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Abstract

When a suprathreshold luminance flash, presented as an increment on a large background field, accompanies a coincident equiluminant flash, the chromatic threshold is reduced. Early studies suggested that the chromatic facilitation grows large at small test size. We have measured detection thresholds for test spots with diameters from 5 min-1°. Even for the smallest size the chromatic red-green sensitivity (specified in cone-contrast coordinates) is greater than luminance sensitivity, which has important implication for what "the eye sees best". Facilitation by the luminance flash remains constant at 2x for all sizes contrary to other earlier studies. Further work with 1° flashes indicates that the facilitation results from a demarcation of the chromatic region by luminance features, and is not due to simple reduction of detection uncertainty. We also studied how the L and M cone signals combine in detecting motion. We isolated and measured the properties of two motion mechanisms: a luminance and a spectrally-opponent mechanism which respond, respectively, to the weighted sum or the weighted difference of the L and M cone-contrast signals.

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## Introduction

All of our research relates to the ways that the visual system combines signals from the three spectral cone classes in performing various visual tasks. The emphasis is not on color perception per se, but rather on how chromatic information as well as luminance information is used in detecting form, flicker and motion.

To compare chromatic information with achromatic or luminance information, we must (a) have consistent operational definitions for color and luminance, and (b) have a rational metric which permits comparisons of chromatic and luminance sensitivities. The use of the cone-contrast space (Stromeyer et al. 1985) satisfies both of these goals. As shown in Fig. 1, stimuli are plotted as vectors in a diagram with axes which represent the contrast as seen by the long (L) and middle wave (M) cones. (Short-wave, S, cone contrast can be added as a third dimension, but we generally restrict our attention to long-wavelength lights which do not stimulate S cones.) Typically, the stimulus is a mixture of simultaneous increments and decrements of red and green lights in a given amplitude ratio which is represented by a vector in this diagram. The polar angle of the vector specifies the ratio of excitation of L and M cone types. Stimuli on the horizontal axis (Fig. 1) uniquely stimulate L cones with increments ( $0^\circ$  polar angle) or decrements ( $180^\circ$ )-- these stimuli produce silent substitution of the M cones. Stimuli on the vertical axis uniquely stimulate M cones. Luminance increments and decrements are necessarily found at  $45^\circ$  and  $135^\circ$  respectively since they represent flashes with the same chromaticity as the adapting field. Equiluminant green and red flashes are represented by vectors in the second and fourth quadrants respectively.

Mechanisms which respond to linear combinations of cone contrasts have straight-line detection contours in such a plot. In Fig. 2 the straight lines with slope of  $\sim 1.0$  indicate a red-green chromatic mechanism sensitive to the

linear difference of the L and M cone contrast signals, whereas the lines of negative slope (not necessarily -1.0) indicate a luminance mechanism sensitive to a weighted sum of L and M cone contrast signals.

A central goal of this project is to quantify and compare chromatic and luminance sensitivity, using the cone-contrast metric, for a wide variety of stimuli and tasks. In particular, we are studying small, fovea test spots, flashed for various temporal durations, to see how chromatic sensitivity compares with luminance sensitivity for small and brief stimuli. Another major goal of the project was to examine how suprathreshold luminance contours or edges affect chromatic sensitivity. We are also determining how the various cone signals are combined in detecting motion.

### **Review of Results**

#### Detection Contours for Small Foveal Flashes

Thresholds were measured for 200 ms foveal flashes on a yellow field of 1500-3000 td. For a 1° flash (Fig. 3) sensitivity is 10x higher for chromatic flashes (in the -45° vector direction) than for luminance flashes (+45° vector direction). (The contour has an aspect ratio of 10 -- ratio of thresholds measured on +45° and -45° axes.) Results for four observers show that when the flash is quite small, e.g. 5 min, sensitivity is still 2-3x higher for the chromatic flashes, as shown by the detection contours in Fig. 4. The slope of ~1.0 in Fig. 4 for the chromatic mechanism indicates that even for these tiny flashes the L and M cones contribute equally to red-green chromatic detection. The color of the flash, red or green, can be identified at the same probabilistic threshold as that for which the flash can be detected, supporting our interpretation that this represents detection by a chromatic mechanism.

By adjusting flash duration, we show that for the 1° test, sensitivity for the chromatic mechanism remains higher (3x) than for the luminance mechanism even at the shortest duration (<10 ms). By adjusting test spot diameter at 200 ms

duration, we find chromatic sensitivity to be higher than luminance sensitivity even for the smallest flash tested yet (5 min). These observations have important implications for defining that stimulus which "the eye sees best" (see Future Plans).

#### Peripheral Retinal Sensitivity for Luminance and Chromatic Flashes

In the fovea we find that green and red chromatic flashes (vectors of  $135^\circ$  and  $315^\circ$  in Fig. 1) are equally detectable (have same vector length) over a size range of 5 min to  $2^\circ$  dia. It was conjectured that the peripheral retina might be different, for studies on color-naming and asymmetric color matching demonstrate that the response to green is reduced compared to red (for references, see Stromeyer, *et al.*, 1992, enclosed). Our methods are particularly well-suited for determining whether this chromatic asymmetry reflects the asymmetry of the cone action spectra or reflects an asymmetry in the post-receptoral red-green mechanisms. Detection contours were measured in L and M cone contrast space for a  $2^\circ$ , 200 ms flash on a yellow field. At  $8^\circ$  eccentricity there was no red-green asymmetry, but asymmetry was evident at  $14^\circ$  ecc and the effect was pronounced at  $21^\circ$ . The asymmetry was also confirmed by color-identification at threshold. Since the luminance detection contours measured at  $21^\circ$  eccentricity show equal sensitivity for M cone increments and decrements and similarly for L cone increments and decrements there is no receptor asymmetry for increments and decrements. The asymmetry in chromatic detection must be post-receptoral, not receptor. These results are described in Stromeyer *et al.* (1992--enclosed).

#### Facilitation of Chromatic Detection by Luminance Edges

One of our major goals is to understand better the ways in which edge or boundary information, carried primarily by the luminance system, interacts with chromatic information to determine the color of a region of the visual field. Our

earlier work used simple circular spots and rings to show that the presence of clearly visible luminance edges can lower the threshold for detecting a colored spot by about a factor of two (Cole *et al.*, 1990, enclosed). Our results show that the facilitation is not due to the luminance stimulus reducing the observer's detection uncertainty (Eskew *et al.*, 1991, enclosed). We have demonstrated the luminance and chromatic stimuli must occur nearly synchronously in time for the facilitation to occur (Eskew *et al.*, 1991, draft).

More recent work has focused on spatial variations in the luminance stimulus (the luminance "pedestal"). Fig. 5 shows chromatic detection thresholds as a function of the type of luminance contour presented as a pedestal. Condition F shows the chromatic threshold in the no-pedestal control condition, and condition A shows the standard ring pedestal--facilitation is about two-fold, as usual. Condition B was of great interest: this luminance "incomplete starburst" causes the perception of an illusory contour around the test region, and as the figure indicates, it did reduce 2AFC thresholds. However, contours C and D also facilitated detection, and these produce no illusory contour; thus, we believe the facilitation produced in B is due to the demarcation of the test contour by the line ends, rather than by the illusory contour. Further evidence for this demarcation idea is given in Fig. 6, which shows that as few as three small luminance "dots" arrayed around the outside of the 1° test spot produce nearly the same facilitation as a full ring. This indicates a large spreading of the facilitatory effect of luminance contours.

Another recent finding is that a single vertical luminance line, centered within the test region, can produce a moderate amount of facilitation. Fig. 7 shows this effect as a function of line length. This effect of the centered line is not easily explained, since this luminance contour does not demarcate any edge of the chromatic test: the color is the same on both sides of the luminance contour. The

neural network model of Grossberg and colleagues (Grossberg and Mingolla, 1985) posits that in the absence of luminance edges, color signals diffuse through a network of tightly-coupled cells while luminance edges, by forming barriers to this diffusion, prevent this spreading. This model might produce some of the facilitation results we observe, but it cannot easily explain our result with the centered line, because the diffusion is always radial, so the centered line cannot prevent the color spread. However, as suggested by Grossberg (personal communication), it could be that the finite width of the luminance contour (about 3 min wide) forms a compartment which prevents diffusion; this idea suggests that detection would be facilitated by seeing the color within the luminance line. We have tested this idea by using a very narrow luminance contour (ca. 1 min wide), too narrow to form a compartment. Unfortunately, the test was inconclusive, since facilitation is rather weak and difficult to measure under these circumstances. It was partly for this reason that we have reduced the size of our test spot, in order to attempt to increase the amount of facilitation and make effects like this one easier to measure.

We have used the luminance pedestal paradigm with the 15 min, 10 min, and 5 min test spots to study facilitation for these small foveal stimuli. Our hypothesis, based in part upon the earlier data of Hilz et al. (1974), was that as the chromatic and luminance stimuli were reduced in size, the luminance pedestal would produce a much larger degree of facilitation, with the result that thresholds for chromatic detection on the luminance pedestal would be approximately independent of size. Forced-choice thresholds for four of our observers do not confirm this expectation. The facilitation for chromatic flashes stays constant at a factor of ~2 for test flashes over a large range of sizes from 5 min to 1° dia. A complete pedestal-contrast function for the 5 min chromatic flash was measured showing that the luminance flash has little effect on chromatic detection when the flash

is subthreshold, and the facilitation is constant at about 2x for a wide range of suprathreshold luminance contrasts. Switkes *et al.* (1988), using large grating patterns, and Cole *et al.* (1990), using 1° spots, showed that the pedestal's facilitatory effect is mostly suprathreshold; we have confirmed this finding for tiny spots.

Our attempts to model the facilitation effect continue. As noted above, we have eliminated one major possible explanation: that the luminance edges simply reduce the observer's uncertainty as to the time and place of test occurrence (Eskew *et al.*, 1991). Alternate models include those in which the luminance contours change the gain or integration area of chromatic detection mechanisms. Our theoretical work on modeling these results is ongoing.

#### Cone Inputs to Motion

Another major goal is to study the way in which L and M cone signals are combined in detecting motion.

This project interested us because we thought our methods of plotting detection contours would shed light on the important contemporary issue of whether motion is detected solely by luminance or whether color plays a significant role. Our results with flashes indicate that sensitivity is generally considerably higher for the red-green chromatic mechanism than for the luminance mechanism. This makes it difficult to isolate the less sensitive luminance mechanism. Thus, a second important reason for the study was to use motion *per se* to isolate the luminance mechanism, if in fact it is true that motion is detected largely on the basis of luminance information. We measured detection contours in L and M cone contrast space for a red+green sine grating of 1 cpd on a foveal yellow field of 3500 td. The vertical grating moved left or right and thresholds were measured either for simple detection or for motion (i.e. identifying whether motion was to the left or right). For the motion task we observed two mechanisms: a luminance motion mechanism that responded to a weighted sum



of the L and M cone contrasts and a spectrally-opponent motion mechanism that responded to a weighted difference of the cone contrasts. The opponent mechanism was more sensitive for velocities up to about 9 deg/sec (9 Hz). At a low velocity of 1 deg/sec, the L and M cone contrasts contribute about equally in the spectrally-opponent motion mechanism, but as velocity is increased the M cone input to this mechanism falls rapidly and the mechanism becomes L-cone-dominated.

We devised a method for better isolating each of the two motion mechanisms in order to measure clearly the detection contour for each mechanism, even when one mechanism has much higher sensitivity than the other. This method employs a quadrature paradigm: a slightly suprathreshold counterphase flickering grating (a pedestal) is set to a vector angle in the L and M cone contrast space chosen to stimulate only one motion mechanism, luminance or spectrally-opponent. In other words, the pedestal was set parallel to the contour of the mechanism not to be stimulated. The test is a counterphase flickering grating added to the pedestal in spatial-temporal quadrature phase. Direction identification thresholds are measured for the composite (pedestal+test), using a range of test vectors in L and M cone contrast space. The contours indicate the L and M cone contrast weights for each mechanism.

In addition to measuring the contours for each motion mechanism, we have collected extensive data showing: (1) Within the luminance motion mechanism the temporal phase shift between L and M cones is quite small, whereas (2) within the spectrally-opponent motion mechanism the phase shift may be large even at low frequencies, e.g. 30-50° at 4 Hz. (3) At 4 Hz we have isolated each of the two motion mechanisms and have measured how the pedestal facilitates each mechanism as a function of its contrast (the 'dipper' function). (4) These dipper functions were then used to predict the effects of pedestals of intermediate vector

angles which stimulate both motion mechanisms. The facilitated outputs of the two motion mechanisms appear to summate linearly, after first undergoing an accelerating transduction represented by the dipper function.

We have enclosed three papers on our motion work which have been delivered at meetings.

#### Future Plans

A major thrust of our work in the next year will be to use our new video display system to study the edge-color interaction by systematically varying the spatial properties of the test stimulus. Our video display system permits 12-bit accuracy in the control of the three phosphors of our display system, and will allow very precise linearization and specification of chromaticities. The complex software required for these experiments is being written. The first experiments will involve the measurement of the spatial spread of both facilitation, at threshold, and the spread of suprathreshold "filling-in" (as described in our proposal); if these two phenomena have similar spatial profiles, this will further reinforce our view that the facilitation involves an adaptive change in the spatial integration area of color mechanisms.

In addition, we will complete our major experiments on the I and M cone inputs to motion detection in the next year. After that, we will begin to add motion that stimulates the S cones to see how the S cones contribute to the luminance and the L/M spectrally-opponent motion mechanisms; this work continues the earlier work of Lee and Stromeyer (1989). Our quantitative model of L and M cone contributions to motion will be extended to include all three cone classes.

An exciting new line of research has to do with comparing absolute sensitivities for color and luminance. Watson et al. (1983), in a famous Nature paper, sought to determine "what does the eye see best." They reported that in the luminance domain the best detected foveal flash was  $0.3^\circ$  and 50 ms; its threshold contrast energy was  $-5.6 \log$

deg<sup>2</sup>sec<sup>1</sup> (the spatial-temporal integral of contrast squared), whereas the most-detectable grating patch had a threshold 2-3x lower. We replicated their luminance spot threshold. But our most-detectable red or green chromatic spot (10', 50 ms) had a threshold 10-20x lower, with thresholds expressed in units of cone contrast energy! This important line of research has far reaching implications that go well beyond the study of "color vision" *per se*.

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- Grossberg, S. and Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. Psychological Review 92, 173-211.
- Hilz, R.L., Huppmann, G. and Cavonius, C.R. (1974). Influence of luminance contrast on hue discrimination. Journal of the Optical Society of America, 64, 763-766.
- Lee, J., and Stromeyer, C.F. III (1989) Contribution of human short wave cones to luminance and motion detection. J. Physiol., 413, 563-593.
- Switkes, E., Bradley, A. and DeValois, K.K. (1988) Contrast dependence and mechanisms of masking interactions among chromatic and luminance gratings. J. Opt. Soc. Am, 25, 1149-1162.
- Watson, A.B., Barlow, H.B., & Robson, J.G. (1983) What does the eye see best? Nature, 419-422.

### Participating Professionals

Professor Richard E. Kronauer

Dr. Charles F. Stromeyer III

Dr. Phea T. Eskew, Jr.

Dr. Alex Chaparro (joined the project in the fall of 1990)

### Interactions and Presentations

• Association for Research in Vision and Ophthalmology, Sarasota, Fla. 1990. Drs. Stromeyer and Eskew attended.

Stromeyer presented experiments on motion, while Eskew presented results on the facilitory effects of various luminance pedestals on chromatic detection. Papers enclosed.

- Optical Society of America, Boston, Ma. 1990. Drs. Stromeyer, Eskew, and Chaparro attended. Stromeyer presented results showing that the "minimal motion" technique of Anstis and Cavanagh is unlikely to produce true equiluminance, and Eskew discussed the cone space representation and why chromatic sensitivity is higher than luminance sensitivity under many circumstances. Papers enclosed.

- Association for Research in Vision and Ophthalmology, Sarasota, Fla. 1991. Drs. Stromeyer, Eskew, and Chaparro will attend. Stromeyer will present results using pedestals to isolate the less-sensitive luminance motion mechanism, Eskew will describe chromatic detection experiments in peripheral vision, and Chaparro will discuss our small-spot results. Papers enclosed.

#### Publications and Publications in Progress

Cole, G.R., Stromeyer, C.F. III, and Kronauer, R.E. (1990).

Visual interactions with luminance and chromatic stimuli.

J. Opt. Soc. Am. A, 7, 128-140. **(reprint enclosed)**

Eskew, R.T., Jr., Stromeyer, C.F. III and Kronauer, R.E.

(1991a). The time course of the facilitation of chromatic detection by luminance contours. Paper in progress

(manuscript available upon request).

Eskew, R.T., Jr., Stromeyer, C.F. III and Kronauer, R.E.

(1991b). On the temporal chromatic impulse response function. Paper in progress, (manuscript available upon request).

Eskew, R.T., Jr., Stromeyer, C.F. III, Picotte, C.J., &

Kronauer, R.E. (1989c) Detection uncertainty and the facilitation of chromatic detection by luminance contours.

Journal of the Optical Society of America, 8, 394-403.

**(reprint enclosed)**

Stromeyer, C.F. III, Eskew, R.T., Jr., Kronauer, R.E., & Spillmann, L. (1989) Temporal phase response of the short-wave cone signal for color and luminance. Vision Research, 31, 787-803. (**reprint enclosed**)

Stromeyer, C.F. III, Lee, J., & Eskew, R.T., Jr. (1992) Peripheral chromatic sensitivity for flashes: a post-receptor red-green asymmetry. Submitted to Vision Research (**manuscript enclosed**).

Papers Delivered at Recent Professional Meetings (included since this work not yet ready for publication)

Eskew, R.T., Jr., Stromeyer, C.F. III, & Kronauer, R.E. (1990). Cone-contrast comparison of luminance and chromatic sensitivities for movement, flicker and flashes. Presented at Annual Meeting, Optical Society of America, Boston, MA (**enclosed**).

Chaparro, A., Stromeyer, C.F. III, Eskew, R.T., Jr. & Huang, E.P. (1991). Relative sensitivity of red-green and luminance mechanisms for small spots. Presented at Annual Meeting of Association for Research in Vision and Ophthalmology, Sarasota, FL (**enclosed**).

Eskew, R.T., Jr., Stromeyer, C.F. III & Lee, J. (1991). An asymmetry in the red-green mechanism in the periphery. Presented at Annual Meeting of Association for Research in Vision and Ophthalmology, Sarasota, FL (not enclosed).

Stromeyer, C.F. III, Eskew, R.T., Jr. & Kronauer, R.E. (1990). The most sensitive motion detectors in humans are spectrally-opponent. Presented at the Annual Meeting of Research in Vision and Ophthalmology, Sarasota, FL (**enclosed**).

Stromeyer, C.F. III, Eskew, R.T., Jr. & Kronauer, R.E. (1990). Equiluminance and minimal motion. Presented at Annual Meeting, Optical Society of America, Boston, MA. (**enclosed**).

Stromeyer, C.F. III, Eskew, R.T., Jr., Ryu, A. & Kronauer, R.E. (1991). Separation of luminance and spectrally-opponent motion mechanisms with a quadrature-pedestal paradigm. Presented at Annual Meeting of Association for Research in Vision and Ophthalmology, Sarasota, FL  
**(enclosed)** .

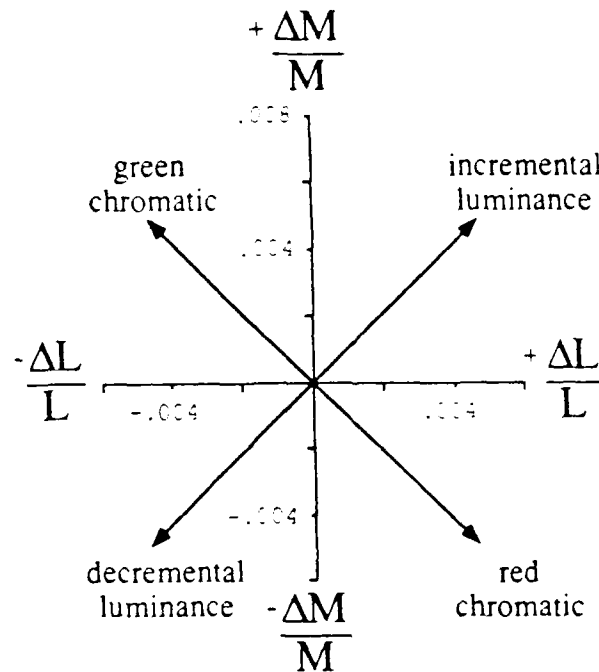


Figure 1.

L and M cone contrast coordinates for various test stimuli.

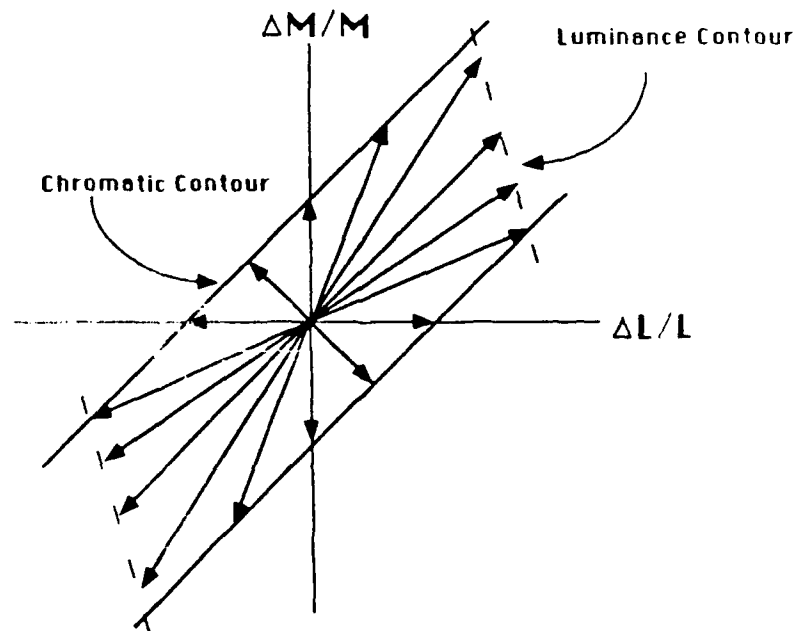


Figure 2. Hypothetical detection contours in the L and M cone contrast coordinates. Luminance mechanism responds to a linear weighted sum of L and M cone contrasts, and the chromatic mechanism responds to a linear weighted difference of L and M cone contrasts.

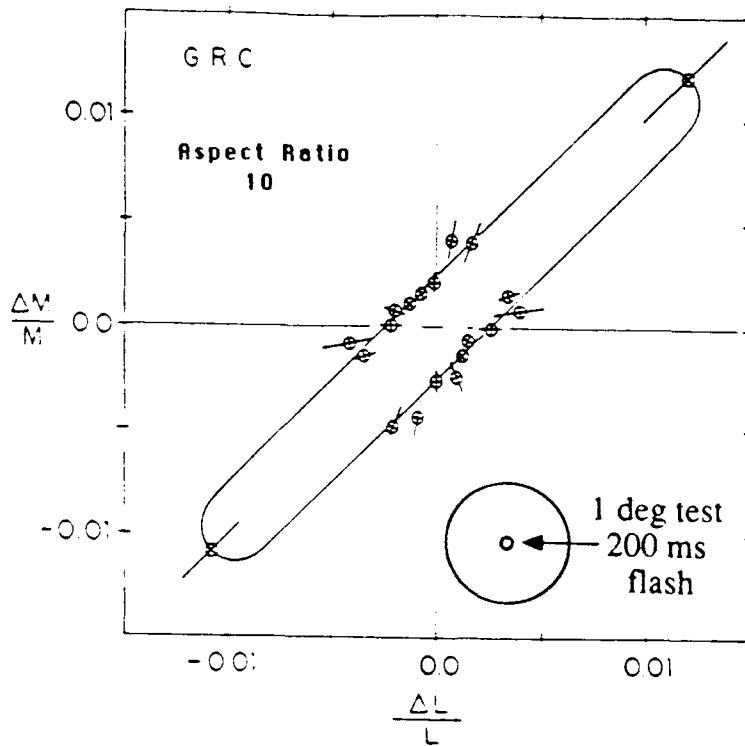


Figure 3. Detection contour for foveal 1°, 200 ms flash on 3000 td yellow field.

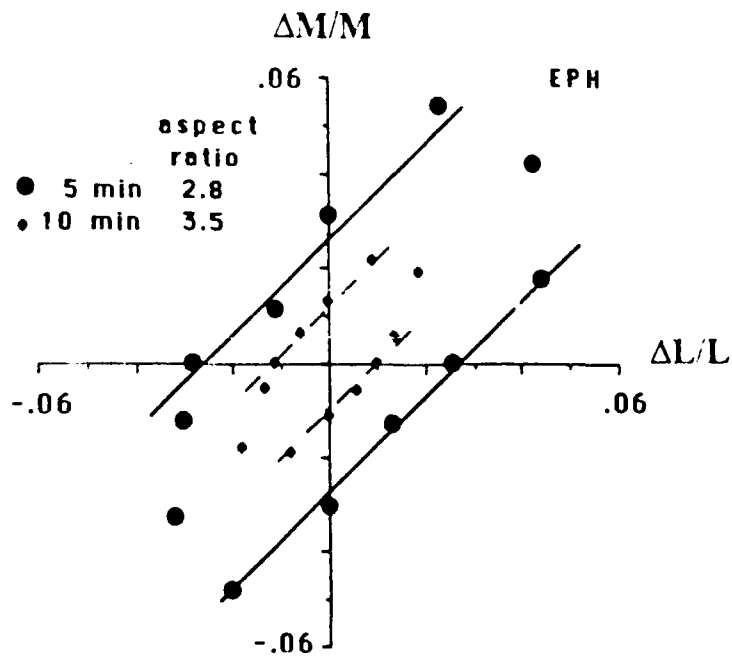


Figure 4. Detection contours for 5 and 10 min, 200 ms flashes on yellow field.



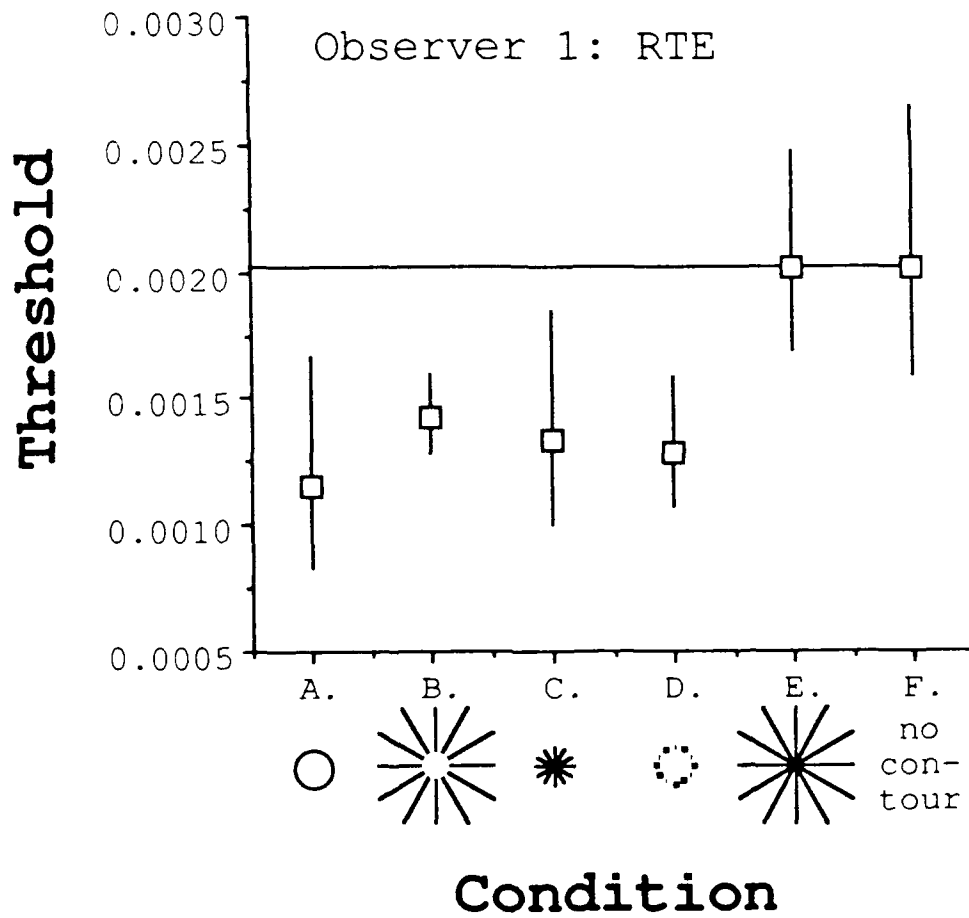
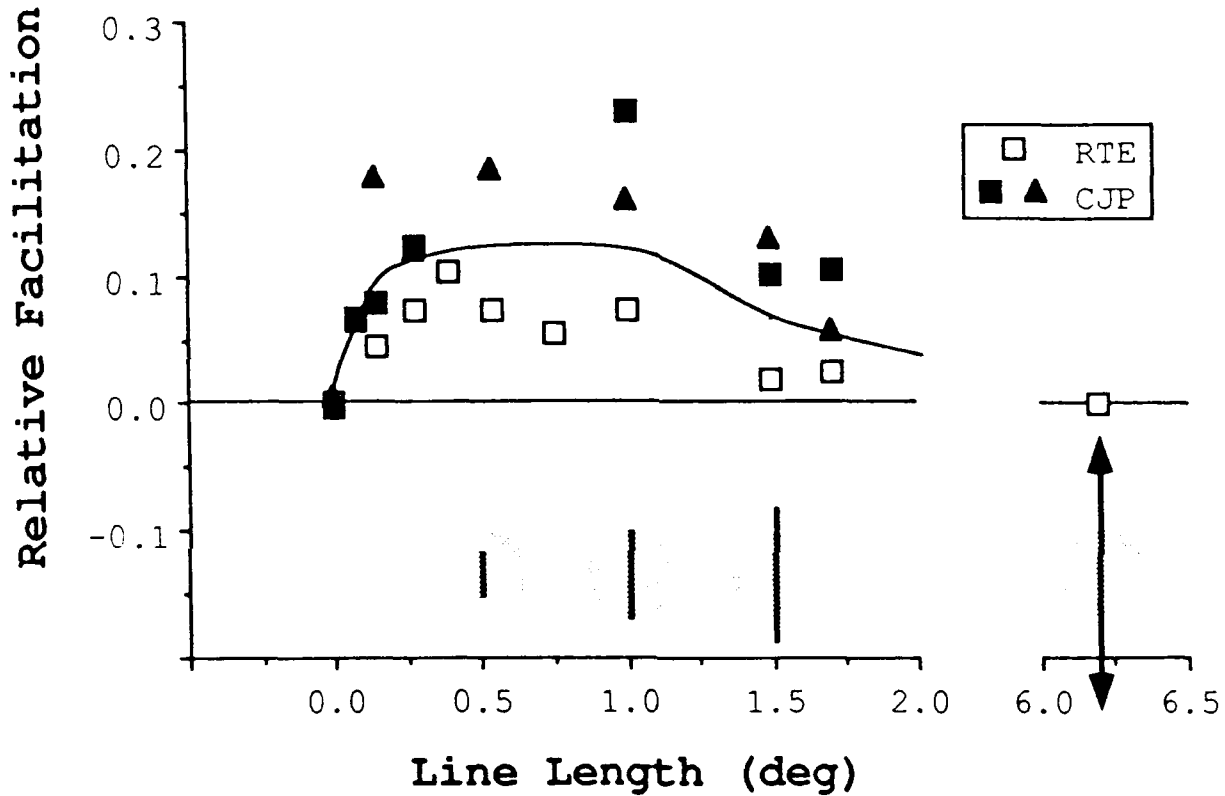


Figure 5. Thresholds for  $1^\circ$ , 200 ms chromatic flash on yellow field. Luminance pedestals A-D produce a clear facilitation of the chromatic threshold.

## Facilitation without Demarcation



**Figure 6.** Facilitation of a 1°, 200 ms chromatic flash on yellow field. The luminance pedestals are line segments. A 3 min wide vertical line produces a small amount of facilitation -- less than 25% of the amount produced by a ring pedestal which completely circumscribes the test. The effect varies slightly with line length, primarily by showing a decrease as the ends of the line are extended outside of the test.

## Facilitation of Chromatic Detection by a Dotted Contour

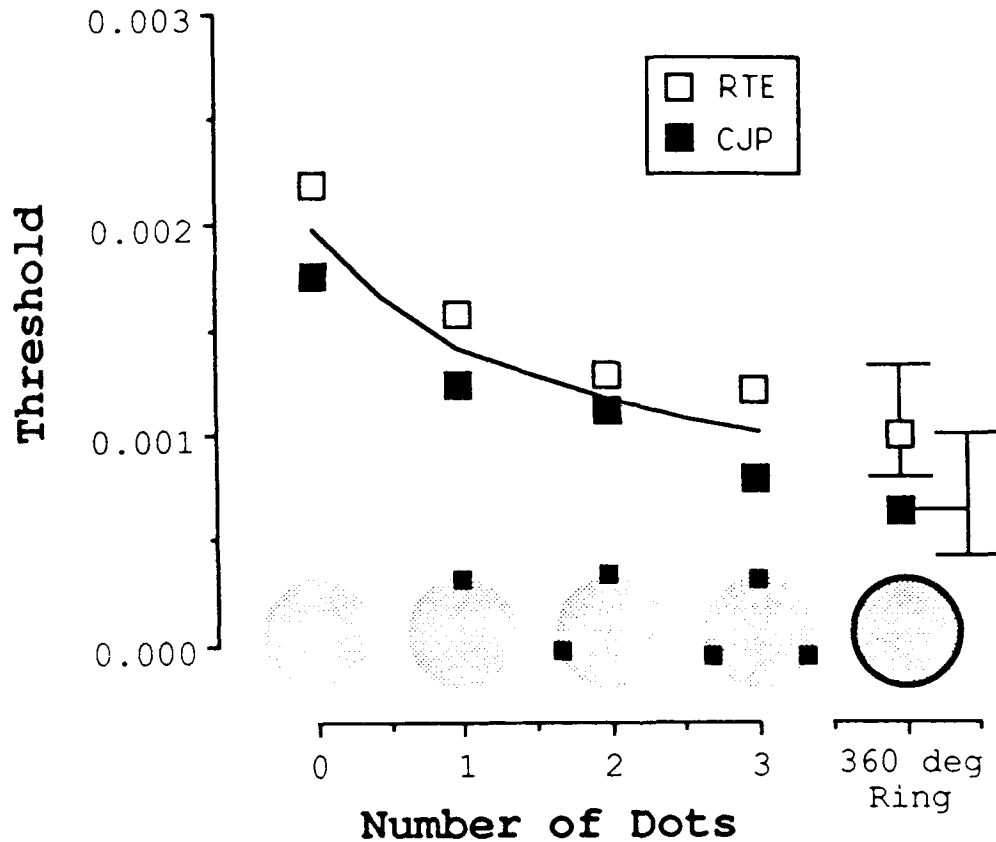


Figure 7. Facilitation of a  $1^\circ$ , 200 ms chromatic flash on yellow field. The pedestals are dots. The threshold is lowered by even one small dot lying on the circumference of the test spot, and three dots produce almost as much facilitation as a complete ring.