XII

THE STILES-CRAWFORD EFFECT AS INSTRUMENT OF RESEARCH

P. L. Walraven, J. J. Vos, and C. J. W. Dunnewold*

Research in vision is mostly characterized by laboriously exploring old fields with new experimental and theoretical techniques. Seldom it is marked by discovery of really new phenomena. One such a discovery was that of the Stiles-Crawford effect in the thirties. Though neither its origin, nor its significance for vision are fully understood, it has proved to be a tool of significance, anyway, in vision research.
For details about the investigations mentioned, we refer to nrs. 86, 111, 115, 128 and 136 *of the cumulative bibliography.*

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Until 1933 it had been implicitly assumed that it did not matter as far as the luminous effect was concerned, through which part of the pupil light entered the eye, just as is the case with a camera. However, Stiles and Crawford (1933) discovered that this is far from true, and that the sensitivity of the retina is dependent upon the direction of incidence of the light. Light passing through the border of the pupil, which produces oblique incidence on the receptors, may easily be some five times less effective in eliciting a visual response than light passing through the centre of the pupil. (Fig. 1).

Absorption by the eye media only plays a minor role in the effect, (Weale, 1961). Numerous investigations have established the effect and have made it clear that the effect is principally of retinal origin. It has been convincingly shown that the effect occurs only in photopic vision and not under scotopic conditions.

A completely satisfactory explanation of the Stiles-Crawford effect has not been given. The most promising explanation was put forward by Wright and Nelson (1936). They based their interpretation on the well known fact that the receptors have a refractive index which is higher than the fluid surrounding them. This should make them act as light conductors and, if they are suitably shaped, as light traps for perpendicularly incident light. Obliquely incident light, however, should partly leak out of the receptors and then only partly reach the visual pigments. This explanation nonetheless leaves a number of questions unanswered. Why should central and peripheral cones, with their difference in shape, show identical Stiles-Crawford patterns? Or

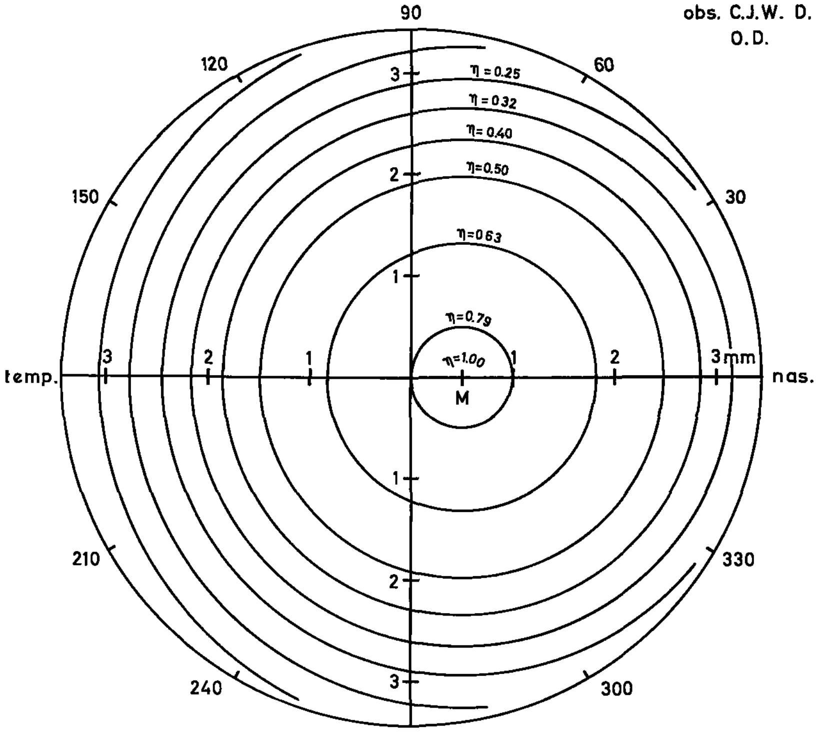


Fig. 1. Normal Stiles-Crawford pattern. The lines of equal luminous efficiency are concentric around a, slightly nasal, centre. Red light.

is this shape difference only an artefact, as suggested by Dowling (1965) on the basis of electronmicroscopic studies of cones? May the directional sensitivity of the individual receptor be much more pronounced than the eye as a whole, as suggested by Enoch (1960), the fact being obscured by a certain degree of disorder in the orientation of the receptors? But, as peripheral rods can hardly be distinguished from central cones, this would imply that rods show less alignment than cones. At the present time there is no reason to believe that this is so.

There are not only many unsolved problems as to the explanation of the Stiles-Crawford effect, but also many areas of ignorance about the role the Stiles-Crawford effect plays in visual performance. In daytime it can not play a role because of the narrowness of the pupil; at night it is of little importance because it is purely a photopic effect. Perhaps its major function is the suppression of entoptic stray light

– which is only another way of saying that light incident through the pupil is favoured. As students of vision, however, we have learned to attribute to the Stiles-Crawford effect quite another kind of significance: that of a powerful tool in visual research. To illustrate this – perhaps teleologically unacceptable – significance we will now give a couple of examples.

A clue to the mechanism of colour vision

Phenomena of colour vision have long been explained on the basis of the existence of three types of cones containing visual pigments absorbing at different spectral bands. A number of psychophysical studies has provided the basis for this assumption. Recent microspectrophotometric studies of cones have provided independent support for this assumption (Marks and McNichol, 1963, Brown and Wald, 1964). These objective measurements provide far less accurate information about cone pigments, however, than do psychophysical experiments. One example of the way psychophysical experiments can give quantitative information on the visual pigments is the determination of the pigment densities from the interrelation between colour vision and Stiles-Crawford effect.

How is the Stiles-Crawford effect related to colour vision? In the first place, it has been shown that the Stiles-Crawford effect is dependent upon wavelength. In the second place a shift in the entrance point on the pupil produces a hue shift as well as a decrease in luminous efficiency. Thirdly, the colour mixture functions change with increasing obliquity of light incidence. Following up suggestions by Stiles (1939) and Brindley (1953), Walraven and Bouman (1960) explored the possibility of relating this whole set of phenomena to certain aspects of absorption of light by the visual pigments. It is in particular the third effect, the break down of the colour match, which directs our attention to the visual pigments. It is hard to imagine how a nervous effect could affect a colour match. Once signals starting from the receptors are equal, the oblique incidence of the light cannot cause any change in the nervous transmission.

It is well known in colorimetry that a colour match cannot be upset unless the shapes of the colour mixture functions change. One possible set of colour mixture functions is the set of absorption curves of the visual pigments themselves. And a change in the shape of the absorption curves can be produced by a change in the optical density of the visual pigment. It follows directly from the exponential law of absorption that the absorption curve of a filter (to which the outer segment of a cone can be compared) broadens with increasing density. This effect starts to be of significance when the absorption in the top of the curve is more than 20%. Now perpendicular versus oblique incidence of the light can be compared with passage of the light through a thick versus a thin filter, respectively. With oblique incidence, the pathway of the light through the visual pigment in the outer segment is shorter than for perpendicular light, due to the light leakage. Thus the change in shape of the pigment absorption as manifest in the breakdown of the colour match is directly coupled to the loss in luminous efficiency as manifest in the Stiles-Crawford effect. This relation is complicated, however, by the fact that only that part of the light loss which occurs in the pigment-containing receptor outer segments is related to the hue effects, whereas the loss of luminous efficiency may be due to loss of light from either the inner or the outer segment. The extent to which the Stiles-Crawford effect is due to light loss in the outer vs the inner segments is not known; thus a direct relationship between the absolute size of the Stiles-Crawford effect proper and the breakdown of the colour match cannot be expected.

If the absorption curves become more narrow with oblique light incidence, this could particularly affect the luminous efficiency at the

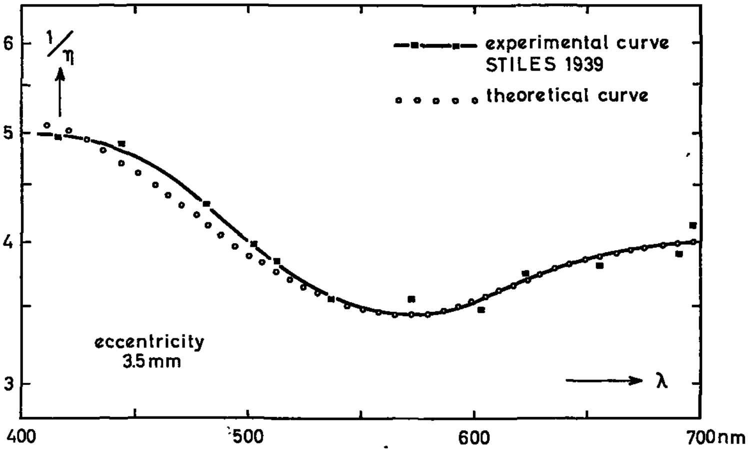


Fig. 2. Dependence of the Stiles-Crawford effect upon wavelength. The dip is attributed to the narrowing of the pigment absorption curves; the asymmetry should be attributed to an inherently stronger Stiles-Crawford effect in the blue cone system. Theoretical curve after Walraven and Bouman (1960).

ends of the visible spectrum with the result that the Stiles-Crawford effect should be smaller in the middle of the spectrum than at either spectral extreme. Such is actually the case, as is shown in Fig. 2. All of the variation of the Stiles-Crawford effect with wavelength cannot be accounted for by a narrowing of cone pigment absorption curves: There is in addition a rise of the Stiles-Crawford effect at the blue end of the spectrum. Stiles (1939) has accounted for this by hypothesing that the blue cones show a larger Stiles-Crawford effect than do the red or the green cones.

The theory that the wavelength dependence of the Stiles-Crawford effect is due to narrowing of the photopigment absorbing curves with oblique light incidence can be tested as follows. If the photopigments are bleached with a bright adaptation light, all pigment concentrations will be reduced to low values, so that the dip in Fig. 2 should disappear. This test has been made by testing the effects of bleaching on the Stiles-Crawford effect at 590 and 650 nm. The pigments have high effective density for light of 590 nm, but not of 650 nm. Bleaching should thus produce little change in the Stiles-Crawford effect at 650, but should produce an increase in the Stiles-Crawford effect at 590 nm. The change in the Stiles-Crawford effect at 590 nm during recovery from bleaching with a 650 nm light, is shown in Fig. 3.

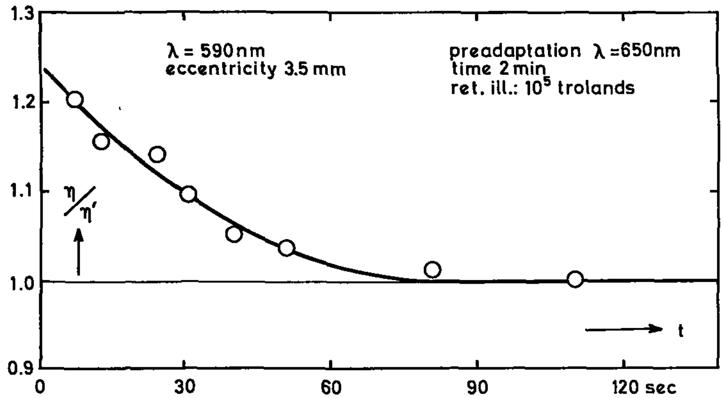


Fig. 3. Recovery of the normal Stiles-Crawford effect at 590 nm after offset of bleaching adaptation light. The Stiles-Crawford factor before and after bleaching is indicated with η and η' respectively.

The recovery rate compares well with the values found by Brindley (1953), who measured the recovery of the breakdown of the colour match. This agreement points again to a common, non-neural origin. At 650 nm, no change in the Stiles-Crawford effect produced by bleaching could be detected. The size of the effect of bleaching, as can be seen from the $t = 0$ value in Fig. 3, is just large enough to make the dip in Fig. 2 fully disappear. In other words, the dip can be completely accounted for by the high pigment concentration.

The absolute value of the pigment concentration cannot be completely specified by these experiments. There remains a certain freedom of choice due to the fact that we do not know to what extent the Stiles-Crawford effect proper is due to leakage from the outer versus the inner segment of the receptors. If the whole process takes place in the outer segments, then a pigment density of 0.3 (corresponding to 50% absorption) is sufficient to explain the phenomena observed. The more the Stiles-Crawford effect takes place in the inner segments, the higher the pigment density must be to account for the phenomena. We can thus specify a minimum density value of 0.3 for the cone pigments at their absorptive peak.

A clue to entoptic scatter

As mentioned before, the significance of the Stiles-Crawford effect in vision might be its suppressive effect on intra-ocular stray light. The receptors are orientated towards the pupil, and thus the normally incident light is accepted with preference to stray light which comes from all directions, scattered as it is by inhomogeneities in the ocular media and at the fundus itself.

With a slight shift in accent one may reformulate the above in the following way. Light scattered at the ocular fundus is, as far as cone vision is concerned, relatively ineffective, and it is independent of the way the primary incident light beam has entered the eye. Stray light from cornea and lens, on the other hand, will be more and more suppressed with increasing eccentricity of incidence, simply because it is subject to the normal Stiles-Crawford effect. Hence we have a means to distinguish between stray light produced in the anterior eye media, and that produced near or at the fundus .We will not go deeper into this subject here, as it is discussed already in more detail in the tenth study, on light scatter at the fundus. We would not fail to mention this aspect, however, within the present context.

As the Stiles-Crawford effect is typically a cone phenomenon, one would expect that the suppressive effects would disappear at scotopic light levels. In fact, indications of this were found (Vos and Bouman, 1959) in measurements of the 'glare capacity' as a function of glare intensity. A difficulty in discussing these data (Vos, 1963) is that we are largely ignorant of the behaviour of the Stiles-Crawford effect – of both rods and cones! – in directions which are obscured by the iris. Our knowledge about the suppression of entoptic stray light rests mainly on guesses, extrapolations, and vague experimental indications. Therefore, any indication about the continuation of the Stiles-Crawford effect outside the pupillar area will be welcome.

One of the sources of information lies in the occurrence of strongly asymmetrical Stiles-Crawford patterns. They suggest, that, in fact, the reduction of the luminous efficiency continues behind the pupil border, so that it reaches values of 0.05 or less. We will return to this problem in the next and last section. Quite another, and as yet unexplored source, might lie in the hue shift of diascleral light. Schouten (1934), who as a first investigated the intensity and spectral distribution of light which enters the eye through the externally visible part of the sclera, noticed a curious hue difference between a light seen through the sclera and the same light when it enters normally through the pupil. His qualitative discription leads one to suspect that he actually noticed a Stiles-Crawford hue shift 'avant la lettre'. More detailed exploration of this Stiles-Crawford effect outside the pupillar area via its hue shift might give a more solid basis for evaluating its suppressive effect on entoptic stray light.

An aid in ophthalmological diagnosis

A third and last example which we will give of possible uses of the Stiles-Crawford effect is in making diagnoses of retinal anomalies, and in following recovery after treatment. Let us make clear, though, that this area is still in an exploratory state; it is far from sure that this application will ever be realized in ophthalmological practice.

We can approach our subject from two sides. The first approach is via the 'Campbell Effect'. In 1958 Campbell found that in looking through a circular aperture of 1 mm diameter placed close to the cornea, visual acuity is maximum when the aperture is over the approximate centre of the pupil. If the aperture is displaced from the centre towards the periphery of the pupil, visual acuity decreases at right angles to the meridian of displacement. It does not decrease, however, in the meridian of displacement. Bypassing the confusion – not the least due to Campbell himself (Campbell, 1960) – about the size and origin of the effect, we can state that a reduction, with increasing eccentricity, of the 'tangential' grating acuity by some 30% must be attributed to causes associated with the Stiles-Crawford effect. An example of this reduction is given in Fig. 4.

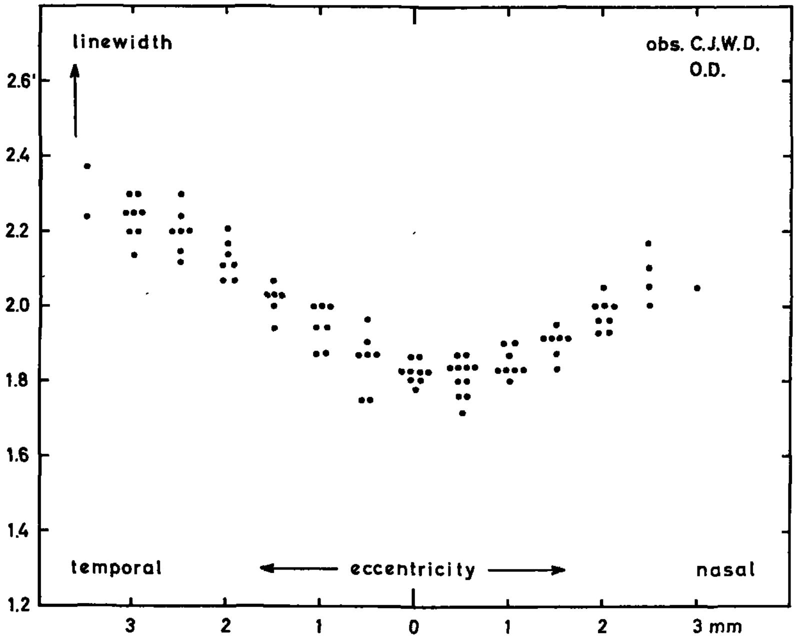
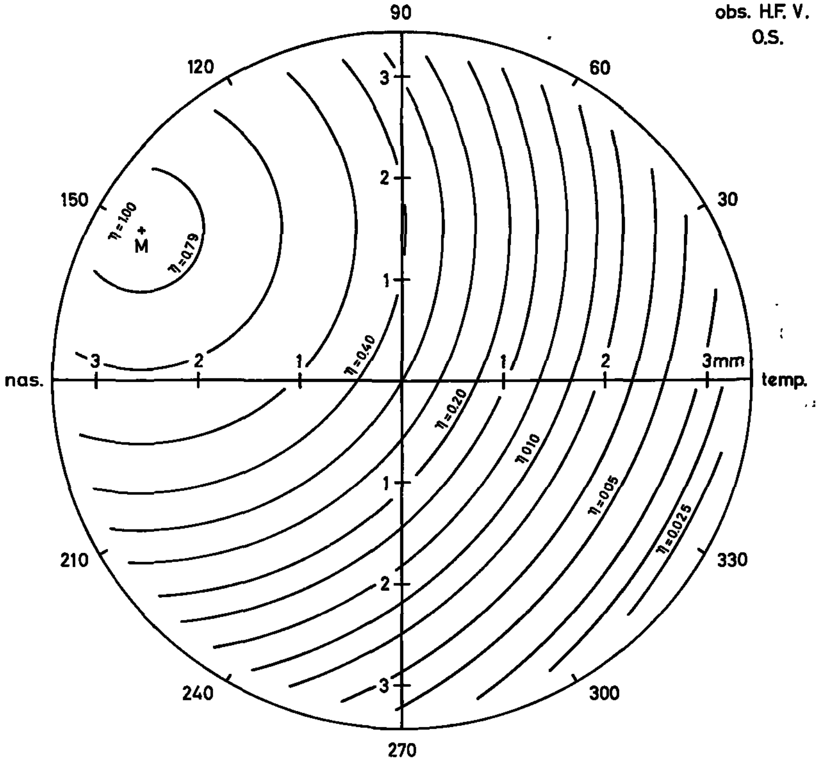


Fig. 4. The just perceptible linewidth as a function of eccentricity of entry of the light beam at the pupil. Same eye, same wavelength as in Fig. 1. Retinal illuminance 5 troland.

The main argument against this effect being due to dioptrical processes, such as spherical aberration, is the coincidence of the maxima of both the visual acuity and luminous efficiency curves in relation to the pupil. This is not only in the normal situation and with such slightly eccentric positions as in the case illustrated in Fig. 4, but also in more anomalous situations where the maximum lies as far as 3 mm off centre (Fig. 5a and b; from Dunnewold, 1964). Qualitatively, this reduction of visual acuity can be interpreted in terms of an increasing leakage of light from one receptor to another, with increasing obliquity of light incidence. But if this is true, one might expect a reduction of visual acuity in such anomalous cases as the just mentioned; the usual



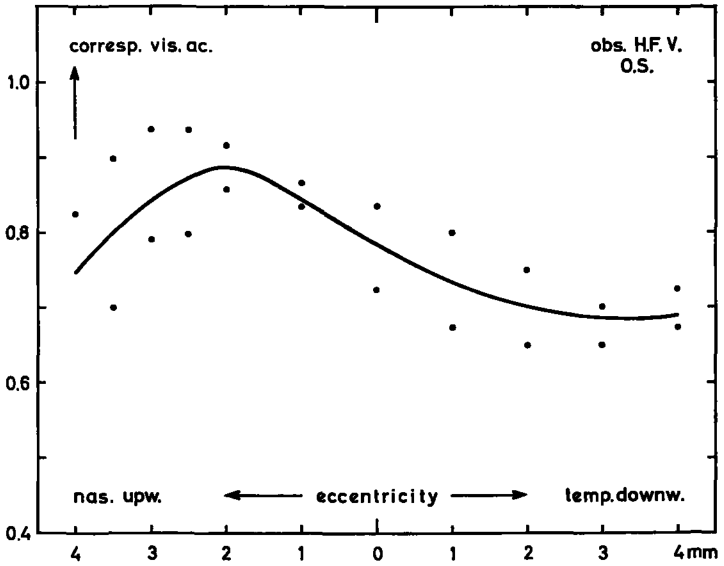


Fig. 5a. Stiles-Crawford pattern of the amblyopic eye of obs. H.F.V.

Fig. 5b. Visual acuity as a function of the point of entry of the light beam in the same eye, along the meridian through the maximum.

clinical test methods are too rough, though, to reveal any such effect in normal cases. For an amblyopic eye with abnormally eccentric position of the Stiles-Crawford top, however, we could measure an acuity effect with Landolt rings (Fig. 5b).

And with that, we have come to the second approach to our subject. In 1957 Enoch described a case of non-squinting amblyopia with abnormally flat Stiles-Crawford effect. Enoch gave an interpretation based on a disturbance of the otherwise orderly receptor orientation and it will be clear that this explanation falls well in line with the reasoning about the origin of the – later discovered – Campbell Effect. Since then, Enoch and coworkers (Enoch, 1959a, 1959b; Fankhauser, Enoch and Cibis, 1961), and Dunnewold (1964) have investigated a number of clinical cases of possible interest, to evaluate the significance of the Stiles-Crawford effect for diagnosis, follow up, and prognosis. Fankhauser, for instance, followed the recovery of retinal strain after light coagulation. Other cases investigated were cases of central serous retinopathy, central retinal oedema, congenital coloboma of the uvea, and prepapillar toxoplasmotic inflammation.

Let us try to summarize the confusing findings.

a. The coincidence of a number of cases of anomalous Stiles-Crawford patterns and ocular disfunction seems to point to a relation. This relation is unclear, however, and only statistical in nature. Typically asymmetric Stiles-Crawford patterns have been found, for instance, without any abnormality in visual performance. Certainly the number of cases investigated is too small to draw definite conclusions.

b. Since the procedure of measuring the Stiles-Crawford effect is time consuming, notwithstanding the development of instruments for clinical measurements of the Stiles-Crawford effect (Vos and Huigen, 1959), further research is called for.

c. The position of the top of the Stiles-Crawford curve with relation to the pupil varies so much from subject to subject, that it is difficult to decide on that basis whether a Stiles-Crawford pattern is anomalous or not. Moreover, the correlation between the positions of the maxima in the left and right eyes of one subject is hardly better than that between the eyes of different subjects. Thus the 'normal' eye can not be used in clinical practice. It is possible, however, that in future it will play a role, notably to diagnose differentially cases of amblyopia, since the Stiles-Crawford effect is the only means of access to problems of receptor orientation. A great deal of laborious research has to be done, however, before we can admit a Stiles-Crawford check into clinical test procedures.

Concluding remarks

We have mentioned three types of application of the Stiles-Crawford effect to other fields. One field is that of colour vision. Here it proved a useful means of obtaining more knowledge, in particular about pigment densities. A second field was that of entoptic light scatter. Here the Stiles-Crawford effect opened the way to being able to distinguish between light scattered in the anterior eye media and at the fundus. Finally its relevance to ophthalmology was discussed. It is not excluded that at some future time the Stiles-Crawford effect will find application in the diagnosis and prognosis of cases of retinal disfunctions.

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