

## THE CHANGE IN COLOR MATCHES WITH RETINAL ANGLE OF INCIDENCE OF THE COLORIMETER BEAMS\*

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**Abstract**—Differences between W.D.W. chromaticities of monochromatic lights obtained with all colorimeter beams incident on the retina “off-axis” and those found for lights striking the retina normally have been studied throughout the visible spectrum on 4 normal trichromats. The results are inconsistent with: (i) the assumption in Weale’s theories of the Stiles–Crawford hue shift that the sets of absorption spectra of the visual pigments catching normally and obliquely incident photons are identical, and (ii) “self-screening” explanations for the change in color with angle of incidence on the retina. The color matching functions of a protanomalous trichromat are inconsistent with the hypothesis that the absorption spectra of the visual pigments catching normally incident photons in his retina are those catching obliquely incident photons in the normal retina.

Stiles–Crawford color effect    Color vision    Color matching

### INTRODUCTION

The color of a monochromatic light changes with its angle of incidence on the retina, say from normal incidence (i.e. from the center of the exit pupil) to oblique incidence (from the exit pupil margin) (Stiles, 1937). “Yellow” lights change to “orange” and desaturate; “blue-greens” become more bluish but increase in saturation. The generally accepted explanation for this effect—the Stiles–Crawford effect of the second kind of SCII (Hansen, 1943)—is that the absorption spectra of the visual pigments in the three species of cones differ for obliquely incident, from those for normally incident, rays (Stiles, 1937; Walraven and Bouman, 1960; Enoch and Stiles, 1961). A minority view (Weale, 1981a, b) requires the same absorption spectra for normal and oblique rays. It accounts

for the changes in hue by *prereceptor* changes alone.

This latter view is surprising for at least three reasons. (i) The color—as distinct from the color matching function (CMF)—of a monochromatic light is generally supposed independent of prereceptor spectral distortions in the observer’s eye. (ii) The assumption of identical spectra for normal and oblique rays is contradicted by earlier evidence of Ripps and Weale (1963, 1964 and 1965) with no hint in the two decades intervening as to why this evidence was no longer relevant. (iii) Enoch and Stiles (1961) found substantial differences in W.D.W. chromaticity between normally and obliquely incident monochromatic lights. Given reasonable assumptions, substantial differences in W.D.W. chromaticities of the same monochromatic light can only be explained by differences in the absorption spectra of the visual pigments involved (Wyszecki and Stiles, 1982). Still, however plausible, the most crucial Enoch–Stiles assumption—that the ordinary additive laws of color matching are valid in matching three normally incident primaries to an obliquely incident test—has recently been rendered suspect (Alpern and Tamaki, 1983).

Brindley (1953) also concluded that the absorption spectra of the pigments absorbing obliquely incident photons are not those absorbing normally incident photons. Alpern and Tamaki (1983) found no grounds for doubting

\*In memory of Günter Wyszecki, in whose laboratory some of these measurements were made and the analysis begun, and who helped in frequent discussions. His last experimental observations were part of this study on the “great trirème” Ottawa Stiles Trichromator of which Günter was justly proud. With this instrument he became the supreme master of the art (as well as the science) of colorimetry. Had he lived to allow it, his name would be listed as an author of this paper.

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the additive laws under Brindley's color matching conditions, in which all beams of the colorimeter traversed the eye together.

Brindley saw that moving from "on-axis" to "off-axis" incidence caused changes in matching similar to those caused by increasing radiance to bleaching levels. He explained both by an extension of Stiles' (1937) hypothesis that one of the visual pigments absorbing normally incident photons at ordinary radiance levels was in high concentration whilst the same pigment absorbing oblique photons (or normally incident photons at bleaching radiances) was dilute. The interpretation has been adopted by subsequent workers, although to explain additional results, the concentration differences have been extended to two or even all three species of cones. The difference between absorption spectra resulting from the application of the Beer-Lambert law of absorption and the spectral distribution of absorption coefficients of likely human cone visual pigments, accounting thereby for the quantitative changes in color matching found, was called "self-screening" by Brindley (1960).

Brindley's experiments were confined to the red-green spectral range and to his eye alone. Aside from a single datum in the same part of the spectrum (Alpern, 1979), they have not been repeated. Since Brindley's results contradict Weale's assumption, the present experiments (in which color matches made with "off-axis" incident colorimeter beams were compared to those obtained with normally incident beams) were undertaken on four normal trichromats to test the generality of the inference that the absorption spectra of pigments absorbing normally incident photons differ from those absorbing obliquely incident photons. A second aim of this work is to provide results for quantitative evaluation of "self-screening" over the entire range of the visible spectrum rather than just the range Brindley studied.

## METHODS

Four normal trichromats were subjects. Three had considerable experience in visual psychophysics experiments but were naive to color matching. The fourth (G.W.), with almost 30 years experience in color matching, was available for only a single set of measurements. Matching was foveal using the maximum saturation method.

The color matching functions (CMFs) of

H.K. and of K.K. were obtained with the Michigan colorimeter. Its details are described in Alpern *et al.*, 1976, and Alpern *et al.*, 1983. Matches were made with successive 1 sec exposures of the test plus desaturating primary followed immediately by 1 sec exposure of the mixture of the other two primaries in alternating presentation, for as long as it took to match. A double monochromator (2 nm halfbandwidth HBW) produced the test beam of wavenumber  $m$ ; the primaries (usually  $451.5 \pm 1.6$ ,  $651.1 \pm 2.1$  and  $550.4 \pm 1.2$  nm) were secured by interference filters. Whatever the instrument primaries, the results were transformed into CMFs with reference primaries of wavenumbers  $15,500 \text{ cm}^{-1}$  (645.2 nm),  $19,000 \text{ cm}^{-1}$  (526.3 nm) and  $22,500 \text{ cm}^{-1}$  (444.4 nm).

Measurements on two other subjects were made on the modified Stiles N.P.L. Trichromator (Stiles, 1955) at the Photometry and Radiometry Section of the Division of Physics of the NRC in Ottawa, Canada (Fielder, 1985). The instrument primaries were the same as the reference primaries, so the CMFs for each test were obtained by direct radiometry immediately after a match. The bipartite halves of the colorimeter field were juxtaposed simultaneously. The upper semicircular field contained the mixture of two primaries; the lower contained the monochromatic test and its desaturant. The chromatic aberration of the eye with peripheral entry fields (Brindley, 1953; Fig. 5, inset) was not corrected, but its impact was minimized by displacing the pupil entry point in a direction parallel to the dividing line of the field and by instructing observers to ignore the colored fringes.

When several color matches were made for a given test, the W.D.W. chromaticity of the mean match together with the major and minor axes of the ellipse defined by mean  $\pm 1 \sigma$  (SD) in the constant  $\bar{g}$  plane were calculated (Brown and MacAdam, 1949).

All results except those of G.W. were obtained with a  $1^\circ$  field. G.W.'s data were obtained with a  $2^\circ$  field (consistent with a large body of previous measurements on his eye). W.D.W. chromaticities of the most recent (1978) set were calculated from the CMFs tabulated on pp. 388-389 of Wyszecki and Stiles (1982) for comparison. The conditions differed only in that in 1978 test radiance was fixed at 1000 td; here it fell below this value for  $m \geq 23,750 \text{ cm}^{-1}$ . [The troland levels for 23,750 (421.1 nm), 24,000 (416.7 nm), 24,250 (412.4 nm) and  $24,500 \text{ cm}^{-1}$

(408.2 nm) were: 518, 286, 154 and 77, respectively.] With two exceptions, there is a remarkable concordance of comparable data between present W.D.W. chromaticities and those calculated from color-matches made six years before. (i) The data for  $m \geq 24,250 \text{ cm}^{-1}$  (violet spectral extreme) differ by an amount larger than the reliability of this highly skilled colorimetrist justifies. We believe this due to the low radiance levels at which the recent data were obtained. (ii) In 1978 G.W. required both the long-wave and the middle-wave primaries to match  $m < 15,500 \text{ cm}^{-1}$ . In 1984 he matched such a test with the long-wave primary alone. The reason for this change is not clear, but insofar as it concerns this present study, the absence of color discrimination makes it impossible to evaluate "self-screening" on G.W. for  $m < 15,500 \text{ cm}^{-1}$ . Considering all the data, the mean  $\pm 1 \sigma$  chromaticity difference between

the maximum saturation CMFs of G.W. in 1978 and those in 1984 was  $0.0145 \pm 0.0153$ . Excluding the above exceptions, it was  $0.0089 \pm 0.0058$ . In the latter instances the residual differences were unsystematic, as if resulting from random measurement errors.

The pupil was dilated with one drop each of 1% cyclopentolate hydrochloride and 2.5% phenylephrine hydrochloride. In the course of long experiments, an additional drop (sometimes two) of the latter mydriatic was added.

### THEORY

$\rho(m)$ ,  $\gamma(m)$ ,  $\beta(m)$  are the normalized spectral distributions of absorption coefficients of the visual pigments in the observers' long-, middle-, and short-wave sensitive foveal cones respectively. Relative extinction spectra, absorptivity spectra, and absorbancy index spectra are

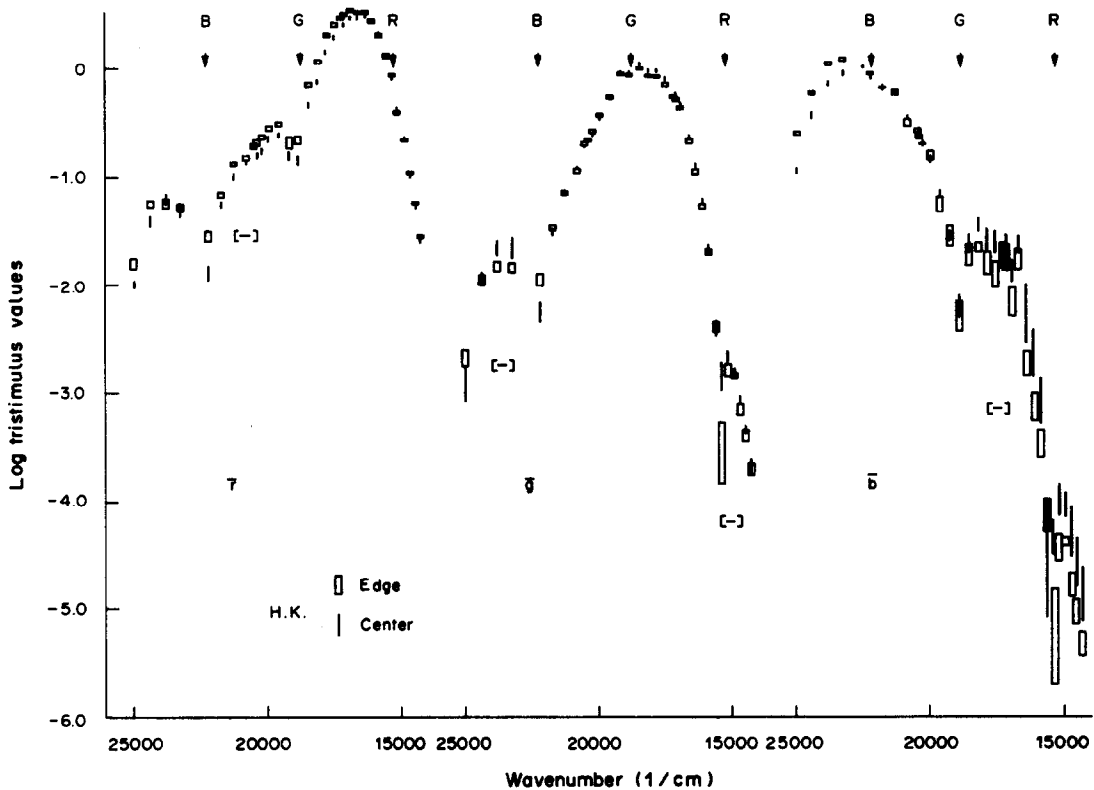


Fig. 1. The color matching functions for 36 monochromatic tests at approximately 10 nm intervals, alternating presentation paradigm (H.K.). Left-hand figure:  $\log r(m)$ ; middle figure:  $\log g(m)$ ; right-hand figure:  $\log b(m)$ . The length of each vertical line is defined by  $\log[\text{mean CMF} + 1 \text{ SEM (standard error of the mean)}]$  and  $\log[\text{mean CMF} - 1 \text{ SEM}]$  for a given "on-axis" match. There were a minimum of 16 matches at 400 nm ( $25,000 \text{ cm}^{-1}$ ) and a maximum of 51 matches at 450 nm ( $22,222 \text{ cm}^{-1}$ ). On average 25 matches were used to obtain these data. The vertical dimensions of each rectangle are defined by  $\log[\text{mean CMF} + 1 \text{ SEM}]$  and  $\log[\text{mean CMF} - 1 \text{ SEM}]$  for a given "off-axis" match. There were a minimum of 11 matches at 400 nm and a maximum of 50 matches at 460 nm ( $21,739 \text{ cm}^{-1}$ ). On average this set was generated with slightly more than 19 matches. Arrows specify the wavenumber of the reference primaries. Logarithms of CMFs in which a given primary was used as a desaturant are shown by [-].

synonyms. In this paper they should not be confused with the term *absorption spectra*.

$f_r(m), f_g(m), f_b(m)$  are the relative spectral absorption factors of the visual pigments in the observers' long-, middle-, and short-wave sensitive foveal cones respectively. In this paper they are used synonymously with the term *absorption spectra*.

$D_r, D_g, D_b$  are the common log optical densities at the wavenumbers of peak absorbance of the visual pigments in the observers' long-, middle-, and short-wave sensitive foveal cones respectively.

$d_r, d_g, d_b$  are the values of  $D_r, D_g, D_b$  respectively for normal retinal incidence and retinal illuminances ( $\leq 10^3$  td) which do not bleach measurable cone pigments.

$\bar{F}(m), \bar{g}(m), \bar{b}(m)$  are the retinal level equal quanta spectrum tristimulus values (or CMFs), i.e. the amounts of the the three reference primaries of wavenumbers  $m_1 = 15,500 \text{ cm}^{-1}$ ,  $m_2 = 19,000 \text{ cm}^{-1}$ ,  $m_3 = 22,500 \text{ cm}^{-1}$  at the retina required to give, by additive mixture, a match to monochromatic lights of wavenumber ( $m$ ) throughout the visible spectrum of equal quantum radiation.

$m_4 = 17,250 \text{ cm}^{-1}$  and  $m_5 = 20,500 \text{ cm}^{-1}$  are the two W.D.W. normalization wavenumbers. For ( $i = 1, \dots, 5$ ) we simplify by substituting  $f_r(i)$  for  $f_r(m_i)$ ,  $\bar{F}(i)$  for  $\bar{F}(m_i)$ , etc.

$u, v, w$  are the long-, middle-, and short-wave W.D.W. chromaticities respectively for all beams normally incident on the retina.

$u', v', w'$  are similar quantities obtained for all beams obliquely incident on the retina.

$$f_r(m) = [1 - 10^{-D_r \rho(m)}] / [1 - 10^{-D_r}] \quad (1)$$

Similar equations define  $f_g(m)$  and  $f_b(m)$  in terms of  $D_g, D_b, \gamma(m)$  and  $\beta(m)$  respectively.

$$\begin{bmatrix} \bar{F}(m) \\ \bar{g}(m) \\ \bar{b}(m) \end{bmatrix} = A^{-1} \begin{bmatrix} f_r(m) \\ f_g(m) \\ f_b(m) \end{bmatrix} \quad (2)$$

$$\text{where } A = \begin{bmatrix} f_r(1) & f_r(2) & f_r(3) \\ f_g(1) & f_g(2) & f_g(3) \\ f_b(1) & f_b(2) & f_b(3) \end{bmatrix}$$

has a nonzero determinant.

$$u(m) = \frac{\bar{F}(m)[\bar{g}'(4)/\bar{F}'(4)]}{\bar{F}(m)[\bar{g}'(4)/\bar{F}'(4)] + \bar{g}'(m) + \bar{b}'(m)[\bar{g}'(5)/\bar{b}'(5)]}$$

$$v(m) = \frac{g'(m)}{\bar{F}(m)[\bar{g}'(4)/\bar{F}'(4)] + \bar{g}'(m) + \bar{b}'(m)[\bar{g}'(5)/\bar{b}'(5)]} \quad (3)$$

and

$$w(m) = 1 - [u(m) + v(m)].$$

Theoretical chromaticity coordinates were calculated by assuming the forms of the spectral distribution of absorption coefficients and peak densities indicated below and applying them to equations (1)–(3). The measured chromaticities were calculated by substituting the empirical (corneal level) CMFs  $\bar{F}(m), \bar{g}(m), \bar{b}(m)$  for their retinal level counterparts in equation (3). Since the W.D.W. normalization obviates differences in matching due to differences in transmissivity of the ocular media (Wyszecki and Stiles, 1982, pp. 347–350), experimental measurements and theoretical predictions of W.D.W. chromaticities are strictly comparable.

*Spectral distribution of absorption coefficients*

To make a reasonably stringent test of “self-screening” theory, sets of spectral distributions of absorption coefficients  $\rho, \gamma, \beta$ —representative of the best estimates of human cone pigments available for the variety of approaches modern technology affords—were evaluated. These included the following:

(a) The mean microspectrophotometric results on 5 short-wave, 45 middle-wave and 58 long-wave sensitive cones from seven human eyes obtained by Dartnall *et al.* (1983).

(b) The human spectral absorption coefficients derived by Estévez (1979) from the 2° pilot foveal color matching functions of Stiles and Burch (1955). Estévez corrected for losses in the ocular media and assumed the peak optical density of 0.3 for each one of the three pigments in the set [Wyszecki and Stiles, 1982, Table 4 (8.2.5), columns 6, 7 and 8 on p. 620].

(c) The spectral distribution of absorption coefficients obtained by Nunn, Schnapf and Baylor (1984) from the photocurrent of single cones of *Macaca fascicularis* illuminated transversely. No short-wave sensitive cones were found in their study; but since their results for (four) long-wave, and (three) middle-wave, sensitive cones were very well fitted by the appropriate fundamentals used in (b), it was concluded that even if a valid estimate of the short-wave fundamental were available, results from including it could not significantly differ from those obtained in (b) for the red-green part of the spectrum where the changes in color were most conspicuous.

(d) The spectral distribution of absorption

coefficients from the absorption factors  $f_r(m)$ ,  $f_g(m)$ ,  $f_b(m)$  derived by Wyszecki and Stiles (1980) from the change in color matching when test radiance was increased to bleaching levels. "Self-screening" and a computer optimization routine were used to determine the most likely shapes of  $f_r$ ,  $f_g$ , and  $f_b$  as well as the most likely peak densities  $d_r$ ,  $d_g$  and  $d_b$ . [To obtain these parameters, Wyszecki and Stiles relied on the spectral transmissivity  $\tau_L(m)$  and  $\tau_M(m)$  of the photostable pigment in the lens and macula, respectively, consistent with data usually applied to normal human eyes. However, they introduced parameters  $\delta$  and  $\epsilon$  to allow for idiosyncratic characteristics of their observer to be included as part of the optimization algorithm. This adjustment,  $\tau(m) = \tau_L^\delta(m) \times \tau_M^\epsilon(m)$ , provides a more accurate correction for prereceptor factors than Estévez, for example, used.] We substituted the values of  $f_r(m)$  at the retinal level [Wyszecki and Stiles, 1982, Table 1 (8.2.6), p. 631] and the value of  $d_r = 0.44$ , emerging from their study, directly into equation (1) to calculate the spectral distribution of the absorption coefficient  $\rho(m)$ . Analogous procedures yielded  $\gamma(m)$  and  $\beta(m)$ .

#### Peak density

Calculations involving equation (1) and similar equations for  $f_g(m)$  and  $f_b(m)$  require knowledge of the peak densities. They were secured in two ways:

(1) *Simple model.* In this case, densities were simply assigned values. For normal incidence they were the values ( $d_r = 0.44$ ,  $d_g = 0.38$ ,  $d_b = 0.45$ ) Wyszecki and Stiles (1980) found to be optimum to fit the changes in CMFs with increase in test illuminance from  $10^3$  and  $10^5$  td. This assignment was not quite so arbitrary as it seems, because it was used only with the  $\rho$ ,  $\gamma$ ,  $\beta$  set emerging from that same study and since the observer in the Wyszecki and Stiles (1980) study (G.W.) was also a subject here. This was also the set used in (d) above. [Note, however, that the earlier study used minimum saturation (Maxwell's) matches; this one used maximum saturation matches. Results from the two methods differ slightly more than the  $\pm 2\%$  imprecision of G.W.'s CMFs lead one to expect (Wyszecki and Stiles, 1982, pp. 379–392).] For oblique retinal incidence,  $D_r = D_g = D_b = 0.0001$  was arbitrarily assumed as representative of a very dilute concentration. This theory is designated

as WS1; the results calculated with it are shown as dotted lines in Figs 4–8.

(2) *Other models.* In all other models the peak densities were calculated by a computer optimization algorithm STEPIT (Chandler, 1965) which minimized the r.m.s. deviations of the theoretical predictions from empirical data. This was accomplished in two stages. In the first, for a given set of absorption coefficients ( $\rho$ ,  $\gamma$ ,  $\beta$ )  $D_r$ ,  $D_g$ ,  $D_b$  were varied parametrically applying equations (1), (2) and (3) to minimize the deviations of predicted W.D.W. chromaticities from the experimental values (normal incidence). All densities in the range 0–10<sup>39</sup> were allowed. With the same values of  $\rho$ ,  $\gamma$ ,  $\beta$ , the second stage was a similar application of STEPIT varying  $D_r$ ,  $D_g$ ,  $D_b$  of the "off-axis" set to minimize the deviations of the predicted changes in W.D.W. chromaticity from the measured changes with oblique incidence. In this stage, "off-axis" peak densities were subject to the constraints

$$d_r \geq D_r > 0$$

$$d_g \geq D_g > 0$$

and

$$d_b \geq D_b > 0 \quad (4)$$

in which  $d_r$ ,  $d_g$ , and  $d_b$  are the values of  $D_r$ ,  $D_g$ ,  $D_b$  yielding the minimal r.m.s. deviations in the first stage.

Three sets of absorption coefficients were evaluated: (i) Dartnall *et al.* (1983) (hereafter DBM), (ii) Estévez (regarded as the same as those of Nunn *et al.*, 1984, hereafter ENSB), and (iii) Wyszecki and Stiles (1980) (hereafter WS2), respectively. In Figs 4–8, predictions with WS2 are drawn with a solid, those by ENSB with a dashed, line.

The iterative calculations leading to the theoretical predictions for H.K. and K.K., the subjects for whom the instrument and reference primaries differed, always began with the calculation of the CMFs at the physical wavelengths actually involved in the matches (i.e. the instrument primaries). These were then transformed into the equivalent CMFs which would have been obtained if the reference primaries had actually been used. However, the results were indistinguishable from those obtained beginning with the assumption that the instrument and reference primaries were identical.

## RESULTS

Figure 1 shows the log CMFs for H.K. (Michigan data) plotted as a function of test wavenumber  $m$ . Logarithms are preferred in the display of CMFs because in different parts of the spectrum the absolute value of the same CMF may differ by several orders of magnitude. [Standard errors of the mean rather than standard deviations are necessary in Fig. 1 because in several instances the standard deviation was larger than the mean, so the limits  $\log(\text{mean} + 1\sigma)$ ,  $\log(\text{mean} - 1\sigma)$  cannot both be plotted.] In the red-green spectral range, Brindley (1953) found—and we confirm—that more red, and less green, primary is generally required in “off-axis” matches than in “on-axis” matches. The results in Fig. 1 show this trend. [The 640 nm test is an exception; elsewhere occasionally only one of the two CMFs differs in the expected direction.]

Unfortunately, the “raw” CMFs plotted in Fig. 1 are not useful for analysis since no allowance is made for prereceptor losses. Hence, results such as those in Fig. 1 were normalized according to equation (3). Figure 2 shows the W.D.W. chromaticity chart resulting.

To make the variability more distinguishable in this figure, ellipses are defined by the standard deviations (*not* standard errors) (see Methods). Solid lines define ellipses of matches made when all the colorimeter beams traversed the pupil center; dashed ellipses show the limits of the chromaticities when these lights traversed the pupil 3.0 mm temporal to the center. Recalling that two means separated by a distance greater than the sum of their standard errors is a conservative indication of a statistically significant difference ( $t$ -test), a glance at Fig. 2 suffices to convince one that generally the differences in mean chromaticities between “off-axis” and “on-axis” matches are both systematic and

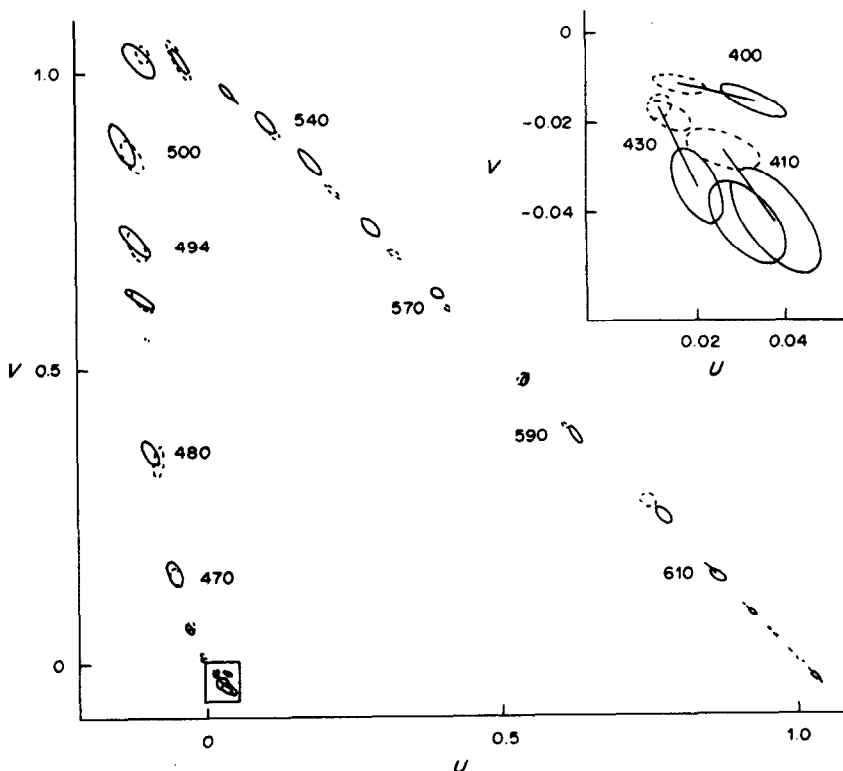


Fig. 2. W.D.W. chromaticity coordinates of the “on-axis” and “off-axis” trichromatic matches of H.K. The matches defining these chromaticities are identical to those producing the CMFs plotted in Fig. 1. The mean of each match is directly related to the mean of the corresponding match plotted in Fig. 1 using equation (3), as described in the text, but the dimensions of the ellipses are defined by  $\pm 1\sigma$  (SD) rather than  $\pm 1$  SEM, plotted in Fig. 1, in order to make the variability more discriminable. The ellipses outlined by the solid lines represent chromaticities of matches made with beams traversing the pupil center. The ellipses outlined by the dashed lines were obtained with all beams traversing the pupil 3.0 mm temporal to the center. The plot at the upper right shows the chromaticities at test wavelengths less than 450 nm with expanded scales.

statistically significant in the red-green part of the spectrum. Similar differences for test wavenumbers between the green and blue primaries are generally smaller and unsystematic; statistical significance of these latter differences is less common. Similar results are found in three of the four subjects. The exception is the single set of results on G.W. plotted as solid arrows in Fig. 3.

A given arrow in Fig. 3 represents the change in chromaticity of the same test: the tail of the arrow is the chromaticity "on-axis", the tip, the chromaticity "off-axis". The dotted arrows in this figure are theoretical; they are discussed below. Although no statistical analysis of G.W.'s results is possible, he was a highly skilled colorimetrist whose settings in repeated color matches have uncertainties of approximately  $\pm 2\%$  in CMFs (Wyszecki and Stiles, 1982,

p. 390). The application of perturbations of this size to several of his matches in both the red-green and blue-green spectral ranges invariably shows that the change in chromaticity with change in angle of retinal incidence shown in Fig. 3 is much larger than the  $\pm 2\%$  perturbation of the "on-axis" match of the same test.

Given a poorer precision of matching in the blue-green, the general trend (a more conspicuous color change with obliquity for  $15,500 < m < 19,000 \text{ cm}^{-1}$  than for  $19,000 < m < 22,500 \text{ cm}^{-1}$ ) is also found (admittedly in a somewhat more subtle form) in Fig. 3. Because matches at  $m_4 = 17,250 \text{ cm}^{-1}$  (unlike those at  $m_5 = 20,500 \text{ cm}^{-1}$ ) involve almost entirely only the "red" and the "green" primaries instead of all three, chromaticity changes for tests near  $m_4$  on the W.D.W. plot must necessarily be smaller

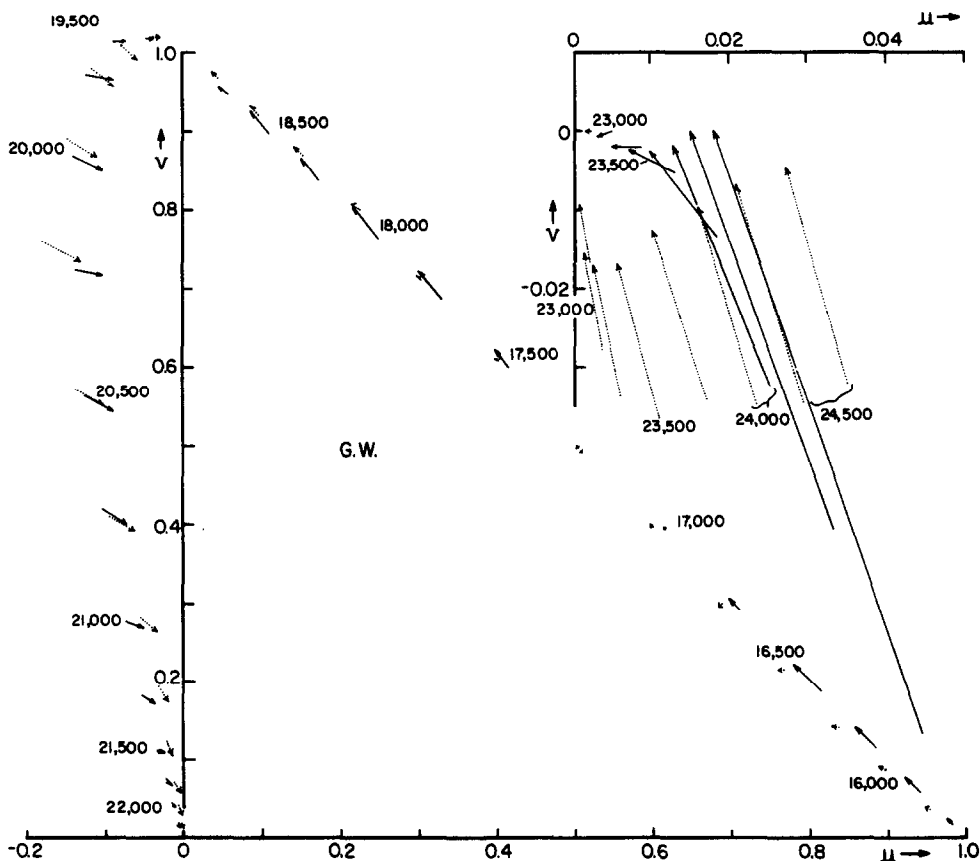


Fig. 3. W.D.W. chromaticity of monochromatic test lights (G.W.)  $2^\circ$  field, simultaneous presentation paradigm. The solid arrows show experimental data: the tail of each arrow represents the chromaticity with all beams traversing the pupil center; the tip of the same arrow represents the chromaticity of the same monochromatic light with all beams traversing the pupil 3.0 mm temporal to its center. Each plotted point is the result of a single measurement, but the CMFs were slightly smoothed prior to conversion to chromaticity coordinates. The dashed arrows are results of the best fitting "self-screening" model (see Table 1). The chart above and to the right shows the chromaticities of all test wavenumbers  $m > 22,500 \text{ cm}^{-1}$  with an expanded scale.

due to the normalization than is the case near  $m_5$ .

Although it is true that in the red-green spectral range more red (and less green) primary is regularly required for a given "off-axis" match than for the same match "on-axis", it does not follow, and Figs 2 and 3 show that it is by no means always the case, that these same color matches for oblique incidence have a larger W.D.W. "red" chromaticity and a smaller W.D.W. "green" chromaticity than for normal incidence.

It is difficult to distinguish between the chromaticities of "on-axis" and "off-axis" matches for  $m < 15,500 \text{ cm}^{-1}$  on the W.D.W. chart, as the results in Fig. 2 make plain. This is no

handicap in studying G.W.'s data (he was a monochromat in this spectral region), but for the other subjects an alternative way of showing the results is used. In it, we plot the change in W.D.W. chromaticities  $\Delta u = u' - u$  (as triangles above),  $\Delta v = v' - v$  (squares, in the middle) and  $\Delta w = w' - w$  (circles, below) as functions of test wavenumber for each set of data separately (Figs 4, 5, 6, and 7).

In these figures the symbols represent experimental means, the lengths of vertical lines specify the 95% confidence limits, of the experimental differences between the W.D.W. coordinate for "off-axis" and "on-axis" matches. Other lines represent changes in chromaticity predicted by "self-screening".

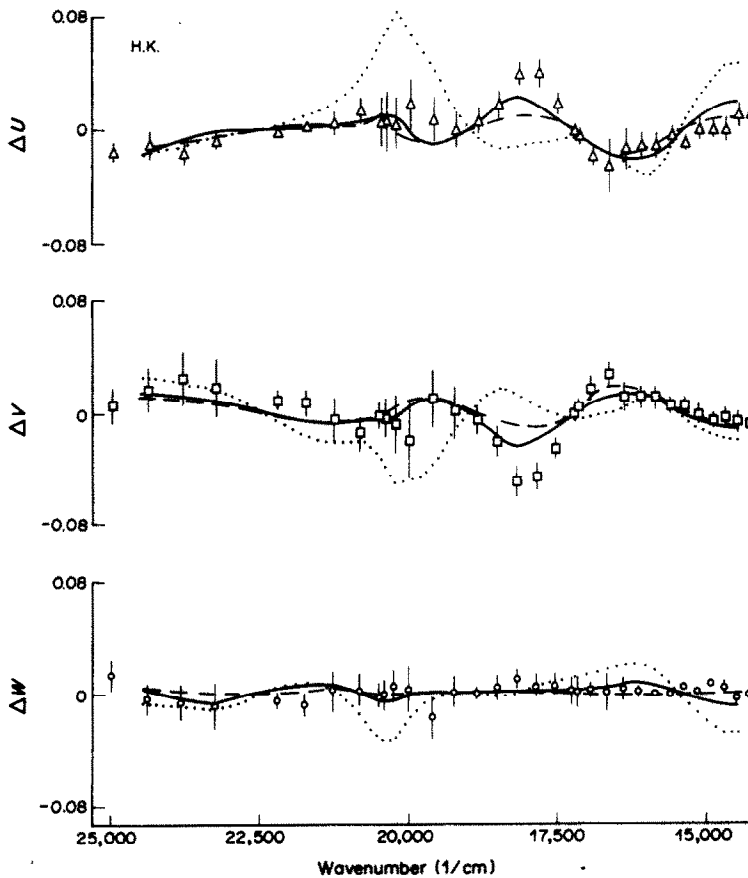


Fig. 4. Changes in W.D.W. chromaticity of monochromatic lights on shifting the point of pupil traverse from the center of the entrance pupil to 3 mm temporal to the center (H.K.). These data are calculated from the results in Fig. 2. The experimental points are: triangles (for  $\Delta u = u' - u$ , above), squares (for  $\Delta v = v' - v$ , in the middle) and circles (for  $\Delta w = w' - w$ , below) which define the changes in the mean chromaticities; the limits of the vertical lines define the 95% confidence limits of these changes. The other lines are predictions of three "self-screening" models: dotted line, WS1, the model with the fewest free curve fitting parameters, is also the poorest description of the change in chromaticity with change in angle of incidence on the retina; solid line, WS2, the best theoretical description of the chromaticity change; dashed line, ENSB. The predictions of DMB are valid only for  $m > 15,500 \text{ cm}^{-1}$  and are not shown. For the details of these fits, refer to Table 1. Weale's original hypothesis predicts that the 95% confidence limit will include zero for all but 5% of the lights tested.



The results in Fig. 2 are replotted in this way in Fig. 4. A comparison of the two figures shows the advantage of plotting chromaticity *change* rather than chromaticities if the experimentally measured 95% confidence limits are compared simultaneously with the predictions of several theoretical models. The chromaticity diagram becomes too cluttered. (Note the dashed arrows in Fig. 3 are predictions of only one model in a figure with no confidence limits included.)

The results for a third observer K.K. are similarly plotted in Fig. 5. These data are of special interest because for all  $m < 19,000 \text{ cm}^{-1}$

this subject managed "off-axis" matches with no recourse to the  $22,500 \text{ cm}^{-1}$  primary. The significance of this result is discussed below.

How do data consistent with theory appear in such a plot? The answer is found in Fig. 6 which gives results from a fourth observer, with more variable matches. They concern a change in chromaticity on shifting the point of pupil traverse from center to a point (2.5 mm nasal) intermediate between the pupil center and its margin. This combination of small angle of obliquity and large variance results in the 95% confidence limits intersecting nearly all the chro-

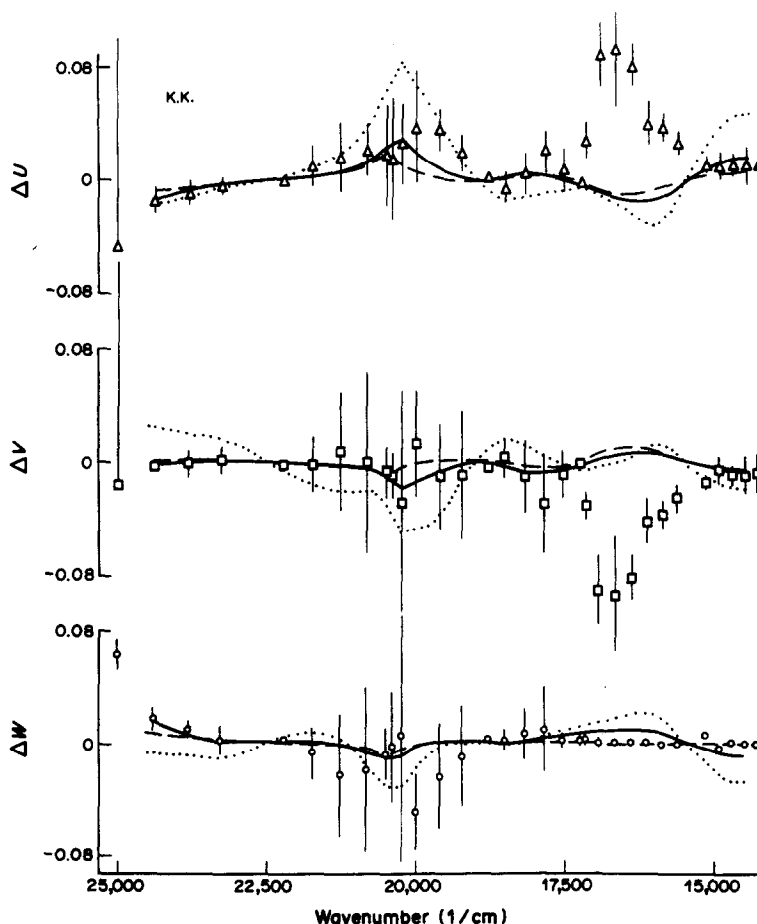


Fig. 5. Change in W.D.W. chromaticity of monochromatic lights on shifting the point of pupil traverse from center to 3 mm temporal pupil margin (K.K.), alternating presentation paradigm. Both the "on-axis" and the "off-axis" experiments were carried out three times at every wavenumber. The experimental points are: triangles (for  $\Delta u = u' - u$ , above), squares (for  $\Delta v = v' - v$  in the middle) and circles (for  $\Delta w = w' - w$ , below) which define the changes in the mean chromaticities; the vertical lines define the 95% confidence limits of these changes. The other lines are predictions of three "self-screening" models: dotted line, the simplest model with the fewest free curve-fitting parameters (WS1), is also the poorest description of the chromaticity changes with change in angle of incidence on the retina; solid line, the best theoretical description of the chromaticity changes (WS2); the dashed line shows the prediction of ENSB. The predictions of DBM are not shown since they are valid only for  $m > 15,500 \text{ cm}^{-1}$ . For the details of the theoretical predictions applied to these data, see Table 1. Weale's original hypothesis predicts the 95% confidence limits will include zero chromaticity change for all but 5% of the monochromatic lights tested. His modified hypothesis predicts the same for  $\Delta u$  and  $\Delta v$  for  $m < 19,000 \text{ cm}^{-1}$ , which for "off-axis" matches were invariably dichromatic.

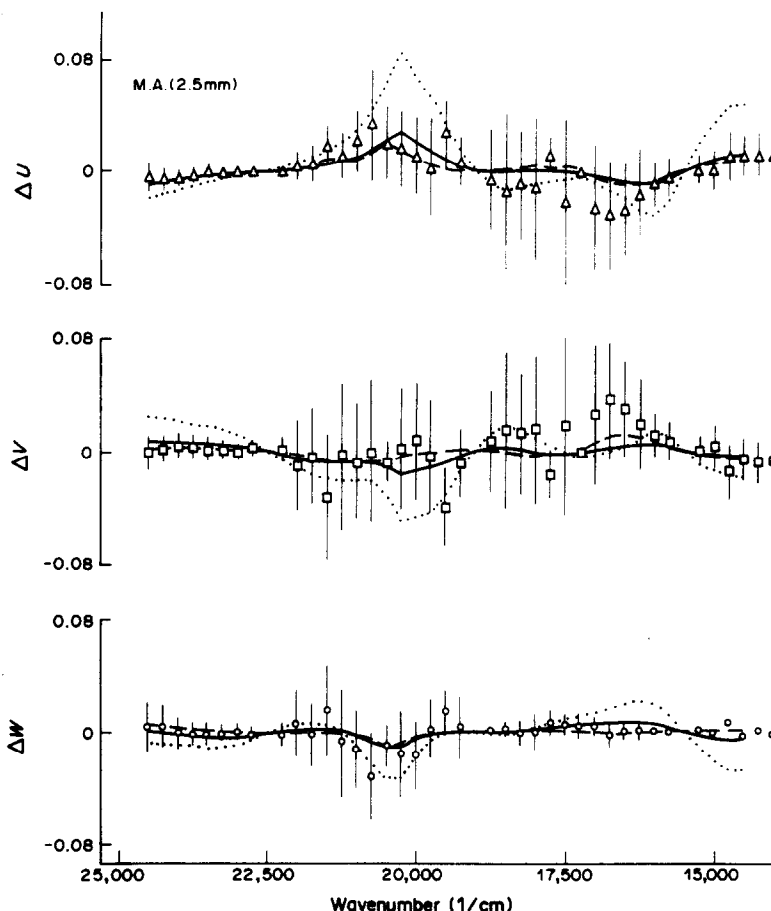


Fig. 6. Change in W.D.W. chromaticities of monochromatic lights on shifting the point of pupil traverse from the center of the entrance pupil to 2.5 mm nasal to the center (M.A.), simultaneous presentation paradigm. Through the center, 6–8 matches ( $m < 19,000 \text{ cm}^{-1}$ ) and 14–17 matches ( $m > 19,000 \text{ cm}^{-1}$ ) were completed; for this oblique pupil traverse 4–7 matches ( $m < 19,000 \text{ cm}^{-1}$ ) and 11–14 matches ( $m > 19,000 \text{ cm}^{-1}$ ) were made. The other details in this figure are to be understood in the way described in the legend to Fig. 4. Note that for this intermediate angle of obliquity on the retina the results exclude only the simplest model (dotted line).

maticities predicted by WS2 and ENSB. Only WS1 (dotted line) is inconsistent with these data.

The changes in chromaticity of matches made with normally incident light and light traversing the pupil margin (3.4 mm temporal) on this same subject are shown in Fig. 7. The 95% confidence limits are still large, but the increased obliquity increases slightly, but definitely, the number of comparisons the 95% confidence limits of which do not intersect theoretical curves.

#### *Individual differences*

Remarkable individual differences in the “red-green” range emerge from this study. For  $19,000 > m > 17,250 \text{ cm}^{-1}$ , the W.D.W. chro-

maticities of “off-axis” matches are more “green” and less “red” than their “on-axis” counterparts for G.W. For H.K. it is precisely the reverse! The others fall between—M.A. closer to G.W., K.K. more like his brother H.K. Analogous differences between the (“on-axis”) W.D.W. chromaticities of individual prot-anomalous compared with those of a given normal trichromat are sometimes found (Bastian, 1976). We do not fully understand such differences, but the dramatic differences in direction found on the W.D.W. plot are not duplicated in the primary chromaticity diagram, where “off-axis” chromaticities are invariably more “red” and less “green” than “on-axis” chromaticities. Individual differences here are differences in degree rather than kind.

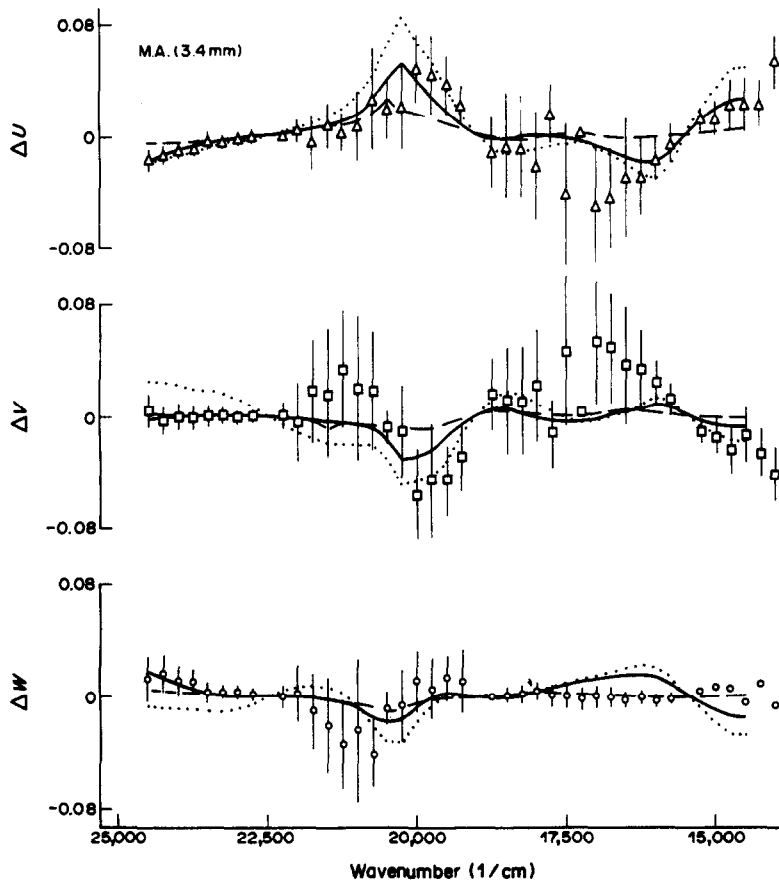


Fig. 7. Change in W.D.W. chromaticities of monochromatic lights on shifting the point of pupil traverse from the center of the entrance pupil to 3.4 mm temporal pupil margin for the same observer whose results are shown in Fig. 6 (M.A.), simultaneous presentation paradigm. For  $m < 19,000 \text{ cm}^{-1}$  there were 8, for  $m > 19,000 \text{ cm}^{-1}$  there were 15–16, “off-axis” matches. The other details in this figure are to be understood in the way described in the legend to Fig. 4. Note in Table 1 that with this increased obliquity, the changes suffice to exclude all theoretical models considered in this paper despite the imprecision of this observer’s color matches.

Evidently, the magnitude of the W.D.W. weighting factor in the yellow ( $\bar{g}_4/\bar{r}_4$ ) or more exactly the ratio of this factor for “off-axis” to the one for “on-axis” matches is important in this transformation. For G.W. this ratio was 0.63, while for H.K. it was 0.74. The others fell between K.K. (0.67), leaning slightly more in the direction of H.K. than M.A. (0.66) does! The most plausible explanation is small second-order differences in the spectral distribution of absorption coefficients in the cone pigments of normal trichromats. Convincing evidence for different absorption spectra of normal cone pigments has been inferred (Alpern, 1987) from the individual  $2^\circ$  color matching data of Stiles and Burch (1955) reported by Trezona (1984).

## DISCUSSION

Are the color changes with retinal angle of incidence associated with different absorption spectra for “on-axis”, than for “off-axis”, matches? According to Weale (1981a, b), they are not. If he is correct, the 95% confidence levels of the color changes will include zero 95% of the time. Figs 4, 5 and 7 show this does not occur (see Table 1 below). When confronted with failures in prediction of the Stiles–Crawford hue shift in the short-wave part of the spectrum by his original theory, Weale (1981a) added the *ad hoc* hypothesis that one of his three prereceptor factors, the cut-off of a high spatial frequencies of obliquely incident rays, does not apply to short-wave sensitive cones because they

(like rods) are not diffraction limited. Though the results in Figs 4 and 7 do not exclude this modification of the original theory, they render it nonetheless improbable since substantial differences in "on-axis" from "off-axis" W.D.W. chromaticities occur in precisely the part of the spectrum for which the contributions of the short-wave sensitive cones to the match are almost negligibly small. The additional certainty provided by exclusion of this *ad hoc* modification of Weale's original hypothesis is afforded by the results  $15,500 < m < 16,750 \text{ cm}^{-1}$  (G.W., Fig. 3) and for K.K. (Fig. 5) for the spectral range  $m < 19,000 \text{ cm}^{-1}$ .

In these examples in the red-green spectral range, "off-axis" matches were dichromatic, i.e. no amount of short-wave primary was required. The only reasonable explanation is that the observers' short-wave sensitive cones made no contribution to the perceptions upon which these matches depended. Under these conditions the attenuation of monochromatic lights by the three prereceptor factors of Weale's theory applies equally to the two types of cones which *do* contribute to those perceptions. The prediction of the modified theory in these instances is then no different from the predictions of the original theory. Since the 95% confidence limits of the changes in chromaticity  $\Delta u$  (or  $\Delta v$ ) in Fig. 5 fail to include zero in more than 60% of the values of  $m$  relevant for this consideration, this observer's results exclude Weale's modified hypothesis. For G.W. (Fig. 3), it may similarly be noted that the chromaticity changes in every one of the four relevant examples in going from "on-axis" to "off-axis" matches were substantially larger than the limits provided by the  $\pm 2\%$  uncertainty of his color matches.

Increasing the obliquity of M.A.'s "off-axis" matches slightly increased the number of examples in which the 95% confidence limits of the matches failed to intersect one theoretical curve or another. Is the frequency of such events sufficient to exclude the model generating a given curve, or is it merely symbolic of measurement imprecision?

We have determined the frequencies that the empirical 95% confidence limits of each W.D.W. chromaticity change falls outside the prediction of each of six models of the color change, including four "self-screening" models and both of Weale's hypotheses. The results are summarized in Table 1.

In this table, the first column identifies the

subject; the second, the theoretical model evaluated; the next column designates the point of pupil traverse. The next four columns specify the predicted peak optical densities and the root mean square deviation of the theoretical from the empirical chromaticities (central entry) and of the predicted changes in chromaticity from the measured changes ("off-axis" traverse). The final four columns list the frequencies the 95% confidence limits of the measured changes in chromaticity fall outside of the theoretical predictions of  $\Delta u, \Delta v, \Delta w$ , respectively, and the averages of the preceding three columns. A rule for conserving theoretical models is that for a given model to be retained, the frequency listed (in this final column) should be no larger than 5.0%.

Inspection of Table 1 reveals that even with this conservative criterion the results suffice to exclude each model for all observers examined. Though the 95% confidence limits of G.W.'s matches weren't measured, previous studies of the repeatability of his ("on-axis") matching (yielding an uncertainty of approximately  $\pm 2\%$  of his CMFs) applied to his results (Fig. 3), lead to a similar conclusion. This can be seen by comparing the fit of the dotted arrows (theoretical predictions) in Fig. 3 to the solid arrows (experimental results). This comparison is made only with the model predicting the smallest r.m.s. deviations from the measured chromaticity changes (WS2) but is generally representative of comparisons provided by the other models as well. Moreover, in the red-green range the underprediction of the theoretical changes is characteristic of the comparisons of theory to results of the other observers as well; the theoretical overpredictions elsewhere in the spectrum are not.

Quantitative difficulties with "self-screening" are clear only when the effect of retinal angle of incidence on color matching is examined—as it is here—throughout the spectrum. One salvation of "self-screening" would be spectral distributions of absorption coefficients different from those used. We are not optimistic that further developments along such lines will be productive. The distributions used are the best estimates emerging from the broad range of different modern approaches: psychophysical, microspectrophotometrical and electrophysiological. Though each distribution makes different predictions from the others, the ensemble differ less from each other than each in turn differs from experimental data.

Table 1. Test of four theoretical models of self-screening theory of SCII and Weale's (1981) original and modified theories of the SC hue shift

Subject	Theoretical model	Point of pupil entry	Optimum theoretical peak optical densities			r.m.s. deviation	Frequency theoretical predictions fall outside the empirical 95% confidence limits for			
			$D_r$	$D_g$	$D_b$		$\Delta u$ (%)	$\Delta v$ (%)	$\Delta w$ (%)	Average (%)
G.W.	WS1	C	0.44	0.38	0.45	0.0337242				
		3 mm T	0.0001	0.0001	0.0001	0.025502				
	WS2	C	0.56	0.29	0.51	0.0294125				
		3 mm T	0.41	0.077	0.38E-7	0.0204955				
	ENSB	C	0.14	0.13	0.69	0.0242927				
		3 mm T	0.11	0.36E-8	0.37E-7	0.0225205				
DBM	C	0.88	0.35	0.31	0.52973					
	3 mm T	0.67	0.89E-6	0.31	0.0230201					
H.K.	WS1	C	0.44	0.38	0.45	0.0430206				
		3 mm T	0.0001	0.0001	0.0001	0.0372239	68	65	61	64.5
	WS2	C	0.78	0.29	0.45	0.0323433				
		3 mm T	0.42	0.19	0.25	0.0149923	42	26	39	35.5
	ENSB	C	0.35	0.12	0.73	0.0224541				
		3 mm T	0.10E-3	0.040	0.50	0.0170741	32	26	19	25.8
DBM	C	1.79	1.27	0.15E-7	0.0684377					
	3 mm T	1.40	1.00	0.50E-7	0.0151215	35	42	12	29.5	
K.K.	WS1	C	0.44	0.38	0.45	0.0441893				
		3 mm T	0.0001	0.0001	0.0001	0.0288397	60	50	60	56.7
	WS2	C	0.76	0.30	0.18	0.0336592				
		3 mm T	0.47	0.11	0.18	0.0140157	30	27	30	28.9
	ENSB	C	0.37	0.14	0.37	0.0225264				
		3 mm T	0.10	0.41E-8	0.37	0.0155286	37	30	10	25.6
DBM	C	1.72	1.23	0.37E-7	0.0664577					
	3 mm T	1.51	1.03	0.15E-7	0.0142894	38	35	8	26.9	
M.A.	WS1	C	0.44	0.38	0.45	0.0459148				
		2.5 mm N	0.0001	0.0001	0.0001	0.0309441	42	26	34	34.2
	WS2	3.4 mm T	0.0001	0.0001	0.0001	0.032400	18	37	55	36.8
		C	0.64	0.28	0.24	0.0398729				
	ENSB	2.5 mm N	0.47	0.14	0.088	0.0174695	0	3	8	3.5
		3.4 mm T	0.30	0.15E-7	0.24	0.0262712	8	13	32	18.4
DBM	C	0.34	0.14	0.30	0.0324238					
	2.5 mm N	0.067	0.11E-6	0.22	0.0165837	0	3	5	2.6	
Average (each match equal weight)	WS1	3.4 mm T	0.19	0.57E-8	0.30	0.0302005	29	26	8	21.0
		C	1.60	1.14	0.21E-6	0.0727143				
	WO	2.5 mm N	—	—	—	—	—	—	—	—
		3.4 mm T	1.49	0.98	0.21E-6	0.0308231	35	18	3	18.6
	WM	C—2.5 mm N	—	—	—	—	5	2	5	4.2
		C—3.4 mm T	—	—	—	—	35	32	22	30.0
Average (each match equal weight)	WS1	C	0.44	0.38	0.45	0.0413409				
		E	0.0001	0.0001	0.0001	0.03267	55	45	68	55.9
	W2S	C	0.75	0.29	0.38	0.0312583				
		E	0.39	0.11	0.32	0.0138687	26	13	19	19.0
	ENSB	C	0.35	0.13	0.64	0.0305846				
		E	0.124E-4	0.46E-8	0.59	0.0161639	23	19	6	16.1
DBM	C	1.74	1.24	0.15E-7	0.0662434					
	E	1.45	1.00	0.15E-7	0.0149882	35	23	8	21.8	
WO						68	48	9.7	41.9	

N = nasal; T = temporal; C = center; E = edge. WS1 = Wyszecki and Stiles 1; WS2 = Wyszecki and Stiles 2; ENSB = Estévez, Nunn, Schnapf and Baylor; DBM = Dartnall, Bowmaker and Mollon; WO = Weale original; WM = Weale modified.

Alternatively, the life of "self-screening" theory might conceivably be prolonged by increasing the number of parameters available in curve-fitting. In this connection, note that the

quantitative models evaluated so far are extensions of the original Stiles model as quantified by Brindley (1953). Walraven and Bouman (1960) developed a more elaborate "self-

screening" model involving a wavelength independent leakage of obliquely incident light at a uniform rate along the outer segment length. The absorption spectrum of the long-wave sensitive cones, for example, then becomes

$$f_r(m) = \frac{D_r \rho(m)}{D_r \rho(m) + A} \left\{ \frac{1 - 10^{-[D_r \rho(m) + A]}}{1 - 10^{-[D_r + A]}} \right\} \quad (5)$$

in which the leakage density  $A$  is zero for normal incidence and increases with increasing angle of incidence on the retina. Attempts to salvage self-screening with this more elaborate theory have been no more successful than the search for a better set of extinction spectra. Increasing the number of free parameters by three leakage densities (one for each cone species) caused only a modest reduction (15%) in the r.m.s. deviations of data from theoretical expectation in Table 2, even in the best case, and improvements were generally an order of magnitude smaller than this. In only one case (for M.A., 3.4 mm T, DBM theory) did the (2.3%) improvements result in a reduction in the frequencies given in the final column of this table (from 18.6 to 17.6%).

The evaluation of theory in the W.D.W. chart avoids the obvious difference in chromaticity between "on" and "off" axis lights due to thickness differences in the lens regions through which the respective beams pass, but it has the difficulty that r.m.s. deviations have been minimized in a chromaticity diagram in which a given distance is not equally perceptible at different loci. Could the unequivocal rejection of "self-screening" emerging be qualified if the minimization were applied in a way not subject to this difficulty? Efforts to evaluate this possibility so far do not offer much hope for the salvation of "self-screening". Two other ways of avoiding the distortions in chromaticity due to losses in the lens have been tried. In the first, lens and macular pigment variability were introduced into the optimization routine following Wyszecki and Stiles (1980). STEPIT minimized the RMS deviations of the log CMFs predicted from those measured for both center and margin of the pupil traverse of the lights, with  $D_r, D_g, D_b, d_r, d_g, d_b$  as the other curve-fitting parameters. In the second, a variant of the von Kries (1899) approach to eliminating eye media distortions with the ratio of two different tristimulus values was tried. The empirical log of the product of the long-wave CMF "off-axis" and the middle-wave CMF "on-axis" divided by the product of the long-wave CMF "on-axis"

and the middle-wave CMF "off-axis" (together with a similar log ratio involving the empirical middle- and short-wave CMFs) were used in a "self-screening" theory in which (given  $d_r, d_g, d_b$  from the first approach)  $D_r, D_g, D_b$  were the curve-fitting parameters used to minimize the r.m.s. deviations of predicted from empirical log ratios. Neither of these approaches predicted results close to the description of the data given by models shown in Figs 4, 5, 6, 7 and 8 when the same domains of  $\rho, \gamma, \beta, D_r, D_g, D_b, d_r, d_g, d_b$  were evaluated.

Individual differences make the average W.D.W. chromaticity change with obliquity difficult to interpret. Nevertheless, it provides a useful control in an attempt to elucidate how the sets of absorption spectra for normally and obliquely incident light differ and, at the suggestion of a reviewer, we computed it. The result (each match weighted equally) is in Fig. 8.

Evidently, the conclusions already inferred from individual data may also be reached by studying this "average" result. Since "off-axis" matches in the red-green range are (in the primary chromaticity diagram) more protanomalous than "on-axis" matches, one might suppose the pigments absorbing oblique photons in the normal retina identical to those catching normally incident photons in the protanomalous retina. We tested this hypothesis by calculating the differences between W.D.W. chromaticities (normal incidence) for the "average data" and those found (also normal incidence) for a protanomalous trichromat retina ( $X$ 's in Fig. 8). If the hypothesis were correct,  $X$ 's should fall within the 95% confidence limits of the changes in chromaticity with change in angle of incidence on the "average" normal retina in all but 5% of the examples in Fig. 8. This prediction fails. Nor is the matter improved if the results on any one subject are similarly compared instead of the average. We infer: the physical-chemical factors determining the wavelength dependency of absorption of oblique photons in the four normal retinas studied here differ from those determining that dependency for normally incident photons in this anomalous fovea.

This does not exclude the existence of a protanomalous subject who will successfully pass a test which this protanomalous trichromat fails so badly. However, the discrepancies between the  $X$ 's and the 95% confidence limits in many of these comparisons are so large this possibility seems remote.

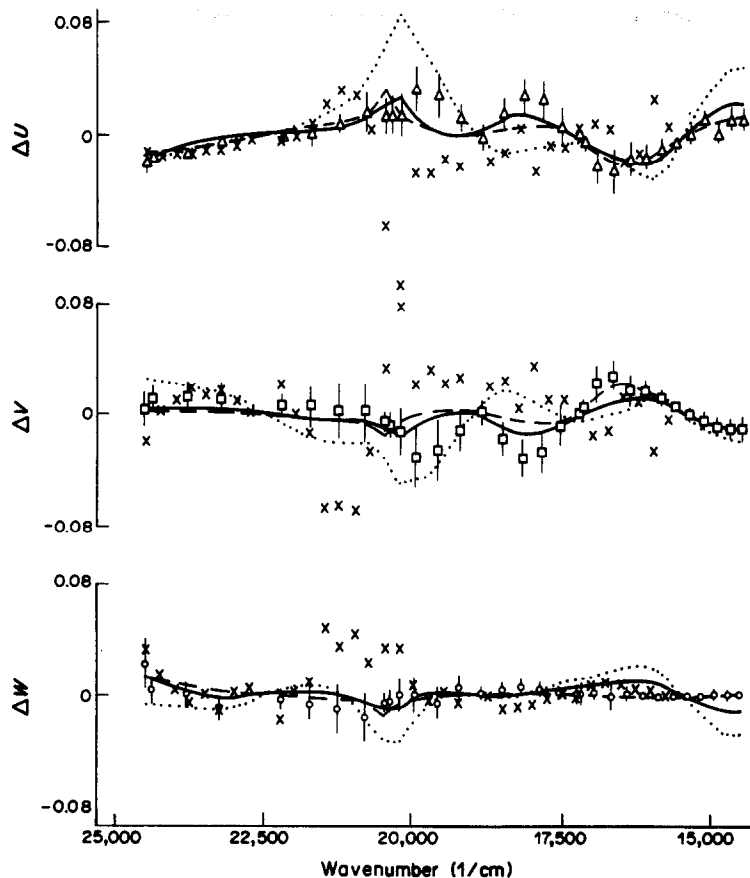


Fig. 8. Change in W.D.W. chromaticities of monochromatic lights on shifting the point of pupil traverse from the center of the entrance pupil to the most extreme position studied, average of the results on four normal trichromats (each match given equal weight). This average included only M.A.'s results "off-axis" at 3.4 mm (i.e. Fig. 7), not those shown in Fig. 6. [In Ottawa the spectrum position is specified in wavenumber; matches covered the range  $14,000 \leq m \leq 24,500 \text{ cm}^{-1}$  in  $250 \text{ cm}^{-1}$  intervals. In Ann Arbor at the time these data were accumulated, spectral position was specified in wavelength; matches covered the range 400–700 nm in 10 nm steps. Consequently in averaging, interpolations were unavoidable. To obtain the results in this figure, the Ottawa data have been interpolated to the Ann Arbor spectral positions (since fewer intermediate positions were sampled), but the average at 400 nm (which requires an extrapolation) has been omitted.] The symbols and the lines have the same interpretations described in the legend of Fig. 4. X's show the differences between the W.D.W. chromaticity of the average results (for normal incidence on the retina) and those of a congenital protanomalous trichromat (also normal incidence on the retina). For interpretation, see text.

But what these physical-chemical factors may be needs more attention. The obvious place to begin is wave-guide theory. Alpern (1983) found a preference for the wave-guide model of Snyder and Pask (1973) over "self-screening" theory in fitting the wavelength dependency of the directional sensitivity parameter  $\rho$  in Stiles's (1937) parabolic equation for SCI for the  $\Pi_j(\mu)$  mechanisms ( $j = 3, 4, 5$ ). The present results also do not exclude models (Wijngaard *et al.*, 1974; Fuld *et al.*, 1979) of "self-screening" in conjunction with wave-guides in explaining SCII. With the exception of Alpern (1983), all these studies

and others (Pask and Snyder, 1975) test such models of SCII, if at all, by their ability to fit "hue shift" data. It remains to be shown how successful they will prove in describing results such as those reported here.

The present results merely show that the action spectra of cones absorbing obliquely incident photons differ from the action spectra of cones absorbing normally incident photons (whether the absorbing cones themselves are the same or distinctly different). They also show that the most generally accepted explanation for this difference is almost certainly wrong!

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