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SPECTRAL SENSITIVITY OF THE FOVEAL CONE PHOTOPIGMENTS BETWEEN 400 AND 500 nm[1]

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Abstract—A comparison was made between the shape of the iodopsin absorption spectrum calculated for appropriate optical density to (1) a set of König-type fundamentals in which the tritanopic copunctal point was set on the alychne and (2) data obtained from red–green dichromats using high intensity heterochromatic flicker procedures which eliminated participation by the short-wavelength sensitive mechanism. The transformation of normal color mixture data resulted in two fundamentals which gave a reasonable prediction of the tritanopic coefficients. The dichromatic *HFP* data corrected individually to average macular pigment agreed with their respective fundamental above 430 nm. The *HFP* data and transformation were converted to a retinal level, quantized and plotted as a function of wavenumber. For the middle-wavelength-sensitive mechanism, the protanopic *HFP* data and its König-type fundamental agreed with the predicted absorption spectrum above 460 nm. The deviations below 460 nm had the shape of the lens absorbance curve. For the long-wavelength sensitive mechanism, the deuteranopic data and its König-type fundamental agreed with the predicted absorption spectrum above 520 nm. The deviations below 520 nm could not be fit solely by the lens absorbance factor used above, but needed in addition, added macular pigment of optical density at 460 nm of *ca.* 0·12. This result was checked by calculating predicted tritanopic coefficients for the two predicted absorption spectra, when the long-wavelength sensitive spectrum was screened by a slight amount (o.d. of 0·12 at 460 nm) of macular pigment. These predicted coefficients agreed with the Wright tritanopic coefficients. We conclude (a) that the shape of the iodopsin absorption spectrum provides a reasonable basis for computation of absorption spectra of the middle- and long-wavelength sensitive cone pigments and (b) that long-wavelength sensitive cones of deuteranopes, tritanopes, and normal trichromats are subject to a selective screening filter of optical density at 460 nm of 0·12 and spectral shape similar to macular pigment.

INTRODUCTION

In an earlier paper (Smith and Pokorny, 1972) we showed that the spectral sensitivities of protanopes and deuteranopes, which may be expressed as transformations of the CIE color mixture data, are similar in shape on their long-wavelength slope to measured isolated visual pigment absorption spectra. It is our purpose to extend this analysis to a consideration of the spectral sensitivity of protanopes and deuteranopes in the wavelength range 400–520 nm. The wavelength range 400–520 nm poses a number of problems.

(a) There is a problem in using protanopic and deuteranopic luminosities. The region 400–520 nm is a region where two photopigments are active. In this study we report protanopic and deuteranopic luminosity using heterochromatic flicker photometry on blue backgrounds at flicker rates above the fusion of the short-wave chromatic mechanism.

(b) There are experimental and theoretical problems with the color mixture data. The experimental problem concerns the exact nature of the color mixture data at short-wavelengths. The 1931 CIE color mixture data (Wyszecki and Stiles, 1967), the Stiles (1955, 1959) 2° data, and Sperling's (1958) data, when transformed into an equivalent primary system, differ in the amount of negative G primary needed at short-wavelengths. Stiles (1955) and Sperling (1958) have commented on the variability of matches at short-wavelengths.

The theoretical problem arises from the fact the 1931 CIE XYZ Standard Observer was set up with underestimated luminance below 460 nm. Hence both the color matching functions and the spectral coefficients are incorrect at short-wavelengths. Judd's (1951) modification involved adjusting the spectral coefficients over a wide spectral range in order to maintain standard source B at the same position in the W.D.W. coordinate system. This procedure does not guarantee the accuracy of the coefficients.

To counterbalance these problems with the color mixture data, we have available an additional tool in the tritanopic color matching characteristics. Since small field foveal color mixture functions of color normal observers (Willmer and Wright, 1945) closely resemble those of tritanopes (Wright, 1952), we assume that tritanopia is a dichromatic reduction form of nor-

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mal trichromacy. Any sensitivity curves we propose for the middle- and long-wavelength sensitive receptors should thus be able to predict the tritanopic spectral coefficients. However, if the CIE coefficients as modified by Judd (1951) are incorrect in the spectral region 400–460 nm, the locus of the tritanopic copunctal point will similarly be in error; transformations based on copunctal points may not be able to predict the Wright (1952) tritanopic coefficients although they will predict the tritanopic confusion wavelengths.

(c) Third, when adjusting the luminosity curves and their CIE transforms for comparison with pigment absorption curves, the corrections for the inert ocular pigments become crucial.

Wyszecki and Stiles (1967) have reviewed lens absorption data from the studies of Ludvigh and McCarthy (1938), Wald (1945), Wright (1951) and Weale (1954). They suggest a curve which may be used to correct spectral response functions to the retinal level. We might point out that only the Ludvigh and McCarthy (1938) tabulations represent the whole eye, the other measurements are for the lens. Boettner and Wolter (1962) and Tan (1971) have shown that the remaining ocular media may represent a 30–50 per cent transmission at 400 nm. The problem is further complicated by the possibility that the spectral transmission curve for the lens may itself be complex (Tan 1971). Three recent studies, Boettner and Wolter (1962), Coren and Girgus (1972), and Tan (1971), support the idea that Wyszecki and Stiles (1967) lens corrections at short-wavelengths (400–500 nm) are spectrally accurate for a young eye. The Boettner and Wolter (1962) study of transmission of ocular media gives a correction for a child's eye similar to the Wyszecki and Stiles correction. Coren and Girgus (1972) have published data showing the effect of age on color matches for 265 observers with an age range of 8–79 yr. Their analysis was based on the Said and Weale (1959) data for relative spectral transmittance. Coren and Girgus (1972) obtained a regression equation, relating lens density at 490 nm to age, which accounted for 83 per cent of the variability of their data. Based on their regression, we can calculate the Wyszecki and Stiles (1967) corrections at short-wavelengths to represent an eye of 15–16 yr. Tan (1971) demonstrated that for aphakic observers, the scotopic spectral sensitivity curve corrected to a retinal level followed the absorption spectrum of rhodopsin measured by Collins, Love and Morton (1952). Tan (1971) then measured scotopic sensitivity in normal observers and subtracted the rhodopsin absorption curve to derive correction factors for the optic media for 16 observers. His data suggest that the Wyszecki and Stiles (1967) corrections are for an eye under 10 years of age.

We have found it difficult to ascertain observer age in many published studies. Most authors used themselves, other laboratory personnel, and undergraduate or graduate students, i.e. an expected age range of 18 or older. It appears that Judd's (1951) modified observer represents an age of about 30–32 yr, which would entail increasing the Wyszecki and Stiles (1967) correction factors by about 1·33 using either the Coren and Girgus (1972) or Tan's (1971) results. For studies involving few observers, inter-individual lens pigmentation may be so great as to make any attempt to increase the Wyszecki and Stiles (1967) correction factor to their average age unsupportable. We have chosen the procedure of adjusting the psychophysical data with the Wyszecki and Stiles (1967) corrections. We then consider if the density difference between the corrected data and a proposed pigment sensitivity curve can be fit by the spectral transmission curve of the optic media adjusted to appropriate density.

Since the publication of Wyszecki and Stiles' (1967) corrections, there have been several new studies of macular pigment absorption (Grützner and Kohlrausch, 1961; Ruddock, 1963; Bone and Sparrock, 1971; Tan, 1971). An extensive review has been published by Vos (1972) who notes that the Wyszecki and Stiles (1967) weighted mean curve continues to provide a reasonable description of the spectral absorption characteristics of macular pigment. The shape of the Vos (1972) weighted mean curve deviates from the Wyszecki and Stiles (1967) tabulation in only minor ways, essentially involving a smoothing of the 490 nm subpeak.

Vos (1972) set the average macular pigment density at λ_{max} to 0·35 on theoretical grounds. However the majority of the studies have found values of 0·4–0·6. The largest data sample, that of Bone and Sparrock (1971), with 49 observers, shows average density at 460 nm of 0·53 with a standard deviation of 0·15–0·20. Thus 95 per cent confidence bounds for the mean of Bone and Sparrock's (1971) data give a value for the macular pigment at 460 nm of 0·53 o.d. $\pm$ 0·06. We have therefore again used the Wyszecki and Stiles (1967) tabulations as a correction factor for macular pigment, setting the average density at 460 nm at 0·53.

(d) Fourth, the concept of a visual pigment nomogram for retinal$_1$ based pigments was based on a comparison of difference spectra. However, as Dartnall (1962) points out, the absorption spectra of isolated pigments are generally similar in shape on the wavenumber axis. The main and *cis*-peaks are usually separated by about 9700 cm^{-1}; the ratio of the absorption minimum (α_{min}) between the *cis*- and main bands to the absorption maximum (α_{max}) of the main band has a limiting value of 0·2. To use pigment absorption data for comparison with psychophysical data at short wavelengths, we have to assume an optical density and calculate the appropriate absorption spectrum. As a first approximation, we have adjusted the Wald, Brown and Smith (1955) iodopsin spectrum to an optical density of 0·3 for comparison with protanopic data and 0·4 for comparison with deuteranopic data. These values of optical density for dichromats were obtained with the same experimental arrangement as for the present study (Smith and Pokorny, 1973).

(e) A fifth problem in the short-wavelength region arises from the possibility of fluorescence either in the

optic media or in the receptors themselves. Such fluorescence could give rise to heightened sensitivity curves which would deviate from a predicted absorption spectrum of the visual pigments. Tan (1971) has discussed the possible role of fluorescence for ultraviolet irradiation (λ:340 nm) in the optic media of aphakes. At 400 nm, according to the Boettner and Wolter (1962) figures on which Tan's calculations were based, the possible percentage of normally transmitted quanta that might arise from a fluorescent process is negligible.

Fluorescence of the lens however remains a problem due to the higher lens absorbance in the visible spectrum. According to Klang (1948) and Trendelenberg (1961), wavelengths up to 400–410 may excite fluorescence in adults (10–54 yr). Various estimates of the spectral distribution of fluorescent light include peaks at 420–430 nm (Le Grand, 1938, 1947) or at 500 nm (Brolin and Cederlund, 1958). Lens fluorescence exited by wavelengths 400–410 nm would not be expected to be a factor in the color mixture or the *HFP* data. As Tan (1971) points out, the secondary emitted quanta would not image focally in the test field but would be scattered in the retina acting as a veil of bluish–green light.

With regard to retinal fluorescence, Tan (1971) distinguishes between fluorescence of the retinal media and fluorescence of photopigments in the outer segments. Tan (1971) found no evidence that a fluorescent substance affected the scotopic spectral sensitivity of aphakes. At higher intensities a different picture emerged. Tan (1971) investigated isolated Π mechanisms in aphakes with high intensity backgrounds. The measurements were made 4–10 min following a 10^6 td white bleach. At the highest intensity of background (4·78–5·22 log td), Tan (1971) found that the Π_3, Π'_4, Π'_5 all showed heightened u.v. sensitivity about 10,000 cm^{-1} from their peak sensitivity. This u.v. sensitivity thus occurred near the predicted *cis*-peak for the appropriate pigments but showed much greater sensitivity than would be predicted from isolated absorption spectra. The high u.v. sensitivity may have resulted from a photosensitive photopigment intermediate or from u.v. excited fluorescence of a stable photoproduct built up by the preliminary white bleach or by the bleaching levels of the backgrounds. Tan's (1971) backgrounds would constitute a 80% steady state bleach according to published human cone pigment kinetics (Alpern, Maaseidvaag and Ohba, 1971). In the visible spectrum, Tan's (1971) measurements of the Π'_4 and Π'_5 mechanisms on aphakes deviate from corrected Stiles data only at wavelengths 400 nm and 410 nm. Thus, even if the heightened sensitivity were caused by a fluorescent stable photoproduct, we would not expect such a process to interfere with sensitivities derived for the visible spectrum from low luminance procedures.

In summary, lens and receptor fluorescence may affect spectral sensitivity. However the effect is confined to wavelengths 400–410 nm and is probably negligible.

TRANSFORMATIONS OF COLOR MIXTURE DATA OF NORMAL OBSERVERS

While many of the transforms using the protanopic and deuteranopic copunctal points used rather arbitrary means to arrive at the coefficient for the $\bar{z}_\lambda$, the Vos and Walraven (1971) approach represents an attempt at a transformation of the full spectrum. They used the dichromatic copunctal points for six of their unknowns; the last three were obtained by assuming that the luminosity function represented a linear sum of contributions from all three receptor mechanisms.

In Fig. 1, the upper portion shows their R and G functions corrected for lens and macular pigment (Wyszecki and Stiles, 1967) and plotted as log relative quantal sensitivity. The continuous lines are our proposed visual pigment absorption spectra based on the

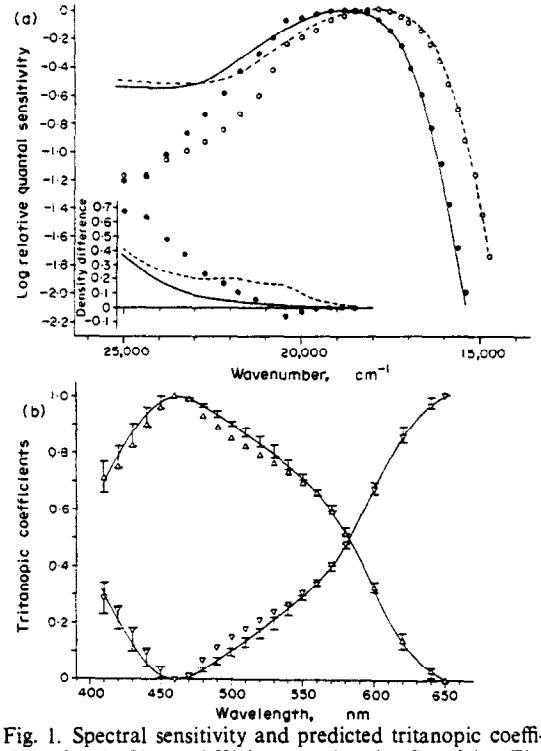

Fig. 1. Spectral sensitivity and predicted tritanopic coefficients for the Vos and Walraven primaries. Panel (a): The symbols show the relative sensitivity of the Vos and Walraven primaries corrected to a retinal level. The continuous and dashed lines represent the predicted visual pigment absorption coefficients based on the shape of the iodopsin spectrum (Wald, Brown and Smith, 1955) calculated for appropriate optical densities. The curves are slid on the horizontal axis to provide a good fit to the symbols on the long-wavelength slope. Inset is the density difference between the G and its predicted absorption coefficient. The solid line is a possible correction for added lens density, the dashed line a correction for increased macular pigment. See text for further explication. Symbols: Vos and Walraven G ●; Vos and Walraven R ○. Panel (b): The symbols show the predicted tritanopic coefficients calculated from the Vos and Walraven primaries. The solid lines are the average and the vertical bars the range of Wright's tritanopic observers. Symbols: r_λ ▽; g_λ △.

iodopsin absorption spectrum (Wald, Brown and Smith, 1955) adjusted to appropriate optical densities. They show no agreement with the Vos and Walraven (1971) functions below 500 nm. Inset is the density difference between the G function and its matching visual pigment spectrum. The solid line near the points shows a correction factor for the lens density for a 20–30-yr-old observer, the dotted line a correction for added macular pigment of 0·15 o.d. at 460 nm (i.e. the standard deviation of the Bone and Sparrock, 1971 data). It is clear that the deviations of the Vos and Walraven G function from the proposed visual pigment spectrum are not solely due to the inert ocular pigments. In the lower panel are shown the predicted tritanopic color matching characteristics calculated using the Vos and Walraven primaries. The solid line is the average of the Wright (1952) data, recalculated for 460 and 650 nm primaries and showing the range of his six observers. The Vos and Walraven (1971) primaries do not fit the Wright (1952) data. The deviations are greater than any of Wright's individual observers.

These data suggest a problem with the Vos and Walraven (1971) primaries. We can consider two possibilities: (a) The Vos and Walraven (1971) model is in error; (b) Judd's (1951) modification of the CIE is in error, in the luminosity curve and or in the coefficients. We turned first to the Vos and Walraven (1971) model: their R and G functions are accurate above 520 nm. Their choice of copunctal point for protanopes and deuteranopes gives a good empirical fit on the long-wavelength slopes of the dichromatic functions. The tritanopic copunctal point is empirically derived from the tritanopic coefficients, and would be in error only if the revised XYZ diagram is in error.

A possible source of error in their model is their description of luminance. They used a linear sum of contributions of the R, G and B functions. We should like to consider the possibility that the short-wavelength-sensitive pigment makes no contribution to the CIE V_λ function. This is not a new idea. Guth, Alexander, Chumbly, Gillman and Patterson (1968), for example have a model of color vision in which the CIE V_λ function is called an achromatic luminance function and receives no input from the short-wave sensitive pigment. Guth and Lodge's (1973) point that *HFP* should be regarded as "achromatic" as compared with, say, brightness matching is based on the fact that *HFP* is obtained above chromatic fusion. A similar argument may be applied to the short-wavelength mechanism, which is known to have a low fusion frequency. With isolated II mechanisms, Brindley, DuCroz and Rushton (1966) found a value of 18 Hz for two observers for the II_1 mechanism. Green (1969) has found values of 20–22 Hz for the high frequency end for two observers at a luminance estimated at 500 td for the II_1 mechanism. Since even low luminance flicker photometry may be performed at 12–16 Hz at short-wavelengths, it is entirely possible that *HFP* data are obtained above the fusion of the short-wavelength mechanism.

Table 1. Transformation with B on alychne

Copunctal points			
Tritanopic	$x_t = 0{\cdot}1748$		
	$y_t = 0$		
Deuteranopic	$x_d = 1{\cdot}40$		
	$y_d = -0{\cdot}40$		
Protanopic	$x_p = 0{\cdot}7465$		
	$y_p = 0{\cdot}2535$		
Luminance			
$SR_\lambda + SG_\lambda = Y_{i\lambda}$			
Solution equations			
$SR_\lambda =$	$+0{\cdot}15514\bar{x}_{i\lambda}$	$+0{\cdot}54312\bar{y}_{i\lambda}$	$-0{\cdot}03286\bar{z}_{i\lambda}$
$SG_\lambda =$	$-0{\cdot}15514\bar{x}_{i\lambda}$	$+0{\cdot}45684\bar{y}_{i\lambda}$	$+0{\cdot}03286\bar{z}_{i\lambda}$

We therefore calculated a set of receptor characteristics, based on a set of three copunctal points plus the proviso that the Y function represents the sum of the R and G functions. In this model, the protanopic and deuteranopic copunctal points were the same as used by Vos and Walraven (1971). The tritanopic copunctal point was set on the alychne, at $x_t = 0{\cdot}1748$. Table 1 shows the equations.

Figure 2 shows the tritanopic coefficients for the transformation. They are somewhat improved over the coefficients obtained from the Vos and Walraven (1971) model. However, coefficients for wavelengths 470, 490–520 nm still lie outside the range of Wright's (1952) observers. If we move the tritan copunctal point to $x_t = 0{\cdot}1739$, the fit improves somewhat. Of course with such a procedure, we are moving further from Thomson and Wright's (1953) empirically determined copunctal point. We think that these remaining discrepancies result from errors in Judd's (1951) revised XYZ diagram at short-wavelengths.

THE LUMINOSITY DATA

Since the attempt to derive visual pigment coefficients from the normal color mixture data was not

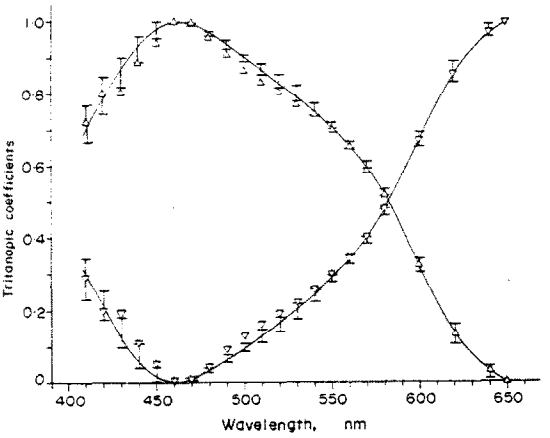

Fig. 2. Predicted tritanopic coefficients for the transformation given in Table 1. The meaning of the symbols, solid lines, and vertical bars are the same as in Fig. 1(b).

completely successful, our next step was to determine luminosities on dichromats using high intensity–high flicker rate *HFP* with blue backgrounds, a method previously used by Miller (1972) and Smith and Pokorny (1973), to reduce the sensitivity of the short-wavelength mechanism. It has become clear to us that the contributions of the various cone outputs to the achromatic system in *HFP* may vary as a function of luminance, flicker rate, and the standard wavelength. Some of our pilot data suggest that normal observers and protanopes show no difference in *HFP* obtained using high luminance–high frequency procedures which eliminate possible short-wavelength receptor response and low luminance–low frequency procedures which allow the possibility of short-wavelength receptor response. The deuteranopic data are equivocal. For the present study we wished to ensure that only one visual pigment could contribute to the dichromats' *HFP* thresholds.

Equipment

The equipment is that described briefly in a previous report (Smith and Pokorny, 1973). A two-channel system placed a 2 mm image of a 75W xenon source at the plane of the observer's pupil. The light from the source was collimated by a lens and then followed by a beam splitter. A variable speed single sector disc placed in the collimated beams allowed alternation of the two channels. In one channel (the variable field) the disc was followed by a lens which focused the image of the arc in the plane of a two log unit metallic neutral density wedge. Light was recollimated, passed through a field stop limiting the field of view to 2 and then focused on 2 mm artificial pupil. Light from the second channel (the standard field) remained collimated after passing the plane of the flicker disk until it was recombined with that of the first channel just before a field stop. Because one of the channels was inverted following the flicker disk, the replacement of one channel by the other was uniform, scanning from top to bottom. The neutral density wedge was driven by a gear motor and the output of a directly coupled potentiometer was read on a voltmeter. The wedge could be controlled by observer or experimenter. Fixed metallic neutral density filters were also used. Interference filters were used to control spectral composition. A series of 13 filters were used with nominal peaks at 400, 405, 410, 420, 436, 445, 453, 464, 480, 502, 540, 580 and 654 nm.

At 8 × 10 rectangular background field was provided by a third channel, using a tungsten iodide source and appropriate filters. A broad band filter (Kodak 47B) was used in the background to depress the short-wavelength sensitive mechanism.

Calibrations

The interference and N.D. fixed filters were calibrated using a Carey-14 recording densitometer. In addition, the neutral filters and the wedge were calibrated in position for each of the interference filters. For this task a United Detector Technology PIN 10 photodiode was used. Three short-wavelength filters 400, 410, and 420 were three-cavity filters (Ditric Optics) with half-band passes of 7–9 nm and visible side bands blocked to 10^{-6}. The remaining interference filters (Schott) had half-band-widths of 10–15 nm.

The relative spectral response of the PIN diode was calibrated by Optronics Laboratories. The calibrated diode was used to check the relative radiance through the interference filters on each experimental day.

An estimate of retinal illuminance was made placing an Ilford SEI exposure photometer in the plane of the artificial pupil for the standard field with the 578 interference filter. The obtained measurement of retinal illuminance was 800 td. The retinal illuminance of the background was ascertained first by establishing a *HFP* match for the 47B filter to the standard illuminance and then by direct homochromatic brightness matching of the variable field to the upper portion of the background. The retinal illuminance of the background was 500 td.

Subjects

The deuteranopes and protanopes were obtained as a result of advertising in the University of Chicago student newspaper. All were males. They ranged in age from 17–34 with an average age of 25. All observers were screened using AO HRR plates, Ishihara pseudoisochromatic plates, the Farnsworth Munsell 100-hue test, and the Nagel anomaloscope. Only those observers who could match in color and brightness both the red (670 nm) and the green (546 nm) to the yellow (589 nm) on the Nagel anomaloscope were accepted as dichromats. All observers had normal corrected acuity and used their customary refractive correction during the study.

Procedure

At the start of each session the observer adjusted the chin rest until his eye was centered on the artificial pupil. The observer then dark adapted for 5 min.

Heterochromatic flicker photometry was performed to a 540 nm standard for protanopes and to a 580 nm standard for deuteranopes. The test wavelengths were presented in random order once in each session. The observer adjusted the radiance of the variable test wavelength until there was a minimal or absent sensation of flicker. The experimenter then adjusted the radiance of the test wavelength in small steps around the observer's setting in order to establish a match range. The flicker rate (22–27 Hz) was adjusted to maintain the match range at 0·04 log unit of radiance.

After an initial practice session, the procedure was repeated on three separate sessions. The data reported are the average data for the three sessions.

Results

Figure 3 shows the log relative energy as a function of wavelength for four deuteranopes (lower panel), and five protanopes (upper panel). The solid lines show the relative sensitivities of the transformations given in Table 1. The deuteranopic points scatter widely across the predicted line. The protanopic points tend to lie above the prediction. Inset in each panel is the density difference between an *HFP* match at 540 nm and 464 nm at 0 and 9 , i.e.: an estimate of macular pigment density for each observer. The protanopes showed less variability in their macular pigment, a finding apparent also in Pitt's (1935) data. The estimated macular pigment density at 464 nm ranged from 0·136 to 0·85 in the deuteranopes and from 0·263 to 0·375 in the protanopes. The estimation may well be an underestimate since according to Polyak (1941) the

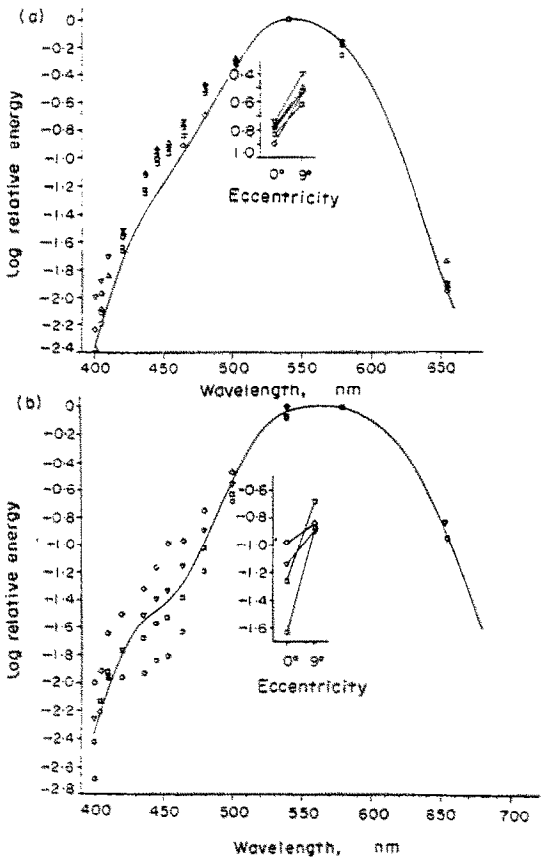

Fig. 3. Log relative energy as a function of wavelength for five protanopes performing heterochromatic flicker photometry to a 540 nm standard [panel (a)] and 4 deuteranopes [panel (b)] performing heterochromatic flicker photometry to a 580 nm standard. The solid lines are the relative sensitivities of the transformations given in Table 1. Inset in each panel is a comparison of the match of 540 nm to 464 nm made with foveal fixation and in the 9° vertical meridian. Symbols for panel (a): Protanopic observer RS ○; MS ▽; DP △; KA □; MG ◇. Symbols for panel (b): Deuteranopic observer MB ○; KG □; NH ▽; JC ◇.

macular pigment may extend to 17°. Further, the procedure implies unprovable (and improbable) assumptions of the identity of optical density, distribution, and sensitivity of the cones at the fovea and 9° vertical meridian. The same problems however are evident in all psychophysical techniques of estimating macular pigment. The measurement does provide us with a method of reducing observer variability due to interindividual variation in macular pigment density.

Figure 4 shows the data corrected for each observer to a macular pigment of d_{max} 0·53, using the Wyszecki and Stiles (1967) spectral correction. The solid lines are again the transformations shown in Fig. 3. They provide a reasonable description of the data except below 430 nm. For wavelengths below 430 nm. the data points tend to cluster above the predictions made by the transformations.

By definition, the transformations are part luminosities of the normal luminosity function. These part luminosities are, of course, determined by Judd's (1951) revised luminosity curve. The Judd (1951) revised luminosity curve fits normal *HFP* data well above 430 nm. The corrections made by Judd were based on the data of Wald (1945) (absolute threshold), Weaver (1949), Thompson (1949), and Ishak (1952) (brightness matching at short-wavelengths), and Gibson and Tyndall (1923) (extrapolation). We have noticed small but consistent deviations of the *HFP* data of Coblenz and Emerson (1917), Sperling (1958), and Wagner and Boynton (1972) from Judd's (1951) revised luminosity function at wavelengths below 430 nm. The Judd (1951) revised luminosity function underestimates *HFP* luminosity (average of studies cited above) at wavelengths 400–430 nm. the difference being 0·41 log unit at 400 nm, 0·29 at 410 nm, 0·20 at 420 nm and 0·15 at 430 nm.

Figure 5 shows the average of the dichromatic data plotted as log relative quantal sensitivity as a function

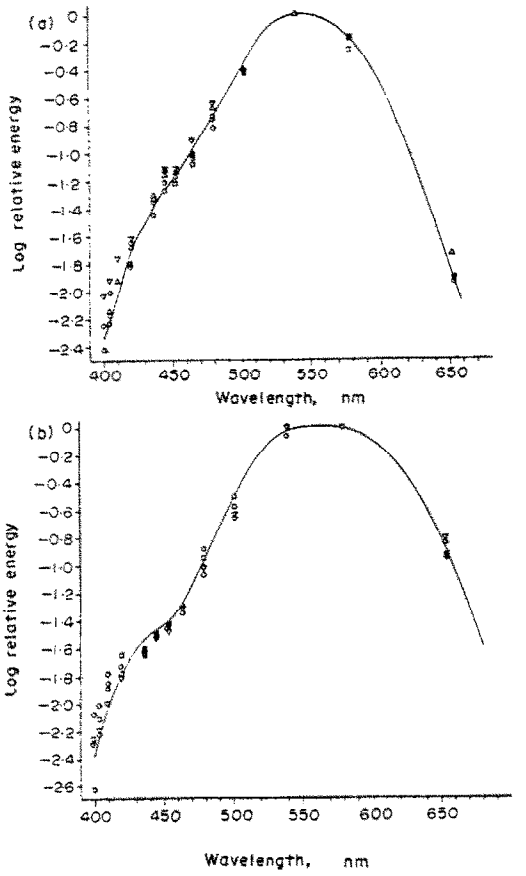

Fig. 4. The data of Fig. 3 corrected individually to have a macular pigment of density 0·53 at 460 nm. The solid lines and symbols are the same as for Fig. 3.

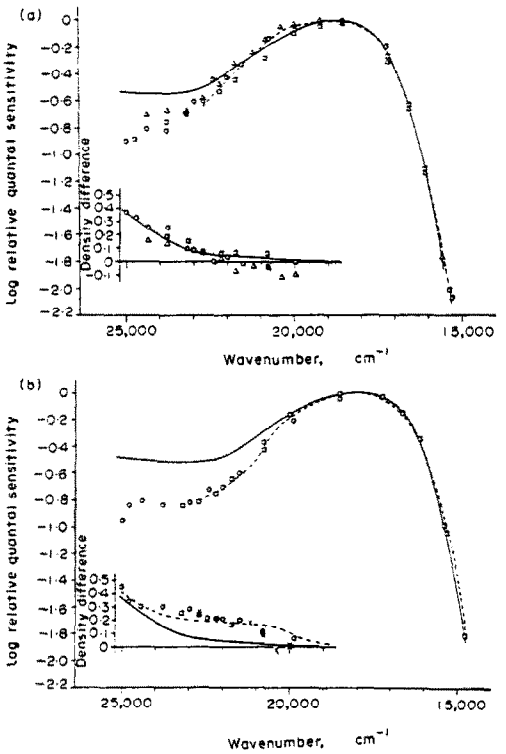

Fig. 5. Log relative quantal sensitivity as a function of wavenumber for protanopes [panel (a)] and deuteranopes [panel (b)]. The dashed lines show the relative sensitivities of the transformations of Table 1 corrected to a retinal level. The solid lines are the predicted visual pigment absorption coefficient as given in Fig. 1. The inset in each panel shows the difference of the psychophysical estimates from the predicted visual pigment absorption coefficient. The solid line in the insets is a factor for added lens density, the dashed line on the inset of panel (b) is a factor for added macular pigment. Symbols: average data of Pitt △; Hsia and Graham □; and the present study ○; all corrected to a retinal level. The crosses on the inset of panel (b) represent the difference between the transformation and its predicted visual pigment absorption coefficient.

of wavenumber. The data were corrected for an average lens and macular pigmentation (d_{max} of 0·53) as tabulated in Wyszecki and Stiles (1967). We have added two extra sets of dichromatic data: (a) Pitt's (1935) protanopic luminosity data were added since in our laboratory we can detect no difference in high and low frequency *HFP* functions for protanopes. (b) The Hsia and Graham (1957) absolute threshold data were added since Pokorny and Smith (1972) reported that using the Hsia and Graham (1957) procedure, absolute thresholds yielded identical results to *HFP* for dichromats,[2] although other procedures (Guth and Lodge, 1973) do not show this identity. The Ikeda (1963, 1964) data suggest that stimulus duration is the determining parameter. The data for the Hsia and Graham (1952, 1957) and Graham and Hsia (1969) procedure (4 msec stimulus flash) suggest that their absolute thresholds follow the absorption coefficient of the most sensitive of the visual pigments. For protanopes and deuteranopes their respective long-wavelength-sensitive pigments appear to be the most sensitive over the full wavelength range, and may thus be compared to the same pigments isolated in the achromatic system by high-flicker rate *HFP*.

The dashed lines show the relative sensitivity of the transformations of Table 1 corrected to a retinal level. The solid lines are the proposed visual pigment absorption spectra based on the shape of the iodopsin absorption spectrum (Wald, Brown and Smith, 1955) calculated for appropriate optical densities. The spectra are slid on the horizontal axis to provide a good fit to the data and transformations on the long-wavelength slope with the result that the spectrum compared with the protanopic functions has a λ_{max} *ca.* 532 nm and that compared with the deuteranopic functions has a λ_{max} *ca.* 555 nm. These estimates for λ_{max} are relative to the accuracy in λ_{max} of the iodopsin spectrum. The data points and the transformations fit the proposed visual pigment spectrum for wavelengths above 520 for deuteranopes and above 460 nm for the protanopes. There is a notch at 490 nm in the data, evident for both classes of observer, which may be an overcorrection of macular pigment at that wavelength (cf. Vos, 1972).

The deviations of the dichromatic data and functions from the proposed visual pigment spectrum become severe at short-wavelengths. Inset in the graphs are the density differences of the dichromatic data points from the proposed visual pigment spectrum. The solid line through these points is a correction of the lens density factor to 1·333 times the Wyszecki and Stiles (1967) tabulations. The solid line provides a good fit of the protanopic deviations, but not of the deuteranopic deviations. The dashed line on the deuteranopic inset which does provide a reasonable fit to the deuteranopic deviations is obtained by adding increased macular pigment of 0·12 optical density at 460 nm to the lens correction.

DISCUSSION

The results show that the dichromatic data and the transformation of the CIE data in the wavelength range 430–700 nm approximate the visual pigment absorption coefficient predicted from the iodopsin

[2] The Pokorny and Smith study allows a comparison of the three tasks (absolute thresholds, *HFP* to 580 nm and *HFP* to 3000°K) for five observers (two protanopes and three deuteranopes). The flicker rate below 500 nm was 10–12 Hz at 4·0 td. There was no difference in the thresholds as a function of method. The data are not replotted for reasons including: (a) we have no independent assessment of macular pigment and too few observers to justify averaging; (b) we could not measure sensitivities at wavelengths below 420 nm; (c) examination of the long-wavelength slope suggests that our calibration procedure was not as precise as that used for this study.

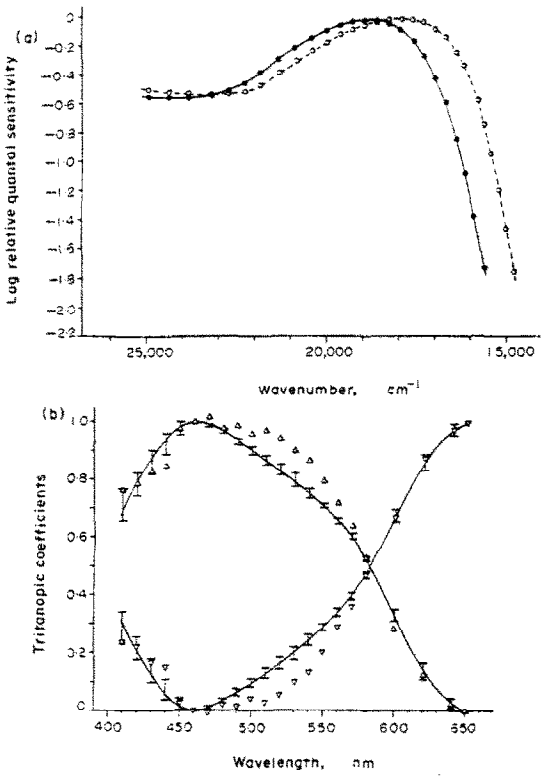

Fig. 6. Panel (a) Log relative quantal sensitivity of the proposed human visual photopigments. The symbols and lines correspond to the continuous lines of Fig. 5. Symbols: Middle-wavelength sensitive ○; long-wavelength sensitive ●. Panel (b) Tritanopic coefficients predicted by the pigment absorption spectra of panel (a). The symbols are the same as those in Fig. 1(b).

absorption spectrum (at appropriate optical density) provided the lens correction factor is increased by *ca.* 1·333 and that a differential macular pigment correction is applied to the middle- and long-wavelength sensitive mechanisms. There is no indication that fluorescence of the optic media or retina has contributed to the measured sensitivities. The data do not show any heightened sensitivity that might be caused by fluorescence.

The added optic media correction factor is that predicted by Coren and Girgus (1972) for 30-yr-olds and agrees with Tan's (1971) data for the age group 20–29. Although such a correction is necessarily *ad hoc*, it is a reasonable correction, given our knowledge of the absorption in the ocular media.

The macular pigment correction presents a different problem: it appears that the deuteranopes have slightly greater average macular pigment. The same result occurs in the transformation of the revised CIE color mixture data, a result which preserves the integrity of the copunctal points. The long-wavelength sensitive cones of normal trichromats are apparently subject to a slightly higher macular pigment than the middle-wavelength sensitive cones. Further, the macular pigment density difference for the two photo-pigments is also true of the tritanope. Figure 6 shows the proposed visual pigment absorption spectra and their predicted tritanopic coefficients without a differential macular pigment correction. It is clear that these coefficients are completely incorrect, the pair of pigments lie too close together to predict the tritanopic coefficients. The next step is to add a small amount (d_{max} of 0·12) of macular pigment to the long-wavelength pigment. The result of this procedure is shown in Fig. 7. The predicted tritanopic coefficients now provide a good fit to the Wright (1952) tritanopic coefficients. The coefficients at 520 nm were checked at a number of values of d_{max} of added macular pigment at 460 nm. The predictions fall within Wright's (1952) observers provided the density of macular pigment added to the long-wavelength sensitive pigment has optical density at 460 nm between 0·09 and 0·16.

We thus conclude that the iodopsin spectrum when adjusted to appropriate density and slid on the wavenumber axis can provide a reasonable description of the visual pigment absorption spectra of the middle- and long-wavelength sensitive foveal cones although we expect minor deviations at the short-wavelengths. Further, we come to the conclusion that we must allow different amounts of macular pigment for the two

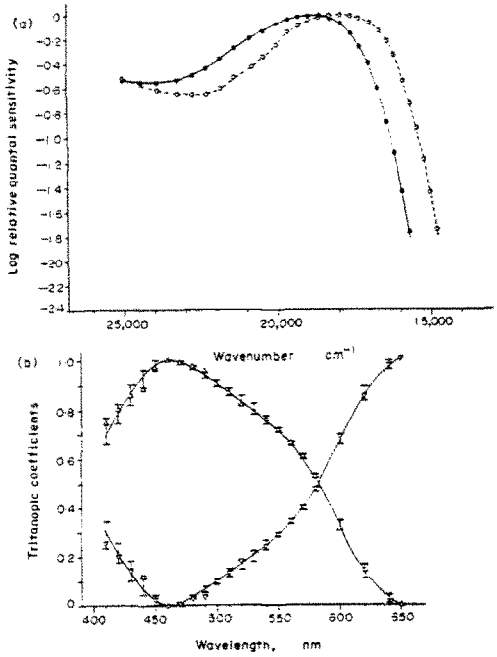

Fig. 7. The effect of adding a selective filter to the proposed long-wavelength sensitive pigment. Panel (a) Pigment absorption curves of Fig. 6 with a macular pigment filter of o.d. 0·12 at 460 nm screening the long-wavelength sensitive photopigment. Panel (b) Tritanopic coefficients predicted by the spectral sensitivities shown in Panel (a). The symbols are the same as those in Fig. 1(b).

classes of cones: namely, maximal optical density of about 0·5 for middle-wavelength sensitive and 0·62 for long-wavelength sensitive cones. This suggestion is not contradicted by the available psychophysical measurements on normal macular pigment, since the predicted apparent average macular pigment density in normals given d_{max} of 0·5 for middle- and 0·62 for long-wavelength sensitive cones would be about 0·57 at 460 nm. However, since the macular pigment is described as lying around the fibers of Henle (Segal, 1950), primarily in the outer plexiform layers (Gass, 1973), or through layers 4–9 of the retina (Polyak, 1941), the assumption of differential pigment density affecting the two classes of cones is somewhat puzzling. A number of alternatives may be considered.

(a) A larger differential optical density of the two photopigments: In order to fit the deutan data to a hypothetical pigment absorption curve, we would need to compute it for dilute optical density. This possibility is contradicted by the results of Miller (1972) and ourselves (Smith and Pokorny, 1973) who find the long-wavelength sensitive pigment to be in density 0·4–0·55. Further, our calculations of predicted tritanopic coefficients based on a larger optical density differential between the two pigments do not fit the Wright (1952) tritanopic data below 440 nm.

(b) Two pigments in long-wavelength sensitive cones: Two pigments each absorbing quanta should look like a pigment with apparently greater sensitivity than the proposed absorption spectrum. We are concerned with a sensitivity which lies below the proposed absorption spectrum.

(c) Intrusion of the short-wavelength mechanism by inhibitory interaction with the long-wavelength mechanism. Such a hypothesis requires that some proportion of normal short-wavelength sensitive receptors exist whose output consists of an inhibitory linkage to the long wavelength sensitive receptors. These short-wavelength sensitive receptors would also be postulated for tritanopia—a possibility since there is no conclusive evidence that tritanopia is a pigment defect. However, our calculations show that predicted tritanopic coefficients for such a system do not agree with Wrights (1952) tritanopic data.

(d) A stable photoproduct of the long-wavelength sensitive pigment acting as a screening pigment: This notion was suggested by Dartnall (1962) for the case of indicator yellow as a screening pigment for rhodopsin. The concept was carefully examined by Goldstein and Williams (1966) who concluded that the low optical densities in human rods and cones preclude stable photoproducts from acting as effective screening pigments. They worked however with Rushton's (1956) value of 0·15 optical density for rods. We allow higher optical densities of 0·3–0·4. Even so, a substantial bleach (probably 50 per cent) would be required to build up an appropriate density of any hypothetical screening photoproduct for long-wavelength sensitive cones, even given optimal conditions for such build-up. Our analysis indicates that the selective filtering of the long-wavelength sensitive cones occurs at luminances ranging from absolute foveal threshold to 800 td.

(e) A substance of spectral shape similar to the macular pigment which is present in the structure of the cones and may occur in both peripheral and foveal cones: The relatively higher density of such a substance in the long-wavelength sensitive cones may reflect a greater length of the outer segment, a result which we might expect based on the higher density of the long-wavelength sensitive cones found by Miller (1972) and Smith and Pokorny (1973). In their estimation of the optical density of human cones, Dobelle, Marks and MacNichol (1969) imply that the optical density will be proportional to the length of the outer segment.

(f) There is the possibility of error in the Wald, Brown and Smith (1955) measurements. At 500 nm the percentage extinction for iodopsin is 50 per cent and we would need to invoke a 10 per cent error in Wald, Brown and Smith's (1955) spectrum. The two estimates using independent techniques made by Wald, Brown and Smith (1955) of iodopsin absorption at 500 nm differed by only 2 per cent.

(g) A remaining alternative would be to state that the deuteranopic curve is the true absorption curve and that the protanopic curve results from a summation such as mentioned in (b) above. Such a hypothesis predicts incorrect tritanopic coefficients. Further we would need to accept that the similarity in shape of the protanopic functions to the iodopsin spectrum is coincidence. We prefer to think that the shape similarities found between the visual pigments of many species in the animal kingdom does extend to the human cone photopigments.

Of these alternatives, the most likely seems to be (d) and (e), which of course are essentially *ad hoc* explanations. Thus we come to the conclusion that our analysis requires a selective screening of long-wavelength sensitive comes by a filter whose spectral transmission is similar or identical to macular pigment. Guild (1931), Wright (1928) and Stiles (1955) found considerable variability in the color matches of normal trichromats for the spectral region 470–500 nm. Wright (1928) points out the different color matches exceed observational error and may indeed reflect receptor differences. From our point of view such variability might reflect variation in differential density of the screening pigment. Further, it appears that the human cone visual pigments are closely similar in shape to the Wald. Brown and Smith (1955) measured absorption spectrum for iodopsin. However we would not be surprised by minor deviations in the spectral region 400–450 nm, the region of greatest uncertainty in both Wald, Brown and Smith's (1955) data and the psychophysics. We conclude that the shape of the iodopsin absorption spectrum provides a basis for calculation of absorption spectra for the middle- and long-wavelength sensitive human cone photopigments.

REFERENCES

Alpern M., Maaseidvaag F. and Ohba N. (1971) The kinetics of cone visual pigments in man. *Vision Res.* **11**, 539–549.

Boettner E. A. and Wolter J. R. (1962) Transmission of the ocular media. *Invest. Ophthal.* **1**, 776–783.

Bone R. A. and Sparrock J. M. B. (1971) Comparison of macular pigment densities in human eyes. *Vision Res.* **11**, 1057–1064.

Brindley G. S., Du Croz J. J. and Rushton W. A. H. (1966) The flicker fusion frequency of the blue-sensitive mechanism of colour vision. *J. Physiol. Lond.* **183**, 497–500.

Brolin S. E. and Cederlund C. (1958) The fluorescence of the lens of the eyes of different species. *Acta ophthal.* **36**, 324–328.

Coblentz W. W. and Emerson W. B. (1918) Relative sensibility of the average eye to light of different colors and some practical applications to radiation problems. *Bull. natn. Bur. Standards* **14**, 167–236.

Collins F. D., Love R. M. and Morton R. A. (1952) Studies in rhodopsin—IV: Preparation of rhodopsin. *Biochem. J.* **51**, 292–298.

Coren S. and Girgus J. S. (1972). Density of human lens pigmentation: *in vivo* measures over an extended age range. *Vision Res.* **12**, 343–346.

Dartnall H. J. A. (1962) The photobiology of Visual Processes. In *The Eye* (edited by Davson H.), Vol. II, pp. 321–533. Academic Press, New York.

Dobelle W. H., Marks W. B. and MacNichol E. F. (1969) Visual pigment density in single primate foveal cones. *Science, N.Y.* **166**, 1508–1510.

Gass J. D. M. (1973) Nicotinic acid maculopathy. *Am. J. Ophthal.* **76**, 500–510.

Gibson K. S. and Tyndall E. P. T. (1923) Visibility of radiant energy. *Scient. Pap. Bur. Stand.* **475**, 131–191.

Goldstein E. B. and Williams T. P. (1966) Calculated effects of "screening pigments". *Vision Res.* **6**, 39–50.

Graham C. H. and Hsia Y. (1969) Saturation and the foveal achromatic interval. *J. opt. Soc. Am.* **59**, 993–997.

Green D. G. (1969) Sinusoidal flicker characteristics of the color-sensitive mechanisms of the eye. *Vision Res.* **9**, 591–601.

Grützner P. and Kohlrausch A. (1961) Der lichtverlust in der macula lutea und das farbensehen von deuteranomalen. *Pflügers Arch. ges. Physiol.* **274**, 318–330.

Guild J. (1931) The colorimetric properties of the spectrum. *Phil. Trans. R. Soc. A* **230**, 149–187.

Guth S. L., Alexander J. V., Chumbly J. I., Gillman C. B. and Patterson M. M. (1968) Factors affecting luminance additivity at threshold among normal and color-blind subjects and elaborations of a trichromatic-opponent colors theory. *Vision Res.* **8**, 913–928.

Guth S. L. and Lodge H. R. (1973) Heterochromatic additivity, foveal spectral sensitivity and a new color model. *J. opt. Soc. Am.* **63**, 450–462.

Hsia Y. and Graham C. H. (1952) Spectral sensitivity of the cones in the dark adapted human eye. *Proc. natn. Acad. Sci.* **38**, 80–85.

Hsia Y. and Graham C. H. (1957) Spectral luminosity curves for protanopic, deuteranopic and normal subjects. *Proc. natn. Acad. Sci.* **43**, 1011–1019.

Ikeda M. (1963) Study of interrelations between mechanisms at threshold. *J. opt. Soc. Am.* **53**, 1305–1313.

Ikeda M. (1964) Further use of the summation index for the study of color vision. *J. opt. Soc. Am.* **54**, 89–94.

Ishak I. G. H. (1952) The photopic luminosity curve for a group of fifteen Egyptian trichromats. *J. opt. Soc. Am.* **42**, 529–539.

Judd D. B. (1951) Secr. Rep. Colorimetry and artificial daylight. In *Proc. 12th Session CIE*: Stockholm. Vol. I. Techn. Comm., No. 7.

Klang G. (1948) Measurements and studies of the fluorescence of the human lens *in vivo*. *Acta ophthal. Suppl.* **31**, 1–152.

Le Grand Y. (1938) Sur la fluorescence du cristallin. *C.r. Acad. Sci.* **207**, 1128–1130.

L. Grand Y. (1947) Nouvelles recherches sur la fluorescence du cristallin. *C.r. Acad. Sci.* **225**, 1031–1032.

Ludvigh E. and McCarthy E. F. (1938) Absorption of visible light by refractive media of the human eye. *Archs. Ophthal.* **20**, 37–51.

Miller S. S. (1972) Psychophysical estimates of visual pigment densities in red–green dichromats. *J. Physiol., Lond.* **223**, 89–107.

Pitt F. H. G. (1935) Characteristics of dichromatic vision, with an appendix on anomalous trichromatic vision. *Spec. Rep. med. Res. Council* **200**, 1–58.

Pokorny J. and Smith V. C. (1972) Luminosity and CFF in oenteranopes and protanopes. *J. opt. Soc. Am.* **62**, 111–117.

Polyak S. L. (1941) *The Retina*. University of Chicago.

Ruddock K. H. (1963) Evidence for macular pigmentation from colour matching data. *Vision Res.* **3**, 417–429.

Rushton W. A. H. (1956) The Rhodopsin density in the human rods. *J. Physiol., Lond.* **134**, 30–46.

Said F. S. and Weale R. A. (1959) The variation with age of the spectral transmissivity of the living human crystalline lens. *Gerontologia* **3**, 213–231.

Segal J. (1950) Localisation du pigment maculaire de la rétine. *C.r. séanc. Soc. Biol.* **144**, Pt. 2, 1630–1631.

Smith V. C. and Pokorny J. (1972) Spectral sensitivity of color-blind observers and the cone photopigments. *Vision Res.* **12**, 2059–2071.

Smith V. C. and Pokorny J. (1973) Psychophysical estimates of optical density in human cones. *Vision Res.* **13**, 1199–1202.

Sperling H. G. (1958) An experimental investigation of the relationship between colour mixture and luminous efficiency. In *Proc. 8th NPL Problems of Color*. (Symposium held at the National Physical Laboratory, September 1957) pp. 251–279. Her Majesty's Stationery Office, London.

Stiles W. S. (1955) Interim report to the commission internationale de l'éclairage, Zurich, 1955, on the National Physical Laboratory's investigation of colour-matching (1955), with an appendix by W. S. Stiles and J. M. Burch. *Optica Acta* **2**, 168–181.

Stiles W. S. and Burch J. M. (1959) N.P.L. colour-matching investigation: final report (1958). *Optica Acta* **6**, 1–26.

Tan K. E. W. P. (1971) Vision in the ultraviolet. Doctoral thesis, Utrecht.

Thomson L. C. (1949) Shape irregularities in the equal energy luminosity curve. *Proc. Phys. Soc., Lond.* **B62**, 787–792.

Thomson L. C. and Wright W. D. (1953) The convergence of the tritanopic confusion loci and the derivation of the fundamental response functions. *J. opt. Soc. Am.* **43**, 890–894.

Trendelenberg W. E. T. (1961) *Der Gesichtsinn. Grundzüge der physiologischen optik, 2nd Edition* (edited by Monje M., Schmidt I. and Schütz E.), pp. 67–69. Springer-Verlag, Berlin.

Vos J. J. (1972) Literature review of human macular absorption in the visible and its consequences for the cone receptor primaries. *Inst. Percept.* RVO-TNO Report No. 12F 1972-17. Soesterberg.

Vos J. J. and Walraven P. L. (1971) On the derivation of the foveal receptor primaries. *Vision Res.* **11**, 799–818.

Wagner G. and Boynton R. M. (1972) Comparison of four methods of heterochromatic photometry. *J. opt. Soc. Am.* **62**, 1508–1515.

Wald G. (1945) Human vision and the spectrum. *Science, N.Y.* **101**, 653–658.

Wald G., Brown P. K. and Smith P. H. (1955) Iodopsin. *J. gen. Physiol.* **38**, 623–681.

Weale R. A. (1954) Light absorption by the lens of the human eye. *Optica Acta* **1**, 107–110.

Weaver K. S. (1949) A provisional standard observer for low level photometry. *J. opt. Soc. Am.* **39**, 278–291.

Willmer E. N. and Wright W. D. (1945) Colour sensitivity of the fovea centralis. *Nature, Lond.* **156**, 119–121.

Wright W. D. (1929) A re-determination of the trichromatic coefficients of the spectral colours. *Trans. opt. Soc. U.K.* **30**, 141–164.

Wright W. D. (1951) The visual sensitivity of normal and aphakic observers in the ultra-violet. *Ann. Psychol.* **50**, 169–177.

Wright W. D. (1952) The characteristics of tritanopia. *J. opt. Soc. Am.* **42**, 509–521.

Wyszecki G. and Stiles W. S. (1967) *Color Science: Concepts and Methods, Quantitative Data and Formulas.* John Wiley, New York.