J. Physiol. (1967), **192**, *pp.* 309–315
With 4 *text-figures*
Printed in Great Britain

DEPENDENCE OF THE MAGNITUDE OF THE STILES–CRAWFORD EFFECT ON RETINAL LOCATION

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(*Received* 17 *January* 1967)

SUMMARY

1. The directional sensitivity (Stiles–Crawford effect) of retinal cones is supposed to be associated with their shape, but only extrafoveal cones have a cone-like shape; cones in the central fovea are elongated and look like rods.

2. To determine whether the directional sensitivity of cones depends on their shape, the Stiles–Crawford effect was measured both in the central fovea and in the parafovea of the human eye.

2. To ensure that the cone population tested was homogeneous, a small brief test flash, brought into the eye through the centre of the pupil, was placed at threshold by varying the intensity of a large adapting field. The directional sensitivity of the cones was determined by finding the efficiency of light to act as an adapting background as a function of position of entry in the pupil.

4. Central foveal cones have a less pronounced directional sensitivity than parafoveal cones and this lends support to the conclusion that the Stiles–Crawford effect is connected with the shape of the retinal receptors.

INTRODUCTION

The retinal directional effect, discovered by Stiles & Crawford in 1933, is essentially confined to cone vision. Evidence for this is seen in the disappearance of the effect when, during dark adaptation, the change-over occurs from cone vision to rod vision (Crawford, 1937), and in the experiments of Flamant & Stiles (1948), who showed that the receptor system not concerned with the Stiles–Crawford effect has the scotopic luminosity curve. While it is true that some directional effect has been demonstrated for rods at extremely high obliquities, it seems to be of an entirely different order of magnitude. This association of the Stiles–Crawford effect with cone rather than rod vision has been found useful where it was necessary to differentiate between the photopic and the scotopic systems (Donner & Rushton, 1959; Fuortes, Gunkel & Rushton, 1961).

Although the exact nature of the mechanism by which obliquely incident light is effectively attenuated remains to be elucidated, the Stiles–Crawford effect is usually regarded as being due to the shape of the cones. However, cones vary considerably in their shape: the foveal cones look very much like rods; only the peripheral cones have the appearance commonly ascribed to cones. Yet in the one study in which a difference was looked for in the Stiles–Crawford effect for central and peripheral vision (Aguilar & Plaza, 1954), none was found. The evidence tends to favour the view that the photopigment molecules are embedded in the lamellae of the outer segments. If indeed the Stiles–Crawford effect is independent of cone shape, one might have to seek an explanation for the difference in directional sensitivity between rods and cones at the level of the fine rather than gross receptor structure, though the differences between lamellar fine structure of the outer segments in cones and rods are too slight to make this a promising lead (Cohen, 1961; Dowling, 1965).

In some respects, however, the study of Aguilar & Plaza (1954), which constitutes the main objection to a linkage of gross cone structure with the Stiles–Crawford effect, is inconclusive: only a few points of entry in the pupil were used, and no clear precautions were taken to segregate the responses of central cones from those of the near periphery. It was, therefore, decided to reinvestigate the influence of retinal position on the Stiles–Crawford effect to see whether it would not be possible, after all, to demonstrate a dependence of its magnitude on retinal location and hence on cone shape.

METHODS

The point of departure of the present study is the observation that even the earliest anatomical drawings (Schultze, 1866) show the central elongated rod-like cones to be confined to a region not much wider than $\frac{1}{2}°$ in diameter. Already $\frac{3}{4}°$ from the centre of the fovea the cones have their more familiar cone-like shape. Elaborate precautions were, therefore, taken to ensure that the cone population, whose directionality was being tested experimentally, remained as homogeneous as possible.

The technique employed was based on Stiles's (1939) finding that light impinging obliquely on the retina was less efficient in inducing sensory excitation regardless of whether it acted as a test stimulus or as an adapting stimulus. Thus, for a given test stimulus to be seen at its incremental threshold, more light had to be provided in the adapting field if the latter was brought into the eye through the edge of the pupil rather than through the centre of the pupil. The magnitude of this decrease in efficiency was the same as that found when the *test* stimulus was moved from central pupillary entry to peripheral pupillary entry.

Inevitable changes in image quality occur when a small object is imaged through different small portions of a dilated pupil. If the small object is to act as a test stimulus whose threshold is to be determined, such changes in light distribution may cause changes in the threshold luminance of the target. Changes in position of entry in the pupil may then introduce changes in increment threshold which are entirely secondary to changes in retinal light spread and not connected with obliquity.

The difficulties associated with possible changes in the point-spread function of the eye as different positions of entry in the pupil are sampled, were obviated in the present experiments by using a small constant-luminance test flash which was always imaged through the centre of the pupil. The directional sensitivity of the cones in the test field was measured by bringing the beam carrying a $7\frac{1}{2}°$ adapting field into the eye through various parts of the pupil and adjusting the energy of this adapting beam so as to place the test flash at threshold. While the shape of the point-spread function may have changed as the adapting beam's point of entry into the eye changed, the illuminance level in the middle of the image of a field that is large compared with the extent of the point-spread function is in practice independent of the exact shape of the point-spread function. The dependence of the Stiles–Crawford effect on retinal location was then studied by first presenting the test flash in the centre of the fovea and then in the parafovea.

The apparatus (Fig. 1) consisted of two Maxwellian view optical beams, brought together by a beam splitter. The source in each beam was a 6 V, 2·75 A compact filament tungsten source. Both lamps were run in parallel from the same D.C. power supply. The filaments were imaged in the pupil with a 2:1 reduction; the filament images were vertical rectangles measuring $\frac{1}{2} \times 1$ mm. One of the beams was used to produce a circular adaptation field on the retina. This beam was exposed continuously, and contained a Wratten no. 99 green filter (peak transmission near 540 nm) as well as a neutral wedge adjustable by the subject. The source for this beam was mounted on a microscope stage allowing the source image to be moved horizontally across the subject's pupil. The second beam was exposed intermittently (0·05 sec every second) by means of a sector disk driven by a synchronous motor. It contained a Wratten no. 29 red gelatine filter, which virtually excludes all light of wave-length shorter than 600 nm. The beam was further attenuated by a neutral filter which brought its retinal illuminance level to 30 photopic trolands of red light.

The subject had his pupil dilated by the instillation into the conjunctival sac of one or two drops of 1 % cyclogyl about $\frac{3}{4}$ hr before beginning the experiment. He was positioned in the apparatus by means of a bite bar so that initially both incoming beams passed through the centre of his dilated pupil. Fixation was achieved by placing in the target plane of the large adaptation field four hairs in the form of two parallel crosses shifted horizontally and vertically by about $\frac{1}{3}°$. There was thus outlined a square of $\frac{1}{3}°$ side length, in the centre of which appeared the 12′ circular test flash for $\frac{1}{20}$ sec every second. For the measurements in the fovea, the subject was instructed to look at the centre of the square; and for parafoveal fixation, the subject was instructed to look at the intersection of one hair line with the right edge of the background. The test flash then appeared 3·75° away from the fovea.

The wave-length separation of the test flash and the background was chosen to favour cone vision over rod vision and the data clearly show that parafoveal cones responded rather than rods, which would have shown no Stiles–Crawford effect.

With the entrance point in the pupil of both the test and adaptation stimuli coinciding, the subject was instructed to move the wedge controlling the luminance of the adaptation field so that the flashing test stimulus was seen at threshold. A reading was taken followed by three further settings; the average of the four settings was plotted. The source in the Maxwellian beam carrying the adaptation field was now moved in 1 mm steps, shifting the point of entry in the pupil in $\frac{1}{2}$ mm steps, and measurements were obtained until the edge of the pupil was reached. The point of entry was now placed back in the centre of the pupil and the procedure repeated until the other edge of the pupil was reached.

The whole procedure was now repeated with parafoveal test flash presentation. The subjects' right eyes were used, and for parafoveal measurements the subjects were instructed to fixate 3·75° to the right, i.e. the test flash fell on the temporal parafoveal retina.

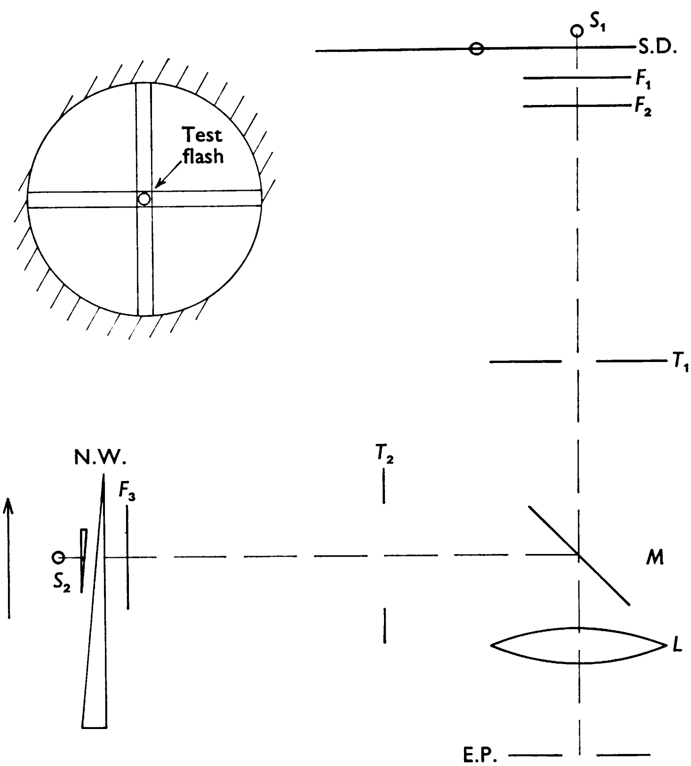

Fig. 1. Schematic diagram of apparatus to measure Stiles–Crawford effect (not to scale). S_1, S_2 tungsten filaments imaged by lens L in pupil of subject's eye. M beam splitter. Source S_2 can be moved in direction indicated, thus varying position of entry in subject's entrance pupil (E.P.) of beam carrying adapting background. S.D., sector disk exposing test beam for 0·05 sec every second. F_1, F_2 neutral and red filter for test flash, F_3 green filter for background, N.W. neutral wedge (with fixed counter wedge), adjusted by subject, varying intensity of background so as to place test flash at threshold. T_1, aperture controlling size of test flash; T_2 aperture controlling size of background. Inset: subject's view of field. Test flash appeared as small (12 min of arc) disk in centre of circular adapting field $7\frac{1}{2}°$ in diameter. For test flash presentation in centre of fovea, subject was instructed to fixate the centre of pattern created by four hairs in plane of aperture T_2; for parafoveal presentation he was instructed to fixate right edge of field at one of the hair lines.

RESULTS

In Fig. 2 the results of the experiment are shown for one of the subjects. In it, the illuminance of the green adapting field is plotted at which the red, 12 min of arc, 0·05 sec, 30 troland test flash is seen at threshold, as a function of point of entry in the pupil of the adapting beam, both for central and peripheral fixation. The mode of presentation—background illuminance increasing downwards—has been chosen to make the curves similar to the ones usually seen to depict the Stiles–Crawford effect.

The fact that the parafoveal curve is higher than the central one is an indication that in general the fovea is more sensitive, for more background light is necessary here to place a given test flash at threshold. The important

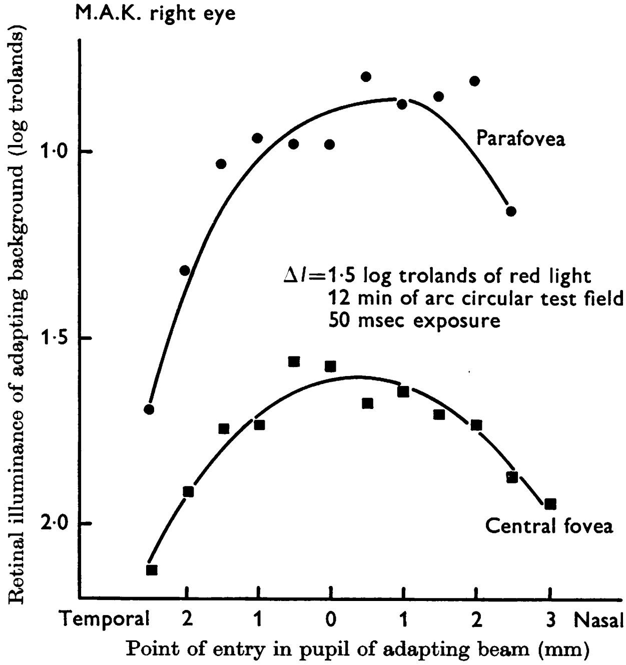

Fig. 2. Retinal illuminance of large green backgrounds necessary to place a constant small, short, red incremental test flash at threshold, as a function of point of entry of adapting light beam along horizontal meridian of pupil. Upper curve, test flash falls 3·75° from fovea; lower, test flash falls on centre of fovea. Note that ordinates show retinal illuminance increasing downwards, so that curves display the directional sensitivity of retinal receptors in the familiar manner.

finding is that while the directional effect of the parafoveal cone retina in this experiment is more or less that given in Stiles & Crawford's original study and the numerous replications since, the directional effect for a population of purely central foveal cones is distinctly less pronounced.

Figure 3 gives the results for another subject, and Figure 4 for still another subject. Two further subjects gave similar results.

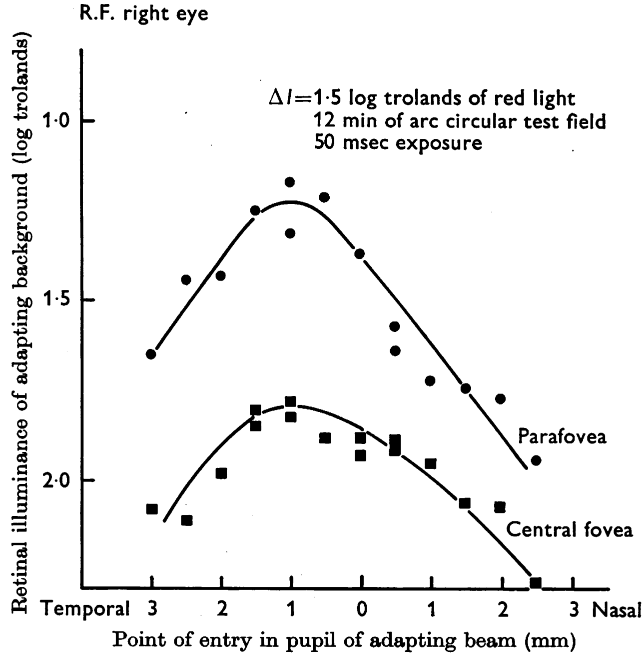

Fig. 3. Results for another subject. See legend of Fig. 2 for details.

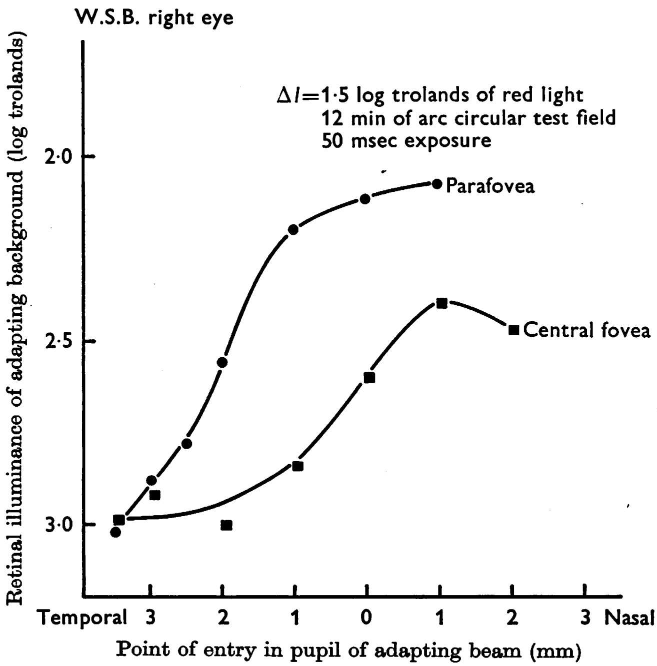

Fig. 4. Results for a third subject. See legend of Fig. 2 for details.

DISCUSSION

The difference between the findings in this paper and previous studies, particularly that of Aguilar & Plaza (1954) who were looking for this phenomenon, is probably due to the experimental arrangement. The very small test flash and the constancy of its site of entrance into the eye ensured the measurement of the directional effect of central foveal cones as it has possibly not been done before. The difference in directional sensitivity demonstrated between foveal and parafoveal cones by all of our subjects is unlikely to be an artifact produced by something in the optical path to the retina, since under the two conditions only minute differences could be involved. The retinal regions used are only about $\frac{3}{4}$ mm apart and light reaching them would share almost all the portions of the cornea, lens and vitreous traversed.

The results in Fig. 4 are particularly interesting since in this subject there is a shearing-over of cones, already observed in one of Flamant & Stiles's subjects (1948), with a consequent uncovering of the shoulder of the Stiles–Crawford effect which is seen when one has a chance to get measurements well away from the centre of the sensitivity lobe. But the parafoveal cones do not exhibit this shoulder. The results were quite repeatable.

The finding that central foveal cones have a less pronounced directional sensitivity than parafoveal cones, coupled with the more elongated, more rod-like, appearance of the foveal cones, lends support to the conclusion that the Stiles–Crawford effect is somehow connected with the shape of the retinal receptors.

This research was supported in part by Grant NB-03154 from the National Institutes of Neurological Disease and Blindness, U.S. Public Health Service, and by a contract between the office of Naval Research and the University of California.

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