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CHANGES IN FIELD SPECTRAL SENSITIVITIES OF RED-, GREEN- AND BLUE-SENSITIVE COLOUR MECHANISMS OBTAINED ON SMALL BACKGROUND FIELDS

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Abstract—When *field spectral sensitivities* of the red- and green-sensitive *colour mechanisms* are determined in the presence of a small steady *background field* (auxiliary conditioning field), spatially coincident with the test field, the resulting curves may be found to be narrowed and shifted away from each other on the wavelength axis. These "sharpened" curves tend to peak at wavelengths of 605 nm and 530 nm respectively. This investigation determines spectral sharpening for variations in the intensity, wavelength, and size of the auxiliary conditioning field, and for variations in the wavelength and duration of the test flash. The following results were obtained.

(1) The intensity-wavelength dependence of an auxiliary field that produces a constant spectral sharpening of the red-sensitive mechanism is indistinguishable from the sharpened field spectral sensitivity curve of the green-sensitive mechanism.

(2) The wavelengths of the test flash at which maximum spectral sharpening of the red- and green-sensitive mechanisms occurs are 610–620 nm and 530 nm respectively.

(3) Spectral sharpening is reduced or eliminated when the test flash has short duration.

(4) No spectral sharpening is apparent at moderate-to-high intensities for the blue-sensitive mechanism.

(5) The variation of spectral sharpening with auxiliary-field size depends strongly on test-field size. This dependence could be made approximately constant when data were scaled according to *cortical magnification factor M*.

(6) Spectral sharpening is abolished, or severely diminished, when the auxiliary field is presented dichoptically.

These findings are considered in relation to an *opponent-process theory* of colour encoding, the site of the coincident auxiliary-field effect and other data on *interactions* amongst colour mechanisms.

INTRODUCTION

In an extensive series of studies, Stiles made use of the two-colour threshold method to derive the *field spectral sensitivities* of long-, medium- and short-wavelength sensitive colour mechanisms of the human eye (Stiles, 1978; see Enoch, 1972, for review). For each colour mechanism defined in these measurements its field spectral sensitivity is evaluated by determining, at each wavelength, 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 (this multiple being typically 1 log unit). For the short-wavelength sensitive mechanism, the use of a short-wavelength test flash is not in itself sufficient to ensure detection solely by that mechanism, and a fixed medium-to-long wavelength *auxiliary* conditioning field is usually introduced to secure adequate suppression of the long- and medium-wavelength sensitive mechanisms. To obtain the field spectral sensitivities of the latter mechanisms, it suffices to use long- and medium-wavelength test flashes respectively, without an auxiliary conditioning field.

Although more than three colour mechanisms were eventually derived in Stiles's measurements, those mechanisms designated as π_5 (long-wave), π_4 (medium-wave) and π_3 (short-wave) have been shown to give close fits to the results of cone microspectrophotometry, after suitable allowance is made for preceptoral absorption losses (Bowmaker *et al.*, 1978; Bowmaker and Dartnall, 1980). These three π mechanisms have also been argued to be good candidates for the fundamental functions of small-field colour matching (Pugh and Sigel, 1978; Estévez and Cavonius, 1977).*

Significantly, if field spectral sensitivity measurements for the long- and medium-wavelength sensitive mechanisms are made in the presence of a small, steady, monochromatic auxiliary conditioning field,

* *Terminology*—Following Stiles, the symbol π_i is used both generically for Stiles's ith mechanism and specifically for test spectral sensitivity; the symbol Π_i is used for field spectral sensitivity. Intensity is expressed as the $\log_{10}$ of the number, 10^N say, of quanta per second per square degree of visual angle, written: N log quanta·sec^{-1}·deg^{-2}; where appropriate, the latter corresponds to a sensitivity: $-$N log quanta·sec^{-1}·deg^{-2}.

spatially coincident with the test field, a marked change may be seen in the shapes of the sensitivity curves (Foster, 1979a, 1980). The peak of the curve for the long-wavelength sensitive mechanism shifts towards longer wavelengths and the peak of the curve for the medium-wavelength sensitive mechanism shifts towards shorter wavelengths. Figure 1 shows typical results for relatively high-intensity coincident auxiliary fields (filled circles), and, for comparison, results for zero auxiliary field (unfilled circles). The data in Fig. 1(a) are for the medium-wavelength sensitive mechanism, for which the test flash had wavelength 516 nm, and in Fig. 1(b) for the long-wavelength sensitive mechanism, for which the test flash had wavelength 664 nm. The continuous curves in (a) and (b) show Stiles's average curves Π_4 and Π_5 (from Wyszecki and Stiles, 1967, Table 7.6).

This displacement and narrowing of the spectral sensitivity curves, hereafter referred to as *spectral sharpening*, may be conveniently characterized by the difference in field sensitivities, at two suitable wavelengths, measured before and after introduction of the coincident auxiliary field. Thus, for the long-wavelength sensitive mechanism, the difference in field sensitivities at 657 nm and 465 nm (arrowed on the abscissa in Fig. 1b) changes from -0.4 log quanta·sec^{-1}·deg^{-2} without the auxiliary field (i.e. sensitivity at 657 nm is 0.4 log quanta·sec^{-1}·deg^{-2} lower than that at 465 nm) to 0.6 log quanta·sec^{-1}·deg^{-2} with the auxiliary field (i.e. sensitivity at 657 nm is 0.6 log quanta·sec^{-1}·deg^{-2} higher than that at 465 nm). The net change in sensitivity difference is thus 1.0 log quanta·sec^{-1}·deg^{-2}. For the medium-wavelength sensitive mechanism (Fig. 1a), the corresponding change in sensitivity difference at 465 nm and 620 nm is 0.7 log quanta·sec^{-1}·deg^{-2}.

Noticeable spectral sharpening effects, albeit smaller than those illustrated in Fig. 1, can also be obtained with weak auxiliary fields, which, for example, raise test-flash threshold by just 0.1 log units (Foster, 1979a). The effect is manifestly not due to "bleaching" adaptation (Rushton, 1965; Hayhoe, 1979a), nor is it due to a transition to the high-intensity π mechanisms π'_4 and π'_5 (Stiles, 1959).

One explanation of spectral sharpening has been tentatively proposed by the present author (see review by Mollon, 1980) within the framework of an opponent-process theory of colour vision (see, for example, Hurvich and Jameson, 1957; Jameson, 1972; Guth and Lodge, 1973; King-Smith and Carden, 1976;

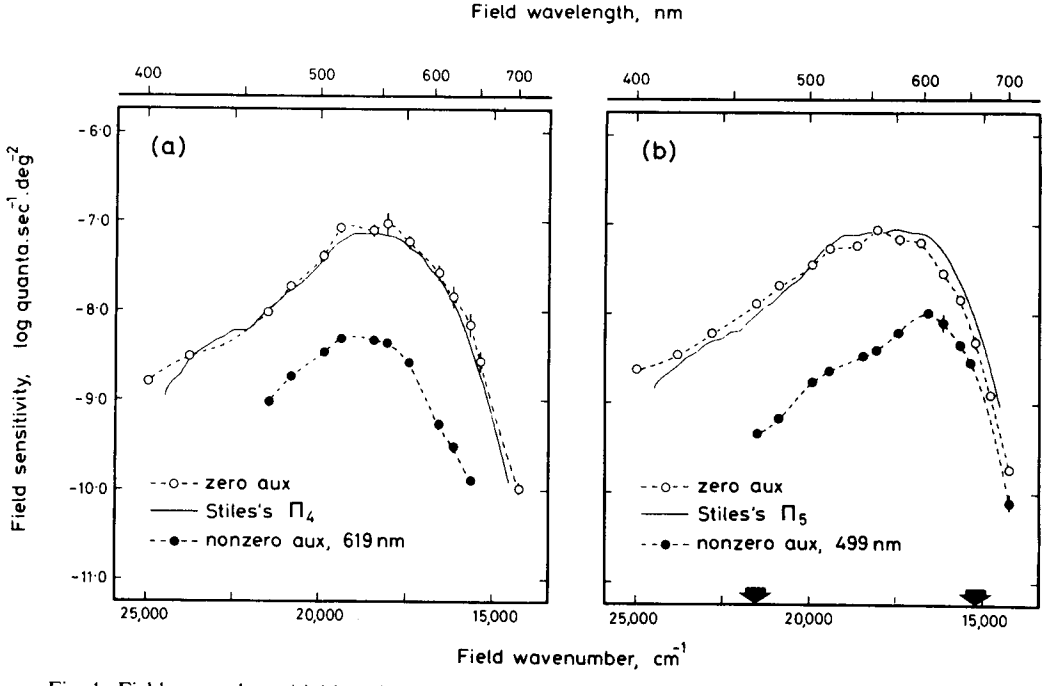

Fig. 1. Field spectral sensitivities of (a) the medium-wavelength sensitive mechanism and (b) the long-wavelength sensitive mechanism determined with zero (unfilled circles) and nonzero (filled circles) steady auxiliary conditioning fields concident with the test field. The reciprocal of the intensity of a 10-deg main conditioning field necessary to raise test flash (increment) threshold by 0.3 log units is plotted against the wavenumber of the main field. In (a) the test flash had wavelength 516 nm and the auxiliary field had wavelength 619 nm and intensity 9.12 log quanta·sec^{-1}·deg^{-2}; in (b) the test flash had wavelength 664 nm and the auxiliary field had wavelength 499 nm and intensity 8.47 log quanta·sec^{-1}·deg^{-2}. The test flash had duration 200 msec and angular subtense 0.15 deg in all conditions. Each point is the mean of six readings and the vertical bars show ± 1 SEM where this is sufficiently large. The continuous curves in (a) and (b) show Stiles's average Π_4 and Π_5 (from Wyszecki and Stiles, 1967, Table 7.6) adjusted vertically in a weighted least-squares fit over the whole wavelength range. No correction has been made for prereceptoral absorption losses. Subject: D.H.F. (Adapted from Foster, 1980.)

Ingling and Tsou, 1977). In such a theory, there are usually assumed to be two types of encoding system, an achromatic system in which cone signals are combined with the same sign, and a chromatic system in which cone signals are combined with different signs. Typically, the achromatic "non-opponent" system encodes luminance and the chromatic "opponent-colour" system encodes hue. There has been much discussion in the literature concerning the precise functional nature of these two systems, and some controversy has arisen over the most appropriate characterization of their spatio-temporal properties (Ingling, 1978; King-Smith and Carden, 1978). For the moment, suppose (following King-Smith and Carden, 1976) that the spatial acuity of the non-opponent system is higher than that of the opponent-colour system (van der Horst *et al.*, 1967; Hilz and Cavonius, 1970). Given this, the non-opponent system should then be more vulnerable to the high spatial-frequency masking that should occur at the coincident edges of the test and auxiliary fields (see, for example, Sternheim *et al.*, 1972; see also Lennie and MacLeod, 1973). If this masking were sufficiently great, the threshold of the non-opponent system should be raised above (or, equivalently, its sensitivity reduced below) that of the opponent-colour system, and detection of the test flash then determined, either mainly or exclusively, by the opponent-colour system. The spectral sensitivities shown in Fig. 1 would then correspond to the field action spectra of the "red–green" channel of the opponent-colour system at some level of activity determined by the intensity and wavelength of the auxiliary field.

Clearly, this is not the only interpretation of spectral sharpening induced by an auxiliary field coincident with the test field, nor the only interpretation based on opponent interactions between colour mechanisms, but it does suggest a number of immediately testable hypotheses, some of which are considered here. In this study, sharpening of the spectral sensitivity curves of the red- and green-sensitive mechanisms* was measured for variations in the intensity, wavelength, and size of an auxiliary conditioning field, and for variations in the wavelength and duration of the test flash. In addition, the effects on spectral sharpening of dichoptic presentation of the auxiliary field were examined, and measurement made for spectral sharpening of the blue-sensitive mechanism.

It should perhaps be emphasized that the present study is intended primarily to reveal some of the qualitative characteristics of the effect and no attempt is made at this stage to model in detail any of the underlying functional processes (compare Ingling and Tsou, 1977; Guth and Lodge, 1973).

* The terms "red-", "green-" and "blue-sensitive mechanism" respectively will be used to cover both the long-, medium- and short-wavelength sensitive mechanisms (π_5, π_4 and π_3) and the corresponding "mechanisms" with sharpened field spectral sensitivities.

METHODS

Stimuli

The test flash was disc-shaped and, depending on the experiment, subtended either 0.15 deg or 1.05 deg at the eye and had duration either 200 msec or 20 msec. The test flash was presented on a steady disc-shaped auxiliary conditioning field, the diameter and intensity of which are given below. A variable-intensity main conditioning field, dia 10 deg, was also present. The stimuli were all concentric and were located at the middle of a 3-deg square array of four tiny lights forming the fixation display. A typical stimulus configuration is schematized in Fig. 2(a). Spectral compositions of the stimuli are given below.

Apparatus

The stimuli were produced by a three-channel Maxwellian-view optical system schematized in Fig. 2(b). Channel 1 gave rise to the test flash; channels 2 and 3 gave rise to the main and auxiliary conditioning fields respectively. The single light source LS was a 24 V 150 W tungsten-halogen lamp, with a compact filament, run from a regulated d.c. power supply. Light was taken from both sides of LS and collimated by lenses L_1 and L_2. The left-hand beam was divided by the semi-reflecting plate SR_1, and the three beams passed through compensated neutral density wedges W_1, W_2 and W_3 and then brought to intermediate foci by lenses L_3, L_4 and L_5 at the stops S_1, S_2 and S_3. The beams were recollimated by lenses L_6, L_7 and L_8, and, after passing through interference filters IF_1, IF_2 and IF_3, transilluminated the stimulus masks A_1, A_2 and A_3. The three beams were recombined, free of ghost images, by the biprisms B_1 and B_2. The lenses L_9 and L_{10} brought the beams to their respective foci at 2-mm artificial pupils P_1 and P_2, each of which was completely filled with light. Stability of head position was maintained with the aid of a dental bite-bar. Precautions were taken to minimize instrumental stray light.

Light output of the source LS was continuously monitored with a silicon photodiode; drift in absolute light level over one hour did not exceed 0.03% of the mean value. The colour temperature of the lamp before filtering was 4400 °K. Transmittances of the compensated wedges W were controlled by pulse-driven d.c. motors which adjusted wedge positions. Additional density was introduced with Wratten neutral density filters.

Glass diffusing plates were inserted at stops S_2 and S_3 to ensure the overall spatial uniformity of the main and auxiliary conditioning fields. The masks A were produced photographically (Kodalith film) and each was mounted in a precision X-Y slide. A silent electromagnetic shutter ES, controlled by an electronic timer, interrupted the test-flash beam at S_1. Rise and fall times of each flash were less than 2 msec.

The spectral compositions of the channels were controlled with Balzers B40 interference filters with

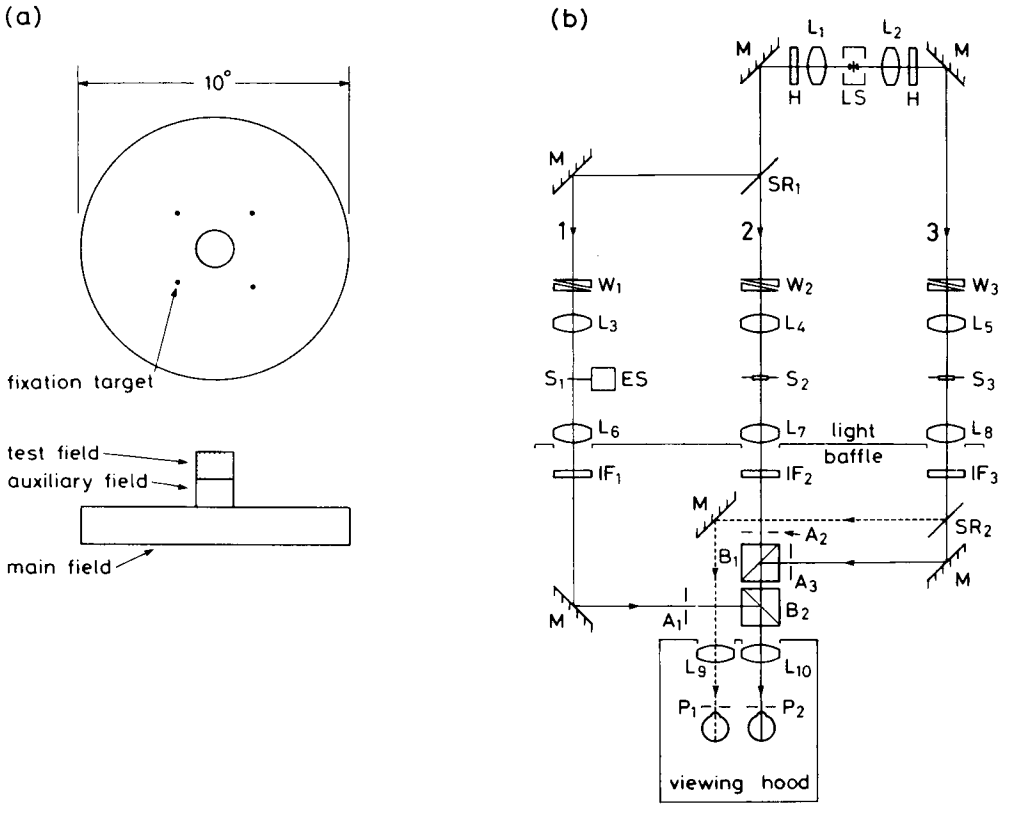

Fig. 2. (a) A typical stimulus configuration. In all experiments except one, the test and auxiliary fields were spatially coincident, both subtending either 0.15 deg or 1.05 deg. (b) Optical system. LS, light source; L, achromatic lens; H, heat-reflecting filter; M, front-silvered mirror; SR, semi-reflecting plate; W, compensated neutral density wedge; S, stop; ES, electromagnetic shutter; IF, interference filter; B, beam-splitter cube; A, stimulus mask; P, artificial pupil.

peak-transmittance wavelengths ranging from 401 nm to 702 nm. Half-height bandwidths of these filters were each not more than 11 nm except for the 401 nm filter, which had bandwidth 14 nm (see *Calibrations*). To reduce unwanted long-wavelength transmission by interference filters with peak-transmittance wavelengths less than 465 nm, a violet gelatin blocking filter, Ilford, No. 621, was attached to each of these filters when they were used to produce conditioning fields for test flashes detected by the red- and green-sensitive mechanisms. Under these conditions, transmittances were thus reduced to between -6.5 and -7.0 log units of maximum over the range 550–700 nm. The heat-reflecting filters H (Balzers, Calflex) had transmittances -1.5 log units of maximum outside the band 400–750 nm.

For some experiments, a monochromator with a holographically recorded grating (symmetrical Czerny-Turner configuration, Applied Photophysics, M300) was used instead of interference filters IF_1 to control the spectral composition of the test flash. The exit slit of the monochromator was set to provide a 10 nm bandpass. Stray-light levels were less than -5.9 log units of the peak transmittance.

Calibrations

Absolute and relative spectral outputs of each channel were measured at the eye position. Calibrations were made by means of a low-noise EG & G silicon photodiode (PV-100A), operated in the photovoltaic mode and connected to a linear amplifier and digital voltmeter. A non-polarizing Schott glass i.r.-blocking filter (BG21) was mounted in front of the photodiode. Departures from linearity of the photodiode system over a 3-log-unit intensity range were less than 0.005 log units.

The absolute and relative spectral responsivities of the photodiode system were determined with a Hilger–Schwarz vacuum thermopile (FT16) with silica window. Additional precautions were taken against leakage of non-visible radiation in the calibrating system. The responsivity of the thermopile itself was calibrated both absolutely and spectrally by the National Physical Laboratory. Departures from spectral uniformity were less than 0.3%.

An independent calibration of the photodiode system was also made with a Ferranti silicon photodiode (MS601) and a linear amplifier used in an earlier study (Foster, 1979a). The latter system had been cali-

brated by Dr B. H. Crawford against a Hilger–Schwarz vacuum thermopile also calibrated at the National Physical Laboratory. The principal calibration and this secondary calibration of the EG & G photodiode system differed in relative spectral terms by no more than 0.03 log units within the range 430–670 nm (0.05 log units outside), and absolutely by 0.09 log units. The principal calibration only was used in the calibration of the present optical system.

The wavelength scale, stray-light and band-pass characteristics of the monochromator were calibrated with light from a low-pressure mercury lamp and a He–Ne laser (results summarized in *Apparatus*). Spectral transmittance curves of the interference filters and gelatin blocking filters were measured on independently calibrated Perkin-Elmer i.r. and u.v.-visible scanning spectrophotometers. For short-wavelength interference filters (peak transmittance wavelengths ≤ 465 nm), transmittance at 600 nm was less than -3.0 log units of maximum, and, with blocking filters attached, transmittance was further reduced by a factor of -4.0 log units (results summarized in *Apparatus*).

Neutral density wedges and filters were calibrated *in situ* at each of the wavelengths used in each of the channels. Computational approximations for the 3-log-unit curves of density vs wedge-reading at each wavelength entailed r.m.s. errors of less than 0.002 log units for the main-field channel (No. 2) and less than 0.006 log units for the other channels.

Procedure

General. At the beginning of each session, the positions of the stimulus masks were adjusted both transversely (X-Y) and longitudinally so that they were seen by the subject to be concentric and in sharp focus. All measurements were made foveally, and subjects dark-adapted for ten minutes at the start of each experimental session. Viewing was, except in one experiment, monocular, and each subject fixated the centre of the fixation display with the right eye. The presentation of the stimulus flash was controlled by the subject. Stimuli could not be presented more rapidly than once every 2 sec. Depending upon the experiment, intensities of the test flash or of the main conditioning field were adjusted by the subject using a push-button control box. (No non-visual feedback on current wedge position was thus available to the subject.)

All threshold measurements were made by a method of adjustment (see below), and the final setting to be recorded was always approached from subthreshold values. Mean threshold values were based on four or six such measurements. (Forced-choice discrimination measurements were occasionally also performed as controls.)

Field spectral sensitivity measurements. Field sensitivity measurements were made by a direct method of field adjustment (see de Vries, 1946). In this technique, the test-flash intensity is raised by a fixed amount (0.3 log units here unless otherwise noted) above absolute threshold (or increment threshold if the auxiliary field is present), and the main 10-deg conditioning field then introduced and its intensity adjusted by the subject to bring the test flash to threshold.

Particular care was exercised to avoid changes in main-field intensity that could give rise to transient adaptation effects (Mollon and Polden, 1977). Thus:

(1) Test flashes were presented only when the eye was adapted to the given main conditioning field.

(2) A sequence of three consecutive field-intensity settings was recorded only when the range of those settings was less than about 0.1 log units.

(3) As a further precaution, measurements were made in runs with decreasing and then increasing (or vice-versa) values of the wavelength of the main conditioning field, in order to counterbalance for order and carry-over effects.

Each mean field sensitivity determination was based on six measurements (or 12 if the counterbalanced runs were repeated).

This procedure for determining field spectral sensitivities is faster than the traditional method (see Stiles, 1978) using threshold-vs-intensity (t.v.i. or t.v.r.) curves obtained for the same range of wavelengths of the main conditioning field. Moreover, it has the advantage that a complete spectral sensitivity function may be derived in one experimental session.

Mollon and Polden (1977) and Sigel and Pugh (1980) have, however, postulated a number of theoretical difficulties associated with the use of a direct field-adjustment method. The hypothesized difficulties are related to phenomena such as transient tritanopia (Mollon and Polden, 1977) and asymmetries in dark- and light-adaptation to the field. They are, *a priori*, unlikely to apply to the counterbalanced, steady-state version of the field-adjustment method used here. Nevertheless, since this report is concerned with changes in the shape of field action spectra derived by this method, it is important that it should be validated empirically. In the Appendix, a control experiment is described in which both the traditional t.v.i. method of Stiles and the present direct field-adjustment method are compared. The two methods gave the same results for unsharpened and for sharpened field spectral sensitivities.

There are two further points that should be noted regarding the dependence of the present experimental findings on methodology. First, as a control on the normality of each subject's colour mechanisms, field spectral sensitivities of the mechanisms π_4 and π_5 were determined by the direct field-adjustment method. Three of the four subjects participating in this study produced spectral sensitivity curves that were well fitted by the corresponding average curves given in Wyszecki and Stiles (1967, Table 7.6); the deviation in spectral sensitivity shown by one subject was traced to abnormal macular pigment absorption, revealed by extrafoveal measurements. Second, most

of the results reported here relate not to the absolute shapes of field spectral sensitivity curves, but to the *changes* in those shapes produced by an auxiliary conditioning field. Variations amongst subjects in the extent of pre-receptoral absorption are not critical with respect to the essential conclusions.

Subjects

Four subjects participated in this study; two female, H.C.B. and R.S.S. and two male, J.N.T. and D.H.F. (the author). Ages ranged from 20 to 35 yr. All had normal colour vision and normal or corrected-to-normal visual acuity. Correcting lenses were placed immediately behind the eyepiece as necessary.

H.C.B. and J.N.T. were unaware of the theoretical background of the study.

EXPERIMENTS

Experiment 1. Intensity effects

(a) Auxiliary-field intensity and spectral sharpening

As explained in the Introduction and Methods, the sharpening of the spectral sensitivity curve of a colour mechanism may be characterized by the change in field sensitivity at two appropriately chosen wavelengths. The present experiment illustrates for the red-sensitive mechanism typical variations in spectral sharpening, measured by this field-sensitivity difference, as auxiliary-field intensity is increased. The wavelength of the test flash was 664 nm and that of the main conditioning field 651 nm and 465 nm. The elevation in test-flash threshold used to determine main-field sensitivity was 0.3 log units (see Methods). The test flash had diameter 1.05 deg and duration 200 msec: the steady spatially coincident auxiliary field had wavelength 531 nm.

Results

Figure 3 shows results for subject J.N.T. Similar results were obtained by subject D.H.F. for a 0.15-deg test flash. The straight line through the data points in Fig. 3 at nonzero auxiliary-field intensities is a weighted least-squares regression line. It is not intended to have any theoretical significance and is included only to show the general linear trend of the data over this restricted range (this trend being highly significant, $P < 0.001$). (Differences in field sensitivities are difficult to measure at auxiliary-field intensities much greater than 9.0 log quanta·sec^{-1}·deg^{-2}, since main-field intensities needed to bring the test flash to threshold become prohibitively great.)

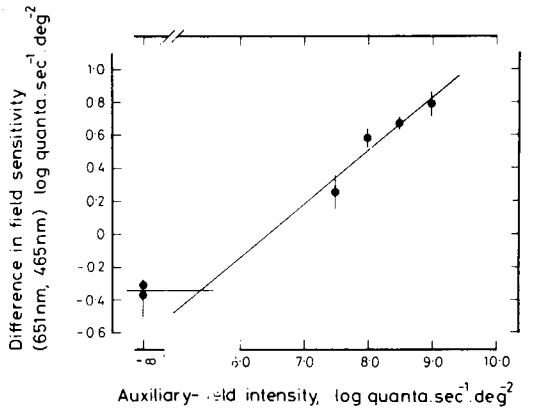

Fig. 3. Difference in main-field sensitivities at the given wavelengths is plotted against intensity of a steady auxiliary conditioning field, wavelength 531 nm, spatially coincident with the test field. The wavelength of the test flash was 664 nm, its dia 1.05 deg and duration 200 msec. Each point is based on twelve readings and the vertical bars show ±1 SEM. Subject: J.N.T.

Comment

Evidently, spectral sharpening of the red-sensitive mechanism increases with intensity of the auxiliary field, at least up to the values used here (see remarks in Experiment 2(b)). The gradient of the sharpening-vs-intensity curve does, however, depend on auxiliary-field wavelength*. This situation contrasts with that for standard t.v.i. curves (see Barlow, 1958; Sigel and Pugh, 1980). The effect of auxiliary-field wavelength on the shape of the field spectral sensitivity curve is examined in the next section. First, there is a methodological question to resolve related to the evaluation of main-field sensitivity. Sensitivity has here been interpreted as the reciprocal of the main-field intensity that, at the chosen wavelength, raises test-flash threshold by a fixed amount, typically 0.3 log units. In the usual measurement of field spectral sensitivities of π mechanisms without an auxiliary field coincident with the test field, the choice of magnitude of this fixed elevation does not (within limits related to the isolation of the mechanism) affect the shape of the curve obtained, only its vertical position. The fact that the measured sharpening of the spectral sensitivity curve induced by the coincident auxiliary field depends upon the intensity of that field might suggest that the observed sharpening should also depend upon the elevation in test-flash threshold.

(b) Effect of magnitude of test-flash elevation

To test the supposition set out above, difference in main-field sensitivities at 651 nm and 516 nm for a 0.15-deg 200-msec test flash, wavelength 610 nm, was determined as a function of the elevation in test-flash threshold used to determine that sensitivity. The intensity of the steady 499 nm auxiliary field coincident with the test field remained fixed throughout at 8.47 log quanta·sec^{-1}·deg^{-2}.

* Spectral sharpening of the green-sensitive mechanism also increases with auxiliary-field intensity. Full spectral sensitivity curves for the red- and green-sensitive mechanisms and an analysis of the intensity dependence of their shapes is to be presented in a subsequent report (D. H. Foster and R. S. Snelgar, in preparation).

Results and comment

Results are shown in Fig. 4. The straight line is a weighted least-squares regression fit (for which there is a highly significant linear trend, $P < 0.001$). Clearly, the smaller the elevation in test-flash threshold used to determine main-field sensitivity, the greater the spectral sharpening that is produced for a given auxiliary-field intensity. In the following experiments, test-flash elevation is fixed at 0.3 log units.

Experiment 2. Effect of auxiliary-field wavelength on spectral sharpening

Two fundamental questions arise in relation to the sharpening of a field spectral sensitivity curve by an auxiliary conditioning field coincident with the test field.

(1) Is the effect a trivial artifact of variations in test-flash detectability resulting solely from variations in contrast of the auxiliary field against the main field? Since the contrast of the auxiliary field depends on both main-field intensity and wavelength, its effect on test-flash detectability could be dependent upon which part of the field spectral sensitivity curve was being determined. If this hypothesis is correct, then auxiliary fields of different wavelength should give rise to different alterations in curve shape. For example, a short-to-medium-wavelength auxiliary field should most strongly affect sensitivity to a long-wavelength main field, whereas a long-wavelength auxiliary field should most strongly affect sensitivity to a short-to-medium-wavelength main field. These hypothesized effects should not be interchangeable by manipulating auxiliary-field intensity. (In preliminary measurements with the red-sensitive mechanism, the variation in contrast of a fixed-wavelength auxiliary field against a main field of variable wavelength and of intensity equated with respect to Π_5 suggests that the above hypothesis is, in any event, an inadequate explanation of spectral sharpening.)

A simple test of this contrast hypothesis is to vary the wavelength of the auxiliary field and at each wavelength determine whether some "standard" sharpened field spectral sensitivity curve can be obtained by adjusting the intensity of the auxiliary field. The facilitation of this potentially protracted procedure depends on the resolution of the second question.

(2) If, at each auxiliary-field wavelength, the intensity of the auxiliary field may be adjusted to produce some "standard" sharpened field spectral sensitivity curve [e.g. for the red-sensitive mechanism as in Fig. 1(b)], then how does the magnitude of this intensity of the auxiliary field vary with its wavelength? That is, what is the action spectrum of the process producing the sharpening of the field spectral sensitivity curve?

Suppose that a standard sharpened field spectral sensitivity curve may indeed be produced at each auxiliary-field wavelength by appropriate adjustment of auxiliary-field intensity. The second question might then be resolved and the results of that used to assist in the resolution of the first.

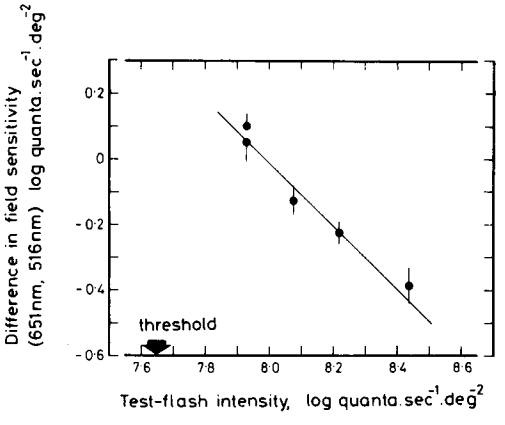

Fig. 4. Difference in main-field sensitivities at the given wavelengths is plotted against the intensity of the test flash, wavelength 610 nm, dia 0.15 deg, and duration 200 msec. The steady auxiliary field coincident with the test field had wavelength 499 nm and intensity 8.47 log quanta·sec^{-1}·deg^{-2}. Each point is based on twelve readings and the vertical bars show ±1 SEM. Subject: D.H.F.

(a) Intensity-wavelength dependence of auxiliary field for constant difference in main-field sensitivity of red-sensitive mechanism at long and short wavelengths

Figure 3 showed a typical increase in spectral sharpening of the red-sensitive mechanism as a function of auxiliary-field intensity. In the present experiment, sections of these sharpening-vs-intensity curves are determined for auxiliary-field wavelengths ranging from 401 nm to 640 nm.

Procedure

The test flash had wavelength 664 nm, dia 0.15 deg and duration 200 msec. The steady auxiliary conditioning field was spatially coincident with the test field and had variable wavelength and intensity. The main conditioning field had dia 10 deg and wavelength either 465 nm or 651 nm. For these conditions, the "standard" spectral sharpening was chosen as 0.3 log quanta·sec^{-1}·deg^{-2} difference in main-field sensitivities at 651 nm and 465 nm (that is, sensitivity at 651 nm is 0.3 log quanta·sec^{-1}·deg^{-2} higher than at 465 nm). This difference represents a shift of 0.6 log quanta·sec^{-1}·deg^{-2} from the zero auxiliary-field condition.

An iterative procedure was used to determine the intensity of the auxiliary field that, at the selected wavelength, produced the required difference in main-field sensitivities at 651 nm and 465 nm. Because of variations in the sharpening-vs-intensity curve (see Experiment 1), a standard "template" for this function

could not be used to facilitate determination of the auxiliary-field action spectrum; see Stiles (1978, p. 19).

The procedure at each auxiliary-field wavelength was as follows.

(1) Absolute test-flash threshold was determined. The auxiliary field was then introduced, its diameter set to 10 deg, and its intensity adjusted to raise test-flash threshold by 0.3 log units (method of adjustment, see Methods). The auxiliary-field diameter was then reduced to 0.15 deg. The auxiliary-field intensity (thus based on the unsharpened field spectral sensitivity curve Π_5) provided the starting point for the next sequence of operations. (The final value of auxiliary-field intensity did not depend on this initial value.)

(2) Test-flash threshold was determined on the coincident auxiliary field (with main field extinguished).

(3) Main fields of 465 nm and 651 nm were in turn introduced and the intensity of each adjusted to raise test-flash threshold by 0.3 log units. (Usual precautions were observed concerning balancing of main-field wavelengths and adjustment of main-field intensities, see Methods.) The difference Δs in main-field sensitivities at 651 nm and 465 nm was computed.

(4) Auxiliary-field intensity was increased or decreased in approx. 0.4-log-unit steps and Δs determined as in (2) and (3), until successive values I_n, I_{n+1} of the auxiliary-field intensity gave sensitivity difference values Δs_n, Δs_{n+1} bracketing the standard value Δs_0 of 0.3 log quanta·sec^{-1}·deg^{-2}.

(5) The intensity of the auxiliary field was then set to a linearly interpolated value:

$$I_{n+2} = ((\Delta s_0 - \Delta s_n)/(\Delta s_{n+1} - \Delta s_n))\cdot(I_{n+1} - I_n)$$

and the actual sensitivity difference Δs_{n+2} redetermined as in (2) and (3). (This measured value Δs_{n+2} obtained from this local linear approximation to I_{n+2} was on all occasions within 0.06 log units of the standard value Δs_0.)

(6) If necessary, a final correction to I_{n+2} was then made by a further linear interpolation, to bring the value of Δs_{n+2} into precise coincidence with Δs_0.

The variance associated with the value of auxiliary-field intensity so determined at each auxiliary-field wavelength was estimated by the same method of local linear approximation to the sharpening-vs-intensity function. It should be noted that although local linear approximations were used in the experimental derivation and fine adjustment of the values for the action spectrum of the auxiliary-field effect, these approximations involve at worst a r.m.s. error of 0.04 log units. (A more important source of error is likely to be drift in test-flash threshold over the course of an experimental run. Without substantially more experimentation, however, any effect of this is difficult to quantify.)

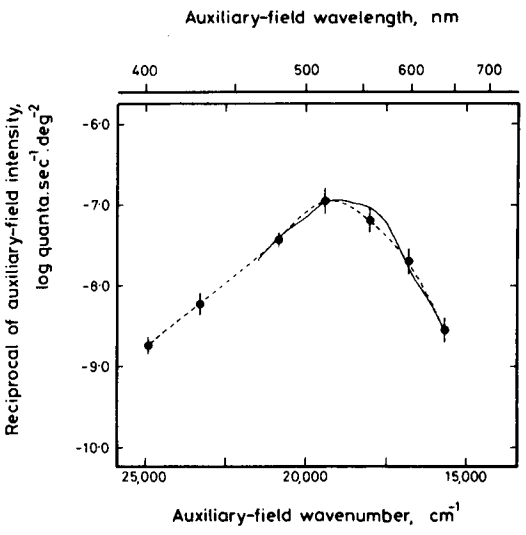

Fig. 5. Action spectrum for spectral sharpening of the red-sensitive mechanism. The reciprocal of the intensity of the steady auxiliary field, coincident with the test flash, necessary to increase the difference in main-field sensitivity of the red-sensitive mechanism at 651 nm and 465 nm by 0.6 log quanta·sec^{-1}·deg^{-2} is plotted against wavenumber of the auxiliary field. The test flash had wavelength 664 nm, dia 0.15 deg and duration 200 msec. The vertical bars show ±1 SEM. The broken curve is obtained by Lagrange interpolation. The continuous curve is the sharpened field spectral sensitivity curve of the green-sensitive mechanism shown in Fig. 1(a), the vertical position of which has been adjusted to give a weighted least-squares fit to the auxiliary-field data. Subject: D.H.F.

Results and comment

Figure 5 shows the measured action spectrum. The reciprocal of the intensity of the auxiliary field required to increase the difference in main-field sensitivity of the red-sensitive mechanism at 651 nm and 465 nm by 0.6 log quanta·sec^{-1}·deg^{-2} is plotted (filled circles) against the wavenumber of the auxiliary field. The vertical bars show ±1 SEM computed as explained above. The broken curve connecting the data points is obtained by Lagrange interpolation. The auxiliary-field action action spectrum clearly peaks at about 520 nm. For comparison, the continuous curve shows the sharpened field spectral sensitivity curve of the green-sensitive mechanism obtained with a 619 nm auxiliary field, intensity 9.1 log quanta·sec^{-1}·deg^{-2} (from Fig. 1a). The latter curve was constructed from the original data by Lagrange interpolation, and is a weighted least-squares fit, by vertical adjustment, to the auxiliary-field data. The fit is good and the unweighted r.m.s. error is 0.12 log units (which is not significant, $\chi^2(4) = 3.00$, $P > 0.5$).

As a control, the unsharpened field spectral sensitivity curve Π_4, obtained under the same conditions, was also fitted, by weighted least-squares, to the auxi-

liary-field action spectrum over the range 480–516 nm (where there is essentially no alteration in the shape of the sensitivity curve of the green-sensitive mechanism). The unweighted r.m.s. error over the whole wavelength range for this fit (not shown in the figure) is 0.36 log units (which is highly significant, $\chi^2(4) = 27.9$, $P < 0.001$). If the fit of Π_4 is extended to the whole wavelength range, the unweighted r.m.s. error is reduced to 0.31 log units (which is still highly significant, $\chi^2(4) = 22.5$, $P < 0.001$). The field spectral sensitivity of the red-sensitive mechanism, spectrally sharpened [Fig. 1(b)] or otherwise, is obviously a poor candidate.

It thus appears that the action spectrum of the process producing the spectral sharpening of the red-sensitive mechanism coincides with that of the spectrally sharpened green-sensitive mechanism.

(b) Field spectral sensitivity of spectrally sharpened red-sensitive mechanism when auxiliary-field intensity is equated with respect to spectrally sharpened green-sensitive mechanism

In the previous section the assumption was made that the difference in field sensitivities of the red-sensitive mechanism at 651 nm and 465 nm is a reliable indicator of the change in overall curve shape. To verify this, complete field spectral sensitivity curves were determined with coincident auxiliary fields of various wavelengths and intensities, equated with respect to a spectrally sharpened green-sensitive mechanism. More generally, such measurements show whether differences in sharpening of a field spectral sensitivity curve arising from changes in auxiliary-field wavelength may be annulled by suitable adjustment of auxiliary-field intensity.

Results and comment

Figure 6 shows three field spectral sensitivity curves of the red-sensitive mechanism determined with different auxiliary fields coincident with the test field. In each case, the 0.15-deg 200-msec test flash had wavelength 664 nm. The wavelengths of the auxiliary fields are indicated. Their intensities were based on the sharpened field spectral sensitivity curve of the green-sensitive mechanism (Fig. 1a). The auxiliary field with wavelength 531 nm had intensity 8.32 log quanta·sec^{-1}·deg^{-2}, that with wavelength 499 nm had intensity 8.47 log quanta·sec^{-1}·deg^{-2}, and that with wavelength 460 nm had intensity 9.12 log quanta·sec^{-1}·deg^{-2}. The middle and lowest curves respectively in Fig. 6 have been shifted downward by 1.0 and 2.0 log units from their correct positions.

The dashed templets (obtained by Lagrange interpolation) are derived from a weighted mean of the three curves, adjusted vertically in a weighted least-squares fit. The similarity in the three spectrally sharpened curves is evident. Each peaks close to 605 nm and each falls off rapidly in relation to Π_5 over medium to short wavelengths. Each also shows a slight dip around 555 nm.

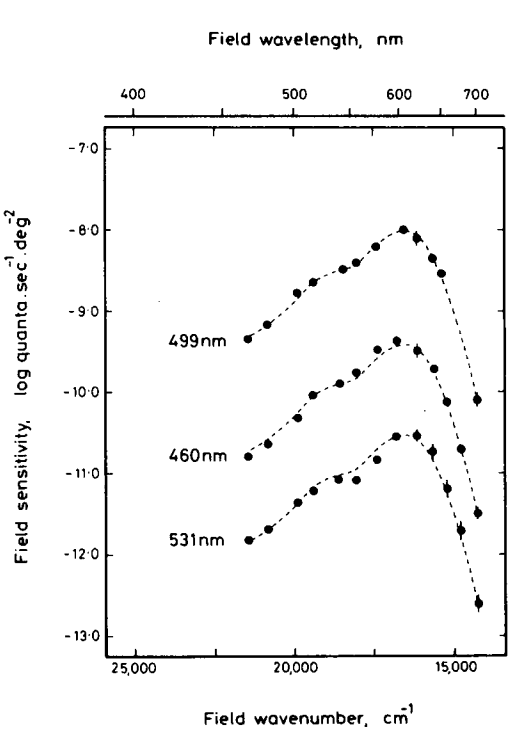

Fig. 6. Field spectral sensitivity curves of the red-sensitive mechanism determined with auxiliary fields of various wavelengths. The reciprocal of the intensity of a 10-deg main conditioning field necessary to raise increment threshold of the 0.15-deg 200-msec test flash, wavelength 664 nm, by 0.3 log units is plotted against the wavenumber of the main field. Data for the middle and lowest curves are displaced downward by 1.0 and 2.0 log units respectively. The wavelengths of the auxiliary fields are indicated; intensities (given in the text) are equated with respect to a sharpened field spectral sensitivity curve of the green-sensitive mechanism. Each point is the mean of six readings and the vertical bars show ± 1 SEM where this is sufficiently large. The broken curves are derived from a weighted mean of the three curves adjusted vertically in a weighted least-squares fit. Subject: D.H.F.

A detailed analysis of the shapes of the curves reveals significant differences between them ($\chi^2(22) = 69.8$, $P < 0.001$), although these differences are small in magnitude. For example, the unweighted r.m.s. error (deviation from the weighted mean) is 0.05 log units. Certainly, if there do exist contrast effects of the kind discussed at the beginning of this section, they are not an important factor in determining sharpening of field spectral sensitivity curves.

Experiment 3. Effect of test-flash wavelength on spectral sharpening

The examples of sharpening of field spectral sensitivity curves given in preceding sections were obtained with just three test-field wavelengths: 664 nm and 610 nm for the red-sensitive mechanism, and 516 nm for the green-sensitive mechanism. (These values were chosen to achieve good isolation of the corresponding unsharpened π mechanism on zero

auxiliary field.) The present experiment illustrates how spectral sharpening depends on test-flash wavelength.

Procedure

Spectral sharpening for the red- and green-sensitive mechanisms was measured for a range of test-flash wavelengths. Which of these mechanisms actually detects the test flash depends on test-flash wavelength, and the range of the latter was therefore restricted to 570–670 nm for the red-sensitive mechanism, and to 480–580 nm for the green-sensitive mechanism. For the red-sensitive mechanism, a 0.15-deg 200-msec test flash with variable wavelength was presented on a fixed spatially coincident auxiliary field, wavelength 531 nm and intensity 8.32 log quanta·sec^{-1}·deg^{-2} (compare data in previous section). The 10-deg main conditioning field had wavelengths μ_1 and μ_2 of 657 nm and 503 nm for subject R.S.S. and 651 nm and 503 nm for subject D.H.F. For the green-sensitive mechanism, the arrangement was similar except that the spatially coincident auxiliary field had wavelength 619 nm and intensity 8.69 log quanta·sec^{-1}·deg^{-2} and the 10-deg main conditioning field had wavelengths μ_1 and μ_2 of 503 nm and 621 nm for both subjects.

For each of these two colour mechanisms, field sensitivity was measured (as in Methods) at the two selected main-field wavelengths and the wavelength of the test-flash varied over the appropriate range.

Results

Figures 7(a) and (b) show results for subjects D.H.F. and R.S.S. respectively. In each case, the filled symbols represent the difference in main-field sensitivities at the selected main-field wavelengths μ_1 and μ_2 plotted against test-flash wavelength for the 619 nm auxiliary field (filled squares), and for the 531 nm auxiliary field (filled circles). The corresponding difference in main-field sensitivities for zero auxiliary field is indicated by the unfilled symbols.

As may be seen, spectral sharpening depends strongly on test-flash wavelength, and the position of maximum sensitivity is clearly defined for each subject. Thus the curve for the 531 nm auxiliary field peaks at 610 nm for subject D.H.F. and at 620 nm for subject R.S.S. The curve for the 619 nm auxiliary field peaks at 530 nm for both subjects.

Comment

It has been assumed that data derived with test-flash wavelengths 480–580 nm on the 619 nm auxiliary field (filled squares in Fig. 7) relate to the spec-

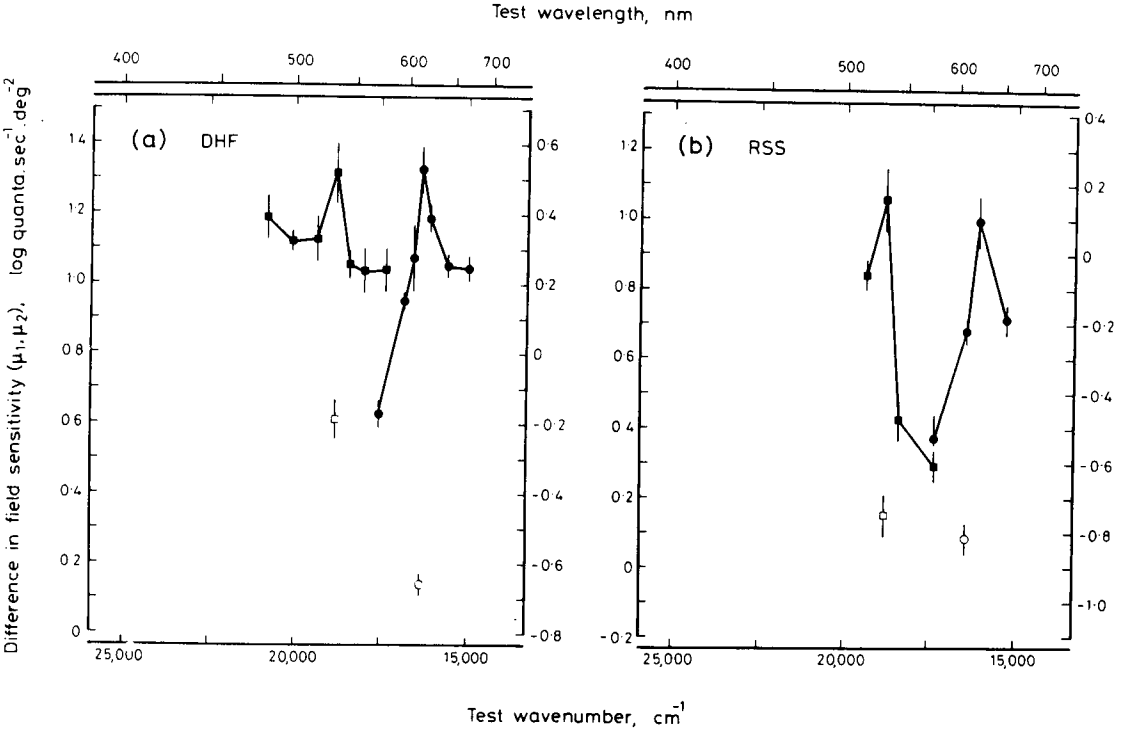

Fig. 7. Effect of test-flash wavelength on spectral sharpening. Difference in field sensitivities at wavelengths μ_1 and μ_2 is shown (filled symbols) as a function of test-flash wavenumber for an auxiliary field, coincident with the test field, of wavelength 531 nm, intensity 8.32 log quanta·sec^{-1}·deg^{-2} (filled circles) and of wavelength 619 nm and intensity 8.69 log quanta·sec^{-1}·deg^{-2} (filled squares). The wavelengths μ_1 and μ_2 of the main conditioning field are given in the text. The difference in main-field sensitivity on zero auxiliary field is indicated by the corresponding unfilled symbols. Each point is the mean of twelve readings and the vertical bars shown ±1 SEM. Subjects: (a) D.H.F. and (b) R.S.S.

trally sharpened green-sensitive mechanism, and the data derived with test-flash wavelengths 570–670 nm on the 531 nm auxiliary field (filled circles in Fig. 7) relate to the spectrally sharpened red-sensitive mechanism. This assumption is supported by the full field spectral sensitivity curves previously obtained for selected test-flash wavelengths: for example, 516 nm for the green-sensitive mechanism (Fig. 1a) and 664 nm for the red-sensitive mechanism (Figs 1b and 6). The effect of small changes in test-flash wavelength only alter the magnitude of the spectral sharpening; as already indicated, large changes (beyond those used here) should shift detection to different mechanisms (except on the long-wavelength side for the red-sensitive mechanism).

In the field spectral sensitivity curves shown in Fig. 1, the peak sensitivity of the spectrally sharpened red-sensitive mechanism is about 605 nm, and that for the spectrally sharpened green-sensitive mechanism is about 530 nm, although the positions of these peaks and the precision with which they may be estimated does depend on the magnitude of the sharpening; compare Fig. 2 in Foster (1979a) with Fig. 1(b) here. (Asymptotic peak values might be theoretically estimated (Sperling and Harwerth, 1971), providing that certain assumptions are made about the nature of the interaction between signals from long- and medium-wavelength sensitive cones.) Nevertheless, the overlap of these field wavelengths for maximum sensitivity with the test wavelengths for maximum sharpening is striking. Discussion of their relationship to other data on opponent-colour processes is postponed until the General Discussion.

Experiment 4. Effect of test-flash duration on spectral sharpening

There is considerable evidence which suggests that the chromatic or opponent-colour system exhibits greater temporal integration, i.e. has lower temporal frequency response characteristics, than the luminance or non-opponent system (de Lange, 1958; Kinney, 1965; Regan and Tyler, 1971; King-Smith and Carden, 1976; Tolhurst, 1977; Stromeyer *et al.*, 1978a; Sternheim *et al.*, 1978). In particular, King-Smith (1975) has proposed explicitly that long-duration test flashes favour detection by the opponent-colour system, whereas short-duration flashes favour detection by the non-opponent system. If the sharpened field spectral sensitivity curves observed in the present experiments were associated with the opponent-colour system, then a reduction of test-flash duration from 200 msec, the value previously used, to much smaller values might be expected to reduce the sharpening effect. Whether or not such a reduction is actually observed presumably depends on how effective the auxiliary field is in securing detection by the opponent-colour system. In any case, there should be no *increase* in spectral sharpening as test-flash duration is reduced.

Procedure

Spectral sharpening for 200-msec and 20-msec test flashes was compared for both the red-sensitive and green-sensitive mechanisms. For the red-sensitive mechanism, a 0.15-deg 607 nm test flash was presented on a steady spatially coincident auxiliary field, which, for both subjects, had wavelength 531 nm and intensity 8.32 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}. As before, the main field subtended 10 deg. Field sensitivity was measured at main-field wavelengths μ_1 and μ_2 of 657 nm and 503 nm. For the green-sensitive mechanism, a 0.15-deg 531 nm test flash was presented on a steady spatially coincident auxiliary field, which, for subject R.S.S., had wavelength 607 nm and intensity 8.59 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}, and, for subject D.H.F., had wavelength 619 nm and intensity 8.69 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}. Field sensitivity was measured for a 10-deg main conditioning field with wavelengths μ_1 and μ_2 of 621 nm and 503 nm.

Results

Figure 8 shows the results. Spectral sharpening, expressed as the difference in main-field sensitivities at the chosen main-field wavelengths μ_1 and μ_2 (see above) is shown (C) for the 200-msec test flash and (B) for the 20-msec test flash, in (a) and (c) for the red-sensitive mechanism, and in (b) and (d) for the green-sensitive mechanism. For comparison, the corresponding difference in field sensitivities is shown (A) for zero auxiliary field (test-flash duration 200 msec).

For both subjects, sharpening of the field spectral sensitivity curves of both red- and green-sensitive mechanisms is strongly diminished by the reduction in test-flash duration ($t(22) \geq 4.29$, $P < 0.001$). In fact, for the red-sensitive mechanism [Figs 8(a) and (c)], difference in field sensitivities with the 20-msec test flash is not significantly different from that with the 200-msec test flash on zero auxiliary field ($t(22) \leq 0.55$, $P > 0.2$, for both subjects). For the green-sensitive mechanism [Figs 8(b) and (d)], the reduction in sharpening is not complete. Difference in field sensitivities is significantly greater at 20 msec on the nonzero auxiliary field than on zero auxiliary field ($t(22) \geq 2.74$, $P < 0.01$, for both subjects).

Comment

As speculated earlier, a reduction in test-flash duration gives rise to a reduction in spectral sharpening of the red- and green-sensitive mechanisms, consistent with there being a shift from detection by the opponent-colour system to detection by the non-opponent system. This result parallels the finding by King-Smith and Carden (1976) for test spectral sensitivities (see further remarks in General Discussion).

The inequivalence of the effects of reduction of test-flash duration for red- and green-sensitive mechanisms may be related to the asymmetric form of their absorbance curves and the values of wavelength and

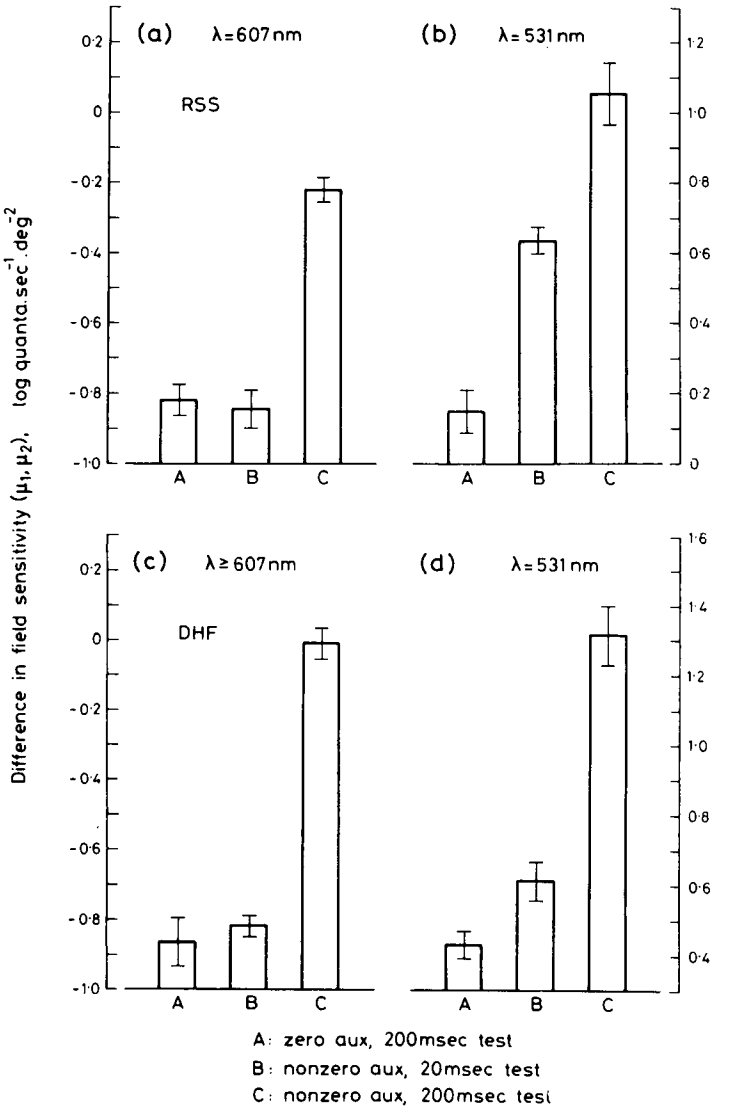

Fig. 8. Effect of test-flash duration on spectral sharpening for (a) and (c) the red-sensitive mechanism and (b) and (d) the green-sensitive mechanism. In each case, difference in main-field sensitivity at wavelengths μ_1 and μ_2 (see text) are shown for (B) 20-msec and (C) 200-msec test flashes on nonzero auxiliary fields and (A) 200-msec test flashes on zero auxiliary field. Wavelengths λ of the 0.15-deg test flash are indicated (for condition A in (c), test-flash wavelength was 664 nm). Wavelengths and intensities of the auxiliary fields are given in the text. Each point is the mean of 12 readings and the vertical bars show ± 1 SEM. Subjects: (a) and (b) R.S.S., (c) and (d) D.H.F.

intensity of an auxiliary field that will produce symmetric effects on the opponent-colour system (J. D. Mollon, 1981, personal communication). Thus, the presumed opposing effects of (a) the auxiliary field in shifting detection to the opponent-colour system, and (b) the short-duration test flash in shifting detection to the non-opponent system need not be the same for the two mechanisms.

Experiment 5. Spectral sharpening of the blue-sensitive mechanism

Several authors have suggested that signals from short-wavelength sensitive cones do not have access to the luminosity channel (Guth *et al.*, 1968; Mollon and Krauskopf, 1973; Smith and Pokorny, 1975; Stromeyer *et al.*, 1978b, 1979). Indeed, Mollon and Polden (1979) and Polden and Mollon (1980) have proposed that the psychophysically defined blue-sensitive mechanism may reveal quite general properties of opponent-colour channels.

The hypothesis under tentative consideration in the present study is that the sharpening of the field spectral sensitivity curves of the red- and green-sensitive mechanisms by an auxiliary field coincident with the test field is the result of a shift from detection by the non-opponent system to detection by the opponent-

colour system. Given that signals from blue-sensitive receptors are indeed transmitted only by the opponent-colour system, then introduction of the coincident auxiliary field should produce no change in shape of the field spectral sensitivity curve of the blue-sensitive mechanism.

Procedure

To ensure that the mechanism detecting a short-wavelength test flash is the blue-sensitive mechanism, it is customary to introduce a large, steady medium-to-long-wavelength auxiliary conditioning field, in the manner of Stiles (1953, 1978). The intensity of this auxiliary field was computed on the basis of a standard t.v.i. curve (see Stiles, 1953) determined with a 200-msec 1.05-deg test flash, wavelength 421 nm, and a concentric, steady 10-deg conditioning field, wavelength 576 nm. (The test-flash diameter of 0.15 deg used for the red- and green-sensitive mechanisms would here be inappropriate because of small-field tritanopia. Note, however, that spectral sharpening of for example the red-sensitive mechanism is obtainable for coincident test and auxiliary fields of dia 0.15 deg or 1.05 deg, see Experiment 1 and Experiment 6.) On the basis of this t.v.i. curve, the 576 nm auxiliary field was fixed in intensity at 9.31 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}, which ensured adequate isolation of the blue-sensitive mechanism (see below). A field spectral sensitivity curve for the 1.05-deg 421 nm test flash was determined on this 10-deg auxiliary conditioning field in the usual fashion (Methods). The auxiliary field was then reduced in diameter to 1.05 deg so that it was spatially coincident with the test field and the field spectral sensitivity curve redetermined.

Results

Results for subjects D.H.F. and R.S.S. are shown in Figs 9(a) and (b) respectively. In each figure, field spectral sensitivity on the 10-deg auxiliary field is shown by the unfilled circles, and that for the coinci-

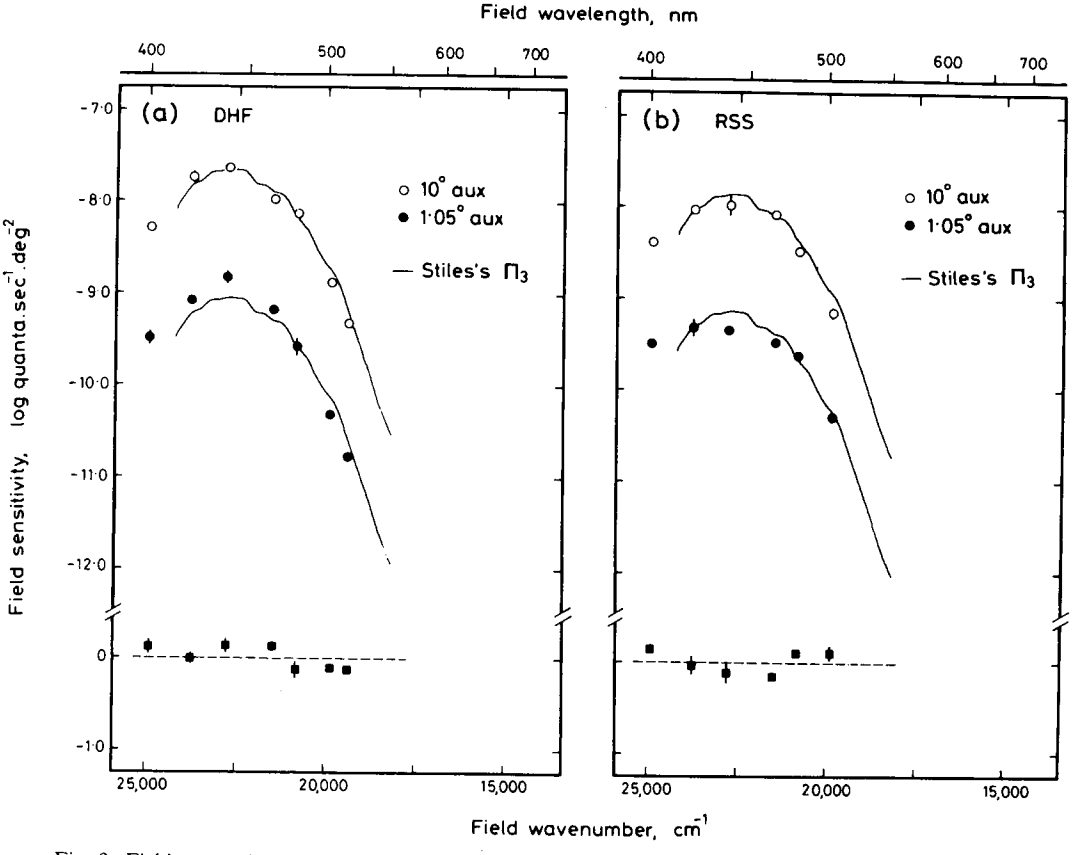

Fig. 9. Field spectral sensitivity of the blue-sensitive mechanism for a 10-deg auxiliary field (unfilled circles) and a 1.05-deg auxiliary field concident with the test field (filled circles). The latter data have been displaced downward by 1.0 log units. The reciprocal of the intensity of a 10-deg main conditioning field necessary to raise increment threshold of a 200-msec 1.05-deg test flash, wavelength 421 nm, by 0.3 log units is plotted against the wavenumber of the main field. The 1.05-deg and 10-deg auxiliary fields each had wavelength 576 nm and intensity 9.31 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}. The smooth curves are Stiles's average π_3 (from Wyszecki and Stiles, 1967, Table 7.6) adjusted vertically in a weighted least-squares fit over the whole wavelength range. The data points shown by the filled squares are the differences in the field spectral sensitivities for the 10-deg and 1.05-deg auxiliary fields, adjusted for zero weighted mean. Points shown by the circles are the mean of six readings. The vertical bars show ± 1 SEM where this is sufficiently large. Subjects: (a) D.H.F. and (b) R.S.S.

dent 1.05-deg auxiliary field by the filled circles. The latter data have been displaced downward by 1.0 log units for clarity. The smooth curve through each set of points is Stiles's average curve Π_3 shifted vertically in a weighted least-squares fit over all wavelengths. (For wavelengths below 513 nm, Stiles's average mechanisms π_1 and π_3 (from Wyszecki and Stiles, 1967, Table 7.6) have essentially the same field spectral sensitivity functions; r.m.s. difference in shape is less than 0.038 log units.)

For both the 10-deg and 1.05-deg auxiliary fields, the data for each subject are moderately well fitted by the Stiles curve (r.m.s. error less than or equal to 0.21 log units in all cases), bearing in mind the large inter-subject differences that can arise from variations in macular pigment absorption for wavelengths less than about 530 nm (Wyszecki and Stiles, 1967, p. 218).

The difference between the field spectral sensitivities obtained for the two sizes of auxiliary field are shown by the filled squares at the bottom of Figs 9(a and b) (for zero weighted mean). There is clearly no narrowing or sharpening of the field spectral sensitivity curves analogous to that exhibited by the red- and green-sensitive mechanisms (as for example in Figs 1a and b) when the auxiliary field is made coincident with the test field. Although there are significant differences between the curves for the blue-sensitive mechanism for the two sizes of auxiliary field ($\chi^2(6) = 22.4$ for D.H.F. and $\chi^2(5) = 38.75$ for R.S.S., $P < 0.01$ for both), the unweighted r.m.s. deviation from concurrence is just 0.11 log units, for both subjects.

Comment

The simple possibility cannot be ruled out that the auxiliary field was not sufficiently intense to produce spectral sharpening of the blue-sensitive mechanism (recall that the Fechner fraction of the blue-sensitive mechanism is much higher than that of the red- and green-sensitive mechanisms). But this explanation seems implausible since significant sharpening of the field spectral sensitivity curve of the red-sensitive mechanism may be obtained with coincident auxiliary fields so weak that test-flash threshold is increased by no more than 0.1 log units (Foster, 1979a); in the present experiment, the 576 nm auxiliary field raised test-flash threshold for the blue-sensitive mechanism by at least 0.5 log units. It should also be noted that the fact that the spectral sensitivity curves are compared here for 1.05-deg and 10-deg auxiliary fields and not for 1.05-deg and zero auxiliary fields (as was done, for example, for the red-sensitive mechanism) is not critical. The field spectral sensitivity of the red-sensitive mechanism is essentially the same whether it is obtained on a 10-deg auxiliary field or on a zero auxiliary field.

As an alternative to the hypothesis advanced in the introduction to this section, the absence of spectral sharpening for the blue-sensitive mechanism might be explained in the following way. The blue-sensitive mechanism is known to have poor spatial frequency response characteristics (Stiles, 1949; Brindley, 1954; Green, 1968; Kelly, 1973). Whatever the processes are that underlie the spectral sharpening of the red- and green-sensitive mechanisms, in order for sharpening to be revealed it is necessary to have good coincidence of the boundaries of the auxiliary conditioning field and test field. The blue-sensitive mechanism, with its reduced spatial acuity, is presumably incapable of transmitting this information, and for this reason might be expected not to exhibit spectral sharpening. Nevertheless, as will be shown in Experiment 6, a reduction in spatial acuity in the region of the boundaries of the test and auxiliary fields is not in itself sufficient to eliminate spectral sharpening. The range of auxiliary-field sizes over which sharpening may occur is merely extended.

A phenomenon that may be relevant to the present findings concerning the blue-sensitive mechanism is the "minimally distinct border" effect (Boynton and Kaiser, 1968; Wagner and Boynton, 1972; Tansley and Boynton, 1978; Tansley and Glushko, 1978). When the two fields of a bipartite field are adjusted so that the border is minimally distinct, the two half fields may be considered to be equated with respect to the non-opponent system (Wagner and Boynton, 1972). Significantly, the residual strength of the border is found to depend on the relative activity of the long- and medium-wavelength sensitive cones, and not on activity of the short-wavelength sensitive cones (Tansley and Boynton, 1978).

Experiments 6. Effect of auxiliary-field size on spectral sharpening

In preceding experiments, spectral sharpening of the red- and green-sensitive mechanisms has been measured for 1.05-deg and 0.15-deg test flashes presented on steady auxiliary fields coincident with the test field. It is certainly true that if the auxiliary field is made very large (e.g. 10 deg) relative to the test field, spectral sharpening is abolished (Foster, 1979a). As has been implicitly assumed, the coincident auxiliary-field effect is not due to a general failure in field additivity, analogous to that reported for the blue-sensitive mechanism π_1 (Pugh, 1976; Augenstein and Pugh, 1977). In addition, the red-sensitive mechanism π_5 has been argued to show no evidence of systematic deviations from additivity (Sigel and Pugh, 1980; compare Boynton, Das and Gardiner, 1966).

To clarify the role of auxiliary-field size, sharpening of the field spectral sensitivity curve of the red-sensitive mechanism is here measured as a function of auxiliary-field diameter for two fixed test-field diameters: 0.15 deg and 1.05 deg.

Procedure

Experimental conditions differed slightly amongst the three subjects participating in this experiment. For subject H.C.B. the 200-msec test flash had wave-

length 664 nm and appeared concentrically superimposed on a steady 480 nm auxiliary field, intensity 7.96 log quanta·sec^{-1}·deg^{-2}; the 10-deg main conditioning field had wavelengths μ_1 and μ_2 of 465 nm and 651 nm. For subjects R.S.S. and D.H.F., the 200-msec test flash had wavelength 607 nm and appeared concentrically superimposed on a steady 531 nm auxiliary field, intensity 7.60 log quanta·sec^{-1}·deg^{-2}; the 10-deg main conditioning field had wavelengths μ_1 and μ_2 of 465 nm and 657 nm. The relatively low intensities of the auxiliary fields (compare conditions for results illustrated in Fig. 1) were selected to reduce the effects of scattered light in the region of the test field.

Results

Results for the 0.15-deg test field are shown in Figs 10(a) and (b) and for the 1.05-deg test field in Figs 10(c) and (d). Spectral sharpening of the red-sensitive mechanism, defined by the difference in field sensitivities of the mechanism at the two selected main-field wavelengths μ_1 and μ_2, is plotted against auxiliary-field diameter in degrees.

For auxiliary fields close in size to the test field (diameter indicated by an arrow on the abscissa) there is marked spectral sharpening which is eliminated when the auxiliary field is made sufficiently small or large (the value depending on test-field diameter). Thus, with the 0.15-deg test-field (Figs 10a and b), significant spectral sharpening occurs for auxiliary-field diameters between about 0.05 and 0.35 deg; with the 1.05-deg test field (Figs 10c and d), for auxiliary-field diameters between about 0.8 and 1.3 deg.

Comment

Spectral sharpening evidently varies far less rapidly with auxiliary-field diameter for the larger of the two test fields, and this raises the question of the most appropriate parameterization of the test- and auxiliary-field sizes. Plots of spectral sharpening against log diameter of the auxiliary field are found to be highly dissimilar, although on such a scale, the rate of variation of spectral sharpening is greater for the 1.05-deg test field than for the 0.15-deg test field. There is, however, a natural parameterization of the sizes of the test and auxiliary fields that leads to much greater uniformity in these spatial characteristics of spectral sharpening, as is shown below.

It was suggested in the Introduction that the coincident auxiliary field gives rise to spectral sharpening by high spatial-frequency masking at the coincident edges of the test and auxiliary fields. The efficiency of this masking depends *a priori* on the "closeness" of the test and auxiliary fields, closeness presumably being evaluated with respect to the spatial response characteristics of the (non-opponent) system being affected. But spatial response characteristics are known to vary with retinal eccentricity of the test stimulus in a manner well described by a formula (Drasdo, 1977; Rovamo and Virsu, 1979; Virsu and Rovamo, 1979) equivalent to that expressing the eccentricity dependence of cortical magnification factor M. This factor relates degrees of visual angle to the projected distance in mm on the visual cortex (Daniel and Whitteridge, 1961). Cortical magnification factor correlates well with the density of retinal ganglion cell receptive fields (Rovamo and Virsu, 1979). The dependence of M (in mm·deg^{-1}) on eccentricity θ (in deg) may be summarized (Drasdo, 1977) as

$$M(\theta) = 11.5/(1 + 0.59\theta).$$

To obtain the function, f say, that maps points in the visual field onto points on the cortex (or its homothetic equivalent), M must be integrated, whence

$$f(\theta) = (11.5/0.59)\cdot\ln(1 + 0.59\theta).$$

Figures 10(e) and (f) show the spectral sharpening data of Figs 10(a)–(d) replotted against M-scaled auxiliary-field diameter in mm cortex, where the latter value is computed from deg of visual angle by means of the function f (data for H.C.B. and R.S.S. shifted vertically to overlap with data for D.H.F.). Although the two sets of characteristics do not concur exactly, their qualitative agreement is good and the spatial range over which spectral sharpening occurs is now of the same order.

Note again that although the abscissa scale is mm cortex, any homothetically related equivalent of that scale, for example, one based on the density of ganglion cell receptive fields, would do equally well. The important point is that when variations of visual acuity with retinal eccentricity are taken into account, the spatial dependence of spectral sharpening is rendered substantially constant.

Experiment 7. Effect of dichoptic presentation on spectral sharpening

Stromeyer *et al.* (1980) have demonstrated that colour-selective spatial adaptation of the short-wavelength pathway is strongly monocular. Westheimer (1967) and Hayhoe (1979a) have also shown that there is no binocular transfer of cone-mediated spatial sensitization (see General Discussion). The present experiment determines whether spectral sharpening also fails to occur when the steady auxiliary conditioning field is presented dichoptically.

Procedure

The 200-msec test flash and main conditioning field were presented as usual to the right eye; the steady auxiliary field was presented either to the left eye or, as a control, to the right eye. To faciliate accurate visual alignment of the dichoptically presented test and auxiliary fields, the diameters of the fields were fixed at 1.05 deg, and an additional tiny fixation spot was introduced at the centre of each. The resulting 5-dot fixation array was presented to each eye in the dichoptic condition, and the same array used for the

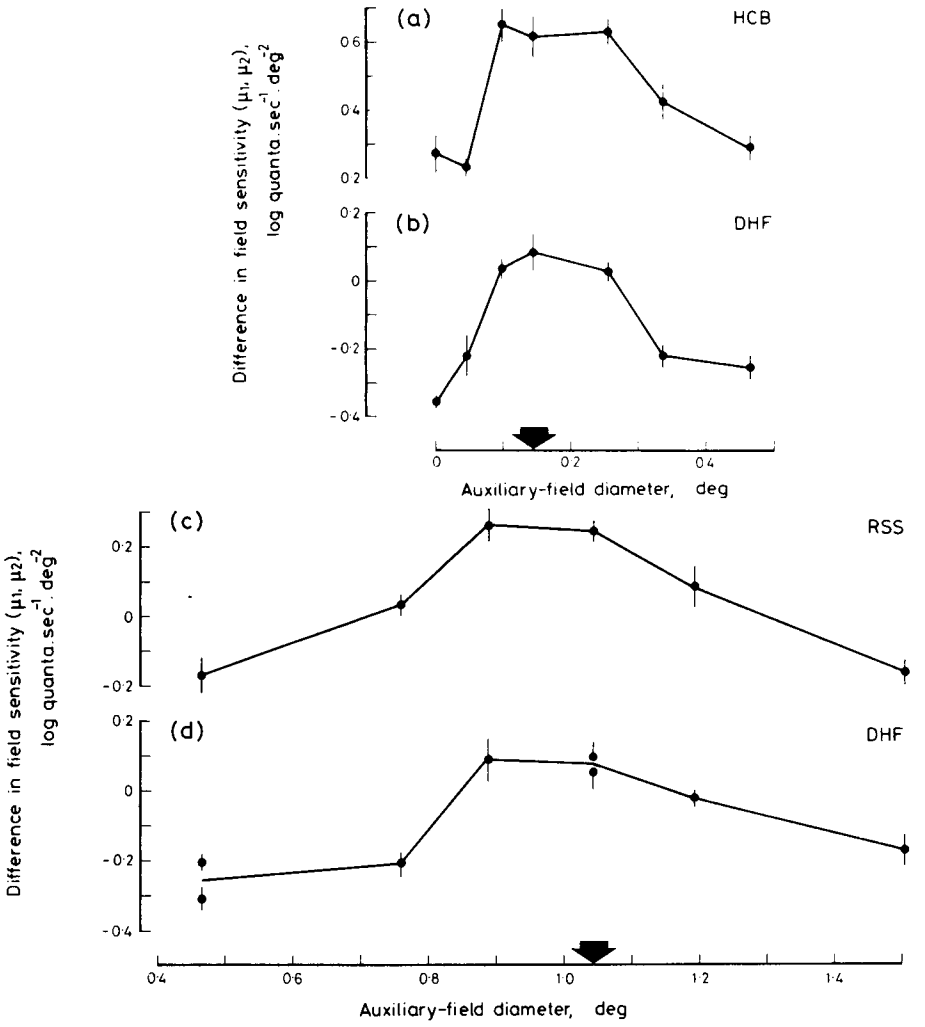

Fig. 10. (a–d). Spectral sharpening as a function of auxiliary-field size. Difference in field sensitivity at wavelengths μ_1 and μ_2 (see text) for a 200-msec long-wavelength test flash is plotted against auxiliary-field diameter in (a) and (b) for a 0.15-deg test flash, and in (c) and (d) for a 1.05-deg test flash. The arrows on the abscissae indicate the test-field size. Each point is the mean of twelve readings and the vertical bars show ±1 SEM. Subjects: H.C.B., R.S.S., D.H.F.

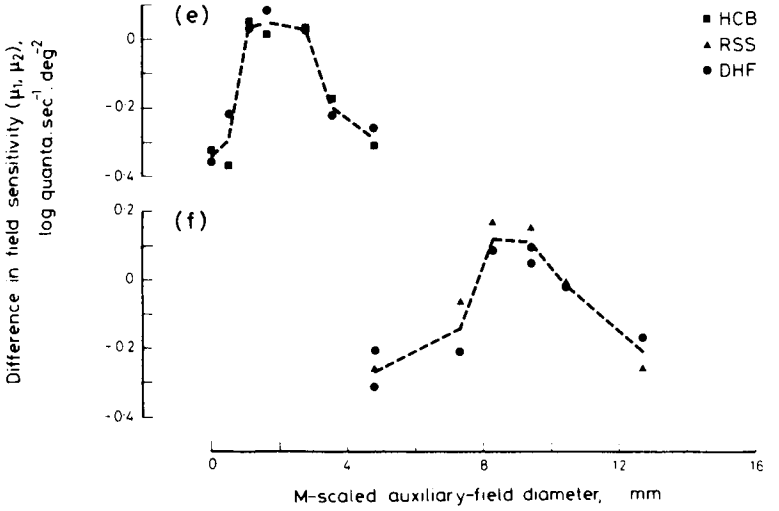

Fig. 10. (e) and (f). Differences in field sensitivities shown in (a)–(d) replotted against auxiliary-field diameter transformed by the integral of the magnification factor and expressed in mm cortex. For further details, see text.

monoptic control condition. Apart from this modification to the fixation array, the procedure for measuring sharpening of the field spectral sensitivity curve, in this case of the red-sensitive mechanism, was the same as for previous experiments.

The 200-msec 1.05-deg test flash had wavelength 664 nm. The steady, visually coincident auxiliary field (presented to the same or opposite eye) had wavelength 480 nm and relatively low intensity 7.96 log quanta·sec^{-1}·deg^{-2}. The 10-deg main conditioning field (presented to the same eye as the test flash) had wavelengths 465 nm and 651 nm.

Results and comment

Figure 11 shows results for subjects H.C.B. and D.H.F. For each subject, spectral sharpening, measured by the difference in field sensitivities at the two main-field wavelengths, is shown (A) for zero auxiliary field, (B) for the auxiliary field presented to the opposite eye, and (C) for the auxiliary field presented to the same eye.

There is no significant spectral sharpening when the auxiliary field is presented dichoptically: differences between this condition and the zero auxiliary-field condition are not significant for either observer ($t(22) < 1.46$, $P > 0.05$), although for subject H.C.B. the magnitude of the dichoptic effect is larger than that for zero auxiliary field. In contrast, for the monoptic condition, there is highly significant spectral sharpening ($t(22) = 6.50$, $P < 0.001$, for both subjects), despite the minor modification to the fixation array.

The absence or severe diminution of spectral sharpening for dichoptic presentation of the auxiliary field is of course consistent with a retinal origin to the auxiliary-field effect, but does not preclude a more central process that is monoptically driven. For further comment, see General Discussion.

GENERAL DISCUSSION

As declared in the Introduction, the present study was designed to reveal some of the qualitative properties of the sharpening of field spectral sensitivity curves obtained when a small, steady auxiliary conditioning field is made spatially coincident with the test field.

It appears that the sharpening effect is not an artifact of the method adopted for measuring field spectral sensitivities (Methods and Appendix), nor of accidental colour-contrast effects existing between the main conditioning field used to determine sensitivity and the inducing auxiliary field (Experiment 2(b)). One possible explanation of spectral sharpening, outlined in the Introduction, has been often cited: by virtue of the different spatial frequency response characteristics assumed for the achromatic, non-opponent system and the chromatic, opponent-colour system, the coincident auxiliary field is supposed to cause a shift in the mechanisms determining detection from the former system to the latter.

In the following section, the compatibility of this interpretation with the results reported in this investigation are briefly reviewed. Subsequent sections consider the relationship of test and field action spectra for the opponent-colour system, the site of the coincident auxiliary-field effect, and the relationship of the present findings to other studies on interactions amongst colour mechanisms.

Opponent-process theories and spectral sharpening

Consider the evidence for the hypothesis that the sharpened field spectral sensitivity curve obtained with an auxiliary field coincident with the test field is determined mainly or exclusively by the opponent-colour system.

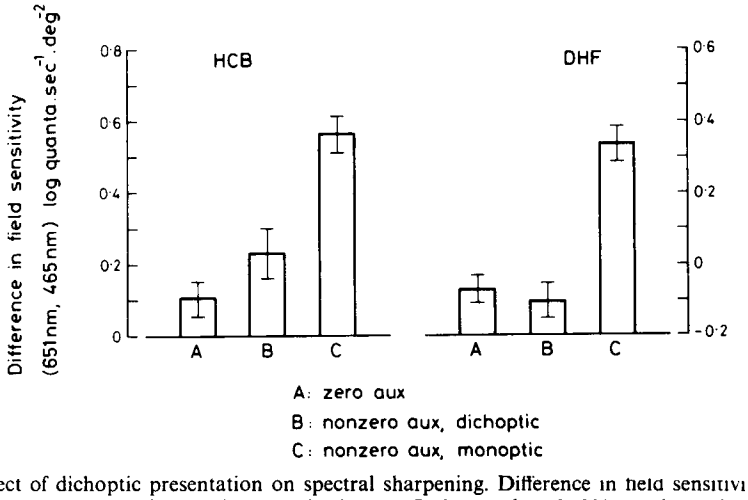

Fig. 11. Effect of dichoptic presentation on spectral sharpening. Difference in field sensitivity at wavelengths 651 nm and 465 nm for a 200-msec 1.05-deg test flash, wavelength 664 nm, determined with zero auxiliary field (A), and with a steady 1.05-deg auxiliary field, wavelength 480 nm and intensity 7.96 log quanta·sec^{-1}·deg^{-2} presented dichoptically (B) or monoptically (C). Each point is based on 12 readings and the vertical bars show ±1 SEM. Subjects: H.C.B. and D.H.F.

First, the changes in shape of the field spectral sensitivity curves for the red- and green-sensitive mechanisms are in opposite directions, and the curves tend to peak at wavelengths of about 605 nm and 530 nm (Fig. 1). In addition, when spectral sharpening of the red- and green-sensitive mechanisms is measured as a function of test-flash wavelength, peak sharpening occurs at wavelengths of 610–620 nm and 530 nm respectively (Experiment 3). These wavelengths are the same as those for extrema in the average chromatic valences of the red–green opponent channel reported by Werner and Wooten (1979) using the cancellation method of Jameson and Hurvich (Hurvich and Jameson, 1957; Jameson, 1972). They also coincide with the wavelengths at which peaks occur in test spectral sensitivity curves when the latter are determined on large white background fields with long-duration flashes (Stiles and Crawford, 1933; Sperling and Harwerth, 1971; King-Smith and Carden (1976); Klingaman and Zrenner, 1981). These curves have been argued to be the result of opponent-colour processes (see next section). Thus the peaks in these curves are preserved for high-frequency flicker stimuli if a hue-detection rather than simple detection criterion is used (Klingaman, Zrenner and Baier, 1980).

Second, when the intensity and wavelength of the auxiliary field are varied to yield a constant spectral sharpening of the red-sensitive mechanism, the resulting auxiliary-field action spectrum coincides with the field spectral sensitivity of the mechanism complementary to the spectrally sharpened red-sensitive mechanism, namely, the spectrally sharpened green-sensitive mechanism [Experiment 2(a)].

Third, reduction of test-flash duration from 200 msec to 20 msec reduces or abolishes spectral sharpening of the red- and green-sensitive mechanisms (Experiment 4), consistent with evidence cited in that section that the opponent-colour system shows greater temporal integration than the non-opponent system.

Fourth, an auxiliary field coincident with the test field gives no spectral sharpening of the blue-sensitive mechanism at moderate-to-high intensities of the auxiliary field (Experiment 5), consistent with evidence cited in that section that signals from short-wavelength sensitive cones have access only to the opponent-colour system.

Circumstantially, an explanation of the coincident auxiliary-field effect based on an opponent-process theory appears plausible, although a number of caveats should be expressed. The appeal to processing by the opponent-colour system is through its presumed spatial, temporal and spectral characteristics as revealed in simple detection paradigms. No experiments have been performed here involving colour matching or colour naming (compare King-Smith and Carden, 1976; Klingaman *et al.*, 1980). Informal introspections on the appearance of the test stimuli for short- and long-duration test flashes (Experiment 4) are, however, consistent with the hypothesized achromatic and chromatic encodings of these stimuli. Although the supposed spatial, temporal and spectral characteristics of the opponent-colour system are consistent with most of the effects reported here, no detailed predictions are available to enable quantitative estimates to be made of the interdependence of opponent-colour and non-opponent systems, and the degree of opponency within an individual red–green or blue–yellow channel (compare Ingling, 1977; Ingling and Tsou, 1977; Jameson and Hurvich, 1972). In the event, some aspects of the distinction between opponent and non-opponent systems may be artificial in view of the findings by Gouras and Zrenner (1979) that tonic ganglion cells in monkey can appear colour-opponent at low temporal frequencies and lose this property at high temporal frequencies (see also Klingaman *et al.*, 1980).

An alternative *post hoc* explanation of some of the present results, particularly those relating to the dependence of spectral sharpening on auxiliary-field intensity, might be contrived by working directly with the estimated interactions between the long- and medium-wavelength sensitive cone mechanisms (see, for example, Sperling and Harwerth, 1971), but it is not easy to see how such an explanation could provide a general framework for the remainder of the experimental data (see King-Smith and Carden, 1976).

Relationship of field action spectra to test action spectra

A desirable property of any essentially unitary colour mechanism is that the spectral sensitivity of that mechanism should be qualitatively the same whether determined by test or by field measurements (see Stiles, 1978). Only field spectral sensitivities have been measured here (thus Experiment 3 determined spectral sharpening as a function of test-flash wavelength, not test-flash threshold as a function of test-flash wavelength). Data on test spectral sensitivities obtained with the present paradigm are to be reported subsequently (R. S. Snelgar and D. H. Foster, in preparation). There are, however, other relevant data on test action spectra available. Thus, when test spectral sensitivity is measured for a large (e.g. 1 deg), long-duration (e.g. 200 msec) flash on a moderate-to-high luminance (e.g. $\geq$1000 td) white background, three peaks are observed at or near 440 nm, 530 nm and 610 nm (Stiles and Crawford, 1933; Sidley and Sperling, 1967; Sperling *et al.*, 1968; Sperling and Harwerth, 1971; King-Smith and Carden, 1976; Klingaman and Zrenner, 1980).

As Sperling and Harwerth (1971) have pointed out, it is not possible to represent these peaks as the upper envelope of the spectral sensitivities of independent short-, medium- and long-wavelength sensitive cones. To fit their data, Sperling and Harwerth developed a specific model based on the assumption of a linear subtractive interaction between signals from long- and medium-wavelength sensitive cones, with no

interaction involving signals from short-wavelength sensitive cones.

A more general approach to the modelling of these test action spectra was adopted by King-Smith and Carden (1976), who measured test spectral sensitivities on large white backgrounds for 20 Hz flicker and for long- and short-duration flashes, using both simple detection and colour-detection criteria. These authors proposed that a large white adapting field preferentially reduces sensitivity of the achromatic, non-opponent system, and that a relatively large and long-duration test flash favours detection by the chromatic, opponent-colour system. In particular, they argued that for a 1-deg 200-msec test flash presented on a 1000-td white background, its detection at all wavelengths, except those in the yellow region, is mediated by the opponent-colour system.

If, as has been suggested, detection is mediated by the opponent-colour system in the present paradigm, then the field spectral sensitivity curves obtained are the field action spectra of the opponent-colour system. An incidental advantage of measuring such action spectra is that they may be derived for almost the whole of a mechanism's wavelength range. Only with the use of very intense adapting fields can substantial portions of a test action spectrum be normally revealed (Wald, 1964).

Site of the coincident auxiliary-field effect

The results of Experiment 7 show that there is no significant spectral sharpening produced under dichoptic presentation of the auxiliary field, and this suggests that the effect of the coincident auxiliary field must be either retinal or more centrally determined by monocular processes. (Compare analogous results by Mollon and Polden (1977) for transient tritanopia, and by Stromeyer *et al.* (1980) for spatial adaptation involving the blue-sensitive mechanism.) The fact that the areal dependence of spectral sharpening depends on the mean eccentricity of the stimuli in a manner described by cortical magnification factor (Experiment 6) lends particular support to the notion of a post-retinal monocularly driven site.

It is, however, important to distinguish between (a) the site at which the coincident auxiliary field is assumed to exert its influence in shifting detection from the non-opponent system to the opponent-colour system, and (b) the site (or sites) at which the actual opponent-colour encoding takes place. The two types of site need not coincide, and the above assertions imply only a centripetal limit to the location of the opponent-colour interactions.

Other related experiments on interactions among cone mechanisms

It is well known that suitably small, steady backgrounds raise thresholds for very small test stimuli (desensitization) and that increasing the size of the background lowers thresholds for those stimuli (sensitization) (Crawford, 1940; Westheimer, 1965, 1967). Sensitization cannot be produced dichoptically (Westheimer, 1967; Hayhoe, 1979a) although the time course of the after-effects of the background suggest the existence of a central component in the effect (Hayhoe, 1979b).

With regard to the possible existence of interactions between signals from different cone mechanisms in sensitization, McKee and Westheimer (1970) have reported that the long- and medium-wavelength sensitive mechanisms operate independently of each other; thus, a test flash detected by long-wavelength sensitive cones is affected by the background only in so far as the background excites long-wavelength sensitive cones.

It is difficult to relate immediately the results of sensitization-desensitization experiments to the present findings on spectral sharpening. It might be supposed that desensitization and the present coincident auxiliary-field effect arise through common processes. But there are fundamental differences in stimulus goemetry: the spectral sharpening examined here is obtained with test flashes of dia 0.15–1.05 deg and duration 200 msec; in Westheimer and McKee's paradigm for cone-mediated sensitization the test flashes have diameters of the order of 0.03 deg and durations of the order of 10 msec, conditions that here would be chosen to selectively stimulate the *non-opponent* system.

Evidence for interactions between signals from different π mechanisms under dynamic conditions, as opposed to the above-described static conditions, has been presented by Boynton *et al.* (1964) and Ikeda *et al.* (1970), who used spatially coincident, double test flashes of various wavelengths presented on large, medium- and long-wavelength conditioning fields. The double test flashes were presented simultaneously, and the authors found evidence under these conditions for an inhibitory interaction between signals from the long- and medium-wavelength sensitive cones. Stromeyer *et al.* (1978c) performed related experiments with spatially coincident double test flashes of long and medium wavelengths presented on large bright yellow adapting fields. The double test flashes were presented in both simultaneous and sequential modes. They found that large (1 deg), long-duration (200 msec) double flashes gave rise to cancellation when presented simultaneously, but facilitation when presented sequentially. Significantly, the cancellation effect largely disappeared for short-duration flashes (10 msec) or small test fields (0.04 deg). (Compare the present Experiment 4.) The authors interpreted their results in terms of colour-differencing, opponent mechanisms.

Stromeyer *et al.* (1978c) also found that long-wavelength flashes were in general strongly affected by medium-wavelength flashes, whereas medium-wavelength flashes were less strongly affected by long-wavelength flashes. An analogous asymmetry in the effects of the coincident auxiliary field on spectral sharpening is also evident here (compare, for example,

Figs 1a and b). Klingaman and Zrenner (1981) have also reported the same kind of asymmetries in the effects on test spectral sensitivity curves for long- and medium-wavelength sensitive mechanisms after adaptation to large chromatic and achromatic backgrounds: the antagonistic effect of the green-sensitive mechanism on the red-sensitive mechanism appears greater than in the opposite situation (see also Sperling and Harwerth, 1971; King-Smith and Carden, 1976).

Dynamic interactions involving signals from *different* parts of the retina have been examined in the phenomenon of metacontrast masking. In this phenomenon the visibility of a test flash is reduced by the subsequent presentation of a briefly flashed background close to but not overlapping the test region (Stigler, 1910; Alpern, 1953; Kahneman, 1968; Weisstein, 1972; Lefton, 1973). It was suggested by Alpern and Rushton (1965) that signals from different π mechanisms did not interact in metacontrast masking. Subsequent work has, however, shown that metacontrast-type interactions between signals from long- and short-wavelength sensitive cones can be demonstrated over a range of stimulus onset asynchronies (Foster, 1979b; see also Yellott and Wandell, 1976). With regard to the present discussion concerning opponent and non-opponent encodings, Bowen *et al.* (1977) have proposed that a necessary condition for metacontrast masking is activity generated within the luminance system. As has been argued by Foster (1979b), the occurrence of strong metacontrast masking within the short-wavelength pathway, and thus presumably outside the luminance system (see introduction to Experiment 5 here), implies that this hypothesis cannot be generally true. This assertion has been confirmed and extended by Reeves (1981) in a study addressed specifically to the question of metacontrast masking involving hue changes. Reeves has shown that pronounced masking can be obtained for a range of hue-substitution stimuli, providing that the magnitude of the hue change is sufficiently great.

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APPENDIX

Comparison of direct field-adjustment and t.v.i. methods

A control experiment was performed to compare the traditional t.v.i. method of Stiles and the present direct field-adjustment method (see Methods). Field sensitivity for the red-sensitive mechanism [the one most sensitive to the coincident-auxiliary field effect (see Fig. 1)] was measured with and without an auxiliary field coincident with the test field at two main-field wavelengths, 465 nm and 657 nm, by (1) the traditional t.v.i. method of Stiles, and (2) the present direct field-adjustment method.

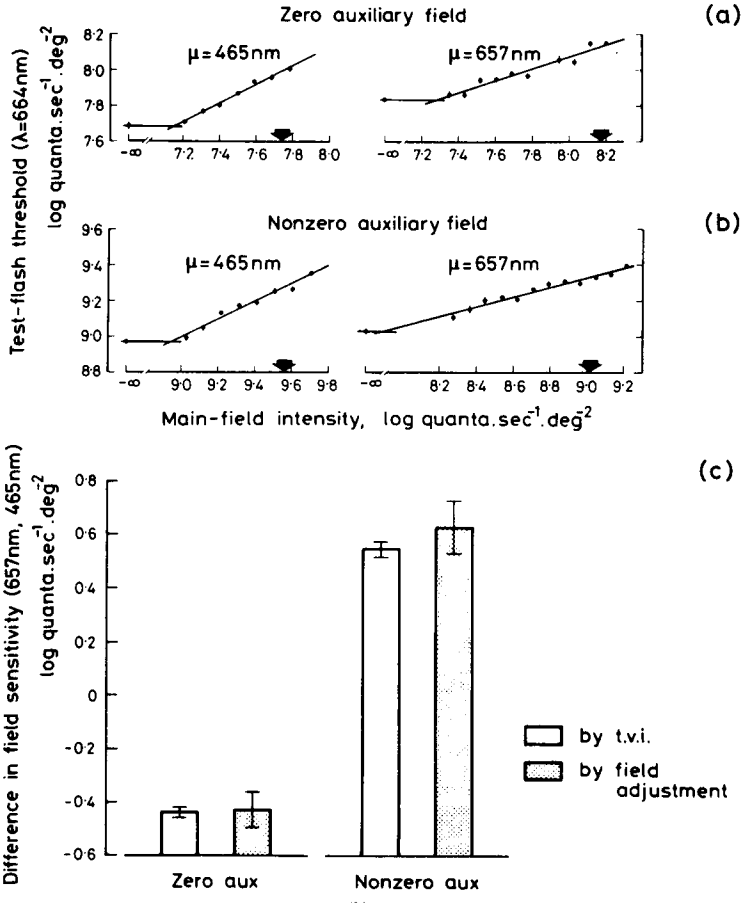

Fig. 12. (a) and (b) Test-flash threshold as a function of main-field intensity for (a) zero auxiliary field, and (b) nonzero auxiliary field. The wavelengths λ and μ of the test and main conditioning fields respectively are shown. The auxiliary field coincident with the test field had wavelength 531 nm and intensity 8.32 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}. Each point is the mean of six readings and the vertical bars show ± 1 SEM where this is sufficiently large. The arrows on the abscissae show the main-field intensities that raise test-flash (increment) threshold by 0.3 log units. (c) Difference in main-field sensitivities at the wavelengths obtained from the t.v.i. measurements in (a) and (b) (unshaded columns) and by direct main-field adjustment (shaded columns). Each difference value in the latter determinations is based on 12 readings. The vertical bars show ± 1 SEM. Subject: D.H.F.

The test flash had wavelength λ fixed at 664 nm, dia 0.15 deg and duration 200 msec. The spatially coincident, steady auxiliary field, when present, had wavelength 531 nm and intensity 8.32 log quanta·sec^{-1}·deg^{-2}. The steady main conditioning field had wavelengths 465 nm and 657 nm, and dia 10 deg.

Figure 12 shows results for the two methods. The graphs in (a) and (b) of Fig. 12 relate to the t.v.i. method and show test-flash threshold against main-field intensity for main-field wavelength μ as indicated, for (a) zero auxiliary field, and (b) the above-specified nonzero auxiliary field. For all four sets of data, points showing test-flash thresholds at nonzero main-field intensities are well fitted by least-squares regression lines (all correlation coefficients $r \geq 0.97$, $P < 0.001$). That these fits are linear over these restricted intensity ranges is not intended to have any theoretical significance; the fits are used only to facilitate the computation of the main-field intensities (indicated by arrows on the abscissae) at which the test-flash threshold is raised 0.3 log units above its zero main-field value.

In the direct field-adjustment method, the test flash was set 0.3 log units above its threshold value on zero or nonzero auxiliary field, and the main field, of wavelength μ either 465 nm or 657 nm, adjusted directly to bring the test flash to threshold.

In Fig. 12(c) plots of the difference in field sensitivity at 657 nm and 465 nm are shown by the unshaded columns for the t.v.i. method (differences of the field-intensity values in (a) and in (b)) and by the shaded columns for the direct field-adjustment method. The vertical bars show ± 1 SEM. The two methods clearly give the same differences in field sensitivities both in the zero auxiliary-field condition and in the nonzero auxiliary-field condition, confirming the reliability of the field-adjustment method and the robustness of the spectral sharpening effect.

It may be seen in Fig. 12(c) that in both auxiliary-field conditions the SEMs for the differences in main-field sensitivities are larger for the field-adjustment method than for the t.v.i. method. Note, however, that the latter method entailed approximately eight-times as many readings as the former. As evidenced in the main text, SEMs for data points derived in the direct field-adjustment method are generally of the order of 0.05 log units (for $n = 6$), much smaller than the measured shifts in spectral sensitivity due to spectral sharpening.