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TEST AND FIELD SPECTRAL SENSITIVITIES OF COLOUR MECHANISMS OBTAINED ON SMALL WHITE BACKGROUNDS: ACTION OF UNITARY OPPONENT-COLOUR PROCESSES?*

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Abstract—It has been shown that for human foveal vision the *test spectral sensitivity* curve obtained in the presence of a large white background exhibits peaks at about 440, 530 and 610 nm and a small dip or notch at about 580 nm. Additionally, *field spectral sensitivity* curves for the medium- and long-wavelength sensitive *colour mechanisms* when derived in the presence of a small monochromatic background (auxiliary field) spatially coincident with the test field are sharper than the corresponding Stiles's Π mechanisms and peak at about 530 and 605 nm. The short-wavelength sensitive colour mechanism shows no such effect, the peak remaining at about 440 nm. The test spectral sensitivity curve obtained on a large white background and the *sharpened* field spectral sensitivity curves obtained on a spatially coincident, monochromatic auxiliary field have each been interpreted in terms of an *opponent-process* theory of colour vision: the response of the non-opponent luminance system is considered to be reduced by selective achromatic adaptation (with the large white background) or by selective *contour masking* (with the spatially coincident auxiliary field). The present study combined the two techniques of achromatic and spatial adaptation: a small white auxiliary field spatially coincident with the test field was used in measurements of both test and field spectral sensitivities. Under these conditions, it was found that the test spectral sensitivity curve showed more clearly defined peaks and a deeper notch at about 580 nm than when obtained on the large white background and that the test curve was well fitted by the upper envelope of the short-wavelength and sharpened medium- and long-wavelength field spectral sensitivity curves, suggesting the possibility that three unitary opponent-colour mechanisms may underlie test and field spectral sensitivities. A test of this hypothesis is proposed concerning the effect of auxiliary-field chromaticity on the position of the notch at about 580 nm in the test spectral sensitivity curve.

INTRODUCTION

The spectral sensitivity curve obtained for foveal detection of a long-duration monochromatic test flash on a large white background characteristically shows peaks at approximately 440, 530 and 610 nm (Stiles and Crawford, 1933; Sidley and Sperling, 1967; Sperling and Harwerth, 1971; King-Smith and Carden, 1976; Verriest and Uvijls, 1977; Zrenner and Krüger, 1981; Zrenner, 1982; Klingaman and Zrenner, 1982). Stiles (1978, p. 5) reported that the results obtained by Stiles and Crawford (1933) (with a white surround to the test field, rather than with a uniform field) initially suggested that, for a given white conditioning stimulus, the test spectral sensitivity curve might be "the resultant of three single peak component curves of fixed shape, whose different heights . . . varied as the intensity of the conditioning stimulus was increased . . . (and) that in all probability these component curves would correspond to the spectral threshold sensitivities of the three colour systems postulated in trichromatic theory". Subsequently, however, Stiles (1978) and others (Sperling and Harwerth, 1971; King-Smith and Carden, 1976) have argued that test spectral sensitivity curves obtained on white backgrounds cannot be represented as the upper envelope of cone-mechanism spectral sensitivities: although the short-wavelength peak is well fitted by the upper portion of the curve for the short-wavelength sensitive cone mechanism, the medium- and long-wavelength peaks are poorly fitted by the curves for the medium- and long-wavelength sensitive cone mechanisms.

Opponent-process theory

Sperling and Harwerth (1971) were the first to propose and establish a model based on inhibitory interactions between signals from long- and medium-wavelength sensitive cones to describe these peaks in test spectral sensitivity obtained on a white background. King-Smith and Carden (1976) related this inhibitory interaction to the red-green opponent-colour channel of an opponent-process theory of colour vision (Jameson and Hurvich, 1955; Hurvich and Jameson, 1957; Jameson, 1972; Guth and Lodge,

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1973; Ingling and Tsou, 1977). Such a theory usually assumes two parallel systems: a non-opponent system, which transmits cone signals combined with the same sign, and which typically signals luminance; and an opponent-colour system, which transmits cone signals combined with different signs, and which typically signals hue. King-Smith and Carden (1976) proposed that the detection of a given test flash should be determined by that system which is most sensitive under the particular set of conditions of test-flash wavelength, size and duration and background spectral composition and intensity. Critical properties of the two systems have been postulated as follows.

(1) Relative to the non-opponent system, the opponent-colour system has poorer high spatial frequency response or greater spatial integration (van der Horst *et al.*, 1967; van der Horst and Bouman, 1969; Hilz and Cavonius, 1970; Granger and Heurtley, 1973; King-Smith and Carden, 1976; Sternheim *et al.*, 1978; Stromeyer *et al.*, 1978a; Stromeyer and Sternheim, 1981; Mullen, 1982). (See comments below on comparison with physiological data.)

(2) The opponent-colour system has lower response to temporal transients or greater temporal integration (de Lange, 1958; Regan and Tyler, 1971; King-Smith and Carden, 1976; Kelly and van Norren, 1977; Tolhurst, 1977; Sternheim *et al.*, 1978; Stromeyer *et al.*, 1978a; Sternheim *et al.*, 1979; see also Klingaman *et al.*, 1980; Bowen, 1981; Dain and King-Smith, 1981).

(3) The sensitivity of the non-opponent system is preferentially depressed by white backgrounds of moderate to high intensities (King-Smith and Carden, 1976; King-Smith and Kranda, 1981).

It should be emphasized that these proposed characteristics relate to a general, psychophysically defined, opponent-colour system. Such a system may reflect the activity of an ensemble of retinal colour-opponent cells that, individually, have spatial characteristics (Gouras, 1968; de Monasterio and Gouras, 1975; de Monasterio, 1978) different from colour-opponent cells in some areas of visual cortex (Gouras, 1972; Dow and Gouras, 1973; Zeki, 1977). As Mollen (1982) has cautioned, the various psychophysical and electrophysiological characterizations of opponent-colour processes need not always coincide (for relevant discussion, see Ingling, 1978, and King-Smith and Carden, 1978).

None of the three properties listed above should be taken as decisive in controlling the relative contributions of opponent-colour and non-opponent systems (King-Smith and Carden, 1976; Foster, 1981; Finkelstein and Hood, 1981, 1982). The use of a relatively large (e.g. 1 deg) and relatively long (e.g. 200 msec) test flash on a large white background should, however, facilitate detection by the opponent-colour system. Indeed King-Smith and Carden (1976) demonstrated that the test spectral sensitivity curve obtained with a simple detection criterion in this experimental paradigm corresponds, over most of the spectrum, to the spectral sensitivity curve obtained with the use of a colour-detection criterion, the latter presumably representing the spectral sensitivity of the opponent-colour system. Near 580 nm, there is a notch in the curve that is deeper when the colour-detection criterion is used than when the simple detection criterion is used. King-Smith and Carden (1976) suggested that in the latter case the luminance system is more sensitive than the opponent-colour system in the region near 580 nm.

Field spectral sensitivities on small backgrounds

Consider now the field spectral sensitivity of a colour mechanism. This is evaluated by determining, at each of a range of wavelengths, the reciprocal of the intensity (in quantum units*) of a large monochromatic background (conditioning field) that raises the threshold intensity of a small superimposed test flash, of fixed wavelength, by a constant multiple of its value on zero field (Stiles, 1953; Wyszecki and Stiles, 1967). The resulting sensitivity function reflects an adaptational sensitivity of the mechanism concerned and, unlike test spectral sensitivity, it may be evaluated for essentially all of the mechanism's spectral range. The field spectral sensitivities of Stiles's mechanisms π_5 (long-wave), π_4 (medium-wave) and π_3 (short-wave) are well fitted by the results of cone microspectrophometry, after allowance for prereceptoral absorption losses (Bowmaker *et al.*, 1980; Bowmaker and Dartnall, 1980), and have been argued to be good candidates for the fundamental functions of small-field colour matching (Pugh and Sigel, 1978; Estévez and Cavonius, 1977; see also Wyszecki and Stiles, 1980).

One of us has recently shown (Foster, 1979, 1980, 1981) that if the field spectral sensitivity curves of the medium- and long-wavelength sensitive mechanisms, corresponding normally to Stiles's mechanism Π_4 and Π_5, are obtained with a long-duration test flash superimposed on a steady monochromatic "auxiliary" conditioning field, *spatially coincident* with the test field, then the resulting curves may appear narrowed or sharpened with their peaks shifted in opposite directions along the wavelength scale. Thus, the field spectral sensitivity curve of the long-

Terminology—Intensity is expressed as $\log_{10}$ of the number, 10^N say, of quanta per second per square deg of visual angle, written, for clarity, as N log quanta·sec^{-1}·deg^{-2}; where appropriate, the latter corresponds to a sensitivity: $-N$ log quanta·sec^{-1}·deg^{-2}. The symbol π_i is used, after Stiles, both generically for Stile's ith mechanism and specifically for test spectral sensitivity; the symbol Π_i is used for field spectral sensitivity. The terms "long-wavelength sensitive mechanism", "medium-wavelength sensitive mechanism" and "short-wavelength sensitive mechanism" are used to cover π_5, π_4 and π_3 (or π_1) and the corresponding "mechanisms" with sharpened field spectral sensitivities (Foster, 1981).

wavelength sensitive mechanism π_5, normally rather flat-topped with maximum sensitivity at about 575 nm (Stiles, 1959), becomes attenuated on the short-wavelength side and acquires a relatively sharp peak at about 605 nm (Foster, 1980, 1981). The field spectral sensitivity of the medium-wavelength sensitive mechanism π_4, also fairly flat-topped with maximum sensitivity at about 540 nm (Stiles, 1959), becomes attenuated on the long-wavelength side and peaks more sharply at 530 nm (Foster, 1980). (These effects may be obtained at relatively low stimulus intensities, Foster, 1981.) The field spectral sensitivity curve of the short-wavelength sensitive mechanism π_1 (or π_3) shows no sharpening with a coincident auxiliary field of moderate-to-high intensities (Foster, 1981). Similar wavelengths for maximum effect of a post-receptoral interaction involving pattern adaptation were reported by Hendricks *et al.* (1982).

Foster (1981) suggested that these results, like those for test spectral sensitivities on large white backgrounds, might be interpreted within the framework of an opponent-process theory of colour vision. The basic hypothesis is that high spatial-frequency adaptation or contour masking occurs where the boundaries of test and auxiliary fields coincide (Fry and Bartley, 1935; Sternheim *et al.*, 1972; Lennie and MacLeod, 1973). The spatial transient that would normally be responded to by the luminance system (see references above) is suppressed. Provided that field spectral sensitivity data are obtained with main conditioning fields so weak that the suppressive effect of the auxiliary field is not seriously reduced (Foster, 1981) and receptor adaptation is minimized, the resulting sharpened field spectral sensitivity curves should represent activity mediated by channels within the opponent-colour system and, for sufficiently intense auxiliary fields, correspond to *field action spectra*. Evidence for this hypothesis is considered in the Discussion section of this paper.

Enhanced isolation of the opponent-colour system and comparison of test and field spectral sensitivities

To summarize: there is a close correspondence between (a) the wavelengths at which there are peaks in the sharpened long- and medium-wavelength field spectral sensitivity curves obtained on a monochromatic auxiliary field coincident with the test field and (b) the wavelengths at which peaks occur in the long- and medium-wavelength regions of the test spectral sensitivity curve obtained on a large white background. As outlined above, both types of spectral sensitivity curve have been explained by supposing that they result from a preferential reduction in sensitivity of the non-opponent system: in the case of field spectral sensitivity, by contour masking with the coincident monochromatic auxiliary field; in the case of test spectral sensitivity, by the adaptive effects of the large achromatic background. It seemed plausible that a combination of the two techniques, the one spatial, the other spectral, should more efficiently achieve isolation of the opponent-colour system.

The effectiveness of this paradigm was tested in the present study. It was proposed to compare test and field spectral sensitivities obtained under the same conditions of background (auxiliary-field) configuration and spectral composition. *A priori*, the expectation would be normally (de Monasterio, 1979) that test and field action spectra mediated by one cone mechanism and antagonized by another should have opposite shapes in the spectral region where the cone-mechanism signals interact. If, under the present conditions, a test spectral sensitivity curve could be represented as the upper envelope of three distinct field spectral sensitivity curves, then this might suggest the operation of *unitary* opponent-colour mechanisms or channels, each with a spectral sensitivity that was qualitatively the same whether determined directly by test measurements or indirectly by field measurements.

METHODS

Stimuli and apparatus

In each experiment the monochromatic test flash was disc-shaped, of dia. 1.05 deg, and duration 200 msec. The steady white background (auxiliary field) was also disc-shaped, of dia. either 1.05 or 10.0 deg and luminance 1000 td, with colour temperature 3400 K. For field spectral sensitivity measurements, a disc-shaped variable-intensity monochromatic main conditioning field, dia. 10.0 deg, was introduced. The stimuli were all concentric and were centred at the middle of a 3-deg square fixation array of four tiny red or white lights.

The stimuli were produced by a three-channel Maxwellian-view optical system (Foster, 1981) with as light source a single tungsten-halogen lamp run from a regulated d.c. power supply. The test field and (where appropriate) the main conditioning field were produced by channels 1 and 2; the steady, white auxiliary field was produced by channel 3. Transmittances of the channels were controlled by compensated neutral density wedges and Wratten neutral density filters. The spectral compositions of channels 1 and 2 were controlled with Balzers B40 interference filters with half-height full bandwidths each less than 9 nm except for a 461-nm filter which had half-height full bandwidth 14 nm. The time course of the test flash was controlled by a silent electromagnetic shutter that interrupted the channel at an intermediate focus. Rise and fall times of each flash were less than 2 msec. The geometry of the stimuli was determined by masks inserted in the channels. Precautions were taken to minimise instrumental stray light. The stimuli were viewed through a 2-mm artificial pupil. Stability of head position was maintained with the aid of a dental bite-bar. Further details of the experimental apparatus and its calibration are given in Foster (1981).

The intensity of the white auxiliary field was set by means of an MDB match (Boynton and Kaiser, 1968; Wagner and Boynton, 1972) against a 562-nm field, of luminance 1000 td, from one of the monochromatic channels. As a control for this setting of the white field, an indirect heterochromatic match was made against a tungsten lamp calibrated at the National Physical Laboratory. (This lamb was kindly supplied by Dr B. H. Crawford.)

Procedure

At the beginning of each experimental session, the positions of the stimulus masks were adjusted so that they were seen by the subject to be concentric and in sharp focus. Where necessary, small corrections to the alignments of the masks were made as the wavelength of the test flash was varied. Each subject dark-adapted for 10 min before commencing the observation session. Viewing was monocular and subjects fixated the centre of the fixation display with the right eye. The onset of the test flash and its intensity (or, in measurements of field spectral sensitivity, the intensity of the main-conditioning field) were controlled by the subject using push-button switch boxes. Stimuli could not be presented more rapidly than once every 2 sec.

All threshold measurements were made by a method of adjustment, final values being approached from subthreshold values. For measurements of test spectral sensitivity, procedure was standard. The main conditioning field was blocked, the test flash at the given wavelength was presented on the 1.05- or 10.0-deg white auxiliary conditioning field, and the intensity of the flash set to threshold by the subject. For measurements of field spectral sensitivity, a method of direct field adjustment was used (Foster, 1981). The test flash of wavelength appropriate to the mechanism of interest was set 0.3 log units above *increment* threshold (on the 1.05- or 10.0-deg white auxiliary field), the main 10.0-deg conditioning field was then introduced, and its intensity adjusted by the subject to return the test flash to threshold. This method, under the constraints described by Foster (1981, Methods), has been shown to be efficient and accurate (Foster, 1981, Appendix)*. In field spectral sensitivity determinations, the wavelength of the test flash was fixed, for all subjects, at 422 nm for the short-wavelength sensitive mechanism and at 608 nm for the long-wavelength sensitive mechanism; for the medium-wavelength sensitive mechanism, it was fixed at 521 nm for subjects S.G. and R.S.S. and at 531 nm for subject D.H.F. The choice of these wavelengths was guided by the results of measurements made by Foster (1981) on the variation of spectral sharpening with test-flash wavelength for a monochromatic auxiliary field; in particular, for the long-wavelength sensitive mechanism, spectral sharpening at 610–620 nm was at least 0.3 log units greater than that at wavelengths less than 600 nm or more than 650 nm. There is also evidence (R. S. Snelgar, unpublished data) indicating that, when a white auxiliary field is used, greater spectral sharpening is produced with a 608-nm test flash than with a 658-nm test flash.

In both test- and field-sensitivity measurements wavelengths were varied in ascending and then descending order (or vice-versa). Three consecutive threshold settings were recorded at each wavelength on each traverse; thus, mean threshold values were based on six measurements in a balanced design.

Subjects

Three subjects, with normal colour vision and normal or corrected-to-normal visual acuity, participated in this study: one female, R.S.S. (co-author) and two male, S.G. and D.H.F. (co-author). Ages ranged from 24 to 36 yr. S.G. was unaware of the purpose of the experiment.

RESULTS

Figure 1(a), (b) and (c) show results for subjects R.S.S., S.G. and D.H.F. respectively. In each figure, the upper two curves joining points indicated by open circles show test spectral sensitivities on the 1000-td white auxiliary field, dia. 10.0 deg (broken curve) and 1.05-deg (continuous curve). The three lower continuous curves connecting points indicated by solid symbols show field spectral sensitivities for the long-wavelength (solid squares), medium-wavelength (solid circles), and short-wavelength (solid triangles) sensitive mechanisms obtained on the 1.05-deg white auxiliary field†. The test-flash wavelength for each field spectral sensitivity curve is indicated. In all cases, sensitivity is expressed as log reciprocal intensity in quanta $\cdot \sec^{-1} \cdot \deg^{-2}$. The vertical bars show ± 1 SEM where this is sufficiently large to be displayed. The only adjustments to the vertical positions of the data in each figure are as follows. The field

*As noted earlier, to compare test and field spectral sensitivities under the same adaptational conditions and to minimize receptor adaptation, the intensity of the main conditioning field should be kept relatively low. Previous work (Foster, 1981) has shown that spectral sharpening decreases (linearly) with magnitude of elevation in test-flash threshold used to make the field measurement. For sufficiently intense main fields, the spatially coincident auxiliary field becomes ineffective and pure receptoral adaptation dominates. The elevation in test-flash threshold of 0.3 log units used here, rather than the standard 1.0 log units used by Stiles (1978), was a compromise designed to achieve minimum disturbance by the main field and ease of measurement by the field-adjustment method (Foster, 1981). Measurements of t.v.i. data over this region (Foster, 1981) showed the gradient to be varying monotonically with no evidence of subsidiary branches. A smaller elevation in test-threshold, e.g. 0.2 log units, would be unlikely to affect the sharpness or location of the principal maxima, upon which the present conclusions depend.

†The curves were drawn by computer-controlled plotter using a local Lagrange interpolation.

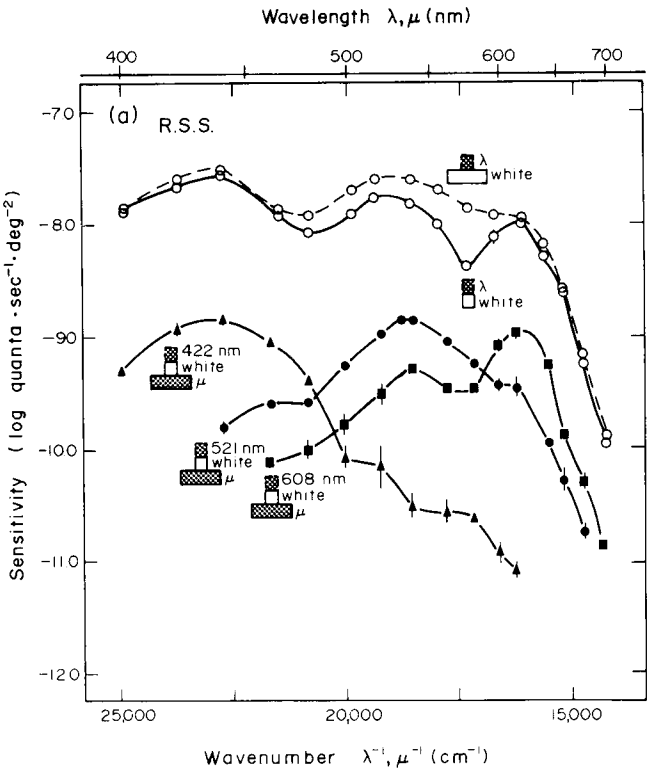
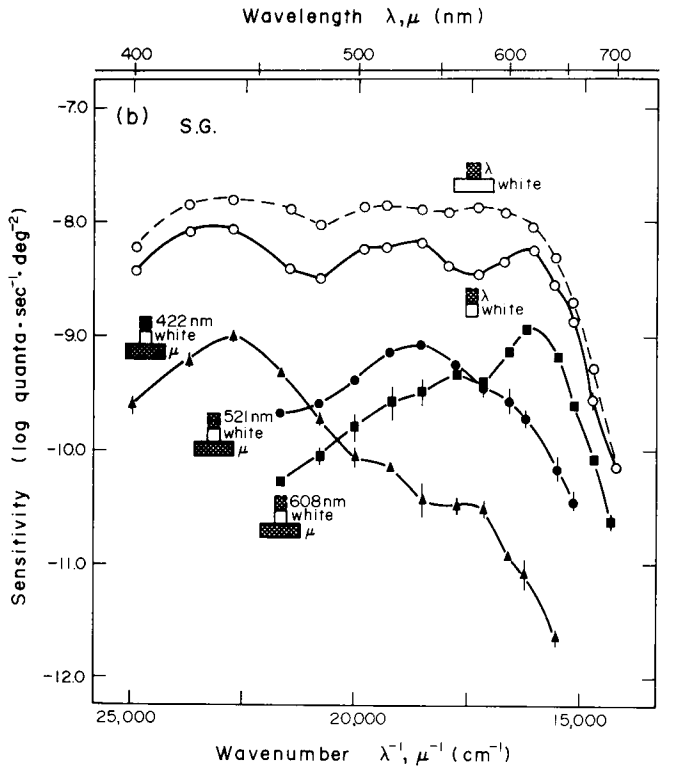


Fig. 1. (a) The upper two curves show test spectral sensitivities obtained on a large (10.0-deg) white background (open circles, broken line) and on a small (1.05-deg) white background spatially coincident with the test field (open circles, continuous line). Log reciprocal threshold intensity of the test flash is plotted against wavenumber λ^{-1} of the test flash. The lower three curves show field spectral sensitivities obtained on the small white background spatially coincident with the test field for the short-, medium- and long-wavelength sensitive mechanisms (solid triangles, circles and squares respectively). Log reciprocal intensity of a 10.0-deg main conditioning field necessary to raise test-flash (increment) threshold by 0.3 log units is plotted against the wavenumber μ^{-1} of the main field. The curve for the short-wavelength sensitive mechanism has been displaced downwards by 0.5 log units. All other curves are in their correct positions. The white background, of angular subtense 10.0 or 1.05 deg, had luminance 1000 td and colour temperature 3400 K. The test flash had angular subtense 1.05 deg and duration 200 msec in all conditions. The wavelength of the test flash used in each measurement of field spectral sensitivity is indicated in the diagram. Each point is the mean of six readings and the vertical bars show ± 1 SEM where this is sufficiently large. Subject: R.S.S. (b) The field spectral sensitivity curve of the short-wavelength sensitive mechanism has been displaced downwards by 1.0 log units. The curve for test spectral sensitivity on the small auxiliary field has been raised by 0.3 log units. All other curves are in their correct positions. Other details as for Fig. 1(a). Subject: S.G. (c) The field spectral sensitivity curve of the short-wavelength sensitive mechanism has been displaced downwards by 1.0 log units. All other curves are in their correct positions. Other details as for Fig. 1(a). Subject: D.H.F.

spectral sensitivity curve for the short-wavelength sensitive mechanism (solid triangles) has been displaced downwards by 1.0 log units for subjects S.G. and D.H.F., and by 0.5 log units for subject R.S.S., thus showing peak sensitivity at approximately the same level as that for the medium- and long-wavelength sensitive mechanisms, whose positions are veridical. The test spectral sensitivity curve obtained on the 1.05-deg white auxiliary field for subject S.G. (open circles, continuous curve, Fig. 1b) has been raised by 0.3 log units. All other curves are in their correct positions.

To compare the fit of the three field spectral sensitivity curves, as a group, to the test spectral sensitivity curve obtained on the same 1.05-deg white auxiliary field, a computer-based linear interactive modelling technique was used (GLIM, Baker and Nelder, 1978). (Where data with non-corresponding wavelengths were to be compared, values were estimated by local Lagrange interpolation.) Table 1 summarizes the results. The values tabulated are, for each subject and section of the spectrum, the constants (in log units) which, when added to the corresponding field curve, gave minimum (least-squares) overlap at or close to the region of peak sensitivity. The lack of fit of the upper envelope of the resulting field curves to the test curve is indicated by the values tabulated under SD full fit, which take into account



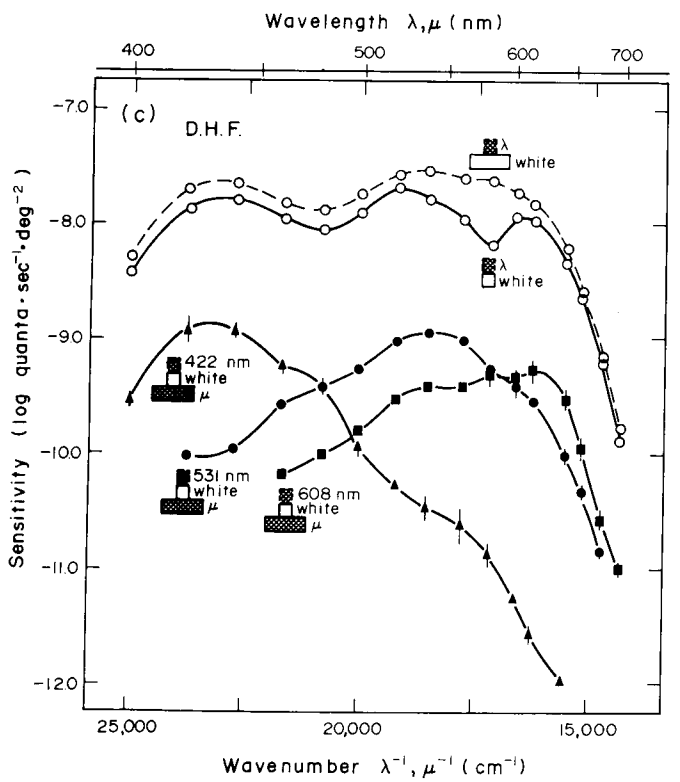


Fig. 1(b) and (c). See legend for Fig. 1(a).

Table 1. Difference in test and field sensitivities (±1 SEM) in log units

Subject	Short-wave	Medium-wave	Long-wave	SD full fit
R.S.S.	0.80 (±0.05)	1.19 (±0.08)	1.02 (±0.05)	0.11
S.G.	−0.23 (±0.05)	0.59 (±0.04)	0.41 (±0.06)	0.09
D.H.F.	0.15 (±0.05)	1.30 (±0.05)	1.25 (±0.04)	0.09

Differences in test and field sensitivities were computed by determining the constant (dependent on colour mechanism) which when added to that mechanism's field sensitivity gave minimum (least-squares) overlap at or close to the region of peak sensitivity. An estimate of a quantity (in log units) related to the Weber–Fechner fraction for each mechanism can be derived by a change in the sign of the values shown and addition of 0.3 log units. Note for each subject the similarity in these values for medium- and long-wavelength sensitive mechanisms. The values tabulated under SD full fit represent the lack of fit in log units of the test spectral sensitivity curve and the upper envelope of the field spectral sensitivity curves when adjusted vertically by the differences shown and allowances made for the number of degrees of freedom. For further details, see text.

the number of degrees of freedom (in all cases 3) allowed in the fit. Adjustments to the additive constants to improve further the fits of the envelopes produced little decrease in SD, at most 0.01 log units. Note that no attempt has been made to introduce probability summation effects. The significance of the additive constants and their relationship to the "Weber–Fechner fractions" of the underlying mechanisms is discussed in the following section.

DISCUSSION

Effect of auxiliary-field diameter on test spectral sensitivity: improved isolation of the opponent-colour system

For all three subjects, the test spectral sensitivity curves obtained on the 10.0-deg white auxiliary field [Fig. 1(a)–(c), open circles joined by broken curves] show the typical three (fairly smooth) peaks, here at about 435, 525 and 580–620 nm (compare Sperling and Harwerth, 1971; King-Smith and Carden, 1976). As conjectured, a marked improvement in the delineation of those peaks occurred when the white auxiliary field was reduced in diameter to 1.05 deg so that it was spatially coincident with the test field [Fig. 1(a)–(c), open circles joined by continuous curves]. In the long-wavelength end of the spectrum, a clear peak emerges at 605–615 nm. Also, the notch in the test spectral sensitivity curve near 580 nm, supposedly characteristic of the opponent-colour system, is considerably deepened in the presence of the 1.05-deg auxiliary field: the increase in depth is 0.35–0.50 log units for each of the three observers. This and the sharpening of the peaks in the region of 520 and 610 nm were achieved in two subjects (D.H.F. and R.S.S.) with little shift in overall test sensitivity. The position of the peak of the short-wavelength sensitive mechanism remained unchanged at about 435 nm.

Operationally, it appears that an improved isolation of the opponent-colour system can be achieved by combining the two techniques of spatial and achromatic desensitization of the non-opponent system. Such a technique may have clinical applications in the determination of spectral sensitivities of the opponent-colour system in patients with inherited or acquired defects of the visual pathway (e.g. Verriest and Uvijls, 1977; Zisman *et al.*, 1978; Klingaman *et al.*, 1980; Alvarez *et al.*, 1980; Zrenner and Krüger, 1981). The use of simple detection thresholds rather than thresholds for the appearance of colour, the latter sometimes associated with difficulties involving criterion effects and constraints on stimulus excursion, may be preferable for determining opponent-colour test spectral sensitivity curves with inexperienced subjects.

Sharpened field spectral sensitivities

The lower three curves joining the solid symbols in each of Fig. 1(a)–(c) show, for the three subjects, field spectral sensitivities for the long-, medium, and short-wavelength sensitive mechanisms on the 1.05-deg white auxiliary field. The most obvious change in curve shape relative to the corresponding Stiles's mechanism is for the long-wavelength sensitive mechanism. Stiles's Π_5 normally has a smooth peak at about 575 nm; instead, with the small auxiliary field, the long-wavelength sensitive mechanism is narrowed with a sharp peak at about 620 nm. On the short-wavelength side, a subsidiary peak is also apparent, the magnitude and position of which varied from subject to subject (compare field spectral sensitivities obtained on monochromatic fields, Foster, 1981, Figs 1(b) and 6). For two subjects (R.S.S. and S.G.), this subsidiary peak is large enough to define a dip at about 580 nm. [Finkelstein and Hood (1981, 1982) have also shown a dip at 580 nm in field spectral sensitivities obtained in a different experimental paradigm: a test flash was presented on a large white auxiliary field and the main conditioning field was flashed, with onset coincident with that of the test flash.]

Minimum half-height half-bandwidths for the spectrally sharpened long-wavelength sensitive mechanism were about 25 nm [Fig. 1(a) and (b)]. Action spectra obtained electrophysiologically from red-sensitive colour-opponent cells in rhesus monkey

show similar subsidiary maxima or shoulders on the short-wavelength side (e.g. de Monasterio *et al.*, 1975; Dow and Gouras, 1973), and comparable values for half-height half-bandwidths for these action spectra have been reported by de Monasterio and Schein (1982) at various levels in the visual pathway of the monkey (compare Zeki, 1980). VEP measurements (Regan, 1974) of action spectra, under conditions which it now seems may have facilitated opponent-colour responses, have also shown a shoulder on the short-wavelength side of the red-sensitive mechanism.

The effects of the spatially coincident auxiliary field on the medium-wavelength sensitive mechanism were less marked. (Asymmetries in the interactions of long- and medium-wavelength signals have also been reported by Stromeyer *et al.*, 1978a and Klingaman and Zrenner, 1982.) But, like the spectrally sharpened long-wavelength sensitive mechanism, the medium-wavelength sensitive mechanism shows evidence of a subsidiary peak or shoulder, here on the long-wavelength side. For two subjects (R.S.S. and D.H.F.), there is also evidence of a complementary shoulder on the short-wavelength side of the medium-wavelength sensitive mechanism. The field spectral sensitivity curve of the short-wavelength sensitive mechanism underwent no apparent sharpening.

The notion that field spectral sensitivities, like those of Fig. 1, obtained on an auxiliary field coincident with the test field represent activity involving the opponent-colour system has been argued previously (Foster, 1981) for data obtained with a monochromatic auxiliary field. The absence of sharpening of the field spectral sensitivity curve of the short-wavelength sensitive mechanism was explained there by the hypothesis that this mechanism inputs signals only to the opponent-colour system (Guth *et al.*, 1968; Mollon and Krauskopf, 1973; Smith and Pokorny, 1975; Stromeyer *et al.*, 1978b; 1979; Mollon and Polden, 1979; Polden and Mollon, 1980).

Comparison of test spectral sensitivity with the upper envelope of field spectral sensitivities

It is evident that, with the 1.05-deg auxiliary field, the wavelengths for maxima in test sensitivity correspond well to the wavelengths for maxima in the field spectral sensitivities of the long-, medium- and short-wavelength sensitive mechanisms. Moreover, when the vertical positions of the field curves were allowed to vary, the upper envelope of those curves provided a close fit to the corresponding test spectral sensitivity curve; the SD associated with the difference between the two curves was less than or equal to 0.11 log units (with 3 d.f. associated with the fit), for all subjects (Table 1). These SDs are larger than the SEMs associated with mean test and field sensitivities, and could presumably be reduced by introduction of probability summation effects or other adjustments to the model, with a concomitant increase in the number of degrees of freedom. Note that little relative displacement of the field curves for the long- and medium-wavelength sensitive mechanisms was required to make the fit to the medium-to-long wavelength section of the test spectral sensitivity curve on the 1.05-deg auxiliary field. In particular, the notch near 580 nm in the latter curve was reproduced in the corresponding section of the upper envelope of the long- and medium-wavelength field curves (Fig. 1), *without adjustment to their vertical positions**.

The rationale for allowing vertical position of the field curves to vary, when they were fitted to the test curve, was based on the assumption that the opponent-colour channel giving rise to a particular field curve had a level of adaptational sensitivity quantified by an unknown "Weber–Fechner fraction" (defined for a given set of stimulus conditions, flash duration, auxiliary-field intensity, etc). Estimates for a quantity (in log units) related to the Weber–Fechner fraction for each mechanism can be derived from the additive constants shown in Table 1 by a change in the sign of the constant and the addition of 0.3 log units (the elevation in test threshold produced by the main conditioning field). Note that it is the relative values of the estimates that are more important here; absolute values are likely to be distorted by the elevating effect of the steady auxiliary field. Direct comparison with the Weber–Fechner fraction for Stiles's mechanisms π_1, π_4 and π_5 (Stiles, 1959) is not possible, for the reason just mentioned, and because Stiles's data were defined for a 1-log-unit elevation in test threshold by the main conditioning field. Nevertheless, the data derived from Table 1 do show some similarities with Stiles's data. Thus, the Weber–Fechner fraction for the short-wavelength sensitive mechanism is higher than those for the sharpened medium- and long-wavelength sensitive mechanisms, and the latter two mechanisms have similar values. A complicating factor in any more detailed analysis, however, is that the contribution of direct adaptation at receptoral (as opposed to post-receptoral) sites is presently unclear (see below).

As Stiles assumed in the case of π mechanisms (Stiles, 1953, 1959), the coincidence of test and field spectra is a critical property in establishing the unitary nature of a colour mechanism. The present suggestion that opponent-colour channels may have adaptational sites which have the same spectral sensitivity as that determined by direct test measurement is based on three factors: first, the sharpening of field spectral sensitivity curves obtained on coincident auxiliary fields is controllable by such factors as the

*The notch near 580 nm in the envelope of the sharpened field spectral sensitivity curves of the long- and medium-wavelength sensitive mechanisms should not be confused with the notch observed for some subjects in the sharpened field spectral sensitivity curve of the long-wavelength sensitive mechanism (Fig. 1), also observed by Finkelstein and Hood (1981, 1982) in field spectral sensitivity curves obtained with the flashed-field paradigm.

duration, relative size and wavelength of the test flash commensurate with the supposed characteristic properties of the opponent-colour system (Foster, 1981); second, the test spectral sensitivity obtained on a coincident auxiliary field is very close to that determined with a colour-detection criterion (compare present test data with those of King-Smith and Carden, 1976); third, under the same experimental conditions, test and field spectra are closely congruent, both locally, in the positions of the maxima along the wavelength scale, and over the full spectrum, when possible differences in channel sensitivity are taken into account. (Note that it is not claimed here that the apparently similar opponent-colour interactions revealed in test and field spectra are necessarily invariant under changes in adaptational state, see e.g. Sperling and Harwerth, 1971.)

The detailed situation is almost certainly more complicated than that outlined above: although the fall-off in sensitivity on the short-wavelength side (<610 nm) of the sharpened field spectral sensitivity curve of the long-wavelength sensitive mechanism (Fig. 1) is probably due to the fall-off in sensitivity at the post-receptoral adaptational site of the corresponding opponent-colour channel, it may not be true that the fall-off on the long-wavelength side (>620 nm) is due entirely to the same processes. Rather, it might be reasoned that the latter fall-off is the result of direct changes in receptor sensitivity (de Monasterio *et al.*, 1975; J. D. Mollon, personal communication). Recall, however, that field spectral sensitivities were determined under conditions intended to cause less adaptation of receptors than of the opponent-colour system. It should be emphasized that receptoral adaptation need not always be insignificant.

The disconfounding of adaptational effects at receptoral and post-receptoral sites (or groups of sites) by psychophysical experiment may not in general be easy (see e.g. King-Smith and Kranda, 1981), although, for the short-wavelength pathway, substantial analysis has been possible (Pugh and Mollon, 1979). More direct electrophysiological techniques have been used involving the local electroretinogram (e.g. Boynton and Whitten, 1970; Valeton and van Norren, 1979). In the present case, exploratory theoretical modelling has suggested that a plausible "red-green" difference signal that fits the short-wavelength fall-off (<610 nm) also fits the immediate long-wavelength fall-off (>620 nm) (Foster and Snelgar, 1983).

One approach to testing the hypothesis of identical test and field spectral sensitivities for opponent-colour channels is to determine whether those changes in stimulus conditions that affect the shape of the test spectral sensitivity curve, or some section of it, affect similarly the shape of the upper envelope of the field spectral sensitivity curve. It is pertinent that the field curves for the long- and medium-wavelength sensitive mechanisms are, without vertical adjustments, almost in their correct relative positions for their upper envelope (from 500 to 700 nm) to fit the test spectral sensitivity curve (Fig. 1). Dr J. D. Mollon has suggested (personal communication) that the position of the notch in the test spectral sensitivity curve, near 580 nm in Fig. 1, may vary with the colour temperature of the coincident auxiliary field. If this is so, and the present hypothesis concerning the correspondence of test and field spectra is correct, then the notch in the upper envelope of the field curves should shift in the same way as for the test curve. In fact, if the sharpening of individual field curves is not much altered by small changes in chromaticity of the white auxiliary field, then a more precise prediction is possible, as follows. If a small amount of red light is added to the white auxiliary field, then the field curve for the long-wavelength sensitive mechanism should move down relative to the curve for the medium-wavelength sensitive mechanism and the notch in the envelope of the field curves and in the test curve should move to longer wavelengths. Conversely, if the auxiliary field is made more green-blue, then the notch in the field envelope and in the test curve should shift to shorter wavelengths.

In conclusion, we note that the initial speculation mentioned by Stiles (1978, p. 5) concerning the composition of test spectral sensitivities on white backgrounds may still prove to be relevant (at least for the situation of coincident test and background fields), except that the underlying "component curves of fixed shape" might now be interpreted as corresponding, over most of the wavelength range, to the sharpened field spectral sensitivity curves of opponent-colour mechanisms.

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