Directional sensitivity of the retina: 75 years of Stiles–Crawford effect

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The reduction of the brightness when a light beam’s entry into the eye is shifted from the centre to the edge of the pupil has from the outset been shown to be due to a change in luminous efficiency of radiation when it is incident obliquely on the retina. The phenomenon is most prominent in photopic vision and this has concentrated attention on the properties of retinal cones, where responsibility has yet to be assigned to factors such as differences in shape, fine structure and configuration, and membrane anchoring of photopigment molecules. Geometrical optics and waveguide formulations have been applied to the question of how light is guided in receptors, but details of their geometry and optical parameters even if they become available will make calculations complex and of only moderate generality. In practice, the diminution of oblique light helps visual performance by reducing deleterious influence of ocular aberrations and of glare caused by light scattering when the pupil is wide. Receptor orientation can come into play in ocular conditions due to mechanical disturbance and has been shown to have potentiality as a tool for clinical diagnosis. Currently, open questions include microanatomical and molecular differences between rods and cones, the coupling of the optical image of the eye with the transducing apparatus in the photoreceptors, possible phototropism and more convincing methods of estimating the actual spatial distribution of photon events as it affects visual resolution.

Keywords: photoreception; retinal rods and cones; waveguides; optical image in the eye; phototropism

1. INTRODUCTION

A prominent design feature of the vertebrate eye is that all individual receptor elements share the same light-admitting aperture. It has a number of consequences. Chief among them is enhanced resolution and light-gathering capacity while simultaneously increasing compactness. This improvement is, however, associated with optical and biological problems of developing and maintaining a suitable refraction apparatus and a matching cellular structure for image analysis.

Both of these factors are at the root of an interesting phenomenon, genuinely unexpected and surprising when it was first noted 75 years ago, marking it as one of the major discoveries in visual science of the twentieth century. Its full explication continues to provide challenges.

As automobile traffic became prevalent in the 1920s, W. Stanley Stiles, a young physicist starting his government career in the National Physical Laboratory in Teddington, England, was assigned to look into street lighting and headlight features. He concentrated on visibility and glare, and derived an equation for veiling glare, which is still used today (Stiles & Crawford 1937). One variable is the size of the eye’s pupil because, insofar as intraocular factors are involved, the larger the bundle of rays entering the eye, the more the scatter and stray light. Photography was then not as well developed as it would be in subsequent decades, and online electronic devices quite far in the future. Therefore, Stiles hit on the idea, previously suggested in Germany, of gauging an observer’s pupil size by subjectively measuring the quantity of light reaching the retina—the larger the pupil, the brighter a given object should appear. Stiles was nothing if not a sophisticated vision researcher. Familiar with the convoluted relationship between stimulus luminance and subjectively reported brightness, he insisted on rigorous measurements. Together with his young collaborator, B. H. Crawford, also a career researcher in the National Physical Laboratory, he used a nulling technique, in which two independently controlled beams entered an eye: a narrow beam through the centre of the pupil and a wider beam filling the whole pupil. Both came from the same source and covered the same retinal area and the two alternated in time. The subject was instructed to adjust the intensity in the wider beam for minimum flicker. This should yield values in accord with the ratio of the full pupil area to that of the narrow central beam. When, to validate the procedure, a comparison was made with actually measured pupil areas, a consistent discrepancy was found: the equivalent luminance from a 30 mm² pupil was found to be only twice that from a 10 mm² pupil. In other words, to match the apparent brightness of a beam entering the eye through a 10 mm² pupil, the light entering through a 30 mm² pupil had to be reduced by only a factor of two instead of the expected three if linear summation of pupil area held. Thus, the Stiles–Crawford (1933) effect was born.

2. THE PUPIL AS AN APERTURE ADMITTING RADIATION INTO THE EYE

Some features of the eye’s optical imagery are relevant. It helps at the outset to pare the situation down to a single
monochromatic point source at infinity whose beam of parallel rays is focused on the retina. This can subsequently be enlarged to the more general case of sources that are extended in space or in the wavelength domain.

Geometrical optics gives a serviceable description of the role of the eye’s pupil in admitting the rays that contribute light to the image formed on the retina (figure 1). To a first approximation, the rays passing through the centre of the pupil strike the retina head-on. The rays coming in near the edge of a fully dilated pupil (approx. 8 mm in diameter) will have an obliquity of approximately 10°. In visual experiments, although the object and its resultant retinal image remain fixed, the location and size in the pupillary plane of the rays can be controlled either by placing an artificial aperture in front of the eye or by a special mode of imagery, called Maxwellian viewing, in which auxiliary optical components in the light beam limit the pupillary region through which it passes into the eye. In either case, the data to be discussed are based on the effect of the pupil entry point on the way light affects the visual process.

Geometrical optics with its rays and ideal point images is only a first approximation of the true situation; generally, consideration in terms of wave optics is demanded. Though the wavelength of light is then no longer neglected, operative parameters for geometrical optics, e.g. surfaces separating media of differing refractive index, remain applicable.

Based on diffraction calculations for the special case of a round pupil and no aberrations, the pattern in the plane of focus is the familiar Airy disc, whose diameter is related directly to the wavelength and inversely to the pupil aperture. The more general case of other locations in the image space and of wavefronts deformed by aberrations is less tractable but, once all the parameters are known, can in principle be solved. Although the ideal is seldom realized in practice, it can be approximated these days by adaptive optics that render the wavefront entering the eye’s image space perfectly spherical by applying suitable corrective deformations to the incoming wavefront. But this deals only with the shape, not with the amplitude of the wavefront across the aperture. Opacities and attenuation by absorption and scatter can produce quantitative changes in the radiation propagated through the intracocular media. In any individual situation, they would have to be taken into consideration for a realistic estimate of the distribution of the electromagnetic disturbance in retinal locations. In addition, when the retinal receptor cell has a dimension of the order of the wavelength of the radiation, even retinal image specification in terms of free-field diffraction patterns does not suffice for a full description of the receiving process.

3. LUMINOUS EFFICIENCY OF RADIATION IN ITS DEPENDENCE ON PUPIL ENTRY

(a) Troland’s original proposition and the troland unit

In vision to differentiate between Fechner’s ‘outer’ and ‘inner’ psychophysics, i.e., between an object’s impression on the sensorium and the perception it generates, requires making a distinction between the optical properties of the actual objects and those of their associated retinal images. Where light intensity is concerned, the pupil diameter obviously is a variable and should be factored in to ensure an accurate estimate of the degree of retinal stimulation. Hence, Troland (1917) introduced a new unit of visual stimulation for which the luminance of the source (in Cd m⁻²) is multiplied by the pupil area (in mm²) (Troland 1917).

This unit, since called the troland, has been employed widely and was regarded as a great advance over merely quoting source emission. Using the energy flux from a source of 1 Cd m⁻² (in lumens sr⁻¹ retinal area⁻¹), and the pupil area, visual stimulation could be defined in photopic or scotopic trolands and, based on the known luminous efficiency of radiation for either photopic or scotopic vision, assigned absolute values in such units as photons receptor⁻¹ s⁻¹. This was invaluable when it came to studying the absorption and concentration of visual pigments in the course of dark and light adaptation.

Implicit in the usage of such a unit is linearity: increasing the pupil area by a factor of 10 could be exactly offset by reducing the source’s emission to a tenth. This was taken for granted until Stiles and Crawford demonstrated it to be false.

(b) Discovery of directional sensitivity

After Stiles & Crawford (1933) noted the lack of reciprocity between pupil area and light needed for equal brightness, they conducted more detailed investigations of the variation of the luminous efficiency of light for various pupil locations. Using narrow eccentric pencils and adjusting the light in them to match the brightness produced by a constant beam passing through the centre of the pupil, they found the curve shown in figure 2. It has been replicated innumerable times and it applies to both vertical and horizontal displacements in the pupil. Quantitatively, it is well characterized by the equation

$$\log(\eta_y) - \log(\eta_x) = \rho \times r^2,$$

where \(\eta_y\) and \(\eta_x\) are the luminous efficiencies of a narrow bundle entering, respectively, at the peak of the curve and at a distance \(r \) millimetres from the peak, which is usually, though not invariably, close to the centre of the pupil. It has been found sufficient to describe the shape by the single parameter \(\rho\), which is typically approximately 0.05. That is, there is approximately a threefold reduction in

Figure 1. Schematic eye with a wide pupil showing two identical bundles of rays from a distant object focused on the retina that enter through different pupillary regions: A, the centre, and B, near the edge. Stiles & Crawford (1933) discovered that, in photopic vision, the oblique incidence of beam B causes a prominent diminution of luminous efficiency, since called the Stiles–Crawford effect.
appearance of a patch of monochromatic light produced by a beam entering through the centre of the pupil with an otherwise identical one through the edge; no matter how he changed the quantity of light, their colour was never the same. According to the trichromatic theory, a specific colour perception depends on the relative effect of a beam on the three wide-band cone colour channels. This chromatic Stiles–Crawford effect therefore means that a monochromatic beam entering obliquely produces a different ratio of responses in the three types of cone from one that enters head-on.

Over the years, two related phenomena have been described. When comparing the brightness of a patch of retina illuminated alternately by beams entering through two opposite edges of the pupil, transient changes were observed even when other tests indicated that for steady-state illumination their brightness was equal (Makous 1968). It takes several tens of seconds for the transients to die down. Equal brightness does not mean full equivalence of cone stimulation.

The other phenomenon, also transient, relates to an aspect of optical stimulation usually left unattended in mammalian vision, polarization of light. When the plane of polarization of a beam entering through the edge of the pupil is suddenly shifted through 90° from radial to tangential, there is a transient change in the effective stimulation of the illuminated patch of retina, as measured by increment threshold of a superimposed spot (de Groot 1979). This does not occur with central pupil entry; quantitatively as a function of pupil locations, this effect maps well on the conventional Stiles–Crawford function.

Directional sensitivity is also a feature of invertebrate photoreceptors (Snyder & Menzel 1975) but the emphasis in this review is on its manifestation in the human, where it was first discovered and remains most relevant.

4. RETINAL RECEPTORS

Once physical transmission defects in the eye media and in pre-receptor layers of the retina have been eliminated and post-receptor neural factors discarded, attention centres on the retinal receptor cells and, particularly, in view of the dissimilar photopic and scotopic Stiles–Crawford effects, on rod–cone differences.

A variety of morphological factors bears on the approach to an explanation of directional sensitivity (figure 3). The overall shape of cones varies depending on their retinal location, the ones in the centre of the fovea having thin, long outer segments resembling rods. Cell shape in vivo has to be deduced from the microscopic picture presented in histological sections, whose preparation invariably introduces some artefacts and distortions. However, the consensus, across almost 200 years of histology, is that cone’s outer segments are tapered (cone-like!), though the taper in the foveal centre is very slight (Borwein et al. 1980). Cones differ from rods at the levels of the cell nucleus, the inner segment and the joining portion, called the ellipsoid; however, in all these dimensions, cone measurements vary markedly between the fovea and the retinal periphery, where the cells are several times wider and prominently tapered (figure 4).

The phototransduction process takes place in the outer segments. Cone photopigments are located in folds of the cell membrane and the rod pigment
rhodopsin in stacks of intracellular discs (figure 5). These polar molecules have a forward-pointing directional acceptance lobe, which at the maximum would follow a cosine law, cosine squared if the calculation is in terms of the intensity of the radiation. For light entering near the edge of a very wide pupil (say, 8 mm in diameter) when the obliquity angle is 10° or less, this would reduce acceptance by only a few per cent and is quite insufficient to account for the actual attenuation of obliquely incident light in cone vision.

What finally matters is the electromagnetic disturbance not in free space but in the location where interaction with the photopigment molecules takes place, for that is the beginning step in the process of vision. No treatment of the problem is complete unless this is addressed. It involves possible guidance of light into the receptors and within them to the place where the photopigment molecules are located. This in turn depends on how electromagnetic radiation is affected by photoreceptor shape and optical parameters.
5. GUIDING OF LIGHT INTO RECEPTORS

Quite soon after their first histological identification, retinal receptors were suspected on experimental and theoretical grounds to act as light pipes (reviewed by Helmholtz; Southall 1924/1962). This concept gained momentum in the middle of the twentieth century with the development of radar and then a little later of fibre optics. Radar detection uses waveguides as antennae; their theory is based on the behaviour of electromagnetic waves in structures whose dimensions are of the order of the wavelength of radiation and whose shapes allow the calculation of the distribution of energy within them. The Italian physicist Toraldo di Francia (1949) pointed out the similarity between the radar waveguides and retinal receptors and the possibility that it may offer an explanation of the Stiles–Crawford effect, in particular, since directional sensitivity is a known feature of waveguides. Early attempts to simulate the retinal process by measuring the acceptance of micro-waves by scaled-up models of retinal cones did indeed reveal such directionality (Jean & O’Brien 1949; O’Brien 1951; Enoch & Fry 1958).

When glass fibres were made with diameters of the order of the wavelength of visible radiation and their industrial application demanded fuller analysis of their performance, theoretical study of optical principles that were also relevant to retinal receptor optics became possible.

Required first of all was knowledge of the optical constants, in particular the refractive index of the intracellular space and the refractive index difference at the cell’s membrane (Barer 1957). With this information, models were formulated, of which the one shown in figure 6 is a widely used example (Snyder & Pask 1973). All such models are abstractions and postulate receptors with smooth surfaces in the form of circular cylinders, sometimes joined by a truncated cone. Light is allowed entry at only one transverse aperture, and all media are homogeneous and isotropic. On the back of these models, calculations of two kinds could be performed (Snyder 1975).

The first type of calculation uses only geometrical optics and traces the initial refraction of the rays entering the receptor and their subsequent multiple internal reflections as the light path is contained within the receptor.

More relevant are the calculations in which the waveguide properties of such models are investigated; they demonstrate not only directional sensitivity for incident radiation, but also the existence of so-called modes, i.e. internal geometrically defined patterns of heightened and lessened energy concentration (Stiles 1962), as well as light loss through leaking of radiation...
outside the confines of the receptor. The nature of the modes depends crucially on all the material factors of shape, optical parameters of the media, angle of incidence and so on. Modes have been demonstrated not only in optical fibre models (Snitzer & Osterberg 1961) but also, if only indirectly, in actual mammalian retina preparations (Enoch 1963).

There cannot be any doubt that receptors do not just passively accept radiation. Their morphological structure as well as the media constituting and surrounding them contribute to a complex and possibly uneven intra-receptor light distribution, and almost certainly to directional sensitivity. The search for the proximal cause of the Stiles–Crawford effect is properly concentrated here. Yet in spite of the elegant mathematical nature of the waveguide calculations, the distance separating such formulations from the real situation is vast and the assumptions are as yet quite simplistic (Horowitz 1981).

Receptor surfaces are neither smooth nor of geometrically ideal shape, the media far from homogeneous and isotropic, and the cells unlikely to have acceptance of radiation restricted to only one transverse plane and nowhere else along their length. When these conditions are relaxed to account for the actual biological situation, the pattern of energy distribution will be less sharply delineated than currently pictured in theoretical expositions. Still, it has been convincingly argued that the application of electromagnetic theory is not only appropriate but also cannot be left out of consideration. Ahead is the difficult transition from abstract models to the actual biological preparation. A specific example is the following: the transient brightness change on a sudden displacement of the pupil of a beam carrying light of equal steady-state brightness suggests the existence of more than one pool of photopigment molecules: does it imply more than one system of waveguide modes, or an acceptance of light over some length of the receptors rather than in just one transverse plane?

### 6. PHOTOPIGMENTS

The conversion of radiation energy into the immediate stimulus for vision is its interaction with the photopigments that lead to the cis–trans isomerization in the chromophore component. It occurs in all classes of pigments; rod and cone pigments differ in their spectral absorption curves and also in their regeneration rates. These differences arise from a relatively few amino acid substitutions in the otherwise highly conserved opsin molecular composition and structure (Carroll & Jacobs 2008).

Rods and cones differ, in addition, to the manner in which the pigment molecules are held inside the receptors. The membranous discs in which they are anchored are invaginations of the outer cell membranes in cones, whereas, in rods, the discs are separate intracellular structures (figure 5). The spatial pattern of their distribution in the membranes, yet to be determined with precision, may also differ (Nickell et al. 2007).

Photopigment molecules are polar with their axis pointing along the long axis of the cells and are capable of rotating around this axis. This is demonstrated by the fact that head-on, the direction of polarization does not matter, but dichroism is exhibited for light shined side-on, with polarization parallel to the long axis being more effective in pigment bleaching (Harosi & Malerba 1975). The explanation for the transient polarization Stiles–Crawford effect mentioned above is obviously to be found here.

As yet little firm knowledge is available about the pigment concentration. This has relevance in the Stiles–Crawford effect of the second kind. When the photopigments are present in a highly concentrated form, the shape of their spectral absorption curve can change substantially with changes in concentration by a process called ‘self-screening’ (Brindley 1953). This is adduced to account for the change in chromaticity when the beam is obliquely incident on the receptors. Such arguments draw attention to the role of pigment concentration in connection with passage of light through receptors (Walraven & Bouman 1960; Enoch & Stiles 1961). Waveguide interpretations propose changes in the bunching of energy in locations inside the receptors, whereas in geometrical–optical descriptions of the Stiles–Crawford effect, oblique incidence manifests itself in the difference in passage length of light through the receptor. The effect of pigment density may turn out to be quite dissimilar in the two.

Because there remain doubts whether overall receptor shape alone will suffice to account for the Stiles–Crawford effect, differing susceptibility to internal light patterning due to rod–cone differences in photopigment structure and anchoring cannot at this time be ruled out.

### 7. RECEPTOR ORIENTATION AND PHOTOTROPISM

Retinal receptor outer segments are parallel and their direction is more or less perpendicular to the outer shell of the eyeball. If the latter were a sphere, they would point to its centre. In fact, they are directed towards the centre of the pupil (Laties & Enoch 1971). Is this the result of an original developmental scheme or does it betray the existence of an active process, a phototropism?

There is some evidence. In subjects made to wear contact lenses with artificial apertures decentred by a few millimetres with respect to their natural pupils, the Stiles–Crawford function peak often undergoes a small (approx. 1 mm) compensatory shift (Enoch & Birch 1981) with a time course of approximately 5 days, and returns to its previous position with the same time course after removal of the lens (Applegate & Bonds 1981). On the other hand, many patients retain a Stiles–Crawford function with a peak near the edge of the natural pupil throughout life. This occurs particularly in myopes with posterior staphyloma and a consequent tilt of the posterior wall of the eyeball (Westheimer 1968). Such findings do not necessarily contradict the existence of phototropic displacements, because even when deliberately induced, it is small and may not suffice to overcome myopic eyeball distortions.

Attempts to change the Stiles–Crawford effect by prolonged occlusion, predicated on the theory that this would lead to a disarray of receptors when deprived of active phototropic influence, have not been conclusive (Kono et al. 2001).

Although the molecular machinery for cell motility exists in teleost photoreceptors (Burnside 2001), it has yet to be demonstrated in the mammal. Even then, there remains the possibility that the responsibility for light-induced receptor realignment lies not with the receptors themselves but with the interleaved processes of the retinal pigment epithelium, which does contain the
macular degeneration (Kanis 1975). As an example of its possible role in ophthalmic diagnosis, the Stiles–Crawford function is abnormal in some cases of amblyopia (Enoch 1967) and age-related cataract. The evidence against this view is that in primate eyes carefully prepared to preserve globe shape for histological examination, there is no sign of receptor splaying (Laties 1969); outer segments in mixed cone and rod parafovea are lined up neatly in parallel (figure 7).

On the other hand, in some pathological conditions, mechanical factors such as stretch, buckling and tearing can cause receptor disarray (Enoch et al. 1981). Ciliary muscle contraction during a maximum accommodation effort is known to exert a pull on the retina and this is supported by the demonstration of a consequent shift of the peak of the Stiles–Crawford function (Blank et al. 1975). As an example of its possible role in ophthalmic diagnosis, the Stiles–Crawford function is abnormal in some cases of amblyopia (Enoch 1967) and age-related macular degeneration (Kanis et al. 2008), implying that the foveal cones in these patients lack orderly alignment.

8. VISUAL CONSEQUENCES OF THE STILES–CRAWFORD EFFECT
If one adopts a teleological view, the prominent cone Stiles–Crawford effect has arisen because it confers some advantages in photopic vision that do not apply to scotopic vision. Where high light sensitivity and low dark noise are of the essence, and resolution can be sacrificed, all the light entering through the largest possible aperture needs obviously to be used. This describes the rod system that, whatever the ultimate shape of its acceptance lobe is found to be, exhibits little, if any, attenuation across even a widely dilated pupil.

The cone system, on the other hand, has quite different imperatives. Its operation does not, as with rods, require a high level of sensitivity and low thermal noise, instead it is built for fast adaptation, good discrimination in the wavelength domain and, above all, high resolution. In the human, peripheral zones of the pupil suffer from optical aberration; the eye’s optics are optimal, i.e. diffraction limited, only for pupil diameters of approximately 3 mm and imagery does not improve further, and, in fact, often suffers when pupils are 6 mm or wider. The elaborate neural apparatus for pupil aperture control associated with light stimulation and with accommodation and convergence in close-up viewing seems intended to restrict the incoming light bundle to a maximum operating diameter of approximately 4 mm. The Stiles–Crawford effect can be seen then as an adaptive mechanism serving the same purpose: to downplay the aberrated light from wider pupils. At this stage, it is not clear whether the compaction of acceptance to a narrow forward lobe is in aid of overall improvement of efficiency or whether it is more in the nature of a defence mechanism to screen out oblique light. Waveguide theories, for example, postulate leakage of radiation out of receptors; geometrical optics traces oblique beams through the long outer segment of several receptors with a resultant loss of location specificity. In both of these formulations, the introduction of a Stiles–Crawford effect would serve the purpose of discarding light with untoward properties rather than of rearranging it for greater efficiency.

Finally, the question of intraocular stray light is pertinent. Scatter occurs on passage through the eye media; in addition, light reflected from the fundus can produce an effect resembling an integrating sphere. For these reasons, and especially with wide pupils, the amount of light reaching receptors obliquely may on occasion be considerable; angular restriction of its acceptance can aid performance in both increment detection (by reducing the overall ‘veiling’ background) and resolution. This argument is most pertinent for cones, but would also apply to rods if their directional sensitivity is ultimately found to be narrower than expected for dipole molecules.

9. OPEN QUESTIONS
Seventy-five years after its original description, the Stiles–Crawford effect still presents scientific challenges on several fronts. Some are due to lack of full understanding, even after all this time, of fundamental issues, some have arisen more recently because major progress and new tools in relevant research areas have generated a new spate of questions, and, finally, some practical applications, in particular clinical ones, await cultivation.

(a) Receptor optics and retinal image computation
The topic begins with the way in which the intact eye processes incoming radiation to generate the electromagnetic disturbances in the retinal region. Since Stiles and Crawford’s days, enormous progress has been made in replacing purely schematic systems of imagery with actual measurements in the intact eye of the retinal image and its quality (Westheimer 2006). New instrumental tools such as coherent light sources and adaptive optics are constantly advancing the field in enabling, even if as yet only for experimental purposes, the production of

Figure 7. A photomicrograph of a small section of the parafoveal mixed rod–cone retina in a macaque, especially prepared to preserve as best as possible the in vivo orientation of the receptors. Reprinted with permission from Laties (1969).
predetermined retinal images and making information available about retinal structure and function, on a real-time individual basis. Thus, a prerequisite is about to be met, viz. full knowledge of the distribution of electromagnetic disturbances in the retinal plane. But that is not enough. The arc then has to be closed between it and the proximal visual stimulus, which are the intra-receptoral photon events. To the extent that the coupling between the two is problematic, our knowledge remains incomplete.

Because the current formulations of how radiation, once it reaches the retina, is guided into the outer segment of the retinal receptors are based on models that have only a remote resemblance with the actual situation, the mathematical function for receptor directional sensitivity, needed for the computation by diffraction theory of intracellular light in individual receptors, is not available.

As an interim solution, it is feasible to perform optical image calculations by standard diffraction theory using the known wavefront deformation of a particular eye and folding in the Stiles–Crawford effect, as manifested in that eye for the applicable viewing conditions, as an attenuation of the wavefront towards the pupil edge (Westheimer 1959; Carroll 1980). There is as yet no theoretical underpinning of this approach; it may have validity for waveguides exhibiting only a single mode (Vohnsen 2007) but cannot be seen at this time to be universally valid when the actual waveguide properties of receptors are not known. The approach has at least the advantage of highlighting that for a given object and a given eye under identical focusing and pupil aperture conditions, the effective retinal image will differ depending on the retinal directional sensitivity of the receptor population that is being addressed (Carroll 1980).

If model building and computation are in the end inadequate, one awaits biological markers that would make overt the spatial distribution of photo-isomerizations from the distal end of photoreceptors following transillumination, are only indirect probes and do not as yet reveal details of events internal to the receptors.

Once a fuller understanding of the interaction of the ocular image and receptor optics has been reached, one can expect an interesting and neglected phenomenon to be tackled anew. It is the diminution of acuity for line or grating targets oriented orthogonally to a pupil displacement of the entering beam that carries them, discovered by Campbell (1958) 50 years ago.

(b) Microanatomy and molecular biology of retinal receptor cells

In a parafoveal region containing both rods and cones, the Stiles–Crawford function differs in a major way between the two classes of cell, even though the shape of their outer segments is similar. The rod–cone difference is very prominent and dwarfs that between cones in different retinal locations with widely varying shapes and but not too dissimilar Stiles–Crawford functions (Westheimer 1967). Rods and cones must therefore differ in more subtle ways than just shape to account for their observed directional sensitivity to obliquely incident light. Investigations here would thus have to concentrate on other anatomical features yet to be fully identified, on categorical structural differences such as the membrane folding in cones and stacking of discs in rods, and properties of the photopigment molecules and the mode of their anchoring in addition to those already identified.

(c) Dynamic changes in receptor orientation

Small changes in peak retinal directional sensitivity can be induced by temporary manipulation of the incoming light beams, but the results are inconsistent and in some cases even contradictory. Experiments here are heroic, requiring lengthy wearing of contact lenses with displaced pupils, exacting measurements and extensive controls. Patients with pupil abnormalities or pathology might provide good evidence, but the combination of a stable and confined abnormality, absence of confounding conditions and readiness to be thoroughly tested will make them rather rare.

Phototropism implies motility and the presence of the suitable molecular apparatus in human cones has still to be established beyond doubt. A possible role of the retinal pigment epithelium with its identified molecular machinery for motility and processes enveloping receptors has yet to be explored.

(d) The Stiles–Crawford effect as a clinical tool

New instrumentation in ophthalmoscopy is allowing better visualization of the retina and the in vivo and in situ recognition of pathological conditions. Changes in the orientation of retinal receptors, still beyond the resolution limit of these devices, would therefore continue to need essaying by optical or psychophysical procedures. The existence and extent of traction on the retina associated with intra- and extra-ocular muscle activity has yet to be fully elucidated and the Stiles–Crawford effect is clearly an appropriate probe here. Especially in myopic and other eyes at risk for retinal detachment, this seems a valuable direction of research. Otherwise, normal eyes with compromised visual acuity (ambylopaia) sometimes also demonstrate abnormal or absent directional sensitivity, but it is still not certain whether the reduction of foveal acuity is commensurate with the degree of receptor disarray needed to abolish the Stiles–Crawford effect were it the sole factor. Owing to the etiological diversity of ambylopaia and hence of the individual prognosis, tests by means of the Stiles–Crawford effect for receptor disarray are proving to have clinical usefulness.

For these and some of the other practical applications, rapid and minimally invasive measuring methods would be welcome. Psychophysical procedures are laborious, demanding and require elaborate instrumentation. Quickly administered objective tests of retinal receptor orientation would therefore be widely welcomed, but light reflected from the fundus cannot be used without sifting for non-visual components (He et al. 1999).

10. SUMMARY

On its 75th anniversary, Stiles and Crawford’s remarkable discovery, in psychophysical tests to solve a practical question relating to glare from automobile headlights, continues to challenge our understanding of photoreception at the cellular and molecular level. The electromagnetic aspects of the channelling of light into narrow segments of retinal cones have been handled so far only in abstract models; subtle morphological differences in rods

and cones, not as yet fully identified, play a role; the anchoring of photopigment molecules in membranes may be involved; possible phototropism of retinal cells still needs elucidation; and there is wide scope for the use of the Stiles–Crawford effect in clinical diagnosis.

REFERENCES


