

# Color Discrimination and Adaptation

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We have measured color discrimination in the isoluminant plane under rigorously controlled adaptation conditions. Two regimes were studied. Under the first regime the observer was adapted to the region of color space in which the discriminations were made. Thresholds for detecting changes along the  $S - (L + M)$  axis are a linearly increasing function of the excitation of the S cones. Thresholds for detecting changes along the  $L - M$  axis are independent of the locus of adaptation along this axis. The straightness of these functions is inconsistent with the theory that second stage mechanisms are more sensitive in the middle of their operating ranges. No convincing evidence of interactions in the effects of adaptation locus or test stimuli was observed. Under the second regime the observer was adapted to one point in color space and the stimuli to be discriminated were located in other places in color space. Discrimination seems to be limited primarily by mechanisms maximally sensitive to modulation along the isoluminant cardinal axes but evidence suggestive of the operation of higher order mechanisms was also found.

Color discrimination   Adaptation   Chromatic mechanisms

## INTRODUCTION

A central problem in color vision is how color discrimination varies over color space. This problem has been attacked theoretically and experimentally by Helmholtz (1891), Schrödinger (1921), Stiles (1946) and Wright (1941) among others. One of the most elegant experiments on the problem was that of MacAdam (1942).

MacAdam designed a special color mixer which produced a bipartite disc consisting of a fixed half-field and a variable half-field. Both halves were mixtures of lights derived from the same source and passed through the same two color-selective filters. The experimenter determined the relative amount of the two lights in the fixed half and the observer repeatedly adjusted the relative amount of the lights in the variable half. A large number of color filter sets were selected and trimmed by additional neutral filters so as to produce equally luminous primaries at many different points in the C.I.E. diagram. By using a number of carefully chosen sets of these filters, fixed lights at the various points in the diagram could be obtained with several pairs of filters, thus allowing one-half of the field to be adjustable along several different lines through those points.

The basic data were the standard deviations of the matches made along the different lines. These were used to construct equal discriminability ellipses about a number of points in the C.I.E. diagram. The projection of the MacAdam ellipses on the chromaticity diagram proposed by MacLeod and Boynton (1979) is presented in

Fig. 1. The variation of the orientation and the lengths of the major and minor axes of these MacAdam ellipses over the diagram is complex and is not compatible with any simple theory of color discrimination. A further problem is that different patterns of ellipses and large variability of the ellipses have been reported when repeated measurements were made for the same observer (Wyszecki & Fielder, 1971).

The differences may be due to the way adaptation was controlled in the experiments. MacAdam (1942) presented his 2-deg diameter bipartite field in the center of a 42-deg uniform surround having a chromaticity that approximated C.I.E. illuminant C and that was about half the luminance of the matching stimuli. Since the observer was concentrating on the matching stimuli, his central retina was presumably adapted to the matching stimuli with some marginal contribution of the surround. In other experiments (Wyszecki & Fielder, 1971) the observers were encouraged to move their gaze over the field including the neutral surround so as to control adaptation.

The powerful effect the state of adaptation has on discrimination was shown by Craik (1938). In his experiments the target, modulated in luminance at 2 Hz around a test luminance level, briefly replaced a steady field whose luminance determined the adaptation level. The threshold amplitude of the modulation was typically a minimum when the adaptation and test luminances were equal and increased markedly when the test luminance was either greater or less than the adaptation luminance. It has been suggested that similar effects of adaptation occur with chromatic stimuli (Brown, 1952; Pointer, 1974; Loomis & Berger, 1979).

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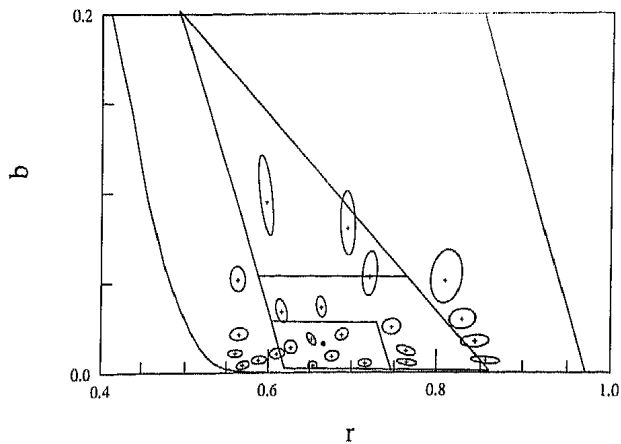


FIGURE 1. MacAdam (1942) ellipses projected on the MacLeod-Boynton (1979) chromaticity diagram. The primaries of the television monitor used in the present work plot at the corners of the triangle which defines the chromaticities obtainable isoluminantly if the luminance is not greater than that of the least luminant (blue) primary. The area enclosed by the larger quadrilateral defines the chromaticities obtainable when the luminance was equal to that of the red primary. The area enclosed by the smaller quadrilateral defines the chromaticities obtainable when the luminance was 50% of the maximum possible.

These facts led us to believe that more orderly results, possibly indicative of the operation of simple processes underlying discrimination, might be obtained if adaptation were precisely controlled. In measuring the variation of color discrimination over color space we can define two useful conditions with respect to adaptation. In one condition, the observer is adapted throughout the experiment to the same point in color space at which the discriminations are made. In the second condition, the observer is adapted to a fixed stimulus throughout the experiment. The stimuli to be discriminated vary widely in chromaticity and are briefly presented. Both conditions are of both theoretical and practical interest. It will be seen that results under each of these special conditions are orderly and suggest the operation of simple mechanisms.

## METHODS

### Equipment

The stimuli were displayed on a Tektronix 690SR color television monitor driven by an Adage 3000 frame buffer controller which generates images on the monitor by reading through the picture memory in a raster scan and interpreting the numbers in each location as a color defined in a 256-element color lookup table. The intensity of each of the three primaries was controlled by a 10-bit digital-to-analog converter. The display was generated at 120 Hz interlaced. Most of the stimuli in the present experiments had a luminance of  $37 \text{ cd/m}^2$ , the exception being in the last experiment in which the luminance was half that value.

### Subjects

Data from four subjects were collected. One author (KG) ran all of the conditions. Three other subjects ran some of the experiments. The data for all the subjects

agree with each other, and in the following data for KG are presented.

### Description of stimuli

We use the color space introduced by Krauskopf, Williams and Heeley (1982) to describe our stimuli (Fig. 2). At the origin is an equal-energy white. There are two chromatic axes,  $L-M$  and  $S-(L+M)$ , which lie within the isoluminant plane and run through the origin. The isoluminant plane of this space is essentially the same as the chromaticity diagram proposed by MacLeod and Boynton (1979), the  $L-M$  axis corresponding to their  $r$  coordinate and the  $S-(L+M)$  axis to their  $b$  coordinate. The spectral sensitivities of the long ( $L$ -), middle ( $M$ -) and short ( $S$ -) wavelength sensitive cones on which this space is based are those derived by Smith and Pokorny (1975). The origin is the equal-energy point (in MacLeod-Boynton coordinates,  $r = 0.667$ ,  $b = 0.016$ ). The range of stimuli that could be produced at the luminance we used ( $37 \text{ cd/m}^2$ ) fell within the parallelogram depicted in Fig. 1.

Our nomenclature, differing from that which has been used previously (MacLeod & Boynton, 1979; Krauskopf *et al.*, 1982; Derrington, Krauskopf & Lennie, 1984), directly expresses the theory implied by the use of the space, namely that independent mechanisms exist somewhere in the visual system whose responses are determined in one case by the difference in the signals generated by the long-wavelength sensitive ( $L$ ) and middle-wavelength sensitive ( $M$ ) cones, in a second case, by the difference between the signals generated by the short-wavelength sensitive ( $S$ ) cones on the one hand and the sum of the  $L$  and  $M$  cones on the other hand, and

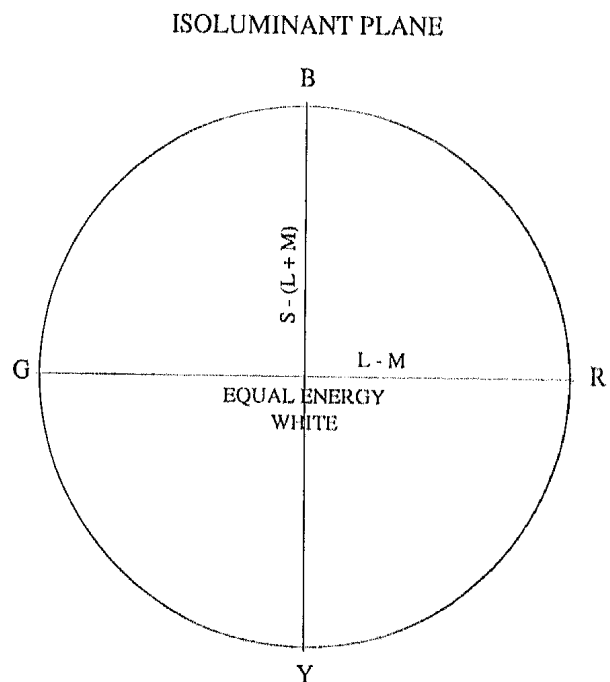


FIGURE 2. Chromaticity diagram used to describe the stimuli. At its origin is a neutral white. Two axes go through this white point. Along the  $L-M$  axis excitation of the  $L$  and  $M$  cones varies so as to leave their sum constant. Along the  $S-(L+M)$  axis only the excitation of the  $S$  cones changes.

in a third the responses are determined by the sum of the signals generated by the L and M cones.

Movement along the L - M axis is achieved by co-varying the excitations of the L and M cones so as to keep luminance and the excitation of the S cones constant. Along the S - (L + M) axis only the S cone excitation varies and the excitation of the L and M cones is constant. This is the only condition under which both luminance and the signal to the L - M mechanism are constant. In another departure from previous usage (Krauskopf *et al.*, 1982; Derrington *et al.*, 1984) we plot increasing excitation of the S cones upward along the S - (L + M) axis in order to agree with MacLeod and Boynton (1979). Along the luminance axis the excitations of all three classes of cones vary in proportion to their values at the white point. Stimuli along this axis provide varying input only to the mechanism which sums the L- and M-cone excitations and a constant input to the two chromatic mechanisms.

It should be noted that the endpoints of the cardinal axes do not correspond to "Unique Hues", as measured by cancellation techniques (Hurvich & Jameson, 1955). While variation along the L - M axis through the white point produces stimuli that appear reddish or greenish, variation along the S - (L + M) axis produces stimuli that appear yellowish-green and purple, not unique yellow and unique blue. Nevertheless, in order to avoid circumlocution, we will occasionally use words like "red" and "green" to refer to stimuli along the L - M axis and "blue" and "yellow" to refer to stimuli along the S - (L + M) axis.

*Procedure*

The observer fixated the center of the television screen which was about 10 deg square. For most of the time the screen was uniformly illuminated with the current adap-

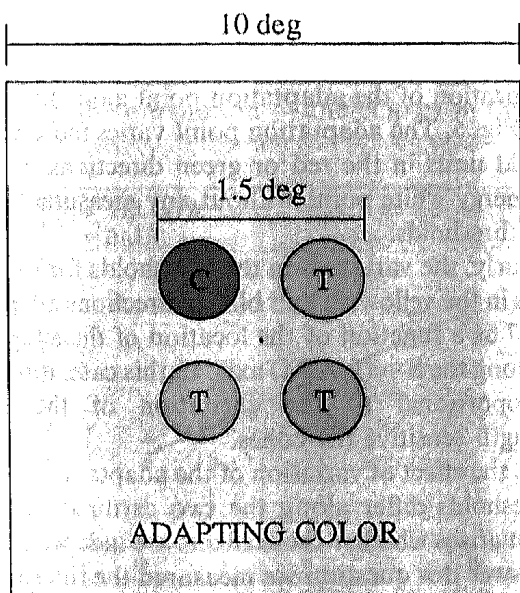


FIGURE 3. Spatial arrangement of the stimuli. The screen was uniformly illuminated by the adapting light. On each trial four disks appeared. Three of them (T) had the same chromaticity, the other one (C) differed slightly. The observers task was to report which one of the disks was different.

ISOLUMINANT PLANE

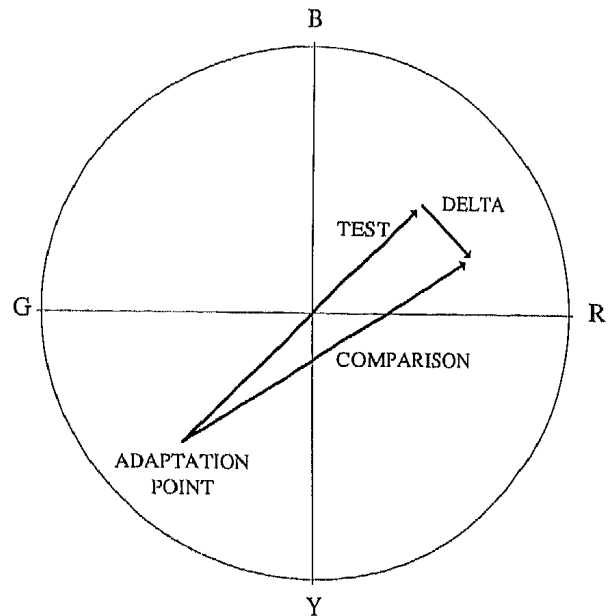


FIGURE 4. Illustration of test and comparison vectors. The adaptation color is set to a fixed point in color space. The test vector is an excursion from that point and defines the color of the three test lights. The comparison vector is the sum of the test vector and a small excursion delta.

tation color. On an experimental trial four discs 36 min in diameter were presented as a Gaussian pulse of  $\pm 3 \sigma$  of 1 sec total duration. The centers of the discs were located at the corners of a 54 min square centered on the fixation point (Fig. 3). Three of the discs were of the same color (test color). The fourth disc (comparison color), randomly located at one of the corners on any trial, differed slightly in color from the test discs. The observer's task was to report which of the discs was different from the others by pressing one of four buttons. A staircase procedure was used to find those comparison stimuli which were just discriminable from the test stimuli. After three consecutive correct responses the difference between the test and comparison stimuli was decreased; after an incorrect response it was increased. The mean of the reversal points of the staircases was used as a threshold estimate.

A graphical representation of the stimuli used in the experiments is given in Fig. 4. The axes of the graph are the L - M and S - (L + M) axes with an equal-energy white as the origin. The *test* vector represents the maximum excursion of the test stimulus, the *comparison* vector represents the maximum excursion of the comparison stimuli. The *delta* vector is the difference between the test and comparison vectors. In any threshold measurement, the amplitude of this vector was adjusted according to the staircase procedure, but its direction was held constant and, therefore, both the direction and the amplitude of the comparison vector might change.

*Description of discrimination contours*

We approximate the discrimination contours with ellipses centered around the test color. In the following we will denote the test color by  $x_T$  with coordinates

$[T_{L-M}, T_{S-(L+M)}]$ , the comparison color by  $x_C = [C_{L-M}, C_{S-(L+M)}]$ , and the adapting color by  $x_A = [A_{L-M}, A_{S-(L+M)}]$ . For a given comparison color  $x_C$  the distance from  $x_T$  is then given as

$$d^2(x_T, x_C) = (x_C - x_T)^T G (x_C - x_T), \quad (1)$$

where the  $2 \times 2$  matrix  $G$  is chosen so that the right hand side of equation (1) never becomes negative, is 0 if and only if  $x_T = x_C$ , and gives identical distances for  $d(x_T, x_C)$  and  $d(x_C, x_T)$ . A matrix that fulfills these three conditions is called positive definite symmetric. Our goal is to find a matrix  $G$ , so that all colors at threshold are an equal distance from the test color. If  $t_\delta$  is the measured threshold along a given direction  $\delta$ , we define  $x_\delta = x_T + T_\delta \times \delta$ . To find the best fitting ellipse we then minimize

$$[(x_\delta - x_T)^T G (x_\delta - x_T) - 1]^2 \quad (2)$$

summed over all directions  $\delta$  in which we measure thresholds.

The matrix  $G$  completely defines an ellipse. There are other ways ellipses can be parameterized, and some of these parameters will be used in later descriptions. We will call the longest extent of an ellipse its major axis and denote it by  $a$ . The minor axis will be denoted by  $b$ . It is in the direction orthogonal to the major axis. The orientation of the major axis will be called  $\theta$ . In addition it is of special importance to us to know the semilength along the axes of our coordinate systems, we will call them  $\sigma_{L-M}$  and  $\sigma_{S-(L+M)}$ .

Fitting the data with ellipses is not guided by a particular theory, but was done because most theories predict results that can be approximated by ellipses.

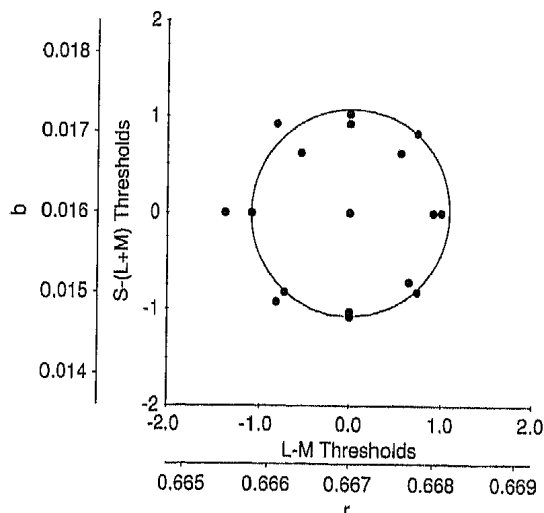


FIGURE 5. Thresholds for detecting changes in different directions from an equal-energy white point. The  $L-M$  threshold unit was set at the average of thresholds for changes from the white point in both directions along the  $L-M$  axis and the  $S-(L+M)$  threshold unit by averaging the thresholds for changes from the white point in both directions along the  $S-(L+M)$  axis. The outer scales give the MacLeod-Boynton values for the stimuli. Note that the scale size for these units is slightly different on the two axes. The total range of stimuli available was about 45 and 12 threshold units in either direction from the equal-energy white point along the  $L-M$  and  $S-(L+M)$  axes respectively.

### Scaling of axes

There are no agreed-upon units for representing the magnitude of stimuli along the  $L-M$  and  $S-(L+M)$  axes. We decided to use as units the thresholds for detecting changes from equal-energy white along each cardinal direction. The results of these measurements for one observer are shown in Fig. 5. In all subsequent plots these threshold units will be used.

The  $b$ -axis of the MacLeod and Boynton (1979) chromaticity diagram was scaled in an arbitrary fashion, the scaling chosen so that the entire spectrum locus just fit inside a square diagram. Therefore it is interesting to note that, expressing the thresholds along these axes in their units,  $\Delta r = 0.0011$  and  $\Delta b = 0.0012$  and furthermore the MacAdam ellipses are approximately circular near the white point in Fig. 1. This is a coincidence. For example, our Fig. 1 is not scaled equally along the two axes. Furthermore, it is likely that the ratio of the thresholds along these two axes would depend on stimulus parameters such as retinal location. There is a small asymmetry in the data. Thresholds for detecting red pulses are smaller than for green pulses. We have not studied this factor in detail.

## RESULTS

Two experimental regimes are of interest. In one case, the observer is always adapted to the point in color space at which the discrimination is made. In terms of the scheme in Fig. 4, this is the case in which the test amplitude is zero. The experimental task is simply to detect at which of the four locations a disc was presented on a particular trial. In the second regime the adaptation point is held constant and the direction and magnitude of the test vector are varied.

### Discrimination at the adaptation point

The variation in the thresholds for detecting changes in the red or green directions are plotted as a function of the location of the adaptation point along the  $L-M$  axis in Fig. 6. The adaptation point varies more than 30 threshold units in the red or green directions from the equal-energy white point without any measurable effect on the thresholds.

Similarly, the variation in the thresholds for detecting changes in the yellowish and bluish directions are plotted in Fig. 7 as a function of the location of the adaptation point along the  $S-(L+M)$  axis. In this case, thresholds are proportional to the excitation of the short-wavelength sensitive (S) cones.

Thus, the effect of variation of the adaptation point on the thresholds differ along the two cardinal axes. The question arises whether these effects are independent. To help answer this question we measured the thresholds in several directions about nine different adaptation points as shown in Fig. 8.

The crosses mark the location of the adaptation points. Stimuli that are just detectably different are indicated by the solid circles. For better readability the

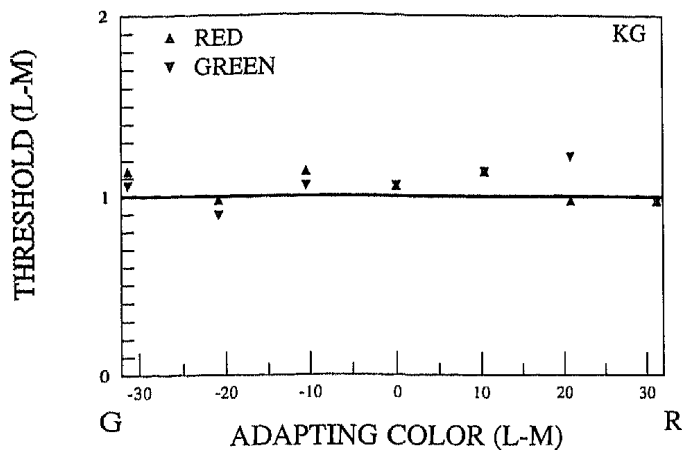


FIGURE 6. Thresholds for detecting reddish (upward pointing solid triangles) or greenish (downward pointing solid triangles) pulses on backgrounds varying along the L - M axis.

distance between the adaptation points and the threshold stimuli has been multiplied by 3.

We fit the data with ellipses having major and minor axes along either the L - M or S - (L + M) axes. We assumed that the semiaxis along the L - M axis is constant for all adaptation conditions while the semiaxis along the S - (L + M) axis varies linearly with the position of the adaptation stimulus along the S - (L + M) axis (which is equivalent to assuming that the length of the semiaxis is proportional to the excitation of the S cones).

This model with only three parameters appears to fit the data quite well. The lengths of the best fit semiaxes at the white point are 1.03 threshold units along the S - (L + M) axis and 1.24 threshold units along the L - M axis. The length of the semiaxis along the S - (L + M) axis is given by  $\sigma_{S-(L+M)} = 1.03 + 0.0357(T_{S-(L+M)} - A_{S-(L+M)})$ . The root mean-squared-error of fitting equation (2) to the ellipses was 0.14. When we removed the restrictions imposed by the above model and fitted an unconstrained ellipse to each data set (9 x 3 parameters) this error decreased only slightly to 0.12. There is no systematic variation of the orientation of the ellipses in that case.

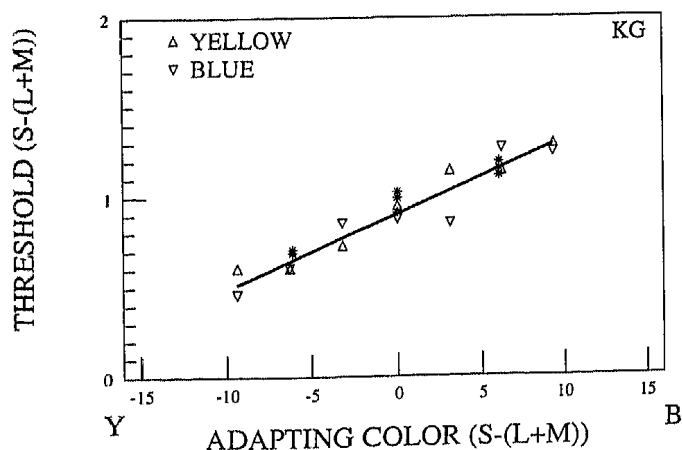


FIGURE 7. Thresholds for detecting yellowish (upward pointing open triangles) or bluish (downward pointing open triangles) pulses on backgrounds varying along the S - (L + M) axis. The stars indicate data points that had different values along the L - M axis.

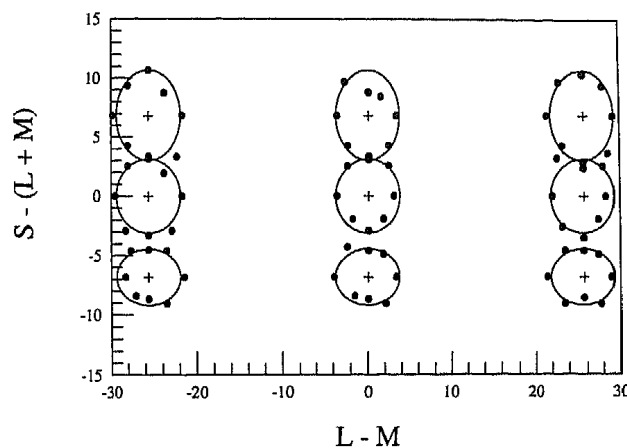


FIGURE 8. Thresholds for detecting pulses on nine different backgrounds. The ellipses are enlarged by a factor of 3.

Therefore there is no indication of interaction when the adaptation point is moved in both directions simultaneously.

*Discrimination away from the adaptation point*

The conditions used in the next set of experiments are depicted in Fig. 9. In these experiments both the test and comparison stimuli were excursions along the same cardinal axis. The observer was adapted to an equal-energy white throughout the experiment.

As shown in Fig. 10, discrimination thresholds increased linearly with the amplitude of the test vector. The results for stimuli varying along the L - M axis appear more regular but it should be noted that the scales of the two graphs are different. Test vectors of as much as 40 threshold units could be used along the L - M axis but of no more than 10 threshold units along the S - (L + M) axis.

In order to increase the size of the test vector we took measurements with the adaptation point set at about 20 threshold units from equal-energy white in the red direction along the L - M axis (Fig. 11). The results of this experiment agree with those in Fig. 6 in that the thresholds for detecting pulses along the L - M axis are independent of the absolute location of the test vector along this axis. The thresholds depend only on the difference between the test vector and the adaptation point, and are lowest at the adaptation point, just as in luminance discrimination (Craik, 1938).

Krauskopf *et al.* (1982) showed that habituation along one cardinal axis had no effect on thresholds for detecting changes along another cardinal axis. We wished to know if chromatic discrimination reveals similar independent effects. The conditions for the next set of experiments are depicted in Fig. 12. In these experiments the test vectors were also excursions along one of the cardinal axes while the difference vectors varied along the other.

The results of these experiments are given in Fig. 13. Thresholds for discrimination of excursions along one cardinal axis are independent of the magnitude of test vectors along the other cardinal axis. This is true for difference vectors along the S - (L + M) axis even when

the amplitude of the test vector is as much as 40 threshold units on the L - M axis.

This suggests that discriminations may be mediated independently within mechanisms selectively responsive along the cardinal axes. In order to examine this question further we measured discrimination thresholds in 8 directions about test vectors in 16 directions around the equal-energy white adaptation point. The results are presented in Fig. 14. We fit ellipses independently to the 16 sets of data.

We have considered two theories which might account for the data. One is that discrimination is performed by mechanisms selectively responsive along cardinal axes. The other assumes that there is a multiplicity of mechanisms tuned in different directions about the isoluminant

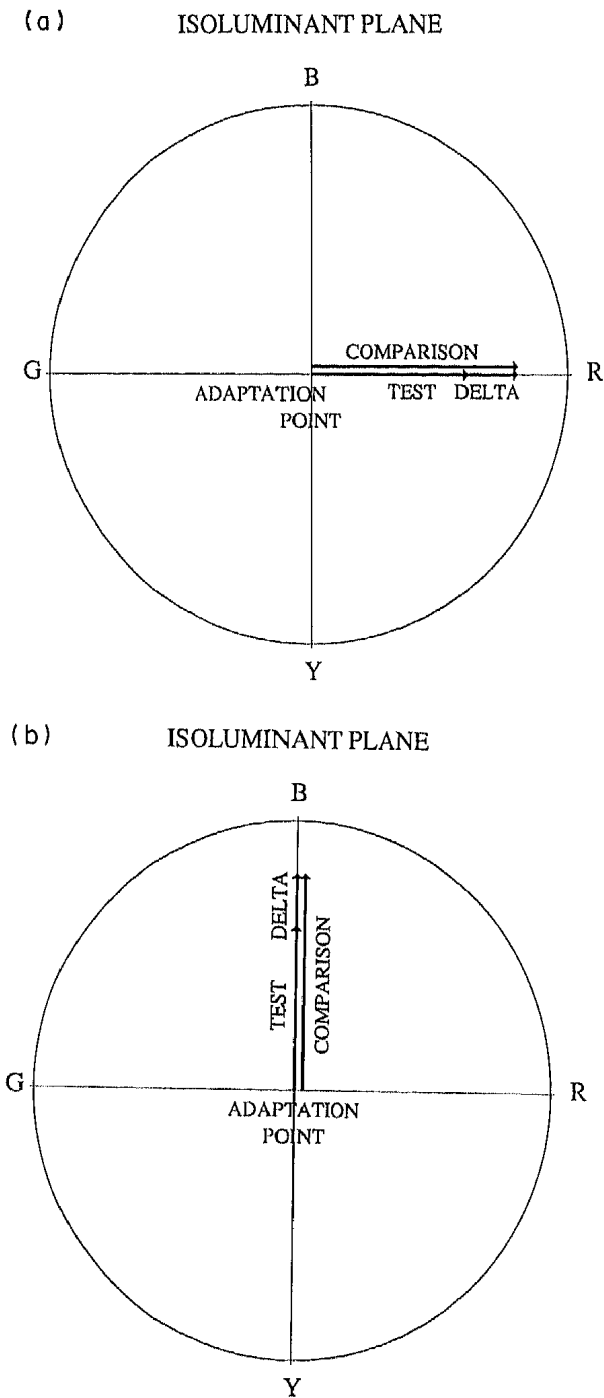


FIGURE 9. Conditions for test vector and delta vector along the same cardinal direction. (a) Both along the L - M axis. (b) Both along the S - (L + M) axis.

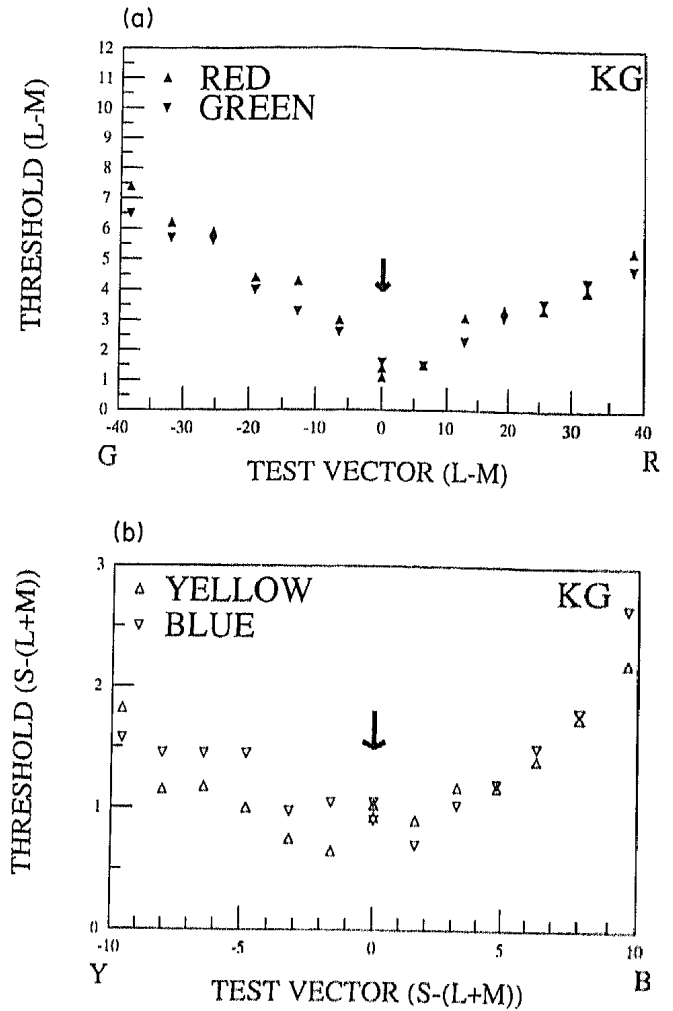


FIGURE 10. Thresholds for detecting deltas when delta and test lie on the same cardinal direction. (a) Along L - M axis. (b) Along S - (L + M) axis. The arrow indicates the adaptation point, which was white.

plane and that discrimination thresholds in any direction are elevated in proportion to the excitation, by the test stimulus, of the mechanisms relevant to discrimination.

These theories lead to different predictions about the variation of the orientation of the ellipses with the azimuth of the test vector. On the first theory it is expected that the orientation of the major axes of the ellipses will be parallel to the cardinal axis nearer the test

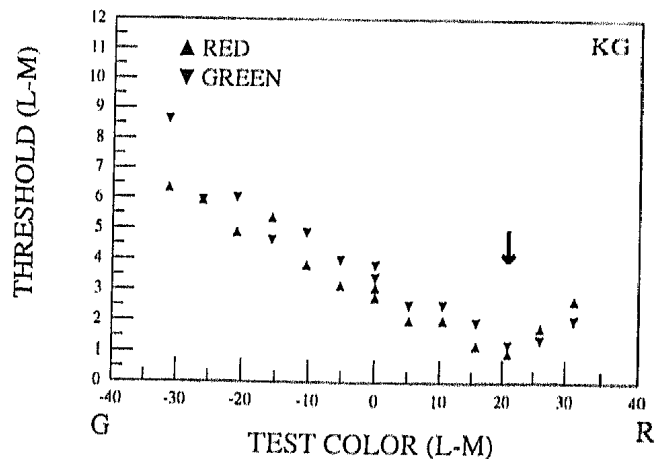


FIGURE 11. Thresholds for detecting deltas along the L - M axis, with test and delta on the same axis and adaptation to a red background (indicated by the arrow).

vector except for test vectors 45 deg removed from the cardinal axes where the ellipses will degenerate into circles. This theory also predicts that the ratio of the major to minor axes of the ellipses should be maximal for test vectors along the cardinal axes and should equal 1 for test vectors 45 deg away from the cardinal axes. On the second theory it is expected that the major axes of all the ellipses will point toward the origin. The data don't support either theory. In the first and third quadrants the ellipses tend to be parallel to the axes except for the 45 and 225 deg directions where they are approximately circular. However, the ellipses in the other two quadrants tend to point toward the origin, indicating that a multitude of mechanisms mediate the discriminations.

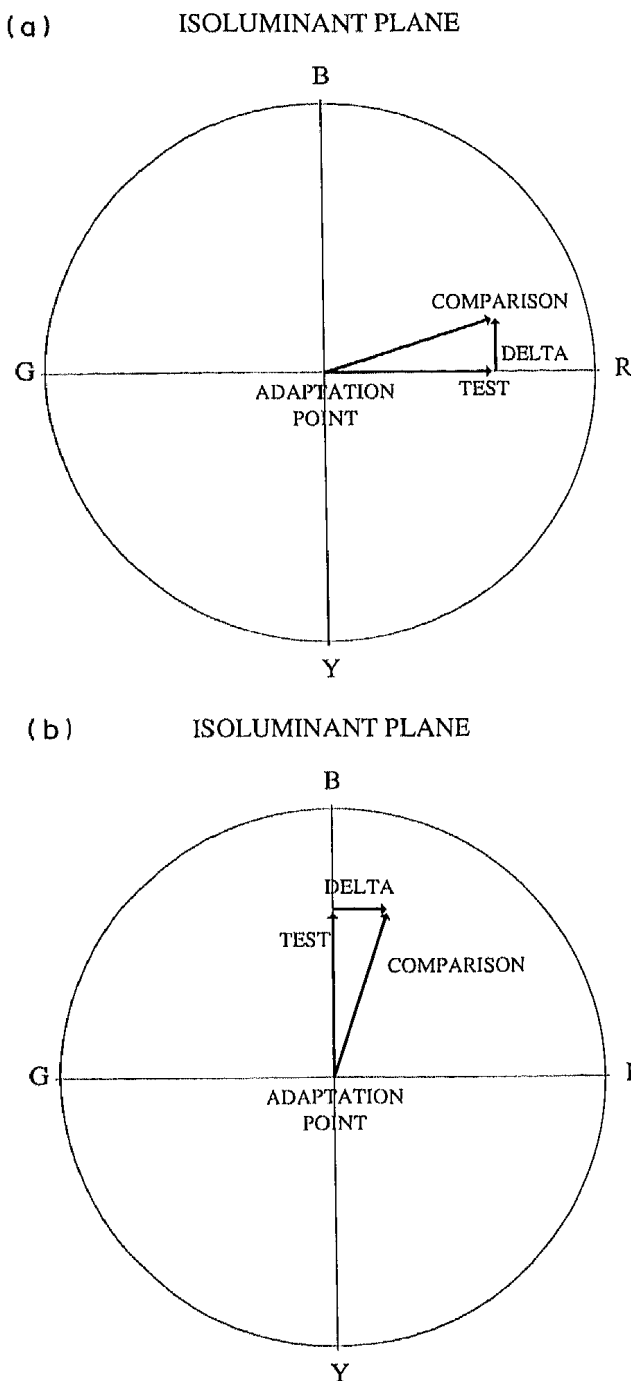


FIGURE 12. Conditions for test vector and delta vector along different cardinal directions. (a) Test on L-M and delta on S-(L+M). (b) Test on S-(L+M) and delta on L-M.

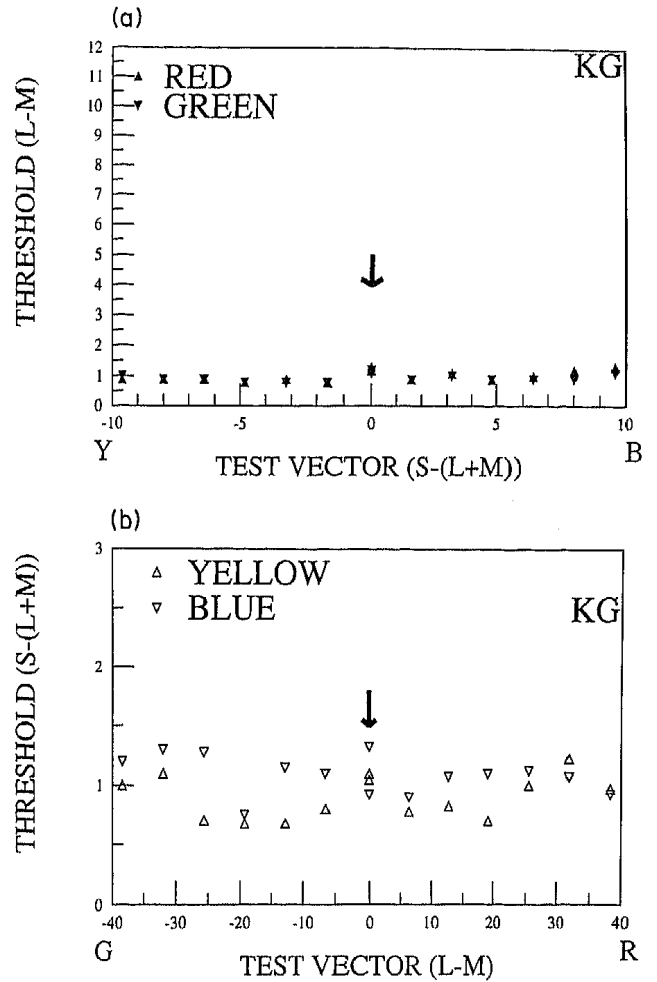


FIGURE 13. Thresholds for detecting deltas when delta and test lie on different cardinal directions. (a) Test on L-M and delta on S-(L+M). (b) Test on S-(L+M) and delta on L-M.

DISCUSSION

The adaptation state of the eye has profound effects on the size of color discrimination thresholds. When the observer is adapted in the vicinity of the lights to be discriminated the thresholds are constant for changes along the L-M axis (Fig. 6). However, when the stimuli to be discriminated are removed from the adaptation point the thresholds increase by as much as 7 times when the observer is adapted to a white background

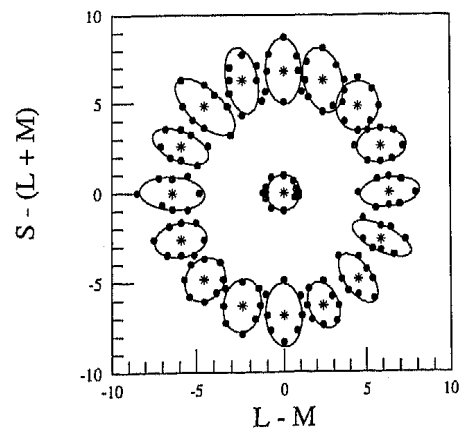


FIGURE 14. Discrimination ellipses for test vectors equally spaced in 16 directions around the white point. The adaptation point was white.

[Fig. 10(a)], and even more when the adaptation point is changed to a saturated red (Fig. 11).

We have found it useful to consider two distinct situations: (1) When thresholds for differences from the point at which the eye is adapted are measured, and (2) when the eye is adapted to a particular point in color space and the thresholds for discriminating pairs of colors at some distance from that point are measured. The results obtained under these conditions are profoundly different.

#### *Color discrimination at the adaptation point.*

Thresholds for changes in color from the adaptation point follow a very simple pattern. Thresholds in the  $S - (L + M)$  direction vary linearly with the excitation of the short-wavelength sensitive cones. These test stimuli produce a change only in the S-cone input. Thus, the detection is a pure S-cone increment (or decrement) threshold task. Thresholds are independent of the value of the  $L - M$  component of the adaptation stimulus.

*Theories of discrimination.* The MacAdam (1942) ellipses are replotted in Fig. 1 as projections on the lower right corner of the MacLeod-Boynton (MacLeod & Boynton, 1979) chromaticity diagram. This plot demonstrates that the thresholds for discriminating changes parallel to the  $b$ -axis tend to increase with increasing S-cone excitation. This feature of the MacAdam data was pointed out by LeGrand (1949) and is very well confirmed by our results in Figs 7 and 8. The data plotted in these figures show a linear dependence of the thresholds in the  $S - (L + M)$  directions as a function of the locus of the adaptation point. LeGrand suggested that discrimination thresholds tended to increase when the excitations of the red or green cones were greater than their values for white stimuli. Boynton and Kambe (1980) and Nagy, Eskew and Boynton (1987) have also concluded that this was true. Our results in Figs 6 and 8 fail to show such an effect. We think this difference is likely to be due to our more rigorous control of adaptation but further experiments are needed to test the correctness of this view.

Let us consider some theories which might account for chromatic discrimination. For example, it might be hypothesized that the signals within each class of cones are independently detected. A line-element model of color discrimination like that proposed by Helmholtz (1891) is an embodiment of such an hypothesis. In his model, the difference between test and comparison color is given by

$$d^2 = \left[ \frac{\Delta L}{L} \right]^2 + \left[ \frac{\Delta M}{M} \right]^2 + \left[ \frac{\Delta S}{S} \right]^2, \quad (3)$$

where  $L$ ,  $M$ ,  $S$  are the absolute excitations of the photoreceptors when the test color is presented, and  $\Delta L$ ,  $\Delta M$ ,  $\Delta S$  are the differences in photoreceptor excitations between test and comparison colors.

First let us consider predictions concerning the effect of the location of the adaptation stimulus on the  $S - (L + M)$  axis on detection of changes along that axis. Because  $\Delta L/L$  and  $\Delta M/M$  are constant for test and

comparison vectors along the  $S - (L + M)$  axis, equation (3) simplifies to

$$d^2 = \left[ \frac{\Delta S}{S} \right]^2, \quad d = \left[ \frac{\Delta S}{S} \right]. \quad (4)$$

We could also predict the results from the popular idea that the effect of a constant stimulus is to reduce the gain of the cone responses to changes in their inputs. In this case, the detection mechanism would compute the algebraic sum of the signals from the different classes of cones prior to the decision process. On this theory we might expect that the signal in the S cones is given by  $\Delta S/S$  and the assumption that the cone signal has a constant value at threshold directly predicts the results we obtain for signals varying along the  $S - (L + M)$  axis.

Yet another idea is that as the background intensity increases the variance of the response within the cone pathways to a steady field increases in proportion to the intensity. On this theory we would predict, in the case of tests and backgrounds varying along the  $S - (L + M)$  axis, that the thresholds would vary as the square-root of the excitation of the S cones. In fact, the variation is linear but the uncertainty introduced by the quantal fluctuations of the light must have significant effects on the detectability of signals (Krauskopf & Reeves, 1980).

Let us turn to the effect of varying the adaptation point along the  $L - M$  axis on thresholds for changes along that axis. To derive the predictions from the Helmholtz line element theory we rewrite equation (4) leaving out the S term. At the same time we substitute, following MacLeod and Boynton (1979),  $l = L/(L + M)$  for  $L$  and  $m = M/(L + M)$  for  $M$ , noting that  $L + M = \text{constant}$ :

$$d^2 = \left[ \frac{\Delta l}{l} \right]^2 + \left[ \frac{\Delta m}{m} \right]^2. \quad (5)$$

Rearranging terms we get:

$$d^2 = \frac{m^2 \Delta l^2 + l^2 \Delta m^2}{l^2 m^2}. \quad (6)$$

Noting that  $m = 1.0 - l$  and  $\Delta l = -\Delta m$ :

$$d^2 = \frac{[(1.0 - l)^2 + l^2] \Delta l}{(1.0 - l)^2 l^2} \quad (7)$$

and

$$\Delta l = -\Delta m = d \sqrt{\frac{(1.0 - l)^2 l^2}{(1.0 - l)^2 + l^2}}. \quad (8)$$

The dotted curve in Fig. 15 plots the thresholds predicted in equation (8).

If we postulate that the cone signals are scaled according to their mean excitation, and thus that threshold for an isoluminant stimulus is achieved when:

$$c = \left[ \frac{\Delta l}{l} \right] - \left[ \frac{\Delta m}{m} \right]. \quad (9)$$



Following the same line that leads from equation (6) to equation (8), we obtain:

$$\Delta l = -\Delta m = c \frac{lm}{l+m} = c \frac{l(1-l)}{l+1-l} = c(l-l^2). \quad (10)$$

The thick solid curve in Fig. 15 plots the thresholds predicted in equation (10).

The results presented in Figs 6 and 8 were obtained at a luminance of 37 cd/m<sup>2</sup>. As illustrated in Fig. 1, the values of *l* achievable at this luminance ranged from 0.6 to 0.7 and the fact that the thresholds do not seem to vary with locus along the L–M axis might not be confirmed if adaptation were varied over a larger range of *l*. Therefore, we conducted an auxiliary experiment in which discrimination was measured along the L–M axis at a luminance half that previously used. As shown in Fig. 1 this allowed measurements at values of *l* from 0.61 to 0.83. The results of these experiments are presented in Fig. 15. Once again there is no variation in thresholds as a function of *l*. Both of the predictions derived above [equations (8) and (10)] are inconsistent with these results.

If the ability to detect signals were solely determined by the statistical variability of the total number of photons caught by the L and M cone pigments we would expect the thresholds to be invariant with the location of the adaptation point along the L–M axis. The variance of the photon catch in the L cones would be proportional to L and that in the M cones would be proportional to M. Since L + M is constant for variation along the L–M axis, the total variance for an L–M mechanism would be constant. This prediction is illustrated by the thin solid line in Fig. 15. This explanation is not likely to be correct since it would also predict a square-root law for intensity discrimination. Perhaps some other process adjusts the sensitivity according to the total L plus M excitation.

There are empirical grounds for expecting a different trend to the data in Fig. 15. In particular, based on the

results of a number of investigators [Boynton & Kambe, 1980; MacAdam, 1942 (as analyzed by LeGrand, 1949); Polden & Mollon, 1980; Pugh & Larimer, 1980; Stromeyer, Cole & Kronauer, 1985; Wandell & Pugh, 1980], it might be expected that thresholds would be minimal in the middle of the range. It has been theorized that second stage chromatic mechanisms should be maximally sensitive when operating in the middle of their operating range (Pugh & Mollon, 1979). However, most of the evidence comes from experiments in which the adapting luminances were much higher than used in the present study and clear evidence for a marked dependence of the effect on luminance was present.

That there may be important differences in the way adaptation processes function at different luminance levels is suggested by the measurements of the electrical responses of single monkey cone receptors reported by Schnapf, Nunn, Meister and Baylor (1990). They found that cone sensitivities were little effected at low to moderate luminance levels, being reduced by only a factor of two at levels approximately equivalent to 100 cd/m<sup>2</sup>. The luminance levels used in the present experiments were less than half this value. On the basis of Schnapf *et al.*'s results we would not expect that cone signals would be scaled according to their excitation levels under our experimental conditions.

*Color discrimination with the test vector variable*

Our results agree with Craik's (1938) finding that discrimination is best in the vicinity of the stimulus to which the eye is adapted. In fact, our data conform to this generalization better than do Craik's in that our thresholds are always minimal at the adaptation point. However, it remains to be seen whether this is a matter of experimental technique or because of the difference between chromatic and luminance discrimination. On the other hand, that we find better defined minima than Pointer (1974) and Loomis and Berger (1979) suggests that experimental method is critical.

A striking feature of the present data is the absence of any elevation in discrimination thresholds when the test vector varies along one cardinal direction and the difference vector is orthogonal to that direction (Figs 12 and 13).

The results for test and difference vectors which vary only along the cardinal axes are consistent with discrimination being mediated by mechanisms selectively responsive along the cardinal axes. When the task is to detect a reddish pulse, no stimulus is presented at three of the possible loci, and thus the activity in those parts of the field are samples of a circular noise distribution about zero. When the test pulses are in the red direction along the L–M axis and the difference vector is also in the same direction, the four stimuli are nominally identical pulses with the exception of the difference vector. If we assume that detection is mediated only by mechanisms along the cardinal directions, it might be hypothesized that the standard deviation of the size of the internal response to the test pulses increases linearly with their amplitude. The assumed noise distribution is then

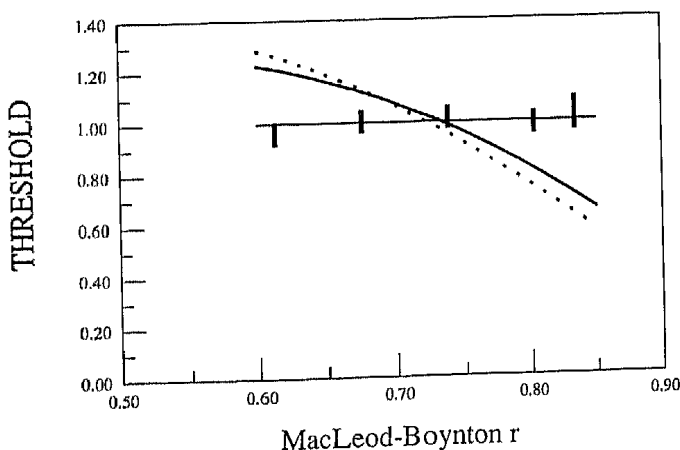


FIGURE 15. Thresholds for detecting red or green pulses on a background varying along the L–M axis, analogous to Fig. 6. Ten thresholds were measured at each point, and the heavy lines plot  $\pm 1$  SE. The three curves indicate predictions from the three different theories discussed in the text. The dotted curve is the prediction of a Helmholtz type model [equation (8)], the thick solid curve for equation (10) and the thin solid line is constant.

elongated along the red direction. Therefore the size of the increment of the test pulse would have to increase linearly with the amplitude of the test pulse to maintain the same signal-to-noise ratio.

This explanation fails when applied to the case in which the increments are orthogonal to the test pulses. In that case, we assume the same elongated noise distribution. Thus the chances of the internal response of one of the test pulses being the most remote from the rest of the responses would increase with test amplitude. Therefore, the magnitude of the increment in the orthogonal direction should increase, but this is contrary to fact. It seems that the information in the stimulus can be evaluated separately within mechanisms selectively responsive along the cardinal directions.

This theory fails to predict the shape of the discrimination ellipses for some cases for non-cardinal test directions. If the discriminations were made solely with mechanisms tuned along the cardinal axes, the major and minor axes would always be parallel to the cardinal axes except for test directions of 45, 135, 225, and 315 deg when the discrimination contour would be circular. Circles are a good fit to the data for tests of 45 and 225 deg, but ellipses with major axes pointing toward the origin fit the data for 135 and 315 deg test stimuli.

The red-green axis, or yellow-blue equilibrium line, of the Hurvich and Jameson (1955) opponent color theory is close to the L - M axis. However, the yellow-blue axis, or red-green equilibrium line, does not correspond to the S - (L + M) axis. Rather it falls close to the negative diagonal of our coordinate system. This makes it attractive to think that discriminations can also be made by using mechanisms sensitive to the "redness" and "greenness" of stimuli.

#### *Number of discriminable colors*

The data from these experiments can be used to calculate the number of discriminable colors. Firstly, since discrimination thresholds are smallest when the observer is adapted to the lights to be discriminated, the largest number of discriminable colors will be obtained under this regime. Because there is no interaction between the two cardinal directions under this regime, the number of discriminable colors is the product of the discriminable colors along the two axes. Neglecting the small increase in threshold along the S - (L + M) axis, we can go 13 threshold units in either direction along this axis. Along the L - M axis thresholds are constant, and we can go 53 threshold units in either direction. Therefore, there are approx. 2750 discriminable colors that we can produce on our monitor in the isoluminant plane at a luminance of  $\text{cd/m}^2$ .

When the observer is adapted to a fixed light, discrimination thresholds rise linearly with the distance of the discriminanda from the adaptation point in the relevant cardinal direction (Fig. 10). If we, following Fechner, sum just noticeable differences (jnds) along each direction, the number of jnds will be proportional to the logarithm of the biggest possible excursion in threshold

units. We obtained 32 threshold steps along the L - M axis, and 14 threshold steps along the S - (L + M) axis. Therefore, there are only 448 discriminable colors under this condition. Because of the logarithmic relationship that number is even further reduced if we change the adaptation point from the central equal-energy-white to another color. For example, if we extrapolate our results to the case of adaptation to a greenish yellow at the corner of our chromaticity diagram we obtain only 180 ( $20 \times 9$ ) discriminable colors.

#### *Practical considerations*

Discrimination thresholds for the same color can change by a factor of 10 when the adaptational state of the eye is changed. This effect should certainly be included in equations used to predict the perceived difference between two colors. When the adaptational state can be controlled, it should be chosen in a way such that the observer is adapted to the discriminanda. Under those conditions discriminability is best. The limitations of performance can be estimated from the results plotted in Fig. 8. In many situations, as for example when color is used for signaling, adaptation to the discriminanda may not be possible. In this case one would use data like those in Fig. 14. Under those conditions the best dynamic range, with the largest number of discriminable colors, can be achieved by adapting the observer to a color in the center (measured in threshold units) of all colors presented.

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