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19. Abstract (cont'd)

Isolation of the red-green mechanism with large test flashes on different colored backgrounds showed that the red-green mechanism responds to an equally-weighted difference of L and M cone contrast on each background. Even for fields as low as 400 trolands, sensitivity is controlled by cone-selective adaptation (as well as second-site adaptation), which is surprising in view of recent physiological recordings suggesting that light adaptation in cones is insignificant below 2000 trolands.

Motion mechanisms receiving L and M cone signals were studied with 1 cpd, flickering and drifting gratings. At low velocity, a spectrally-opponent (SPO) motion mechanism is more sensitive than the luminance (LUM) mechanism, which summates L and M signals. The SPO mechanism has equal L and M contrast weights at low velocity but is L-cone dominated at intermediate and high velocity, whereas the LUM mechanism shows the reverse pattern of weights. The SPO motion mechanism appears distinct from a red-green hue mechanism, for the latter has balanced L and M inputs at all temporal frequencies. The two motion mechanisms can be distinguished by the relative phase shifts of the L and M inputs: large shifts are seen for the LUM mechanism at intermediate frequency (4-9 Hz), where SPO shows very little shifts.

Abstract

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Isolation of the red-green mechanism with large test flashes on different colored backgrounds showed that the red-green mechanism responds to an equally-weighted difference of L and M cone contrast on each background. Even for fields as low as 400 trolands, sensitivity is controlled by cone-selective adaptation (as well as second-site adaptation), which is surprising in view of recent physiological recordings suggesting that light adaptation in cones is insignificant below 2000 trolands.

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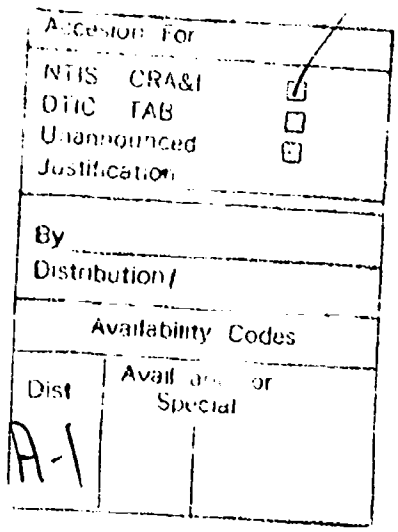


Research Perspective and Overview

Photopic perception is dominated by the most prevalent cones in the human retina—the long (L) and medium (M) wavelength cones. Tests with stationary stimuli show that at threshold the L and M cone signals are reorganized into two linear combinations: a weighted sum which represents a luminance signal, and a weighted difference which conveys chromatic information. At suprathreshold levels there exists a special nonlinear interaction in which the detection of color in a test spot is facilitated by a coincident luminance pedestal. Further tests show that the facilitation is caused by a demarcation of the test spot boundary by the luminance signal, and a small measurable delay accompanies the facilitation process. For a 1° diameter spot the facilitation is no more than a factor of 2, making it difficult to explore features of the mechanism which reduce facilitation, such as misalignment between the luminance contour and the test spot.

Earlier results by Hilz, Huppman and Cavonius (1974) indicated that larger facilitation factors can be obtained with smaller spots. Our experiments with small spots failed to confirm this—the factor of 2 persists for spots as small as 2' dia. The inability to find a larger facilitation places severe demands on both observers and apparatus in trying to define the spatial dependence of the facilitation process. After repeated attempts to get sophisticated, affordable equipment operable, we pursued related research objectives.

These research projects are detailed in sections to follow in a format which emphasizes the physical parameters, the

physiological substrate, the underlying coherence of the projects and their relation to the work of other investigators. In brief summary, we have:

Project 1, generating foveal detection data for spots smaller than 1°. We found that the chromatic mechanism is more sensitive than the luminance mechanism down to at least 2'. Even when test duration is optimized for minimum contrast energy, the chromatic mechanism wins. Chromatic facilitation by the luminance pedestal is never much greater than 2-fold.

Project 2, extending chromatic spot detection to the peripheral retina. The reduced sensitivity to green, compared to red, beyond about 8° eccentricity is shown to reside in the post-receptoral chromatic processing mechanism.

Project 3, defining the adaptation process which underlies Weberian control of detection sensitivity. By generating extended detection contours corresponding to the sensitive red-green chromatic mechanism on a variety of colored adapting fields, we find the most parsimonious explanation for the data to be cone-specific Weberian adaptation followed by second-site decrease in sensitivity for fields different from a yellow of about 580 nm.

Project 4, exploring the perception of motion via the L and M cones using 1 cpd sinusoidal gratings. We find in addition to the anticipated luminance motion mechanism (LUM), a second motion mechanism in which the L and M cones are combined in spectral opposition (SPO). The SPO mechanism conveys the percept of motion but not color. At low temporal frequencies (below about 9 Hz) SPO

is more sensitive than LUM, but above 15 Hz SPO has negligible sensitivity.

Projects 1,2 and 3 are complete and have either been publishe or are in the publication process. Project 4 has an enormous potential scope, and is correspondingly rich in information about visual signal processing structures. With temporal frequency as an additional stimulus parameter, the dynamic properties of the LUM and SPO mechanisms can be appraised: the frequency-dependent magnitudes of responses of the individual cone types represented in each mechanism as well as their relative phase. By varying independently the motion stimuli in the two mechanisms, we can study how motion signals from the two motion mechanisms are combined. Suprathreshold interaction between mechanisms can be quantified. We have laid the groundwork for further studies, first by identifying the various motion mechanisms, and by developing the procedures for isolating the mechanisms in order to study their separate properties and to examine how the mechanisms interact.

Background

When we use our central fovea (which has maximal spatial acuity and contrast sensitivity), information is portrayed by signals from the two spectral classes of cones--the long-wave (L) and middle-wave (M) cones. The majority of our measurements involve the threshold detection of stimuli on a bright yellow field which provides approximately equal adaptation of the L and M cones, and is of sufficient intensity to place both classes of cones in the incremental Weberian region of sensitivity (where our

cone contrast metric described below, is applicable). The test stimuli are comprised of different amplitude mixtures of incremental and decremental red and green test lights. We measure thresholds for many such amplitude ratios, which stimulate the L and M cones in different ratios, both positive and negative.

The detection results are plotted in the two dimensional coordinates of L-cone contrast and M-cone contrast, $\Delta L/L$ and $\Delta M/M$. L-cone contrast, $\Delta L/L$, for example, represents the change in quantal catch in the L cones owing to the test flash, divided by the total L cone quantal catch owing to the steady adapting field.

By plotting thresholds for many different L and M cone contrast ratios, we hope to identify detection mechanisms that respond to the sum of L and M cone contrasts (a luminance mechanism) and other mechanisms that respond to the linear difference of L and M cone contrasts (a red-green opponent, chromatic mechanism or a spectrally-opponent mechanism).

Four projects were pursued using this method during the course of the research project, which we will describe in the following order: (1) What are the most sensitive mechanisms for foveal detection? Do the luminance and red-green mechanisms remain approximately independent? (2) How do the sensitivities of these mechanisms change when the stimuli are presented in the fovea onto peripheral retina? (3) What are the mechanisms controlling light adaptation, as assessed using the easily-isolated red-green mechanism? (4) In detecting motion, how do the signals form the L and M cones combine in different possible motion detection mechanisms? What are the relative L and M contrast cone weights

and temporal phases in each mechanism? Is there a red-green hue mechanism separate from a spectrally-opponent motion mechanism?

The latter motion project is being intensely pursued.

Project 1. Comparison of detection sensitivities of luminance and red-green opponent mechanisms in the fovea, and possible suprathreshold interactions.

"Colour is what the eye sees best" (Chaparro *et al.*, 1993, *Nature*) is our answer to the famous *Nature* paper of Watson, Barlow and Robson, 1983, "What does the eye see best?" They measured thresholds only for luminance stimuli--white, foveal test patterns on a bright white field. To compare detection efficiency for different patterns they expressed thresholds as contrast energy--the square of the contrast integrated over the spatial and temporal dimensions of the pattern. Their best-detected stimulus was a small patch (Gabor) of vertical grating of ~7 cpd, drifting left or right at 4 Hz. They also measured threshold for square shaped incremental flashes of different sizes and durations--the best-detected spot was ~18' and 50 ms.

We used circular flashes (Fig. 1a) on a 3000 troland, 580 nm yellow field. As shown in Fig. 1b, luminance flashes produce equal increments in the contrast of L cones and M cones, and a comparable red chromatic flash is distinguished by only an inversion of the sign of the M-cone contrast component. To show isolation of the red-green mechanism, we first measured full detection contours for 200 ms flashes of either 5' or 10' diameter. Figure 2a illustrates the hypothetical detection

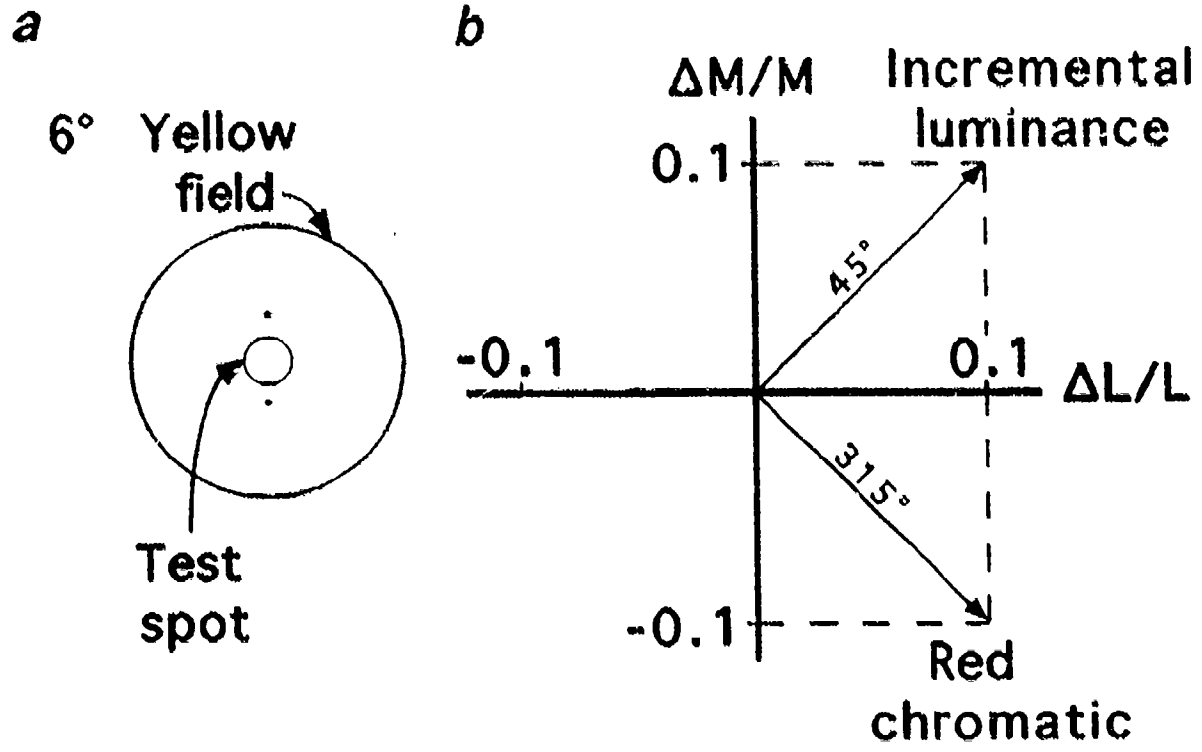


FIGURE 1.

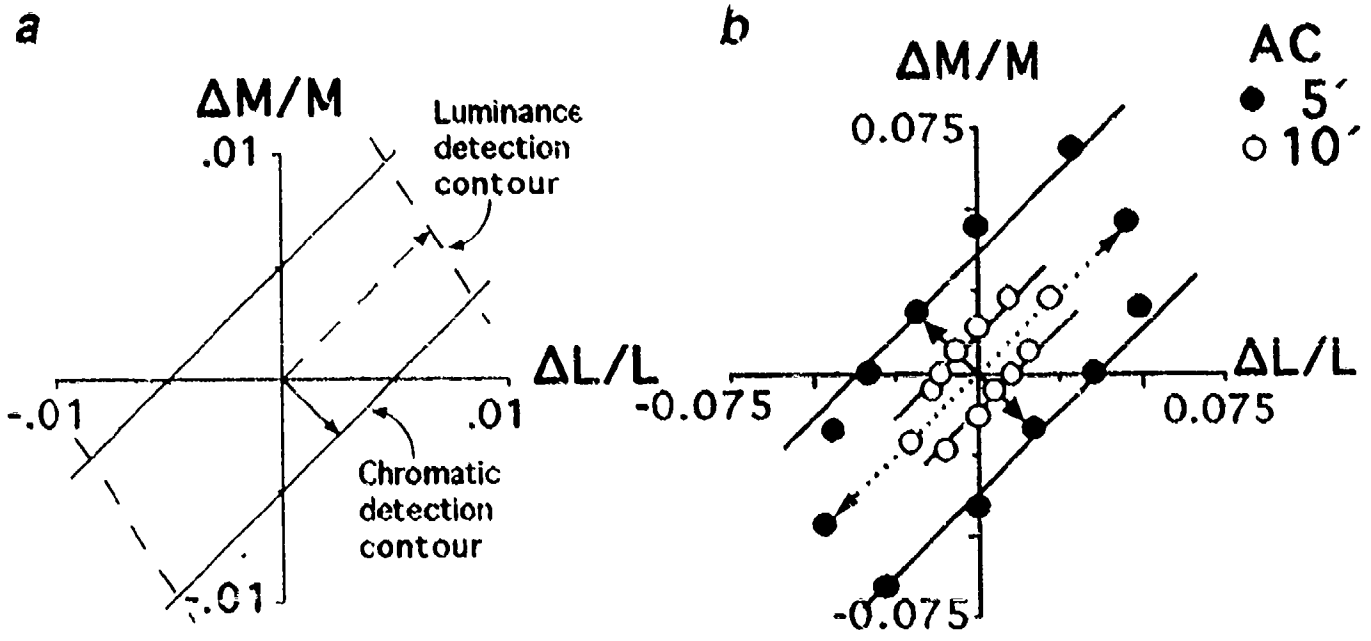
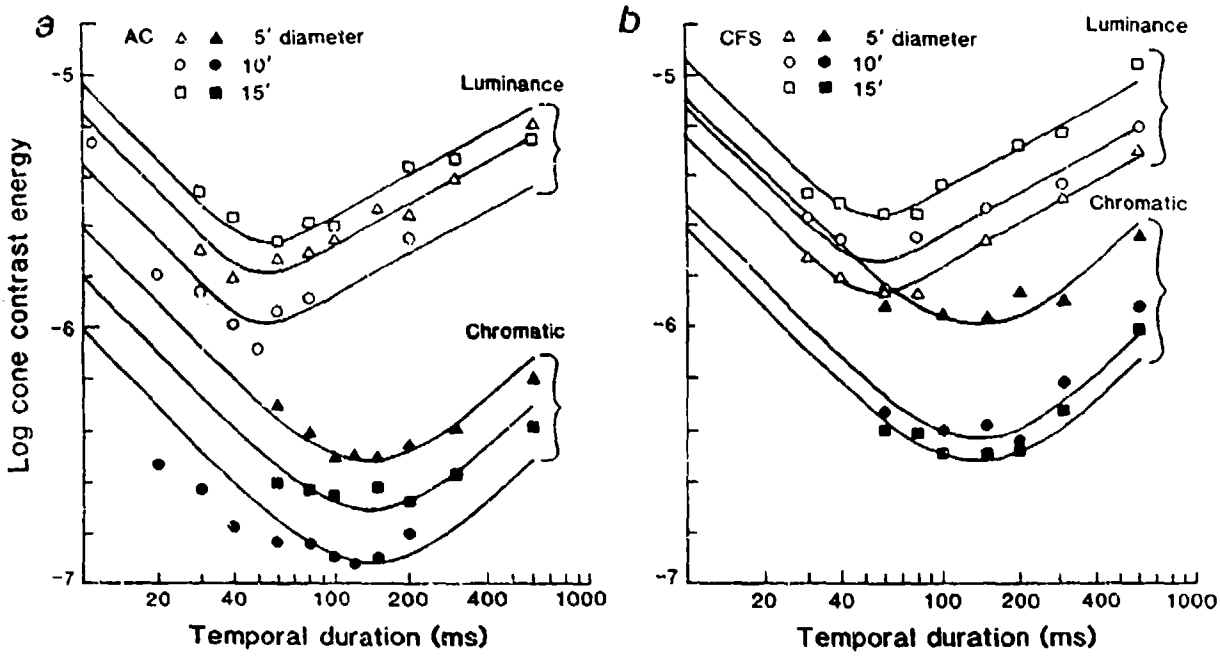


FIGURE 2.

contours we might expect to obtain. The red-green mechanism (as shown by the 'chromatic detection contour') responds to an equally weighted *difference* of L and M cone contrast--hence the detection contour has a slope of ~1.0, given by equation $a\Delta L/Lb\Delta M/M$=constant where $a \cong b$, whereas the luminance mechanism responds to the *sum* of L and M cone contrasts. For a large flash of 1° diameter (Cole *et al.*, 1990), sensitivity is about 10x higher for the chromatic flash (in the -45° vector direction) than for the luminance flash (+45° vector), as indicated by the chromatic contour being 10x closer to the origin than the threshold for the luminance flash. As shown in Fig. 2b, when the test flash is reduced to 10' and 5' diameter, chromatic sensitivity is still better by a factor of 4 and 3. The small red and green flashes appeared reddish and greenish at threshold--the flashes could be identified with the same accuracy with which they could be detected, thus demonstrating detection via a chromatic mechanism. Having revealed isolation of the red-green mechanism at small spot size, we then varied the duration of both the luminance and chromatic flashes to find the duration that yielded the lowest cone contrast energy threshold. As shown in Fig. 3a and 3b, the luminance and chromatic thresholds are lowest at durations of ~60 and 100 ms respectively. Then using these optimal durations, we sought the spot size that yielded the lowest energy threshold (Fig. 3c). Our optimal luminance spot is ~10' diameter and 60 ms duration, similar to that of Watson *et al.*, whereas our optimal chromatic spot shows somewhat higher integration: ~15' diameter and 100 ms duration.


a
AC
5' diameter
10'
15'
Luminance
Chromatic
Log cone contrast energy
-5
-6
-7
20
40
100
200
400
1000
Temporal duration (ms)
b
CFS
5' diameter
10'
15'
Luminance
Chromatic
-5
-6
-7
20
40
100
200
400
1000
Temporal duration (ms)

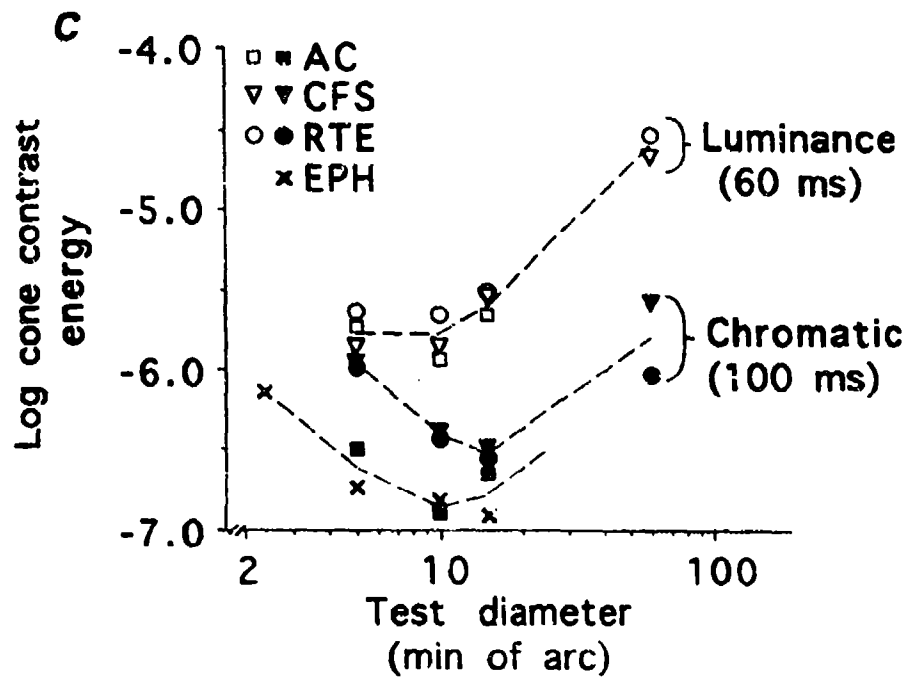

c
AC
CFS
RTE
EPH
Luminance
(60 ms)
Chromatic
(100 ms)
Log cone contrast energy
-4.0
-5.0
-6.0
-7.0
2
10
100
Test diameter
(min of arc)

FIGURE 3.

Surprisingly, the optimal chromatic spot is detected 5-9 fold better than our best luminance spot and 3-8 fold better than Watson's optimal luminance stimulus--the small patch of drifting grating. The high sensitivity to color can be explained by properties of the retinal P, color-opponent cells: their prevalence, high chromatic gain and noise characteristics, provided that the signals are effectively summed.

We have pursued these small spot experiments, decreasing the flash to even smaller size and also examined possible suprathreshold interactions of the luminance and red-green mechanisms. As a preliminary step, we examined whether the Smith and Pokorny L and M cone fundamentals tabulated for the central 2° foveal area, apply adequately at small spot size. If the cones are longer near the center of the fovea, the optical density may change, thereby significantly modifying the shape of the cone spectral sensitivities via self-screening. Large effects of this sort are suggested by earlier work of Pokorny *et al.* (1976). We performed extensive Rayleigh matches (Picotte *et al.*, 1993) with small fields, and observed that in going from a 116' to a 19' field, the effective change in optical density is only ~10%--a factor sufficiently small that we used the unmodified cone fundamentals to represent our data at small spot size.

Our threshold measurements are presented in the enclosed paper "Separable red-green and luminance detectors for small spot size" (Chaparro *et al.*, 1994a, *Vision Research*, In press). We observe that the red-green mechanism responds to the difference of equally weighted L and M cone contrast down to the smallest size

we used (2.3' diameter). At this small size, the red-green mechanism is still ~2x more sensitive than the luminance mechanism for two of the three observers.

Hood and Finkelstein (1983) argue that chromatic mechanisms change their spectral tuning as a function of spot size, so that the L and M weights are *not* constant--they thus argue for a 'variable tuning hypothesis'. In contrast, our results show that the red-green mechanism has constant relative L and M cone weights, or 'fixed tuning', since at all spot sizes the red-green detection contour has a slope of ~1.0, showing that the L and M contrast weights are *equal* and of opposite sign. From this we predict that a luminance flash (a vector of +45° in the L and M cone contrast coordinates) will not directly stimulate the red-green detection, since the +45° vector is *parallel* to the red-green detection mechanism of slope -1.0.

To test this prediction, we measured how detection of a 2.3' chromatic flash is affected by a coincident luminance flash (a 'pedestal'), when the color flash and the luminance pedestal are presented simultaneously. Figure 4 shows the chromatic test threshold as a function of the strength and polarity of the luminance pedestal. The arrow marks the threshold of the luminance pedestals. Pedestals that are subthreshold have little affect on chromatic detection. The independence of chromatic detection is shown, in part, by the fact that the curve for both polarities of the *subthreshold* pedestal (light and dark luminance pedestals) have equally nil effects. (This should be contrasted with the results in Fig. 5 showing strong, asymmetrical dipper functions

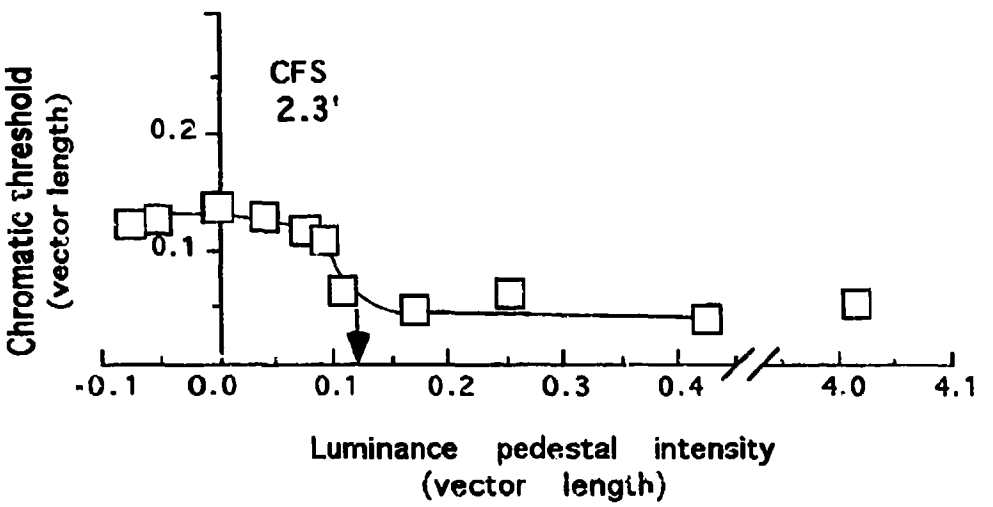


FIGURE 4.

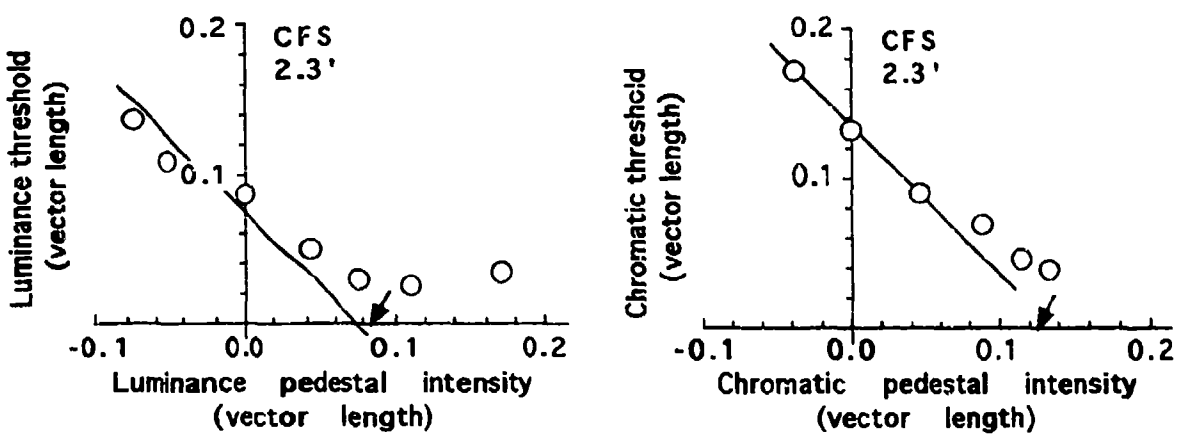


FIGURE 5.

when the test and pedestal are both chromatic or both luminance. In Fig. 5, there is the strong effect of subthreshold pedestal polarity, indicating subthreshold summation within a single mechanism--either chromatic or luminance.) Returning to Fig. 4, we observe that once the luminance pedestal just exceeds threshold, the chromatic threshold descends by a factor of ~2x (facilitation) and intense luminance pedestals do not produce masking. We believe the results show an essential separability of a test into luminance and chromatic components.

One of the major reasons why Hood and Finkelstein proposed their 'variable tuning' hypothesis for chromatic detectors is that wavelength discrimination for small, slightly suprathreshold incremental monochromatic flashes seemed surprisingly good, suggesting that there might be multiple mechanisms with different spectral tuning. However, we believe these observations can be explained by 'fixed' red-green mechanisms with equal and opposite L and M contrast weights, when we take into account chromatic facilitation by the luminance ('pedestal') component of the incremental flash. Our results in Fig. 6 provide evidence for this hypothesis; the figure combines several sets of experiments on one observer using a 2.3' flash. The squares are redrawn from Fig. 4 and show how the chromatic flash threshold varies with luminance pedestal strength: when the pedestal is subthreshold it does not affect the chromatic detection mechanism, and when the pedestal is suprathreshold it facilitates the chromatic threshold by ~2x, causing the chromatic contour to move inward by ~2x. The circles show chromatic identification thresholds (red versus green) on a

luminance pedestal of ~3x threshold. Notice these thresholds lie on the facilitated chromatic detection contours. The open triangles indicate the levels at which threshold incremental flashes [metameric with 550 nm (yellow-green) or 595 nm (orange)], can be discriminated from each other. The adapting field is yellow, metameric with ~580 nm. (The triangles represent wavelength discrimination, like that of Hood and Finkelstein.) Importantly, these flashes can be discriminated when of sufficient intensity to just lie on the luminance-facilitated chromatic contour. Filled triangles show similar discrimination results for flashes metameric (for L and M) with 489 and 610 nm.

A major goal of our grant project was to examine whether chromatic facilitation by a luminance contour increases with small stimulus size, since early work by Hilz *et al.* (1974) showed large effects. As shown by the open symbols in Fig. 7, the chromatic threshold increases strongly as the spot is reduced in size. It would be most advantageous to have this profound decrease in chromatic sensitivity nullified by the presence of coincident suprathreshold luminance contour. The solid triangles in Fig. 7, from Hilz *et al.*, show evidence for such an effect. However our forced-choice results, based on four observers, show that the facilitation remains constant at ~2x at all stimulus sizes.

In summary, at large and small spot size the red-green detection mechanism has fixed spectral tuning--the mechanism responds to an equally weighted difference of L and M cone contrast. The slope of 1.0 for the detection contour implies that luminance flashes of +45° vector angle will not desensitize the

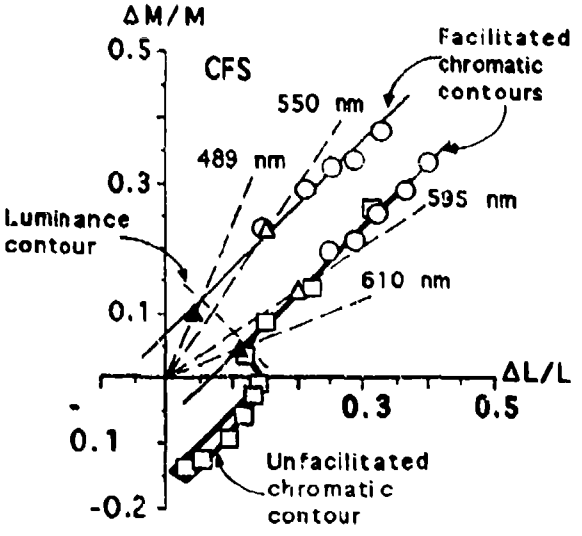


FIGURE 6.

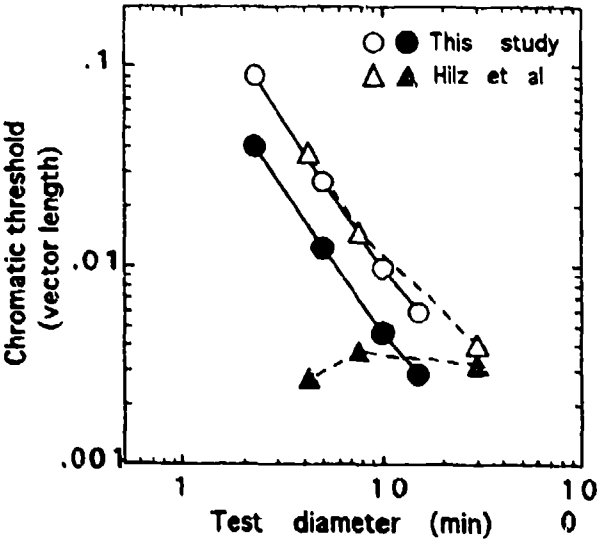


FIGURE 7.

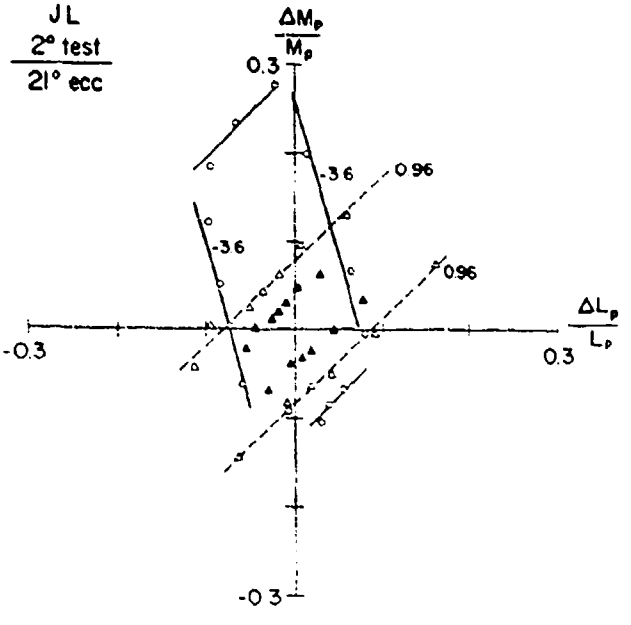


FIGURE 8.

mechanism. Instead, luminance flashes may facilitate the chromatic mechanism by ~2x, and this can account for wavelength discrimination of suprathreshold incremental flashes.

Project 2. Asymmetry in red and green detection in peripheral retina.

Measurement of the 'red' and the 'green' detection contours in the fovea show that red chromatic flashes and green flashes are detected equally well; for example, in Fig. 2b the two chromatic detection contours (2nd and 4th quadrants) are equidistant from the origin. This is true regardless of the color of the adapting field; on a red field, for example, green chromatic flashes are not more detectable than red (Stromeyer *et al.*, 1985).

However, many studies in peripheral retina report that green hues are reported less often than are red (see refs. Stromeyer *et al.*, 1992a), suggesting that green sensations may be selectively attenuated. Is the poor green sensitivity caused by the asymmetries in the action spectra of the L and M cones (red monochromatic incremental flashes produce a greater L/M stimulus ratio than green flashes produce an M/L ratio), or is the poor green sensitivity caused by an asymmetry in the polarity of the response red-green opponent mechanism? We measured (Stromeyer *et al.*, 1992a, paper enclosed), detection contours for 2°, 200 ms flashes on a yellow field at various retinal eccentricities. The red and the green chromatic flashes had similar magnitude thresholds out to ~8° eccentricity, while at greater eccentricities, red flashes were definitely more visible than

green. This asymmetry is shown clearly at 21° eccentricity by the positive-sloped contours fitted to the open circles in Fig. 8. (The triangles show chromatic thresholds facilitated by a suprathreshold luminance pedestal.) The chromatic asymmetry is a property of the chromatic pathways *per se* and does not simply reflect an asymmetry in the polarity of the cone response *per se*, for it can be seen (Fig. 8) that incremental and decremental L-cone flashes have similar thresholds, as do incremental and decremental M-cone flashes--flashes all detected by the extrapolated luminance mechanism.

Project 3. Cone-selective adaptation at low illuminance levels.

By measuring full detection contours for the red-green mechanism on different colored adapting fields, we can clarify some of the surprising recent observations of Krauskopf and Gegenfurtner (1992) on light adaptation. They observed that the threshold for equiluminant red-green flashes was approximately constant on 400-troland backgrounds ranging from yellow-green to orange, and they thus concluded that the detection mechanism is largely unaffected by cone-selective adaptation. Recent recordings by Schnapf *et al.* (1990) of the photocurrent in single, excised primate cones showed evidence for adaptation (a 2-fold gain reduction) only at *high* levels of retinal illuminance--2000 trolands. We asked whether the psychophysical results reflect a lack of cone-selective light adaptation (since they were performed at a low light level of 400 trolands, where the physiology suggests there is little adaptation), or are the results

uninformative about the mechanisms underlying light adaptation, since the measurements are restricted to only the equiluminant test axis. The latter view is supported in our enclosed paper, "Adaptation of human cone signals at low light levels" (submitted to *Nature*).

We measured the red-green detection contour for a 2.2° foveal flash on a large adapting field of 400 trolands, which was either green, yellow or red. Flashes were first plotted (Fig. 9 and 10) in absolute coordinates for M cone trolands (M td) and L cone trolands (L td). The total illuminance change produced by the test flash is the sum of ΔM td and ΔL td produced by the flash (Fig. 9). Thus the equiluminant flashes lie along the -45° diagonal, since a change in ΔL td is balanced by an equal and opposite change in ΔM td.

The dashed line in Fig. 9a shows the expected red-green contour on a yellow field--the contour is straight since the mechanism responds to the linear difference of L and M cone stimulation. Figure 9b shows how the contour is expected to shift on a red adapting field and on a green adapting field if there is cone-selective adaptation. Since the red field exposes the L cones to higher effective illumination than the M cones, the L cones will be more desensitized. This will elevate the threshold for L-cone test flashes, thereby flattening the contour. The green field is expected to have the opposite effect of steepening the contour. Detection contours were measured for both green and red chromatic flashes, and straight contour were fitted to the data (Fig. 10). Figure 11, shows as a function of adapting field

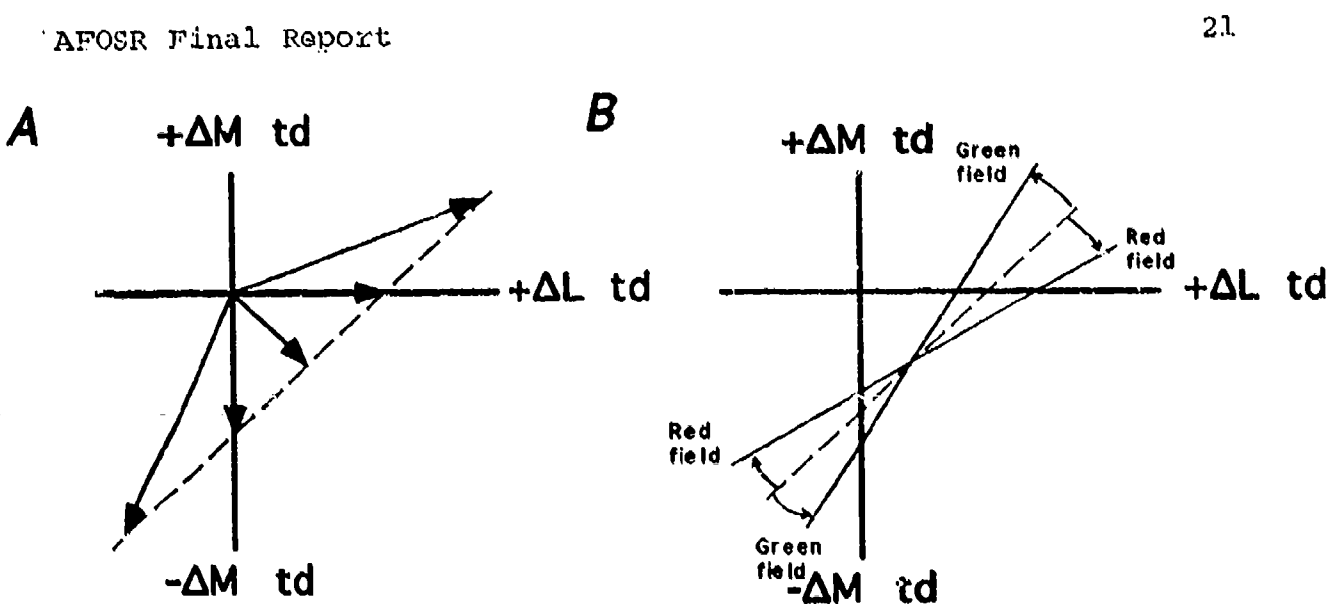


FIGURE 9.

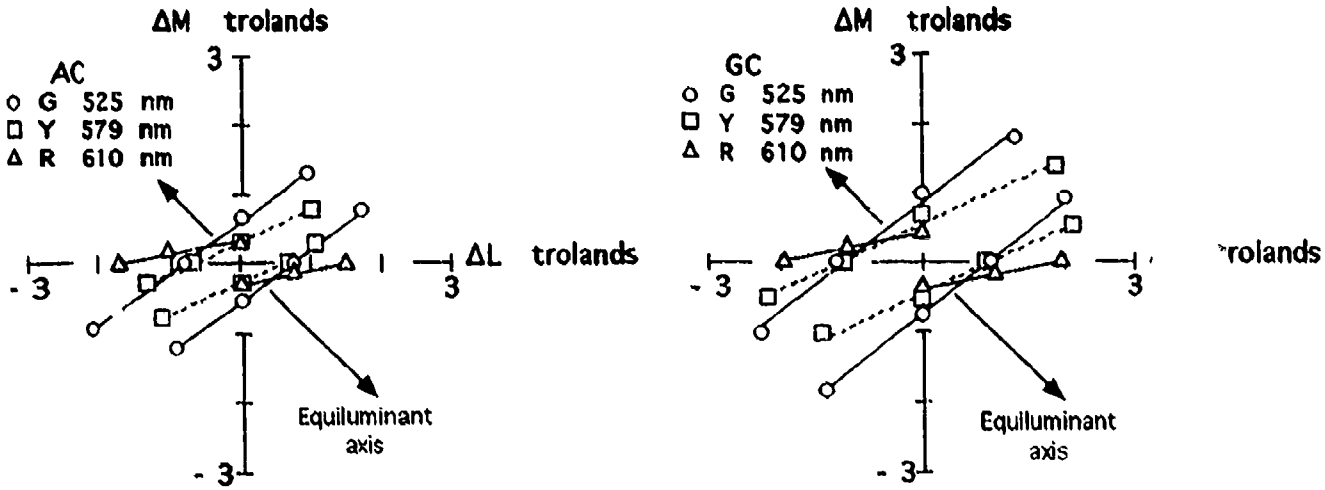


FIGURE 10.

wavelength, thresholds for unique L-cone flashes, unique M-cone flashes and equiluminant flashes. L-cone flashes are most elevated by red fields and M-cone flashes by green fields, showing clear evidence for cone-selective adaptation. Like Krauskopf and Gegenfurtner, we find the equiluminant thresholds vary little with background color--as, also, shown by the fact that the contours in Fig. 10 approximately intersect along the equiluminant axis. This shows that equiluminant flashes are less informative for revealing adaptation, compared to unique L- or M-cone flashes.

We transformed the data in Fig. 10 into cone contrast coordinates (Fig. 12). If the L and M cones adapt in proportion to the degree that they are stimulated by the adapting field, then the L and M *contrast* signals might contribute equally on each adapting field. This implies the contour slope will be approximately 1.0 for each colored background, as we observe. Had the cones not adapted then the slopes would vary over a range of 6-fold, since changing background color changes the mean L/M background ratio by 6-fold (Fig. 10).

An interesting feature in Fig. 12, is that the contours are displaced outward on the red field. This further decrease in sensitivity (over and above the cone-selective adaptation), which dependent on field *color*, is likely caused by second-site adaptation--a partial response saturation at an opponent site where the L and M cone signals are differenced (Pugh & Mollon, 1979; Stromeyer *et al.*, 1985).

Thus our results show clear evidence for cone-selective adaptation at low illuminance levels. Note that, although the

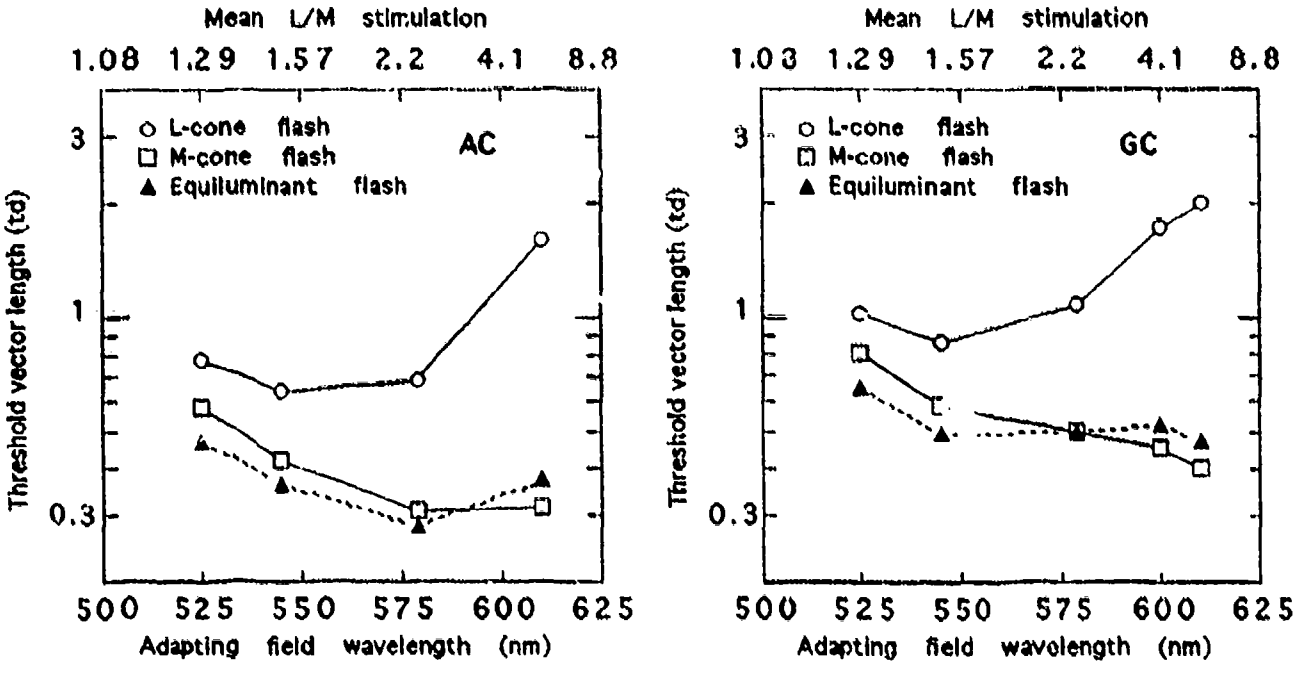


FIGURE 11.

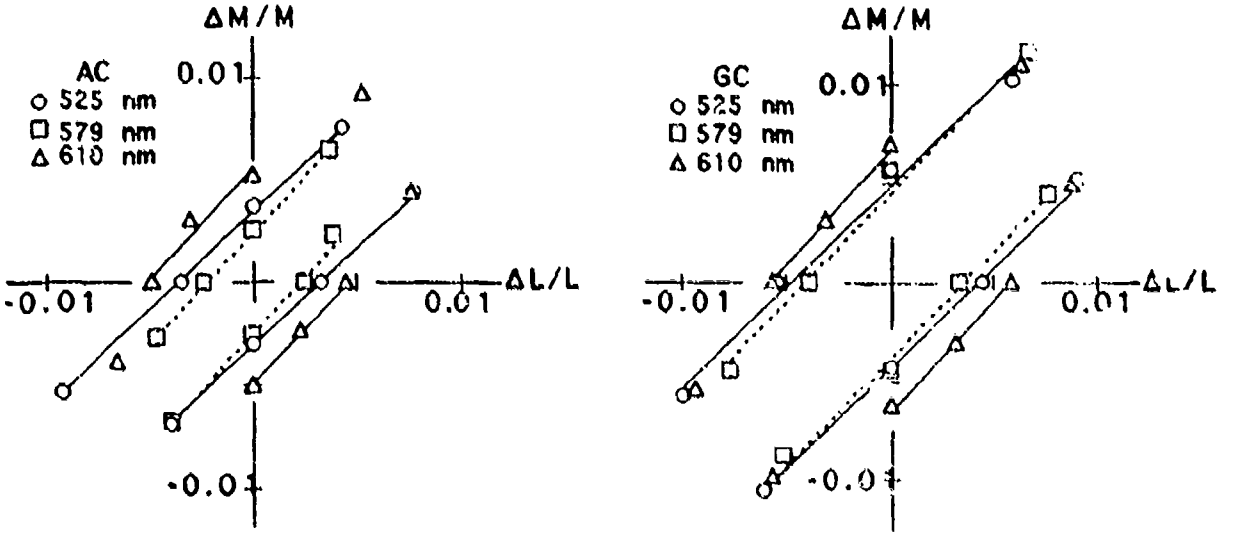


FIGURE 12.

field is 400 trolands, the effective cone illumination is often much lower; the 610 nm field for example produces only about 60 M td and yet the M cones adapt. This adaptation possibly occurs in the cones *per se*, or, at least, at stages prior to the P red-green ganglion cells, which may have cone-selective interneurons (Reid & Shapley, 1992).

We are preparing a more complete report using a larger range of adapting chromaticities and luminances. A major goal is to factor out the role of second-site adaptation so that we can look at the role of cone-selective adaptation over an extensive adapting range.

Project 4. Contribution of L and M cones to the detection of motion.

It has often been suggested that motion is detected by luminance pathways, with chromatic pathways conveying little sense of motion (Livingstone & Hubel, 1987). If these luminance pathways are indeed more sensitive for motion, this should be evident by measuring detection contours in L- and M-cone contrast space. Figure 13 shows our basic stimulus: a 1 cpd, vertical red-plus-green heterochromatic, sine-wave grating is drifted left or right on a ~3500 td foveal yellow field. The grating is made up of red and green components summed in-phase or in antiphase at different amplitude ratios. Each ratio represents a different vector orientation in the L and M cone contrast space. The vector is symmetric about the origin of the space, since the grating modulation is symmetric about the mean.

We measured forced-choice thresholds for both detecting the presence of the pattern and detecting its direction of motion (identifying whether the pattern moved left versus right). Figure 14 (from Stromeyer *et al.*, 1990) shows measurements for a slow drift velocity of 1 deg/sec (or 1 Hz). Thresholds for detecting the pattern are about 8x lower in the -45° chromatic direction (less than 1/10% contrast is needed) than in the +45° luminance direction. In the luminance direction motion can be seen near the detection threshold, whereas in the chromatic direction, contrast must be ~1.6x above the detection threshold to see motion. Clearly, the most sensitive motion mechanism here is chromatic and not luminance.

Although at 1Hz the chromatic detection and motion thresholds contours parallel each other, as velocity is increased the two contours diverge. We believe the chromatic detection contour in Fig. 14 reflects the red-green hue mechanism: at the detection threshold the patterns appear as *red* and *green stationary* stripes and the contour slope is ~1.0, indicating balanced, opponent L and M inputs. We obtained a similar red-green contour of slope ~1.0 for patterns drifting from 1 to 15 deg/sec, using an explicit hue criterion where contrast was adjusted so red and green hue was just apparent (Stromeyer *et al.*, 1993). Over this same velocity range the contour for motion detection steepened considerably: at 1 deg/sec the slope is ~1.0 (Fig. 14), whereas at 9 deg/sec, it is almost vertical (Fig. 15) reflecting a strong attenuation of the M-cone signal (Stromeyer *et al.*, 1990). We have measured complete motion contours on 3 observers from 1 to 21 deg/sec, and detection

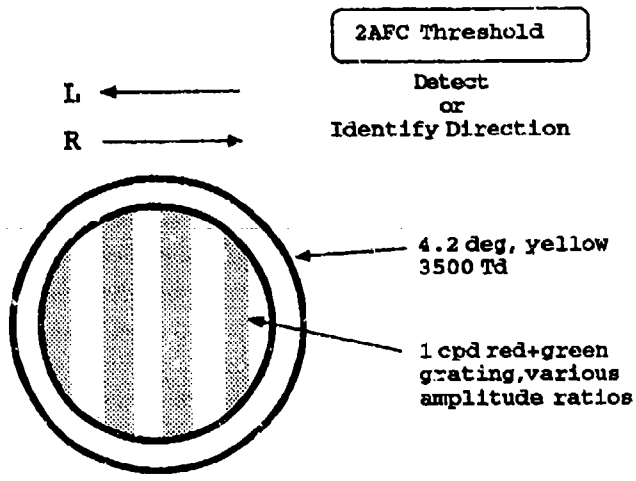


FIGURE 13.

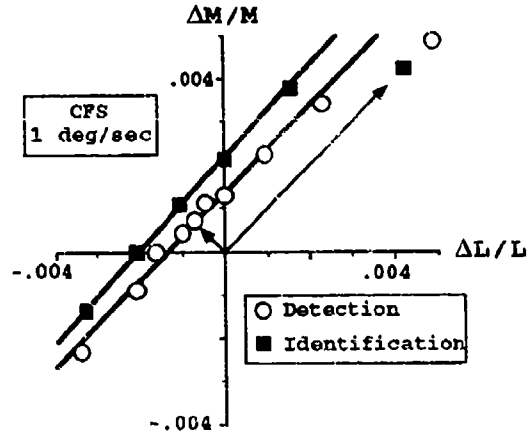


FIGURE 14.

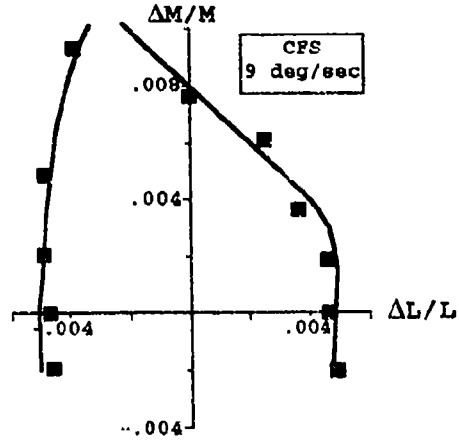


FIGURE 15.

contours over a more limited range. The data suggests there may be three motion mechanisms: a luminance motion mechanism (LUM) that sums L and M signals, a spectrally-opponent motion mechanism (SPO) that responds to the difference of L and M signals, and a red-green hue mechanism (RG) that signals hue and has balanced, opponent L and M inputs.

We have developed techniques to separate the LUM and SPO motion mechanisms (even when one mechanism is much less sensitive than the other), in order to assess the relative L and M contrast weights and relative L and M temporal phases within each of the two motion mechanisms. We use a quadrature protocol (Stromeyer *et al.*, 1984, 1991) for this purpose. Figure 16 shows profiles of two counterphase flickering gratings, of the same spatial and temporal frequency, that are summed with a spatial and a temporal phase difference of 90 deg (they are in spatial-temporal quadrature phase). If the two patterns were, for example, identical luminance gratings, the sum would produce a simple right-moving pattern. Inverting the temporal phase of one pattern relative to the other produces reversed, left motion. Now imagine we could choose the spectral composition of each pattern (its vector orientation in cone-contrast space) so that one pattern stimulated only the luminance motion mechanism (LUM) and the other only the spectrally-opponent motion mechanism (SPO). Each mechanism would signal a standing-wave with no net left or right motion. Both patterns must stimulate a common mechanism to produce motion.

Now let us consider how this technique can be used to measure the less-sensitive LUM motion mechanism at 1 deg/sec (Fig. 14). We

orient the cone-contrast vector angle of one counterphase pattern to be *parallel* to the SPO motion contour. Since the angle is parallel to the SPO contour, the pattern does not stimulate SPO, but does stimulate LUM. We call this counterphase pattern the 'pedestal'--it is kept weak and constant for the experiment. We add, in spatial-temporal quadrature to the pedestal, various counterphase 'test' patterns having different red-green light mixtures (Fig. 17), and measure the test contrast required for discriminating left versus right motion. Figure 18 shows a series of thresholds determined in this manner--this gives the LUM contour slope. Knowing this slope, we can also perform the converse experiment, to measure the SPO contour: we now orient the pedestal slope parallel to the LUM contour, and obtain the thresholds in Fig. 19. Figure 20 shows the *slopes* of the SPO and LUM motion mechanisms obtained with the quadrature protocol and compares them to direction thresholds for simple moving gratings. The SPO contours are similar with both procedures, but the less sensitive LUM contour can only be revealed with the quadrature protocol.

We used the quadrature protocol to measure the L and M weights in the LUM mechanism: at low velocities the L weight predominates over M, whereas at high velocities the weights are more equal. A similar variation in L and M weights with temporal frequency has been observed in retinal M-ganglion cells (Lee *et al.*, 1989). Thus a *single* equiluminant (motion null) setting is not valid at all temporal frequencies--the motion 'photometric' null varies with temporal frequency.

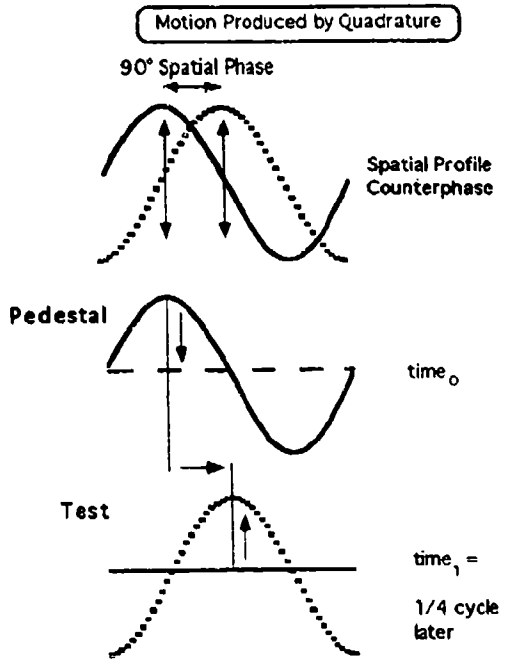


FIGURE 16.

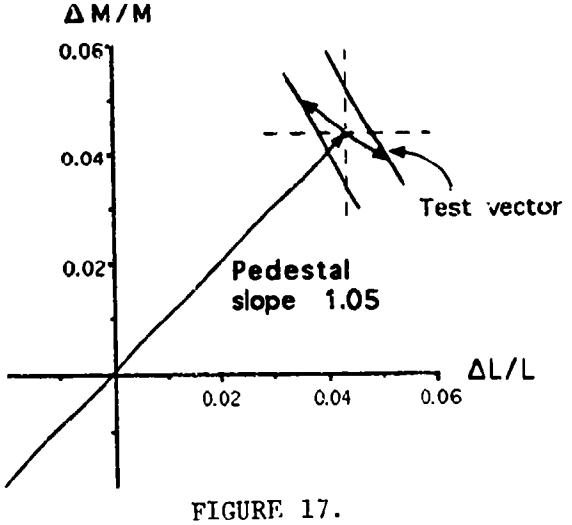


FIGURE 17.

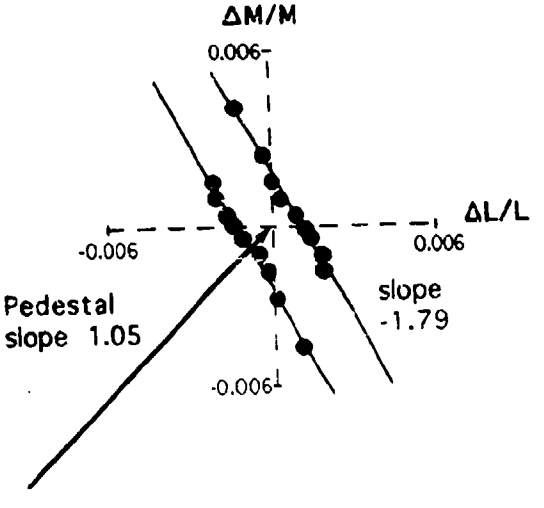


FIGURE 18.

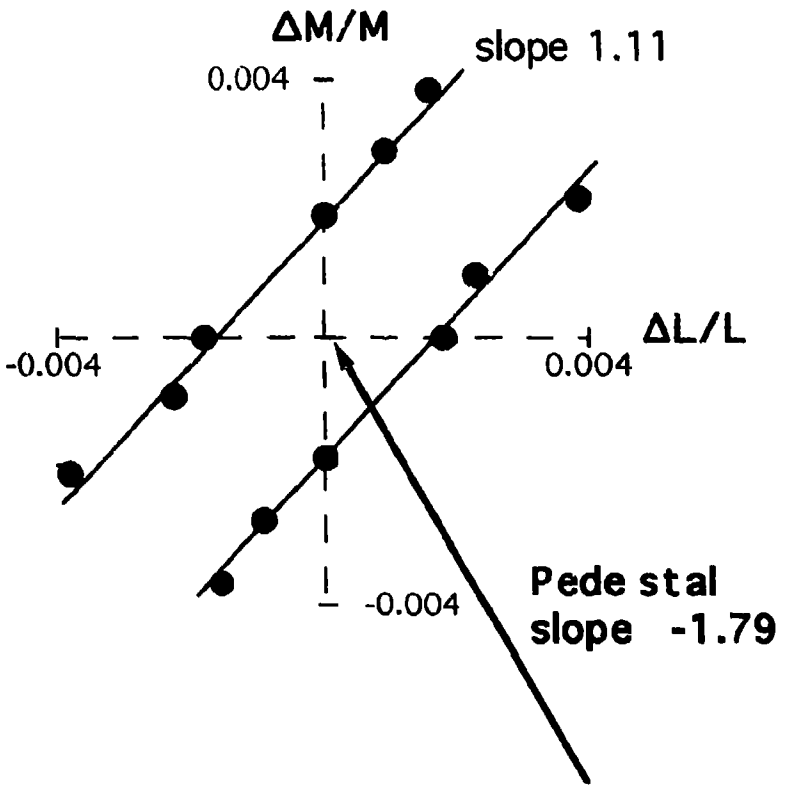


FIGURE 19.

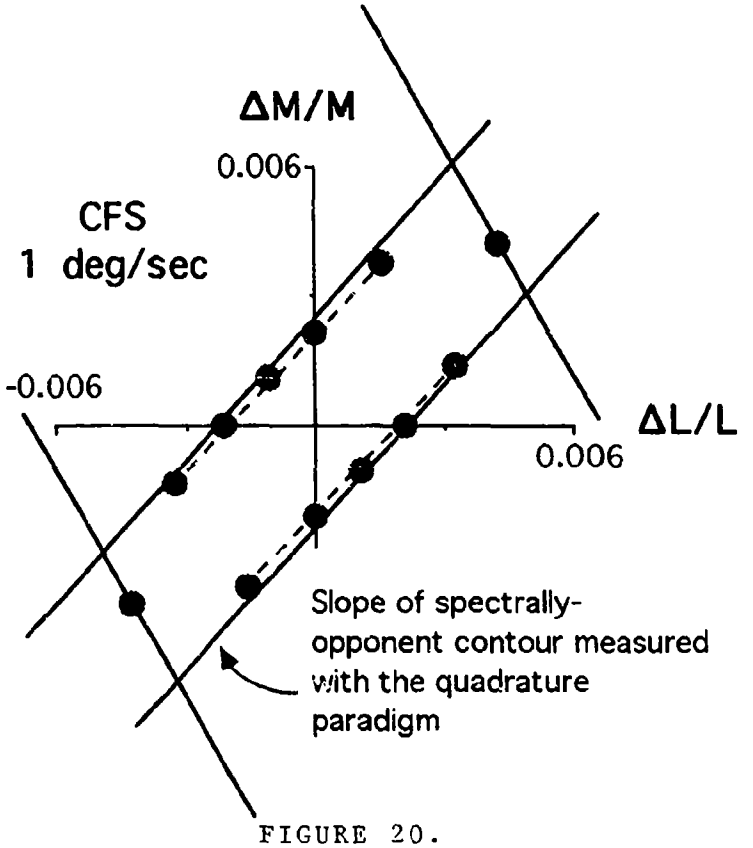


FIGURE 20.

A variation of the quadrature protocol was used to measure the relative temporal phase of the L and M signals within the LUM motion mechanism (Stromeyer *et al.*, 1992b). The counterphase pedestal is again oriented in cone-contrast space to stimulate essentially only LUM. We first pair the pedestal with a pure L-cone counterphase test and then a pure M-cone test. The pedestal and test are in spatial quadrature phase, as before. We vary the temporal phase of each of the L-test and M-test, in turn, to find a motion null. It can be shown mathematically that the L versus M phase shift in LUM is the difference of the phase shifts required to find the motion null for the L-test versus M-test patterns. The phase shifts are surprisingly large: ~30 deg temporal phase lag of the L signal versus M at 4 to 9 Hz, with the phase weakly reversing at 21 Hz. Similar properties have been observed in the retinal M-ganglion cells (Smith *et al.*, 1992). These large phase shifts have important consequences for other investigators, for they indicate that high-contrast nominally 'equiluminant' red-green drifting gratings may directly stimulate the luminance mechanisms. Since the L signal lags M, the 'equiluminant' red and green stripes will not be in effective antiphase--thereby introducing a luminance component.

Preliminary observations suggest that these phase shifts largely disappear when we raise the spatial frequency from 1 cpd to 2 cpd. The large phase shifts in M-ganglion cells are caused by the receptive field surround (Smith *et al.*, 1992), and the higher spatial frequency may better isolate the center response of the

receptive field. Similar measurements of SPO at 1 cpd show only very small phase shifts.

While our data suggest that there are two motion pathways with distinct properties, LUM and SPO, much work remains to understand how signals from these two pathways combine at suprathreshold levels.

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