpendicular to the highly fluorescent pigment epithelial layer. Although cones are present, virtually all receptors appear as rods as observed by light microscopy. (b) Fluorescence micrograph taken in the reasonably far periphery of the same albino rabbit retina. In the peripheral retina the receptors are no longer perpendicular to the pigment epithelial layer. Note again that the inner segments of these mainly rod cells seem to have a larger diameter than the outer segments. This point needs to be further verified histologically. Light would normally pass from below upward. (Courtesy of A. Laties, University of Pennsylvania, Philadelphia, and the Polytechnic Institute of New York, NY)

Fig. 4

2. In a human observer we can readily determine the orientation tendencies of photo-receptors being sampled. The Stiles-Crawford Effect of the First Kind (SCE-1) can be used for this purpose. Examples of remarkable stability in these measured visual responses over time will be considered.

In order to define properly the orientation tendencies of photoreceptors being sampled in an experiment, it is very useful to utilize tests of The Stiles-Crawford Effect of the First Kind (SCE-1) = "The Directional Sensitivity of Retinal Photoreceptors" = the luminous efficiency of the eye for light entering different points in the entrance pupil of the eye.[4-7] For example, JME will ask, *where is the peak of sensitivity directed in a given test meridian f*or beams of light entering the entrance pupil of the eye and imaged at the retinal locus tested? Using such data, one can relate points in the entrance-pupil-of-the-eye to loci in the exit-pupil-of-the-eye, and, based upon such assessments/data, we can deduce where the alignment of the photoreceptors is/was directed. To some extent, it is also possible to assess the quality of the measured function (the shape of the resultant function, the stability of data, the presence of side-lobes, sub-peaks, quality of fixation, etc.).

A useful relationship can be deduced by performing a ray-trace (making use of a representative schematic eye). Schematic eyes are "best estimates" of properties [curvatures, indexes of refraction, position of, and thicknesses of lens elements, etc.] of measured eyes. Using this approach, a 2.5° change in angle of incidence at the retina = 1 mm displacement of the SCE-1 function in the entrance pupil of the human eye.

2A. There is remarkable stability in measured SCE-1 functions over time. Two interesting data sets are presented here as examples.

In normal observers, photoreceptor alignments prove to be remarkably stable over time (i.e., a time period measured in months or years, or a lifetime!). A good example of this is seen in Fig. 5, which presents repeated sets of measurements of the Stiles-Crawford Effect of the First Kind (SCE-1) on the eye of the late W.S. Stiles, who served as the subject. These test data were taken six months apart at the same retinal test locus, at his point of fixation (*fovea centralis*).[6] Also, two different test procedures were employed. These measured results proved to be almost identical in each instance.

As a second example, a quite remarkable experiment was conducted on a well-trained observer, Theodore Grosvenor (T.G.). This "gentle man" recently died. He was first measured by JME when he was a graduate student in 1956. Measurements were repeated 37/38 years later in 1993. In the interim, T.G. had monocular vitreous detachments in each eye. This is a common occurrence with aging; i.e., a contracting and gelatinous vitreous-body, which fills the area of the eye behind the eye lens and in front of the retina, separates from the inner surface of the retina; and there are often associated traction effects. T.G. also later had a retinal detachment, which involved ¼ or more of his left retina (his more normal eye). It was surgically repaired some months before the second set of data were taken. In 1956, T.G.'s visual acuity measured 20/20 in his left eye, and 20/40- in his right eye. In 1993, his visual acuities were 20/25 to 20/30 in his left eye, and 20/60 in his right eye with some apparent loss in image contrast. Please see the source documents[8,9] and Fig. 6.

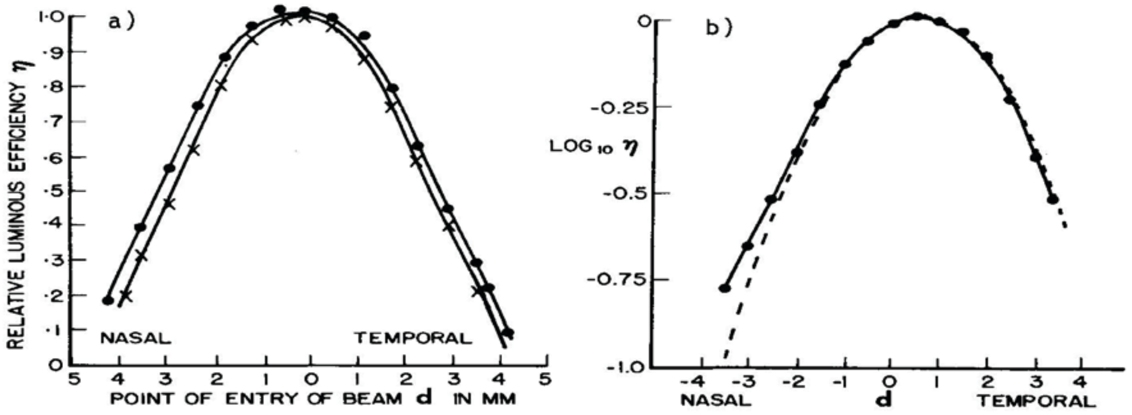
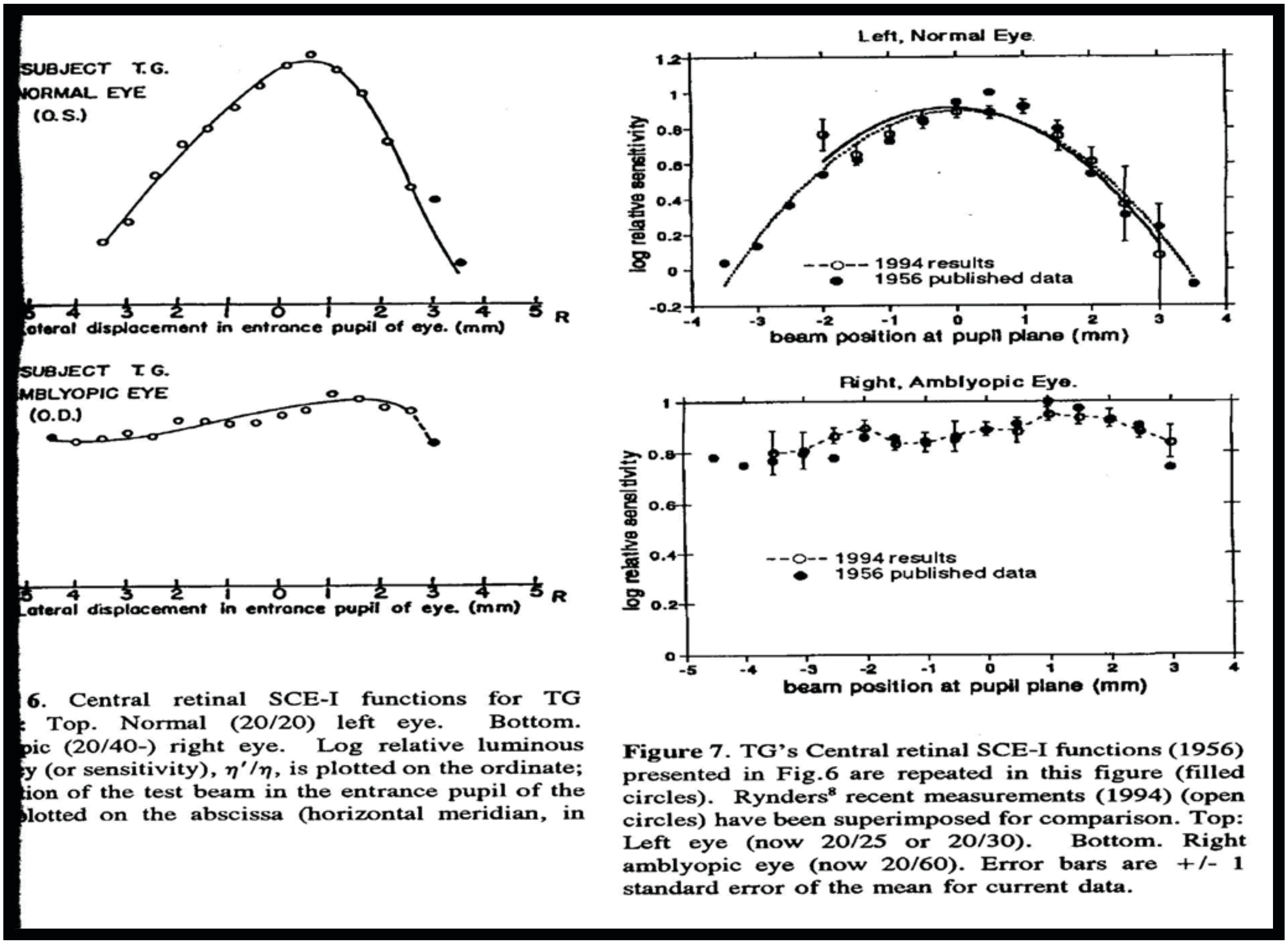


Fig.3.1. (a) The relative luminous efficiency (η) of a foveally viewed target as a function of the horizontal pupillary entry position of the beam. The data are for W.S. Stiles's left eye using a flicker photometric technique. The two curves were taken six months apart [3.1]. (b) Log relative luminous efficiency (log η) of a foveally viewed target as a function of the horizontal pupil entry position of the beam. Data are for W.S. Stiles's left eye using a photometric matching technique. The solid line is drawn through the data points; the dashed line is the best-fitting parabolic equation as described in the text [3.4]

Fig. 5



6. Central retinal SCE-I functions for TG
: Top. Normal (20/20) left eye. Bottom.
pic (20/40-) right eye. Log relative luminous
y (or sensitivity), η'/η, is plotted on the ordinate;
ion of the test beam in the entrance pupil of the
lotted on the abscissa (horizontal meridian, in

Figure 7. TG's Central retinal SCE-I functions (1956) presented in Fig.6 are repeated in this figure (filled circles). Rynders[8] recent measurements (1994) (open circles) have been superimposed for comparison. Top: Left eye (now 20/25 or 20/30). Bottom. Right amblyopic eye (now 20/60). Error bars are +/- 1 standard error of the mean for current data.

Fig. 6

T.G. had a non-normal right eye (e.g., note the SCE-1 data set for that eye), and exhibited modest visual acuity reduction (here an amblyopia) in that eye (amblyopia is a loss of visual acuity not due to an error in refraction).[8,9] Please note, in Fig. 6, the right eye is designated as O.D.; and the left eye is termed O.S. Enoch inferred T.G.'s visual acuity could be due to anomalously aligned photoreceptors (see SCE-1 data in Fig. 6). Enoch termed this anomaly (found in others as well), "receptor amblyopia" (a modest form of amblyopia which could be assigned to this discrete-position in the visual pathway). Note, there are a number of forms of amblyopia, this one being an identifiable one, but it is generally not a major form of amblyopia. The key point here is that there is hardly a discernable difference in these measured SCE-1 functions across a very long span of time. The stability of the SCE-1 functions measured in T.G.'s eyes are truly remarkable!

3. In the vast majority of people tested among normal observers, the common alignment/ photoreceptor fiber-optics or waveguide pointing locus is directed approximately at the Center-of-the-Exit-Pupil-of-the-Optics-of-the-Eye.
3A. Note, the SCE-1 data presented here are for photopic test conditions (that is, vision is measured/assessed at higher light levels). In one eye of Subject P.C. (below), we encounter an exception to this statement. In Fig. 7 (top), SCE-1 data are plotted for each of her two eyes at different retinal test loci sampled on the horizontal meridians of each of her two eyes.

Only those data determined in the horizontal meridian in each eye were plotted on the eye "sections" presented at the top of Fig.7.[10,11] So saying, SCE-1 data were also measured for the vertical meridians of her eyes at these same retinal test loci in her entrance pupil (but those data are not displayed in the illustrations presented above these data sets).

The salient point made here is that *in each of these two eyes, measured retinal receptor alignments in the horizontal meridian tended to follow a different "alignment rule"*.[10,11] The photoreceptors in her right eye tended to align with the-exit-pupil-of- the-optics-of-this-eye, while receptors in the left eye tended to align near to (but a bit in front of) the-center-of-the-retinal-sphere. Data on this subject's eyes were obtained again some time later, but data from each eye were fundamentally unaltered from the initial test sessions.

Wouldn't you know, *she and her family came from Alaska!* A year or so later, JME managed to fund a trip by her sister to JME's laboratory. The question, of course, was whether P.C. had some form of genetic alteration controlling her photoreceptor alignments? In both of her sister's eyes, the retinal receptors aligned with a point at/near to the center of her eye's exit pupils (an expected normal result). It would have been most interesting to obtain the rest of this family for further study and assessment!

Center-of-the-exit-pupil-of-the-optics-of-the-eye-pointing/alignment tends to imply the presence of a system searching for radiant stimuli which when acquired are used in a most efficient manner by the person/animal. On the other hand, center-of-the-retinal-sphere-alignment implies that the waveguide/fiber-optics elements are tending to pack in a manner such that they all tend to align nearly perpendicular to the wall or near-spherical surface of the retinal sphere. The first of these "options" favored survival of the species.

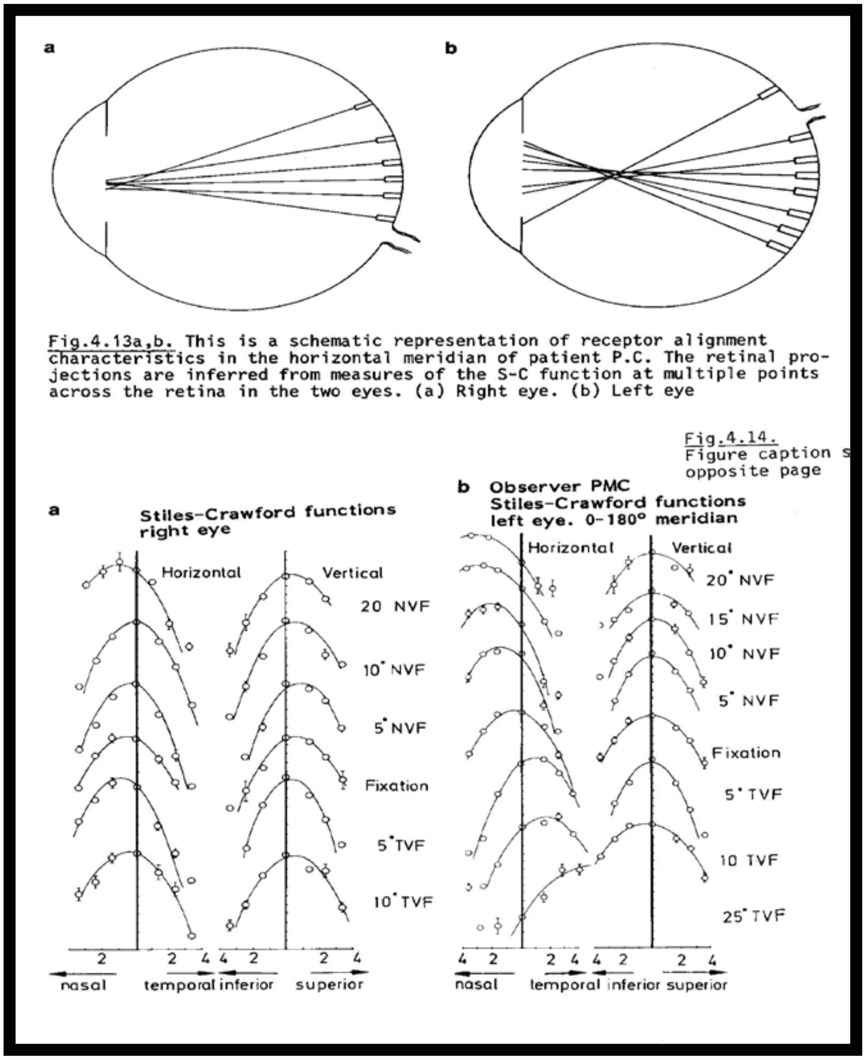


Fig.4.13a,b. This is a schematic representation of receptor alignment characteristics in the horizontal meridian of patient P.C. The retinal projections are inferred from measures of the S-C function at multiple points across the retina in the two eyes. (a) Right eye. (b) Left eye

Fig.4.14.
Figure caption s
opposite page

Fig. 7: reproduced from reference 4, p. 150.

Note, records such as this one were only encountered in 2 or 3 eyes over quite a number of years of testing. And, as noted, this property also seems to be quite stable. In no case defined to date, have *both eyes* of the same individual been affected in this manner!

3B. Repeated serial determinations of the peaks of the SCE-1 function for foveal fixation are plotted in two dimensions for three normal observers (assessed in the entrance-pupil-of the-eye).

It is inferred that the SCE-1 peak distribution measured at the fovea (photopic vision or cone response was sampled in all of studies described Section 3B) aligns approximately with the center of the exit-pupil-of-the-optics-of-the-eye.[12] Here, in Fig. 8, are plotted results of 5 serial measurements of the center of the peak of the SC-1 function determined in two dimensions (the horizontal and vertical meridians) in the entrance pupil of the eye for each one of three trained observers. These five data points were determined on different days, and were assessed at their point of fixation in the eye tested. Note the small variance of these data in their entrance pupil locations. Also observe the small biases encountered (mean displacement of peaks from the pupil center).

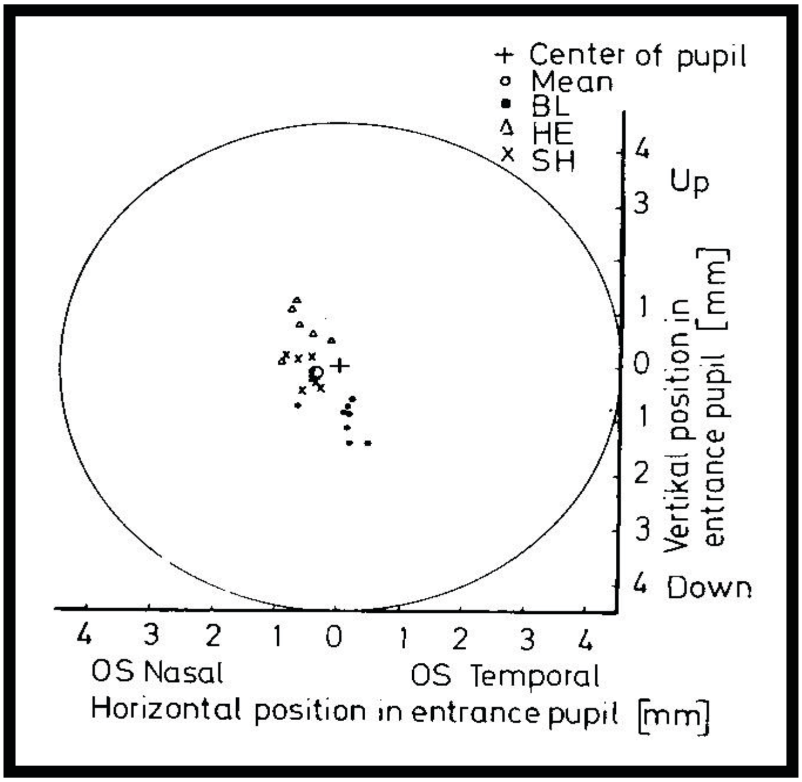


Fig. 8: reproduced from reference 4, p. 140-141.

Each of the sets of SCE-1 peaks for the three subjects measured differs modestly from those of the other two observers (note symbols). The small cross defining the center of they entrance pupil of the eye assumes a round pupil was assessed. It should be noted that the exact size of the dilated pupil and its centrum might have varied modestly on successive days. Once again, 1.0 mm in the entrance pupil of the eye converts to a difference in angle of incidence of 2.5^{o} at the plane of the retinal receptor. Interestingly, there seemed to be a bit more variability in plotted values in the vertical meridian than in the horizontal direction.

3C. Permanent or transient changes in alignments, or measured SCE-1 functions, do occur following trauma, or may be associated with ophthalmic surgery, or are found in ocular disease states. Here, following trauma, there are presented data obtained from an individual who exhibited reorientation-of-his-photoreceptors.

Importantly, within this group of patients, a surprising number of good quality corrections in alignments can/do occur within a reasonable period of time! Of course, there are cases where permanent scarring or cell deaths occur. Shown in Fig. 9 is one example of recovery from trauma. Please compare the top data sets with the successive one presented below in both the horizontal and vertical meridians.[13]

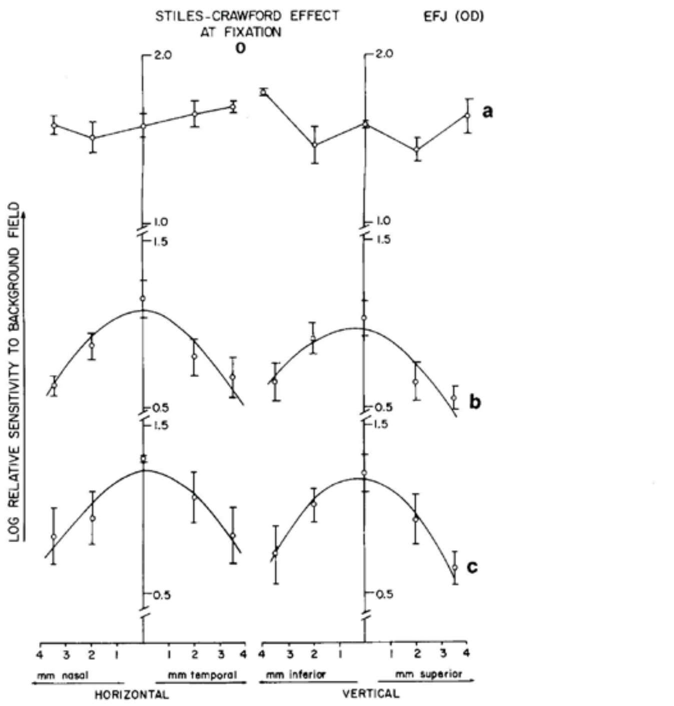


Fig.3.12a-c. Recovery of the S-C function measured at the fixation point in a case of subretinal serous fluid secondary to trauma. Horizontal (left) and vertical (right) traverses of the pupil are shown for three testing dates (top to bottom). Note the severely anomalous S-C functions determined on 5 May (a) and the remarkable recovery in these functions as determined on 26 May (b). No further change was seen from 26 May to 28 July (c). Changes in this subject's S-C functions paralleled the resolution of the retinal pathological [3.75]

Fig. 9: reproduced from reference 4, p. 145.

4. Evidence of a change induced in orientation of photoreceptors due to displacement (shift) of the eye pupil (using a painted iris contact lens incorporating a translated-center-of-the-pupil), and the subsequent recovery of receptor orientation after removal of the inducing stimulus, i.e., following recentration of the eye pupil).

Special black-backed and painted-iris scleral contact lenses for this experiment were obtained and fitted to JME in Germany. In these special lenses, refraction was appropriately corrected, and designated iris-aperture sizes and locations were pre-set. Here, JME was the experimental subject. Note, rotation of the contact lens on JME's eye was greatly limited by adding "prism ballast" to the lens design. The weight of the inferiorly placed prism ballast restricted rotation of the contact lens. And good fitting and use of a lens with a large scleral rim helped to maintain the lens at the designated location on his eye.

Figure 10 shows the measured day-to-day location of the peak of the SCE-1 function relative to the iris aperture built into the lens in two dimensions. The experiment had three phases: 1. During the first (or control) phase, a centered-pupil-iris-contact-lens was worn daily except during SCE-1 testing, and sleep; 2. For the test phase, the decentered-iris-contact-lens was worn for all waking hours except during SCE-1 determinations (scheduled at 3 PM daily in a darkened room); and 3. For the recovery phase, the centered-iris-contact-lens was again worn. Clearly, there resulted translation of the peak of the SCE-1 function in the direction of the translated aperture (but the magnitude of the shift never reached the new iris-center during this experiment). And, one notes the SCE-1 peak reverted to its original position quite rapidly after the special contact lens had been removed. JME's eye pupil was continuously well-dilated throughout. A second contact lens with a centered iris of the same size was available for wear both before and after the displaced contact lens was worn. During SCE-1 testing, no contact lens was worn, but refraction was corrected properly for the dilated pupil, at the time these data were taken. The most detailed/complete write-up of this research appeared in the Philosophical Transactions of the Roy. Soc. Lond.[14] Note: This article contained two independent sections. An error was detected in the execution of first section of this report, and that portion of the whole was subsequently withdrawn. Section 1 was wholly independent of the 2nd experiment described here.[14] The fronts-piece of Ref. 4 (pg. "v") replicates the salient data used in Fig. 10.[4]

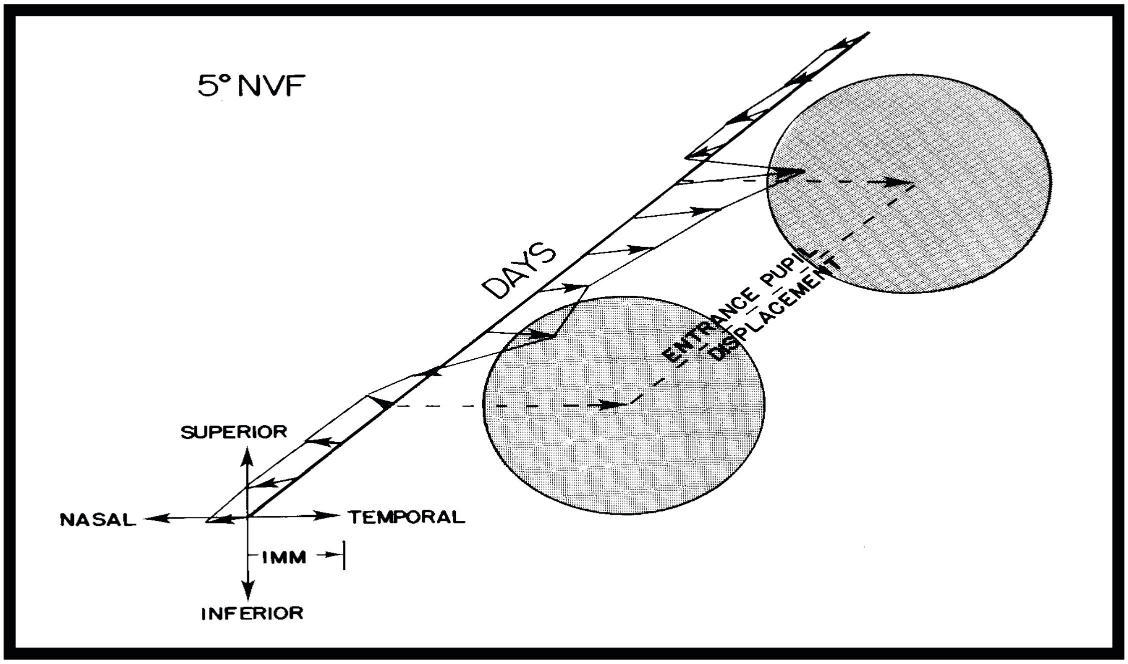


Fig. 10: reproduced from reference 4, p. 145. 4, Frontspiece, Page "v".

5. Separately (but not discussed at any length here), in about 38% of highly myopic individuals, it is found that there occurs noticeable lengthening-of-the-eye often coupled with continued growth of the retina and choroid leading to folding-over and encroachment of those tissues onto the nasal side of the affected myope's optic nerve head.

Such encroachments can cover up to 2/3 of the optic disc! Interestingly, in affected myopic individuals, vision is maintained, but sensitivity is somewhat reduced, within the area of tissue encroachment onto the optic nerve head. Coupled with these changes, there is broad evidence of instability in photoreceptor alignments detected in such individuals.[e.g.,15] So saying, SCE-1 can be assessed at these sites.

The presence of even a small number of center-of-the-retinal-sphere aligning eyes indicates that this may be a throw-back to an earlier state, and that the normal alignment system is not functioning in that eye or in this portion of the retina (central fovea). The fact that orientation in these eyes is stable in time, supports such an argument.

GENERAL DISCUSSION AND CONCLUSIONS

These and other experiments lead to the inevitable conclusion that, in the normal eye, the photoreceptors align remarkably well with the-center-of-the-exit-pupil-of-the-optical-system-of-the-eye. That is, the retina has a dynamic system providing continuous photoreceptor alignment. This powerful phototropic alignment system must have contributed meaningfully to vertebrate survival over a very long time period!

Some Added Dimensions of This Set of Problems (1)

There are additional aspects of this problem which have not been addressed in this brief discussion. As an example, we do not understand at this time how such alterations in photoreceptor alignments come about/occur, i.e., how they make alterations in their physical alignments in the “X”, and “Y” directions in the plane of the retina.

So saying, considerable research on motility of photo-receptors in the third dimension (i.e., in the “Z” direction, i.e., motions towards or away from the exit pupil of the eye or retinal surface) has been conducted by Prof. Beth Burnside, U. of California Berkeley (now retired) and her associates.[16-21] She and others have demonstrated the presence of myosin and actin fibrils within photoreceptors. In particular, she has addressed mechanisms for forward/rearward movements of receptors (rods and cones) in a number of species (such motion(s) are not known to occur in humans). That is, she has studied the inward and outward movement of receptor components in response to changing light levels and/or circadian rhythms. But, comparable mechanisms resulting in lateral alignment alterations (exit-pupil pointing) have not been addressed to date to the writer's knowledge.

Also, the speaker notes there are additional stresses and strains encountered in life which affect photoreceptor alignments. The photoreceptors "live" in an active “World”. That is, they are not like the Guardsmen standing at attention in front of Buckingham Palace in London. For example, with marked accommodation (alteration in the shape and thickness of the eye lens when young individuals view objects of interest at near distances) there is an advance of the anterior (leading edge) of the retina towards the ciliary body in pre-presbyopic individuals (measured to be about 1/2 mm or a bit more). This can result in an increase in the total area of the retina by an estimated $35mm^2$ and associated traction on the retina!

Separately, based upon somewhat dated human-centrifuge-studies, it can be argued that G-forces can alter alignments of photoreceptors, and they may have modest affects on photoreceptor orientations and visual resolution. As but one common example, driving about a circular highway entrance at realistic speeds can induce 3 “G”. Etc.

ORIENTATION OF, AND ORIENTATION CONTROL OF PHOTORECEPTOR WAVEGUIDES IS A POWERFUL FUNCTIONAL SYSTEM!

The speaker has wondered often why such a meaningful set of applications of fiber optics/waveguide function(s) have not been effectively pursued or utilized (to his knowledge) in non-biological applications of fiber optics. Now and again, there seems to be some active interest, but in candor, he has not seen any appreciable success in such ventures. So saying, it is possible that such applications exist and he has just not encountered them.

Here, JME has talked about a number of very refined systems for enhancing fiber optics and waveguide features (and associated responses) of retinal receptors in vertebrates. JME has often wondered if such (admittedly complex in some cases) features might find use in non-biological applications. These fiber optics and waveguide features or "designs" have certainly stood the test of time (!), and contributed to the survival of the fittest! It is JME's hope that such issues as have been considered here might be utilized as models for possible applications in fiber optics systems by those engaged in research in modern optics.

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FIGURE LEGENDS

1. J.J. Gibson's included these two figures in his book "The Senses Considered as Perceptual Systems", Houghton-Mifflin, Boston, 1966, pp. 163-165 (reproduced with permission in Ref. 4, p. 129). He sought to compare a generalized invertebrate eye with a comparable vertebrate eye. Importantly, he also had the general scheme for alignment of vertebrate photosensitive receptors with the source of the visual stimuli (basically, the aperture of the eye. Thus, he addressed both the receptors in the multiple-individual-little-eyes in the invertebrate eye, i.e, .in the individual *ommatidia* = little eyes, and the general scheme for photoreceptors aligned (across the retina) with the single aperture of the vertebrate eye. Gibson was quite correct. So saying, Brücke, in 1843, (quoted by von Helmholtz) understood that "*The axes of those (photoreceptors) which cover the retina in the back of the eye (in a vertebrate eye) are pointed towards the pupil, so that all light that falls on these elements penetrates them nearly parallel to their axes.* See: H. von Helmholtz, Treatise on Physiological Optics 2, Dover, N.Y., 1962, p. 229. This document, (Helmholtz's 3rd edition) had earlier been translated by Prof. James P.C. Southall in the 1920s (Columbia U.) as an OSA English Edition. And later, Gibson had the general scheme for alignment of retinal receptors quite right.

2. The upper part of the figure shows the nature of photoreceptor alignments near the posterior pole of a monkey eye. One can readily distinguish cones from rod photoreceptors. Compare the upper portion of this figure with the appearance of receptors in the far periphery of the same retina seen at the bottom of this figure. Note changes which have occurred in cells shapes, types and frequency of rods and cones, and, in particular, the cell orientations. .

3. This figure is similar in design to Fig. 2, but in this case one observes the retina of a cold-blooded vertebrate, the *Gecko Gecko*. The eye of this lizard is quite a bit smaller than that of the monkey. Top: an area near the posterior pole of the eye is shown, and the bottom shows the peripheral retina of this animal. Courtesy, Prof. Alan Laties, U. of Pennsylvania.

4. This figure shows the retina of an albino rabbit. Once again, the photoreceptor alignment tendencies are similar. This animal is particularly rod-dominant. So saying, there are cones present! The cell morphology appears somewhat different from that seen in the monkey. Interestingly, the section shown on the lower part of this figure is also taken in the periphery, but this photo has been selected from the opposite side of the eye. Note the changes which occur in rods and cones as one goes further into the periphery (in each species of animal). In particular, sizes of inner segments of the cones and rods alter as one goes more into the periphery. Courtesy of Prof. Allen Laties, U. of Pennsylvania.

JME has studied waveguide/fiber-optics properties in living albino rabbits, both from the anterior side, and the posterior side (dissected so that the sclera, the white of the eye, was removed. The retina and choroid are quite clear in the living animal (of course the blood cells in the retinal capillaries are visible) and modal patterns are readily appreciated.

5. These are data of W.S. Stiles, 1937.[6] The overlapped sets of SCE-1 data were measured six months apart in time. Two methods of measurement were employed for SCE-1 determinations, they were use of bipartite fields [two neighboring half fields (test and control)], and flicker photometry [two fields overlapping, one is test and one is control]. When using the latter method (one nulls, or minimizes, the difference to make a match), it is useful to put a little notch in a corner of one of the two fields so one can tell the one stimulus from the other. Basically there was no real change noted here, either in time or with method.

6. These are the data sets for observer T.G. spanning 37/38 years![8,9] Data on the left side of this figure were acquired by JME in 1956. T.G.'s left eye SCE-1 data were essentially normal at that time. His right eye data revealed a non-typical set of SCE-1 data, and it was found T.G. had modest amblyopia in this eye (visual acuity did not improve when a refractive correction was provided). This and other similar cases were designated by JME as having a form of "receptor amblyopia".

In the intervening years, T.G. had vitreous detachments in each eye), as well as a meaningful retinal detachment (surgically corrected in the latter part of 1993 in his better left eye. When tested for SCE-1 in 1994, he had lost a bit of visual acuity (not a great loss) in each eye when his vision and contrast sensitivities were assessed. In spite of his detachments and surgery, when the SCE-1 was re-measured in each of his eyes in 1994 (right side of figure) there was no significant change in his measured SCE-1 functions when these new data were compared to the 1956 data. This is quite amazing! Note, T.G. was a well trained subject.

7. There was encountered a curious finding in 2 or 3 eyes (of different people) over a period of years of testing. In no subject was this finding encountered in both eyes. In normal individuals, retinal receptors tend to align with a point at, or very near to the-center-of-the-exit-pupil-of-the-optics-of-the-eye (e.g., see Fig. 8) [Category 1]. This implied that this response feature is advantageous to vision, and it served to enhance signal (data) processing by the eye of the individual studied. In two individuals and in possibly a third party, receptors in one of their eyes tended to align more closely with a point approaching the center of the retinal sphere [Category 2]. Thus, a different alignment "rule" was being followed in these unique eyes (tested and retested a number of times).

In this figure, only data obtained in the horizontal meridian have been plotted. The top left illustration indicates photoreceptors following an alignment consistent with Category 1; and the top right hand figure favors Category 2. The SCE-1 data upon which these two drawings were based lies below these figures. Note the optic nerve going back to the brain lies at the rear of each eye portrayed. The half of the eye with the optic nerve observed projecting from the eye is the nasal side of the eye, the half-side away from the optic nerve is the temporal side. Zero degrees relates to the fixation point or fovea centralis, or approximately the posterior pole of the eye. Ref. 4, p. 150.

8. In this figure three individuals were tested on five different days in one eye. Each was tested for SCE-1 at their point of fixation in both the horizontal and vertical meridians. Each individual was assigned a different symbol for his/her data plotted in two dimensions. Note, the rather close grouping of each individual's data points, and how close to the center of the eye pupil all of these points were located. Ref. 4, p. 141.

9. This patient had experienced trauma to his right eye (affecting his retinal photoreceptor orientations in two meridians in early February, 1973. This figure shows the recovery of his normal receptor orientations over a modest time period. By July he had essentially fully recovered in both the horizontal and vertical meridians. Ref. 4, p. 145.

10. This particular test was conducted at 5° in the nasal visual field. Here, in the control phase of the experiment, JME recorded his SCE-1 peak in the horizontal and vertical meridians for some days in order to track his SCE-1 data with a centered pupillary aperture; then for the test phase, he wore a displaced aperture contact lens (the location of the de-centered aperture is plotted with grey fill) for some days; and finally, there was a recovery phase when his pupillary aperture was once again centered. Basically, this experiment shows how the receptor orientations were driven by wear (and removal) of the displaced pupil contact lens. What we don't really know, is whether there is an effective limit to the capability of the receptors to follow the luminous stimuli (displaced pupil). Ref. 4, p."v", frontspiece.