

ADAPTATION AND COLOR MATCHING

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Abstract—Crawford's (1965) experiment [*Vision Res.* 5, 71-78], implies that there is a failure of linearity when maximum saturation color matches are compared to Maxwell matches. This implication was tested by making the same maximum saturation matches with and without the superposition of a monochromatic desaturating light. A nonlinearity in color matching for short wavelengths was measured without the possible computational or pre-receptor artifacts in Crawford's design. The data presented are consistent with the hypothesis that this nonlinearity is due to post-receptor interactions and not to a failure of spectral invariance or to the participation in the match of more than three types of photopigments.

Color matching Adaptation Linearity

INTRODUCTION

Maxwell (1860) provided the first empirical evidence for the trichromacy of human vision. From the work of Newton (1704) and Young (1802), he inferred that the result of any mixture of colors, however complicated, may be defined by its relation to three suitably chosen colors: colors that have the same relation to the standard colors, will be identical in appearance, though their physical composition may be different. He published the first determination of color matching functions, using the approach diagrammed in Fig. 1(a). First an observer matches a mixture of the three primaries P_i , P_j and P_k to a standard "White"

$$a_i P_i + a_j P_j + a_k P_k = W. \quad (1)$$

The operations in equation (1) are: "=" refers to a color match between the two sides of the equation, "+" is summation of radiance over each wavelength, and the coefficients are the energy of each primary in the match. The tristimulus values of a spectral light of wavelength λ are found by replacing one of the primaries with the test wavelength. The observer then makes another match to the standard "White"

$$b_\lambda \lambda + b_j P_j + b_k P_k = W. \quad (2)$$

From these two equations, the tristimulus values for λ can be derived algebraically as the coefficients of the P 's

$$\lambda = (a_i/b_\lambda)P_i + [(a_j - b_j)/b_\lambda]P_j + [(a_k - b_k)/b_\lambda]P_k. \quad (3)$$

Guild (1931) devised a new color matching procedure, the "maximum saturation" method, and Stiles and Burch (1955) used this method to measure tristimulus values in a particularly direct way: as shown in Fig. 1(b), a mixture of the test light and the appropriate primary is matched to a mixture of the other two primaries

$$c_\lambda \lambda + c_i P_i = c_j P_j + c_k P_k \quad (4)$$

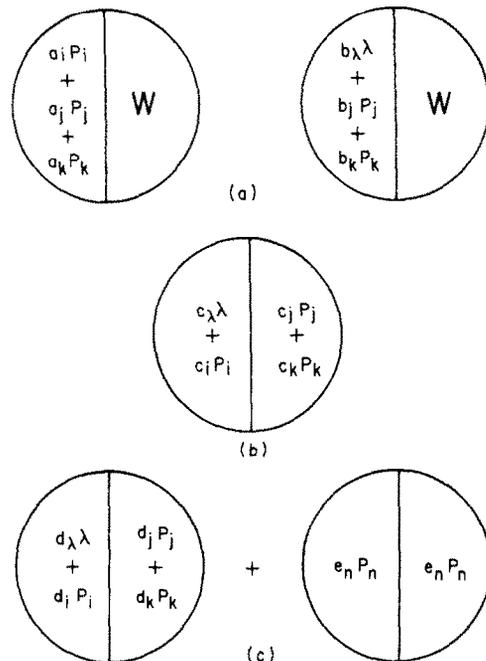


Fig. 1. (a) Maxwell's method for measuring color matching functions. (b) Maximum saturation method for measuring color matching functions. (c) Color matching method used in Experiment 1.

where the coefficients are the radiances of the monochromatic lights. The tristimulus values are derived directly from the equation

$$\lambda = -(c_i/c_z)P_i + (c_j/c_z)P_j + (c_k/c_z)P_k \quad (5)$$

The derivations that lead to equations (3) and (5) assume that the physical operations in equations (1), (2) and (4) can be treated as mathematical operations: a color match as equality, wavelength-by-wavelength summation as vector addition, and the coefficients as scalar multipliers of the unit vectors that represent the primaries and the test wavelengths. This isomorphism between experimental and mathematical operations is implicit in Newton's work and was made explicit by Grassman (1853). In modern terminology (e.g. Krantz, 1975), these algebraic manipulations are justified if a color match is an equivalence relation and if the space of all color matches can be treated as a three-dimensional linear vector space. The identity and symmetry properties of an equivalence relation should be satisfied by the precision of the equipment used in a color-matching experiment. The transitivity property is true only within the limits of color discrimination. To a first approximation, foveal color matches between lights that do not significantly alter the optical density of the visual photopigments satisfy the scalar multiplication (Von Kries, 1896; Trezona, 1954) and superposition (Trezona, 1953, 1954) properties of a linear vector space. The linearity of color matching is the basis of both practical colorimetry and the derivation of photopigment absorption spectra.

Crawford (1956), however, reported a significantly nonlinearity in color vision. For a 2° bipartite field centered on the fovea, Crawford used the same primaries (460, 530 and 650 nm) and a standard "White" (CIE source C), to measure color matching functions of six observers by both Maxwell's method and the maximum saturation method. In a linear vector space, for any basis, an element can be represented as one and only one linear combination of the elements of the basis. Therefore, if normal trichromatic color matching is a three-dimensional linear process, color matching functions measured by these two methods on the same observer using the same primaries should be identical. Crawford found this not to be the case. Crawford's results imply that tristimulus values derived from maximum saturation

color matches do not predict Maxwell matches and vice versa.

It is possible that Crawford discovered this nonlinearity in color-matching where earlier investigators failed to, because he was the first to compare saturated matches to desaturated matches. His experiment was repeated by Wyszecki, who used primaries of wavenumbers 15,500 (645 nm), 19000 (526 nm) and 22,500 cm^{-1} , (445 nm) and a "White" composed of a mixture of his three primaries matched to CIE source D_{65} (Wyszecki and Stiles, 1982). Wyszecki's results plotted in chromaticity coordinates appear similar to Crawford's. In the succeeding sections reference will mostly be made to Wyszecki's results because he also published his data as color matching functions. Wyszecki's data showed that in the long-wavelength region the color matching functions were similar. However, for test wavelengths shorter than the short wavelength primary, there was considerable divergence: the short and long wavelength color matching functions were higher for Maxwell matches than for maximum saturation matches and the middle wavelength color matching function was lower.

There are many possible reasons for these failures of linearity of color matching including photopigments with multiple absorption bands (Wald *et al.*, 1954), photoreceptors with wavelength dependent photon responses (Lamb *et al.*, 1981; Schnapf, 1983), rod intrusion, and post-receptoral interactions (Ingling and Drum, 1973). However, Crawford and Wyszecki's results may just be due to the computational imprecision of Maxwell matches. For some test wavelengths, the energy of one of the primaries in the match [equation (2)] can be very close to the energy in the match to the standard white [equation (1)], so that in equation (3), the tristimulus value is a small difference between two large quantities and so computationally imprecise. Also, Palmer (1980) has mentioned the possibility of the Maxwell spot playing a larger role in the short wavelength maximum saturation matches than in the Maxwell matches.

Linearity of color matches is the basis on which a large part of color vision theory has been developed. Therefore it is important to evaluate directly whether a nonlinearity can be demonstrated using a technique that does not allow computational imprecision or pre-receptoral filters to be a factor in the results. This is the goal of Experiment 1

EXPERIMENT 1

Experiment 1 tested the implication of Crawford's results that tristimulus values derived from maximum saturation matches are different from those derived from Maxwell matches. The approach is diagrammed in Fig. 1(c). The observer made a maximum saturation match on a 2° bipartite field. Identical amounts of monochromatic light were then added to both sides to desaturate the match, and another match was made. The experiment is so designed so that identical physical manipulations and identical computations are made in the two conditions. If saturated and desaturated matches belong to the same linear space, the two sets of matches will be identical within experimental error. If the two conditions yield different color matching functions, then the possible computational imprecision of Maxwell matches can be ruled out as a factor. Moreover, the only difference between the two sets of matches is identical amounts of monochromatic light added to both sides. An identical amount of filtering should take place on both sides in the desaturated condition. Therefore, pre-receptor filters in the eye can also be ruled out as possible causes of any difference between the two conditions.

Equipment

A Moreland Universal Anomaloscope (Moreland and Young, 1974; Pokorny and Smith, 1976) (Fig. 2) was modified for this experiment. Light from a 500 W tungsten halo-

gen lamp run at 120 V from a regulated supply was collimated and passed through two pairs of three-cavity interference filters (Ditric Optics). All the interference filters had half height band-passes of less than 10 nm. The filtered light was adjusted by pairs of opaque slides that selectively blocked the spectrally filtered light. The slides were controlled by knobs with digital read-out. The two slides on the left varied the sum and the ratio of the energies of the two wavelengths on the left. One slide on the right varied the energy of one of the wavelengths and the other varied the ratio of the two wavelengths. The filtered light was focussed on the entrance port of one of two integrating spheres. The exit ports of these integrating spheres served as large sources and a bipartite field was presented in Maxwellian view. A circular field stop of 2° visual angle was used. The added field was supplied by a 150 W tungsten halogen lamp run from a regulated supply. Light from this lamp was collimated and passed through a three-cavity interference filter. The filtered light was focussed on the entrance faces of two cable-sheathed optical fiber bundles. These optical fiber bundles were used to transmit the light to the entrance ports of the integrating spheres. The amount of light passing through each light pipe could be controlled by adjusting the position of the entrance face of the light-pipe. The natural pupil was used. The room lights (Verilux daylight, F15T8VLX lamps with a correlated color temperature of 6200 K) provided ambient illumination of 900 lx.

MODIFIED MORELAND ANOMALOSCOPE

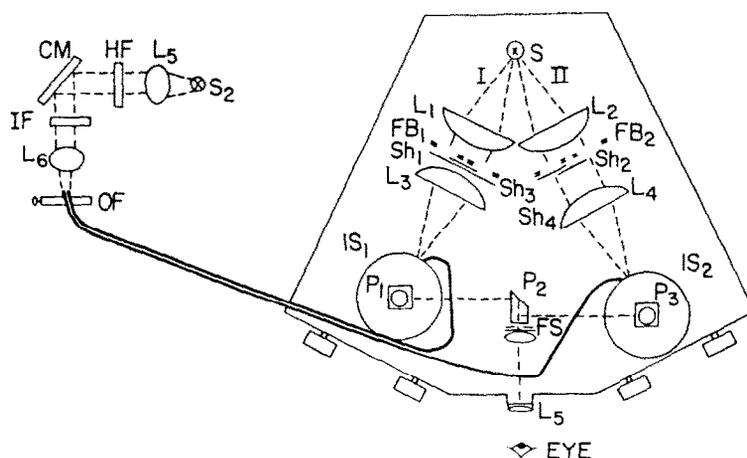


Fig. 2. Diagram of optical equipment used in Experiments 1 and 3. S = light source; L = lens; FB = filter box; SL = slide; IS = integrating sphere; P = Prism; FS = field stop; HF = heat filter; CM = cool mirror; IF = interference filter; OF = optical fibre bundle.

Calibration

The filters were calibrated for peak wavelength and band-pass in the equipment using a laboratory built spectroradiometer and a microammeter. The sensitivity of the spectroradiometer was referenced to a standard lamp of known color and temperature. The relative radiance of the constituents of a color match set by an observer were measured for each match using the spectroradiometer. The luminance of both the match and the added light was measured using an SEI photometer. These measurements were confirmed by relative energy measurements made with the spectroradiometer. The desaturating light was equated visually on the two sides and the setting was confirmed with the spectroradiometer. The luminance of the 430 nm match was 0.43 cd/m² (about 10 effective td; Le Grand, 1957) and the luminance of the 580 nm light was 9.65 cd/m² (about 11.4 effective td).

Observers

Two observers, M.L. and Q.Z., with normal visual acuity and normal color vision (Rayleigh and Moreland (Moreland and Kerr, 1978) match and FM 100 Hue test) were run. M.L. wore correcting spectacles. M.L. was a naive observer with no previous experience with color matches. Q.Z., the author, had previously made color matches.

Procedure

The test wavelengths 410–510 nm in ten nm steps were run in a different pseudo-random order for each observer. The primaries were 450, 546 and 670 nm. Each observer made all 10 matches for a test wavelength in a single session. Matches were made alternately with a 580 nm light on and off. After each match, the observer was asked to judge if the match stayed a match in the alternate condition (a confrontation judgement). To control for possible small differences in the added field on the two sides, the test wavelength for M.L. was in the right hemifield and for Q.Z. in the left hemifield. An additional condition was run at four test wavelengths in which Q.Z. made matches after a 90,000 scot td, 5 minute bleach, supplied by a frosted 60 W tungsten lamp. For the bleached condition and for Experiment 3, the test wavelength was in the right hemifield.

Results

The color matching functions for M.L. are

shown in Fig. 3. In each graph the tristimulus value is plotted as a function of the test wavelength. Five maximum saturation matches (triangles) and five desaturated matches (circles) are plotted for each wavelength. Where points overlap, symbols have been plotted on top of each other. In interpreting the data, a simple statistical consideration will help (Fisher, 1942). The median of the ten matches for a given test wavelength can be taken as a dividing line. Under the null hypothesis of linearity (i.e. no difference between the matches with the added light on or off) and assuming independence of observations, the chance of no overlap between the matches in the two conditions is 2/252 or less than 1%. The chance that four matches in each condition fall on one side of the median and one on the other is 52/252, a little more than 20%. So on the basis of this test, the null hypothesis can only be rejected confidently when there is no overlap between the matches. For M.L., there was no difference in the two conditions for either the 670 or 546 nm tristimulus values: there was considerable overlap for all the test wavelengths. There was a small difference between the two conditions for the 546 nm values for 490 and 510 nm. For the 450 nm color matching function there was considerable overlap for test wavelengths 410 and 460–510 nm. For test wavelengths from 420 to 440 nm, however, even though there is substantial scatter in the matches, the matches do not overlap at any point. The results for observer Q.Z. show the same pattern of overlap and nonoverlap. The logarithm of the median 450 nm tristimulus values for Q.Z. are plotted in Fig. 9.

For each test wavelength, Table I indicates whether an observer accepted a match made in one condition as a match in the alternate condition. For test wavelengths 410–440 nm, matches made in the maximum saturation condition were not accepted as matches when the 580 nm light was added; and matches made in the desaturated condition were not accepted as matches when the 580 nm light was turned off. For test wavelengths 460–510 nm, matches made in one condition were generally accepted as matches in the alternate condition, though fewer matches were accepted by M.L. than by Q.Z. It should be pointed out that interpretation of confrontation judgements is not as straightforward as for repeated matches.

Figure 4 shows 450 nm tristimulus values for matches made by Q.Z. for four test wavelengths with and without the desaturating light under

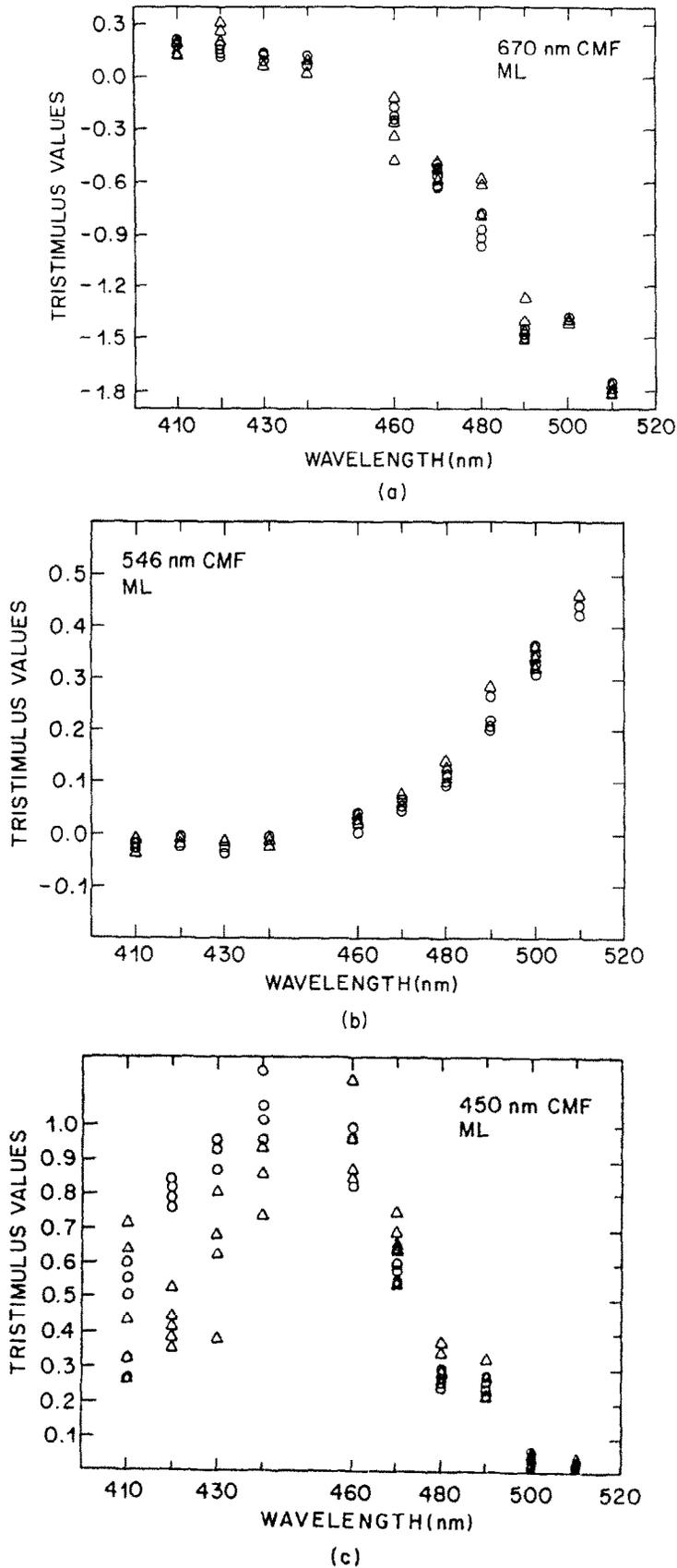


Fig. 3. (a) 670 nm color matching function (CMF) for observer M.L. Δ , maximum saturation matches; \circ , matches made in the presence of a 580 nm desaturating light. The abscissa is labelled with the wavelength of the test color. Tristimulus values are plotted on a linear scale along the ordinate. (b) 546 nm CMF for observer M.L. (c) 450 nm CMF for observer M.L.

Table 1. Confrontation judgements for Experiment 1 for observers M.L. and Q.Z.

Confrontation judgements				
Primaries: 450 nm, 546 nm, 670 nm				
Added light: 580 nm				
Wavelength (nm)	Max saturation (proportion "yes")		Desaturated (proportion "yes")	
	M.L.	Q.Z.	M.L.	Q.Z.
410	0/6	0/5	0/6	0/5
420	0/5	0/5	0/5	0/5
430	0/5	0/5	0/5	0/5
440	0/5	0/5	0/5	0/5
460	3/5	5/5	2/5	1/5
470	1/5	4/5	1/5	2/5
480	0/5	4/5	0/5	4/5
490	0/5	5/5	0/5	5/5
500	5/5	5/5	3/5	5/5
510	2/5	5/5	1/5	5/5

The first column is the test wavelength. The second and third columns show for each observer, the number of maximum saturation matches (numerator) out of the total number of matches (denominator) that are accepted after the 580 nm desaturating light is turned on. The third and fourth columns similarly show the number of desaturated matches accepted after the added light is turned off.

normal ambient adaptation conditions and between five and ten minutes after a 90,000 scot td, 5 min bleach. For 490 and 510 there was overlap as before whereas for 430 and 440 nm, the 450 nm color matching function for the two conditions did not overlap.

Discussion

In order to compare the nonlinearity found in Experiment 1 with the nonlinearity between Maxwell and maximum saturation matches,

Wyszecki's data was transformed to the set of primaries used in this experiment (Fig. 5). Separate linear transformations were done for each set of color matching functions assuming that linearity holds within but not between conditions. In Wyszecki's data, the main difference between saturated and desaturated matches is that for test lights of wavenumbers between $22,750 \text{ cm}^{-1}$ (440 nm) and $23,750 \text{ cm}^{-1}$ (421 nm), the $22,250 \text{ cm}^{-1}$ (450 nm) color matching function is higher for desaturated

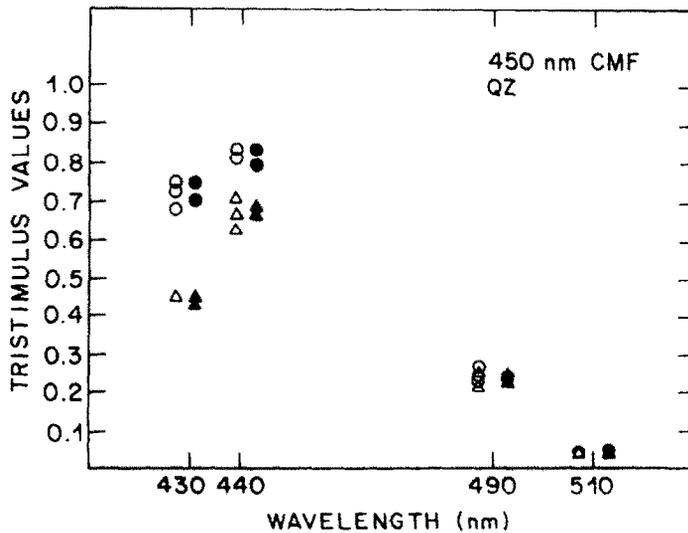


Fig. 4. 450 nm CMF for observer Q.Z. measured under ambient adaptation and on the cone plateau. Symbols and axes as in Fig. 3. Open symbols represent matches made under ambient adaptation. Solid symbols represent matches made on the cone plateau.

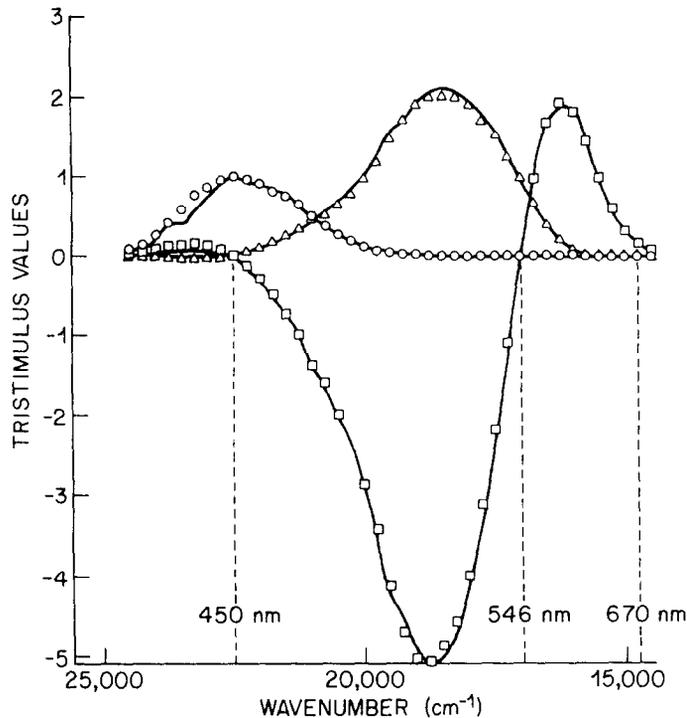


Fig. 5. Color matching functions for G. Wyszecki transformed to the set of primaries used in Experiment 1. Solid lines = maximum saturation matches; symbols = Maxwell matches. "○" = 450 nm CMF, "△" = 546 nm, "□" = 670 nm CMF.

matches. The 546 and 670 nm color matching functions are similar for the two types of matches. These results are similar to the data from the two observers in Experiment 1.

The results of Experiment 1 can be used to rule out some of the possible causes of non-linearity listed in the introduction and to put constraints on the other possibilities. Computational imprecision and pre-receptor filters cannot be the cause of the observed non-linearity for reasons presented above. It is unlikely that rods are contributing to the observed non-linearity since the results are similar for matches made under normal ambient conditions and on the cone plateau. This hypothesis is further explored in Experiment 3. This experiment has two aspects which further constrain acceptable explanations: (a) the 580 nm light only affects LWS and MWS cones; (b) nonlinearity is observed only for test wavelengths shorter than 450 nm.

The data from this experiment are compatible with a possible failure of the spectral invariance of the absorption spectrum of the LWS or MWS photopigment molecules. Human LWS and MWS photopigments fit a nomogram based on Iodopsin (Smith and Pokorny, 1972) which has two absorption bands: a main or alpha band and a beta band that peaks in the ultra-violet

region (Wald *et al.*, 1954). The absorption curve for the LWS photopigment has a local minimum near 440 nm (Smith and Pokorny, 1975). If the two bands of the LWS pigment adapt independently under steady illumination, the height of one of the bands could change relative to the other. In that case, matches which include wavelengths absorbed in both bands, such as the short-wavelengths matches of Experiment 1 would shift with changes in adapting lights. The hypothesis of independent adaptation of alpha and beta band can be tested computationally by multiplying the spectral sensitivity of one of the bands by a constant. For the 580 nm added light, using the fundamentals derived by Smith and Pokorny (1975) for Judd's (1951a) observer, the tristimulus values for 430 nm were derived for various values of the adapting constant from 0.5 to 2.0. This was accomplished by multiplying by the adapting constant, the spectral sensitivity of the LWS cones for those wavelengths in the match that fall in the beta band. These calculations showed that the 450 nm tristimulus value did not change for these adapting constants, but the 670 nm tristimulus value increased rapidly. This hypothesis cannot account for the nonlinearity observed in Experiment 1.

A failure of spectral invariance due to some

other nonlinearity cannot be ruled out. The data are also compatible with more than three photopigments contributing to the matches, because in that case trichromatic color matches do not have to be quantal matches. Experiment 2 will test for the possible failure of spectral invariance in LWS and MWS cones. Experiment 3 will examine the possibility that for short wavelengths, trichromacy is not limited by three photopigments.

EXPERIMENT 2

Experiment 2 was designed to evaluate whether any nonlinear change in either LWS and MWS cones or both could account for the adaptation data. The stimulus was a 2° bipartite circular field, with the two halves separated by a sharp edge. Such a system has been used to equate two lights for luminance by adjusting the radiance of one of them until the dividing border seems minimally distinct (Boynton and Kaiser, 1968). For pairs of lights that fall on tritanopic confusion lines, the dividing border seems to dissolve in the equi-luminance condition (Tansley and Boynton, 1978). A melted border between two lights means that the LWS and MWS cones are each absorbing equal numbers of quanta from the two sides of the bipartite field. Further, the monochromatic wavelength pairs which lead to melted borders depend entirely on the absorption curves of the LWS and MWS photopigments, and are independent of any inert filters in the eye. If either of these absorption curves changes with a particular change in adapting conditions, no pair of lights will give melted borders in both condi-

tions. In this experiment two observers set tritan pairs for fixed amounts of 430 and 450 nm lights. The prediction is that following 580 nm adaptation, the 430 nm pair will no longer be a tritan pair, but the 450 nm pair will not be shifted.

Equipment

A two channel projection system (Fig. 6) was used in this experiment. Light from a 450 W Xenon arc lamp run from a regulated power supply was split into two channels. Light in one channel was collimated, passed through a three-cavity interference filter of wavelength, 430 or 450 nm, reflected onto a pane of separated pieces of diffusing mylar and viewed through the mirrored section of a half-silvered beam splitter cube. Light in the second channel was focussed on the entrance slit of a monochromator with electronic control of wavelength, refocussed on a servo-driven neural density wedge, collimated, reflected and diffused towards the observer's eye through the half-silvered cube. This cube provided perfect juxtaposition of the two half-fields. When lights of identical wavelengths were equated for brightness; the border between the two half-fields could not be discerned. A minor luminance mismatch caused a uniform vertical border to appear. A circular field stop of 2° visual angle was placed next to the cube. The added field was provided by a light from a 150 W tungsten halogen lamp passed through a diffuser, the same 580 nm filter used in Experiment 1, and a circular field stop of 4° visual angle. In the eye piece, an achromatizing lens (Bedford and Wyszecki, 1975) was carefully aligned on its axis to minimize the effects of the

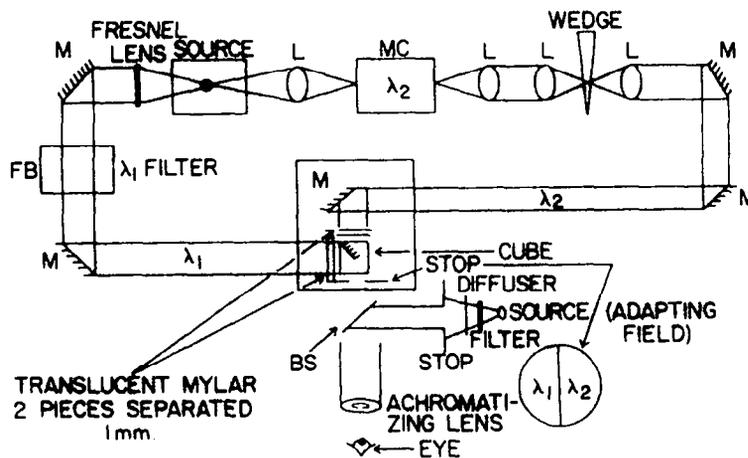


Fig. 6. Diagram of optical equipment used in Experiment 2. L = lens; MC = monochromator; M = mirror; FB = filter box; BS = beam splitter.

chromatic aberrations of the eye. Each observer aligned himself using a bite bar.

Calibration

The neutral density wedge was calibrated with an EG&G digital radiometer. The luminance of the field was measured with an SEI photometer. The luminance of the 430 nm field was 0.34 cd/m² (about 8.4 effective td) and the luminance of the 580 nm added field was 6.84 cd/m² (about 8.8 effective td). This is comparable to 0.43 and 9.65 cd/m² in Experiment 1. The experiment was run in a dark room.

Observers

Two psychophysically experienced observers, R.B. and Q.Z. with normal acuity and color vision were run. R.B. wore correcting contact lenses. The data described in this experiment were obtained after both R.B. and Q.Z. had extensive practice in making MDB adjustments and melting-border judgements.

Procedure

For a fixed amount of 430 or 450 nm light, the observer adjusted the radiance of a longer wavelength light to achieve a minimally distinct border. He then judged whether the border had melted. The 580 nm light was turned on and the procedure repeated. The longer wavelength light was set by the experimenter using a pseudo-random sequence. The observer was not aware of the wavelength of the longer wavelength light. Each session included a number of longer wavelengths at 2 nm intervals for a fixed short wavelength light. Each longer wavelength light was presented thrice in a session. Two to four sessions were run in a day for each observer. An additional condition was run at the 430 nm wavelength in which the observer set minimally distinct borders and made melting border judgements ten times each for 505, 510, 515, 520 and 525 nm presented randomly. One session was run with the adapting light off and on the same day another session was run with the 580 nm adapting light on.

Results

Both observers were able to make reliable MDB settings in both adapting conditions, but neither observer was content with the melting border judgements. The judgements seemed particularly uncertain when the chromatic difference between the two halves was large, and in the 580 nm adapting condition. The range of

Table 2. Melted border judgements for observer Q.Z.

Melted border judgements		
Fixed light 430 nm		
Observer Q.Z.		
λ (nm)	Added field 580 nm	
	Off	On
505	2/10	1/10
510	10/10	9/10
515	6/10	5/10
520	6/10	2/10
525	2/10	2/10

For a fixed wavelength of 430 nm, and for different longer wavelength lights λ the denominators in columns 2 and 3 are the number of MDB settings made with the 580 nm desaturating light Off or On. The numerators are the number of such settings judged to have melted borders between the two hemifields.

wavelengths for which the border seemed to melt was substantially the same for the two adapting conditions.

The additional condition was run to get more precise data for 430 nm, the wavelength at which a nonlinearity was observed in Experiment 1. Table 2 shows the number of times out of ten MDB settings that Q.Z. judged the border between the fields to have melted. In both adapting conditions, 430 nm and 510 nm were the tritan pair for this observer. The mean and standard deviation of the luminance of 510 nm were 0.39 and 0.02 cd/m² for the condition with the adapting light off and 0.37 0.03 cd/m² for the condition with the adapting light on. There was no significant difference (*t*-test) in the luminance at 510 nm between the two conditions.

Discussion

The data in Table 2 show that the tritan pair for observer Q.Z. is the same for the two adapting conditions. Also the luminance of the tritan pair 430 nm and 510 nm is constant across the two conditions. This can only occur if the LWS and MWS spectral sensitivity curves are the same in the two conditions. The 580 nm added light therefore does not cause a failure of spectral invariance.

The next logical possibility is that there are more than three linearly independent mechanisms at some stage peripheral to the stage at which trichomacy is determined, and that they

have different adapting properties. This possibility is tested in Experiment 3.

EXPERIMENT 3

Normal foveal trichromacy is thought to be pigment limited (Brindley, 1970). There are three cone visual photopigments, at least three neural channels, and adaptation invariant quantal matches can be made (von Kries, 1878). The change in matches with adaptation condition shown in Experiment 1 could be due to a fourth photopigment contributing to these color matches. If four linearly independent classes of photopigments are contributing to a trichromatic match, the quantal catch rate may not be equivalent for all four classes of photopigment. An analogous condition is large field normal trichromacy where rods are the fourth active photopigment. Trichromatic matches can be made but they are not radiance invariant (Stiles, 1955), nor are they quantal. These data indicate that rods do not have an independent channel, and in this sense the color mixture data are channel limited (Smith and Pokorny, 1977). At the light levels of Experiment 1, it is possible that rods contribute to some 2° color matches. If rod activity relative to that of cones decreases with increasing luminance level, a series of added lights of different wavelength and energy should change the color match in relation to the scotopic luminance of the added light.

Recently, variability of microspectrophotometric measurements has been interpreted as indicating the possibility that the action spectra of individual cones of a single type in the same eye may vary in wavelength of peak absorption by as much as 20 nm (Dartnall *et al.*, 1983). If this is the case, trichromatic matches would not be equations of quantal absorption in photopigments, but equations at three neural summation pools where inputs from individual cones with slightly different action spectra are summed. Since adaptation may occur within individual photoreceptors (Baylor and Hodgkin, 1974), the action spectra of these summation pools could change with adaptation. If this change has a measurable effect on a particular color match, adapting lights of different wavelengths will shift the match in different directions.

Experiment 3 was designed to test these possibilities. The observers, the equipment and the calibration procedures were the same as for Experiment 1.

Procedure

The two observers, M.L. and Q.Z., matched 450 plus 670 nm to 430 plus 546 nm in four adaptation conditions. In adaptation Condition 1, the energy of each added wavelength was the maximum that the equipment permitted. The wavelength of the added lights were 500, 520, 530, 540, 550, 560, 570, 580, 590, 600, 620 and 660 nm. The luminances of the added light in this condition were 2.0 cd/m² for 500 and 660 nm and between 6.0 cd/m² and 15.2 cd/m² for 520–620 nm. In adaptation Conditions 2 and 3 each added light was attenuated by a 0.8 and 1.4 log unit neutral density filter respectively. In Condition 4, matches were made with no added light. A session included all the matches for added light of one wavelength. The order of the wavelengths was determined by a separate pseudo random sequence for each observer. Each session was run twice. The approximate positions of the matches on a CIE 2 deg/ chromaticity diagram are shown in Fig. 7.

Results

The 450 nm tristimulus values were higher for Condition 1 than for Condition 4 for added light of wavelengths 540–620 nm, but the 670 and 546 nm color matching functions had similar values for all the adapting wavelengths. There was no difference in the color matching functions between Condition 4 and Conditions 2 and 3. The 450 nm tristimulus values for the two matches made by each observer for added wavelength in Condition 1 minus the mean 450 nm tristimulus value of all matches made with no added light, are plotted in Fig. 8. Also plotted on the same scale are the photopic luminance (solid line), the scotopic luminance (dashed line) and the LWS cone excitation (dotted line) of the added lights, all arbitrarily scaled to 0.5 at 540 nm.

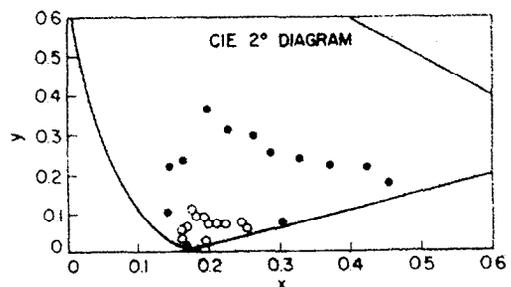


Fig. 7. Chromaticity of matches made in Experiment 3 on a CIE 2° chromaticity diagram. ● = Condition 1, ○ = Condition 2, ▲ = Conditions 3 and 4.

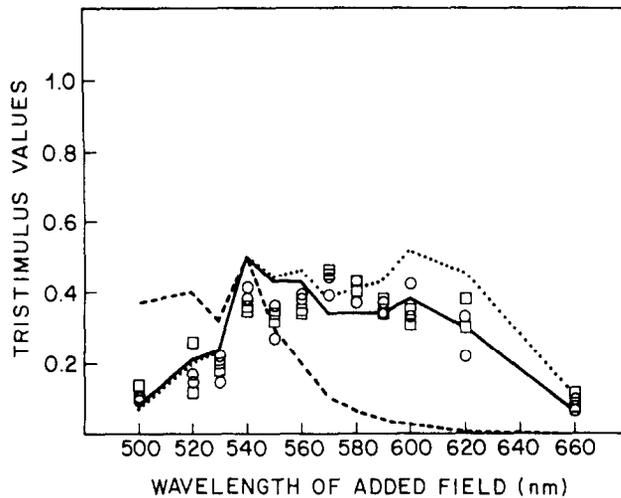


Fig. 8. 450 nm tristimulus values for Condition 1 minus the 450 nm values for Condition 4 for observers M.L. and Q.Z., compared to photopic and scotopic luminance and LWS cone excitation of the desaturating field. \circ , difference in 450 nm values for Q.Z.; \square , difference in 450 nm values for M.L.; solid line connects photopic luminance values of the added field; dashed line connects scotopic luminance values; dotted line connects LWS cone excitation values. The three derived curves for the desaturating lights are plotted on the same scale as the change in tristimulus values and are all scaled to 0.5 at 540 nm.

Discussion

For both observers, the change in the 450 nm tristimulus values is roughly proportional to the photopic luminance of the desaturation light in Condition 1 and is not proportional to the scotopic luminance of the desaturating light (Fig. 8). This reduces the possibility that rods contribute to the nonlinearity.

The distribution of λ_{\max} within photoreceptor classes also does not account for the nonlinearity in the match studied in this experiment. Adapting lights of wavelength 520–620 nm cover the complete range of MWS and LWS

λ_{\max} found by Dartnall *et al.* (1983). Adaptation to different lights would have the effect of shifting effective λ_{\max} for LWS and MWS cones in different directions. If this shift has a measurable effect on a color match, the color match should be disturbed to different parts of color space by different added lights. The results of Experiment 3 show that all the added lights that disturb the match increase the amount of 450 nm primary used in the match and have no measurable effects on the 546 and 670 nm primaries. Therefore, changes in effective λ_{\max} do not account for the effect of the added lights.

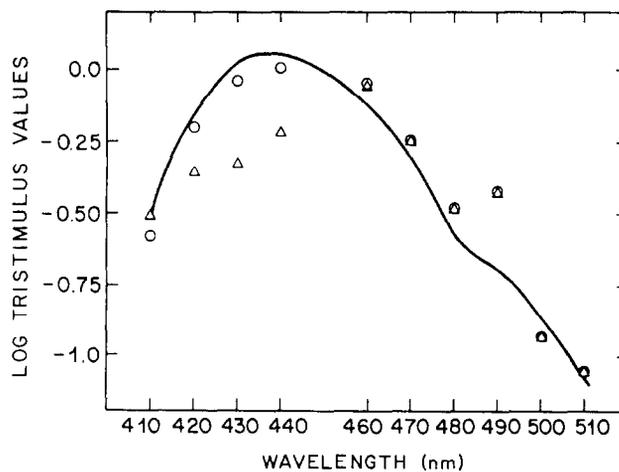


Fig. 9. Logarithm of the 450 nm CMF for Q.Z. compared to the logarithm of Stiles' π_1 . Δ , maximum saturation matches; \circ , desaturated matches; solid line, interpolated values of π_1 field spectral sensitivity normalized to one at $22,250 \text{ cm}^{-1}$.

DISCUSSION

Matches that do not involve SWS cones, e.g. Rayleigh matches, are stable with changes in adaptation (Smith and Pokorny, 1970). Therefore, the SWS cone mechanism may be the possible origin for nonlinearity in color matching. The main difference between maximum saturation matches in the short wavelengths and Maxwell matches for this part of the spectrum is that in the desaturated condition there is more excitation of LWS and MWS cones relative to the excitation of SWS cones. The first experiment was designed to examine if the relative excitation of LWS and/or MWS cones interacts with the spectral sensitivity of the SWS cone mechanism. Two of the primaries 546 and 670 nm were chosen because they do not excite SWS cones to any appreciable extent. If linearity exists at the level of quantal absorption, at the color match the SWS quantal catch will be equal for the test wavelength and 450 nm. Therefore, the color matching function corresponding to the 450 nm primary will be identical to the SWS cone spectral sensitivity (Judd, 1933; Bongard and Smirnov, 1955; Hollins and Montalbana, 1973).

The estimates of SWS cone spectral sensitivity obtained in Experiment 1, can be compared to the π_1 field sensitivity curve (Stiles, 1959). The primary lobe of π_1 is thought to reflect SWS cone mechanism sensitivity (Pugh, 1976). The logarithm of the 450 nm CMF for QZ measured in the two conditions of Experiment 1 and the mean π_1 data of Stiles (1959) normalized to one at $22,250 \text{ cm}^{-1}$ are plotted in Fig. 9. There is reasonable agreement with the estimate derived from matches made in the presence of the 580 nm desaturating field, but not with the estimate derived from maximum saturation matches. The results of Experiment 1 can be interpreted as a demonstration of a change in shape of the SWS cone mechanism's spectral sensitivity for wavelengths shorter than 450 nm in response to a change in LWS and MWS cone excitation relative to SWS cone excitation.

The results of Experiment 3 show that all added lights that disturb the color match, do so in a fashion similar to the 580 nm added light of Experiment 1. The data shown in Fig. 8 are not sufficient to construct an action spectrum for the mechanism that alters the SWS cone sensitivity, but some psychophysically defined color mechanisms can be rejected. The change in the color match is roughly proportional to the photopic

luminance or the LWS excitation of the added lights. This seems to rule out a contribution from the red-green opponent mechanism and the MWS cone mechanism, but not the yellow-blue, luminance, or LWS cone mechanisms. If such interactions play a part in the nonlinearity, they do so at a stage subsequent to quantum absorption.

Ingling and Drum (1973) present one model of such an interaction that accounts qualitatively for the shift in chromaticity coordinates reported by Crawford. Their model postulates that for desaturated matches the LWS and SWS receptor classes become linked and feed into the same channel, and predicts a compensating trade-off between the long-wavelength and short-wavelength primaries from the quantal (maximum saturation) match to the neural (Maxwell) match. This prediction is refuted by Wyszecki's color matching functions where the observer set more of both long and short-wave primaries for Maxwell matches than for maximum saturation matches. Wyszecki's data are incompatible with any model that postulates a trade-off between quanta caught by LWS and quanta caught by SWS cones. In Experiment 1 also, when desaturation increases the amount of the 450 nm primary used in a match, there is no measurable compensating decrease in the 670 nm primary.

A satisfactory model for this nonlinearity would have to account for the rejection of matches made in alternate adapting conditions in Experiment 1, and for the larger amount of 450 nm light used in desaturated color matches in Experiments 1 and 3. It is possible that matches made in one adapting condition are rejected in the alternate adapting condition because of changes in acceptable match width. Short wavelength maximum saturation matches may be rejected when a desaturating light is added, because this can lead to an improvement in hue discrimination (Tyndall, 1933). A desaturated match may be rejected when the light is turned off, because this leads to a decrease in brightness and hence to an improvement in brightness discrimination. The tungsten halogen source used in these experiments has least power in the short wavelengths, so the greatest relative improvement in brightness discrimination occurs for the short wavelength desaturated matches. It is also possible that the 450 nm tristimulus values differ between the adapting conditions because the match range is asymmetric around the quantal match for the short-

wavelength maximum saturation matches. An analogous situation arises in two-dimensional Rayleigh matches if the R and G primaries differ from one of the analytic modes (Pokorny and Smith, 1977). Direct experimental tests have to be done before a model of neural interactions that incorporates these suggestions is formulated.

The question may arise whether the non-overlapping sets of matches are samples from nonoverlapping match ranges, or whether there is some single combination of the three primaries that yields a "quantal match" that is stable under adaptation. Since the evidence reported in this paper is consistent with a post-receptoral cause for the nonoverlap, it is likely that such a match does exist. It is possible that the observers in Experiment 1 did not find the quantal match because of the relatively large match ranges for the short-wavelength matches coupled with the difficulty of a search for a point in a three dimensional space. The nonlinearity reported in this study is present only for three test wavelengths 420, 430 and 440 nm. These are also the wavelengths with the greatest inter-observer variability in color matches due to variability in lens and macular pigment (Zaidi *et al.*, 1982). This explains why a system of colorimetry based on 2 field matches has been widely applied with unambiguous results. In color vision theory, post-receptoral factors have been thought to have no influence on color matches; the demonstration that this assertion is false for some matches may be important.

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