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ISOLATION OF OPPONENT-COLOUR MECHANISMS AT INCREMENT THRESHOLD*

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Abstract—An experimental examination was made of some paradigms designed to isolate the opponent-colour system at increment threshold. The effectiveness of a uniform white conditioning field spatially coincident with a 1.05-deg uniform test field was assessed by measuring intensity thresholds for simple detection and for colour discrimination. Values were obtained both by a method of adjustment and by a two-interval forced-choice procedure. For sufficiently high luminances of the conditioning field (3000 td or greater) little or no difference was found between simple-detection and colour-discrimination thresholds over the critical test-flash spectral range 520–620 nm, implying that the paradigm produced almost complete isolation of the opponent-colour system at increment threshold. A control experiment in which thresholds were obtained for a conditioning field larger than the test field gave less satisfactory isolation; near 580 nm the luminance system was found to be at least 0.3 log unit more sensitive than the opponent-colour system. A comparison was also made of the spatially coincident field paradigm with a paradigm in which a modified test stimulus of low temporal and spatial frequency content was presented on a large conditioning field. Test spectral sensitivity curves for simple detection obtained by a method of adjustment showed little difference in effectiveness in opponent-colour isolation.

Opponent-colour system Luminance system Spectral sensitivity Spectral sharpening

INTRODUCTION

There are three characteristic peaks at approximately 440, 530, and 610 nm in the spectral sensitivity curve obtained by increment-threshold measurements of a long-duration, circular, monochromatic test flash presented on a large white conditioning field. The three peaks have been demonstrated for the human eye in many studies (e.g. Stiles and Crawford, 1933; Sidley and Sperling, 1967; Sperling and Harwerth, 1971; King-Smith and Carden, 1976; Verriest and Uvijls, 1977; Harwerth and Levi, 1977; Kuyk, 1982; Snelgar and Foster, 1982; Foster and Snelgar, 1983a; Zrenner, 1983). Examples of such test spectral sensitivity curves are shown in Fig. 1 (open circles); they were obtained for the subjects who took part in the present study (methods as in Foster and Snelgar, 1983a, and as in Experiments 1 and 3 below). Evidence suggesting that the peaks at about 530 and 610 nm result from activity in the red-green opponent-colour channel of an opponent-process system has been reviewed in Foster and Snelgar (1983a). A specific assumption is that sensitivity of the non-opponent luminance system is depressed as a result of achromatic adaptation produced by the white conditioning field (King-Smith and Kranda, 1981). More detailed descriptions of post-receptoral colour processing have been offered by Mollon (1982), Ingling and Martinez-Uriegas (1983), and Hood and Finkelstein (1983).

The dip at about 580 nm in the curves shown in Fig. 1 (open circles) is also a feature of the test spectral sensitivity curve obtained under the conditions summarized above. The fact that the dip is relatively shallow under those conditions is probably due to intrusion by the luminance system in that region of the spectrum (King-Smith and Carden, 1976). It is, however, possi-

*Some of the data reported here were contained in a paper presented to The Colour Group (Great Britain), January 1985, and in a Communication presented to the Physiological Society (Foster, Scase and Snelgar, 1986). Correspondence should be addressed to Dr D. H. Foster, Department of Communication and Neuroscience, University of Keele, Keele, Staffordshire, ST5 5BG, England.

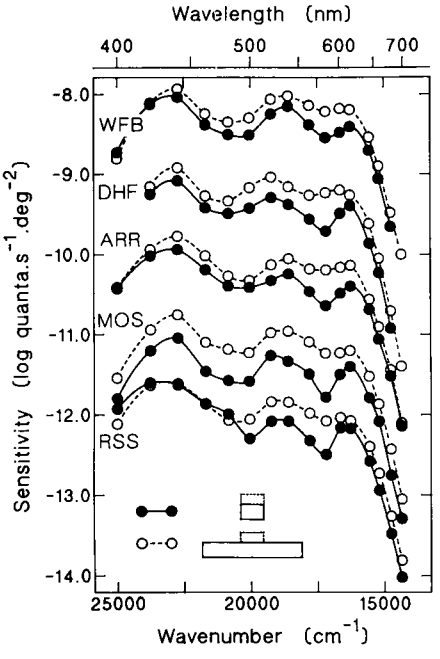

Fig. 1. Test spectral sensitivity curves obtained for simple detection of a 1.05-deg test flash presented on a large (10.0-deg) white auxiliary field (open symbols, broken line) and on a small (1.05-deg) white auxiliary field spatially coincident with the test field (solid symbols, continuous line). Log reciprocal intensity of the test flash is plotted against wavenumber λ^{-1} of the test flash. Thresholds were obtained by a method of adjustment. The white auxiliary field gave retinal illuminance 3000 td and had colour temperature 3400 K. The test flash had duration 200 msec. The pairs of curves, displaced downwards by 1.0 log unit successively, are for different subjects as indicated. Each point is the mean of six readings and the vertical bars show ± 1 SEM where sufficiently large.

ble to depress further the sensitivity of the luminance system relative to that of the opponent-colour system by manipulating the experimental paradigm according to the differential sensitivities of the two systems. The activity of the opponent-colour system may then be revealed more completely: the dip at about 580 nm becomes a deeper trough and the peaks at about 530 and 610 nm become sharper and more clearly defined. Three classes of experimental paradigms have been described that secure or facilitate detection by the opponent-colour system. The critical features of these paradigms were as follows.

(1) Colour-discrimination criterion

As well as determining threshold by the usual criterion of simple detection of the test flash, King-Smith and Carden (1976) used a criterion of colour detection or discrimination from white. Their assumption was that thresholds for colour detection are determined by and reflect the sensitivity of the opponent-colour system. This assumption is made here also. For a colour-detection criterion the test spectral sensitivity curve has a deep trough at about 580 nm (King-Smith and Carden, 1976), presumably representing a state of equilibrium in the red-green opponent-colour channel. (The position of the equilibrium point need not be fixed at 580 nm; see Discussion.) Thresholds for colour detection may, however, be difficult to obtain, unless two-interval forced-choice discrimination methods are used.

(2) Spatially coincident auxiliary field

The test flash used in traditional measurements of test spectral sensitivity (some listed above) is usually bounded by sharp edges, both spatially and temporally. Such a stimulus, even presented on a large white conditioning field, is unlikely to be optimal for measurements of opponent-colour function for, in general, the luminance system is more sensitive than is the opponent-colour system to the high spatial and temporal frequencies present in the stimulus. (Evidence in support of this assertion has been reviewed in Foster, 1981; see also Stromeyer *et al.*, 1978, and Mullen, 1985.) This and the next class of paradigm exploit these differential sensitivities in different ways.

If the large white conditioning field is made spatially coincident with the test field then the high spatial-frequency adaptation or masking that occurs at the boundary of the stimulus is thought to depress further the sensitivity of the luminance system (Snelgar and Foster, 1982; Foster and Snelgar, 1983a; see Foster, 1981, for discussion of this paradigm in measures of field spectral sensitivity). The conditioning field spatially coincident with the test field is referred to as the *small auxiliary field*, and the large conditioning field as the *large auxiliary field*, following the notation introduced by W. S. Stiles. Test spectral sensitivity curves for simple detection obtained with a small auxiliary field are shown in Fig. 1 (solid circles) for the subjects who took part in the present study (methods as in Foster and Snelgar, 1983a, and as in Experiments 1 and 4 below). In comparison with the test spectral sensitivity curve obtained with the large auxiliary field (open circles), there was a marked increase in the depth of the trough at about 580 nm and an improvement in the delineation of the peaks at about 530 and 610 nm with the

small auxiliary field (solid circles). The latter curves are similar to those obtained by King-Smith and Carden (1976) using a colour-detection criterion and a large white auxiliary field.

(3) Low-frequency test stimuli

Some approaches to the isolation of the opponent-colour system have employed test stimuli with modified spatial and temporal profiles that eliminate the spatial and temporal transients at the stimulus edges. The "low-frequency" test stimulus of Thornton and Pugh (1983a,b) had bell-shaped spatial and temporal distributions which were designed so that the Fourier spectra had most energy concentrated at low frequencies. The test spectral sensitivity curves obtained with this low-frequency test stimulus presented on a large white auxiliary field (Thornton and Pugh, 1983a) were similar to those in Fig. 1 for the small auxiliary field (solid circles).

If the extent and periodicity of the stimulus are increased the relative power at low frequencies may be still further enhanced. Thus Mullen (1987) used monochromatic sinusoidal gratings superimposed on a large white auxiliary field; for spatial frequencies less than 1 deg^{-1} and a temporal frequency of 0.8 Hz the spectral sensitivity curves obtained for contrast sensitivity were also similar to the curves in Fig. 1 for the small auxiliary field (solid circles). Evidence was presented, however, which led to the conclusion that the opponent-colour system did not contribute to detection at 577 nm, even though sensitivity of the luminance system was depressed in that region.

There were two main objectives in undertaking the present experiments. The first was to assess whether use of a small white auxiliary field did fully isolate the opponent-colour system at increment threshold. This was decided operationally, by reference to the corresponding test spectral sensitivity curve for detection of colour. As noted below, this approach, although safe, may have been rather conservative. Nevertheless, of all the above-cited studies describing opponent-colour spectral sensitivities, only King-Smith and Carden (1976) reported direct comparisons with colour detection data. Because wavelength-independent variations in sensitivity were not of interest here, adjustment of the relative vertical positions of simple-detection and colour-detection curves were allowed to achieve maximum overlap on a logarithmic scale, under the constraint that at no wavelength should simple-detection threshold exceed colour-detection threshold. Coincidence of the curves implied isolation of the opponent-colour system over the spectral range studied; departures from coincidence, most evident in the region about 580 nm, gave a direct measure of the amount by which the luminance system was more sensitive at threshold than the opponent-colour system over that portion of the spectrum. This estimate was conservative for although perception of colour necessarily entailed activity in the opponent-colour system, the converse need not have applied.

The second objective was to compare directly the small-auxiliary-field paradigm with the low-frequency-test-stimulus paradigm. The two are in some respects complementary, but comparisons of test spectral sensitivities obtained by the two methods have not previously been made in the same subjects. In fact, under the same conditions, little difference in effectiveness was found between the two paradigms.

In initial measurements, described in Experiment 1 below, thresholds were obtained by a method of adjustment. This traditional method provides an accurate and efficient procedure for obtaining simple-detection thresholds, but, for colour-detection judgements, threshold settings are more difficult to make, and a two-interval forced-choice (2IFC) method was therefore introduced. A range of luminance levels of the auxiliary field was tested in these measurements to determine whether there was a limiting effect in the depression of the sensitivity of the luminance system relative to the opponent-colour system. Sperling *et al.* (1967) and Harwerth and Levi (1977) showed that the dip at about 580 nm obtained for a simple-detection criterion with a large white auxiliary field deepened with increasing luminance of that field, reaching a maximum in depth for luminances of 10,000 or 3000 Td respectively. It seemed plausible that increasing the luminance of the small auxiliary field would also decrease sensitivity of the luminance system, offering the possiblity that the trough at about 580 nm obtained for simple detection would eventually converge on the trough obtained for colour detection.

EXPERIMENT 1

Simple-detection and Colour-detection Thresholds by Method of Adjustment

As explained in the Introduction, one aim of

the present study was to assess the effectiveness of the small auxiliary field in isolating the opponent-colour system at threshold for simple detection. In this exploratory experiment, simple-detection and colour-detection thresholds were measured on the small auxiliary field over a range of wavelengths spanning the critical region of the trough at about 580 nm and over a range of luminances of the small auxiliary field corresponding to 300, 1000, 3000, 10,000, and 30,000 td. Instead of absolute judgements of stimulus colour in the colour-detection measurements, a reference white was introduced and the test stimulus judged against that. Formally the task was therefore one of colour discrimination.

Methods

Stimuli and apparatus. The monochromatic test flash was circular, of dia. 1.05 deg, duration 200 msec, and wavelength ranging from 520 to 623 nm. In the colour-discrimination experiments a white comparison flash identical in size, shape, and duration to the monochromatic test flash was also used; its colour temperature was adjusted with colour-correcting filters to be close to that of the auxiliary field. The steady small white auxiliary field was circular, of dia. 1.05 deg, and of varying luminance, with colour temperature 3400 K. The monochromatic test flash and the white comparison flash were each presented concentrically on the small auxiliary field either separately or as a test sequence with an interstimulus interval of 1 sec.

The stimuli were produced by a three-channel Maxwellian-view optical system (described fully in Foster, 1981) with as light source a single tungsten-halogen lamp run from a regulated d.c. power supply. Transmittances of the channels were controlled by compensated neutral density wedges and Wratten neutral density filters (NDFs). The spectral compositions of the monochromatic test fields, produced by channel 2, were controlled with Balzers B40 interference filters with half-height full-bandwidths each less than 9 nm. The comparison white flash was produced by channel 1. The time-courses of the stimulus flashes (monochromatic and white) were controlled by silent electromagnetic shutters that interrupted the relevant channels at intermediate foci. Rise and fall times of each flash were each less than 2 msec. The white auxiliary field, produced by channel 3, could be set to give a retinal illuminance of 300, 1000, 3000, 10,000 or 30,000 td. The settings were obtained by means of minimally distinct border matches (Wagner and Boynton, 1972) against a 562 nm reference field. The spatial geometry of the stimuli was determined by photographic masks inserted in the channels. Precautions were taken to minimize instrumental stray light. The stimuli were viewed through a 2-mm artificial pupil with an achromatizing lens and correcting lenses for non-emmetropic subjects. Stability of head position was maintained with the aid of a dental bite-bar. Further details of the apparatus and its calibration are given in Foster (1981).

Subject. One subject, R.S.S. (co-author) participated in this experiment. She had normal colour vision and corrected Snellen acuity of 6/5, and was aged 31 yr.

Procedure. At the beginning of each experimental session, the positions of the masks were adjusted so that the stimulus fields appeared concentric and in focus. Where necessary, small corrections to the alignments of the masks were made as the wavelength of the test flash was varied. The subject dark-adapted for 10 min before commencing the observation session. Viewing was monocular and the subject fixated the centre of the small auxiliary field with the right eye. The intensity of the test flash and its onset were controlled by the subject using push-button switch-boxes. Stimuli were not presented more rapidly than once every 2 sec.

Measurements of simple-detection and colour-discrimination thresholds for the monochromatic test flash were obtained by a method of adjustment, for 10 wavelengths ranging from 520 to 615 nm. Simple-detection thresholds were obtained as described in Foster and Snelgar (1983a). In each experimental session, measurements were made with test-flash wavelengths in ascending and then descending order for one auxiliary-field luminance. In the same session, detection threshold for the white comparison flash was determined for use in subsequent measurements of colour-discrimination threshold. Colour-discrimination thresholds were set as follows. In each experimental session, auxiliary-field luminance was fixed. The neutral density wedges in channels 1 and 2 were first set by the experimenter so that the white comparison flash and the monochromatic test flash were each at detection threshold as determined previously. Next, the wedge in channel 1 was electronically yoked to that in channel 2 so that the push-button control box varied the intensities of the white comparison flash and the

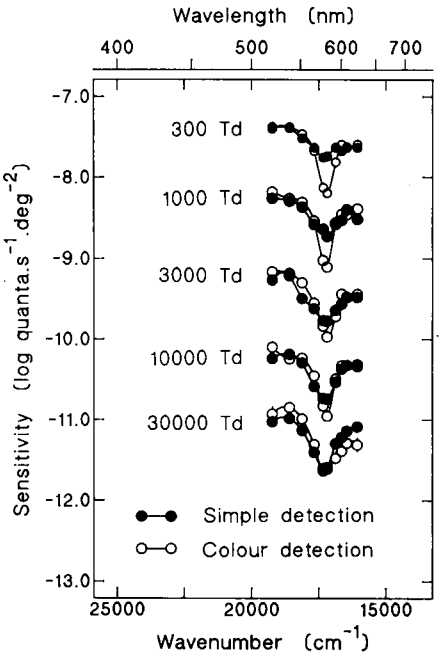

Fig. 2. Test spectral sensitivity curves obtained for simple detection (solid symbols) and for colour discrimination (open symbols). The 1.05-deg test flash had duration 200 msec and was presented on a small white auxiliary field spatially coincident with the test field. Thresholds were obtained by a method of adjustment. The pairs of curves, displaced downwards successively by 0.5 log unit, are for different luminances of the small auxiliary field as indicated. Each point is the mean of six readings and the vertical bars show ± 1 SEM where sufficiently large. Subject: R.S.S. Other details as for Fig. 1.

monochromatic test flash in unison (the gradients of the two wedges being almost identical). The two flashes were presented as a test sequence: the monochromatic test flash followed by the white comparison flash with an interstimulus interval of 1 sec. The subject, using a method of adjustment, then set the yoked wedges so that the monochromatic test flash could just be distinguished from the white comparison flash on the basis of colour. This procedure was repeated at each wavelength of the monochromatic test flash. Wavelength was varied in ascending and then descending order (or vice-versa). For both simple-detection and colour-discrimination measurements, three consecutive threshold settings were recorded at each wavelength on each traverse. Mean threshold values were thus based on six measurements.

Results

Results are shown in Fig. 2. Sensitivities in log quanta. sec^{-1} deg^{-2} are plotted against test-flash wavenumber. Solid symbols indicate data for simple detection and open symbols for colour discrimination. The vertical bars show ± 1 SEM where sufficiently large. The pairs of curves (each pair displaced successively downwards by 0.5 log unit) are for increasing luminance of the small auxiliary field as indicated. For simple detection the trough at about 580 nm became progressively deeper with increasing auxiliary-field luminance. The trough for colour discrimination, however, remained substantially the same over auxiliary-field luminances of 300–10,000 td. (At 30,000 td the relative sensitivity for colour discrimination at short and long wavelengths was different from that at lower luminances, and also the SEMs were larger than at any other luminance.)

To quantify these changes in trough depth, the difference between mean sensitivity over 577 and 582 nm and over the regions 520–566 and 593–623 nm was calculated for simple detection and for colour discrimination at each auxiliary-field luminance from 300 to 30,000 td. For simple detection, there was a monotonic increase in trough depth relative to that at 300 td at each successive luminance level: values were + 0.06, + 0.12, + 0.19, and + 0.26 log unit as luminance increased from 1000 td. For colour discrimination, the differences in trough depth relative to that at 300 td were essentially constant: values were + 0.07, − 0.10, − 0.02, and − 0.17 log unit (where there was a change in curve shape) as luminance increased from 1000 td. The difference between trough depths for simple detection and colour discrimination decreased with increase in auxiliary-field luminance: values were + 0.42, + 0.43, + 0.19, + 0.20, and − 0.01 log unit as luminance increased from 300 to 30,000 td (a positive value indicating a less deep trough for simple detection).

Comment

For luminances of the small auxiliary field of 30,000 td isolation of the opponent-colour system was effectively complete. For auxiliary-field luminances of 3000 and 10,000 td a small residual difference (of the order of 0.2 log unit) between simple-detection and colour-discrimination thresholds was evident at wavelengths close to 580 nm. Thresholds for colour discrimination are, however, notoriously difficult to set by a method of adjustment, even for an experienced observer. For subsequent experiments involving colour-discrimination thresholds a

two-interval forced-choice (2IFC) method was therefore used.

EXPERIMENT 2

Simple-detection and Colour-discrimination by 2IFC Method

In contrast to the procedure followed in Experiment 1, simple-detection and colour-discrimination thresholds were measured here in the same session to offset day-to-day variations in sensitivity; blocks of the two types of measurement were interleaved to offset ordering and carry-over effects within sessions. Differences in thresholds were then computed. A 2IFC method for determining threshold was used both as a control on Experiment 1 and to obtain data from a less practised observer. There were two parts to this experiment. The first part quantified the difference between simple-detection and colour-discrimination thresholds over the same spectral region as explored in Experiment 1. It was expected that any residual differences would be greatest in the region about 580 nm. A fixed auxiliary-field luminance of 3000 td was used, for this gave reasonably good isolation of the opponent-colour system, as Experiment 1 showed, without being uncomfortably bright. Thresholds were determined on the small auxiliary field by two subjects, and, to provide a quantitative control on the effects of auxiliary-field size (see Fig. 1), thresholds were also determined by one of the subjects on the large auxiliary field. The second part of the experiment quantified the effect on opponent-colour isolation of varying the luminance of the small auxiliary field. Simple-detection and colour-discrimination thresholds were determined at 582 nm over a range of auxiliary-field luminances.

Methods

Stimuli and apparatus. For the measurement of wavelength dependence, the monochromatic test flash and the white comparison flash were as in Experiment 1 except that the wavelength of the monochromatic test flash was varied over the range 520–615 nm in rather larger steps. The small auxiliary field was also as in Experiment 1, except that its luminance was fixed at 3000 td. The large auxiliary field was circular of dia. 10 deg, and had the same colour temperature and luminance as the small auxiliary field. When the large auxiliary field was in use stimuli were centred at the middle of a 3-deg, square, fixation array of four tiny white lights. Otherwise, the apparatus was as in Experiment 1. For the measurement of luminance dependence, the wavelength of the monochromatic test flash was fixed at 582 nm, and the luminance of the small auxiliary field was varied over the range 300–30,000 td. Other conditions were as in Experiment 1.

Subjects. R.S.S. and M.O.S. (co-author) took part in this experiment. M.O.S. was male, had normal colour vision and corrected Snellen acuity of 6/5, and was aged 22 yr.

Procedure. Data for only one test-flash wavelength or for only one auxiliary-field luminance were collected in a session. Subjects fixated with the right eye the centre of the small auxiliary field or, for the large auxiliary field, the centre of the fixation display. At the beginning of the experimental session, six preliminary measurements of simple-detection threshold were made by a method of adjustment first for the monochromatic test flash and then for the white comparison flash. The wedges in channels 1 and 2 were then set to the mean positions thus obtained and remained fixed for the remainder of the experiment. The intensity of the stimulus flashes was now controlled by the experimenter using NDFs inserted at a point common to channels 1 and 2. Intensities were altered pseudorandomly over the range approximately -0.5 to $+0.5$ log unit in steps of approximately 0.1 log unit. In the 2IFC determinations of colour-discrimination threshold, one interval contained the monochromatic test flash and the other interval contained the white comparison flash; the interstimulus interval was 1 sec. Ordering of the intervals was pseudorandom. The subject initiated the test sequence on an audible cue, and indicated (forced-choice) whether the monochromatic test flash occurred in the first or second interval. In the 2IFC determinations of simple-detection threshold, the procedure was similar except that one interval contained the monochromatic test flash and the other interval was empty. The subject indicated the interval in which the flash occurred. Each threshold was based on 500 trials comprising five blocks of 100 trials, each block consisting of ten trials at each of ten stimulus intensities. Blocks of colour-discrimination trials were alternated with blocks of simple-detection trials. An experimental session lasted approximately 3.5 hr.

Results

Results for wavelength dependence are shown

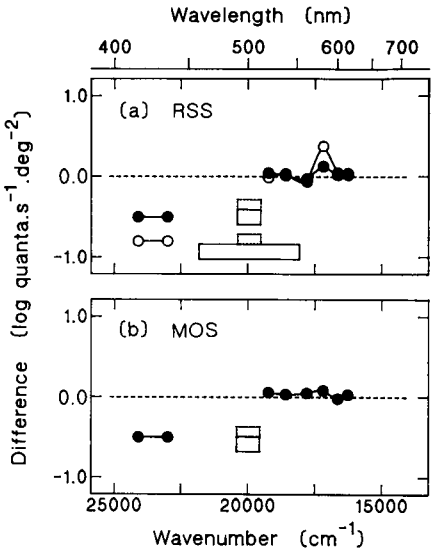

Fig. 3. (a) Difference in sensitivity for simple detection and for colour discrimination of a 1.05-deg test flash presented on a large white auxiliary field (open symbols) or on a small white auxiliary field spatially coincident with the test field (solid symbols). Difference in log intensities of the test flash is plotted against wavenumber λ^{-1} of the test flash. Thresholds were obtained by a two-interval forced-choice procedure. Each point shows the difference between the thresholds each of which was based on 500 trials and the vertical bars shows ± 1 SEM where sufficiently large. Subject: R.S.S. Other details as for Fig. 1. (b) Subject: M.O.S. Measurements were made for the small auxiliary field only. Other details as for (a).

in Fig. 3. The difference between threshold for colour discrimination and that for simple detection is plotted as a function of test-flash wavenumber; if more light was required for colour discrimination then the result is shown positive. Solid symbols show differences in threshold on the small auxiliary field and open symbols on the large auxiliary field [Fig. 3(a) only]. Vertical bars show ± 1 SEM where sufficiently large. For subject R.S.S. [Fig. 3(a)] the differences between simple-detection and colour-discrimination thresholds on either auxiliary field did not exceed $+0.04$ or -0.06 log units at all wavelengths except 582 nm where the difference was 0.13 and 0.37 log unit on the small and large auxiliary fields respectively. For subject M.O.S. [Fig. 3(b)], who made measurements on the small auxiliary field only, the difference between the two thresholds at 582 nm was 0.08 log unit, and not more than 0.06 log unit elsewhere.

Results for luminance dependence are shown in Fig. 4. The difference between threshold for colour discrimination and that for simple detection at 582 nm is plotted as a function of auxiliary-field luminance. Differences are again shown positive if more light was required for colour discrimination. There is an evident monotonic decrease in threshold difference with increasing auxiliary-field luminance. For R.S.S. [Fig. 4(a)] the difference was reduced from 0.38 log unit at 300 td to 0.14 log unit at 3000 td and at 10,000 td, and to -0.01 log unit at 30,000 td. For M.O.S. the difference was reduced from 0.40 log unit at 300 td, to 0.01 log unit at 10,000 td and to 0.09 log unit at 30,000 td.

Comment

These forced-choice measurements confirmed the preliminary conclusions of Experiment 1. First, a large white conditioning field was not sufficient to isolate the opponent-colour system over the whole trough region. Some indication of the greater sensitivity of the luminance system at 582 nm is given by the difference, 0.37 log unit, between colour-discrimination and simple-detection thresholds obtained by subject R.S.S. on the large field. The small auxiliary field was clearly more effective in isolating the opponent-colour system: at 582 nm the difference between colour-discrimination and simple-detection thresholds was 0.13 log unit for R.S.S., and 0.08 log unit for M.O.S.

Second, almost complete isolation of the opponent-colour system can evidently be

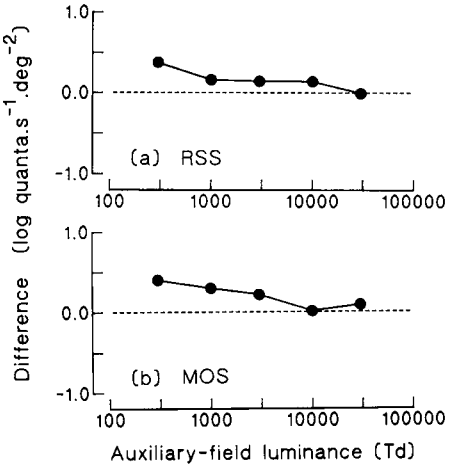

Fig. 4. (a) Difference in sensitivity for simple detection and colour discrimination for a 1.05-deg test flash of wavelength 582 nm presented on a small auxiliary field of various luminances. Each point shows the difference in log units between thresholds value each of which was based on 500 trials; the vertical bars show ± 1 SEM where sufficiently large. Subject: R.S.S. Other details as for Fig. 3. (b) Subject: M.O.S. Other details as (a).

achieved at simple-detection threshold by use of a sufficiently intense auxiliary field spatially coincident with the test field. If there is a limiting effect in the action of this auxiliary field it would seem to occur at 10,000 or 30,000 td. For a large auxiliary field, a limiting effect may be at 3000 td (Harwerth and Levi, 1977) or 10,000 td (Sperling *et al.*, 1967).

EXPERIMENT 3

Comparison with Low-frequency-test-stimulus Thresholds

In this experiment, the small auxiliary-field paradigm was compared with the low-frequency-test-stimulus paradigm of Thornton and Pugh (1983a). Simple-detection thresholds for a low-frequency test stimulus were determined by a method of adjustment, with wavelengths spanning most of the visible spectrum. Experiments 1 and 2 showed that the small auxiliary field could produce almost complete isolation of the opponent-colour system; the results obtained there were accordingly used to assess the effectiveness of the low-frequency test stimulus.

Methods

Stimuli and apparatus. The low-frequency monochromatic test flash had the spatial profile of a radially symmetric Gaussian with half-height full-width of 1.0 deg, and the temporal profile of a Gaussian with half-height full-width of 200 ms*. The white comparison flash was not used. Other stimuli were as described above. The additional interference filters used had characteristics as described in Experiment 1, except for a 461-nm filter which had half-height full-bandwidth of 14 nm.

Subjects. R.S.S., M.O.S., D.H.F. (co-author), and W.F.B. took part in this experiment. D.H.F. and W.F.B. were male with normal colour vision. D.H.F. had corrected Snellen acuity of 6/4, and was aged 40 yr. W.F.B. had corrected Snellen acuity of 6/6 and was aged 34 yr. A.R.R. who made measurements for the sharp test flash only on the small and large auxiliary field (Fig. 1) was female, had normal colour vision and corrected Snellen acuity of 6/5, and was aged 22 yr.

Procedure. Threshold was measured for the monochromatic low-frequency test stimulus, with the spatial and temporal profiles described above, presented on a large white auxiliary field. Threshold was also measured for the monochromatic test flash with sharp-edged spatial and temporal profiles presented on a spatially coincident white auxiliary field. Both auxiliary fields were of luminance 3000 td. Subjects made these measurements by a method of adjustment for simple detection only. For each stimulus paradigm, measurements were made in two sessions, the one with ascending and the other with descending order of wavelengths. Other details of the measurement procedure were as in Experiment 1.

Results and Comment

Results are shown in Fig. 5. Sensitivity in log quanta. $sec^{-1} \cdot deg^{-2}$ is plotted against test-flash wavenumber. Solid symbols show thresholds obtained with the sharp stimulus on the small auxiliary field, replotted from Fig. 1, and open symbols show thresholds obtained with the low-frequency stimulus on the large auxiliary field. It can be seen that, although relative sensitivity to the two types of test stimulus varied from subject to subject (possibly because of different relative threshold criteria), the shapes of the two test spectral sensitivity curves particularly in the region about 580 nm were broadly similar. For each subject, the difference in sensitivity between 582 nm and the mean over the regions 520–562 and 601–615 nm was calculated. The

*The spatial profile of the low-frequency test stimulus was obtained by placing a photographic mask at an appropriate position in the channel to give a defocussed image. This position was determined and the image quality assessed by means of a linear photodiode system mounted on a travelling microscope placed after the exit pupil. The profile of the sharp 1.05-deg stimulus was also measured by the same method and, with this as a reference, the mask giving rise to the low-frequency stimulus was adjusted so that the stimulus had a half-height full-width of approximately 1 deg. Its profile was sampled at 14 points along a diameter of the field. The data were analysed by means of a generalized linear interactive modelling technique GLIM (Baker and Nelder, 1978), and the profile was found to be well fitted by a Gaussian function (proportion of variance accounted for was 95.2%). The temporal profile of the low-frequency test stimulus was controlled by two polaroid filters placed in the channel, the one static and the other rotated through 180° by a stepping motor controlled by a microcomputer. The speed of rotation of the stepping motor was set so that the half-height full-width of the time-varying intensity was 200 ms. Light output was sampled at 24 points over its time-course. The data were analysed by means of GLIM and the temporal profile was also found to be well fitted by a Gaussian function (proportion of variance accounted for was 96.8%).

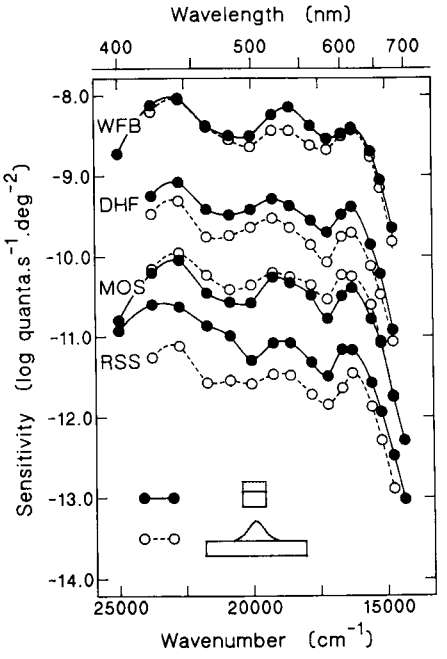

Fig. 5. Test spectral sensitivity curves obtained for simple detection of the previously used sharp-edged test flash presented on a small white auxiliary field spatially coincident with the test field (solid symbols, continuous line, replotted from Fig. 1) and for simple detection of a low-frequency test stimulus presented on a large white auxiliary field (open symbols, broken line). The low-frequency test stimulus had Gaussian spatial and temporal profiles with half-height full-widths of 1 deg and 200 msec respectively. Thresholds were set by a method of adjustment. The pairs of curves, displaced downwards by 1.0 log unit successively, are for different subjects as indicated. Each point is the mean of six readings and the vertical bars show ± 1 SEM where sufficiently large. Other details as for Fig. 1.

differences in trough depth for W.F.B., D.H.F., M.O.S., and R.S.S. were respectively -0.02, $+0.09$, -0.11, and -0.04 log unit, where a positive result corresponds to a less deep trough for the low-frequency test stimulus. This difference was significant for both D.H.F. and M.O.S. (respectively $t = 2.27$ and -2.25, d.f. $= 30$, each $P < 0.05$, two-tailed), but the differences were in opposite directions and numerically small. Overall, it was concluded that the two paradigms were equally effective in revealing activity of the opponent-colour system.

DISCUSSION

In Experiment 1 simple-detection threshold was measured by a method of adjustment. The trough in spectral sensitivity at about 580 nm progressively deepened with increasing auxiliary-field luminance and reached its lowest values at auxiliary-field luminances of 3000–10,000 td, where the curves were very close to those obtained for colour discrimination in the same experiment. In contrast, for colour discrimination, the trough in spectral sensitivity remained fairly stable over all luminances of the auxiliary field. The concurrence of detection and discrimination troughs at auxiliary-field luminances of 3000 td or higher provided strong support for the hypothesis that the small auxiliary field secured isolation of the opponent-colour system at simple-detection threshold.

This hypothesis was further supported by the two-interval forced-choice measurements of simple-detection and colour-discrimination threshold in Experiment 2. The difference between the two thresholds was greatest at 582 nm, and this difference was reduced almost to zero for auxiliary-field luminances of 10,000–30,000 td. It was also evident that use of a large auxiliary field with a spatially and temporally sharp-edged test flash did not secure complete isolation of the opponent-colour system, failing by 0.37 log unit at 582 nm for a luminance of 3000 td.

These results confirmed previous suggestions of Foster and Snelgar (1983a) concerning the effectiveness of a small auxiliary field in revealing opponent-colour function at simple-detection threshold. There, as in Experiment 1 here, a method of adjustment was used. It may be noted that although colour-discrimination thresholds provide, in principle, a direct measure of opponent-colour sensitivity, the preferred procedure entails some 2IFC method, which, in turn, requires many more presentations of the stimulus. The 2IFC thresholds obtained in Experiment 2 were based on 500 trials each, which may be compared with about 60 trials with the method of adjustment.

Experiment 3 compared the effectiveness of the small-auxiliary-field paradigm with the low-frequency-test-stimulus paradigm. For all four subjects, there was essentially no difference between the two sets of results in the region of the troughs near 580 nm: differences in depths were 0.11 log unit or less. The supposed mechanisms of isolation were, however, different in the two cases: the small auxiliary field actively caused high spatial-frequency adaptation or masking of the luminance system, whereas the low-frequency test stimulus provided little or no stimulus transients to which the luminance system might respond.

The paradigm of an auxiliary field spatially coincident with the test field may be applied in a variety of investigations of opponent-colour processes where complete or near-complete isolation is desirable, both in the fovea and at other localized retinal sites. Most of the studies in which a large auxiliary field was employed, some cited in the Introduction, used central presentation of the test flash. Three peaks in the test spectral sensitivity curve have been shown at stimulus eccentricities of 1.5° (Harwerth and Levi, 1977), 5° (Stiles and Crawford, 1933), and 6° (Verriest and Uvijls, 1977). For the more peripheral retina, however, it seemed that the peaks at 530 and 610 nm were much less prominent (Wooten *et al.*, 1975; Verriest and Uvijls, 1977). Instead, a broad maximum was usually found with peak sensitivity at about 550 nm and it was generally assumed that opponent-colour processes do not operate or operate weakly on signals from receptors situated in the peripheral retina. Interestingly, Kuyk (1982) found that the three peaks in the test spectral sensitivity curve could be obtained in the peripheral retina if the test field was made sufficiently large (e.g. 5.5 deg of visual angle at 45° eccentricity). The paradigm of the small auxiliary field, developed by Foster (1979) for measurements of field spectral sensitivity (see below), was also used by Krastel *et al.* (1983, 1984) who showed that a three-peaked test spectral sensitivity curve, with a deep trough at about 580 nm, could be obtained in the peripheral retina if the test and auxiliary fields were large (e.g. 16 deg of visual angle at 33° eccentricity).

A small auxiliary field was first used to reveal activity of the opponent-colour system in measures of field spectral sensitivity with either a monochromatic (Foster, 1979, 1980, 1981; Foster and Snelgar, 1983b) or white auxiliary field (Foster and Snelgar, 1983a). An almost exactly analogous paradigm, exploiting the sensitivity of the luminance system to *temporal* transients, has also been used (Finkelstein and Hood 1981, 1982). In this method a test flash was presented on a steady, large white auxiliary field and a flashed large main field, the onset of which was temporally coincident with that of the test flash. A single field spectral sensitivity curve was obtained with peaks at 600 nm *and* 540 nm, and a dip at 580 nm.

It should be noted that, in general, the imposition of a particular stimulus property or set of properties need not always ensure isolation of the opponent-colour system or luminance system. Thus, a test flash which is small, or brief, or both (properties which should favour detection by the luminance system) may under suitable conditions give rise to field spectral sensitivity data that show shifted and sharpened peaks characteristic of opponent-colour function (Foster, 1981; Finkelstein and Hood, 1981, 1982). Moreover, the shape of the spectral sensitivity curve of the opponent-colour system, determined by either test or field variation, need not be fixed, and will alter if the equilibrium points of the constituent opponent-colour channels are shifted by chromatic adaptation. Thus for the red-green channel, the deep trough in the test spectral sensitivity curve and the cross-over point of the sharpened long- and medium-wavelength field spectral sensitivity curves obtained by Foster and Snelgar (1983a) both occurred at about 580 nm because the small auxiliary field used in those experiments was white. If the chromaticity of the auxiliary field, either large or small, is changed, however, then the position of the trough in the test spectral sensitivity curve may also change (Sperling and Harwerth, 1971; Thornton and Pugh, 1983b; Foster and Snelgar, 1986). A parallel effect occurs in the cross-over point of the sharpened long- and medium-wavelength field spectral sensitivity curves, a result which suggests a quasi-invariance of opponent-colour processes (Foster and Snelgar, 1986).

In conclusion, the present results show that a small auxiliary field spatially coincident with the test field provides an effective device for depressing the sensitivity of the luminance system and revealing opponent-colour activity. It has, moreover, the advantage that opponent-colour function may be explored over small regions of the visual field, a property which may have particular significance in the investigation of retinal and optic-nerve pathologies (Foster *et al.*, 1985).

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