CARDINAL DIRECTIONS OF COLOR SPACE

JOHN KRAUSKOPF, DAVID R. WILLIAMS* and DAVID W. HEELEY†

Bell Laboratories, Murray Hill, NJ 07974, U.S.A.

Abstract—Thresholds for detecting changes in color are raised following viewing a field sinusoidally modulated in color over time. This effect is highly selective. For example, thresholds for detecting reddish and greenish changes from white are raised following viewing a field varying in a reddish-greenish direction, but not after viewing one varying in a yellowish-bluish direction. Similarly thresholds for yellowish and bluish changes from white are raised following viewing a field varying along a yellowish-bluish axis but are not altered by exposure to reddish-greenish variation. Thresholds for chromatic changes are not raised following viewing a field varying in luminance. Thresholds for changes in luminance are raised following viewing a field varying in luminance but not altered by exposure to purely chromatic variation. Since this selectivity is found only for these directions and not intermediate directions in color space we conclude that these directions are cardinal, that is, signals varying along these directions are carried along separate, fatiguable, second stage pathways. The results conform to the expectations of opponent process theory with the important exception that the yellowish-bluish cardinal direction is a tritanopic confusion line and not a red-green equilibrium line.

INTRODUCTION

Modern theories of color vision typically incorporate two stages: a well-established first stage that includes the three types of cone receptors each with its own photopigment, and a more tentative second stage that includes mechanisms whose signals depend on quantal absorptions in more than one cone type. The interactive nature of the so-called second stage is widely accepted, receiving support from many kinds of evidence such as color appearance assessed with the cancellation technique (Hurvich and Jameson, 1957), detection of mixtures of chromatic stimuli (Boynton *et al.*, 1964; Guth *et al.*, 1969; Guth and Lodge, 1973; Krauskopf, 1973; Kranda and King-Smith, 1979), transient tritanopia (Mollon and Polden, 1975), field additivity experiments (Pugh, 1976), and increment thresholds for spectral lights presented on achromatic backgrounds (Sperling and Harwerth, 1971). In addition, a large body of physiological evidence beginning with the work of Svaetichin (1956) and De Valois (1965) has shown that signals from different cone types are combined in an opponent fashion. Still there is little agreement about the specific interactions between cone signals that occur beyond the receptors.

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*Present address: Center for Visual Science, University of Rochester, Rochester, NY 14627, U.S.A.

†Present address: University of St Andrews, St Andrews, Fife, Scotland.

‡We have chosen to use the word "habituation", while others might prefer "adaptation", "fatigue", "desensitization", etc.

§There were reliable individual differences. D.R.W. required more 441.6 nm light for his white matches than J.K. and is known to have a relatively dense macular pigment. Since this short wavelength contributed little to the luminance of the white, this variation had insignificant effects on the luminance measurements.
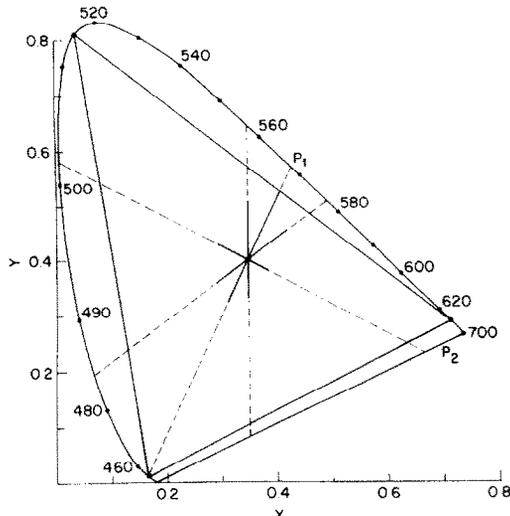
Prolonged viewing of temporally modulated fields raises the thresholds of detecting changes in chromaticity and luminance (Guth *et al.*, 1976; Benzschawel and Guth, 1978; Krauskopf, 1976, 1980; Jameson *et al.*, 1979). We have used a method of selective habituation to delineate the second stage mechanisms objectively, measuring the changes in color discrimination produced by exposure to fields that are temporally modulated in color space‡. The test stimuli we used for this purpose were color changes of a field from neutral white rather than test flashes superimposed on backgrounds as in the typical increment threshold procedure. Thus, in principle, we could measure thresholds dependent on but one second stage mechanism.

METHODS

The apparatus is a computer controlled color mixer described elsewhere (Krauskopf *et al.*, 1981) that produces virtually any temporal variation in chromaticity and luminance to which the eye can differentially respond, within the limits imposed by the three primary sources. The sources are three lasers emitting light at 632.8, 514.5 and 441.6 nm referred to hereafter as the red, green and blue primaries, respectively, that are mixed to form a spatially uniform 2° circular field fixated by the observer. A spectrally calibrated PIN diode, incorporated in the equipment, measured the intensity of the primaries before and after each experimental session. The retinal illuminances of the primaries were computed in trolands with the aid of the CIE photopic luminosity function. Flicker photometric measurements confirmed the appropriateness of these values for each of our observers§.

Before beginning the experiments, each observer determined a mixture of the three primaries that

Fig. 1. Chromaticity digram depicting the eight test directions (shown as dotted lines) and four habituation axes (shown as solid lines) for observer J.K., whose white point is at the intersection of these axes. The provisional cardinal chromatic axes are labeled P_1 (yellowish-bluish) and P_2 (reddish-greenish).

appeared white to him. He did this by adjusting the red and blue primaries while the green primary was kept fixed at half of its maximum output. No reference was used. The illuminances of each primary in trolands required to produce a neutral white were stored in a separate file for each observer and used to set the mean luminance and chromaticity in each experimental session.

To simplify specification of the experimental conditions we tentatively defined two chromatic and one luminance direction in color space. The chromatic axes are depicted on the CIE chromaticity diagram in Fig. 1. A provisional reddish-greenish axis was defined by equation 1 where L_R, L_G and L_B are the luminances of the 632.8, 514.5 and 441.6 nm primaries, respectively and W_R, W_G and W_B are constants representing the luminances of these primaries for the white match.

$$L_R + L_G = W_R + W_G \qquad (1A)$$

$$L_B = W_B. \qquad (1B)$$

Increasing the output of the red primary while decreasing the output of the green primary by the same amount in trolands constitutes a change in the reddish direction. Reversing the sign of the changes in the primaries produces a change in the greenish direction. A provisional yellowish-bluish axis was defined

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*We have chosen to use the terms yellowish, bluish, reddish and greenish to describe these provisional directions to distinguish them from directions that correspond to unique yellow, blue, red and green. In fact, as shown below, the reddish-greenish provisional axis is almost identical to the unique red-green direction but the yellowish-bluish provisional axis does not coincide with the unique yellow-blue direction but the tritanopic axis through the white point.

by equation 2.

$$0.5 (L_R + L_G) + L_B = W_R + W_G + W_B \qquad (2A)$$

$$L_R - W_R = L_G - W_G. \qquad (2B)$$

Increasing the output of the blue primary while decreasing both the green and red primaries each by half as many trolands constitutes a change in the bluish direction. Reversing the sign of the changes produces a change in the yellowish direction*. Simultaneous increase in all three primaries in proportion to their mean luminance constitutes an increment along the luminance axis, and a proportional decrease in all three primaries constitutes a luminance decrement.

The thresholds reported in this paper are analogous to modulation thresholds. For example, thresholds in the reddish direction were measured in terms of $\Delta L_R/W_R$ and those in the greenish direction in terms of $\Delta L_G/W_R$. It should be noted that the latter is not equal to $\Delta L_G/W_G$ for while according to equation 2 ΔL_R is equal to ΔL_G, W_R is not equal to W_G. The modulation measure used in the other provisional primary direction is $\Delta L_B/W_B$. The interpretation of absolute modulation thresholds is theory dependent. The conclusions drawn in this paper are based on *changes* in modulation thresholds.

Time-course of habituation

Figure 2 illustrates the experimental procedure employed in a preliminary experiment. The observer viewed a steady white field for 30 sec, after which thresholds for detecting changes from white in the reddish-greenish direction in color space were measured with a yes–no staircase procedure. Thresholds for these same directions were remeasured after viewing the habituation field. The test stimulus illustrated in Fig. 2 is a pulse with a gaussian temporal waveform in the reddish direction from the neutral white. This waveform was chosen to minimize the high temporal frequency content of the test pulse, favoring detection of chromatic variation relative to achromatic variation (Kelly and van Norren, 1977).

Figure 3 presents the results of such an experiment to illustrate the size and the time–course of the desensitization effect of viewing of a sinusoidally varying habituation field. The habituation stimulus varied in the equiluminous reddish-greenish direction for 30 sec at a frequency of 1 Hz and an amplitude that was the largest that could be generated within the rules defined above. Note that the habituation stimulus is produced by sinusoidally modulating each of the laser primaries while keeping their time-averaged luminance the same as that of the neutral white. Gaussian pulses (SD = 250 msec, total duration = 1.5 sec) were presented at 3.0 sec intervals for 60 sec following the offset of the habituation stimulus. Two separate series of test pulses were alternately presented, one after each presentation of the habituation stimulus. In one series the first test pulse began immediately at the end
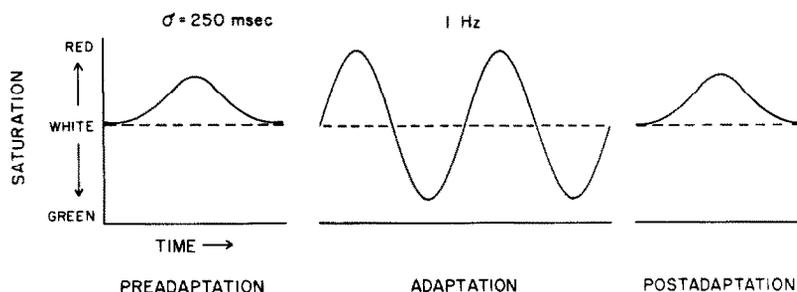
Fig. 2. Gaussian test pulses whose amplitude is varied to measure threshold before and after exposure to sinusoidal variation in color space whose mean level is a neutral white. A reddish test pulse and a reddish-greenish habituation stimulus are depicted.

of the last cycle of the habituation stimulus, while in the other it occurred after a delay of 1.5 sec. The two series combined provided a threshold measurement every 1.5 sec. The observer reported whether each pulse was visible by pressing one or two buttons. If the observer reported seeing a pulse, its amplitude for that time slot on the next presentation was reduced by 0.1 log units (except on the first trial on which the change was 0.2 log units). The amplitude was increased by the same amount if the observer reported not seeing a pulse. No change was made and the trial did not affect the computed threshold on the rare occasions when the observer failed to respond before the next pulse was presented. At the end of the test period the habituation stimulus was presented again initiating a new cycle. Ten to twenty cycles were run within an experimental session, the data from which were stored and used as initial values for a later session. The mean of the log amplitudes of the pulses presented in each time slot, excluding the first three trials that were used to locate the thresholds approximately, were taken as estimates of the thresholds for that interval. The retinal illuminance of the field was fixed at 50 td throughout the experiment.
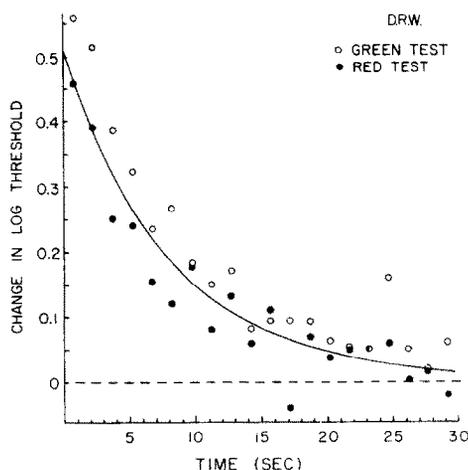

Fig. 3. Time–course of the desensitizing effect of viewing a field varying sinusoidally at 1 Hz in the reddish-greenish direction on a gaussian pulse in the reddish direction having a standard deviation 250 msec and a total duration of 1500 msec. Habituation period—15 sec. Mean illuminance —50 td. Observer—D.R.W.

In Fig. 3, thresholds are initially about 0.5 log units higher than their asymptotic values. An exponential recovery curve with a time constant of 8 sec fits the data well. Further experiments showed that roughly 15 sec viewing of the habituation field was sufficient to produce maximal changes in threshold. Experiments in which both the habituating stimulus and test pulses were either changes in luminance or changes in our provisional yellowish-bluish direction produced similar recovery curves. Similar data were obtained with a second observer.

Effect of modulation depth of habituation stimulus

These results suggested the use of the following "top-up" procedure that was used in the remaining experiments. After an initial 30 sec exposure to the observer's white field, thresholds in several directions in color space were measured using randomly interleaved staircases. The habituation field was then viewed for 30 sec. A second set of threshold measurements were made using the interleaved staircase procedure but with a 5 sec reexposure of the habituation field preceding each test presentation. An interval, typically 0.5 sec, elapsed between the end of the habituation stimulus and the beginning of test pulse during which the field was white. At the end of the test pulse, the field remained white until the observer responded, at which time the habituation stimulus resumed.

For reddish and greenish test pulses and reddish-greenish habituation stimuli, Fig. 4 plots the ratio of the thresholds following exposure to the habituating stimuli relative to control thresholds obtained without habituation, as a function of the amplitude of modulation of the habituating stimulus.

Selectivity of habituation for chromatic stimuli

Are the threshold-elevating effects of viewing a light varying sinusoidally along one axis in color space confined to test stimuli in the same direction as the habituating stimulus or do they generalize to other test directions as well? Thresholds were measured in four directions (D.R.W.) or eight directions (J.K.) in each experimental session before and after viewing a field varying along one of our two provisional chromatic axes. Thresholds were measured in 16 direc-
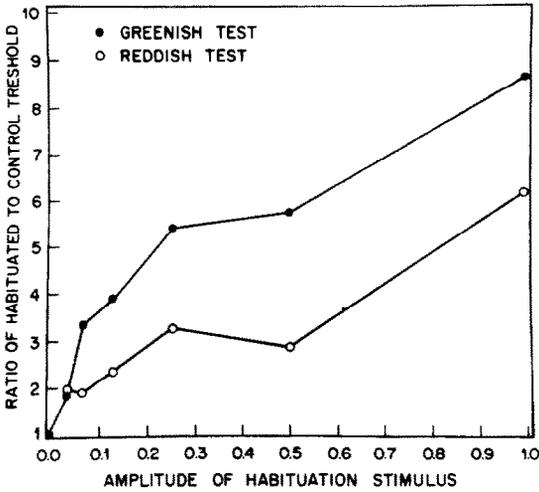
Fig. 4. Effect of amplitude of reddish-greenish sinusoidal habituation on the ratio of the habituated to the control thresholds for detecting reddish (R) and greenish (G) pulses, using the top-up procedure described in the text. Observer: J.K. Mean illuminance: 50 td.

tions altogether for D.R.W. and in eight for J.K. Figure 1 plots the white point for J.K. on the CIE chromaticity diagram, showing the eight test directions from white used. The solid lines labeled P_1 and P_2 represent the habituation axes used for this observer. The stimuli used for the second observer (D.R.W.) were similar though the mixture of primaries he chose as a neutral white was somewhat different than that chosen by J.K. Therefore, there is a slight difference between the loci of P_1 and P_2 and the white points for the two observers.

The directions chosen for test and habituation stimuli were equally spaced around the color circle in the following sense. Thresholds measured in each of the provisional primary directions were used to define unit vectors in these directions. Intermediate vectors were defined in terms of these vectors. For example, we denote the "reddish" direction as $0°$ and the "yellowish" direction as $90°$. A unit vector in the "yellowish-red" direction at $22\frac{1}{2}°$ is defined in terms of the instrument provisional axes as the sum of $\sin(22\frac{1}{2})$ times the variation of the laser primaries at threshold in the yellowish direction and $\cos(22\frac{1}{2}°)$ times their threshold variation in the reddish direction.

The thresholds before habituation were about 1/100 of the full variation possible in the reddish and greenish directions but only 1/15 of the full variation in the yellowish and bluish directions. We wished to use habituation stimuli that were roughly equal multiples of thresholds in all cases. Therefore, the amplitudes of all the habituation stimuli were set at roughly 15 times threshold.

The upper parts of Figs 5 and 6 plot in polar form (for J.K. and D.R.W., respectively) the changes in thresholds caused by habituation. The major axes of the plots are the provisional axes. The bold lines with arrow heads show the direction of variation of the
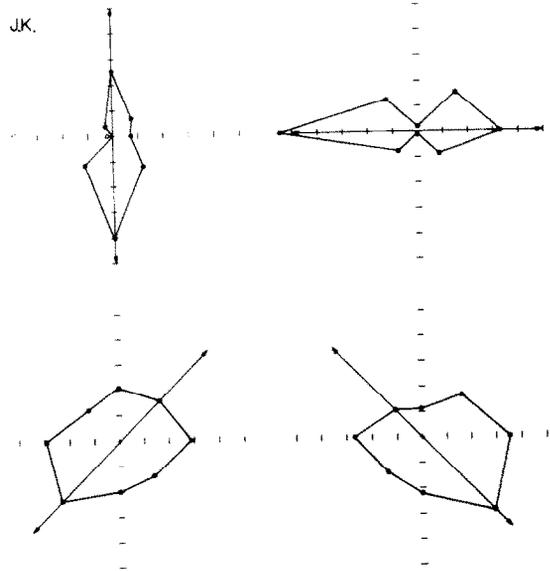

Fig. 5. (Upper) changes in thresholds resulting from viewing fields varying along the provisional cardinal axes. See text for details. Observer—J.K. (Lower) Changes in thresholds resulting from viewing fields varying along directions halfway between the provisional cardinal axes.

habituation stimuli. The center of each graph is the locus of no change in threshold. Solid symbols plot the elevation of log threshold for specific test pulse directions following habituation, unfilled symbols represent cases in which log threshold was lower following habituation. Tick marks represent increments of 0.1 log units.

The results for both observers show strong selective changes in threshold. For J.K. thresholds are raised by between 0.25 and 0.55 log units in the direction of habituation and virtually unchanged in the orthogonal directions. The thresholds for D.R.W. are
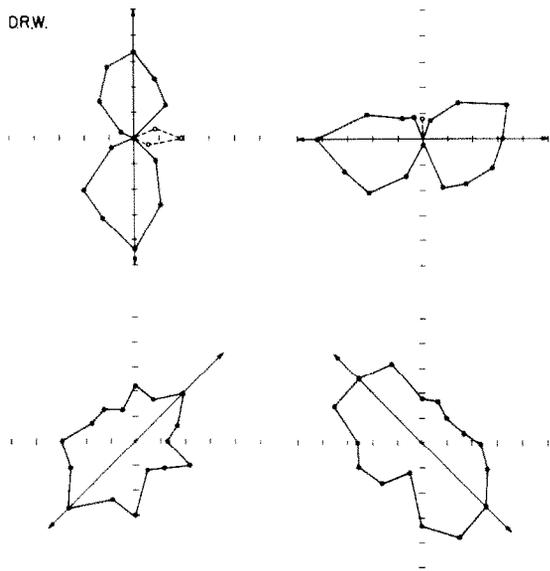

Fig. 6. Effects of chromatic habituating stimuli on detectability of chromatic test pulses for observer D.R.W.
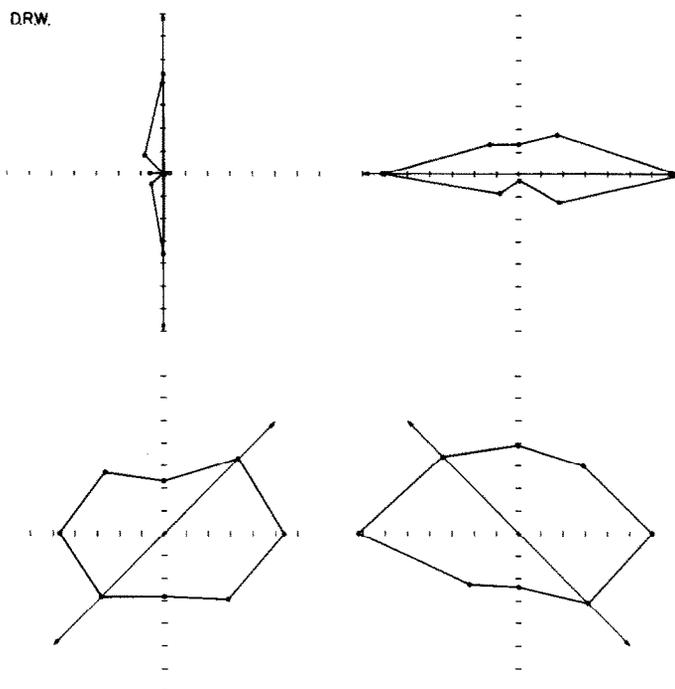
Fig. 7. Effects of purely chromatic (horizontal), purely achromatic (vertical), and mixed habituating stimuli on detectability of test pulses in these same directions for observer D.R.W.

higher by between 0.30 and 0.45 log units in the habituation direction and are essentially unchanged in the orthogonal directions. The average SEM based on variability between four sessions was 0.04 log units for D.R.W. and 0.07 log units for J.K. These results imply that signals from stimuli varying along our provisional cardinal axes are transmitted, at least in part, along separate pathways.

The question immediately arises whether these axes are unique or whether any arbitrarily chosen axis for the habituating stimulus has associated with it some "orthogonal" test direction for which thresholds are not elevated. To answer this we repeated the experiment with the habituation axes rotated by 45° in the equiluminance plane. The results (Fig. 5 lower) for J.K. show little evidence of a selective effect; thresholds are fairly uniformly elevated in all directions around the color circle. Those for D.R.W. (Fig. 6 lower) also show that thresholds are elevated in all test directions. However, there is some tendency for the threshold elevation to be selective.

Selectivity of habituation for mixtures of chromatic and luminance stimuli

The data for habituating and test stimuli confined to the equiluminance plane suggest that there are two main chromatic axes. Is it possible to distinguish a third "intensive" axis as well? To answer this question, the selective habituation procedure was repeated with test and habituation stimuli that varied in luminance as well as in chromaticity. As before, two pro-

visional axes were chosen, the reddish-greenish axis used in the previous experiment, and the luminance axis defined above. Habituation stimuli varying in four directions were used, two of which represented our provisional axes, and two of which were oriented 45° with respect to the provisional axes. In each case, the habituation stimuli were the maximum amplitude that could be produced within the limits imposed by the primary sources. The temporal frequency used was 4 Hz. Eight test directions from the mean neutral white were used; the standard deviation of the gaussian test pulse in each direction was 50 msec.

The results for one observer (D.R.W.) for the reddish-greenish axis are shown in Fig. 7. Habituation to a stimulus varying only in luminance (vertical) and not in chromaticity (horizontal) elevates thresholds for detecting incremental and decremental test pulses but has little or no effect on the detectability of reddish or greenish equiluminous pulses. Conversely, habituation to reddish-greenish chromatic modulation elevates thresholds for detecting reddish and greenish test pulses but has little or no effect on the detectability of luminance increments and decrements. On the other hand, habituation stimuli that vary both in chromaticity and in luminance elevate thresholds in all directions as shown in the lower half of Fig. 7. There is little evidence for any selective threshold elevation in this case, though thresholds for chromatic test pulses are uniformly elevated more than those for luminance test pulses. The essential features of these results were replicated on a second observer. Experiments that used a mixture of our yellowish-bluish

chromatic axis and our luminance axis also revealed selective habituation effects.

Locus of habituation

We conducted these experiments with the time averaged intensity of each of the laser primaries, and therefore the time averaged quantum catch of each cone type, held constant to prevent changes in the state of adaptation of the eye that depend on the d.c. component of the field. The a.c. component of the habituating field could reduce sensitivity at any adaptable site, either prior to or beyond the point where signals from more than one cone type combine. The experiment just described, however, shows that the habituation effects measured here must occur at sites receiving input from more than one cone type. The variation of energy impinging on a separate classes of cone receptors was never greater when the habituating field was varied chromatically than when it was varied in luminance at 100% modulation. This was so for two reasons. One was an instrumental one. The observers required more trolands from the green primary than from the red to produce a neutral white and thus the amplitude of variation in the reddish-greenish direction was limited by the number of trolands in the red primary. The amplitude in the yellowish-bluish direction was even more severely limited since the number of trolands contributed by the blue primary to the white match was much smaller than that contributed by either the red or green primaries. The second reason was that each of the primaries has some effect on at least two of the three classes of cone; therefore even if the amplitude of variation of the primary lights were as great in the chromatic case as in the luminance case, the amplitude of variation of the cone signals would be smaller.

If the observed sensitivity losses occurred at sites prior to the point where signals from different cone types combine, with the proviso that these losses increase monotonically with increasing modulation (see Fig. 4), there should be greater changes in thresholds following viewing 100% luminance modulated fields than fields varying chromatically. Since viewing luminance modulated fields produces negligible effects on the detectability of chromatic tests, we conclude that the desensitizing effects occur in parts of the visual system at or beyond the point where signals from different classes of cones combine. This conclusion was reinforced by the finding in informal experiments that the desensitizing effect of chromatically varying fields transferred from one eye to the other.

Selective habituation with sawtooth waveforms

Our experiments support the theory that there are three sets of pathways that respond selectively to variation in the reddish-greenish direction, a yellowish-bluish direction, and a luminance direction. We now turn to the question of whether different pathways are used in the detection of reddish changes vs greenish changes and yellowish changes vs bluish changes.
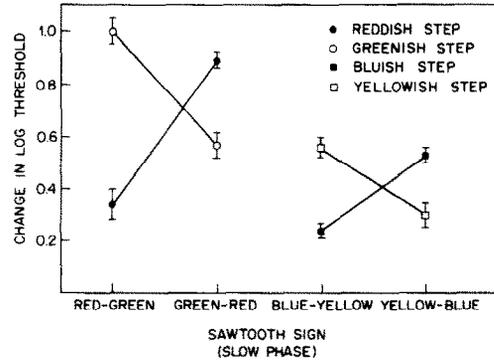

Fig. 8. Changes in thresholds resulting from viewing fields varying in color in a sawtooth fashion as a function of time. Test stimuli step changes in chromaticity. Observer— D.R.W. Mean illuminance = 500 td.

The method was adopted from previous work that supported the hypothesis that increments and decrements in luminance are, at least in part, transmitted over separate pathways (Krauskopf, 1980). We studied the effects on detection of chromatic changes of fields varying in chromaticity in a sawtoothed fashion as a function of time. In these experiments the tests were step changes in chromaticity. The color of the field changed abruptly and remained changed until the observer responded. The top-up procedure described above was employed. The results are presented in Fig. 8. Thresholds were raised more for reddish tests than greenish tests when the slow phase of the sawtooth was a change from greenish to reddish and vice versa. A similar pattern obtained in the yellowish-bluish case. We conclude that the pathways used for detecting changes in the two directions from white along each chromatic axis are in part separate. It is interesting that the direction of the asymmetry of the effect of sawtoothed variation is opposite in the chromatic case to that found from previous work in the luminance case, where, thresholds were raised more for steps in the direction corresponding to the fast phase of the sawtoothed wave. We have no explanation for this difference. However, the logic of the experiment still holds: the ability to elevate threshold selectively in one direction relative to another must imply that stimuli in these directions are processed in part, at least, by different mechanisms.

CARDINAL DIRECTIONS AND UNIQUE HUES

Our results agree with opponent mechanism theories in finding evidence for three major mutually orthogonal sets of pathways. In one important way, however, our results contradict previous theories that identify the cardinal axes of color space on the basis of color appearance. Our yellowish-bluish cardinal axis does not correspond to a red-green equilibrium line but rather corresponds more closely to a tritanopic confusion line.
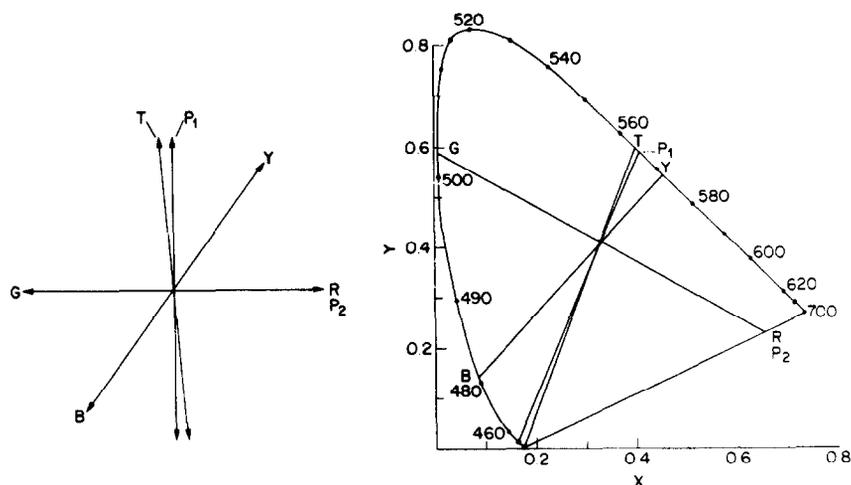
Fig. 9. Color space in terms of our provisional axes (P_1 and P_2) and CIE chromaticity diagram showing unique red-green axis (R-G, coincident within experimental error with cardial axis, P_1), trianopic axis (T), and unique yellow-blue axis (Y-B) for observer J.K.

The following experiments speak to this point. The apparatus was programmed so that the field varied sinusoidally at 1 Hz. The luminance was held constant and the observer used a knob to control the direction of variation within the plane of the color circle. Observers found it easy to select an axis in which the field varied from red to green while minimizing bluish or yellowish variations, and another axis in which the field varied from yellow to blue without appearing reddish or greenish. After making each selection the axes were recorded in terms of the relative contribution of our provisional axes. Our unique red-green axis (yellow-blue equilibrium axis) determined in this way agrees well with our provisional reddish-greenish axis but our unique yellow-blue axis (red-green equilibrium axis) is substantially different from our provisional yellowish-bluish axis; the latter varies from a reddish-blue to a greenish-yellow. These axes are shown in Fig. 9 for observer J.K. plotted both on the color circle defined by our provisional axes and in the CIE chromaticity diagram. Similar results were obtained for observer D.R.W.

In a second set of measurements, we used Brindley's technique (1953) for inducing "artificial tritanopia" to identify the tritanopic confusion line running through the white point. The same computer program was used. Between settings the observer viewed an intense 449 nm field intended to desensitize his short wavelength cones. He then adjusted the chromatic axis of a field varying sinusoidally at 1 Hz in the equiluminance plane until the flicker was minimized. Our yellowish-bluish cardinal direction corresponds closely to the tritanopic confusion line determined by this method and not to a classical red-green equilibrium line (see Fig. 9).

To be certain that the cardinal axis defined by the habituation procedure corresponds more closely to a tritanopic axis than a red-green equilibrium axis, we

wished to improve the precision with which we could specify the cardinal axes by the selective habituation procedure.

Figures 10 and 11 present results of experiments in which the test and habituations stimuli were in the near vicinity of the provisional cardinal directions. The changes in thresholds are plotted against the direction of the habituation stimulus. Ten of the 12 curves show the least desensitization for the middle habituating stimulus. In the case of reddish-greenish habituation stimuli, the middle value was the provisional cardinal direction. The middle value in the yellowish-bluish habituation stimuli was the tritanopic confusion line for this observer that is very little removed from our provisional yellowish-bluish axis. His red-green equilibrium axis is more than 40° from the minimum identified with the tritanopic axis shown in Fig. 10. This was confirmed with observer D.R.W. who invariably showed larger threshold elevation for detection of reddish or greenish pulses following red-green equilibrium habituation than tritanopic habituation. Our provisional reddish-greenish axis corresponds well with both observers' choices of a yellow-blue equilibrium axis.

DISCUSSION

The results presented here demonstrate that there are three main cardinal axes in color space revealed by habituation to temporally varying lights. Thus, these experiments generally support opponent color theory (Hurvich and Jameson, 1957). However, the present results conflict with Hurvich and Jameson's analysis in an important respect, namely by identifying one of the cardinal chromatic axes with a tritanopic confusion line and not with a unique yellow-blue (red-green equilibrium) line.

Evidence as summarized by Ingling (1977) suggests that the short-wavelength sensitive cones contribute
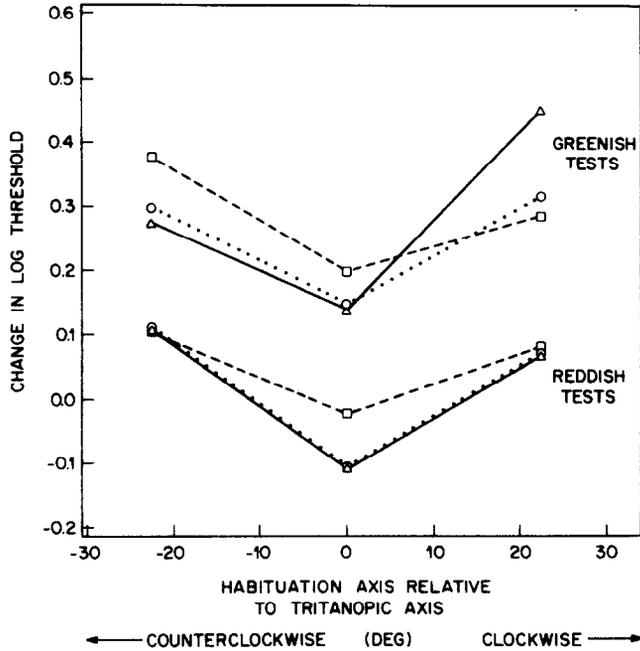
Fig. 10. Effects of three habituation stimuli in the vicinity of tritanopic axis through white on detection of test pulses in the vicinity of the red and green directions. A value of zero on the abscissa corresponds to the tritan line; positive values on the abscissa correspond to clockwise rotation of the adaptation vector in the space defined by our provisional axes. Test stimuli as follows: □—bluish-red or yellowish-green; O—red or green; △—yellowish-red or bluish-green. Results for greenish tests displaced upward by 0.2 log units. Habituation frequency = 1 Hz, gaussian test pulse, standard deviation = 250 msec, total duration = 1500 msec. Mean illuminance = 50 td. Observer—J.K.

to redness, and consequently require inclusion in a "red-green opponent channel" defined by the criteria of the cancellation technique and color appearance. However, the red-green channel defined by our ha-

bituation procedure requires no input from the short wavelength cones. Rather, the cardinal habituation direction that fails to elevate threshold for red and green pulses is a direction in which only the short
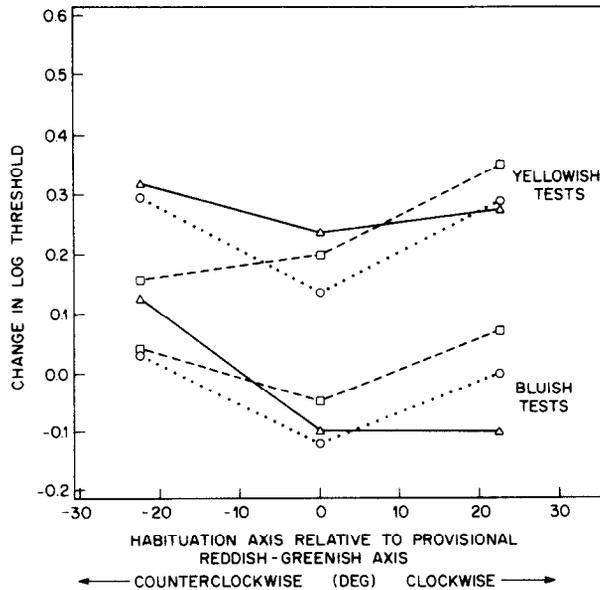

Fig. 11. Effects of habituation stimuli in the vicinity of the reddish-greenish provisional axis on detection of test pulses in the vicinity of the tritan directions from white. Conditions are the same as in Fig. 10 with test and adaptation stimuli interchanged. Test stimuli as follows: O—tritanopic stimuli; □—stimuli rotated 22.5° counterclockwise relative to the tritan line; △—stimuli rotated 22.5° clockwise relative to the tritan line. Results for yellowish tests displaced upward by 0.2 log units.

wavelength cones are modulated, with the ratio of long and middle wavelength cone excitation held constant. The field appears to vary in redness and greenness when modulated along this tritanopic confusion line. Yet such a habituation stimulus fails to reduce the detectability of red and green test pulses. Chromatic flicker modulated along a red-green equilibrium line (the locus of points in color space that appear neither reddish nor greenish), on the other hand, does reduce the detectability of red and green test pulses. Once the relation between second stage opponent mechanisms and locus of unique hues is abandoned, there is no basis for expecting that there are only two second stage chromatic mechanisms. That habituation has little or no desensitizing effect only when the habituation stimulus is along one of our two cardinal axes and the test along the other, however, does support the idea that there are only two major chromatic mechanisms.

However, our data do reveal some second-order deviations from the predictions of a simple two mechanism theory. First, the results of one of the observers (D.R.W.) suggest a residual selective habituation effect of stimuli at 45° with respect to the cardinal axes. There may be two populations of mechanisms with their maximum sensitivities distributed about the cardinal axes. Stimuli along the cardinal axes would be much more effective with respect to one distribution than the other, but stimuli at other directions would preferentially affect subsets of each population, resulting in a residual selectivity. Another possible explanation is that there is yet another set of adaptable mechanisms at a third level in the visual system, tuned to many directions around the color circle, that derive their inputs from the second stage mechanisms. A particular mechanism on this level might respond best when the second stage mechanisms are activated in the correct proportion. This possibility raises the intersting question, at what level are color changes detected?

A second deviation from the predictions of a simple theory invoking only two chromatic mechanisms is the suggestion of an increase in sensitivity to red test pulses following exposure to a habituating stimulus that predominantly modulates the short wavelength sensitive cones, an effect found for only one observer (D.R.W.). We prefer not to speculate about this since the result is ephemeral and may have a methodological explanation.

Our result that there exist three main axes in color space contrasts with recent physiological evidence (De Monasterio and Gouras, 1975) that there are at least 12 kinds of color opponent ganglion cells in the rhesus monkey. Our results imply six mechanisms if a separate mechanism is involved in detection in opposite directions along each cardinal axis.

Habituation is found even when the amplitude of the habituating stimulus is near threshold (see Fig. 4) and with relatively brief exposure times, which suggests that these effects could be important for vision under ordinary circumstances. We are not prepared to speculate about what role they might play.

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