

SPATIAL INFLUENCES ON COLOUR OPPONENT CONTRIBUTIONS TO PATTERN DETECTION

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Abstract—The contribution of colour opponent mechanisms to detection thresholds is investigated at different spatial frequencies by presenting monochromatic, sinusoidal gratings on a uniform white background. Colour opponent mechanisms, characterised by a triple peaked spectral sensitivity function, determine threshold at low spatial frequencies (below 1 c/deg) and their contribution flattens the Weber function. They display low pass spatial frequency characteristics, becoming relatively more sensitive than non-opponent mechanisms as spatial frequency decreases. Colour opponent contributions are not revealed when the test grating and background are presented dichoptically.

Colour opponency Spectral sensitivity Spatial frequency

INTRODUCTION

One approach to the study of colour opponent mechanisms is to isolate their response at detection threshold. This can be achieved by selecting stimulus arrangements to which the opponent mechanisms are the most sensitive, so allowing their responses to determine detection at threshold. There is now considerable evidence to suggest that detection by colour opponent mechanisms is favoured if test stimuli are presented on a constant white or yellow background field (Sloan, 1928; Stiles and Crawford, 1933; Sperling and Harwerth, 1971; King-Smith and Carden, 1976; King-Smith and Kranda, 1981; Foster and Snelgar, 1983; Thornton and Pugh, 1983a, b; Stromeyer *et al.*, 1985). Test spectral sensitivity measurements made with such backgrounds reveal a characteristic triple peaked function. The long and medium wavelength peaks in sensitivity are both too sharply peaked and are in the wrong spectral locations to correspond to the peaks of cone action spectra. However, they can be more satisfactorily explained by the presence of inhibitory interactions between medium and long wavelength cones, of the type which are believed to underlie colour opponent processing (Sperling and Harwerth, 1971; Thornton and Pugh, 1983a, b; see also review by Mollon, 1982).

Successful isolation of colour opponent mechanisms at threshold also depends on the choice of spatial and temporal parameters for

the test stimuli. King-Smith and Carden (1976) demonstrated that the triple peaked spectral sensitivity function is revealed using a 1 deg test spot and a long exposure time (200 msec), whereas either a smaller size of test spot or of shorter presentation time produced a different unimodal spectral sensitivity function. They also suggest that colour opponent responses may be integrated over a greater spatial area than luminance based responses. Various subsequent studies support the observation that relatively large spot stimuli (≥ 1 deg), especially if blurred, favour detection by colour opponent mechanisms (e.g. Kranda and King-Smith, 1979; Polden and Mollon, 1980; Thornton and Pugh, 1983a, b; Stromeyer *et al.*, 1985). Studies of contrast sensitivity functions to sinusoidal chromatic gratings indicate that chromatic mechanisms are relatively more sensitive to low spatial frequencies than to higher ones (Van der Horst and Bouman, 1969; Mullen, 1985). Thus, overall, while these results suggest that large spot sizes favour detection by colour opponent mechanisms, a systematic investigation of the spatial characteristics of the test stimuli which isolate colour opponent mechanisms at detection threshold has not been made.

The present study aims to investigate the range of spatial frequencies and the spectral conditions which favour the use of colour opponent mechanisms at detection threshold. Monochromatic sine-wave gratings are presented on a white background field, and the

gratings are sinusoidally modulated at a low temporal rate (0.8 Hz) since colour sensitivity is greatest at low temporal frequencies and luminance sensitivity is reduced (Kelly and Van Norren, 1977). This work has been presented in a preliminary form (Mullen, 1982).

METHODS

Stimuli and apparatus

The stimulus consists of a monochromatic sinusoidal test grating superimposed on a uniform tungsten white background (see Fig. 1). The test grating is sinusoidally phase reversed at a low temporal rate of 0.8 Hz. It subtends 10 deg viewed at 170 cm, and the white background subtends 17.5 deg. The grating is viewed monocularly and a small fixation spot is placed in its centre. The stimulus is viewed with a natural pupil unless the mean luminance is varied during the experiment, in which case, the subject's pupil is dilated with 1% cytopentolate hydrochloride at least 45 min before the experiment and a 4.5 mm artificial pupil is used.

The test grating is displayed on a Joyce display screen fitted with a white P4 phosphor. The spectral wavelength of the grating is variable; it is viewed through narrow band interference filters whose full band widths at 50% transmittance are in the range 22–26 nm. The quantal intensities of the gratings at different wavelengths were calibrated using a UDT (United Distributor Technology) radiometer, calibrated from an internally calibrated Pritchard spectroradiometer. For all spectral sensitivity measurements, the grating quantal intensities were equated using calibrated neutral density filters (Barr and Stroud, type ND).

These ND filters are also used to reduce the background illumination (I_B). The background is produced using a projector containing the condenser lens only, with a fine ground glass diffuser in front of this lens. The background has a colour temperature of 3300 K. The background and test grating are combined optically with a beam splitter.

The amplitude of the grating can be varied to determine threshold, and its amplitude at threshold is termed modulation threshold (MT).

$$MT = 1/2(I_{\max} - I_{\min})$$

I_{\max} and I_{\min} are the peak and trough values respectively of the sinusoidal test grating, and are of quantum irradiance measured in quanta per second, per square degree ($q\ s^{-1}\ deg^{-2}$) in the experiments on spectral sensitivity, but are of retinal illuminance measured in trolands (td) in all other experiments. The modulation threshold is calculated from a knowledge of the calibrated Michelson contrast (C) and the mean retinal illuminance (Experiments 1 and 3) or quantum irradiance (Experiments 2 and 4) of the test grating (I_T) since

$$MT = C \times I_T.$$

Modulation sensitivity is the reciprocal of the modulation threshold. The modulation depth of the grating is varied using a digital attenuator. Grating contrasts were calibrated using a UDT radiometer. The mean illuminances of the test grating and background are calculated from measurements made with a calibrated SEI spot photometer.

Procedure

A single staircase procedure is used to determine threshold; this is similar to a method of

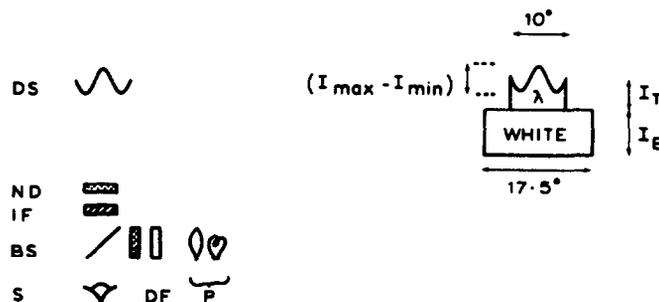


Fig. 1. *Left*: the apparatus used to produce the stimulus, which is shown on the right. DS, display screen; ND, neutral density filter; IF, interference filter; BS, beam splitter; DF, ground glass diffuser; P, projector; S, eye of subject. *Right*: the stimulus is a sinusoidal, monochromatic grating of wavelength (colour), presented on a white background. See methods for a definition of I_{\min} , I_{\max} , I_B and I_T .

adjustment (Cornsweet, 1962). The grating contrast at the start of the experimental run is chosen randomly to be either above or below threshold, and thereafter the grating is displayed continuously, rather than in discrete trials, in order to reduce temporal transients. After a criterion number of reversals, from the subject seeing to not seeing the stimulus, the stimulus, the run is terminated. Threshold is taken as the mean of the last six contrasts displayed. A mean of at least four experimental runs is obtained for each plotted data point.

Dichoptic presentation

For one experiment the test grating and white background are presented dichoptically, the test grating to the right eye and the background to the left eye. Fusion is aided by presenting one half of a circular fixation mark to each eye. When the mark appears as a complete circle it indicates that fusion has occurred and thresholds are determined.

Subjects

At least two and in some cases three subjects were used for each experiment. Data for two subjects are shown in the figures. For the experiment involving dichoptic presentation only one subject was used. All subjects performed normally on the Ishihara test for colour deficiency and the Farnsworth-Munsell 100 hue test. In addition, K.T. (the author) was tested and performed normally on the Nagal anomaloscope.

RESULTS

Experiment 1: Weber functions

In this experiment modulation thresholds to two different spatial frequencies of test grating are measured at different white background illuminances. A low spatial frequency test grating of 0.3 c/deg and a medium spatial frequency of 6 c/deg are used. At each white background illuminance, thresholds to both the spatial frequencies of test grating are measured before the background illumination is increased. These functions are measured for three different colours of test grating: green (526 nm), yellow (577 nm) and orange (602 nm).

The results for the green, orange and the yellow test gratings are shown in Fig. 2 for subject K.T., and results for the green and the

yellow gratings are shown in Fig. 3 for subject C.P. Modulation threshold is plotted as a function of the mean illuminance of the whole stimulus, which comprises the sum of the variable white background illuminance and the fixed mean illuminance of the test grating. The first data point of each function shows thresholds for the monochromatic test grating presented alone when the illuminance of the background is zero. The data points thereafter are measured at increasing illuminances of the white background.

These results show that, in the case of the green and orange test gratings, the thresholds to the two spatial frequencies behave very differently. Initially, thresholds to the monochromatic test grating presented alone are higher for the 0.3 c/deg stimulus than for the 6 c/deg one, however as the background illuminance is increased, thresholds to the two spatial frequencies become almost equal to each other. This relative change in the modulation thresholds has arisen from a flattening of the threshold function for the low spatial frequency (0.3 c/deg) grating. In both subjects this flattening of the 0.3 c/deg function occurs when the background illuminance is approximately twice as great as the test grating illuminance. In contrast, the data for the 6 c/deg green and orange test gratings lie close to a slope of unity over the whole range of background illuminances, behaving in accordance with Weber's law. While similar results are found for the orange and green test gratings, the results for yellow gratings follow a different pattern. For the yellow stimulus, thresholds to both the 0.3 and 6 c/deg stimuli fall close to a Weber slope of unity (Figs 2 and 3). Thresholds to the 6 c/deg grating were consistently lower than those for the 0.3 c/deg gratings, and there is no indication of the flattening which was found for the green and orange low spatial frequency stimuli.

It has been well established, using monochromatic gratings, that contrast sensitivity is constant or the Weber slope is close to unity at these spatial frequencies and photopic illuminances (Van Nes and Bouman, 1967; Daitch and Green, 1969; Barlow, 1972). Thus the results suggest that as the white background illuminance is increased there is a change in the mechanism which determines detection thresholds for the green and orange gratings at low spatial frequencies. Such a switch in the detecting mechanism may be revealed by a corresponding change in spectral sensitivity.

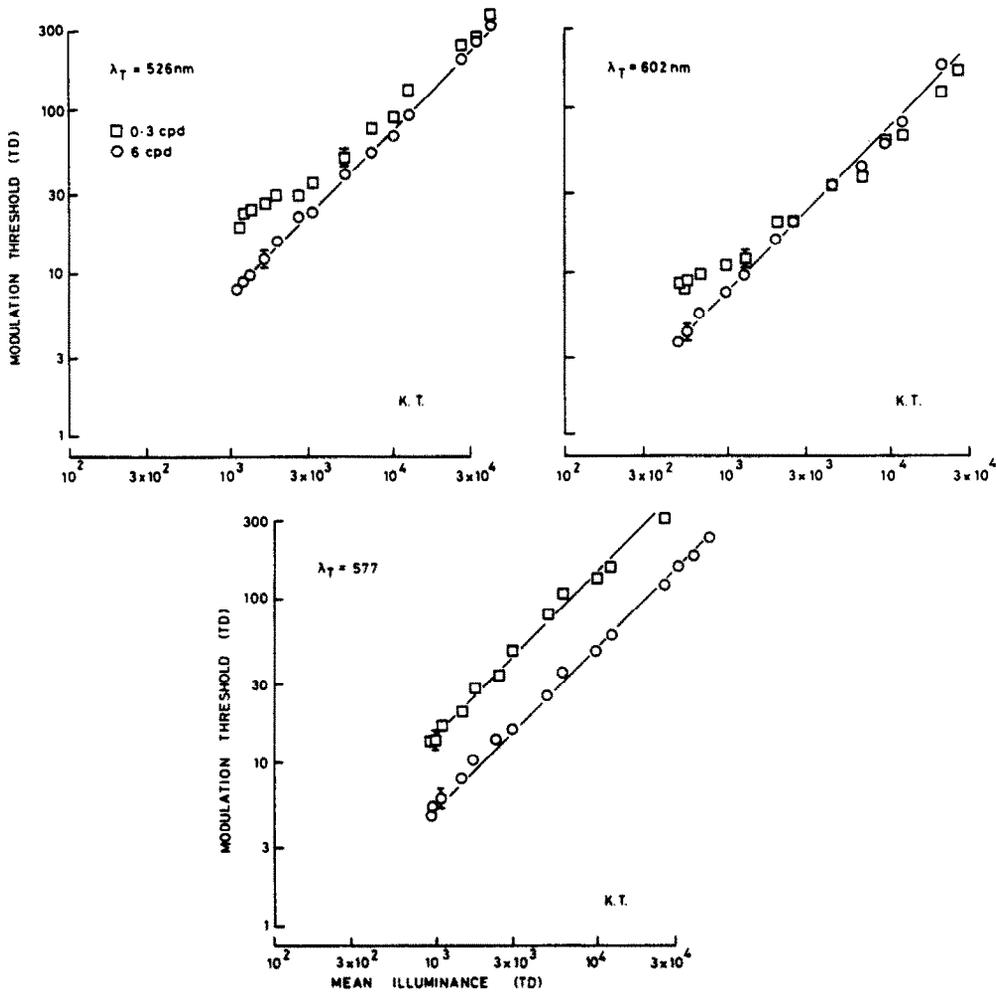


Fig. 2. Modulation thresholds to a test grating, at increasing illuminances of a white background (see methods for a definition of modulation threshold). The abscissa shows the mean illuminance of the whole stimulus which comprises the sum of the fixed mean illuminance of the test grating and the variable background illuminance. The first data point of each function shows threshold for the test grating alone with no background, and all following points are measured at increasing background illuminances. Squares (□) show results for a 0.3 c/deg test grating and circles (○) show result for a 6 cpd grating, each graph shows the results for one wavelength of test grating (λ). Test grating wavelengths are: 526, 602 and 577 nm. The solid line has a slope of unity. The subject is K.T.

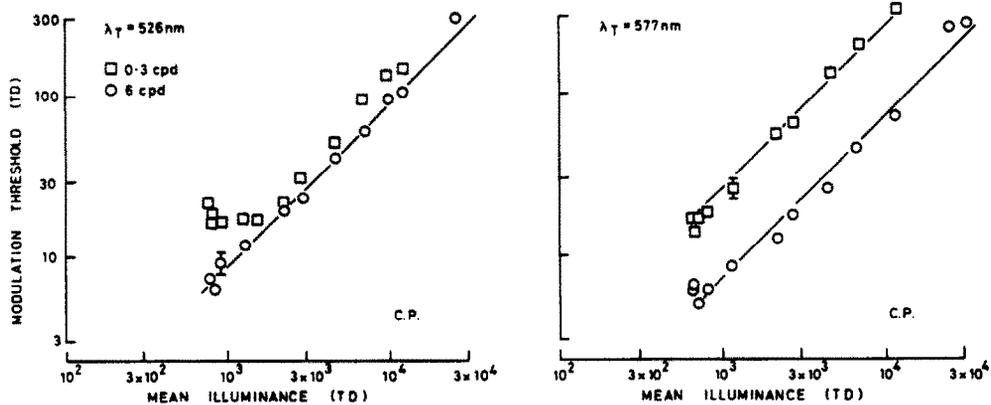


Fig. 3. Modulation thresholds to a test grating for increasing illuminances of a white background. Symbols and axes are the same as for Fig. 2. Two test grating wavelengths (λ_T) are shown; 526 and 577 nm. The subject is C.P.

Experiment 2 spectral sensitivity

In this experiment, the spectral sensitivity of the detecting mechanisms was measured for a range of spatial frequencies. Thresholds were measured for different wavelengths of test stimulus while the white background was fixed at a constant photopic illuminance (I_B), given in the legend of Fig. 4. All of the stimuli presented, consisting of the test grating and background combined, were equal in quantal intensity. However, fixing the quantal intensity of the test grating means that its illuminance (I_T) will vary across the spectrum, and hence the illuminance of the whole stimulus ($I_B + I_T$) will also vary. This effect was minimized by setting I_B to be large compared to I_T . For example, for subject K.T. the grating illuminance comprised only 8% of the total illuminance at 550 nm, and so the maximum change in the illuminance of the whole stimulus will be rather less than this.

The results for two subjects are shown in Fig. 4. Modulation sensitivity is plotted as a function of the test grating wavelength for five spatial frequencies: 0.3, 0.6, 1, 3 and 6 c/deg. The curves have been vertically displaced. At low spatial frequencies below 1 c/deg there is evidence for a triple peaked spectral sensitivity function. The peaks occur for subject K.T. at around 602, 520 and 450 nm, and there are troughs at 580 and

490 nm. A similar curve is found for the second subject (C.P.), although the green-blue peak is less clearly defined. At the medium spatial frequency of 6 c/deg a different, unimodal spectral sensitivity function is found for both subjects, which has a peak at around 550 nm and is similar to the standard luminous efficiency (V_λ) function. At intermediate spatial frequencies a mixture of the triple peaked and single peaked response functions are found; the yellow trough disappears and a combination of peaks appears as the spatial frequency increase.

Figure 5 shows the unshifted spectral sensitivities to the 6 and 0.3 c/deg grating for the two subjects. For wavelengths below 525 nm and above 600 nm sensitivity to the low spatial frequency grating is greater than sensitivity to the 6 c/deg stimulus. However at 570 nm, sensitivity to the 0.3 c/deg stimulus is considerably less than to the 6 c/deg grating.

In summary these spectral sensitivity results show that the deviation from the Weber slope and improvement in detection of the green (526 nm) and orange (602 nm) low spatial frequency gratings shown in the first experiment are associated with a triple peaked spectral sensitivity function; these wavelengths fall close to the medium and long wavelength peaks of spectral sensitivity. For reasons outlined in the introduction and described more fully

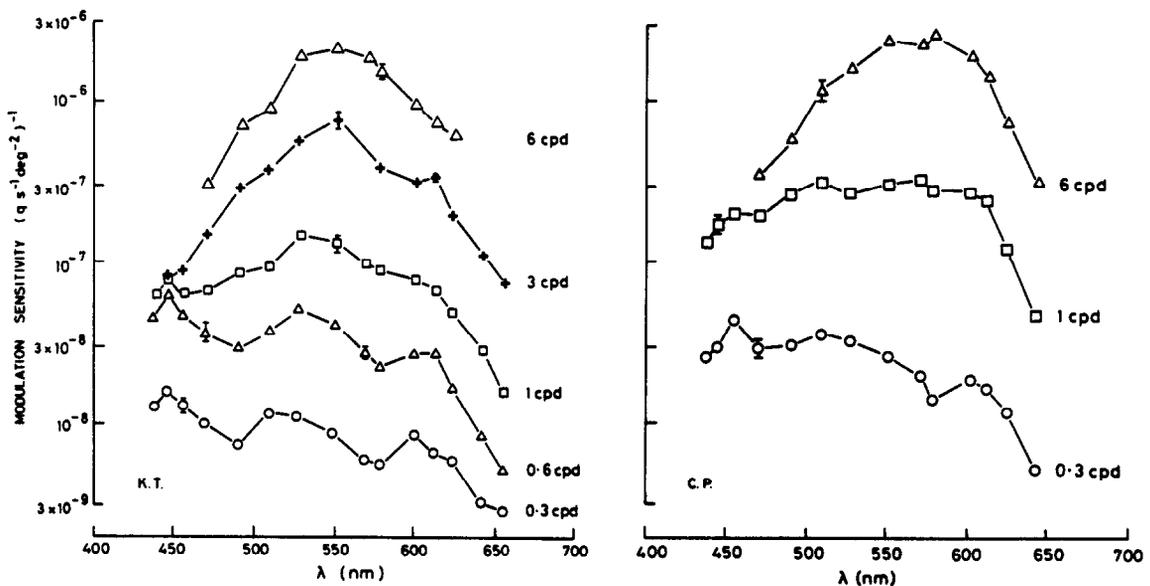


Fig. 4. Modulation sensitivity as a function of the wavelength of a test grating, shown for two subjects (K.T. and C.P.). The mean quantal irradiance of each test grating is $4 \times 10^8 \text{ q s}^{-1} \text{ deg}^{-2}$. Gratings are presented on a uniform white background of 3800 td for subject K.T. and 1500 td for subject C.P. Each function shows the results for a different spatial frequency of test grating, ranging from 0.3 to 6 c/deg. The curves have been vertically displaced upwards from that for 0.3 c/deg.

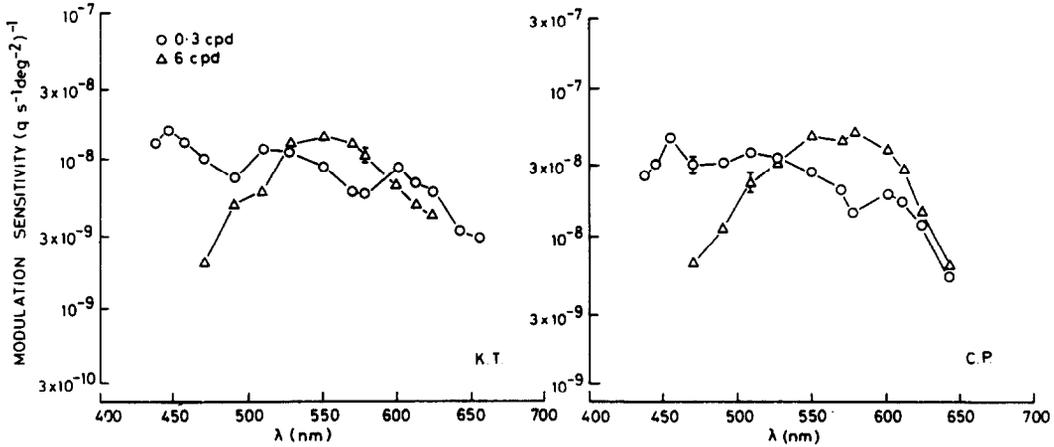


Fig. 5. Modulation sensitivity at different wavelengths of test grating. The data of Fig. 4 for two spatial frequencies, 6 and 0.3 c/deg, are shown unshifted on the modulation sensitivity axis. See legend of Fig. 4 for details.

in the discussion, this spectral sensitivity function suggests that postreceptoral, opponent colour mechanism are determining detection thresholds (Sperling and Harwerth, 1971; King-Smith and Carden, 1976; Thornton and Pugh, 1983a, b). In contrast, the detection of the higher spatial frequency (6 c/deg) stimulus is associated with a unimodal spectral sensitivity function. The interpretation of these spectral sensitivity function is considered in the discussion.

Experiment 3: spatial frequency functions

This experiment investigates the spatial characteristics of the contribution of opponent col-

our mechanisms to detection thresholds over a range of spatial frequencies. Modulation sensitivities to the green (526 nm), orange (602 nm) and yellow (577 nm) test gratings, presented on the white background, were measured as a function of spatial frequency and the results for two subjects are shown in Fig. 6. The modulation functions have been scaled so that they match in sensitivity at 6 c/deg. Thus sensitivities to each colour of test grating have been matched on the unimodal spectral sensitivity function, shown in Fig. 5. The number of spatial cycles displayed in the stimulus for the lower spatial frequencies is indicated on the figure.

The results show that the shape of the sub-

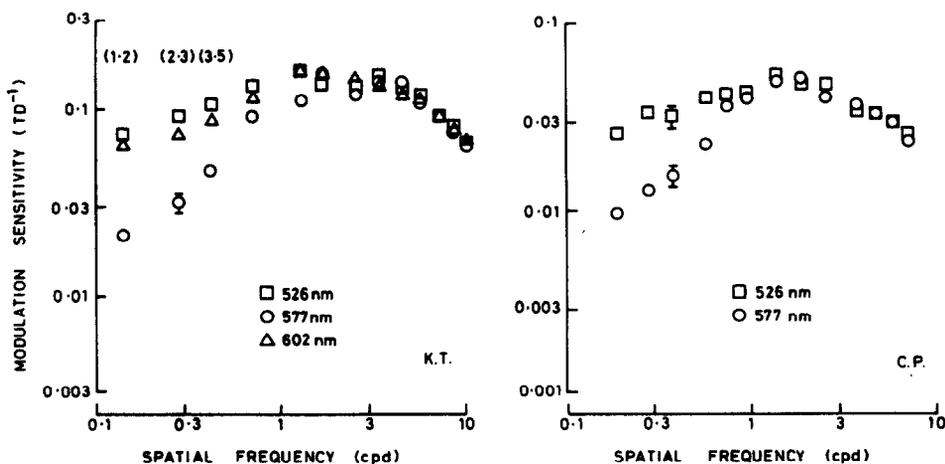


Fig. 6. Modulation sensitivity as a function of spatial frequency for two subjects. Results for three different wavelengths of test grating are shown for subject K.T. (526, 577 and 602 nm), and two wavelengths of test grating are shown for subject C.P. (526 and 577 nm). The curves for each subject have been matched at 6 cpd, according to the spectral sensitivity function shown in Figs 4 and 5. The number of spatial cycles displayed is shown in parentheses if it falls below 4. The white background illuminance is 3800 td for subject K.T. and 1500 td for subject C.P.

ject's modulation sensitivity function depends on the colour of the test grating. Below 1–2 c/deg sensitivity to the orange and green test stimuli is maintained as spatial frequency decreases, showing little attenuation for low spatial frequencies. The slight loss in sensitivity may be partly accounted for by the low number of spatial cycles displayed in the stimulus (Findlay, 1969; Savoy and McCann, 1975; Howell and Hess, 1978). However significantly greater low spatial frequency attenuation occurs for the yellow (577 nm) test grating. As spatial frequency decreases, sensitivity to the yellow test grating falls increasingly below sensitivity to the green and orange stimuli; this difference reaches half a log unit at the lowest frequency of 0.12 c/deg. In the higher spatial frequency region above 2–3 c/deg, modulation sensitivities for all three colours of test grating fall along the same curve. Coincidence at 6 c/deg only is determined by the scaling procedure.

The spectral sensitivity functions shown in Figs 4 and 5 suggested that low and medium spatial frequencies are detected by two different mechanisms. In which case the curves found here for the orange and green test gratings would represent the upper envelope of the sensitivities of these mechanisms to different spatial frequencies. The mechanism sensitive to the low frequencies has an opponent colour spectral sensitivity function and low pass spatial frequency characteristics.

Experiment 4: Dichoptic presentation of test stimulus and background

This experiment tests for the dichoptic transfer of the effects of the white background on modulation thresholds. An absence of dichoptic transfer would suggest that the psychophysical effects are determined in a monocular, possibly precortical site. The experimental conditions were similar to those used in the spectral sensitivity experiments and are described in the methods. The monochromatic test grating and the white background were presented to different eyes. The subject only made threshold settings when fusion was known to have occurred (see Methods).

Modulation sensitivity was measured as a function of the wavelength (colour) of the test grating for 0.3 c/deg stimuli both with and without a white background. The results are shown in Fig. 7. Although thresholds are quite variable owing to the difficulty of the task, sensitivity to the test gratings with dichoptic presentation of the background is essentially uniform across the spectrum. This is to be expected if the test gratings are within the Weber illuminance range (Van Nes and Bouman, 1967). The triple peaked spectral sensitivity function obtained for monocular presentation of the test grating and background for this subject is indicated on the figure by the broken line. There is no indication that this function

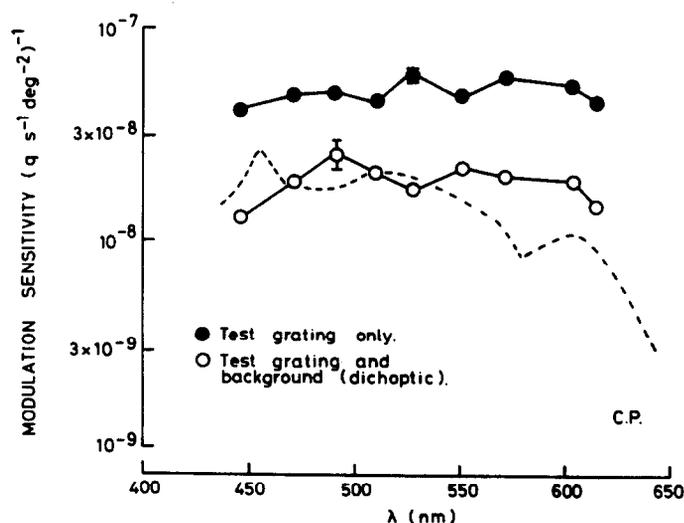


Fig. 7. Modulation sensitivity as a function of test grating wavelength for dichoptic presentations of the test stimulus and white background (hollow circles) and for the presentation of the test grating alone (solid circles). The background illuminance is 1750 td. The spatial frequency of the test grating is 0.3 cpd. The dashed line shows the spectral sensitivity function obtained for this subject at 0.3 c/deg when the test stimuli and background are monocularly presented (see Fig. 4).

occurs under dichoptic viewing conditions. However the background has some adaptive effect dichoptically since sensitivity is lower in its presence than when the test gratings are presented alone. Thus these results indicate that the triple peaked spectral sensitivity function is not produced dichoptically, and suggest that the neural interactions subserving it occur at a monocular, possibly precortical, site. These findings are supported by those of Foster (1981) who reports field spectral sensitivity functions, believed to be based on opponent colour interactions, which fail to be produced under conditions of dichoptic viewing. Other colour opponent threshold effects have also been reported which cannot be produced dichoptically (Sternheim *et al.*, 1979; Stromeyer and Sternheim, 1981; Polden and Mollon, 1980; see Discussion).

DISCUSSION

The results of Figs 2 and 3 reveal a flattening in the Weber function for red and for green monochromatic test gratings on a white background which only occurs for the low spatial frequency used (0.3 c/deg) and is absent at the higher spatial frequencies (6 c/deg). The effect is also absent for yellow test gratings of either spatial frequency. This effect suggests the intrusion of a mechanism which determines detection threshold under these specific spatial and spectral conditions.

A similar phenomenon has been reported by Sternheim *et al.* (1978), and Stromeyer and Sternheim (1981) under different spectral conditions, in which detection depends on a red sensitive mechanism. When a red (633 nm) grating on a red auxiliary field was presented on a green (565 nm) adapting field thresholds were found to be lowered. The effect was also spatially dependent, occurring only at the lowest spatial frequencies used (0.5, 1 c/deg), and was associated with a flattened π_3 sensitivity function. A weaker effect was found for green test gratings on red fields.

A reversal of the Weber function has also been found for spot stimuli under conditions which isolate a blue mechanism and has been termed combinative euchromatopsia (Polden and Mollon, 1980). These effects have been found not to transfer dichoptically (Stromeyer and Sternheim, 1981; Sternheim *et al.*, 1979; Polden and Mollon, 1980). The results of Fig. 7 indicate that this is also the case for the present

effect, strengthening the similarity between the present and previous deviations from the Weber function, and suggesting that these results are compatible with processing occurring at a monocular, possibly precortical sites.

In Figs 4 and 5, a marked change in spectral sensitivity was found in association with the flattening of the Weber slopes. At low spatial frequencies (below 1 c/deg) the detection of the test grating has a triple peaked spectral sensitivity function. At higher spatial frequencies (6 c/deg) a unimodal broadly peaked spectral sensitivity function occurs, whereas at intermediate spatial frequencies the response appears to be a mixture of these two types of function. Thus these results indicate that the flattening of the Weber functions shown in Figs 2 and 3 is due to the contribution at detection thresholds of a mechanism with a triple peaked spectral sensitivity function.

A similar type of spectral sensitivity function has been revealed previously using large spot stimuli of 1–2 deg (Sloan, 1928; Stiles and Crawford, 1933; Sperling and Harwerth, 1971; King-Smith and Carden, 1976; Foster and Snelgar, 1983) or a spatial Gaussian profile (Thornton and Pugh, 1983a, b), all with a long presentation time. It is known that the function is too sharply peaked and furthermore that the peaks are in the wrong spectral locations to be attributable to isolated receptor mechanisms. However, there is evidence that this function reflects inhibitory interactions occurring between red and green cone types, of the sort which are believed to subserve opponent colour processing (Sperling and Harwerth, 1971; Ingling and Tsou, 1977). Subadditivity of threshold mixtures of light has been found to occur in association with this spectral sensitivity function which strengthens the argument that it represents the outputs of red/green and possibly blue/yellow opponent colour mechanisms (Krandt and King-Smith, 1979; Thornton and Pugh, 1983a, b). Experiments by Stromeyer *et al.* (1985) also demonstrate that inhibitory medium and long wavelength cone interactions subserve the detection of large and blurred spot stimuli presented on chromatic adapting fields, providing the test and background field differ sufficiently in chromaticity. Yellow adapting fields produced the strongest chromatic response (see also Wandell, 1985).

There is also evidence to suggest that this function coincides with the ability of the subject to determine the colour of the test spot at its

detection threshold. King-Smith and Carden (1976) have shown that a test spot, whose detection is characterized by a triple peaked sensitivity function, can be as easily discriminated from white as it can be detected. Furthermore, measurements of wavelength discrimination at detection threshold under the same conditions reveal that wavelength pairs which fall across the peaks of this function can be as easily discriminated as detected (Mullen *et al.*, 1985). Thus, the weight of evidence described here indicates that a triple peaked spectral sensitivity function is associated with detection at threshold by opponent colour mechanisms. In this case, we may conclude from the results of Figs 4 and 5 that at low spatial frequencies (below 1 c/deg, at 0.8 Hz) the subject is using the colour contrast in the stimulus to make a colour discrimination at threshold. Thus, the role of the white background in this type of experiment may be to add colour contrast to a stimulus, which is originally monochromatic, hence allowing detection to be based on opponent colour discriminations. This conclusion is supported by the results of Stromeyer *et al.* (1985) which give a systematic description of the test and background chromaticities favouring detection by red/green opponent mechanisms.

At higher spatial frequencies (6 c/deg) a unimodal sensitivity function with a broad peak around 550 nm was obtained. There is evidence to suggest that this type of function *can* represent the activity of achromatic mechanism sensitive only to intensity differences in the image. For example, when the $V\lambda$ function is obtained using high flicker rates colour differences cannot be seen in the stimulus. In this case detection is most probably based on additive interactions between medium and long wavelength cone types (see Boynton, 1979).

Using the approach already described, King-Smith and Carden (1976) have shown that such a unimodal spectral sensitivity function is also obtained for the detection of small test spots (0.05 deg), and the shape of the function is similar to that obtained using flicker photometry. Although Ingling (1978) has pointed out that a similarity in shape between the spectral sensitivity for an achromatic flicker response and the response to small spots does not necessarily imply that both are detected by the same mechanism (see also Guth and Lodge, 1973). However, King-Smith and Carden found that in the mid-spectral regions detection thresholds fell considerably below those for colour recog-

nition, and thus they concluded that this spectral sensitivity function reflects the activity of an achromatic luminance system which mediates the detection of these small stimuli, although opponent colour mechanisms may influence detection at each end of the spectrum.

Further results from Finklestein and Hood (1982), and Hood and Finklestein (1983), however, show that the interpretation of the $V\lambda$ function must be approached with some caution. Although the *test* spectral sensitivity for a small, brief flash (10', 40 msec) has a unimodal $V\lambda$ -like shape, the *field* spectral sensitivity for a flash of 580 nm reveals a different function and indicates a strong red/green opponent colour influence. Threshold subadditivity for red and green flashes was also found, supporting an opponent colour influence on detection. Incomplete additivity for small spots (0.04 deg, 200 msec) has been reported by Stromeyer *et al.* (1978) who also found that the colours of the stimuli could be named at above chance level close to their detection thresholds. Thus, overall, these results show that detection thresholds with a unimodal spectral sensitivity function may be influenced by opponent colour mechanisms.

In the light of this evidence, various possibilities should be considered. Firstly, that a luminance mechanism cannot necessarily be well isolated and separated from opponent colour mechanisms by the use of small and/or brief test stimuli. Such stimuli, which are sharply presented in space and time, will contain a relatively wide range of spatial and temporal frequencies. Instead, the use of stimuli isolated to high spatial and/or temporal frequencies may produce a more effective isolation of achromatic mechanisms. The stimuli used in the present experiments will be better isolated in spatial and temporal frequency than spot stimuli since they are sinusoidally presented.

Secondly, the results of Finklestein and Hood may suggest that the opponent and non-opponent mechanisms do not exist independently of each other. It is possible that the achromatic and chromatic mechanisms revealed in Figs 4 and 5 do not represent the outputs of two independent mechanisms, but for example, may reflect the processing of both colour and luminance information within one neural channel. The present results show that a colour opponent mode of processing at detection threshold is favoured by low spatial frequency stimuli whereas a non-opponent mode is fav-

oured by higher spatial frequencies: similar effects can be predicted for single colour opponent cells (Ingling and Drum, 1973; Ingling and Martinez, 1983).

The results of Fig. 6 have indicated the spatial characteristics of opponent colour mechanisms. The function obtained (modulation sensitivity vs spatial frequency) appears to be the upper envelope of two mechanisms, of which one operates at low spatial frequencies and has low pass spatial characteristics. Thus these results suggest that colour opponent mechanisms, which determine detection below 1 c/deg, have low pass spatial characteristics. This contrasts to the band pass characteristics which are obtained for achromatic, luminance gratings (Campbell and Robson, 1968; Van Nes and Bouman, 1967), and suggests that, as spatial frequency is reduced, luminance sensitivity falls increasingly below colour sensitivity.

Interestingly, the yellow test gratings have revealed spatial frequency functions which differ markedly from those for the green and orange stimuli. The yellow gratings are associated with band pass spatial characteristics similar to those obtained for luminance gratings and do not show the low pass spatial characteristics associated with the detection of chromatic gratings (Van der Horst and Bouman, 1969; Mullen, 1985). No flattening of the Weber function occurred at low spatial frequencies for yellow stimuli, suggesting that opponent colour mechanisms do not contribute to their detection. Thus, taken together, these findings suggest that the yellow test grating is detected on the basis of its luminance contrast. This implies that the minimum in spectral sensitivity found at this wavelength represents a fall to luminance contrast detection. Since the difference between sensitivity to yellow test gratings and to red or green test gratings becomes greater as spatial frequency decreases (Fig. 6), the trough in spectral sensitivity will deepen at lower spatial frequencies, and probably corresponds to the decline in luminance contrast sensitivity relative to colour contrast sensitivity.

In support of these results, experiments by Thornton and Pugh (1983a, b) show that when a low spatial frequency test stimulus (of Gaussian distribution) is used a deeper trough is found at yellow than when a spot stimulus is used which contains high spatial frequencies. However, subadditive interactions were found at threshold between blue and yellow test lights, which indicate the involvement of blue/yellow

opponent interactions at threshold in this trough of spectral sensitivity. These results may be reconciled with the present experiments if both a blue/yellow colour opponent and an achromatic mechanism may potentially contribute to detection in and around the trough. The two mechanisms may lie closely together in the spectrum and be close together in sensitivity, in which case complete isolation of one or other at threshold would be unlikely.

Finally, comparisons may be drawn between the results described here and those obtained using a different approach. While the method used here relies upon the choice of stimulus parameters to favour the use of opponent colour responses over luminance responses at threshold, another approach is to eliminate the "unwanted" achromatic information in the stimulus by matching the intensities of the different colours in it such that only its colour contrast determines threshold; such stimuli may be termed "isoluminant". This latter approach reveals results which are comparable to those described here since the detections of both red/green and blue/yellow chromatic sinusoidal gratings have low pass spatial frequency characteristics (Van der Horst and Bouman, 1969; Granger and Heurtly, 1973; Mullen, 1985). These comparisons give additional support to the conclusion that the opponent colour thresholds revealed in this investigation are based on the detection of the colour contrast in the stimuli at threshold.

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