

## LIGHT CAPTURE BY HUMAN CONES

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### SUMMARY

1. The variation in visual efficiency of light with varying pupillary entry (the Stiles–Crawford effect) was measured to determine the proportion of light incident on the cones that escapes them without recovery by other cones.

2. The variation in detectability of interference fringes with varying pupillary entry of the interfering beams was measured to determine the proportion of incident light that was *recaptured* by cones in the dark stripes after escaping cones in the bright stripes of the fringes.

3. By exclusion, these observations determine the variation, with varying pupillary entry, in the proportion of incident light that was *captured* and absorbed by the first cones it entered.

4. Some 70–90% of the light absorbed by the cones when it passes through the centre of the pupil, is entirely lost to the visual system if it passes instead through the margin of the (dilated) pupil.

5. Over half the light that cones absorb when the light enters the margin of the pupil is light that has previously passed through other cones.

6. If the spread of recaptured light is assumed to be Gaussian, its standard deviation is at most one minute of visual angle.

7. Such recaptured light makes a previously unknown contribution to the various Stiles–Crawford effects.

### INTRODUCTION

Light entering the pupil of the eye at its centre more effectively stimulates the eye than light entering near the pupil's edge (Stiles & Crawford, 1933). Light from the margin of the pupil falls on the receptors at an oblique angle and tends to escape before being absorbed. This is undisputed, but it only partially explains this Stiles–Crawford effect, for a full explanation must tell where the escaped light goes. Ultimately, such escaping light must: (1) pass back out of the eye; (2) be absorbed by inert structures; or (3) be absorbed by other receptors. Certainly not much passes back out of the eye. Most must pass between cones to the pigment epithelium where it is absorbed by inert pigments. Yet, estimates of the spatial distribution of such escaped light (cf. especially, Miller & Snyder, 1973) suggest that some of the light

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that escapes cones (even foveal cones) must impinge on neighbouring cones where it is subject to recapture. Such light that escapes one cone and is recaptured by its neighbours would have the same effect on conventional measurements of the Stiles–Crawford effect as if it had remained in the original cone; however, such light must reduce the contrast, or visibility, of gratings cast onto the retina. It is puzzling, then, that Green (1967) observed no such loss of contrast when he measured the visibility of interference fringes produced by beams passing through different parts of the pupil. Consequently, we have replicated and extended his observations. We find that under conditions not tested by Green, the expected loss of contrast does occur.

#### LIST OF SYMBOLS

- $d$  = pupillary position at which light enters  
 $d_0$  = pupillary position at which entering light is most effective  
 $\Delta d$  = separation of interfering beams in the plane of the pupil  
 $\Delta I$  = flux density at threshold for a test flash  
 $I_B$  = flux density of background light against which a test flash is presented  
 $I_0 = I_B$  for light entering the pupil at  $d_0$   
 $I$  = ratio of flux density with a given effect at entry  $d$ , to that with the same effect at  $d_0$  (the inverse of the Stiles–Crawford effect)  
 $c_{1-3}$  = free parameters of the threshold *versus* intensity curve (eqn (2))  
 $c_{4-6}$  = free parameters of the Stiles–Crawford effect (eqn (5))  
 $C$  = Michelson contrast of threshold fringes at the retina  
 $C_0 = C$  when  $d = d_0$   
 $C^*$  = Michelson contrast of threshold fringes at the site of absorption in the cones  
 $i_u$  = unrecovered light ( $I - 1$ )  
 $i_c$  = captured light ( $C_0/C$ )  
 $i_r$  = recaptured light ( $1 - i_c$ )  
 $i_e = i_u + i_r$  (escaped light)  
 $f$  = spatial frequency of a grating  
 $p$  = amplitude of the optical transfer function  
 $\sigma_f$  = standard deviation of the optical transfer function  
 $\sigma_x$  = standard deviation of the spread function  
 $\theta$  = retardation angle

#### METHODS

##### *Apparatus*

A conventional two-channel Maxwellian system was used to measure the Stiles–Crawford effect. Rotation of a prism just behind the aperture stop of one channel moved the image of the stop, which was 1 mm in diameter, in the plane of the observer's pupil with little or no movement of the image of the field stop on the retina. The small movement of the retinal image associated with highly eccentric passage through the pupil was compensated by adjustment of the field stop imaged on the retina.

A different apparatus was used to erect sinusoidal gratings on the observer's retina. This was done through interference between two beams created by splitting the output of a 1 mW He–Ne laser. The essential features of the design, shown in Fig. 1, follow that of Williams (1985*a*). The

light first passes through a variable beam-splitter, VB, that permits regulation of the relative powers of the interfering beams. The beams then pass through acousto-optic modulators, Mo, which together control the time-averaged contrast of the interference fringe, as described below. The spatial filters, F, remove spatial noise from the beams and expand them. After collimation by lenses,  $L_{1,3}$ , images of the pinhole apertures are formed by lenses  $L_{2,4}$ . After the beams are combined by the cube  $C_2$ , they are again collimated, by lens  $L_5$ , and images of the apertures are focused by lens  $L_6$  in the observer's pupil. Field stops, S, are focused by the same lens on the observer's retina. A linear polarizer just in front of the eye ensures that the two beams fall on the eye in the same state of polarization. For some experiments, this was removed, and crossed polarizers were inserted in the interfering beams just before they combined at cube  $C_2$ , and the power of the beams at the eye was readjusted to equality.

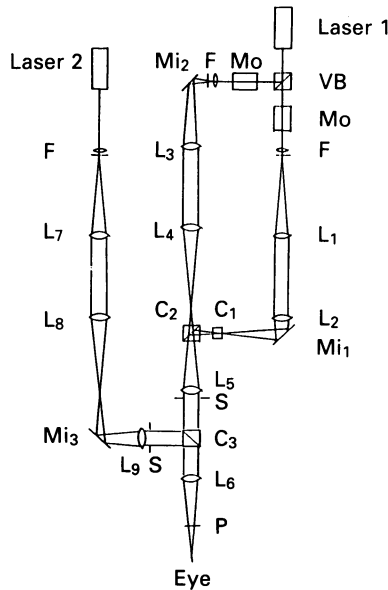


Fig. 1. Schematic diagram of the interferometer. The apparatus is explained in the text. VB, variable beam-splitter; Mo, acousto-optic modulator; F, spatial filter;  $L_{1-9}$ , lenses;  $C_1$ , cube controlling spatial frequency and orientation;  $C_{2,3}$ , beam-splitter; S, field stop;  $Mi_{1-3}$ , mirrors; P, linear polarizer.

Rotation of cube  $C_1$  about perpendicular axes moves the image of one of the pinhole apertures along the two perpendicular co-ordinates of the observer's pupil. As the distance and relative orientations of the two images determine, respectively, the spatial frequency and orientation of the resulting fringes, this cube controls those properties of the resulting fringe.

Contrast of the fringes was controlled through the action of the two acousto-optic modulators, which chopped each beam into 1 ms pulses separated by 1.5 ms. The relative phase of the pulses was under computer control: when they were simultaneous, interference between the two beams on the retina produced a sinusoidal grating of 100% contrast (flickering at 400 Hz); when the pulses alternated, so that one was off whenever the other was on, interference between the beams was not possible, and a zero contrast grating was formed (i.e. two homogeneous fields, each flickering at 400 Hz). Gratings of graded contrast were achieved by varying the temporal overlap of the pulses from the two beams, thus varying the proportion of time the pulses interfered. As the rate of alternation of the fields was well above the observers' flicker fusion frequency, a steady grating was seen, the contrast of which was equal to the proportion of time during which the

fields overlapped. As such variations of timing were not detectable except by their effects on the fringe contrast, forced-choice determination of fringe thresholds was possible.

Because threshold contrasts sometimes approached the smallest contrasts (0.78%) available from our apparatus at the beginning of these experiments, contrast was reduced by addition of a uniform field of light from a second laser, except in experiments where maximum contrast might be needed. This light passed through a series of elements directly analogous to those of the other channels, except the initial beam splitter and acousto-optic modulators. The pupillary image of the pinhole, which was under the control of the mirror,  $M_3$ , was positioned in the observer's pupil midway between the two beams of the other laser.

Both apparatuses were equipped with a calibrated, three-co-ordinate manipulator that held the observer's bite-board and a clinically prescribed lens that corrected the observer's myopia and astigmatism. The entry of the laser beams through the pupil was varied by moving the subject's head, with due allowance for the small beam displacement caused by movement of the lens.

### Stimuli

To measure increment thresholds, discs of either 1 or 2 deg were presented to the fovea for 100 ms every 2 s, against a steady, concentric background of 4.8 deg. Light in both fields passed through a 630 nm interference filter placed just before the eye.

To measure contrast thresholds, gratings were presented with 632.8 nm light in a 1.5 deg circular field at 500 td. Grating contrast was zero between trials and assumed the value of the test contrast during one of a pair of 500 ms tones, separated by 100 ms. Spatial frequency was determined by the separation of the interfering beams, according to the relation (Green, 1967):

$$f = 27.6\Delta d, \quad (1)$$

where  $\Delta d$  mm is the separation of the beams in the pupil of the eye, and  $f$  is the spatial frequency in cycles  $\text{deg}^{-1}$ .

*Calibrations.* The power of each laser beam was measured and equalized before each run at the location of the eye by a United Detector Technology (USA) 61 Optometer with a QED-200 detector. Occasional checks were made after sessions to establish that power was constant over the course of the sessions. Filters were calibrated *in situ*. That contrast of the fringes corresponded to the proportion of temporal overlap between pulses of the interfering beams passed by the modulators was checked down to 2% by scanning them with a pinhole aperture and displaying the output of the radiometer on a storage oscilloscope (No. 7613, Tektronix, USA) with adjustable offset (No. 7A22 preamplifier). The relation between beam separation and spatial frequency of the fringes specified above was checked in the range from 1 to 15 cycles  $\text{deg}^{-1}$  by adjusting the frequencies so that the gratings were in identical phase at the edge of a 1 deg aperture, and by counting the number of lines. Confirmation that the beam separations in a magnified image were correct at these frequencies supports the assumption that the relationship was correct at the higher frequencies as well.

### Procedures

Increment thresholds were obtained by the method of adjustment, with the wedge offset randomly in direction and amount between trials. We always passed the light in the test flash through the centre of the pupil to keep it in good focus, but we varied the pupillary entry of the background field, which was large enough (4.8 deg) to avoid any effects its image quality might have on thresholds for the test flash at its centre.

Contrast thresholds were measured by an adaptive, two-interval forced-choice procedure (Watson & Pelli, 1983) with feedback. Thresholds (75% correct) were based on fifty trials. Several such thresholds were determined under each set of conditions, and the standard errors reported below refer to the variability among these separate threshold determinations. Contrast thresholds for horizontal and vertical gratings were measured by beams passing through positions varying along both horizontal and vertical diameters of the pupil. Depending on the orientation of the fringes, the two beams either entered the pupil at different points on the meridian along which they varied, or they straddled the meridian. When the beams entered at different points along the meridian measured, beam intensities were adjusted to compensate for the Stiles-Crawford effect, although this compensation is not critical; optical theory (Born & Wolf, 1970) shows that a mismatch of beam intensities as great as 4:1 reduces contrast by only 20%, and we confirmed the

applicability of this conclusion to the present work by control observations near the temporal edge of observer B.C.'s pupil, where sensitivity to the beams differs by 2:1.

The sequences of replications were counterbalanced to bring out any systematic changes of sensitivity. None were observed.

#### Observers

Both observers had normal colour vision and myopia (before correction):  $-4$  D for B.C. and  $-5$  D for W.M. The pupils were dilated by dual application of 1% Mydriacyl 25 min before the experiment and afterwards when necessary to prevent constriction of the pupil. Each observer used the right eye.

## RESULTS

### *Total light lost*

Our first step was to measure variations of the light lost to the visual system with varying angles of incidence on the retina. We did this by measuring how much light must be added to compensate for the lost light. This is the same as measuring the Stiles-Crawford effect.

We measured sensitivity to light in a test flash but varied the pupillary entry of the background light. To infer how much light is lost by changing its pupillary entry, it is useful to know the relationship between amount of background light and sensitivity to the test flash, and whether this relationship is affected by changing the entry of the background light. Figure 2 shows such threshold *versus* intensity curves, obtained with background light passing through either the centre or margin of the pupil (3 mm towards the temporal side). The curve is a template of the form:

$$\log \Delta I = c_1 \log (c_2 I_B + c_3), \quad (2)$$

where  $\Delta I$  is the threshold intensity,  $I_B$  is the background intensity, and  $c_{1-3}$  are free parameters.

The parameters  $c_1$  and  $c_3$  depend on the observer. Only the parameter  $c_2$  depends on the entry of the background light through the pupil. For observer B.C.,  $c_2$  is 3.16 times greater (0.50 units on the logarithmic scale) when the background light enters the centre of the pupil than when it enters near the margin; for observer W.M., it is 2.75 times greater (0.44 units on the logarithmic scale). The data obtained with the background light passing through the margin of the pupil have been translated leftwards by these amounts to bring them into coincidence with the data for background light entering the centre of the pupil. Evidently, after this shift, a single curve or template suffices to describe both sets of data. The ratio of  $c_2$  under these two conditions represents the relative effectiveness of light passing through these two pupillary loci. That is, 3.16 units of light passing through the margin of B.C.'s pupil has the same effect as 1 unit of light passing through the optimal location. It is just as though 2.16 out of every 3.16 units of light passing through the margin of the pupil are lost to the visual system. Therefore, we take these results as a means of estimating the amount of light that was lost to the visual system that would not have been lost had it entered the optimal locus in the pupil.

Next, thresholds were found with the background entering through several different parts of the pupil. In each case the background intensity was adjusted on the basis of pilot data to yield approximately equal thresholds. Then the values of

$c_2$  necessary to fit the data were determined. Finally,  $I$ , the relative increase of light necessary to compensate for the effect of moving its pupillary entry from the optimal location, is found by the relation :

$$I = c_2 I_B / I_0. \tag{3}$$

Stiles-Crawford curves are conventionally plotted to show variations of sensitivity with varying pupillary entry. The focus here, however, is on losses of light with

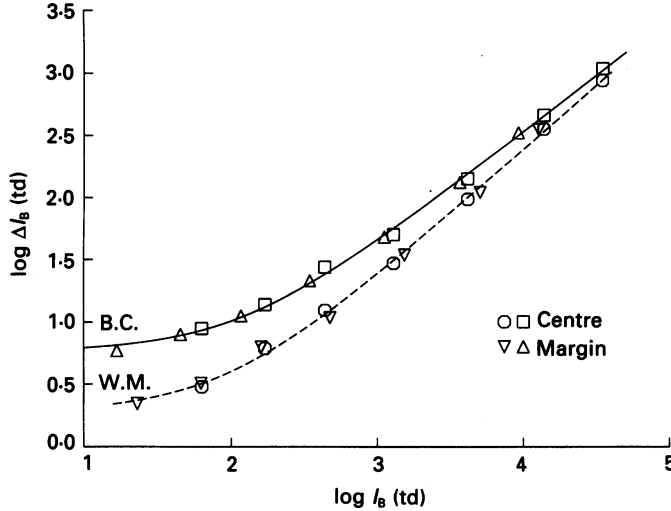


Fig. 2. Increment threshold at varying background intensity. The background light passed through either the centre or margin of the pupil (3 mm towards the temporal side); test light, through the centre of the pupil. Background and test flash intensities are in log Trolands. Squares and octagons represent data from central pupillary entry; triangles, marginal pupillary entry. Data obtained with marginal pupillary entry from observer B.C. were translated 0.5 log units to the left; those from observer W.M., 0.44 log units to the left. Curves are least-squares fits of eqn (2), with the following parameters: for B.C.,  $c_1 = 0.906$ ,  $c_2 = 0.0609$  and  $c_3 = 6.88$ ; for W.M.,  $c_1 = 1.031$ ,  $c_2 = 0.0203$  and  $c_3 = 1.811$ .

varying pupillary entry. If a unit amount of light entering the optimal location of a pupil has the same effect as a greater amount,  $I$ , entering a different part of the pupil,  $d$ , then the difference

$$i_u = I - 1, \tag{4}$$

must represent the amount of light lost when the light enters at  $d$  that is not lost when the light enters at the optimal location. We call this *unrecovered* light, for it is light that has escaped without recovery (or recapture). Dividing this difference,  $i_u$ , by the total light incidence through a given pupillary entry,  $I$ , yields the proportion of light incident at  $d$  that is lost. We ignore light that is lost to the system in any case, such as light that passes all the way through the cones without absorption and light that never enters a cone at all, which may be substantial (van Bloklend & van

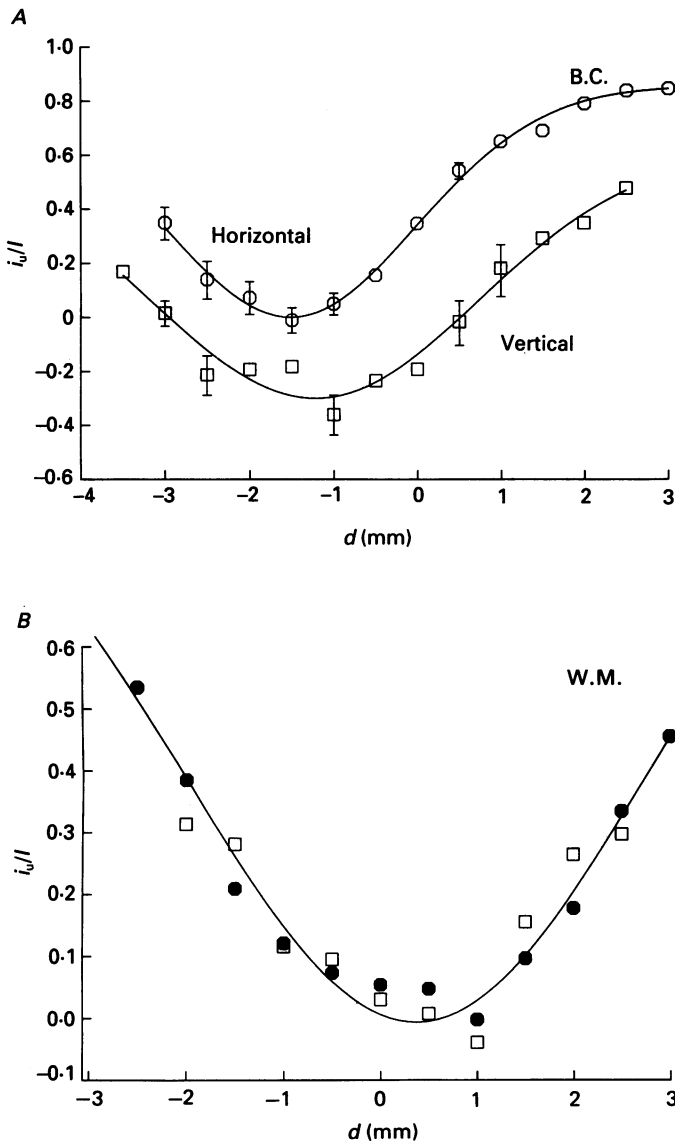


Fig. 3. The proportion of light entering the pupil at varying locations that escapes the cones without recapture (unrecovered light). *A*, horizontal and vertical meridians of B.C. Positive values of  $d$  represent temporal or superior pupil; negative values, nasal or inferior pupil. Each point represents the average of three sessions of five thresholds per condition. The vertical bars, which enclose  $\pm 1$  standard error of the mean of the three sessions, are omitted where they are smaller than the symbols. Curves are least-squares fits of eqn (5), with the following parameters: for the horizontal meridian,  $c_4 = 0.86$ ,  $c_5 = -1.51$  and  $c_6 = 2.13$ ; for the vertical meridian,  $c_4 = 0.92$ ,  $c_5 = -1.22$  and  $c_6 = 2.76$ . The data and curve for the vertical meridian have been shifted downwards 0.3 units for clarity. *B*, both meridians for W.M. Sign conventions are identical to part *A*. Squares are the current data collected along the vertical meridian. Filled octagons are the averaged results of data collected by various other methods, with standard errors approximately equal to the size of the symbols. Parameters for eqn (5) are:  $c_4 = 0.97$ ;  $c_5 = 0.37$ ; and  $c_6 = 3.33$ .

Norren, 1986). Figure 3 shows the proportion of unrecovered light,  $i_u/I$ , with varying pupillary entry. The curves, fitted by least squares, are of the form:

$$i_u/I = c_4\{1 - e^{[(d-c_s)/c_s]^2}\}. \quad (5)$$

The results with 1 deg test flashes are more variable but not significantly different.

The open symbols in Fig. 3B show the data gathered here from observer W.M. For comparison, the filled symbols show the averaged results of data collected from the same observer by various methods over a period of 20 years. As there are no systematic differences between these results, and as the standard errors of the filled symbols are small (approximately the size of the symbols), we have fitted the curve to the more extensive set of data and use them for the rest of this work. As there are also no systematic differences between horizontal and vertical traverses of the pupil, they have been combined.

Thus, the vertical differences between the points on these curves and the minima of the corresponding curves show the proportion of light entering different parts of the pupil that escapes the visual system without recovery (unrecovered light). These results are used in the following work to estimate such light losses and to compensate for them experimentally when necessary.

#### *Recaptured light*

The previous experiment allows computation of the amount of light that escapes the cone system without recovery,  $i_u$ . However, some entering light, denoted  $i_r$ , may escape the cones it originally enters and then be recovered or *recaptured* by neighbouring cones. So the total amount of light that *escapes* the cone into which it originally entered is the sum of the unrecovered and the recaptured light:

$$i_e = i_u + i_r. \quad (6)$$

We distinguish the spatial modulation of flux density at the entrance to the cones from the spatial modulation of quantal absorptions in the outer segments of the cones. Light escaping one cone and recaptured by its neighbour reduces the latter but not the former. Any difference between the two betrays the existence of such recaptured light. The observer's visual system determines the threshold modulation of quantal absorptions,  $C^*$ , but the experimenter knows only the threshold modulation of retinal illuminance,  $C$ . We assume that the threshold modulation of quantal absorptions,  $C^*$ , is independent of the pupillary entry of the light. Then any variation of retinal constant threshold with pupillary entry must reflect variation of recaptured light,  $i_r$ .

Figures 4 and 5 show just how retinal contrast threshold varies with pupillary entry. Sensitivity to 40 cycle  $\text{deg}^{-1}$  gratings decreases when the light passes through the pupil some 2 mm or more from the maximum of the Stiles-Crawford curve (Fig. 4). Displacements of both vertical and horizontal gratings along both vertical and horizontal medians produce this loss of contrast sensitivity. However, the losses are somewhat greater when the direction of displacement is perpendicular to the orientation of the grating. We attribute this loss of contrast sensitivity, then, to escape of light from the cones under the bright bars and recapture by cones in the dark bars.



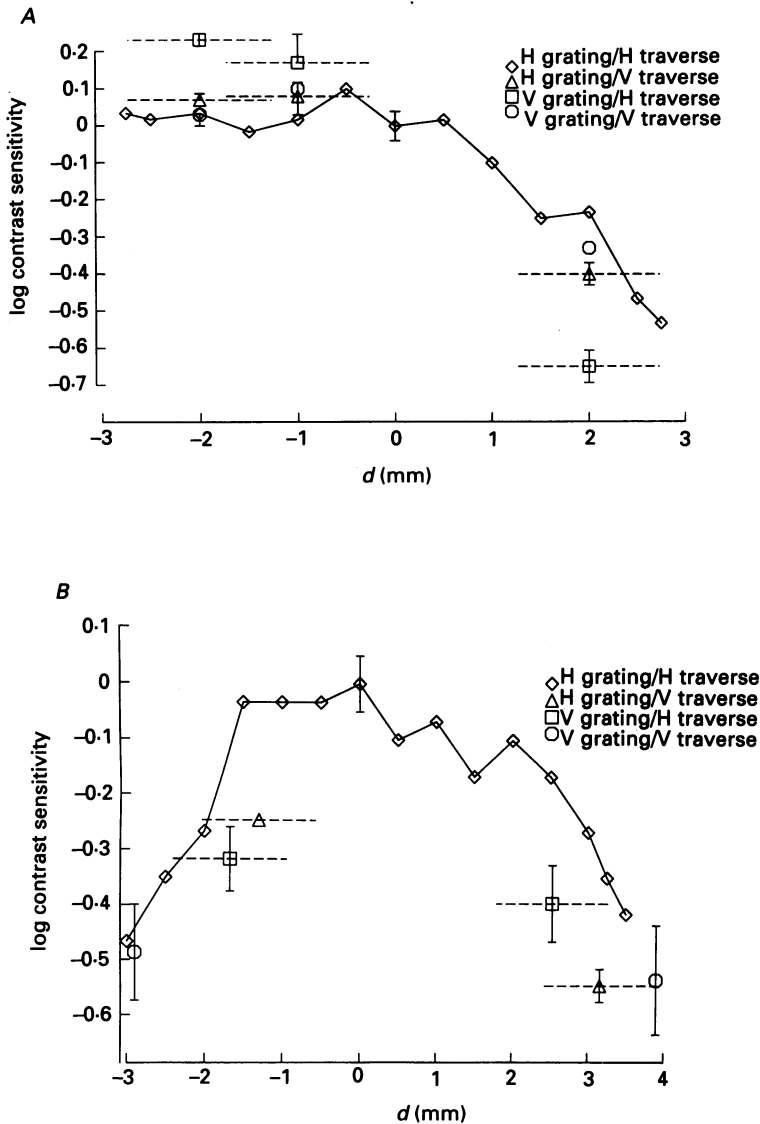


Fig. 4. Log contrast sensitivity to 40 cycle  $\text{deg}^{-1}$  fringes produced by coherent beams entering the pupil at varying positions. The end-points of the horizontal lines of dashes passing through the data points show where the beams producing the gratings entered the pupil when they were on the meridian varied instead of straddling it. As the data from the horizontal (H) traverse of the pupil with horizontal fringes are the most extensive, they are connected by lines to distinguish them more clearly from the other data. The vertical bar at the centre position represents the mean standard error for these data. For ease of comparison and because the sensitivities to fringes of different orientation are not necessarily identical, the data for each of the four conditions are normalized so that their sensitivities are equal at the centre of the pupil. This required an upward shift of 0.20 for W.M.'s data from all vertical (V) gratings, and an upward shift of 0.07 and 0.16 for W.M.'s and B.C.'s data, respectively, from the vertical traverse of horizontal gratings. *A*, observer B.C.; *B*, observer W.M.

Sensitivity to 14 cycle  $\text{deg}^{-1}$  gratings, on the other hand, shows no such evidence of systematic variation with entry of the light in the pupil (Fig. 5). To reach the dark bar of a 14 cycle  $\text{deg}^{-1}$  grating, light escaping a cone at the centre of a bright bar must travel nearly 3 times as far before recapture as it does with a 40 cycle  $\text{deg}^{-1}$  grating. We show next that this is further than it goes.

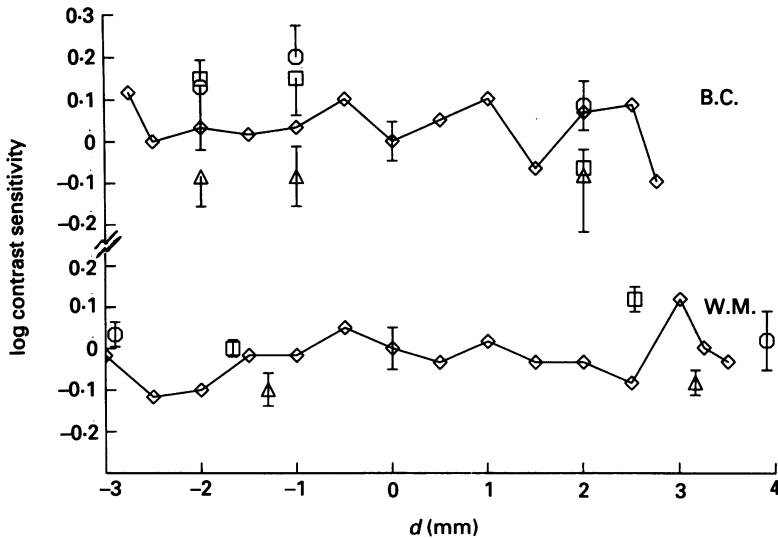


Fig. 5. Log contrast sensitivity to 14 cycle  $\text{deg}^{-1}$  fringes produced by coherent beams entering the pupil at varying positions. Symbols are the same as for Fig. 4. B.C.'s data from the vertical traverse of horizontal gratings was shifted downward 0.18 units on the log scale; all other shifts were less than 0.08 units.

### *Amount and distribution of recaptured light*

#### *Data*

The preceding experiment shows that bringing the light of interference fringes through the margin of the pupil decreases their visibility only when the spatial frequency of the fringes is high, and we take this as evidence that light spreads along the retina only a limited distance before recapture. In this experiment we measure the amount and distribution of such recaptured light by measuring contrast sensitivity to fringes of varying spatial frequency when the light enters the pupil either at the centre or near the margin of the pupil.

For observer B.C., marginal entry is 2.5 mm temporal from centre; for observer W.M. it is 2.9 mm inferior from centre. The beams straddled, perpendicularly, the pupillary meridian along which they were displaced; thus, the orientation of the fringes was vertical for W.M. and horizontal for B.C. These particular entries take advantage of idiosyncracies of the observers' respective Stiles-Crawford effects.

Two replications were done: one with three thresholds (fifty trials each) per entry position at six (W.M.) or eight (B.C.) spatial frequencies, and the other with two

thresholds per entry position at ten spatial frequencies. Figure 6 shows the raw data from the first replication. The difference between each pair of thresholds must represent a loss of image contrast associated with the peripheral pupillary entry. Then a plot of the ratios of the two contrasts qualifies as an optical transfer function. This is shown for both replications in Fig. 7.

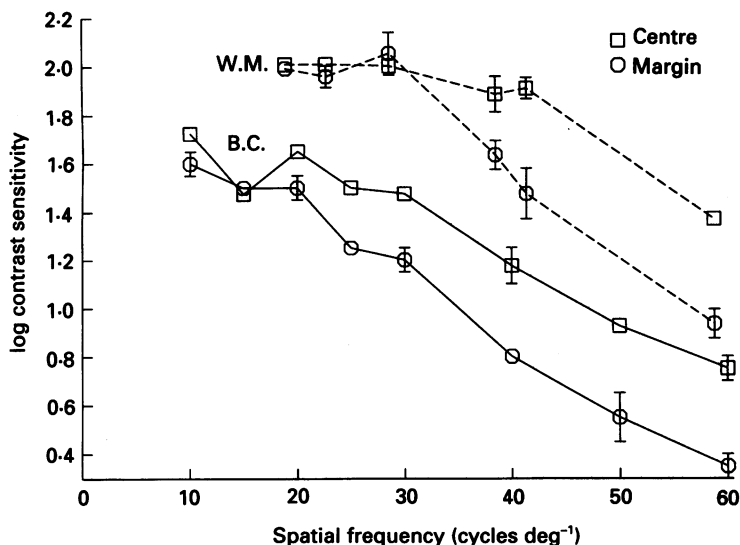


Fig. 6. Log contrast sensitivity to fringes of varying spatial frequency at two pupillary entries: centre (squares) and margin (circles) of the pupil. The data for W.M. have been shifted upwards 0.4 units for clarity. The bars, which enclose  $\pm 1$  standard error of the mean, are omitted where they are less than the size of the symbols.

As these data represent the exponential of the difference between two (log) thresholds, their variability is not surprising. The curves (explained below) are Gaussians of the form:

$$C_0/C = 1 - p(1 - e^{-\frac{1}{2}(f/\sigma)^2}) \tag{7}$$

Values of  $p$  and  $\sigma$ , are, respectively, 0.66 and 28 cycles deg<sup>-1</sup> for B.C., and 0.63 and 49 cycles deg<sup>-1</sup> for W.M.

*Quantitative analysis*

One wishes to know two things about the recaptured light: (i) how much of the light absorbed by a cone was trapped by it on first incidence and how much was recaptured after escaping another cone; and (ii) how far does light that has escaped one cone spread before being recaptured by another?

*How much?* The first question is answered by the asymptotes of the curves in Fig. 7. When the spatial frequency of a grating (erected by light passing through the margin of the pupil) approaches zero, the loss of contrast caused by the spread of

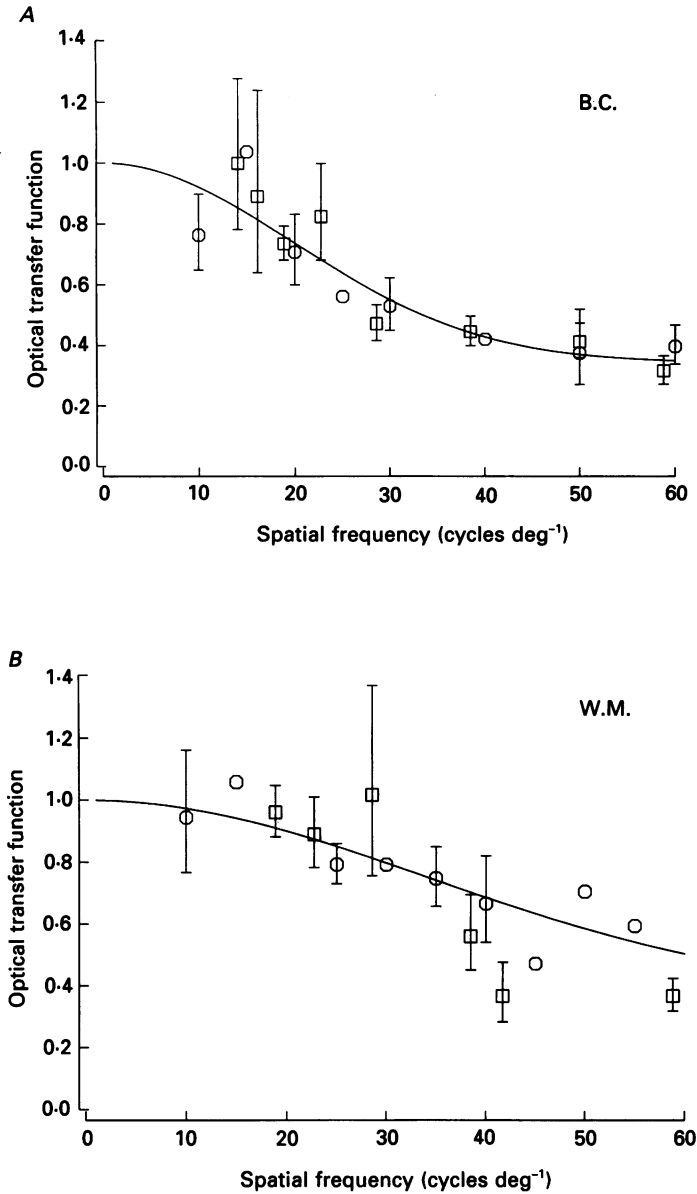


Fig. 7. Optical transfer function. This is the contrast sensitivity to fringes passing through the margin of the pupil, divided by the contrast sensitivity to fringes passing through the centre of the pupil (linear scale). The vertical bars are as for Fig. 3. Different symbols represent different replications. *A*, observer B.C.; *B*, observer W.M. The estimate of the point at 20 cycles deg<sup>-1</sup> for W.M. is omitted because it lies outside the figure and is more than ten standard errors from the maximum possible value.

recaptured light also approaches zero; and so the total modulation is due to the sum of both captured and recaptured light, which is all the absorbed light. That is:

$$i_c + i_r = 1. \tag{8}$$

Therefore, the contrast at the site of absorption,  $C^*$ , is the same as that at the entrance to the cones,  $C$ , and in this case it is also the same as it would be if the light passed through the centre of the pupil:

$$C^* = C_{f \rightarrow 0} = C_0. \tag{9}$$

As the spatial frequency increases, however, modulation of the recaptured light, which must spread from its site of incidence before being absorbed, eventually approaches zero, and the curves in Fig. 7 approach the asymptote  $(1 - p)$ . (The form of the curve is unimportant here, as long as it approaches a lower asymptote.) Any remaining modulation must be due to light captured by the cones on which it falls. The modulation of such captured light is attenuated only by summation over the aperture of the capturing cone, and we assume such summation has similar effects on fringes of a given frequency, whether the light passes through the centre or margin of the pupil. Therefore,

$$C^* = C_{f \rightarrow \infty} i_c. \tag{10}$$

Equations (9) and (10) (each for  $C^*$ ), then yield:

$$i_c = C_{f \rightarrow 0} / C_{f \rightarrow \infty} = 1 - p, \tag{11}$$

and this, with eqn (8), yields,

$$i_r = p. \tag{12}$$

Then when the light enters the margin of the pupil, the estimated values of  $i_r$ , the proportion of light absorbed by one cone, that has previously escaped another cone, are 0.66 for W.M. and 0.63 for B.C.

*How far?* This question is answered by *spread functions* that can be derived from the shape of the transfer functions in Fig. 7. Although we cannot argue that Gaussian curves best fit the data, they are reasonable approximations, considering the variability; and they have the attractive property that they yield line spread and point spread functions that also are Gaussian. (The spread function is continuous even though the cone mosaic is discrete, for a pair of cones that exchange light can have any orientation relative to the orientation of the gratings used to measure it. As a spread function describes only the net spread of light perpendicular to the geometric image of a line, exchange of light between cones with an oblique orientation to the line, or between cones straddling the line, causes a spread smaller than the diameter of a cone. The line spread function, then, represents the statistical summation of all such exchanges along the length of the line, the greatest proportion of which may be small compared to the diameter of a cone.) Such spread functions have the same standard deviation,  $\sigma_x$ , which is related to that of the transfer function,  $\sigma_f$ , according to the equation:

$$\sigma_x = (2\pi\sigma_f)^{-1}. \tag{13}$$

For observer B.C., the best estimate of the standard deviation of the spread

functions,  $\sigma_x$ , is 41 minutes of visual angle; and the best estimate of the proportion of absorbed light that is recaptured,  $i_r$ , is 66%. If  $\sigma_x$  is allowed to vary freely, the lower fiducial limit (all such limits cited here are 0.95 limits) of  $i_r$  is 44% ( $\sigma_x$  then equals 56 min), and of course it cannot exceed 100% ( $\sigma_x$  equals 25 min). The fiducial limits on  $\sigma_x$ , if  $i_r$  is allowed to vary freely, are 22 min ( $i_r$  equals 100%) and 67 min ( $i_r$  equals 50%). If  $i_r$  is fixed at its optimum of 66%, then the limits of  $\sigma_x$  are 29 and 56 min; and if  $\sigma_x$  is fixed at its optimum of 41 min, then the limits of  $i_r$  are 49 and 83%.

The data of W.M. are noisier. Fiducial limits for  $i_r$  are 21 and 100%; and for  $\sigma_x$ , 11 and 89 min. Fixing  $\sigma_x$  at its optimum of 18 min changes the lower limit of  $i_r$  to 56%; and fixing  $i_r$  at 63% constrains  $\sigma_x$  to the range 15–38 min.

These results show that half or more of the light absorbed from a homogeneous field entering the pupil near its edge is absorbed by cones other than those on which it originally falls, most of it coming from adjacent cones.

### *Polarization*

The gratings in these experiments were created by interference between two beams originating from the same laser. Such interference produces gratings of maximum contrast only when the two beams are of equal intensity and identical states of polarization at the site of absorption. Any change of polarization in one of these beams by, say, the ocular media, that is not reproduced identically in the other, could reduce the contrast of the test gratings. Observations were therefore made to examine such effects and any influence they might have on these observations.

The rationale depends on the fact that perpendicularly polarized beams do not interfere at all. Any change of polarization of one beam that is not exactly reproduced in the other destroys the mutually perpendicular polarization of the two beams and causes them to interfere. Thus any change of polarization that might *reduce* the contrast of gratings produced by interference necessarily *introduces* interference between perpendicularly polarized beams. And a test for interference between perpendicularly polarized beams is a sensitive test for the effects of concern. Since the converse is not true (for example, passing perpendicularly polarized beams through a linear polarizer at 45 deg to both introduces interference between them, but has no effect on the contrast of interference between identical beams), it is a conservative test.

The entire pupil was scanned along horizontal and vertical meridians with cross-polarized beams separated by 0.02 mm (0.5 cycles deg<sup>-1</sup>), 0.5 mm (14 cycles deg<sup>-1</sup>) and 1.5 mm (40 cycles deg<sup>-1</sup>). Nowhere could interference be detected when the beams were separated by only 0.02 mm.

The 14 cycle deg<sup>-1</sup> interference fringes associated with the 0.5 mm separation were visible at all locations tested. The threshold contrast was 0.20 at the centre of B.C.'s pupil and 0.45 at 2.5 mm to the temporal side. This is opposite to what would happen if polarization contributed to the phenomena of Figs 4, 6 and 7.

The 40 cycle deg<sup>-1</sup> fringes associated with the 1.5 mm separation had a threshold contrast of 0.20 when the beams entered at the central position of B.C.'s pupil, but could not be seen everywhere. Particularly, they were not visible 2.5 mm to the temporal side (cf. Figs 6 and 7).

If  $\theta$  is the retardation angle of linearly polarized light after entering the centre of the pupil and passing through the ocular media, then  $C = 0.20 \sin \theta$ . From Fig. 4, B.C.'s threshold contrast at the retina for 40 cycle  $\text{deg}^{-1}$  gratings,  $C = 0.067 \cos \theta$ ; then  $\theta$  is 18 deg, and this 18 deg retardation reduces the contrast of the 40 cycle  $\text{deg}^{-1}$  gratings by about 5% ( $\cos 18 \text{ deg} = 0.95$ ), which is too small to measure. As the threshold 40 cycles  $\text{deg}^{-1}$  for gratings produced by crossed polarized beams is higher everywhere else in the pupil, the retardation and its effects are smaller everywhere else.

#### DISCUSSION

##### *Fate of incident light*

Where the light enters the pupil affects where it goes after it enters a cone. Figure 8 shows schematically the fate of light that enters the pupil at different locations and, hence, is incident on the cone at different angles. Part *A* illustrates the finding that nearly all the light entering a cone parallel to its axis is captured and absorbed either by that cone or by the pigment epithelium behind the cone. Part *B* illustrates the finding that some part ( $i_u$ ) of the beam ( $I$ ), when incident at small angles, escapes the cones (cf. Fig. 3) but fails to enter neighbouring cones (cf. Fig. 4) before hitting the pigment epithelium. Part *C* illustrates the finding that there are two components of the part ( $i_e$ ) of the light ( $I$ ) incident on a cone at a large angle that escapes: light recaptured by neighbouring cones  $i_r$  and unrecovered light that is absorbed by the pigment epithelium,  $i_u$ .

The classic measurements of the Stiles–Crawford effect reflect only the light that escapes the cones *without* recapture (i.e. is unrecovered). But the present observations allow an estimate of  $i_e/I$ , the total proportion of *incident* light (not proportion of *absorbed* light, as was estimated from Fig. 7) that escapes the first cone it enters. This includes both lost and recaptured light. It is plotted in Fig. 9, along with estimates of the proportion of captured ( $i_c/I$ ) and recaptured ( $i_r/I$ ) light. The irregularity of the curves is understandable, for each point represents the difference between two thresholds followed by conversion to an absolute scale from the log scale on which the variance of the observations is homogeneous.

The small proportion of incident light absorbed by the first cone it hits ( $i_c/I$ ) when the light enters the pupil far from its centre is noteworthy. The retina, when illuminated by such light, is drenched with light that passes through the cones with little effect on them. Light that escapes the cones and is not recaptured ( $i_u$ ), then, is invisible stray light, and recaptured light ( $i_r/I$ ) is visible stray light. It is also noteworthy how little of the stray light that escapes one cone is recaptured by its neighbours. Evidently, the cones very efficiently reject such stray light, as predicted by van Bloklant & van Norren (1986).

Small as the proportion of incident light that is recaptured is ( $i_r/I$ ), the total proportion of incident light that is absorbed ( $i_r/I + i_c/I$ ) is also small. And so, with eccentric pupillary entry, half or more of the light absorbed in each cone is light that originally entered a different cone.

##### *Escape versus non-capture*

If light passed straight through a cone without deviation: (a) no light would be

scattered out of the plane of incidence, and contrast sensitivity to gratings parallel to the plane of incidence would not depend on the incident angle of the light, as it does (cf. Fig. 4); and an obliquely incident ray of light that just clipped the lip of a cone's outer segment in this experiment would hit the pigment epithelium at a

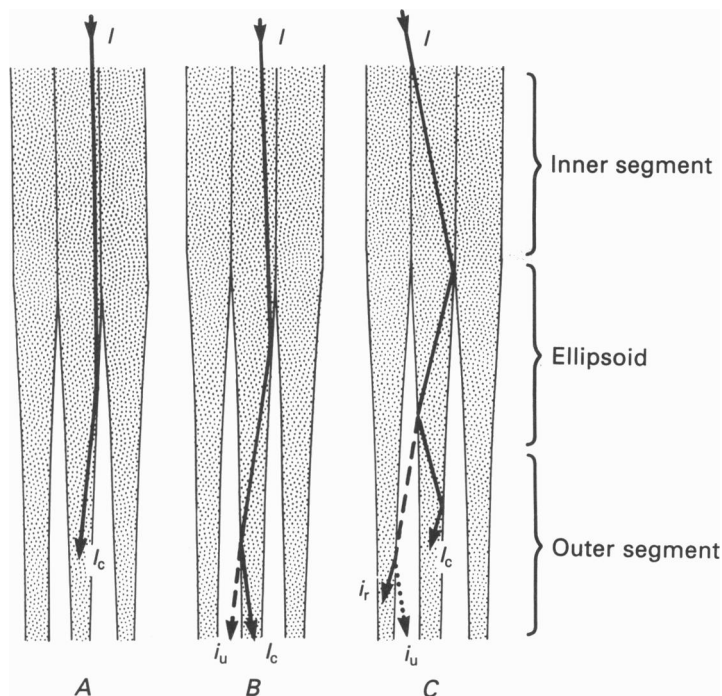


Fig. 8. Schematic model of Stiles-Crawford effect. *A*, all the light entering a cone parallel to its axes is captured and absorbed either by that cone or by the pigment epithelium behind the cone. *B*, when incident at small angles, some part ( $i_u$ ) of the beam ( $I$ ) escapes the cones, but fails to enter neighbouring cones before hitting the pigment epithelium. *C*, at larger angles of incidence, there are two components to the part ( $i_e$ ) of light that escaped from the origin cone: light recaptured by the neighbouring cones ( $i_r$ ) and unrecovered light that is ultimately absorbed by pigment epithelium ( $i_u$ ).

distance  $10\ \mu\text{m}$  (124 minutes of visual angle) from the tip of the cone, passing on its way through some four or five cones. This is further than it goes (cf. Fig. 7). Therefore, escaped light is temporarily trapped, or at least deviated in its course, by the first cone it hits before its escape.

#### *Other assumptions*

##### *An alternative to stray light*

These observations show that light passing through the margin of the pupil produces interference fringes of reduced detectability, but only when the fringes are of high spatial frequency. A possible explanation we have not yet considered is that the distribution of light from beams passing through the margin of the pupil differs



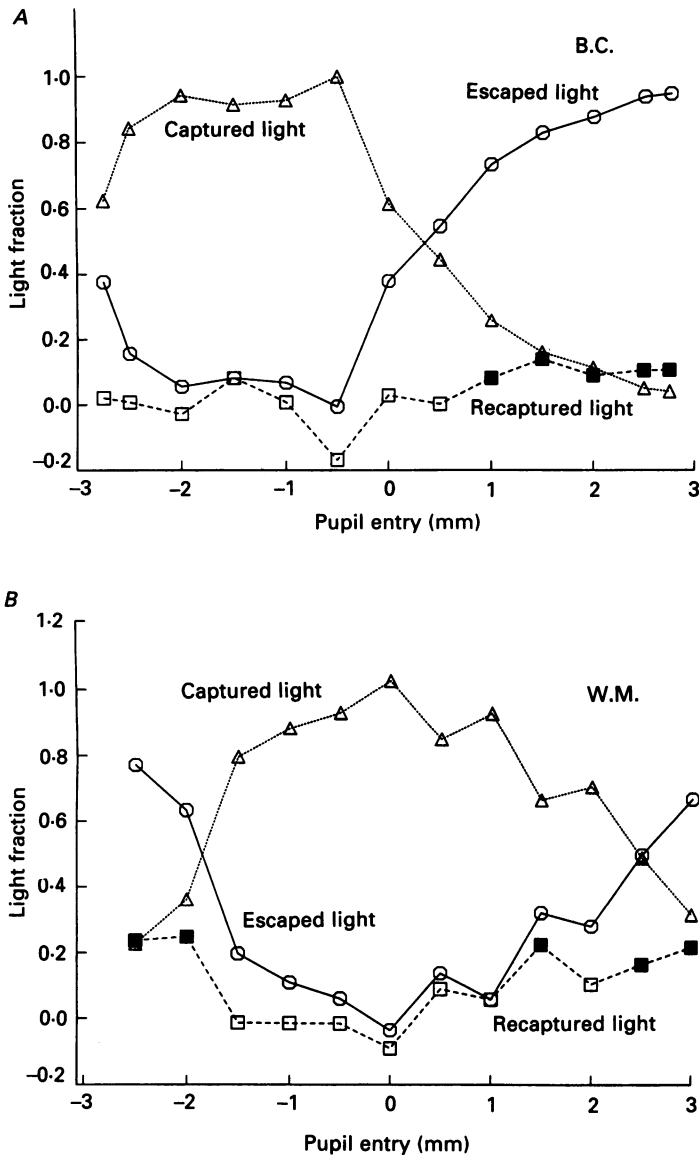


Fig. 9. Fate of incident light: triangles connected by the dotted line represent captured light,  $i_c/I$ , the proportion of incident light that is absorbed by the first cone it hits; octagons connected by continuous lines represent escaped light,  $i_e/I$ , the proportion of incident light that escapes the first cone it hits; squares connected by dashed lines represent recaptured light,  $i_r/I$ , the proportion of incident light that escapes, and then is recaptured by the neighbouring cones. Estimates are based on the assumption that threshold contrast without light recapture is 0.044 for A (the mean of the thresholds for positions -2.75-0 mm in Fig. 4A), and 0.042 (the mean of the thresholds for positions -1.5 to +1 mm in Fig. 4B) for B. To obtain the proportion of incident light that is recaptured,  $i_r$  is divided by  $I$ . Points representing recaptured light that differ reliably from zero are filled. The crossing of the curves for  $i_c/I$  and  $i_e/I$  in A is also reliable. A, observer B.C.; B, observer W.M.

enough at the site of absorption to decrease their interference. Imagine, for example, that an obliquely incident beam produced a power density distribution in cross-section within the cone, i.e. a modal pattern (cf. Enoch, 1961; Snyder & Pask, 1973) with the shape of an hour glass. If two interfering beams enter the pupil at different locations along the circumference of the pupil, then the respective patterns associated with each beam will not coincide exactly, although they may overlap. Increasing the spatial frequency of fringes produced by the two beams requires increasing their separation, and this rotates the two patterns in opposite directions and decreases the overlap between their power distributions. As maximal interference occurs only when the power densities of the interfering beams are uniformly equal to one another, the contrast of the fringes would decrease with increasing spatial frequency.

Too little is known about the optics of human cones to exclude this possibility entirely, but present evidence suggests that the outer segments of foveal cones are too small relative to the 632.8 nm light used here to support modal patterns of sufficient complexity (Snyder & Pask, 1973). Only the lowest order mode can be sustained, a radially symmetrical pattern that decreases in power density monotonically from its centre (cf. Enoch, 1961, for example).

On the other hand, optical theory demands the stray light (Miller & Snyder, 1973) that seems the only alternative. Although Miller and Snyder emphasized in their paper the escape of light from peripheral as opposed to foveal cones, their computations show that the taper of the ellipsoids of foveal cones produces the necessary stray light as well. Therefore, we have adopted the stray light interpretation here and explored its implications.

### *Mode coupling*

The interpretation offered here supposes that light escapes one cone to the extracellular space before entering another. An alternative is that some of the so-called recaptured light passes directly from one cone to another, as by mode coupling (Wijngaard & Heyker, 1975). However, Wijngaard and Heyker's computations (1975) lead them to conclude that mode coupling is not significant for the human fovea. In any case, for most purposes it matters little which interpretation is adopted, and so we have chosen the interpretation that assumes less.

### *Coherence of stray light*

We have assumed that light escaping a cone loses its coherence with respect to the light in neighbouring cones, so that these two components of light could be considered mutually incoherent. This undoubtedly is an oversimplification. On the other hand, it seems even less likely that the coherence of such scattered light would be wholly preserved. And so the scattered light may be partially coherent.

Such partial coherence can have opposite effects. To the extent that the phase of scattered light is *not* preserved, recaptured light may increase speckle. Such speckle raises thresholds for gratings more than an equal amount of incoherent light (Williams, 1985*b*). (That is why the contrast thresholds observed here are lower than is typical with incoherent light.) This would cause *overestimation* of the recaptured light. Interference fringes such as were used here are, however, subject to substantial

speckle under any conditions, and no increase associated with eccentric pupillary entry was obvious to the observers.

To the extent that the relative phases of the scattered and unscattered light in the cones *are* preserved, recaptured light has the same effect as captured light, and so recaptured light would be underestimated. van Meeteren & Dunnewold (1983) have argued that measurements with coherent light do underestimate the retinal losses of contrast on which these estimates of recaptured light depend.

So, until the residual coherence of recaptured light is determined, and until its indirect effects through speckle are separated from its direct effect on contrast, the present estimate stands as the best available.

#### *Properties of the ocular media*

Dichroism and depolarization in the pathway of the absorbed light are excluded by the finding that (closely spaced) cross-polarized beams produce no visible interference fringes. Thus, even the modest depolarization observed by van Blokland (van Blokland, 1985; van Blokland & van Norren, 1986) in light reflected from the human fundus is not present in the absorbed light. These findings are consistent with Wijngaard's observation (1971) that transmission through frog rods depolarizes light less than 1%.

We attribute the visibility of fringes produced by cross-polarized beams separated by 0.5 mm or more to variation of birefringence across the cornea (van Blokland & Verhelst, 1987). This certainly contributes also to the point-to-point variability of the data in Figs 4 and 5.

#### *Implications for the Stiles-Crawford effects*

The existence of significant amounts of recaptured light require modification of quantitative theories of the Stiles-Crawford effect (e.g. Snyder & Pask, 1973), and it increases the number of free parameters allowed for explanation of puzzling aspects of the Stiles-Crawford effect, such as Stiles-Crawford II (Enoch & Stiles, 1961; Alpern, 1986), and the transient Stiles-Crawford effect (Makous, 1968).

The Stiles-Crawford effect is greater in the parafovea than in the fovea (Westheimer, 1967). This could be attributed to greater escape of light from parafoveal cones, or to less recapture. The greater taper angle of cones outside the fovea might conceivably reduce escape, but Miller & Snyder (1973) have argued that it would do just the opposite. The greater distance among parafoveal cones, however, ensures reduced recapture, and so differences in the amount of recaptured light must account for at least part of the difference between foveal and parafoveal Stiles-Crawford effects. Had the present observations been restricted to a smaller area of the fovea, where the cones are smallest and most densely packed, even more recaptured light might have been observed. Thus, recaptured light might contribute to the especially shallow Stiles-Crawford effect that has been reported for this region of the fovea (Starr, Fitzke & Massof, 1979).

The waveguide properties of individual rods and foveal cones are similar (Enoch, 1967; Horowitz, 1981), but the Stiles-Crawford effect for the rod system is much shallower than that of the cone system (Crawford, 1937; Alpern, Ching & Kitahara, 1983), and clusters of rods accept light over a far greater span of angles than

individual isolated rods (Enoch, 1967; Tobey & Enoch, 1973). Thus clustered rods perform differently from isolated rods and from clustered cones. Clustered rods recapture more light than isolated rods, which recapture none, and perhaps clustered rods also recapture more light than clustered cones. Although it is unlikely that more light escapes rods than cones, for Fig. 9A shows that the proportion of incident light that can escape cones approaches 100%, nevertheless the close packing of rods compared with the spaces between cone outer segments must increase recapture in rods.

### *The Campbell effect*

Green's purpose (1967) in measuring contrast sensitivity with interference fringes was to establish how much of the Campbell effect (1958) is due to the optical properties of the retina as opposed to off-axis aberrations of the eye's optics. He observed nothing attributable to the retina. We have observed a loss of contrast that must occur within the retina. As we did not assess the pre-retinal loss of contrast, we have no good estimate of the relative losses attributable to retinal and pre-retinal optics. If illumination is decreased enough to dilate the natural pupil to the size where the retinal Campbell effect is observed, however, then the spatial frequencies that can be detected are too low to show it. On the other hand, if illumination is increased to allow detection of the fine gratings that are sensitive to the retinal effect, the natural pupil constricts too much to allow the eccentric entry necessary to produce the retinal effect. Thus, Green's original conclusion that optical cross-talk does not affect contrast sensitivity holds with a natural pupil. This happy trade-off, between pupil size and spatial resolution, that protects the visual system from the effects of the retinal scatter studied here, may not be fortuitous.

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