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THE CONTRAST SENSITIVITY OF HUMAN COLOUR VISION TO RED–GREEN AND BLUE–YELLOW CHROMATIC GRATINGS

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SUMMARY

1. A method of producing red–green and blue–yellow sinusoidal chromatic gratings is used which permits the correction of all chromatic aberrations.

2. A quantitative criterion is adopted to choose the intensity match of the two colours in the stimulus: this is the intensity ratio at which contrast sensitivity for the chromatic grating differs most from the contrast sensitivity for a monochromatic luminance grating. Results show that this intensity match varies with spatial frequency and does not necessarily correspond to a luminance match between the colours.

3. Contrast sensitivities to the chromatic gratings at the criterion intensity match are measured as a function of spatial frequency, using field sizes ranging from 2 to 23 deg. Both blue–yellow and red–green contrast sensitivity functions have similar low-pass characteristics, with no low-frequency attenuation even at low frequencies below 0·1 cycles/deg. These functions indicate that the limiting acuities based on red–green and blue–yellow colour discriminations are similar at 11 or 12 cycles/deg.

4. Comparisons between contrast sensitivity functions for the chromatic and monochromatic gratings are made at the same mean luminances. Results show that, at low spatial frequencies below 0·5 cycles/deg, contrast sensitivity is greater to the chromatic gratings, consisting of two monochromatic gratings added in antiphase, than to either monochromatic grating alone. Above 0·5 cycles/deg, contrast sensitivity is greater to monochromatic than to chromatic gratings.

INTRODUCTION

The aim of this paper is to examine the spatial characteristics of human colour vision. For luminance vision this has been done by measuring a contrast sensitivity function: the ability of the visual system to detect luminance contrast at different spatial frequencies. The experiments described here aim to make comparable contrast sensitivity measurements for colour vision, by using grating stimuli which vary sinusoidally in colour.

A few previous studies have attempted to determine spatial sensitivity to red–green sinusoidal gratings, in which the two colours are matched in luminance to create an isoluminant stimulus (e.g. Schade, 1958; Van der Horst & Bouman, 1969; Granger & Heurtley, 1973; Kelly, 1983). Only one of these reports measurements using

blue–yellow sinusoidal stimuli (Van der Horst & Bouman, 1969). However, there are many difficulties associated with these investigations. First, the chromatic aberrations of the eye are likely to produce luminance artifacts in colour gratings at medium and high spatial frequencies. Transverse aberrations, or a chromatic difference of magnification, have not been corrected in previous isoluminant experiments. Corrections for longitudinal aberrations, or a chromatic difference of focus, have sometimes been made (Van der Horst & Bouman, 1969; Kelly, 1983). Secondly, a luminance match between the two colours in the stimulus has generally been made by using flicker photometry at one temporal and spatial frequency (Van der Horst & Bouman, 1969; Granger & Heurtley, 1973) and it has been assumed that this match is appropriate for all the other spatial and temporal frequencies used. However, red–green brightness matches may alter with temporal frequency (Ives, 1912; Börnstein & Marks, 1972), and so temporal and possibly spatial-frequency-dependent changes in brightness matches may have produced artifacts in previous isoluminant studies.

Thirdly, previous measurements have not extended to very low spatial frequencies and very few spatial cycles have been displayed at the lowest frequencies. A spatial cycle number below four or five is known to reduce sensitivity to luminance gratings (Findlay, 1969; Savoy & McCann, 1975). The lowest chromatic frequency that has been used while displaying four cycles is 0·4 cycles/deg (Granger & Heurtley, 1973) although often the lowest frequency measured with this cycle number has been higher at, for example, 1·4 cycles/deg (Van der Horst & Bouman, 1969). Furthermore, these latter measurements only extended down to spatial frequencies of 0·7 cycles/deg and for luminance gratings at comparable cycle numbers, low-frequency attenuation does not occur until below 0·5 cycles/deg (Howell & Hess, 1978). Thus, the previous studies have not satisfactorily investigated colour sensitivity to low spatial frequencies and the effects of reducing the spatial cycle number have not been distinguished from possible low-frequency attenuation below 0·5 cycles/deg. Finally, in previous investigations comparisons between colour and luminance sensitivities have not been attempted. This is partly because there is no adequate definition of colour contrast available which can be used for all colour combinations and does not depend on theoretical assumptions about post-receptoral cone interactions. Previous measures of colour sensitivity, such as purity (Van der Horst & Bouman, 1969) and wave-length discrimination, are difficult to relate to luminance contrast sensitivities.

The experiments described in this paper aim to overcome these problems in the following ways. (1) A different method of producing chromatic stimuli is used which permits correction of all chromatic aberrations. (2) Quantitative criteria are used to judge the most appropriate intensity match for creation of an optimum chromatic stimulus, and this match is adjusted separately at all spatial frequencies. (3) A very large field size is used which allows low spatial frequencies to be presented, without thresholds being affected by a low number of spatial cycles. (4) The stimulus is arranged so that the same contrast scale is used to determine thresholds for both chromatic and luminance gratings. This enables simple calculations to be made of the contrasts of the chromatic and luminance stimuli to individual cone types.

METHODS

The stimulus and procedure

A red–green chromatic grating was produced by displaying two gratings, each on Joyce display screens with white (P4) phosphors. These gratings were viewed through narrow band interference filters to produce their colour (Fig. 1). Interference filters with peak transmissions at 526 and 602 nm were chosen as these wave-lengths are at the peaks of both the human opponent colour spectral

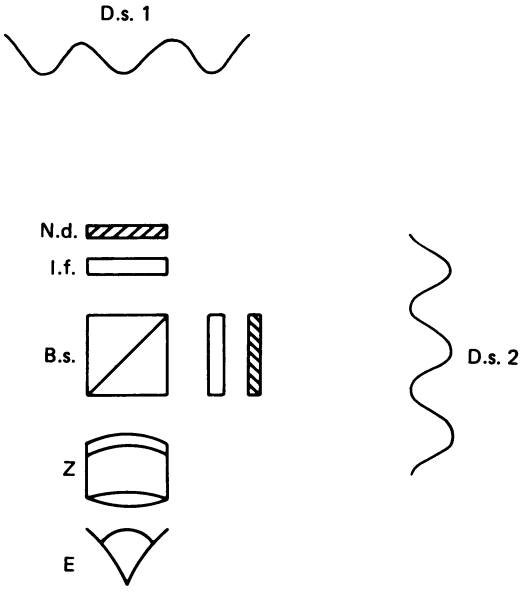

Fig. 1. A diagram of the experimental apparatus used to create the red–green and blue–yellow chromatic gratings. B.s., beam splitter; d.s. 1, d.s. 2, display screens Nos. 1 and 2; E, eye of observer; n.d., neutral density filter; Z, Zeiss telescope (× 3); i.f., interference filter. Interference filters with peak wave-length transmissions of 602 and 526 nm were used to produce a red–green chromatic grating and filters with peaks at 470 and 577 nm were used for the blue–yellow grating.

sensitivity function (Sperling & Harwerth, 1971) and the chromatic response function of Hurvich & Jameson (1955). Thus, this red–green wave-length pair causes maximal modulation in the red–green chromatic response function but modulates the blue–yellow response function by only 12%. The two monochromatic gratings were combined optically 180 deg out of phase to form the composite chromatic grating. The chromatic grating patch was circular and ranged from 9·2 to 10·3 cm in diameter, depending on the correction made for the chromatic difference of magnification (described later). The remainder of the display screen was masked off with a diffuser; thus, at all contrasts used, the grating patch was set in a uniform surround of the same mean colour and reduced mean luminance. A fixation mark appeared at the centre of the chromatic grating. Viewing was monocular with a natural pupil and at a distance of 82 cm from each display screen. A Zeiss telescope (× 3) could be placed directly in front of the eye. Viewing with the eye-piece close to the eye optically enlarged the grating and the field size, whereas viewing with the objective lens close to the eye optically reduces the image; it was thus equivalent to changing the viewing distance, and enabled the field size to be varied from 2·2 to 23·5 deg. The stimulus was phase reversed sinusoidally at 0·4 Hz.

The same method was used to produce a blue–yellow chromatic grating, but using interference filters with peak transmissions at 470 and 577 nm. 577 nm falls at the trough of the red–green

opponent spectral sensitivity function, and 470 nm is close to the blue peak. A filter transmitting light at the blue peak was not used because it severely reduced the mean luminance of the stimulus. This blue–yellow wave-length pair causes 74% modulation in the blue–yellow chromatic response function, but only 5% modulation in the red–green response function. Thus, the choice of the two wave-length pairs has been made on the basis of our knowledge of the post-receptoral colour opponent responses to different wave-lengths. As far as possible, chromatic gratings have been created which maximally stimulate one opponent colour system, and as such cause little modulation in the other opponent colour system.

Contrast of either component grating in the chromatic stimulus is defined by the usual formula:

$$C = \frac{I_{\max} - I_{\min}}{I_{\max} + I_{\min}},$$

where $I_{\max}$ and $I_{\min}$ are the peak and trough luminance values respectively of the monochromatic grating. The contrasts of the two component gratings were yoked together electronically, although their respective mean luminances may differ. Thus, $C_{526} = C_{602}$ and $C_{470} = C_{577}$ at all luminances. To find threshold, contrast is varied and at threshold the reciprocal contrast of either grating may be taken as the contrast sensitivity. Contrast output on the display screen was measured for a range of input contrasts using a UDT (United Detector Technology, model 40X) light-meter. Output contrast was linearly related to input contrast, and contrasts shown in the following experiments are the true, calibrated values.

Contrast output was also measured as a function of the spatial frequency on the display screen, using a psychophysical procedure which avoids the use of any additional optical apparatus with unknown modulation transfer characteristics. The subject set contrast thresholds for a range of gratings which consisted of pairs of stimuli identical in retinal spatial frequency (in cycles/deg) and retinal field size, but differing only in their screen spatial frequency (in cycles/cm) and viewing distance. Thus, any differences found between the thresholds for a pair of stimuli are likely to be due to the loss of contrast on the display screen at higher spatial frequencies. The results, shown in Fig. 2, reveal a non-linear relation between contrast output and screen spatial frequency; contrast output declines markedly above 0·4 cycles/cm and the loss is 40% at 2 cycles/cm. In the following experiments, screen spatial frequencies above 1·8 cycles/cm were not used. All contrast values quoted are of contrast output calibrated from the data of Fig. 2. The results of this psychophysical procedure agree well with results obtained from optical measurements of contrast loss for the same type of apparatus (Hess & Baker, 1984). Natural pupil sizes for the red–green stimuli were around 4 mm, and 6 mm for the blue–yellow stimuli. All mean luminances were measured using a calibrated SEI spot photometer.

Contrast thresholds were determined by a single staircase procedure (Cornsweet, 1962), begun at a randomly selected contrast above or below threshold. The grating was displayed continuously to increase the speed of threshold setting and to reduce considerably temporal transients. A mean of at least four thresholds was obtained for each plotted data point. The largest standard deviation of the thresholds is marked on each data curve. A 6809 Motorola microprocessor was used on-line to control the stimulus production and presentation, and data collection.

Three subjects were used in the experiments; K.T. (the author), R.M.C. and S.C.S. At least two subjects, and in some cases three, were used in each experiment. All subjects wore their normal correcting lenses, and performed normally on the Farnsworth–Munsell 100 hue test and the Ishihara test for colour blindness.

Correction of chromatic aberrations

This method of grating production has the advantage over the use of colour TV displays in that it allows the chromatic difference of focus and the chromatic difference of magnification of the eye and other optics to be corrected. The difference of focus may be corrected by placing a negative lens in the path of the shorter wave-length of the grating pair or a positive lens in the path of the longer wave-length, before the two component gratings are combined by the beam splitter.

It is also possible to measure the magnitude of this correction directly. The stimulus was arranged such that in the top half of the test patch one monochromatic square-wave component grating was displayed, whereas in the bottom half the other one appeared. The subject fixated on the longer-wave-length member of the pair (602 or 577 nm) with the help of a fixation mark. A series of negative correcting lenses was placed in front of the shorter-wave-length stimulus (470 or 526 nm)

until the subject saw this stimulus in sharpest focus simultaneously with the longer-wave-length grating. This method indicated that a correction of −1 D was required for the blue grating in the blue–yellow pair and a correction of −0·5 D was required for the green grating in the red–green pair. These values are close to previous calculations (see Wyszecki & Stiles, 1967) and were used in the present experiments.

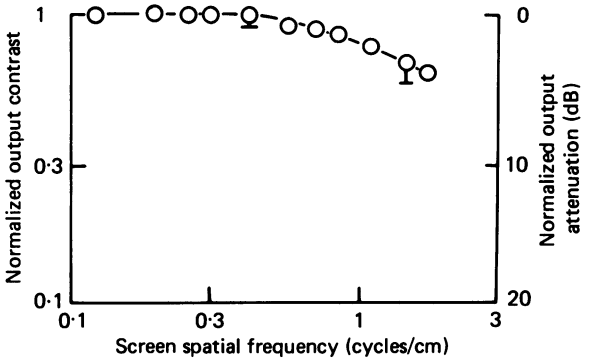

Fig. 2. Output contrast (c) normalized to contrast threshold as a function of screen spatial frequency (cycles/cm). A psychophysical method, described in the text, is used to calculate output contrast. Output contrast declines after 0·4 cycles/cm. Real contrast may be calculated from the curve by multiplying the uncalibrated input contrast by the normalized output contrast, or by adding the normalized output attenuation to the uncalibrated input attenuation. The smallest and largest standard deviations are shown. Attenuation (dB) = $20 \times \log 1/c$.

This empirical method of measuring the chromatic difference of focus is convenient to use since theoretical calculations become complex when the telescope is used to magnify or minify the stimulus, and will depend on the design of the telescope. When the telescope was used to magnify, very little correction was required for the short-wave-length gratings (−0·25 D for the 470 nm grating only). When the telescope was used to minify, much larger correcting lenses were needed, since for this reverse viewing condition a small difference of focus at the eye requires large correcting lenses at the eye-piece. A +3 D lens for the yellow grating in the blue–yellow stimulus, and a +2 D lens for the red grating in the red–green stimulus were found to be the best corrections.

The chromatic difference of magnification of the eye, and any additional optics in use, can be corrected by making independent adjustments to the spatial frequency of one of the component gratings. This was done by adjusting the X-gain on the appropriate display screen. Magnification differences are easily detected by displaying the two component gratings as square waves; overlap of adjacent bars produces a bright strip of a different colour which can be removed by adjusting the magnification of one grating.

Wave-length-dependent diffraction effects did not need correction as high frequencies, greater than 6 cycles/deg are not used (Van der Horst, de Weert & Bouman, 1967). While the chromatic aberrations are being corrected the subject's head is held in place using a dental bite bar and this line-up is maintained throughout the experiment. When the corrections have been made the gratings are displayed sinusoidally in space to produce a sinusoidal red–green or blue–yellow chromatic grating.

RESULTS

The removal of achromatic contrast

When creating stimuli which vary only in colour, an important problem is to establish the basis on which the intensities of the colours in the stimulus should be matched. Furthermore, it has frequently been assumed that a match made at one

spatial or temporal frequency will apply to all other frequencies. However, there is evidence to suggest that stimuli matched in luminance, for example by flicker photometry, will appear equally bright only under high spatial or high temporal frequency conditions, whereas under other low-frequency conditions luminance

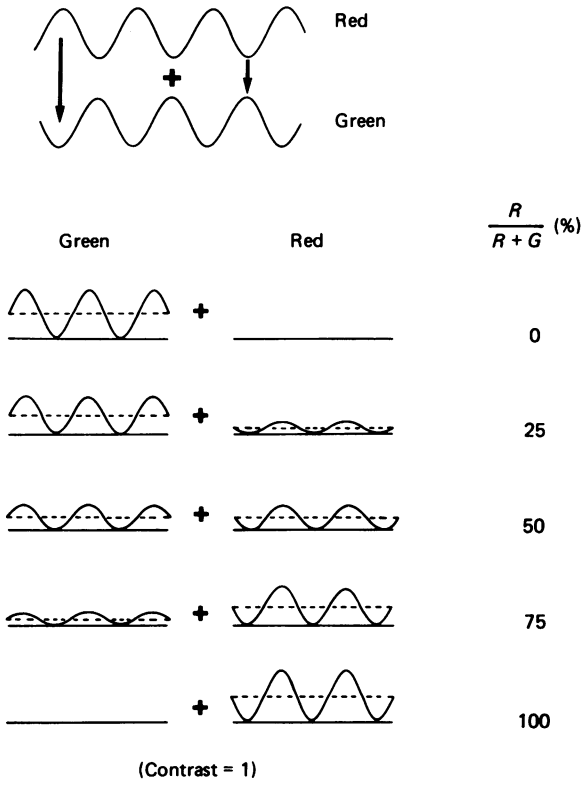

Fig. 3. A diagram of the luminance profiles across space of the red and green component gratings which are added 180 deg out of phase to produce a sinusoidal red–green chromatic stimulus. The ratio of red (R) to green (G) mean luminances in the chromatic grating is variable, and is expressed as the percentage of red light in the mixture. The mean luminance of the whole stimulus ($R+G$) is constant. The contrasts of the component red and green gratings are always equal and are at a value of 1 in this Figure. Contrast is varied to determine threshold. The same method is used to produce a blue–yellow chromatic grating, and the blue to yellow ratio is expressed as the percentage of yellow in the mixture.

matched stimuli will contain brightness differences (Ives, 1912; Börnstein & Marks, 1972; Myers, Ingling & Drum, 1973). Thus, there is a need to devise an appropriate criterion and a quantitative method for matching the intensity of the two colours in the stimulus which may be used at all spatial and temporal frequencies.

In this experiment, the ratio of the mean luminances of the two component gratings in the stimulus was varied over a wide range, and the subject's contrast sensitivity to the stimulus was measured at selected points. The criterion for the choice of the

intensity match was the luminance ratio at which the contrast sensitivity to the chromatic grating differs most from the contrast sensitivity to the monochromatic gratings. The method is illustrated for the red–green grating in Fig. 3. In this case, the ratio has been expressed as the percentage of red (R) in the red–green mixture. The range begins and ends with a red or green monochromatic stimulus that has luminance contrast but no colour contrast, and in the middle region the stimulus will

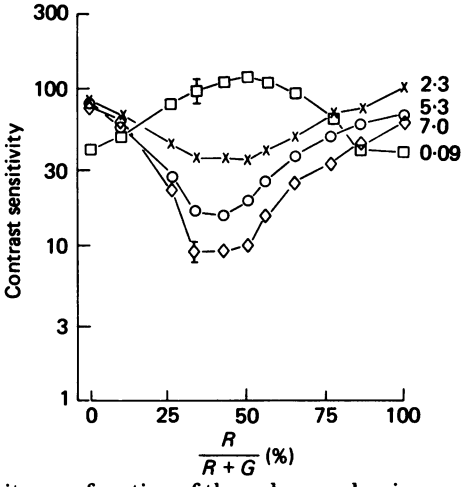

Fig. 4. Contrast sensitivity as a function of the red–green luminance ratio in the stimulus, expressed as the percentage of red in the mixture. Four spatial frequencies are shown (cycles/deg): ×, 2·3; ○, 5·3; ◇, 7·0 and □, 0·09. Vertical bars indicate ±1 S.D.. The subject is R.M.C.

have maximum colour contrast and minimal luminance contrast. Over-all there is no net change in the mean luminance of the composite stimulus; although R/G varies, $R+G$ was arranged to be at a constant photopic luminance (15 cd/m^2). The same method is used to vary the colour ratio in the blue–yellow stimulus. The ratio is expressed as the percentage of yellow in the mixture. The mean luminance of the composite stimulus ($B+Y$) remains constant at 2·1 cd/m^2.

Contrast sensitivity for one spatial frequency was measured at eleven or twelve percentages in the red–green or the blue–yellow range. The run was then repeated but beginning with the opposite colour in the range to avoid any effects due to chromatic adaptation. This was repeated for a range of spatial frequencies. Thus, the experiment examines the effect on detection of a monochromatic grating when a second grating of a different colour is added out of phase in various proportions. Typical results for the red–green grating are shown in Fig. 4, and for the blue–yellow grating in Fig. 5. The subject's contrast sensitivity is plotted as a function of the luminance ratio. The set of curves in each Figure represents a range of spatial frequencies.

The spatial frequency of the stimulus has a profound influence on the results. For low spatial frequencies (below 1 cycle/deg) the subject is less sensitive to the monochromatic conditions at either end, but as luminance contrast is reduced sensitivity *increases* reaching a maximum. However, for the higher spatial frequencies

the reverse occurs: the subject is most sensitive to the two monochromatic conditions, and in between sensitivity *decreases* reaching a minimum. Thus, under low spatial frequency conditions sensitivity is greatest when there are colour differences in the stimulus, whereas at higher frequencies sensitivity is greatest when the stimulus has only luminance contrast.

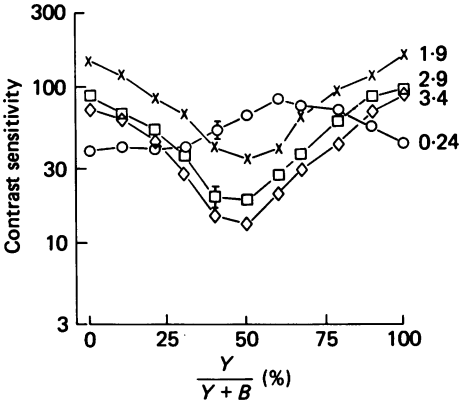

Fig. 5. Contrast sensitivity as a function of the blue–yellow luminance ratio in the stimulus, expressed as the percentage of yellow in the mixture. Four spatial frequencies are shown (cycles/deg): ×, 1·9; □, 2·9; ◇, 3·4 and ○, 0·24. The subject is K.T.

For the blue–yellow contrast sensitivities (Fig. 5) the minimum at high spatial frequencies shifted relative to the maximum at low spatial frequencies. The low spatial frequency (0·24 cycles/deg) maximum occurs at 60% yellow, or higher. At 1·9 cycles/deg a minimum occurs at 50% yellow, and the remaining curves at 2·9 and 3·4 cycles/deg both have minima at 45% yellow. All spatial frequencies in this Figure were displayed with the same field size (6·5 deg). Thus, for this subject (K.T.) as for others, there is a shift in the intensity match with spatial frequency of about fifteen percentage points. Most of this change occurs below 2 cycles/deg. Less blue is required at the low spatial frequency maxima than at the high spatial frequency minima, indicating that the effective intensity of the 470 nm wave-length is relatively lower at high frequencies. The red–green threshold data, shown in Fig. 4, are suggestive of a similar but much smaller shift. The low spatial frequency maxima occur at 55% red, and the minima occur at 50 and 47% red for 2 and 3 cycles/deg respectively. For other subjects a similar pattern occurs. This effect is not more than 7%, but resembles the blue–yellow results in that relatively more of the shorter-wave-length (526 nm) light is required at the criterion match as spatial frequency increases up to 2 cycles/deg. Thus, for both red–green and blue–yellow stimuli a luminance match between colours, which occurs at 50% red or 50% yellow, does not predict the maxima or minima of contrast sensitivity.

It can also be seen from these results that the minima at high spatial frequencies become more sharply defined, making an accurate choice of intensity match more critical, since small differences in the match have quite large effects on sensitivity. These minima continue to increase in depth from 2 to 7 cycles/deg.

All subjects were asked to report any changes in the appearance of the gratings at threshold, at the different intensity ratios. The appearance varied from a homochromatic condition, where the bars appeared to be of a uniform colour but varying in brightness, to a heterochromatic condition where hue differences could be distinguished at threshold. At low spatial frequencies, colour differences could be

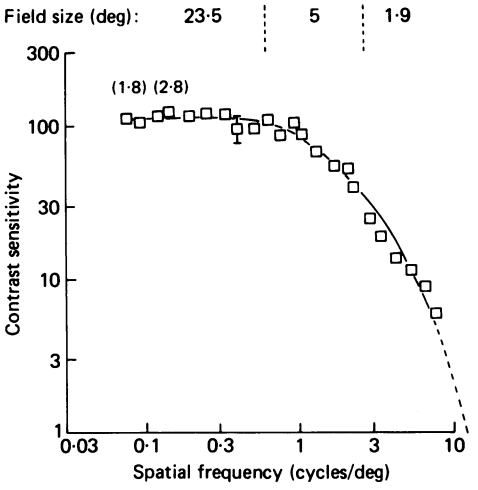

Fig. 6. Contrast sensitivity as a function of spatial frequency for a red–green grating (□; 526, 602 nm). Slightly different red–green ratios were used at different spatial frequencies to obtain the criterion intensity match of the two colours. The lowest numbers of spatial cycles displayed are indicated in parentheses. The continuous curve was fitted by eye. The method of extrapolation (dashed line) is described in the text. The subject is R.M.C. See also the upper curve of Fig. 7 for results of subject K.T.

detected at threshold for most of the intensity ratios. However, for the highest spatial frequencies used, such heterochromatic colour thresholds occurred at only 2 or 3 intensity ratios, and these always coincided with the minima of sensitivity. These observations strongly suggest that colour differences are detected at threshold at the intensity ratios which produce the maximal and minimal sensitivities. They also emphasize the need for an accurate, quantitative method of determining the match since, at high spatial frequencies, only a narrow range of intensity ratios produce colour detection thresholds. Furthermore, at the intensity ratios which occur at and around the maxima and minima of contrast sensitivity, the two colours in the grating appear as bars of equal brightness. Many subjects comment on the unusually vivid or 'fluorescent' appearance of the colours at these points.

The chromatic contrast sensitivity function (c.s.f.)

Measurements of the sensitivity of colour vision to different spatial frequencies can now be made using the criterion that the maxima and minima indicate the best intensity ratio for the two colours in the chromatic grating. For a range of spatial frequencies, results similar to those of Figs. 4 and 5 were obtained, and intensity ratios at the maxima and minima selected for determining the contrast sensitivities which are plotted in Figs. 6 and 7. The largest field size (23·5 deg) used in the experiment

enabled frequencies as low as 0·17 cycles/deg to be displayed with over 4 cycles present. Thus, low spatial frequency sensitivity could be assessed without being affected by a reduced cycle number, since if more than four spatial cycles are present contrast sensitivity is independent of the cycle number and the field size (Howell & Hess, 1978).

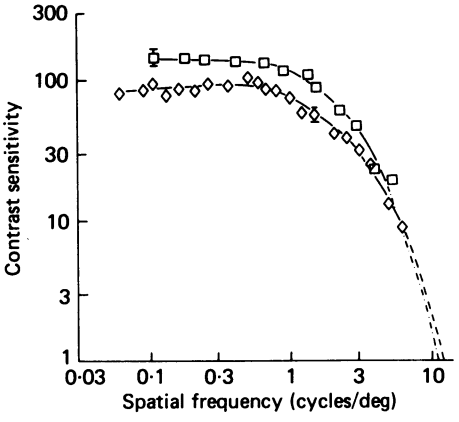

Fig. 7. Contrast sensitivities as a function of spatial frequency for a blue–yellow grating (◇; 470, 577 nm) and a red–green grating (□; 602, 526 nm), both for subject K.T. Different blue–yellow ratios were used at different spatial frequencies to obtain the criterion intensity match of the two colours. Slightly different red–green ratios were also required for the criterion match. The continuous curve was fitted by eye. The method of extrapolation (dashed line) is described in the text.

The results obtained using red–green gratings are shown in Fig. 6 for R.M.C. and in the upper curve of Fig. 7 for K.T., the blue–yellow results for K.T. are shown in Fig. 7. Sensitivities to both blue–yellow and red–green stimuli have low-pass characteristics, with no decline in sensitivity for spatial frequencies below 0·1 cycles/deg. Previous declines found (e.g. Kelly, 1983) may have been due to the low number of cycles displayed.

Sensitivity to the red–green and blue–yellow stimuli declines at spatial frequencies above 0·8 cycles/deg. Sensitivity to the red–green medium and higher spatial frequencies is lower than has been previously reported and by extrapolation, red–green chromatic resolution fails at 11–12 cycles/deg for R.M.C. and K.T. (The method of extrapolation is described later.) Previously, resolutions above 25 cycles/deg have been suggested. Resolution of the blue–yellow grating also fails at around 11 cycles/deg for both subjects K.T. and S.C.S. (no Figure). This compares with an acuity of above 20 cycles/deg, obtained using blue–yellow sine-wave stimuli (Van der Horst & Bouman, 1969). These chromatic acuity values are investigated more fully in a later section.

Fig. 7 shows a comparison between the red–green and blue–yellow sensitivities obtained from the same subject (K.T.). The two c.s.f.s are remarkably similar and have much the same high spatial frequency decline. The only significant difference occurs in the low spatial frequency region where the blue–yellow sensitivity is consistently about 0·15–0·2 log units lower.

Comparisons between colour and luminance c.s.f.s

The colour and luminance c.s.f.s differ in shape, but we do not know how their relative sensitivities compare. Comparisons of sensitivity are difficult since there is no adequate definition of colour contrast available which can be applied to all colour combinations, and does not depend on theoretical assumptions about post-receptoral

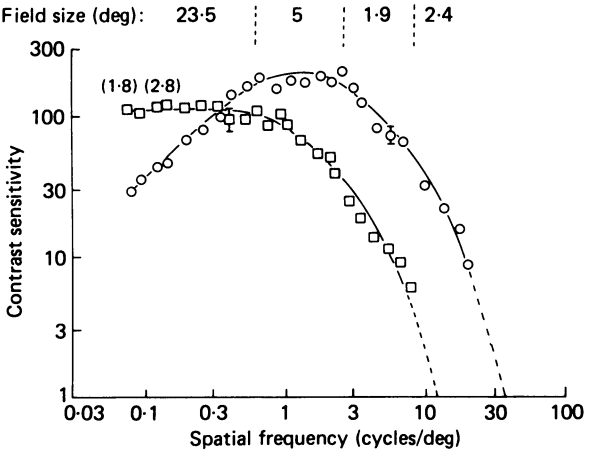

Fig. 8. Contrast sensitivity as a function of spatial frequency for the red–green grating (□; 526, 602 nm) and a green monochromatic grating (○; 526 nm). The data for the chromatic grating are taken from Fig. 6. The subject is R.M.C.

cone interactions. None of the previous measures of chromatic sensitivity, such as wave-length discrimination or purity, translate readily into the luminance domain. Measures of purity have resulted in the two component luminance gratings being presented at different contrasts, making comparisons with luminance sensitivity difficult. In the present experiments, the contrasts of the two component gratings are always held equal to each other, and at threshold the reciprocal contrast of either grating is taken as contrast sensitivity. Thus, as a working measure, the same contrast scale is used to determine detection thresholds for both the luminance and chromatic gratings. More direct and quantitative comparisons of sensitivity can also be made of the level of the cone responses since it is relatively simple to calculate the contrast of the luminance and chromatic gratings to each cone type.

The results shown in Figs. 4 and 5 give an initial indication of how contrast sensitivity changes as luminance contrast is removed and chromatic contrast is added to the stimulus. The present experiment extends these comparisons over the complete spatial range. The data for the chromatic gratings were taken from Figs. 6 and 7. Data for the luminance gratings were obtained by either using the pure green grating (0 % red condition) to make the red–green comparison, or using the pure yellow grating (100 % yellow condition) to make the blue–yellow comparison. Luminance and chromatic comparisons were each made at the same mean luminances. The choice of monochromatic grating is not important since Van Nes & Bouman (1967) have shown that the wave-length of a monochromatic luminance grating does not affect

contrast sensitivity provided the stimuli have the same mean luminance. The results for the comparison between sensitivities to the red–green chromatic grating and the green monochromatic grating are shown in Fig. 8. The blue–yellow chromatic and yellow monochromatic comparisons are shown in Fig. 9.

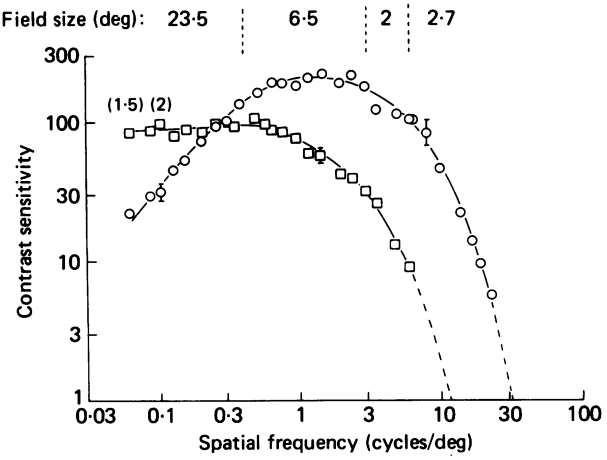

Fig. 9. Contrast sensitivity as a function of spatial frequency for the blue–yellow grating (□; 470, 577 nm) and a yellow monochromatic grating (○; 577 nm). The data for the chromatic grating are taken from Fig. 7. The subject is K.T.

The results show that the contrast sensitivity to both red–green and blue–yellow gratings is greatest below 1 cycle/deg, whereas luminance contrast sensitivity peaks at 0·8–4 cycles/deg. For the low spatial frequencies, the combination of the red and green monochromatic gratings in antiphase can be seen when neither grating can be seen alone. This difference in contrast sensitivity reaches 0·6 log units and may increase at even lower spatial frequencies. Results obtained on another subject (K.T.) are very similar. The same effect occurs for the blue–yellow stimuli. For low spatial frequencies, contrast sensitivity to the combination of monochromatic gratings in antiphase is greater than to the monochromatic grating alone. This difference reaches 0·5 log units at 0·1 cycles/deg. For another subject (S.C.S.) the difference was slightly less (0·4 log units). Above cross-over points at 0·3–0·5 cycles/deg for all subjects, contrast sensitivity becomes greatest to the monochromatic stimuli, and it is luminance vision which has the higher acuity.

Comparisons of chromatic and luminance acuity

Previous studies using isoluminant techniques have produced a wide range of values for chromatic acuity. In most studies, extrapolations have to be made by eye from threshold measurements obtained at lower spatial frequencies. Such procedures, using purity as the measure of chromatic sensitivity suggest acuity values for red–green gratings that range from 25–30 cycles/deg (Van der Horst & Bouman, 1969) to 50 cycles/deg and equal to luminance acuity (Schade, 1958). Two studies which include measurements made using blue–yellow sine or square-wave stimuli suggest

an acuity greater than 20 cycles/deg (Van der Horst *et al.* 1967; Van der Horst & Bouman, 1969). Studies which have attempted to measure acuity using isoluminant sine- or square-wave gratings of variable wave-lengths have also reported a similar range of acuity values from 20 to 30 cycles/deg (Hilz, Hupperman & Cavonius, 1974),

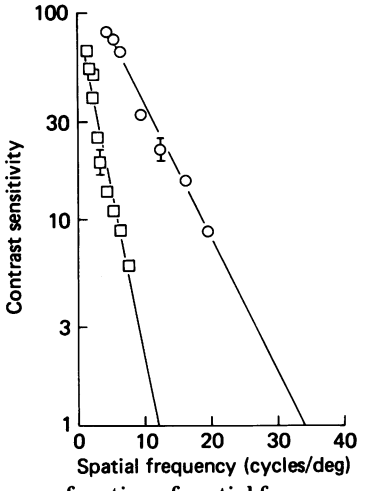

Fig. 10. Contrast sensitivity as a function of spatial frequency, plotted on semilogarithmic coordinates. The data for red–green gratings (□; 602, 526 nm) and green monochromatic gratings (○, 526 nm) are taken from Fig. 8. Linear regression lines are fitted to the data and extrapolated to a contrast sensitivity of 1 (100% contrast) to indicate acuity. Low spatial frequency data have been omitted (see text for further details). The subject is R.M.C.

and bar frequencies of 46 cycles/deg reported to equal luminance acuity under similar conditions (Cavonius & Schumacher, 1966). The purpose of the following calculations is to make accurate predictions of colour and luminance acuity on the basis of the new contrast sensitivity measurements obtained here.

The high spatial frequency data points for the luminance and chromatic gratings were replotted on semilogarithmic coordinates. All the data points which occur after the peak sensitivity of the colour or luminance contrast sensitivity functions are included in the plot. In effect, the medium and high spatial frequency points that occur at or below a contrast sensitivity of 100 were included. A linear regression line was fitted to each function and extrapolated to a contrast of 100% (contrast sensitivity = 1) to predict acuity.

Results for red–green stimuli are shown in Fig. 10 and the blue–yellow results in Fig. 11. Visual inspection reveals that the regression lines fit the data points well. Red–green chromatic acuity is 11–12 cycles/deg, compared to the luminance acuity of 34–36 cycles/deg at the same mean luminance for subjects R.M.C. and K.T. Blue–yellow chromatic acuity is around 11 cycles/deg, closely resembling red–green acuity, compared to the luminance acuity of 32–33 cycles/deg, for subjects K.T. and S.C.S.

Luminance acuity is lower than might be expected. This is probably due to the

relatively low mean luminance of the stimuli which will reduce sensitivity to very high spatial frequencies. However, comparisons with the results of previous chromatic studies can be made since equivalent or higher luminances have been used in the present experiments.

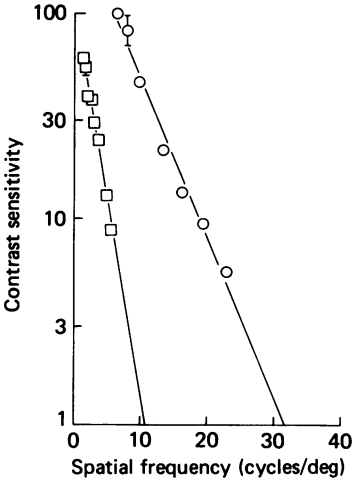

Fig. 11. Contrast sensitivity as a function of spatial frequency, plotted on semilogarithmic coordinates. The data for blue–yellow gratings (□; 470, 577 nm) and yellow monochromatic gratings (○, 577 nm) are taken from Fig. 9. Linear regression lines are fitted to the data and extrapolated to a contrast sensitivity of 1 (100% contrast) to indicate acuity. Low spatial frequency data have been omitted (see text for further details). The subject is K.T.

Thus, these results indicate that chromatic acuity, based on hue discriminations of sinusoidal chromatic gratings, is lower than previously thought at 11–12 cycles/deg for both the red–green and blue–yellow stimuli. Possible explanations for the higher sensitivities and acuities found in previous studies are considered in the Discussion.

Note on colour appearance

At suprathreshold levels these purely chromatic sine-wave gratings are square wave in appearance. For example, no intermediary shades of yellow are seen between the red and green peaks and little variation occurs in the appearance of these colours within each bar. A similar effect occurs for the blue–yellow stimulus, where no intermediary blue–whites are seen. The unexpected absence of yellow between regions of red and green, and the absence of other such 'transition' colours, has been commented on before, both in the spectrum (von Helmholtz, 1909), and using overlapping linear ramps of red and green (Campbell, 1983). Below about 0·3 cycles/deg, this effect disappears and the chromatic gratings become more sinusoidal in appearance.

DISCUSSION

These experiments have revealed a shift with spatial frequency in the intensity match which produces the maximum change in contrast sensitivity. The shift is most prominent for blue–yellow gratings and shows that the effectiveness of blue light

relative to yellow in the match, decreases as spatial frequency increases up to 2 cycles/deg. There is also a suggestion of a similar but smaller shift in the red–green match, where the effectiveness of green light decreases relative to red at the higher spatial frequencies. The question arises as to what causes these changes in match point. Wave-length-dependent diffraction effects are unlikely since the shift occurs at relatively low spatial frequencies, below 6 cycles/deg. Also, diffraction would cause a relative decrease in the contrast of the red or yellow grating, and so would produce a shift in the opposite direction at higher spatial frequencies. Small differences in focus between the two colours due to longitudinal chromatic aberrations might cause an apparent shift in an intensity match, by reducing the contrast of one colour. However, in the present experiments chromatic aberrations have been corrected, and a considerable change in match still occurs for blue–yellow stimuli at very low spatial frequencies below 1–2 cycles/deg. Any small residual differences in focus between the two colours are unlikely to affect thresholds at these low spatial frequencies (Campbell & Green, 1965).

Another possible explanation is that blue cones or rods contribute to the match under low spatial frequency conditions, but not at higher spatial frequencies, therefore decreasing the effectiveness of short wave-length light in the match at these higher frequencies. It is known that the sensitivity of the 'isolated' blue system decreases above 1–2 cycles/deg and is considerably reduced by 5–6 cycles/deg (Kelly, 1974; Green, 1972), which is broadly compatible with the shift occurring at low spatial frequencies. The fact that the shift is considerably greater for the blue–yellow match than for the red–green one is compatible with a blue-sensitive mechanism being involved. Rod sensitivity also declines above 1 cycle/deg (Green, 1972). However, rods are unlikely to contribute to threshold since, at threshold, different colours can be seen in the stimulus. These results suggest that spatial frequency influences brightness perception; and are compatible with other evidence which shows that brightness differences are not always predicted by the standard V_λ luminosity function (Ives, 1912; Börnstein & Marks, 1972; Myers *et al.* 1973).

These results have shown that acuities for the red–green and blue–yellow gratings are very similar, namely 10–12 cycles/deg. Although our knowledge of post-receptoral colour processing is very limiting, the wave-length pairs for the two gratings were chosen so as to optimally stimulate either the red–green or the blue–yellow opponent colour system, and each causes very little response in the opposite opponent system (see Methods). Thus, it is likely that the detection of the red–green and blue–yellow gratings is by the red–green and blue–yellow opponent colour systems respectively. It is interesting that the red–green colour acuity is so low in view of the dense distribution of red and green cone types in the retina. The acuity for the blue–yellow grating agrees well with recent estimates of the acuity of the 'isolated' blue mechanism, also at 10–14 cycles/deg (Stromeyer, Kranda & Sternheim, 1978; Williams, Collier & Thompson, 1983). Thus, the results may suggest that the sparse distribution of blue cones in the retina is not the only factor limiting blue–yellow grating acuity. Previous measurements have suggested much higher chromatic acuity values ranging from 20 to 30 cycles/deg to normal luminance acuities. The methods used here allow accurate measurements of sensitivity to chromatic high spatial frequencies to be made since a quantitative way of making an intensity match has been adopted; the accuracy of this match is shown to be most important at high

spatial frequencies. Furthermore, corrections have been made for both types of chromatic aberration, reducing or eliminating luminance artifacts in the stimulus. In the experiments, the subjects could all detect the colour differences in the matched stimulus at threshold, at all spatial frequencies measured, suggesting that these thresholds are based on colour discriminations.

Reports by some other authors suggest that previous measurements of sensitivity to medium and high spatial frequency chromatic gratings are not based on the perception of colour differences. For example, Granger & Heurtley (1973) found that colour differences in the stimulus at threshold disappear at spatial frequencies above 3 cycles/deg, and that the remaining brightness differences could not be nulled by readjusting the colour match. Such effects might be explained if the medium and high spatial frequency thresholds were based on luminance artifacts in the stimulus produced by chromatic aberrations. Cavonius & Schumacher (1966), who measured acuities to chromatic gratings, did not look for colour differences in the stimulus but reported a wave-length discrimination function at 30 cycles/deg which is very unlikely to be based on hue discriminations. Another possibility which should be considered in this case is that the spectral sensitivity of the achromatic detecting mechanism changes at spatial frequencies greater than those used in the present experiment introducing brightness differences into the stimulus. If two achromatic detecting mechanisms were available then brightness differences could not be nulled simply by readjusting the brightness match. Further experiments eliminating all luminance artifacts at spatial frequencies above 7 cycles/deg are in progress to test these possibilities.

In the experiments described here, comparisons have been made between contrast sensitivities to luminance and chromatic gratings. Although contrast sensitivity to monochromatic gratings does not change with the wave-length (colour) of the stimulus, providing the mean luminance is constant (Van Nes & Bouman, 1967), the over-all contrast sensitivity to the chromatic gratings will depend on the particular colour pairs which they contain. Thus, any comparisons of sensitivity to luminance and chromatic gratings will be influenced by the colours of the pairs in the chromatic stimulus. For the comparisons made here, wave-lengths were chosen to coincide with the peaks of the opponent colour spectral sensitivity function and the chromatic response function (see Methods), and so the over-all contrast sensitivity to the chromatic gratings is unlikely to be greatly increased, but may be decreased, by using different wave-lengths. Also, measurements made of modulation sensitivities to different wave-length combinations (Butler & Riggs, 1978) confirm that sensitivity is relatively high to the colour pairs used here.

Both red and green gratings in the red–green stimulus will stimulate both medium- and long-wave-length cone types and even at isoluminance the stimulus will contain intensity differences to individual cone types. Thus, comparisons between the luminance and colour c.s.f.s can also be made in terms of their cone contrasts. Calculations have been made in the Appendix which show that, at the red–green ratio used for subject R.M.C. in the low spatial frequency chromatic grating, the contrast of this grating to a mechanism with the spectral sensitivity of long-wave-length cones is 18 % of the contrast of either component grating. For a mechanism with the spectral sensitivity of medium-wave-length cones, the contrast of the chromatic grating is 39 %

of the contrast of either component grating. These values at the criterion red–green match for another subject (K.T.) are also given in the Appendix.

The comparisons of contrast sensitivities have revealed that at low spatial frequencies the two monochromatic gratings combined in antiphase can be seen when neither grating can be seen alone. For example, at the lowest spatial frequency contrast sensitivity to the red–green grating is 3·8 times greater than to the green grating presented alone (subject R.M.C., Fig. 8). However, when considered in terms of cone contrasts, this effect is considerably greater. The modulations of the long-wave-length cones which can be detected in the chromatic condition are 21 times smaller than those which can be detected for the monochromatic grating presented alone. For medium-wave-length cones, modulations 10 times smaller can be detected when the stimulus is in the chromatic (antiphase) condition than when either monochromatic stimulus is presented alone. Thus, at low spatial frequencies a chromatic grating can be detected on the basis of considerably smaller receptor modulations than can a luminance grating. This interesting effect is presumably mediated by the post-receptoral extraction of colour opponent signals, involving the combination of different cone outputs.

Finally, the psychophysical results reported here are relevant to the neurophysiology of primate colour vision. The evidence has shown that the relative sensitivities of the visual system to colour and luminance contrast change with spatial frequency. Since colour opponent cells are likely to respond to both colour and luminance contrast (Ingling & Drum, 1973), it can be predicted that the relative sensitivity of these single cells to colour and luminance contrast is spatial frequency dependent. Thus, these psychophysical results emphasize the importance in future neurophysiological studies of considering spatial variables when determining the colour and luminance contrast sensitivities and the spectral sensitivities of single cells.

APPENDIX

The following calculations are of the effective contrast (C_c) of a chromatic grating, composed of two monochromatic gratings added in antiphase, for a single cone type.

The quantal intensity profile (I_c) of the chromatic grating is described by:

$$I_c = M_1\alpha_1 + M_2\alpha_2 + (a_1\alpha_1 - a_2\alpha_2)\sin\omega x,$$

where $\frac{\omega}{2\pi}$ is its spatial frequency and x is space. The contrast of the grating is:

$$C_c = \frac{a_1\alpha_1 - a_2\alpha_2}{M_1\alpha_1 + M_2\alpha_2},$$

where: 1, 2 are subscripts denoting the wave-lengths of the component gratings; M_1, M_2 are the mean quantal intensities of each component grating; a_1, a_2 are the amplitudes of each component grating; α, β denote the spectral sensitivity weightings for the wave-lengths of the two component gratings for long (α)- and medium (β)-wave-length cone types.

If the contrasts of the two component gratings are equal and at a value C

$$M_1 = a_1/C,$$
$$M_2 = a_2/C$$

and

$$C_c = \frac{a_1\alpha_1 - a_2\alpha_2}{a_1\alpha_1 + a_2\alpha_2} \times C. \quad (1)$$

If the ratio of the luminance of component grating No. 1 to component grating No. 2 is L, their quantal intensities are equated by:

$$a_1 V_1 = L a_2 V_2,$$

or

$$a_1 = L a_2 V, \quad (2)$$

where $V = V_2/V_1$; V_1, V_2 are the standard V_λ luminous efficiency weightings of the component wave-lengths.

Substituting eqn. (2) in eqn. (1):

$$C_c = \frac{LV\alpha_1 - \alpha_2}{LV\alpha_1 + \alpha_2} \times C. \quad (3)$$

For the red–green chromatic grating used in the present experiments, wave-length No. 1 is 526 nm and wave-length No. 2 is 602 nm

$$V_{526} = 0{\cdot}8012,$$

$$V_{602} = 0{\cdot}6054.$$

Therefore, $V = 0{\cdot}7556$.

Cone spectral sensitivities may be taken from the Smith & Pokorny (1975) cone sensitivity functions, based on colour matching data (see Boynton, 1979).

For long-wave-length cones (α)

$$\alpha_{526} = 0{\cdot}4526,$$
$$\alpha_{602} = 0{\cdot}4905.$$

For medium-wave-length cones (β)

$$\beta_{526} = 0{\cdot}3484,$$
$$\beta_{602} = 0{\cdot}1149.$$

The data in Fig. 4 for subject R.M.C. show that the criterion intensity match at low spatial frequencies is at 50% red. Thus the green to red luminance ratio (L) = 1.

Using these values in eqn. (3) gives:

$C_c = -0{\cdot}1784 \times C$ for long-wave-length cones, or 18% of C;

and

$C_c = +0{\cdot}3923 \times C$ for medium-wave-length cones, or 39% of C.

For subject K.T., the intensity match at low spatial frequencies is at 55% red. Thus, the green to red luminance ratio (L) = 0·8182.

Using these values in eqn. (3) gives:

$C_c = -0{\cdot}2735 \times C$ for long-wave-length cones, or 27% of C;

and

$C_c = +0{\cdot}3043 \times C$ for medium-wave-length cones, or 30% of C.

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