SPECTRAL SENSITIVITY OF COLOR-BLIND OBSERVERS AND THE CONE PHOTOPIGMENTS

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INTRODUCTION

One of the most powerful tools in the analysis of human color vision is the data obtained from color mixture experiments. The requirements of a color match are that the quantal catch for each pigment be identical for both sides of the match. Thus color mixture data must be linear transforms of the absorption curves of the visual pigments. However, hypothesized visual pigments conforming to Dartnall's standard shape for visual pigments cannot be expressed as transformations of the CIE color mixture data (Brindley, 1960; Le Grand, 1969).

Further, many estimates of the chromatic receptor mechanisms, independent of the color mixture data, do not conform to the standard shape proposed by Dartnall. For example, Dartnall (1962) has remarked that the action spectra of pigments measured from protanopic and deuteranopic eyes by reflection densitometry (Rushton, 1963a, 1965), are both too narrow to fit the standard shape. Stiles (1959) has demonstrated that the rhodopsin absorption curve fits the Stiles' $n_1$ mechanism. The $n_1$ mechanism also provides a good fit to the short-wave cone mechanism observed in blue monocone monochromats (Alpern, Lee and Spivey, 1965). Stiles (1959) found that the rhodopsin absorption curve gave an adequate fit to the $n_4$ mechanism, although small but systematic deviations of the $n_4$ function from the rhodopsin absorption curve are evident in the data. The $n_5$ mechanism does not fit a rhodopsin absorption curve, showing large deviations on the long-wavelength side of the maximum. Stiles (1959) recognized that the $n_5$ mechanism did not represent the sensitivity of a single rhodopsin-type pigment or a simple mixture of two rhodopsin-type pigments. Inglis (1969) has also noted that the rhodopsin absorption curve fits the $n_5$ function better than the $n_4$ and $n_5$ functions.

Boynton (1963) has compared the $n_4$ and $n_5$ mechanisms with data from protanopes and deuteranopes, using his own (Boynton, Kandel and Onley, 1959), and Hsia and Graham's (1957) data. He found that the protanopic sensitivity curve was narrower than the Stiles $n_4$ mechanism. The major deviations were on the long-wavelength side of the maximum. The deuteranopic sensitivity curve fitted the Stiles $n_5$ mechanism on its long-wavelength side, but deviated on the short-wavelength side of its maximum. Boynton (1963) concluded that neither $n_4$ nor $n_5$ represented a pigment absorption curve. The analysis also suggests that the protanopic and deuteranopic sensitivity curves would not fit Dartnall's standard shape for visual pigments.

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2 Although direct measurements of the absorption spectra of single human cones have been made (Marks, Dobelle and McNichol, 1964; Brown and Wald, 1964), the precision of the measurements does not allow for an unequivocal statement concerning the applicability of Dartnall's standard shape.
WILLMER (1955) has made a direct comparison of the rhodopsin absorption curve to protanopic and deuteranopic absolute sensitivity. His data showed a good fit of the rhodopsin absorption curve to protanopic sensitivity. The deuteranopes' sensitivity lay below the rhodopsin absorption curve at wavelengths longer than 660 nm with a maximum deviation of 0.4 log unit, at 700 nm. The protanopic and deuteranopic sensitivities proved a better fit to the rhodopsin absorption curve than we would expect based on BOYNTON'S (1963) analysis. We therefore compared luminosity data of protanopes and deuteranopes from a number of investigators. We found that, while the data of PIT (1935), HECII and HSIA (1947), HSIA and GRAHAM (1957), and ALPERN and TORII (1968a, b) all agree as to the shape of the relative sensitivity functions for protanopes and deuteranopes, Willmer's data for both protanopes and deuteranopes were more sensitive than those shown by the other authors for wavelengths longer than 580 nm. Willmer's data thus do not agree in shape with other acceptable estimates of protanopic and deuteranopic luminosity.

These psychophysical data suggest that the standard shape of a visual pigment absorption coefficient proposed by Dartnall for retinal1 pigments is inapplicable to the middle- and long-wavelength sensitive human cones. The standard shape, however, has been a valuable tool in its own right in visual pigment research. DARTNALL (1953) proposed it when he noted that the positive portion of (hydroxylamine) difference spectra of many visual pigments superimposed when plotted relative to their $\lambda_{max}$ on a wavenumber axis. In 1967, a standard shape for visual pigments based on retinal2 was developed independently by Munz and Schwanzara (1967) and Bridges (1967a). Although there have been theoretical treatments of the long-wavelength slope (e.g. Lewis, 1955), there is no general explanation of either of the proposed standard shapes. Both have been successful in fitting difference spectra of many extracted visual pigments.

The concept of a standard shape for visual pigments used together with color mixture data would be of considerable strength when applied to the theory of normal and anomalous human color vision. The purpose of this paper is to consider the evidence that the best estimates of the human cone receptor mechanisms are also estimates of pigment absorption curves.

**BASIS OF COMPARISON BETWEEN NOMOGRAM AND SPECTRAL SENSITIVITY—CHOICE OF DATA**

DARTNALL and Goodeve (1937) have elucidated the conditions under which valid comparisons may be made between a psychophysical spectral sensitivity curve and a visual pigment absorption spectrum. These are:

1. The relative sensitivity of the psychophysical data should be calculated for an equal quantum spectrum.

2. Corrections must be made for the selective filtering of the ocular media. The estimates of average densities of human lens and macular pigment necessary for such corrections are available in Wyszecki and Stiles (1967).

3. Only one visual pigment can be active to contribute to the sensitivity curve. This condition can be fulfilled for the human chromatic mechanisms provided data within a narrow wavelength range from certain types of color-blind observers are used.

**Short-wavelength sensitive mechanism**

The narrow high intensity spectral sensitivity function of the blue monocone monochromat peaks at 440 nm (Blackwell and Blackwell, 1961; Grützner, 1964; Pokorny,
Spectral Sensitivity of Color-blind Observers

Smith and Swartley, 1970). It has the same spectral shape and sensitivity as the \( \pi_1 \) mechanism (Alpern, Lee and Spivey, 1965), and may be assumed to represent the short-wave sensitive response of normal observers between 400 and 500 nm after appropriate corrections are made for lens and macular pigmentation.

**Middle- and long-wavelength sensitive mechanism**

The spectral sensitivity functions of protanopes and deuteranopes in the wavelength range 500–700 nm may each be assumed to represent the response of a single class of cones. The contribution of the short-wavelength sensitive mechanism is small if present and confined to wavelengths below 500 nm (De Vries, 1948). Retinal densitometry (Rushton, 1963a, 1965) has demonstrated that partial bleaching does not change the difference spectrum of the single pigment observed in a propanopic or deuteranopic eye. Mitchell and Rushton (1971a, b) have demonstrated that the same pigment (which they call chlorolabe) is present in normal and propanopic eyes, and another pigment (which they call erythrolabe) is present in normal and deuteranopic eyes. Their estimates of the spectral sensitivities of these pigments fit Pitt’s (1935) measurements of protanopic and deuteranopic luminosity. Although there is still question concerning a possible sensitivity loss in all deuteranopes, most deuteranopes do show a loss for wavelengths below 580 nm relative to normals. This loss occurs both for threshold and for above threshold measurements of luminosity (Pokorny and Smith, 1972).

(4) Under conditions 1–3, the spectral sensitivity curve may be compared to the function giving the spectral variation of light absorbed by the visual pigment in situ (Dartnall, 1953). Dartnall (1961) has shown that density spectra obtained from suspensions of outer segments are practically identical to density spectra obtained in solutions. He concluded that it is correct to compare appropriately corrected psychophysical data with absorption spectra of visual pigments with one proviso. In the retina, where the cells are aligned on the optic axis, the effective optical density may be 50 per cent higher than when they are oriented at random in a suspension. This difference, however, is a quantitative one which may be treated by determining the absorption spectrum which best fits the psychophysical data. The absorption spectrum is related to the density spectrum by the equation:

\[
\frac{I_{\text{abs}}}{I_{\text{inc}}} = 1 - 10^{-D\lambda}.
\]

When \( D\lambda \) is small (\(<0.1\)), the difference between the absorption and density spectra is small. The psychophysical spectral sensitivity curve may be compared to the extinction curve for the pigment. If \( D\lambda > 0.1 \), then an appropriate absorption curve may be prepared using the equation above.

In application to human cones, the question of density is unresolved. Microspectrophotometry (Brown and Wald, 1964; Marks, Dobelle and MacNichol, 1964) and retinal densitometry (Rushton, 1963b) give low estimates of density for the cone pigment. Neither type of experiment indicates a differential density in the middle- and long-wavelength sensitive cones. However, the concept of high pigment densities (O.D. > 0.5) in the long-wavelength sensitive cones was invoked by Brindley (1953) to explain the break-down in normal color matches following bleaching adaptations. Brindley (1955) calculated that the pigment concentration in normal long-wavelength sensitive cones must be greater than 0.5 for his observers.

Inglis (1969) has questioned Brindley’s hypothesis, summarizing the evidence that pigment concentration is similar in the middle- and long-wavelength sensitive cones.
MITCHELL and RUSHTON (1971a) have recently shown that the protanopic luminosity function measured by brightness matching is identical at 200 td and 40,000 td, a level calculated to bleach 50 per cent of the pigment. A high pigment concentration in the cones demands a broader shoulder in the 200 td than in the 40,000 td brightness matching data. DARTNALL (1967) demonstrated this fact in his interpretation of the dark- and light-adapted ERGs of the green rods of frogs (DONNER and REUTER, 1962) which have an O.D. of 0.7. We conclude that these data indicate a density of pigment in the middle- and long-wavelength sensitive cones < 0.5.

COMPARISON OF SPECTRAL SENSITIVITY AND DARTNALL'S STANDARD SHAPE FOR VISUAL PIGMENTS

The data points of Fig. 1 are the spectral response of the short-wavelength mechanism for an equal quantum spectrum. Three sets of data are shown: brightness matches made by a blue monocone monochromat with a 1° field (BLACKWELL and BLACKWELL, 1961), increment thresholds made by a blue monocone monochromat with a 12' field (POKORNY, SMITH and SWARTLEY, 1970), and measurements of the $\pi_1$ mechanism (400–500 nm) of four normal observers made by STILES (1953, 1959 as tabulated in WYSZECKI and STILES, 1967). All the data were calculated in terms of an equal quantum spectrum, corrected for an average density of lens and macular pigment (as tabulated in WYSZECKI and STILES, 1967), and plotted as a function of wavenumber (cm$^{-1}$). The solid line follows the absorption coefficient for the standard shape of a visual pigment defined by Dartnall for the retinal pigments (tabulated in WYSZECKI and STILES, 1967). When its peak is placed at a wavenumber of 23,180 cm$^{-1}$ (corresponding to 431.4 nm), the standard shape provides an adequate fit to the three sets of data points, particularly in view of the uncertainties sur-

Fig. 1. Log relative quantal sensitivity as a function of wavenumber for blue monocone monochromats. Also shown is the Stiles $\pi_1$ mechanism. All data have been scaled to unit sensitivity at their maxima. The solid line is Dartnall's standard shape for visual pigments, plotted in terms of the absorption coefficient, $\log (a/\lambda_{\max})$, with $1/\lambda_{\max}$ placed at 23,180 cm$^{-1}$ (431.4 nm). Top abscissa shows corresponding wavelength scale.
rounding the correction for macular pigment. The curve shown in Fig. 1 is for pigment in dilute solution. Percentage absorption curves for O.D.s of 0.05, 0.10, 0.20, 0.50, 0.75 and 1.00 were also calculated. The variability of the psychophysical data preclude the possibility of finding a best-fitting absorption curve. All absorption curves with O.D.s up to 0.5 are acceptable fits with the $\lambda_{\text{max}}$ for the best fit moving to shorter wavelengths as O.D. is increased.

The data points of Fig. 2 are the equal quantum spectral sensitivities of protanopes and deuteranopes in the wavelength range 500–700 nm. The data points are those obtained at absolute threshold for a 42', 4-msec flash by HSIA and GRAHAM (1957) and by color mixture and heterochromatic flicker photometry for a 2° field by PITT (1935, data tabulated in WYSZECKI and STILES, 1967). All data points were corrected for an average lens and macular pigment and set to unit sensitivity at their maxima. The dashed line follows the absorption

![Graph](image)

**Fig. 2.** Log relative quanta1 sensitivity as a function of wavenumber for protanopes and deuteranopes. All data have been scaled to unit sensitivity at their maxima, and plotted as $1/\lambda_{\text{max}}-1/\lambda$. The solid line is the corrected log relative quanta1 sensitivity of Vos and Walraven's $G$ function, with $1/\lambda_{\text{max}}$ corresponding to 18,727 cm$^{-1}$ (534 nm) for protanopes and 17,857 cm$^{-1}$ (560 nm) for deuteranopes (bottom abscissa). The dashed line is Dartnall's standard shape, plotted in terms of the absorption coefficient, Log ($a/a_{\text{max}}$), with $1/\lambda_{\text{max}}$ corresponding to 18,426 cm$^{-1}$ (525.6 nm) for protanopes, and 17,557 cm$^{-1}$ (550.7 nm) for deuteranopes (top abscissa). See text for further explanation.

The coefficient of the standard shape of a visual pigment defined by Dartnall for the retinal visual pigments. It is placed to give an average minimal deviation from the data (scale shown at the top of the figure), corresponding to a $\lambda_{\text{max}}$ of 525.6 nm for the corrected protanopic data and a $\lambda_{\text{max}}$ of 550.8 nm for the corrected deuteranopic data. The solid line is given by VOS and WALRAVEN's (1971) $G$ function (a linear transformation of color mixture data congruent with the color confusions and spectral sensitivity of protanopes) with $\lambda_{\text{max}}$ of 534 nm when corrected for lens and macular pigment absorption and expressed in quanta (scale shown at the bottom of the figure). The corrected protanopic data is placed on the same scale ($\lambda_{\text{max}} = 534$ nm). The corrected deuteranopic data is assigned a $\lambda_{\text{max}}$ of 560 nm.
The two sets of data points superimpose on the figure. The protanopic and deuteranopic sensitivity functions have the same shape on a wavenumber axis. The Vos and Walraven (1971) $G$ function provides the better fit to the data points. There are slight but consistent deviations of the data points from Dartnall’s standard shape which are not evident for the $G$ function. The long wavelength slope of Dartnall’s standard shape is too shallow to fit the data. This leads to overestimation of the sensitivity (0.16 log unit) at long wavelengths and underestimation of the sensitivity (0.09 log unit) at intermediate wavelengths. Absorption spectra with higher values of O.D. show even greater deviations from the data.

RELATION OF PSYCHOPHYSICAL DATA OF COLORBLIND OBSERVERS TO THE COLOR MIXTURE DATA OF NORMALS

The deviations of the protanopic and deuteranopic sensitivities from the standard shape for retinal, visual pigments are small but consistent. That they must be real hinges on our starting point. No linear transformation of the color matching data gives three fundamentals consistent with the standard shape for visual pigments. If corrected spectral sensitivities of the blue monocone monochromat, protanope, and deuteranope do represent the cone pigments, then they should fit a linear transformation of the color matching functions of the normal observer.

The Vos and Walraven (1971) fundamentals are König fundamentals. They are based on dichromatic color vision with the view that both protanopia and deuteranopia represent loss systems. Other König type fundamentals are those described by Bouma (1942), Judd (1945), and De Vries (1948b). These authors give their transformations in terms of the CIE 1931 standard observer. Vos and Walraven (1971) used Judd’s (1951) revised trichromatic functions.

The middle-wavelength functions of these authors, when scaled to unit sensitivity at their maxima, all agree closely. The functions peak at 534 nm when corrected for an average lens and macular pigmentation, and calculated for an equal quantum spectrum. They provide a good fit to the protanopic data. Vos and Walraven’s $G$ function was shown in Fig. 2. It has the equation: $G = -0.15516x + 0.45693y + 0.0306z$, where $x$, $y$, and $z$ are Judd’s (1951) revised functions.

The long-wavelength functions differ depending on the copunctal point (convergence of dichromatic confusion lines on the CIE XYZ chromaticity diagram) associated with the equation. Bouma (1942), Judd (1945), and De Vries (1948b) give equations associated with copunctal points between $x_d = 1.08$, $y_d = -0.08$, and $x_d = 1.21$, $y_d = -0.21$. There is considerable variability in reports of the deuteranopic convergence point. Nimeroff (1970) has calculated a weighted mean convergence point based on five studies using 29 observers. The values are $x_d = 1.53$, $y_d = -0.53$, which give a predicted deuteranopic sensitivity

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3 The Bouma (1942), Judd (1945), and De Vries (1948b) equations for protanopic sensitivity using the 1931 CIE standard observer are:

- **Bouma**: $V' = -0.4136x + 1.70y + 0.1017z$;
- **Judd**: $W_p = -0.46x + 1.355y + 0.101z$;
- **De Vries**: $G = -0.402 + 0.93y + 0.028z$.

4 The Bouma (1942), Judd (1945), and De Vries (1948b) equations for deuteranopic sensitivity using the 1931 CIE standard observer are:

- **Bouma**: $V'' = 0.1053x + 0.973y - 0.007068z$;
- **Judd**: $W_d = 0.071x + 0.954y - 0.0154z$;
- **De Vries**: $R = 0.145 + 0.93y - 0.028z$.

The equation given for Judd was recalculated using his equations (1) and (8a) (Judd, 1945) using $x_d = 1.08$, $y_d = -0.08$. It does not correspond to that in his paper (p. 206).
(JUDD's 1945 equations using CIE 1931 standard observer) of: \( W_d = 0.4746\bar{x} + 1.3702\bar{y} - 0.10442 \). This function peaks at 562 nm when corrected for an average lens and macular pigmentation. It does not give a perfect fit to the deuteranopic data, which peaks at 560 nm.

Vos and WAlRAVEN (1971) used \( x_d = 1.40, y_d = -0.40 \) as the deuteranopic copunctal point. Their \( R \) function has the equation: \( R = 0.15516\bar{x} + 0.54037\bar{y} - 0.030602 \) where \( \bar{x}, \bar{y}, \) and \( \bar{z} \) are JUDD's (1951) revised functions. The \( R \) function peaks at 560 nm and provides a reasonable fit to the deuteranopic data. Vos and WALRAVEN'S (1971) \( R \) and \( G \) functions have the identical shape when plotted as \( 1/\lambda \) versus \( \lambda \) (average absolute deviation for wavelengths sampled in 10 nm steps between 530 and 700 nm is less than 0.019 log unit).

BOUMA (1942), JUDD (1945), and De VRIE~ (1948b) scaled the \( \bar{z} \) of the 1931 CIE observer for their short-wavelength receptor primary. VOS and WALRAVEN (1971) scaled JUDD's (1951) \( \bar{z} \) for their short-wavelength (\( B \)) receptor primary. The fit to the standard shape of a visual pigment is bad for the 1931 CIE observer, especially on the short-wavelength side of the maximum. For wavelengths below 510 nm, the fit is good for Vos and Walraven's \( B \) function and also for the 1964 CIE supplementary observer, when the standard shape proposed by Dartnall is placed at 23,000 cm\(^{-1}\) (corresponding to 435 nm). It should be noted that the blue monocone data, corrected for lens and macular pigment and plotted on an equal quantum spectrum, peaks at 431 nm, and that there is no way to shift the \( \bar{z} \) to shorter wavelengths.

COMPARISON WITH OTHER PUBLISHED ABSORPTION SPECTRA

The finding that the spectral sensitivities of protanopes and deuteranopes have the same shape is suggestive that they represent a pigment absorption curve. We considered and rejected the possibility of an inert pre-receptoral long-wavelength filter. Calculated deviations of the protanopic and deuteranopic curves from Dartnall's standard shape have the same shape but are displaced on the wavenumber axis. Vertical adjustment does not bring them into alignment. The similarity in shape of the two spectral sensitivities tends to rule out the possibility of two long-wave filters (or wave-guides) selective for the two classes of cones.

Since it seems likely that the middle- and long-wavelength sensitive human cone photopigments are based on Vitamin A\(_1\) (HECHT and MANDELBAUM, 1938; WALD, JEGHERS and ArMINio, 1938; BROWN and WALD, 1963; RUSHTON, 1968), we here consider the possibility that Dartnall's standard shape does not apply to all retinal\(_1\) photopigments. The deviations of the human spectral response from the standard shape occur at long wavelengths and are noticeable when plotted in terms of log quantal sensitivity. The usual practice in plotting absorption spectra of visual pigments is to use a linear scale. Examining DARTNALL'S (1962) comparison of iodopsin (WALD, BROWN and SMITH, 1955) and a rhodopsin with \( \lambda_{\text{max}} \) of 498 nm, we noticed that the iodopsin curve is consistently below the rhodopsin curve on the long-wavelength side of the maximum. Figure 3 shows a logarithmic plot of WALD, BROWN and SMITH's (1955) data points (their Table VII, last column) for iodopsin with \( \lambda_{\text{max}} \) at 562 nm. The dashed line is Dartnall's standard shape for visual pigments with \( 1/\lambda_{\text{max}} \) placed at 17,794 cm\(^{-1}\) (562 nm). The solid line is given by the VOS and WALRAVEN (1971) \( G \) function, corrected for an average lens and macular pigment, converted to a quantal spectrum, adjusted to unit sensitivity at its maximum, and shifted on the frequency axis to a \( \lambda_{\text{max}} \) of 562 nm. There are systematic deviations of the iodopsin data from the standard shape. The iodopsin data give a better fit to the VOS and WALRAVEN (1971) \( G \) shape than to Dartnall's standard shape.
Wavelength, nm

$\begin{array}{c}
500 \\
550 \\
600 \\
650 \\
700 \\
\end{array}$

\[ -2 \leq \log \left( \frac{a}{a_{\text{max}}} \right) \leq -1.4 \]

\[ \text{VOS and WALRAVEN (1971)} \]

\[ \lambda_{\text{max}} \text{ to fit the G shape was sometimes of longer wavelength by 2 or 3 nm than the published } \lambda_{\text{max}} \text{ (due either to the concentration variable or the technique of curve fitting). We were unable to replot microspectrophotometric data.} \]

The results of this review may be summarized as follows:

(a) All the photopigments with $\lambda_{\text{max}} \approx 500$ nm do fit Dartnall's standard shape, including those of amphibians (LYTHGOE, 1937; WALD, 1938; COLLINS and MORTON, 1950;
DARTNALL, 1967), fishes (MUNZ, 1964; BRIDGES, 1965a, b, 1967b; MUNZ and BEATTY, 1965; SCHWANZARA, 1967; BEATTY, 1969; BRIDGES and YOSHIKAMI, 1970b; McFARLAND, 1970), reptiles (CRESCITELLI, 1956, 1963; WALD, BROWN and KENNEDY, 1957), birds (BLISS, 1946; WALD, BROWN and SMITH, 1955; BRIDGES, 1962; CRESCITELLI, WILSON and LILYBLADE, 1964; SILLMAN, 1969), and mammals (CRESCITELLI and DARTNALL, 1953; CRESCITELLI, 1958; WALD and BROWN, 1958; BRIDGES, 1959). This result is expected since the standard shape was prepared from such pigments. (b) The P433, of frogs described by DARTNALL (1967) fits Dartnall's standard shape. (c) All the fish pigments with $\lambda_{\text{max}}$ below 500 nm fit the standard shape (DENTON and WARREN, 1956; MUNZ, 1958a, 1964; CRESCITELLI, 1969). Of the fish pigments peaking above 500 nm, those with $\lambda_{\text{max}}$ at 511 or 520 nm (MUNZ, 1956, 1958b, 1964; BRIDGES, 1965a, b, 1967; MUNZ and BEATTY, 1965; SCHWANZARA, 1967; BEATTY, 1969; BRIDGES and YOSHIKAMI, 1970a, b; McFARLAND, 1970) fit the standard shape. The P530, of Scomberomorus sierra (mackerel) described by MUNZ (1964) fits the $G$ shape with $\lambda_{\text{max}}$ of 532 nm. (d) The P478, pigment of Gekko gekko fits the standard shape. Three lizard pigments fit the $G$ shape: The P524, of Phyllyrus (CRESCITELLI, 1956) and P521, of Gekko gekko (CRESCITELLI, 1963) fit the $G$ shape with $\lambda_{\text{max}}$ of 526 and 523 nm respectively. The pigment of Hemidactylus turcicus (CRESCITELLI, 1963) fits the $G$ shape with $\lambda_{\text{max}}$ of 530 nm. (e) Among birds, the iodopsins with $\lambda_{\text{max}}$ 561–562 nm, reported by BLISS (1946), WALD, BROWN and SMITH (1955), and CRESCITELLI, WILSON and LILYBLADE (1964), fit the $G$ shape. The P544, pigment of the pigeon reported by BRIDGES (1962) fits the standard shape. Figure 4 shows the difference spectra of six visual pigments which fit the $G$ shape.

There is a dichotomy of the pigments by their $\lambda_{\text{max}}$. Pigments with $\lambda_{\text{max}}$ at or below 520 nm fit Dartnall's standard shape. Pigments with $\lambda_{\text{max}}$ above 520 nm conform to the $G$ shape. There is one exception: the 544, pigment of the pigeon reported by BRIDGES (1962).
COMMENT

The short-wavelength sensitive mechanism measured as the high intensity cone response in blue monocone monochromats and as the \( \pi_1 \) mechanism in normals (400-500 nm) fits Dartnall's standard shape for retinal pigments. The best estimate of the short-wavelength pigment derived from color mixture data also fits the standard shape, but there is a discrepancy of 3-4 nm in the placement on the wavelength axis. The middle- and long-wavelength sensitive mechanisms measured as the spectral sensitivity of protanopes and deuteranopes (in the wavelength range 500-700 nm) deviate from the standard shape, but share the same shape on a wavenumber axis. This shape is identical to measured absorption spectra of some visual pigments of birds, lizards, and one fish. The corrected protanopic and deuteranopic sensitivities are congruent with a linear transformation of color mixture data of normal observers. These facts support the hypothesis that the corrected protanopic and deuteranopic sensitivities are estimates of pigment absorption curves.

We also show that the use of a logarithmic scale—which is an appropriate treatment of psychophysical data—reveals that the density spectra of \( A_1 \) derived visual pigments are described by two rather than one standard shape. The \( \lambda_{\text{max}} \) appears to determine which shape is appropriate. Visual pigments with \( \lambda_{\text{max}} \leq 520 \) nm fit Dartnall's standard shape; those with \( \lambda_{\text{max}} > 520 \) nm fit the Vos and Walraven G shape. It might be noted that a cut-off of 520 nm for \( A_1 \) derived pigments corresponds to about 560 nm for \( A_2 \) derived pigments, using Dartnall and Lythgoe's regression relating the \( \lambda_{\text{max}} \) of \( A_1 \) pigments to the \( \lambda_{\text{max}} \) of \( A_2 \) pigments (Dartnall and Lythgoe, 1965). The absorption spectra of the \( A_2 \) derived visual pigment, P620\(_2\) (Wald, Brown and Smith, 1953; Marks, 1965; Liebman and Entine, 1967, 1968; Liebman and Grande, 1971) is narrower than the standard shape for retinal visual pigments ( Bridges, 1967a; Liebman and Entine, 1967, 1968). Thus it may prove that two shapes are also necessary to describe the \( A_2 \) derived visual pigments.

Finally we would like to point out that the estimates of the human visual photopigments derived from psychophysical data have correlates measured in other species. The estimates of the short-wavelength sensitive pigment (\( \lambda_{\text{max}} 431 \) or 435 nm) may be compared with the green rods of frogs (\( \lambda_{\text{max}} 432-433 \) nm; Dartnall, 1967; Liebman and Entine, 1968). The estimate of the middle-wavelength sensitive pigment (\( \lambda_{\text{max}} 534 \) nm) may be compared with the pigments of the mackerel, Scomberomorus sierra (\( \lambda_{\text{max}} 532 \) nm; Munz, 1964) and the lizard, Hemidactylus turcicus (\( \lambda_{\text{max}} 530 \) nm; Crescitelli, 1963). The long-wavelength sensitive pigment (\( \lambda_{\text{max}} 560 \) nm) may be compared to the iodopsins measured in fowl (\( \lambda_{\text{max}} 561-562 \) nm; Bliss, 1946; Wald et al., 1955; Crescitelli, Wilson and Lilyblade, 1964) and the salt water turtle, chelonia mydas mydas (\( \lambda_{\text{max}} 562 \pm 3 \) nm; Liebman and Grande, 1971).

Note added in proof:

Professor Le Grand has kindly supplied us with copies of two of his papers (Les Pigments des cônes chromatiques. Die Farbe 19, 15, 1970, and About the Photopigments of Colour Vision. Mod. Prob. Ophthalm. 11, 186, Karger, Basel, 1972). In these papers, he develops independent evidence that the human cone photopigments have narrower spectral bandpass than rod pigments. Le Grand suggests that cone pigments have a different prosthetic group (still based on Vitamin A) than rod pigments.

REFERENCES


Abstract—A comparison was made between Dartnall’s standard shape for visual pigments and the spectral sensitivities of the short-, middle-, and long-wavelength sensitive cone receptor mechanisms of man. Data from blue monocone monochromats, protanopes, and deuteranopes were chosen as reliable estimates of each of the three classes of cone sensitivities. The short-wavelength sensitive mechanism fits the standard shape. The middle- and long-wavelength sensitive mechanisms have the same shape on a wavenumber axis but do not fit Dartnall’s standard shape for visual pigments. The shape of the middle- and long-wavelength sensitive mechanisms also describes some other published absorption spectra of visual pigments with $\lambda_{\text{max}} > 520$ nm, notably the iodopsins found in birds.

Résumé—On compare la courbe standard de Dartnall pour les pigments visuels avec les sensibilités spectrales des mécanismes récepteurs des cônes humains pour les courtes, moyennes et grandes longueurs d’onde. On utilise les données relatives aux monochromates à cônes bleus, aux protanopes et aux deuteranopes comme des estimations sérieuses de ces trois classes de sensibilités des cônes. Le mécanisme des courtes longueurs d’onde est en accord avec la courbe standard. Les mécanismes sensibles aux moyennes et grandes longueurs d’onde ont la même forme avec un axe en nombre d’ondes, mais ne sont pas en accord avec la courbe standard de Dartnall pour les pigments visuels. La forme de ces mécanismes s’accorde aussi avec d’autres données publiées sur l’absorption des pigments visuels tels que $\lambda_{\text{max}} > 520$ nm, en particulier l’iodopsine trouvée chez les oiseaux.

Zusammenfassung—Die spektrale Empfindlichkeit der auf kurze, mittlere und lange Wellenlängen ansprechende Zapfenmechanismen wurde mit derjenigen der Standardform für Sehstoffe (nach Dartnall) verglichen. Als verlässliche Schätzung für die spektrale Empfindlichkeit wurden die Daten von Monochromaten, die nur blauempfindliche Zapfen sowie die von Protanopen und Deuteranopen benutzt. Der für kurze Wellenlängen empfindliche Mechanismus stimmt mit der Dartnallschen Standardform überein. Die für mittlere und lange Wellenlängen empfindlichen Mechanismen haben, aufgetragen über der Wellenzahl, die gleiche Gestalt. Sie stimmen aber nicht mit der Dartnallschen Standardform für Sehstoffe überein. Die gefundene Form der Empfindlichkeitskurven für lange und mittlere Wellenlängen beschreibt auch einige andere veröffentlichte Absorptionsspektren von Sehstoffen mit $\lambda_{\text{max}} > 520$ nm, insbesondere die des Iodopsins, das bei Vögeln gefunden wird.

Резюме—Было сделано сравнение между стандартной формой кривой Дартнелла для зрительных пигментов и спектральной чувствительностью колбочек человека, чувствительных к коротко-, средне- и длинноволновой областям спектра. Данные о пигментах моноcone монокроматов, протанопах и дейтеранопах были выбраны как надежная оценка каждого из трех классов колбочковой чувствительности. Коротковолновая чувствительность совпадает со стандартной формой. Средневолновую и длинноволновую чувствительности имеет ту же самую форму на оси волновых чисел, но не совпадает со стандартной формой кривой Дартнелла для зрительных пигментов. Форма средневолновой и длинноволновой чувствительности аналогична форме некоторых других опубликованных спектров поглощения зрительных пигментов с $\lambda_{\text{max}} > 520$ нм, а именно иодопсинов, найденных у птиц.