Linearity of hue cancellation in sex-linked dichromacy

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The results of several recent studies concur in the finding that for normal trichromats red–green hue-cancellation data obey linearity properties over rather general conditions, but for most observers yellow–blue hue-cancellation data do not. It is of interest to examine the question of cancellation linearity in sex-linked dichromats under the assumption that they represent reduced systems. We measured both the wavelength of the spectral achromatic point over a large range of intensities and yellow–blue hue-cancellation functions over the full spectrum and at several luminance levels in protanopes and deuteranopes. Both sets of data for the two types of dichromat satisfy linearity properties. These results are consistent with a model in which both cone receptor response functions have the same form. Implications for trichromatic opponent-response functions are considered.

INTRODUCTION

Experiments on the nature of the opponent-response functions have shown that the red–green process behaves in a linear fashion over a more general set of conditions than does the yellow–blue system.[1–6] The data in support of this assertion arise from hue-cancellation experiments in which either the mixture of two fixed-wavelength lights or the wavelength of a single spectral light is varied to obtain lights that appear neither red nor green (unique yellow, unique blue, or achromatic) for red–green cancellation or neither yellow nor blue (unique red, unique green, or achromatic) for yellow–blue cancellation. These unique hues, or more generally cancellation end points, may be regarded as equilibria for underlying opponent-response functions.[7] As such they represent criterion responses (the zero response) and may serve as suitable probes with which to infer the properties of these underlying response functions. Equilibrium hues must obey two laws if hue-cancellation data are related linearly to the color-matching functions and the cone-photopigment quantum catch[8]; these are scalar invariance and additivity.

(1) Scalar invariance: If a light is an equilibrium hue for a given opponent system, then with an increase or decrease in its intensity it must remain an equilibrium hue for that opponent system.

(2) Additivity: If two lights are equilibrium hues with respect to the same opponent system, then their mixture in any proportion must be an equilibrium hue with respect to that same opponent system.

It is the violation of the scalar invariance property for unique red (but not necessarily for unique green) for most observers that has led to the rejection of a linear model for the yellow–blue system.[2,4] The inability to find a satisfactory linear combination of candidate cone photopigments that predicts yellow–blue hue cancellation data (for most observers) is also consistent with a nonlinear yellow–blue process.[3] Recently, significant additivity failures have been demonstrated as well for yellow–blue cancellation.[5,6]

Although several analyses have been attempted, no completely satisfactory model of the yellow–blue nonlinearity has been found.[2,3,6,9] The main difficulty of adequately accounting for the behavior of the yellow–blue system is that the nonlinearity varies from individual to individual.[2,3,5] Also, little consideration has been given to the nature of models that would predict at least one invariant point in chromaticity space, as appears to be necessary, at least for some observers.[2]

In the hope of gaining some insight into the normal trichromatic yellow–blue system, we sought to analyze a simpler visual system. Sex-linked dichromats display the requisite characteristics of such a simpler system. For 2-deg foveal fields, these observers behave as if they possess only two cone photopigments.[10]

From studies in unilateral dichromats, there is some evidence that sex-linked dichromats have only one opponent mechanism, the yellow–blue system.[11] However, these data have been controversial in that pure dichromacy has not been well established. In addition, two recent studies challenge the notion that dichromats show simple loss of an opponent system.[12,13] The purpose of the present experiment was to test the linearity properties of the yellow–blue equilibrium points in protanopes and deuteranopes. In the first experiment we determined whether these hue equilibria obeyed the

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scalar invariance property. Previous studies of this issue have been restricted to a range of retinal illuminance spanning no more than 1 log unit.[14,15] The present study extends such measurements considerably.

The possibility exists that there is a residual red–green system in some dichromats. In addition to the long-wave lobe of the red–green system innervated by the long-wave-sensitive cones, there is evidence that shortwave redness in trichromats is contributed by the shortwave-sensitive cones.[16] Thus, in protanopes with the long-wave-sensitive mechanism missing, red–green opponent antagonism contributed by the shortwave and midwave mechanisms may remain. In the deuteranopes, for whom the midwave cones are missing, there would be no residual red–green antagonism.

Whether there is a red–green system present does not affect the validity of the present study. What matters is whether the observers can make judgments based on yellowness and blueness. The appearance of the residual hue sensation at yellow–blue equilibrium is irrelevant to the question of whether the equilibrium locus, itself, is invariant with intensity.

If the dichromatic system is the simpler system that we have assumed, i.e., composed of two cone photopigments and, at least, one opponent system, and if the scalar invariance property is satisfied, then it is not necessary to test additivity. In this case, other hue equilibria will be metameric to the spectral achromatic point, except for an intensity factor, provided that Grassmann's laws of color matching hold. Tests of additivity under these circumstances can be shown to be no more than tests of Grassmann's laws of color matching. However, a number of recent studies have demonstrated a need to acknowledge more than two photopigment inputs in putative dichromats under certain conditions.[17–22] If this were the case under our conditions, then it is possible that by restricting our attention only to the spectral equilibrium we would have overlooked conditions that do reveal nonlinearities. Thus, to test more generally the linearity properties of the dichromatic yellow–blue system, we also measured hue-cancellation and color-matching functions and attempted to relate these two sets of data to each other by a linear transformation.

METHODS

Observers

One of the authors and three students solicited from introductory psychology classes at Brown University served as observers. Each prospective dichromat was screened initially with the Farnsworth Panel D-15. Each observer who failed the D-15 was subsequently tested on four color-matching tasks: (1) an isomeric match (590 nm ≡ 590 nm), (2) a Rayleigh match (550 nm ≡ 590 nm and 590 nm ≡ 650 nm), (3) a midspectral match (450 nm + 650 nm ≡ 500 nm), and (4) a neutral-point match in which the experimenter varied the wavelength and the observer varied the intensity of a monochromatic light to match it to a broadband white with CIE chromaticity coordinates $x = 0.40$ and $y = 0.42$.

The purpose of the isomeric match was to provide practice in performing color matching on a Maxwellian-view system. The observer was required to rate this match in terms of how nearly identical the two halves of the field appeared in all aspects of color (i.e., hue, brightness, and saturation) on a 10-point scale, where 10 referred to a complete match with respect to these three perceptual attributes. In all cases, the isomeric match was given a rating of 9 or 10. On inquiry, ratings of 9 were found to result from small differences in the distribution of dust particles visible in Maxwellian view on the two sides of the bipartite field.

On subsequent matches the observer was instructed to use the same rating scale. Only observers who rated all their metameric matches at least as high as their isomeric matches were chosen to participate in the experiment.

Four observers were obtained by using this procedure, two protanopes and two deuteranopes. All had normal visual acuity, and none wore glasses or contact lenses.

Apparatus

The apparatus has been described in detail by Werner and Wooten.[3] Up to three channels of a four-channel Maxwellian-view system were used in the present experiments. Two channels were optically identical and had a common source, a 1000-W xenon-arc lamp (Hanovia). For both of these channels (1 and 2), the source was brought to focus on the entrance slit of a 500-mm grating monochromator (Bausch & Lomb).

Neutral-density filters and stray-light-blocking filters were placed in collimated portions of the optical system. Circular neutral-density wedges, a shutter, and an achromatizing lens were placed at focused images of the source. A circular aperture that defined a 1.05-deg field conjugate with the observer's retina was used for all experiments described except where otherwise specified. The third channel was obtained from a second 1000-W xenon-arc lamp. The construction of this channel was similar to that of channels 1 and 2 except that a 250-mm grating monochromator was used. The three beams were brought to a focus in the plane of the observer's right pupil as an image of 1 mm in diameter.

Each neutral-density wedge was attached to a continuous one-turn potentiometer with a stable reference voltage across it that could be read on a digital voltmeter. The shutter was driven by a Uniblitz shutter drive (Vincent Associates), and the timing was controlled by a variable timer mechanism with error of less than 1%.

An auxiliary channel for pupillary alignment could be brought into the system by moving a beam splitter into the final collimated portion of the system. The experimenter viewed the observer's pupil against a reticle consisting of a cross hair and concentric circles, the center of which was aligned with the optical axis of the system and conjugate with the source images.

The observers used a dental impression bite bar and adjustable forehead rest to keep in a fixed position throughout a session. The bite bar and forehead rests were attached to a sturdy milling table that was movable in three orthogonal directions.

Additional details of the apparatus can be found elsewhere.[23]

Calibrations

Each xenon arc was powered by a regulated, dc power supply (Oriel Corporation). The current was maintained at 42 A. The energy output of the monochromators was calibrated on a daily basis with a PIN-10 silicon photodiode (United De-

tector Technology Corporation) that was previously calibrated against a standard that was traceable to the National Bureau of Standards. A linear readout system (United Detector Technology Corporation) was used to measure the current output of the photodiode. All energy calibrations were performed with the 1.05-deg field stop in place. Neutral wedges and filters were calibrated in place in the optical system. Interference-blocking filters were used to reduce stray light and secondary spectra from the monochromators over the ranges 400–490 nm and 640–700 nm. These blocking filters were calibrated on a Cary Model 17 recording spectrophotometer (Varian).

The monochromator slits in channels 1 and 2 were set to a half-amplitude bandpass of 5 nm while channel 3 was set to a half-amplitude bandpass of 10 nm. The monochromators were calibrated at the start of the study against interference filters with known transmission peaks of 451 and 650 nm, as well as with the zero-order spectrum. During the course of the study these calibrations were periodically rechecked for the zero-order spectrum and the 451-nm filter.

Retinal illuminance was determined by a normal trichromat with an SEI photometer and checked with a Macbeth illuminometer at 575 nm using the method of Westheimer.[24] Reported troland values are for the appropriate luminous efficiency function for that observer.[25]

Procedure

To obtain the spectral achromatic points, the method of constant stimuli was used. Ten luminance levels were chosen ranging from 0.5 to 5.0 log Td for the protanopes and from 0.3 to 4.8 log Td for deuteranopes in steps of 0.5 log unit. The order of presentation of the illuminance levels was randomized across days. All levels were run before any were replicated. Two levels were chosen for a given experimental session, although sometimes there was time for only one. The dimmest level of the two was always presented first to minimize cumulative effects of adaptation. Observers were initially dark adapted for 15 min. A session typically lasted 2 h with a 10-min break in the dark between different illuminance levels.

Each wavelength was presented at equal retinal illuminance corrected for the appropriate dichromatic luminous efficiency function.[19] To minimize bias, no fixation point was used.[26] Instead, the observer was directed to notice after 15 min in the dark that when he fixated straight ahead, he could just discern with peripheral vision the circular outlines of the first apparatus lens (about 9.5-deg radius) that was made visible by low levels of ambient light. He used this information to direct his gaze in order to obtain a foveal view of the stimulus. The observer kept his eyes closed except just before and during stimulus presentation.

If the observer saw the stimulus foveally, he responded with a report of either blue or yellow. He then responded with an estimate of the saturation of the stimulus on a scale of 1 to 5, where 1 was reserved for stimuli that appeared achromatic and 5 was assigned to stimuli that appeared definitely blue or yellow. The results of these saturation estimates have been presented elsewhere.[27] The observer could ask to see the stimulus as often as necessary to obtain a foveal view. If it was necessary to repeat the stimulus, the experimenter waited a minimum of 20 sec before the second presentation.

Some studies have shown evidence of anchoring behavior with the method of constant stimuli used for this type of judgment.[14,15] Using the following procedure, we found no evidence for anchoring in pilot studies. The length of the stimulus set (10–15 nm) and the region of the spectrum in which it was centered (6-nm range) were randomized across sessions. Within sessions, the observer was permitted to discard stimuli that appeared clearly yellow or blue. For a given illuminance level, six random orders of wavelength were generated. The entire range was presented before continuing to the second random order, and so forth. Since the observer discarded many stimuli early in the session, each stimulus was presented at most six times. Each observer was given two or three practice sessions at different intensity levels to familiarize him with the task and in order for the experimenter to obtain some idea of the region of the spectrum within which the achromatic point would be found.

Hue Cancellation

The isocancellation technique[9] was used to measure sensitivity functions. To measure the blue lobe a standard stimulus of 575 nm (570 nm for observer KK) was presented at 1.5, 2.5, or 3.5 log Td. The observer varied the radiance of a series of bluish test lights of shorter wavelength than that of his achromatic point in a mixture with the yellowish standard to obtain a light that appeared neither yellowish nor bluish.

To measure the yellow lobe the reverse procedure was used. A set of three blue standards was used. Each blue standard was set at a wavelength of 445 nm, and the canceling test stimuli were presented at longer wavelengths than that of the achromatic point. As in the case of the blue lobe, the observer varied the radiance of the test stimuli to produce a mixture that appeared neither yellow nor blue. The height of the yellow lobe was specified by the amount of 445-nm light that canceled the series of three yellowish standards referred to above.

At the beginning of a session, the observer was allowed to practice the cancellation task with continuous stimulus presentation. The standard was set at a predetermined level for the first part of the session for that day. With a test stimulus adjusted so that it appeared in yellow–blue equilibrium, the achromatizing lens was adjusted laterally and vertically to eliminate any colored fringes seen by the observer. Following this adjustment, the observer was dark adapted for 15 min. At the end of this period, the observer was presented with a field composed of a mixture of the standard field and a test field. The stimulus appeared against a dark background with no fixation point and was cycled on for 3 sec and off for 7 sec. In adjusting the mixture to the yellow–blue equilibrium endpoint, the observer was further advised to avoid adjustments that caused the stimulus to appear strongly blue or yellow and to approach the end point from both directions to avoid excessive adaptation to one or the other hue.

To measure the blue lobe, test wavelengths were chosen every 10 nm from 400 nm to a wavelength slightly shorter than the achromatic point. For the yellow lobe, wavelengths were chosen every 10 nm starting as near the achromatic point as feasible until the longest wavelength shorter than or equal to 700 nm for which the system produced enough energy to cancel the hue in the standard was reached. The spectrum was traversed in both directions twice for a given luminance level. Thus four measurements were obtained at each wavelength on a given day. The order in which the spectrum

was initially presented was alternated across sessions and across standard levels. Each lobe at each standard level was determined twice on separate days. Each observer was given at least two practice sessions before data were collected.

Color Matching

The minimum saturation (or Maxwell) method of color matching was used.[28–30] A 1-deg bipartite field was presented in Maxwellian view. In half of the field, the comparison half, a light of fixed spectral composition, of fixed radiance, and of low saturation was presented (hence the name "minimum saturation method"). For this purpose, the monochromatic light of the wavelength at the mean value of each observer's achromatic point was presented at 316 photopic Td. The other half-field consisted of either a mixture of a 445-nm light and a test light of longer wavelength than that of the achromatic point or a mixture of 630-nm and a test light of shorter wavelength than that of the achromatic point. The test lights were chosen in 10-nm steps between 400 and 700 nm. The observer varied the intensity of both lights in the mixture field to obtain a metameric match. The observer was instructed to make identity matches and to inform the experimenter if such matches were not possible.

Within a single session, measurements were obtained only from the part of the spectrum corresponding to a single fixed-wavelength primary. During the session, the wavelength of the test light was chosen by one traverse of the spectrum in both directions. Thus two measurements were obtained at each wavelength in a single session. The direction in which the spectrum was initially traversed was alternated across sessions. Each portion of the spectrum was measured in two separate sessions, resulting in a total of four measurements at each wavelength.

RESULTS

Figure 1 presents the proportion of yellow responses as a function of wavelength for several luminance levels for two observers. Since the observers' responses were limited to only two responses, the proportion of blue responses is one minus the proportion of yellow responses. The filled and unfilled symbols represent across-day replications of the same conditions. At short wavelengths the observer never responded with yellow and at long wavelengths he always did. In an intermediate region the proportion of yellow responses is an increasing function of wavelength. Except at the lowest intensity levels tested, the slopes in this intermediate range are steep. Typically the transition from 0 to 100% yellow responses is complete within 1 to 3 nm.

On inquiry, all observers referred to the hues in the intermediate region as grayish or white. At low intensities, observer CH sometimes used the terms greenish or pinkish.

The smooth curves in the graphs represent logistic functions that were fitted to the data using a least-squares criterion with the minimization subroutine STEPIT.[31] From the fitted curves, the wavelength that was responded to on 50% of the trials as yellow and 50% of the trials as blue was interpolated and termed the achromatic point.

The mean wavelengths of the achromatic point for each luminance level and observer are plotted in Fig. 2. The mean achromatic points (±SD) determined across all luminance levels for each observer are KK, 493.0 ± 1.63; BG, 500.5 ± 1.76;

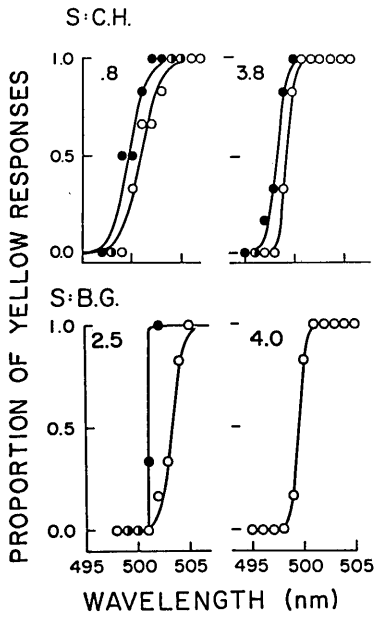

Fig. 1. Proportion of yellow responses as a function of wavelength in the vicinity of the achromatic point for deuteranope, CH, and protanope, BG. The level of retinal illuminance at which the judgments were obtained is indicated in log trolands in the upper left-hand corner of each graph. The filled and unfilled symbols represent different experimental sessions. The smooth curves represent a least-squares fit of a logistic function.

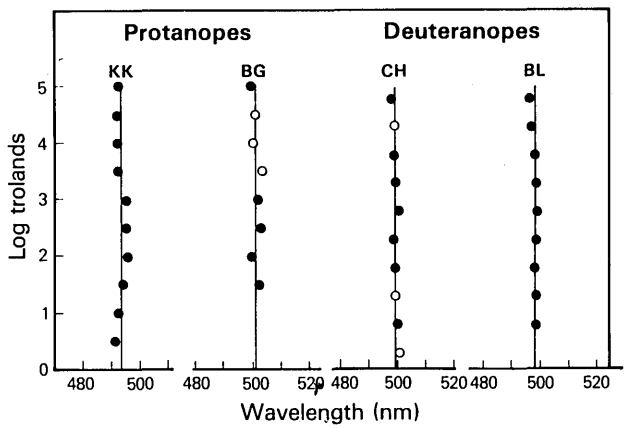

Fig. 2. Achromatic points as a function of retinal illuminance for two protanopes and two deuteranopes as derived from yellow–blue judgments. Filled symbols represent the means of 2–5 experimental sessions. Unfilled symbols represent a single experimental session. Vertical lines represent the grand mean wavelength of the achromatic point for a particular observer. Standard deviations in all cases are the size of the symbols or smaller.

CH, 499.3 ± 1.39; BL, 498.1 ± 0.97. A small amount of variation in the achromatic locus is present for each of the four observers. There appears to be a shift of the achromatic point of 1 to 4 nm in the short-wavelength direction for luminances above 4 log Td. KK also shows a small shift in this direction below 2 log Td. A one-way analysis of variance, however, did not lead to a rejection of the null hypothesis of scalar invariance for three of the four observers (KK, $F = 3.232$, $df = 4, 18$ $0.05 > p > 0.01$; BG, $F = 1.081$, $df = 3, 9$ $p > 0.05$; CH, $F = 0.676$, $df = 4, 13$ $p > 0.05$; BL, $F = 3.329$, $df = 3, 14$ $p > 0.05$). Because the slopes of the psychometric functions are so steep, a small change in the position of the achromatic point can

Table 1. Mean Difference Between Achromatic Points Determined Within a Single Session

Observer	x (nm)	s	t	df	
KK	−1.09	1.62	−1.90	7	$p > 0.05$
BG	−1.27	2.45	−1.27	5	$p > 0.20$
CH	−0.73	1.89	−1.08	7	$p > 0.20$
BL	−1.49	1.02	−4.14	7	$p < 0.001$

result in a large change in the proportion of yellow responses at a wavelength in the intermediate region. A small change in wavelength on a single day might be significant, but the larger across-day variation would hide a change with retinal illuminance. To assess whether a systematic within-day shift with retinal illuminance was present for the days that two levels were measured in a single session, we tested whether the difference between the higher and lower levels was significantly different from zero. The results of this test, shown in Table 1, indicate that while the mean shift was always to a shorter wavelength at higher levels, only for one observer (BL) are the shifts statistically significant.

The single consistent trend across observers is a slight shift in the shortwave direction of the achromatic locus at very high retinal illuminances. Although our statistical analyses have shown this to be in general an insignificant shift on the wavelength axis, they have given us no insight as to whether this trend represents a large or small change in underlying response. For example, because the shortwave cone mechanism is changing rapidly in sensitivity in this spectral region, a small change in wavelength may represent a rather large change in its input to the opponent-response function. The vertical lines fitted to the data in Fig. 2 are located at the mean values of the achromatic point over the whole range tested. These lines represent the best fit of a linear opponent-response model for the data:

$$R(I, \lambda) = \tau(\lambda)[k_1 I(\lambda)\beta(\lambda) - k_2 I(\lambda)\alpha(\lambda)], \quad (1)$$

where R is the response output, τ is the preretinal transmission factor, α, β are shortwave-sensitive and midwave- or long-wave-sensitive mechanisms, I is radiance, and k_1, k_2 are wavelength-independent weighting coefficients. When R is constrained to equal zero, the expression becomes independent of the intensity and preretinal transmission factors. To evaluate the power of the fit of this model we need a set of alternative models against which to judge it. For this purpose, we chose a model of the form

$$R(I, \lambda) = k_1[I(\lambda)\tau(\lambda)\beta(\lambda)]^p - k_2[I(\lambda)\tau(\lambda)\alpha(\lambda)]^q. \quad (2)$$

The fitting of this model may be implemented simply by noting that if we set R equal to zero, add the second term on the right to both sides, and take the logarithm of both sides we obtain

$$\log I(\lambda)\tau(\lambda)\beta(\lambda) = n \log I(\lambda)\tau(\lambda)\alpha(\lambda) - c, \quad (3)$$

where $n = q/p$ and $c = (\log k_1/k_2)/p$.

Although this model may not represent the full set of alternative models possible, it has the following advantages: (1) What seemed to be a four-parameter model is shown to depend actually on only two parameters (n, c); (2) in this form, fitting the model becomes a linear-regression problem that is extremely simple to implement; (3) the degree of nonlinearity may be varied in a systematic fashion by varying the parameter n; and (4) the homogeneous family of models of which the linear model is a member represents the special case in which $n = 1.0$.

Figures 3 and 4 represent all the data that went into Fig. 2 transformed to the coordinates appropriate for fitting Eq. (3). The cone fundamentals and preretinal factors used were those of Estévez.[32] Values in the intermediate wavelengths were obtained by linear interpolation. The solid lines represent the best-fitting straight line to the data. Table 2 contains the parameters of the fits. In only one case does the slope significantly differ from unity and in this case by only 2.2%. For comparison the best fitting lines of unity slope are reproduced in Figs. 3 and 4 as dashed lines. There seems to be remarkably little variation in the achromatic locus over an extended range of retinal illuminance.

Hue Cancellation

The hue-cancellation data obtained from one protanope and one deuteranope are presented in Figs. 5 and 6, respectively. Consider how the blue lobe for 1.5 log Td (filled circles) was obtained. Each point represents the intensity of a test light necessary to cancel a 1.5-log Td yellowish standard. We have

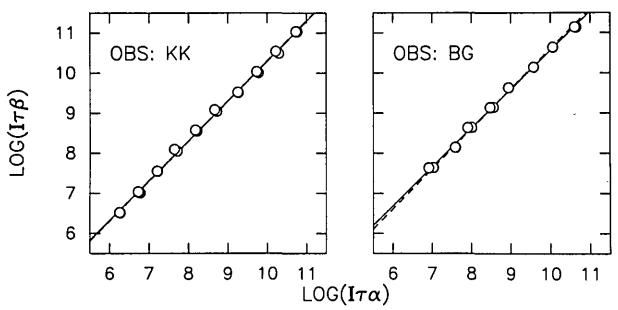

Fig. 3. Achromatic points for two protanopes transformed to the coordinate system implied by Eq. (3) from text using the midwave-sensitive, $\beta(\lambda)$, and shortwave-sensitive, $\alpha(\lambda)$, fundamentals of Estévez.[32] Solid line indicates best-fitting line by least squares. Dashed line indicates best-fitting line of unit slope.

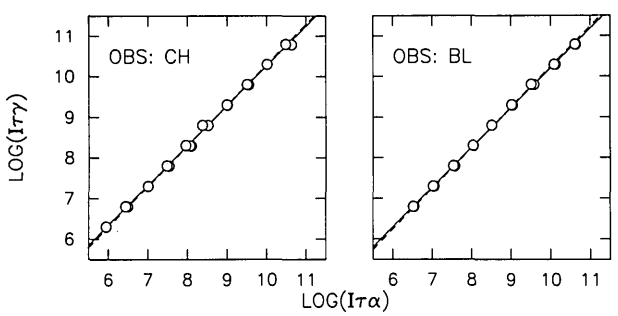

Fig. 4. Achromatic points for two deuteranopes plotted in a similar fashion as that of Fig. 3 using long-wave-sensitive, $\gamma(\lambda)$, and shortwave-sensitive, $\alpha(\lambda)$, fundamentals of Estévez.[32] Other details as in Fig. 3.

Table 2. Results of Fit of Eq. (3) to Achromatic Point Data

Observer	n	c	r^2	t	df	
KK	0.994	−0.360	0.998	−0.65	21	$p > 0.40$
BG	0.971	−0.861	0.998	−1.99	11	$p > 0.05$
CH	0.981	−0.457	0.998	−1.86	16	$p > 0.05$
BL	0.978	−0.425	0.999	−3.70	16	$p < 0.01$

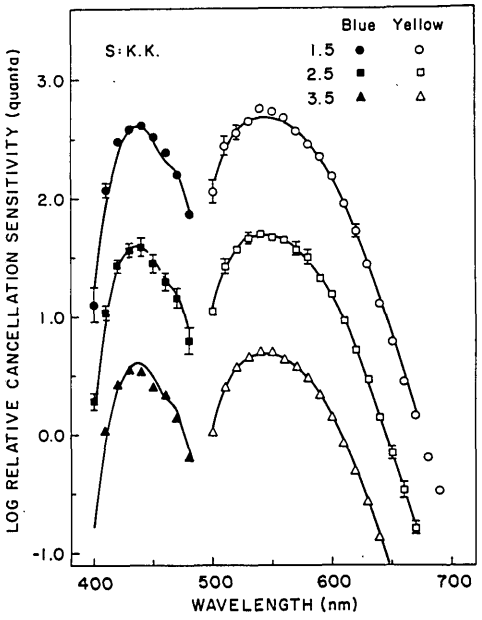

Fig. 5. Log cancellation sensitivity plotted as a function of wavelength for three standard levels for protanope, KK. Reference standard for the blue lobe (filled symbols) was a 570-nm light at 1.5, 2.5, or 3.5 log Td. To obtain the yellow lobe (unfilled symbols) a 445-nm reference standard was used. Error bars represent ±1 SEM. Smooth curves are the best fitting linear combination of the observer's own color-matching functions.

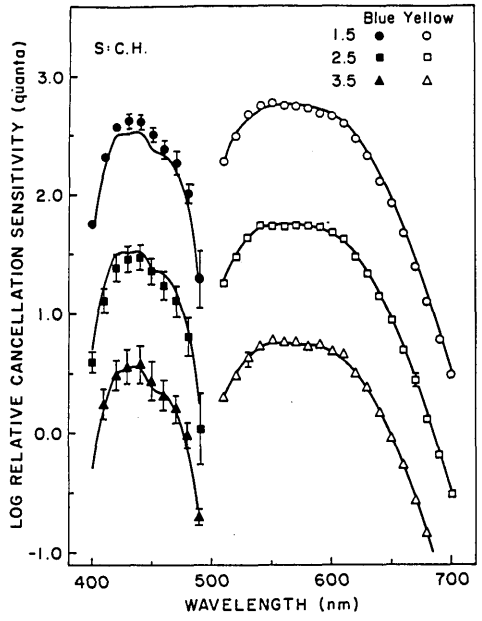

Fig. 6. Log cancellation sensitivity for deuteranope, CH. Reference standard for the blue lobe was a 575-nm light at 1.5, 2.5, or 3.5 log Td. Other details as in Fig. 3.

plotted the logarithm of the reciprocal of this quantity measured at the cornea as an index of cancellation efficiency of bluish lights and have labeled it cancellation sensitivity. Increasing the yellowish standard by 1 and 2 log units (filled squares and triangles) results in the data being displaced vertically downward by 1 and 2 log units, respectively.

In a similar fashion, each of the unfilled circles represents the intensity of a yellowish test light necessary to cancel the bluish standard at the wavelength 445 nm. The intensity of the bluish standard was chosen to fall approximately on the blue lobe generated by the 1.5-log-Td yellowish standard.[33] Increasing this bluish standard by 1 and 2 log units (unfilled squares and triangles) results in the cancellation data being displaced vertically downward by approximately 1 and 2 log units, respectively.

The average of the standard errors of the mean (SEM's) for each observer were KK, 0.037; BG, 0.050; CH, 0.052; BL, 0.037. Within sessions SEM's at all wavelengths were less than 0.05, except at wavelengths nearest the spectral achromatic point at which the variability was about twice as great. Near the spectral achromatic point, the test light appeared to contain only a small amount of hue, and observers found that they had to add a large amount of the test light to cancel the hue of the standard. However, as the brightness of the mixture increased, the hue appearance became swamped or veiled by the white component. Under these conditions observers experienced difficulty choosing a criterion point. Most of the other variability apparent in the data resulted from across-day factors.

If the dichromatic yellow–blue response function is linear, then the hue-cancellation data are related to the underlying cone photopigment sensitivities by a linear transformation. Unfortunately, we do not have precise knowledge of the photopigment functions (nor of the preretinal transmission factors). However, assuming Grassmann's laws of color matching and that two lights are metameric when they produce the same quantum catch rate in the classes of cones present, color-matching functions (CMF's) are related to the cone-absorptance functions by a linear transformation. Thus we can determine whether an individual's CMF's are related to the hue-cancellation data by a linear transformation.

Color Matching

The minimum saturation CMF's for one protanope and one deuteranope are presented in Figs. 7 and 8. For test wavelengths above 530 nm and below 470 nm, the amount of the fixed-wavelength primary becomes asymptotic. This behavior has been documented elsewhere for this type of matching situation[30,34,35] and indicates that under these stimulus conditions sex-linked dichromats behave as monochromats in these spectral regions.

The errors associated with these matches were found to be quite small, even for the limited number of observations per wavelength ($n = 4$). Over the whole spectrum, observers claimed that they were able to obtain identity matches using only two primaries. Thus we find no need to postulate the presence of a third photopigment under these stimulus conditions.

The matching equations for these data can be represented as follows:

$$I(\lambda) + I_{630}(\lambda) \equiv I_{\lambda_0}, \quad \lambda < \lambda_0,$$
$$I(\lambda) + I_{445}(\lambda) \equiv I_{\lambda_0}, \quad \lambda > \lambda_0, \tag{4}$$

where $I(\lambda)$ is the quantum flux of the test beam, $I_{445}(\lambda)$ and $I_{630}(\lambda)$ are the quantum fluxes of the fixed-wavelength primaries, I_{λ_0} is the quantum flux of the comparison field, and the + symbol indicates superposition of lights.

To relate the CMF data to the hue-cancellation data, the above equations must be transformed such that a single set of primaries is used over the whole spectrum. From the data we obtained the values of the two fixed-wavelength primaries

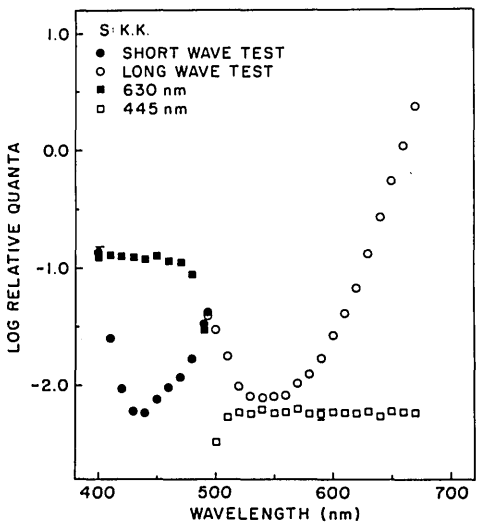

Fig. 7. Minimum saturation color-matching functions for protanope, KK. Filled symbols refer to the conditions in which a short-wavelength test light was mixed with a 630-nm light. Unfilled symbols represent the condition in which a long-wavelength test light was mixed with a 445-nm test light. Circles indicate the intensity of the test light used in the match. Squares indicate the intensity used in the fixed-wavelength primary. All matches were made to a 493-nm comparison stimulus set at 2.5 log Td. Error bars represent ±1 SEM.

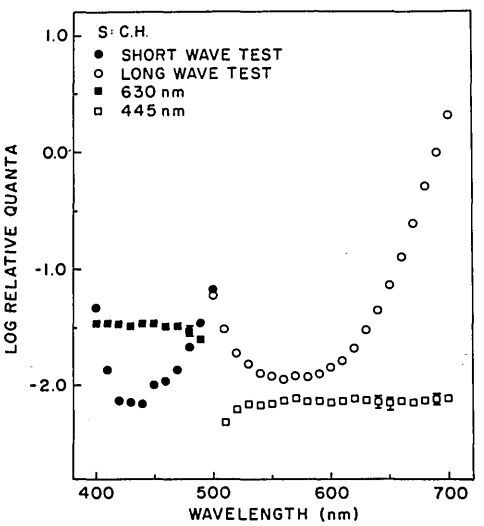

Fig. 8. Minimum saturation color-matching functions of deuteranope, CH. Comparison standard was set at 500 nm at a retinal illuminance of 2.5 log Td. Other details as in Fig. 5.

that when mixed together matched the comparison field. This match can be represented as

$$\bar{I}_{630} + \bar{I}_{445} \equiv I_{\lambda_0}, \tag{5}$$

where $\bar{I}_{630}$ and $\bar{I}_{445}$ indicate the radiances of the two fixed-wavelength primaries needed to match the comparison field. By substitution of the left-hand side of expression (5) for I_{λ_0} in Eqs. (4) the CMF's for primaries at 445 and 630 nm, p_{445} and p_{630}, are obtained:

$$p_{445}(\lambda) = \bar{I}_{445}/I(\lambda); p_{630}(\lambda) = [\bar{I}_{630} - I_{630}(\lambda)]/I(\lambda), \quad \lambda < \lambda_0,$$

$$p_{445} = [\bar{I}_{445} - I_{455}(\lambda)]/I(\lambda); p_{630}(\lambda) = \bar{I}_{630}/I(\lambda), \quad \lambda > \lambda_0.$$

Using these primaries, the coefficients for the CMF's could be found that minimized the squared deviations between the CMF's and the hue-cancellation data. To implement the search for these coefficients, the minimization subroutine STEPIT[31] was employed. The deviations were minimized in logarithmic space since this transformation appears approximately to equalize variance across wavelength for both sets of data.[38] All the data from a single observer were fitted at once. The fits were run from multiple starting points to reduce the risk of obtaining a local minimum of the error function.

The best-fitting linear combination of the CMF's for the observers in Figs. 5 and 6 appear as the smooth curves. For KK the rms error is 0.042 log Td, and for CH it is 0.055 log Td. These deviations are on the order of variability in the raw data. For CH, there appear to be systematic departures from the fits in the blue lobe. These can be traced to some misplacement of the relative heights of the two hue-cancellation lobes since there do not appear to be systematic changes in the shapes of these lobes with intensity.

DISCUSSION

The data support the assertion that sex-linked dichromats display scalar invariance of the achromatic point. Massof and Bailey[14] and Hurvich and Jameson[15] measured the spectral achromatic point over a small range of intensities and did not find evidence for a lack of scalar invariance. Starr[35] tested both cancellation linearity using mixtures and Grassmann's laws of color matching in dichromats. Grassmann's laws were found to hold for a 3-log-unit range. Scalar invariance of hue cancellation was found to hold over a similar range. The present study confirms and extends his observations to cover a 4-log-unit range.

Relation of Isocancellation and Conventional Hue Cancellation

The method of hue cancellation used in the present study differs from hue cancellation as it has been measured conventionally. In the original paper of Jameson and Hurvich,[37] the canceling stimuli were of fixed wavelength and were varied in intensity by the observers to eliminate the opponent hue of a series of lights from an equal-brightness spectrum. Subsequently the canceling lights were adjusted as if they had been mixed with a series of lights from an equal-energy spectrum. This is the reverse of the present procedure in which the fixed-wavelength stimuli are also of fixed intensity and the observer varies the intensity of the test stimuli.

The present procedure has been studied in detail for normal trichromats by Donnell[9] and has been termed by him "isocancellation." Under the assumption of linearity, it may be shown that conventional cancellation yields a curve that is proportional to cancellation sensitivity as defined in the present paper. We measured a conventional cancellation curve for one of our deuteranopes, BL, and found it to be identical within experimental error to his cancellation sensitivity curve except for a proportionality factor.

Romeskie and Yager[38] reported conventional cancellation data obtained from one protanope and one deuteranope. Both sets of data were well fitted by a linear combination of iodopsin extinction spectra with average corrections for preretinal media. Ikeda and Ayama reported conventional

cancellation data from one protanope. They showed that this observer's data were linearly related to the CMF's of the CIE standard observer.[39] The present comparison between each observer's *own* CMF's and hue-cancellation data depends on no assumptions about underlying photopigment distributions, preretinal media corrections, or similarity of the observer to a standardized average. If we seek to relate these fits to the cone pigment quantum catch, we need only make the well-accepted assumption that the CMF's are a linear combination of each observer's own cone photopigment absorptance functions.

As stated in the Introduction, the reason for gathering both the cancellation and CMF data subsequent to the first experiment was to rule out any nonlinearity that might be due to interaction from a third spectral mechanism. Indeed, in normal trichromats, spectral unique green has been reported to obey scalar invariance while other portions of the yellow–blue equilibrium locus do not.[2,4] One would think that if this were our aim, it would have been more to the point simply to prove that our dichromats never required a third primary by allowing them the use of one. Given the construction of our optical system, this was inconvenient to do. In lieu of this experiment, we have tried to demonstrate that the linearity properties hold over the whole spectrum.

The results from both the achromatic point determinations and the fit of the CMF's to the hue-cancellation data lead us to conclude that, unlike most normal trichromats, the sex-linked dichromat displays linear yellow–blue hue-cancellation data.

Model

We have shown that the hue equilibria of the sex-linked dichromat's yellow–blue response function obey linearity properties. This does not necessarily mean that the response function behaves linearly at values away from the hue equilibria. Recall that the hue equilibria may be regarded as zero crossings of the opponent-response function. It is not difficult to construct diverse classes of nonlinear functions whose zero crossings behave in a linear fashion (i.e., the kernels form linear subspaces).[8,40,41] This is especially true if one needs to consider only two photopigment inputs to the opponent stage, as with dichromats.

If it is assumed that the opponent interaction between receptor outputs is linear, we can constrain the functional form of one of the receptor functions if the other is known. Specifically, linear opponent interaction and the existence of at least one equilibrium point that obeys scalar invariance implies that both receptors display the same functional form:

$$R(I,\lambda) = r\left[I\frac{\beta(\lambda)}{\beta^*}\right] - r\left[I\frac{\alpha(\lambda)}{\alpha^*}\right],$$

where r is the receptor function and α^* and β^* are scaling constants (see Appendix A for proof).

In support of the assumption of linear interaction, we note that visual physiologists have provided evidence of linear interaction between classes of cone mechanisms in opponently coded cells in the primate visual system.[42]

Response Functions with Three Cone Inputs

With the same assumptions applied to a three-receptor system, it can be proven (see Appendix A) that a response function of the following form is sufficient to generate at least one scalar invariant equilibrium point:

$$R(I,\lambda) = k_1\left\{r_1\left[I\frac{\beta(\lambda)}{\beta^*}\right] - r_1\left[I\frac{\alpha(\lambda)}{\alpha^*}\right]\right\} + k_2\left\{r_2\left[I\frac{\gamma(\lambda)}{\gamma^*}\right] - r_2\left[I\frac{\alpha(\lambda)}{\alpha^*}\right]\right\}, \quad (6)$$

where $\gamma(\lambda)$ is the additional cone spectral sensitivity curve and γ^* is a scaling constant. For any point in chromaticity space for which $[\alpha(\lambda), \beta(\lambda), \gamma(\lambda)] = (\alpha^*, \beta^*, \gamma^*)$, $R = 0$ for all I.

This model demonstrates, for example, that, contrary to what has been stated in the literature,[6] exponential receptor nonlinearities with different powers on different receptors could in principle produce an invariant locus of white. Note, however, that this form of the model does *not* require that two different receptor functions necessarily be associated with a single photopigment. Both r_1 and r_2 could be the same. In that case, the model reduces to

$$R(I,\lambda) = k_1 r\left[I\frac{\alpha(\lambda)}{\alpha^*}\right] + k_2 r\left[I\frac{\beta(\lambda)}{\beta^*}\right] + k_3 r\left[I\frac{\gamma(\lambda)}{\gamma^*}\right], \quad (7)$$

where $k_1 + k_2 + k_3 = 0$. Note that these response functions by construction will produce at least one invariant locus, but they will display additivity only if r is linear. Thus receptors with the same functional response are sufficient to guarantee linear hue-cancellation behavior in a dichromat but do not provide such a guarantee for a trichromat.

Response Function with at Least Two Invariant Loci

The above response functions were derived under the assumption that at least one invariant equilibrium locus existed. If an additional invariant locus exists, then a much more severe constraint can be placed on r. As is shown in Appendix A, assuming at least two invariant loci constrains the receptor functions to take one of three forms: (1) homogeneous of degree p, (2) logarithmic, or (3) zero everywhere. Obviously, the third solution is extraneous for our purposes.

Now, consider the space of functions generated by Eq. (6), the family of response functions with at least one invariant locus. The class of functions just derived forms a subset of this space. The complement of this subset represents a class of models with exactly one invariant locus. In other words, the set of response functions with form given by Eq. (6) constrained so that the receptor functions are neither logarithmic nor homogeneous of degree p will have just one invariant locus. No prediction can be made about where in chromaticity space this invariant point will be found. That will depend on both the exact form of r and the various scaling constants.

The qualitative properties of these models provide a means of deciding between (or against) them. To test these models, it is necessary to determine the entire equilibrium surface for an opponent system. If there is more than one scalar invariant locus, we can reject any model like Eq. (6) in which the receptor functions are not logarithmic or homogeneous of degree p. If there are any noninvariant loci, then we can reject models that use logarithmic or homogeneous of degree p receptor functions, since receptor functions of this form predict scalar invariance of all hue equilibria. Finally, the presence of no invariant loci allows us to reject Eq. (6) altogether.

It should be noted, however, that the above predictions

degenerate in certain cases. For example, at the spectral unique yellow locus for the red–green system (about 580 nm), the shortwave-sensitive cones make a negligible contribution. If the coefficients of the midwave- and long-wave-sensitive receptor functions [k_2 and k_3 in Eq. (6)] are approximately equal in magnitude and much larger than k_1 and if the receptor functions are the same, then we would expect unique yellow to display scalar invariance for the same reason that it is displayed by our dichromatic model. The presence of this degenerate scalar invariant point in no way excludes a second truly invariant point, say, near unique blue or white. Thus a model of the form discussed above could account for the scalar invariance of unique yellow and blue.[1,4,43] However, unless the receptor functions are linear, nonadditivity is predicted.[44]

We know of no studies that have determined the entire equilibrium surface for either the red–green or the yellow–blue system. A definitive test of this class of models is awaited.

APPENDIX A

In this appendix we investigate the constraints imposed on response functions by the assumption of invariant equilibrium points. In order to derive the various classes of models described in the discussion, we will use the following notation: $\alpha(\lambda)$, $\beta(\lambda)$, $\gamma(\lambda)$, photopigment absorption spectra as a function of wavelength; r_i, $i = 1$–3, receptor response; I, intensity scaling factor; k_i, $i = 1$–3, wavelength-independent coefficients; R, opponent response.

Dichromatic Model

The dichromatic model is the simplest to derive. We take the opponent response, R, to be a summation of receptor functions $R = k_1 r_1[I\alpha(\lambda)] + k_2 r_2[I\beta(\lambda)]$. Then the existence of at least one wavelength, λ^*, such that $R = 0$ for all I, yields

$$k_1 r_1(I\alpha^*) + k_2 r_2(I\beta^*) = 0, \tag{A1}$$

where $\alpha^* = \alpha(\lambda^*)$, $\beta^* = \beta(\lambda^*)$. Since Eq. (A1) is valid over the entire range of I, it states that r_1 and r_2 are functionally related. To bring out this relationship, set $I\alpha^* = x$; then

$$r_1(x) = -\frac{k_2}{k_1} r_2\left(\frac{\beta^*}{\alpha^*} x\right).$$

A symmetric form results if we write

$$r_2 = r\left[I\frac{\beta(\lambda)}{\beta^*}\right],$$

in which case

$$r_1 = -\frac{k_2}{k_1} r\left[I\frac{\alpha(\lambda)}{\alpha^*}\right].$$

Thus, leaving out an unimportant factor, $-k_2/k_1$, we can write

$$R = r\left[I\frac{\alpha(\lambda)}{\alpha^*}\right] - r\left[I\frac{\beta(\lambda)}{\beta^*}\right]. \tag{A2}$$

Trichromatic Model

With the inclusion of a third receptor function, the opponent response has the form $R = k_1 r_1[I\alpha(\lambda)] + k_2 r_2[I\beta(\lambda)] + k_3 r_3[I\gamma(\lambda)]$. An invariant equilibrium, λ^*, then implies

$$k_1 r_1(I\alpha^*) + k_2 r_2(I\beta^*) + k_3 r_3(I\gamma^*) = 0 \tag{A3}$$

for all values of I. Considerations of the sort used earlier show that Eq. (A3) implies

$$r_1(x) = -\frac{k_2}{k_1} r_2\left(\frac{\beta^*}{\alpha^*} x\right) - \frac{k_3}{k_1} r_3\left[\frac{\gamma(\lambda)}{\gamma^*} x\right].$$

A more symmetrical form appears if we prepare our function by taking

$$r_1 = r_1\left[I\frac{\alpha(\lambda)}{\alpha^*}\right], \quad r_2 = r_2\left[I\frac{\beta(\lambda)}{\beta^*}\right], \quad r_3 = r_3\left[I\frac{\gamma(\lambda)}{\gamma^*}\right].$$

It then follows that, at $\lambda = \lambda^*$,

$$k_1 r_1(x) = -k_2 r_2(x) - k_3 r_3(x),$$

and hence

$$R = k_2\left\{r_2\left[I\frac{\beta(\lambda)}{\beta^*}\right] - r_2\left[I\frac{\alpha(\lambda)}{\alpha^*}\right]\right\} + k_3\left\{r_3\left[I\frac{\gamma(\lambda)}{\gamma^*}\right] - r_3\left[I\frac{\alpha(\lambda)}{\alpha^*}\right]\right\}.$$

Thus the presence of at least one invariant point implies the need for at most two different receptor functions.

If on grounds of parsimony we assume only one receptor function, then

$$R = k_1 r\left[I\frac{\alpha(\lambda)}{\alpha^*}\right] + k_2 r\left[I\frac{\beta(\lambda)}{\beta^*}\right] + k_3 r\left[I\frac{\gamma(\lambda)}{\gamma^*}\right], \tag{A4}$$

where

$$k_1 + k_2 + k_3 = 0. \tag{A5}$$

We next consider the effect of a second invariant equilibrium, at say wavelength $\bar{\lambda}$. It then follows from Eq. (A4) that

$$k_1 r(I\mu_1) + k_2 r(I\mu_2) + k_3 r(I\mu_3) = 0, \tag{A6}$$

with $\mu_1 = [\alpha(\bar{\lambda})/\alpha(\lambda^*)] = \bar{\alpha}/\alpha^*$, etc. valid for all I. Without loss of generality, let

$$1 \geq a = \frac{\mu_2}{\mu_1} \geq b = \frac{\mu_3}{\mu_1}.$$

Then to satisfy Eq. (A5) write $k_2 = k_1(-\frac{1}{2} - \theta)$, $k_3 = k_1(-\frac{1}{2} + \theta)$, where $-\infty < \theta < \infty$. If we set $I\mu_1 = x$, then Eq. (A6) becomes

$$r(x) = \frac{1}{2}[r(ax) + r(bx)] + \theta[r(ax) - r(bx)]. \tag{A7}$$

Equation (A5) is homogeneous in r, and r = constant is a solution but of no interest.

To examine the possibility of other solutions we transform Eq. (A7) by introducing

$$y = \ln x, \quad r(x) = f(y), \quad c = \ln a, \quad d = \ln b.$$

Then Eq. (A7) becomes

$$f(y) = \frac{1}{2}[f(c + y) + f(d + y)] + \theta[f(c + y) - f(d + y)]. \tag{A8}$$

The Fourier transform

$$\hat{f}(k) = \int \exp(-iky) f(y)\,dy$$

applied to Eq. (A8) yields

$$\hat{f}(k)\left[1 - \left(\frac{1}{2} + \theta\right)\exp(ikc) - \left(\frac{1}{2} - \theta\right)\exp(ikd)\right] = 0. \quad \text{(A9)}$$

Therefore $\hat{f}(k)$ vanishes unless

$$1 - \left(\frac{1}{2} + \theta\right)\exp(ikc) - \left(\frac{1}{2} - \theta\right)\exp(ikd) = 0 \quad \text{(A10)}$$

or

$$\left(\theta + \frac{1}{2}\right)[1 - \exp(ikc)] = \left(\theta - \frac{1}{2}\right)[1 - \exp(ikd)].$$

Before considering Eq. (A10) observe that if k_0 is a simple zero of Eq. (A10), then, to within a multiplicative constant, Eq. (A9) has the solution

$$\hat{f}(k) = \frac{1}{2\pi}\,\delta(k - k_0). \quad \text{(A11)}$$

This in turn leads to

$$f(y) = \exp(ik_0 y)$$

or

$$r(x) = \exp(ik_0 \ln x) = x^{ik_0} = x^{p_0},$$

where in general p_0 is complex. Since $r(x)$ represents a response it is unlikely that it depends sinusoidally on input. We therefore restrict attention to real p_0 and hence pure imaginary k. We set

$$ik = p$$

so that Eq. (A10) is

$$\left(\theta + \frac{1}{2}\right)(1 - a^p) = \left(\theta - \frac{1}{2}\right)(1 - b^p). \quad \text{(A12)}$$

Note from Eq. (A12) that $p = 0$ is always a solution. There is just one other solution. To see this, observe that if

$$\frac{\theta + \frac{1}{2}}{\theta - \frac{1}{2}} = \frac{\ln b}{\ln a},$$

then $p = 0$ is a double root and $\delta'(k)$ is also a solution to Eq. (A9). This then implies that $r = \ln x$ is a solution to Eq. (A7). To summarize, we have shown that if R, Eq. (A4), has two invariant equilibrium points, the cone function r must be a constant, proportional to a power function x^p, or proportional to the logarithm.

Finally, it should be observed that although our deliberations used spectral lights the results apply to arbitrary lights, in which case $I\alpha(\lambda)$ is replaced by $\int I(\lambda)\alpha(\lambda)d\lambda$ [$I(\lambda)$ is the spectral illumination density], and so forth.

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