

Selective cone suppression by the L–M- and M–L-cone-opponent mechanisms in the luminance pathway

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We investigated how transient changes of background color influence the L- and M- (long- and middle-wavelength-sensitive-) cone signals in the luminance pathway. Motion identification thresholds were measured for a drifting sinusoidal grating (1 cycle/deg) modulated along different vector directions in L- and M-cone contrast space. The color of a central 4-deg-diameter region was briefly altered (500 ms) by incrementing or decrementing either L- or M-cone excitation. Incrementing L-cone and decrementing M-cone excitation produced a field that appeared reddish relative to the yellow surround. Likewise, incrementing M-cone and decrementing L-cone produced a field that appeared greenish. Motion identification thresholds were obtained on the yellow field following the brief color transitions. The results show that the threshold for the L-cone direction was selectively elevated by the background substitution of incrementing L-cone and decrementing M-cone excitation (shift toward reddish color). The same substitution, however, did not affect the threshold in the M-cone direction. Similarly, the threshold for the M-cone direction was selectively elevated by the background substitution of incrementing M-cone, decrementing L-cone excitation (shift toward greenish) without affecting the threshold in the L-cone direction. Experiments using the motion quadrature paradigm confirmed that these effects occur within the luminance mechanism. These results indicate that the activation of L-on plus M-off signals suppresses the L-cone signal and that the activation of L-off plus M-on signals suppresses the M-cone signals in the luminance pathway. We propose a retinal model based on the experimental results. © 1999 Optical Society of America [S0740-3232(99)00506-2]

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1. INTRODUCTION

Several studies have shown that a colored background field affects the ratio of inputs from the long and middle-wavelength-sensitive (L and M) cones to the luminance mechanism. For example, De Vries¹ showed that the equiluminant point of red and green flicker photometry is strongly affected when intense red or blue background is used. Eisner and MacLeod² suggested that such an effect is due to the suppression of L- or M-cone input to the luminance mechanism by the background color.

Recent studies suggested that cone-selective suppression is related to the background hue or to chromatic responses rather than to the mean quantal catch of each cone.^{3–5} Stromeyer *et al.*³ measured flicker detection thresholds for red and blue-green backgrounds, which had identical L-cone excitations, and found that the L-cone signal was suppressed by the red background. Similarly, Stockman *et al.*⁵ showed that the L-cone signal

was suppressed when the background color was changed and the mean L-cone quantal catch was kept constant. They replaced a bright blue background with a bright red background (we call them preceding and concurrent background here) and measured threshold for detecting a flicker stimulus that was superimposed on the concurrent background. They found that the L-cone signal was suppressed by the background substitution and, similarly, that the M-cone signal was suppressed when a bright red background was replaced by a bright blue one. These results suggest the existence of chromatic suppression in the luminance pathway.

The purpose of our study is to specify the relationships between the luminance mechanism and the chromatic mechanisms that suppress it. We modified the method of Stockman *et al.*⁵ in the following ways for that purpose. First, in order to compare the effects of different preceding backgrounds directly, we fixed the color of the concur-

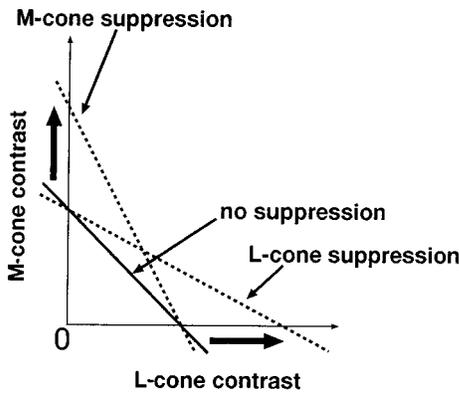


Fig. 1. Hypothetical threshold of the luminance mechanism and its change in slope in L- and M-cone contrast space. A straight line with negative slope of -1 represents a threshold contour detected by the luminance mechanism. When the L-cone signals are selectively suppressed by background substitution, the threshold along the L-cone axis should be elevated, with the consequence that the threshold contour will have a flatter slope. On the other hand, when the M-cone signals are selectively suppressed, the threshold contour will have a steeper slope.

rent background to yellow throughout the experiments instead of using two concurrent backgrounds as in the experiment of Stockman *et al.* Second, the background color was replaced in the direction along either the L- or the M-cone axis in the cone-excitation coordinates (cone luminance space). The suppression may be at the post-receptor cone-opponent site, because the suppression occurs even with silent substitution for each type of cone. Third, we used test gratings modulated along various directions in a cone contrast space to estimate the possible contamination of the chromatic mechanism(s). If the slope of the threshold contour becomes positive, for example, this suggests that the part of the threshold contour is mediated by the chromatic mechanism(s) (that is, L-M or M-L in the space is expressed by a line with a positive slope).

Figure 1 shows the effect of selective suppression on the threshold contour in a cone contrast space. The horizontal axis corresponds to L-cone contrast. Test gratings that are modulated along this axis drive L-cones only and are called L-cone gratings. The vertical axis corresponds to M-cone contrast, and test gratings modulated along this axis drive M-cones only and are called M-cone gratings. Suppose that a solid line with negative slope of -1 represents the threshold contour of the luminance mechanism, which linearly sums the L- and M-cone signals with the same weights. When the L-cone signal is selectively suppressed by background substitution, the threshold along the L-cone axis will be elevated, so that the slope of the threshold contour will decrease. On the other hand, when the M-cone signal is selectively suppressed, the slope of threshold contour will increase, as shown in the figure. Therefore measuring the slope of threshold contour will reveal the existence of the suppression effect.

In experiment 1 we measured the threshold contours in a cone contrast space for motion identification of simple moving gratings with five preceding backgrounds. In experiment 2 we reexamined the effect of the preceding background by quadrature protocol to confirm that the

suppression effect was on the luminance mechanism. Finally, we propose a retinal model to explain the suppression effect and describe the results of a supplemental experiment that support the model.

2. GENERAL METHODS

In this section experimental methods that were used throughout the experiments are described.

A. Apparatus

A stimulus is displayed on a color monitor (Sony Multiscan 17seII) of $19^\circ \times 25^\circ$ screen size, which is controlled by a video controller (Cambridge Research Systems VSG2/3). The resolution of the monitor is 640×480 pixels and the frame rate is 100 Hz. Each phosphor is driven by a 12-bit digital-to-analog converter. Cone excitation is calculated according to the spectral sensitivity function given by Smith and Pokorny⁶ and the spectral radiation of each phosphor, measured by Photo Research PR-704. Two observers, ST and YT, participated in the experiments. They were seated 64 cm in front of the monitor.

B. Stimulus

The spatial and temporal configuration of the stimulus is shown in Fig. 2. As shown in the top part of the figure,

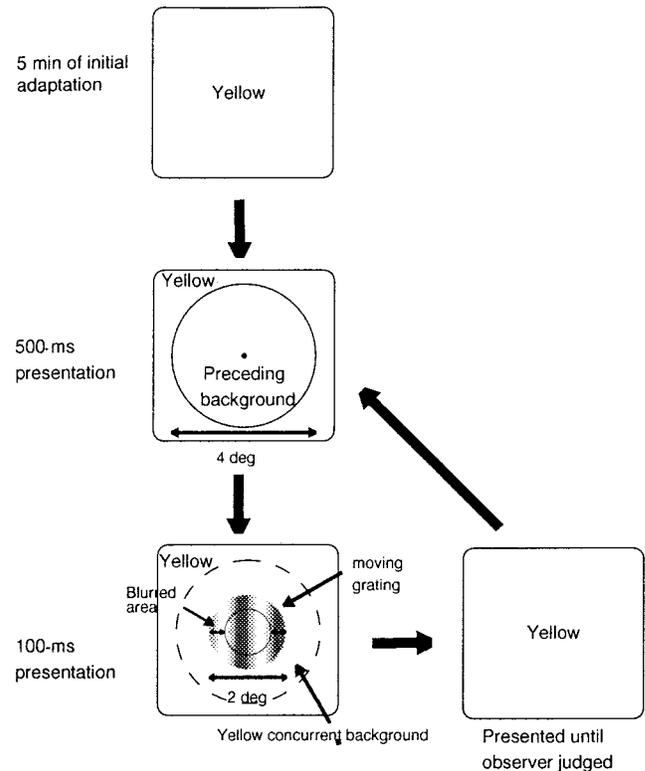


Fig. 2. Spatial and temporal configuration of the stimulus in the experiments. The test grating was displayed in a circular field with a diameter of 2° at the center of the display surrounded by a uniform field of the same color as the average of the test grating. In each trial the preceding background was presented in a circular field of 4° at the center of the display for 500 ms, and then the moving test grating with a yellow concurrent background replaced the field.

before each session each observer was adapted to a yellow adapting field with full screen size for 5 min. The luminance of the adapting field was 35.4 cd/m^2 , which corresponded to the retinal illuminance of 640 td for observer ST and 360 td for observer YT with their natural pupils.

After the initial adaptation a session of experimental trials began. Each trial consisted of (1) 500-ms presentation of a preceding background, (2) 100-ms presentation of the moving test grating on the yellow concurrent background, and (3) presentation of a yellow adapting field that lasted until the judgment of the direction of motion of the test grating was reported. In each session, this trial was repeated until the observer's judgments converged, with use of a staircase procedure.

The preceding background was a circular region of 4-deg diameter and was presented at the center of the screen. The color was altered for 500 ms by incrementing or decrementing either L- or M-cone excitation. Incrementing L-cone and decrementing M-cone excitation produced a field that appeared reddish relative to the yellow surround. Conversely, incrementing M-cone and decrementing L-cone excitation produced a field that appeared greenish. There were five preceding colors, whose positions in the cone-excitation coordinates are shown in Fig. 3. Two of the preceding colors are $\pm 3.0 \text{ cd/m}^2$ away from the mean color of the test grating (the origin in the figure) along the L-cone axis, and the other two are $\pm 3.0 \text{ cd/m}^2$ away along the M-cone axis. We also used the mean color as the preceding background for a control condition. The CIE coordinates of these preceding colors are (0.45, 0.44), (0.34, 0.51), (0.29, 0.56), (0.49, 0.39), and (0.40, 0.47). These preceding colors were chosen to stimulate either the L or the M cones dominantly within the limitation of our apparatus with no change in the stimulation to the short-wavelength-sensitive (S) cones.

The five preceding colors were named +L (light red), -L (dark green), +M (light green), -M (dark red) and Y (yellow), and the five substitution conditions were named +L to Y, -L to Y, +M to Y, -M to Y and Y, respectively. The fractions of the preceding background luminance for L-cone (i.e., r in the cone excitation diagram proposed by MacLeod and Boynton⁷) were 0.69 for +L, 0.61 for +M, 0.64 for -L, 0.73 for -M, and 0.67 for Y (identical to that of the monochromatic light of 570 nm).

After 500-ms presentation of preceding background, a moving test grating and the concurrent background were presented for 100 ms. The test grating was displayed in a circular region of 2-deg diameter at the center of the screen. The circumference of the grating, which was an annular area of 0.24-deg width, was blurred by decreasing the contrast of the grating linearly. The size of the test grating was chosen so that our results could be directly compared with the results by Stockman *et al.*⁵ and Stromeyer *et al.*³ The spatial frequency of the test grating was set to 1 cycle per degree (c/deg) throughout the experiments. It was moved either left or right at 10 Hz, and the observer's task was to make a two-alternative forced-choice of the direction of motion. We used the motion identification task because we felt that it makes the observer's task easier than do flicker detection tasks. It has been shown that the threshold for motion identification and that for flicker detection are similar in foveal

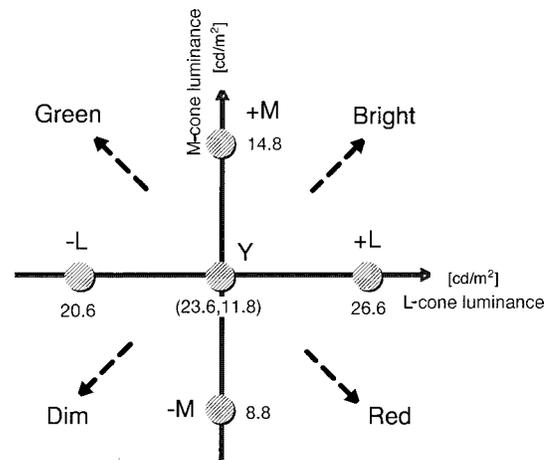


Fig. 3. Five colors of preceding backgrounds used in the experiments in L- and M-cone-excitation coordinates (cone luminance space). Two colors are $\pm 3.0 \text{ cd/m}^2$ away from the average color of the test grating (yellow) along the L-cone axis (-L and +L), and the other two colors are $\pm 3.0 \text{ cd/m}^2$ away along the M-cone axis (-M and +M). We also used as a control a yellow preceding background (Y) that is the same as the concurrent background color. The five substitutions are named +L to Y, -L to Y, +M to Y, -M to Y, and Y. The directions of color and brightness change are indicated by arrows.

vision,⁸ and we assumed that the two processes access the same luminance mechanism.

In experiment 1, a mixture of sinusoidally modulated L- and M-cone signals, which was moved at 10 Hz, was used as a test grating. In experiment 2, a yellow pedestal grating was superimposed on the mixture used in experiment 1, but both gratings were flickered, not moved according to the quadrature protocol proposed by Stromeyer *et al.*⁹ By varying the contrast, we could measure the motion identification threshold along one vector direction in cone contrast space (i.e., vector length). By varying the ratio of the mixture, we could change the vector direction in cone contrast space. Since any pair of two mixtures with 180-deg difference in their directions are essentially the same stimuli, the threshold measurements can be confined to two quadrants of the cone contrast space.

We chose the color of the concurrent background as yellow with $r = 0.67$ because it minimizes the variation in the suppression effect that will occur when the mean luminance level, the temporal frequency, or the spatial frequency of test grating is changed. On the 570-nm yellow field, Pokorny *et al.*¹⁰ showed that the red-green ratio in flicker detection was approximately constant with respect to change in the mean luminance levels. Stromeyer *et al.*¹¹ also showed that the ratio of L- and M-cone inputs to the luminance mechanism was constant with respect to the change in spatial and temporal frequencies.

C. Threshold Measurements

A staircase procedure was used to measure the contrast threshold at which the direction of motion was identified correctly 79% of the time. The contrast was lowered by 0.1 log unit after three successive correct responses and increased by the same amount after each error. Each threshold was estimated from the average of the last 8–12

reversals in one session, and the observers ran two sessions for each condition. Thresholds were measured for 12 different vector directions in cone contrast space (0 to 165 deg in 15-deg steps) in a session by interleaving staircases (one staircase for each direction). Two observers (YT and ST) with normal color vision (Ishihara plates) participated throughout the experiments.

3. EXPERIMENT 1: SIMPLE MOVING GRATING

A. Methods

In this experiment a mixture of sinusoidally modulated L- and M-cone signals was used as a test grating whose spatial frequency was set to 1 c/deg, and it was moved either left or right at 10 Hz. The contrast was modulated along the various vector directions in cone contrast space. Each test grating was presented for 100 ms to isolate the luminance mechanism from the chromatic mechanism(s).¹²

B. Results

The threshold contours of motion identification obtained under five different preceding backgrounds are shown in Figs. 4 and 5 for observers ST and YT, respectively. In each figure the results for five preceding backgrounds are summarized in five panels that are arranged according to the relative positions of the preceding backgrounds. The preceding background is expressed by a symbol in the lower left corner of each panel.

If the luminance mechanism linearly sums L- and M-cone signals, the motion identification thresholds will become a straight line with a negative slope in the cone contrast space. The results, however, show that they are fitted well by an ellipse contour whose principal axis has a negative slope. There are two possible reasons that the threshold contour is expressed as an ellipse instead of lines. First, the shape can be the consequence of the temporal phase shift or the delay between the L- and M-cone signals to the luminance mechanism.^{13,14} There might still be a small phase shift even in the condition of 570-nm-field color for our observers. While Stromeyer *et al.*³ showed that the phase shift is approximately zero on a 570-nm field, they also found relatively large inter-observer differences in the phase shift. However, with the phase shift or delay, it is shown theoretically that the threshold contours determined by the luminance mechanism become an ellipse^{11,15} (see Appendix A). In this case, the direction of the slope of the principal axis of the ellipse corresponds to the slope of the threshold contour without a phase shift.

Second, the threshold near the direction of the principal axis of an ellipse may be determined by chromatic mechanism(s). Since the temporal conditions of the experiment were chosen to isolate the luminance mechanism, the chromatic mechanism(s) could have contributed to the threshold when the sensitivity of the luminance mechanism was very low, i.e., near the direction of the principal axis of the ellipse. In this case the slope of the principal axis should be determined mostly by the data in the high-sensitivity regime, i.e., near the direction of the L+M luminance axis. Indeed, the result shows that the

slope of the principal axis of the ellipse is very similar to the slope of the imaginary line that represents the data in the first (or third) quadrant. Following the above considerations, we used the slope of the principal axis of the ellipse to estimate the relative contribution of the L- and M-cone signals to the luminance mechanism here.

The magnitude of the slope for each substituting condition is shown in the upper-right corner of each panel. The slopes of the -L to Y and +M to Y conditions are 0.74 and 0.66 times smaller, respectively, than the slope of the control condition denoted by Y. On the other hand, the slopes of the -M to Y and +L to Y conditions are 3.69 and

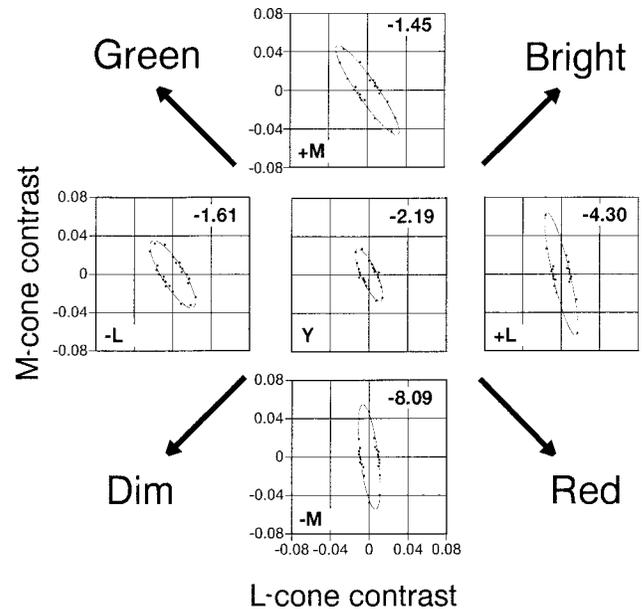


Fig. 4. Motion threshold contours in five substituting conditions in L- and M-cone contrast space for observer ST. The arrangement of the panels corresponds to the arrangement of the preceding background colors in Fig. 3. The value at the upper right of each panel represents the slope of the threshold contour.

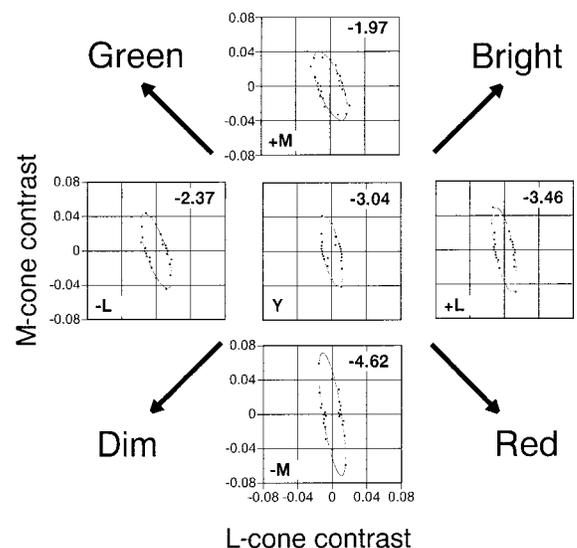


Fig. 5. Motion threshold contours in five substituting conditions in L- and M-cone contrast space for observer YT. The arrangement of the panels corresponds to the arrangement of the preceding background colors in Fig. 3. Configurations are the same as in Fig. 4.

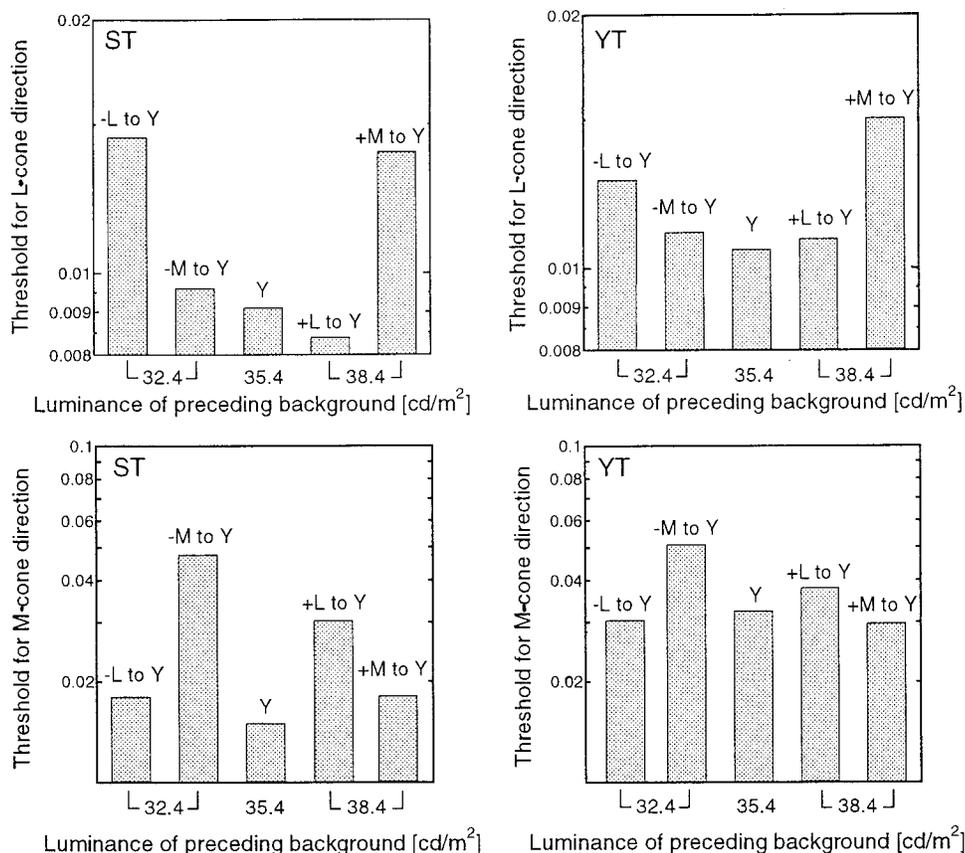


Fig. 6. The thresholds for L- and M-cone direction for two observers. The top row represents the thresholds for L-cone direction (L-cone thresholds), and the bottom row represents the thresholds for M-cone direction (M-cone thresholds). The $-L$ to Y substitution elevated the L-cone thresholds, but it had little effect on M-cone thresholds. The $+M$ to Y substitution also elevated the L-cone thresholds, whereas the substitution had no effect for L-cones. Similarly, $+L$ to Y and $-M$ to Y substitutions elevated the M-cone thresholds, with little effect for L-cone thresholds.

1.96 times larger, respectively, than the slope of the control condition. These results suggest that incrementing L-cone and decrementing M-cone ($+L-M$) signals will suppress L-cone inputs to the luminance mechanism and that incrementing M-cone and decrementing L-cone ($+M-L$) signals will suppress M-cone inputs.

However, the slope change may come from facilitation of the cone signal instead of its suppression. To examine whether it comes from suppression or facilitation, we compared the thresholds for L- and M-cones directly, as shown in Fig. 6. The top-left panel shows L-cone thresholds for observer ST, and the top-right panel shows those for observer YT. The bottom-left panel shows M-cone thresholds for ST, and the bottom-right panel shows those for YT.

As seen in the results, $-L$ to Y substitution elevates L-cone thresholds but has little effect on M-cone thresholds. The same is true for the $+M$ to Y condition. On the other hand, $+L$ to Y and $-M$ to Y substitutions elevate M-cone thresholds but have little effect on L-cone thresholds. From these results, it can be concluded that the slope change comes from suppression, not from facilitation.

The results also suggest that the elevation in the L- or M-cone threshold is not due to the luminance change produced by the background substitution, because the same

amount of luminance changes produced different effects when the chromatic changes were different. For example, elevation of the L-cone threshold can be seen in the $+M$ to Y condition but not in the $+L$ to Y condition despite the fact that the two conditions have identical luminance changes. The same is true for the M-cone threshold.

From these results, two important conclusions can be drawn regarding the possible mechanism of cone-selective suppression. First, the suppression may be at the postreceptoral cone-opponent site, because the suppression occurs in the L- (or M-) cone direction even when the background substitution does not change the activation of the cone (cone silent substitution). Second, there are separate suppression mechanisms in L- and M-cone pathways, because each substitution condition affects only one cone type.

In Section 4 the above results are further examined by a quadrature protocol, and we propose a model of cone-selective suppression on the basis of the cone-opponent mechanism.

4. EXPERIMENT 2: QUADRATURE PROTOCOL

To confirm that the variation of the threshold for motion identification of the test grating that was observed in ex-

periment 1 comes from the suppression of a cone signal in a luminance mechanism, we employed the quadrature protocol to eliminate the contribution of chromatic mechanism(s) in the threshold measurements. It was proposed by Stromeyer *et al.*,⁹ who modified the minimum-motion paradigm that had been developed by Anstis and Cavanagh.¹⁶ Stromeyer *et al.*⁹ applied the protocol to measure the relative contributions from L and M cones to the luminance mechanism.

A. Methods

The experimental procedure is the same as in experiment 1 except for the configuration of the test stimulus. The test stimulus is a superposition of a pair of flickering

sinusoidal gratings: One is a test grating whose color and contrast can be changed, and the other is a luminance pedestal grating whose color and contrast are fixed. They have identical spatiotemporal frequencies of 1 c/deg and 10 Hz, respectively. The phase between the two gratings is shifted by 90 deg in the spatial and temporal domain, that is, in the spatiotemporal quadrature phase. Neither of the gratings alone produces motion perception. When they are presented together in a superimposed form, apparent motion will be perceived from the interaction between the two gratings.

An example of the test stimuli is schematically illustrated in Fig. 7. To simplify the illustration, each sinusoidal grating is shown as a rectangular one. A test grat-

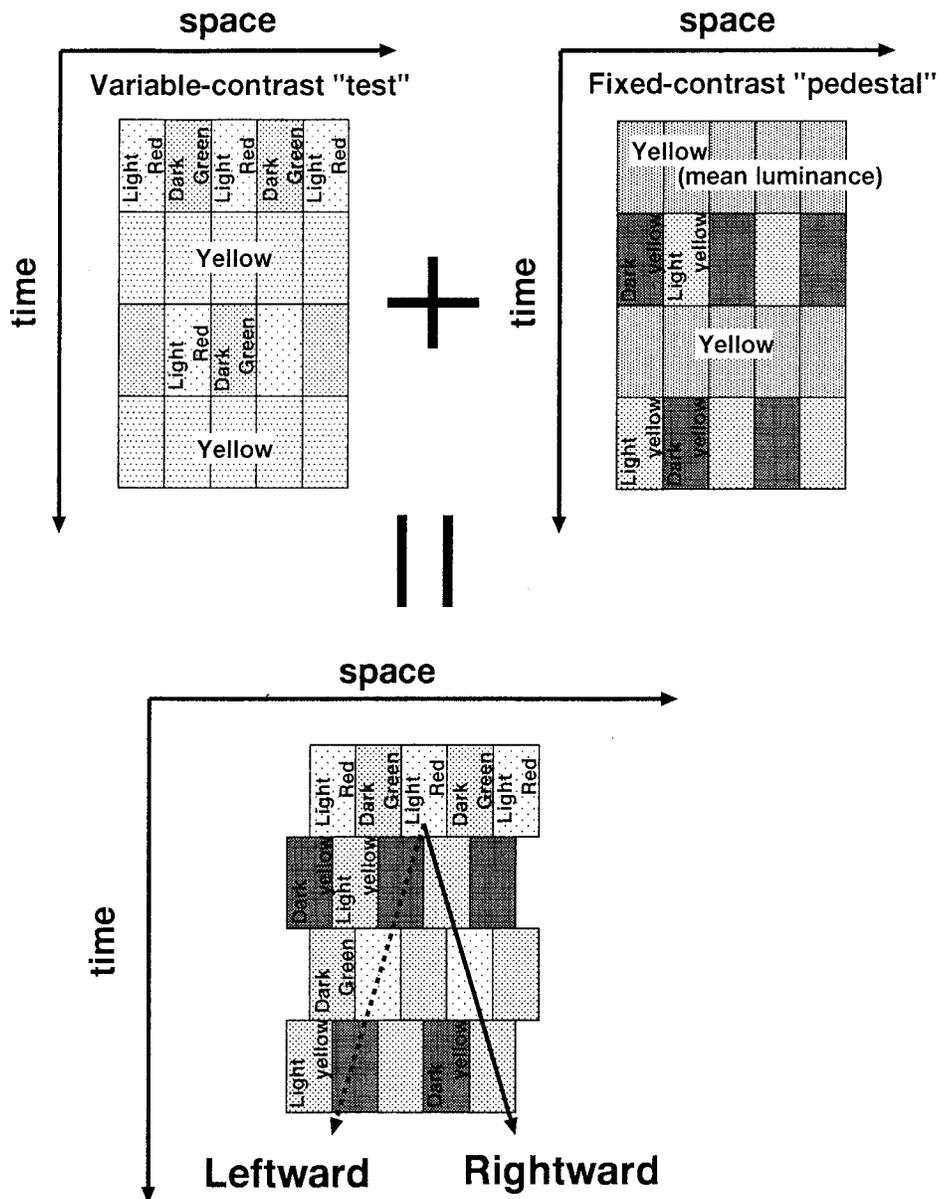


Fig. 7. The spatiotemporal properties of the stimulus in the quadrature protocol. The red-green test stimulus was added to the light-dark yellow pedestal stimulus with a shift of 90° in temporal and spatial phase. Neither of these stimuli alone produces any net motion, and only the interaction of the two stimuli can produce the motion perception. A net rightward motion will be perceived in this case because the luminance of red light is greater than that of green light. Note that rectangular gratings are used to simplify the illustration. The actual stimulus consisted of sinusoidal gratings.

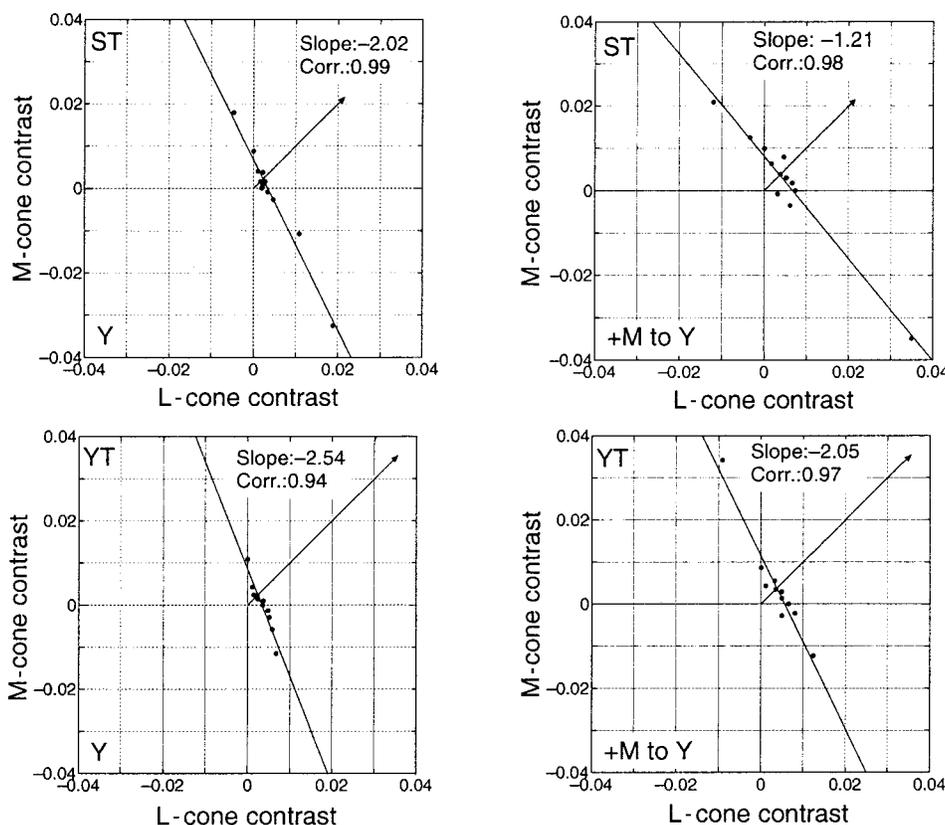


Fig. 8. Motion identification contours assessed by the quadrature protocol in **Y** and **+M to Y** conditions for observer ST (top row) and observer YT (bottom row). The values at the upper right of each panel represent the slope of the fitted line and the correlation coefficient. The arrow represents the pedestal grating used. The fact that the threshold contour in the **+M to Y** condition had a flatter slope than that in the **Y** condition suggests that the **+M to Y** substitution suppressed the L-cone signals.

ing consists of a chromatic grating that is modulated by 135-deg in cone contrast space and is also temporally modulated as shown in the figure. If there is a luminance difference between the red and the green components of a grating, it will produce a motion percept moving either left or right that is induced by a pedestal grating composed of only luminance components.

By adjusting the contrast of the test grating to the threshold at which no motion percept occurs, we can measure motion thresholds of the luminance mechanism. We used a pedestal grating that was modulated at 45 deg in cone contrast space, with the contrast approximately four times larger than the threshold of the simple moving grating. Each test stimulus was presented for 100 ms as in experiment 1. Only the **Y** and **+M to Y** conditions were used in this experiment.

B. Results

The threshold contours obtained by the quadrature protocol in the **Y** and **+M to Y** conditions are shown in Fig. 8. The contours reduced to straight lines for all conditions. To estimate the relative L- and M-cone weights in each condition, we fitted a straight line to the data; it is shown as a solid line in each panel. The correlation coefficients of the fits were greater than 0.94 in every case.

The slope of the fitted line was -2.0 and -1.2 in the **Y** and **+M to Y** conditions, respectively, for observer ST and -2.5 and -2.1 , respectively, for observer YT. These values are close to those obtained in experiment 1. There-

fore it can be concluded that cone-selective suppression occurs only in the luminance mechanism.

5. DISCUSSION

A. Effect of Phase Shift

Strictly speaking, the effect of cone-selective suppression cannot be estimated directly from the slope of the threshold contour. Equation (A3) in Appendix A shows that the phase shift between L- and M-cone signals influences the slope of the threshold contour. In the extreme case, we can think that there is a phase shift of 180 deg between L- and M-cone signals. The slope of the threshold contour is positive in that case. However, there should be no effect of phase shift when threshold elevation is compared for L- and M-cone directions (i.e., Fig. 6). Since phase shifts should not influence the thresholds in either cone direction, the results of each cone direction must be due primarily to the change in cone weights. The fact that the same conclusion was derived from the comparison between the L- and M-cone thresholds and from the original slope analysis indicates that there was little effect of phase shift in our experimental conditions.

B. Selectivity of Suppression

Stockman *et al.*⁵ and Stromeyer *et al.*¹¹ isolated L and M cones by using background substitutions. The results of Stockman *et al.*¹¹ suggest that there are cone-selective suppressions caused by the chromatic mechanism since

the suppression in the L- (or M-) cone direction was produced by a background substitution that did not change the activation of the cone as well as by a background substitution that did not change the luminance. We found that a specific type of chromatic mechanism is responsible for the suppression of each type of cone signal. The increment or “on” state of the signal along the L-cone direction (L-on) and the decrement or “off” of the signal along the M-cone direction (M-off) suppressed the L-cone inputs to the luminance pathway. Similarly, the L-off and M-on signals suppressed the M-cone inputs. In contrast, L-on and M-off did not affect the M-cone inputs, and L-off and M-on did not affect the L-cone inputs. Since the amount of change in the mean quantal catches was the same as that in the conditions, the suppression has to occur at the postreceptoral site, and two independent suppression mechanisms are required. We claim that the L-on plus M-off ($L^+ + M^-$) cone-opponent mechanism suppresses the L-cone signal and that the L-off plus M-on ($L^- + M^+$) cone-opponent mechanism suppresses the M-cone signal (see the model below).

Another important aspect of our results is the experimental conditions. We found selective suppression under conditions that are much less extreme than those used by Stockman *et al.*⁵ and Stromeyer *et al.*,¹¹ although the amount of the suppression was weaker than theirs. They used intense adapting fields to get full isolation (above 1000 td), whereas we used a low adapting intensity to get partial isolation. This indicates that the use of the appropriate test and background colors makes it possible to show the suppression effect without intense lights.

C. Retinal Model of Cone-Selective Suppression

Our results suggest the evidence of two separate cone-opponent mechanisms, each of which suppresses either the L- or the M-cone signal in the luminance pathway. The luminance pathway has been considered to be mediated by parasol retinal ganglion cells projecting to the magnocellular laminae in the lateral geniculate nucleus. We assume that the cone-selective suppression observed in our experiments occurs in the magnocellular pathway since the suppression is within the luminance pathway. To explain our results, we propose a functional model of this suppression process. The structure of the model is illustrated in Fig. 9.

The model consists of three processing stages. The first stage is an input layer composed of cones. The second stage consists of a luminance cell that projects to the cells at a higher stage of the magnocellular pathway. Although the luminance cell might receive inputs from S cones, we do not take this into account, because there was change in stimulation to the S cones in our experiment. The third stage consists of two types of cells, named $L^- + M^+$ and $L^+ + M^-$ cone-opponent cells. The $L^- + M^+$ cell receives signals from the cell that is sensitive to decrements in the L-cone signal and the cell that is sensitive to increments in the M-cone signal. Similarly, the $L^+ + M^-$ cell receives signals from the cell that is sensitive to increments in the L-cone signal and the cell that is sensitive to decrements in the M-cone signal. Since these inputs are sensitive to either increments or decrements along

the L- or the M-cone axis, the cone-opponent cells are considered to half-wave rectify the signals. To realize the selective suppression, the cone-opponent cells modify the output signals of L and M cones by controlling the weights of the signals to the luminance cell ($1 > W_L, W_M > 0$).

The model can explain the pattern of suppression that we found. When an $L^+ + M^-$ cone-opponent cell is stimulated ($-L$ to Y and $+M$ to Y substitutions), the input from the L cone to the luminance cell is reduced. This causes threshold elevation in the L-cone direction. Similarly, when an $L^- + M^+$ cone-opponent cell is stimulated ($+L$ to Y and $-M$ to Y substitutions) the input from the M cone to the luminance cell is reduced, which causes threshold elevation in the M-cone direction. It is also important that the model can explain the small effect of the L-cone threshold in $+L$ to Y and $-M$ to Y substitutions and of the M-cone threshold in $+M$ to Y and $-L$ to Y substitutions. Since there is no connection from the $L^+ + M^-$ cone-opponent cell to the M-cone inputs, no effect of the L-cone threshold is expected in $+L$ to Y and $-M$ to Y substitutions. Similarly, no effect of the M-cone threshold is expected in $+M$ to Y and $-L$ to Y substitutions.

The possible sites of the luminance and the cone-opponent cells in the model are the bipolar and the amacrine cells, respectively. The luminance-type or L + M cells that receive L- and M-cone signals separately are likely to be the diffuse bipolar cells. After the diffuse bipolar cell level, the luminance signal becomes L + M and it is difficult to control L- and M-cone components separately. The reason we think that cone-opponent cells in the model are at the amacrine cell level is less definite, because to our knowledge, no physiological evidence has been reported for the cone-opponent-type cells at the other levels on the retina and people simply discuss the possibility of opponent-type amacrine cells.^{17,18} If this is

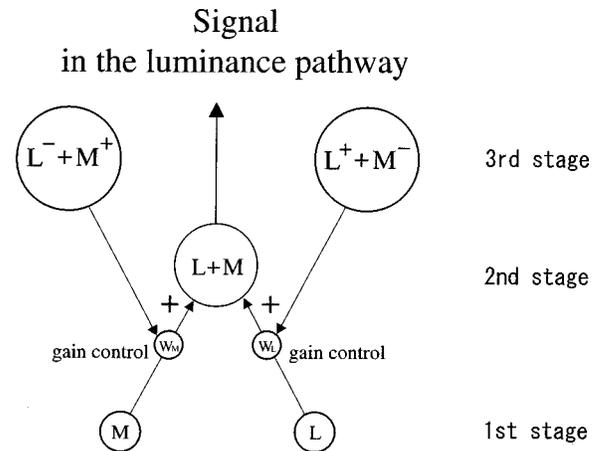


Fig. 9. Retinal model for cone selective suppression in the magnocellular pathway. The first stage is an input layer composed of cones. The second stage consists of a luminance cell that projects to the cells at the higher stage of the magnocellular pathway. The third stage consists of two types of cells, named $L^- + M^+$ and $L^+ + M^-$ cone-opponent cells. The $L^- + M^+$ cell receives the signals from the cell that is sensitive to decrements in the L-cone signal and the cell that is sensitive to increments in the M-cone signal. Similarly, $L^+ + M^-$ cell receives the signals from the cell that is sensitive to increments in the L-cone signal and the cell that is sensitive to decrements in the M-cone signal.

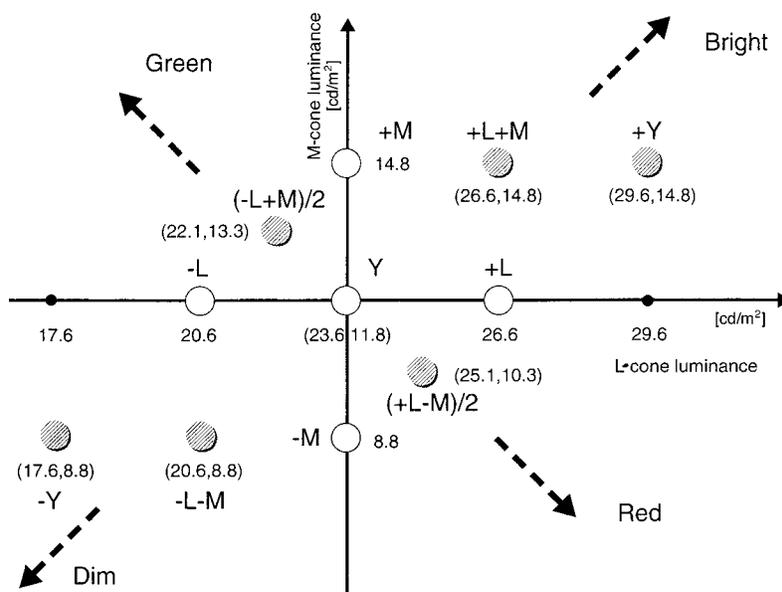


Fig. 10. Six colors of preceding backgrounds of the luminance and equiluminance axes in L- and M-cone luminance space (hatched disks). Two colors are for the equiluminance conditions ($-L + M$ to Y and $+L - M$ to Y), and the rest are for the luminance conditions ($+L + M$ to Y , $-L - M$ to Y , $+Y$ to Y , and $-Y$ to Y). The $+L + M$ and $-L - M$ preceding backgrounds are chosen along a 45–225-deg axis in cone-excitation space and appear bright green or dim red. The $+Y$ and $-Y$ preceding backgrounds are chosen along a monochromatic axis so that the color is not changed. The white disks represent the preceding backgrounds used in experiment 1.

the case, midget bipolar cells are candidates for being the cells projected to the cone-opponent cells, since the L^+ , L^- , M^+ , and M^- components are known. Of course, we have little physiological knowledge related to selective suppression in our conditions, and the physiological site and physiological plausibility of the model are issues to be examined further.

D. Supplemental Experiments: Background Substitutions along the Luminance and Equiluminance Axes

We conducted a supplemental experiment to test our model with additional background substitutions. Two important directions of background substitution that were not examined in the main experiment are the luminance and the equiluminance directions.

Figure 10 shows the six preceding backgrounds. Two are for the equiluminance conditions ($-L + M$ to Y and $+L - M$ to Y), and the rest are for the luminance conditions ($+L + M$ to Y , $-L - M$ to Y , $+Y$ to Y , and $-Y$ to Y). The $+L + M$ and $-L - M$ preceding backgrounds are chosen along a 45–225-deg axis in cone-excitation space and appear bright green and dim red, respectively. The $+Y$ and $-Y$ preceding backgrounds are chosen along a monochromatic axis so that the color is not changed. Along the equiluminance axis, the luminance changes along the L- and M-cone axes were one half of those in the other conditions [i.e., $(-L + M)/2$ and $(+L - M)/2$] because of the limitation of the gamut of the CRT display.

Our model predicts that L-cone threshold will be elevated by the background substitutions that activate $L^+ + M^-$ (i.e., $-L + M$ to Y , $+L + M$ to Y , $-L - M$ to Y , $+Y$ to Y , and $-Y$ to Y) but not by the background substitution of $+L - M$ to Y . It also predicts that the M-cone threshold is elevated by the background substitutions that acti-

vate $L^- + M^+$ (i.e., $+L - M$ to Y , $+L + M$ to Y , $-L - M$ to Y , $+Y$ to Y , and $-Y$ to Y) but not by $-L + M$ to Y . The same threshold measurements as in the first experiment were performed, but only observer ST participated in the experiment.

The panels in Fig. 11 show the L- and M-cone thresholds in the four luminance conditions with the data from the main experiment. The two left panels show the L-cone thresholds, and the two right panels show the M-cone thresholds. The upper panels are for the preceding backgrounds that have the $+L$ or the $+M$ component, and the lower panels are for the preceding backgrounds that have the $-L$ or $-M$ component.

The results shows clear elevation of the L-cone threshold compared with that in the control condition when the preceding background contained the $+M$ or the $-L$ component (dark bars), whereas little influence of background substitution was found in the other conditions. Similarly, clear elevation of the M-cone threshold was found when the preceding background contained the $+L$ or the $-M$ component (dark bars), whereas little influence of background substitution was found in the other conditions. Among the conditions that showed threshold elevation (dark bars), the amount of suppression is similar when the substitution along the axis of concern is the same: $+M$, $+L + M$, and $+Y$ preceding backgrounds for decrements in the M-cone signal (upper-left panel); $+L$, $+L + M$, and $+Y$ preceding backgrounds for decrements in the L-cone signal (upper-right panel); $-L$, $-L - M$, and $-Y$ preceding backgrounds for increments in the L-cone signal (lower-left panel); and $-M$, $-L - M$, and $-Y$ preceding backgrounds for increments in the M-cone signal (lower-right panel). There is only one exception: The threshold in the $-L - M$ condition was higher than the others for a decrement in the M-cone signal. Moreover, the threshold

elevation is larger when the substitution along the axis of concern is larger: $+Y$ in the upper-right panel and $-Y$ in the lower-left panel (see Fig. 10).

Interestingly, the cone-selective suppression is observed even for the case in which the background substitution was along the monochromatic direction ($+Y$ to Y and $-Y$ to Y conditions). The suppression by background substitution without color change cannot be explained by suppressive signals from cone-opponent cells with linear summation of L- and M-cone signals (i.e., $L-M$ or $M-L$) since the difference should be zero in the monochromatic conditions. Two separate mechanisms with half-wave rectification, such as L^-+M^+ and L^++M^- of our model, are necessary to explain the results.

Figure 12 shows the L- and M-cone thresholds in two equiluminant conditions. The results showed that the L-cone threshold was elevated only by the $(-L+M)/2$ preceding background and the M-cone threshold was elevated only by the $(+L-M)/2$, as the model predicts (dark bars in Fig. 12). These results again support our model with two separate mechanisms: the L^++M^- mechanism that suppresses the L-cone pathway selectively and the L^-+M^+ mechanism that suppresses the M-cone pathway selectively.

E. Comparison with Previous Models

Suppression by chromatic signals in the magnocellular pathway is also assumed in the elaborate computational models proposed by Smith *et al.*¹⁷ and Stromeyer *et al.*¹¹ Although their models are for steady backgrounds and therefore may not be directly comparable with ours, it is worth comparing our model with theirs to see the differences. There are three important differences of our model from the previous models. First, on and off cells have different roles in our model. In the models proposed by Smith *et al.*¹⁷ and Stromeyer *et al.*,¹¹ cone-opponent cells are defined as the cells that subtract the L-cone signal from the M-cone signal or vice versa (i.e., $+L-M$ and $+M-L$ cells). On and off cells are considered to be essentially the same units with a sign inversion. This implies that luminance signals (i.e., $+L+M$) do not activate these cells since they will activate L and M cones by the same amount and output signals of the cell are canceled. However, the results of the supplemental experiment show that this is not the case in our experimental conditions. The $+L+M$ preceding background, for example, acted as the $+L$ preceding background for the M-cone input to the luminance and as the $+M$ preceding background for the L-cone input. There is no interaction

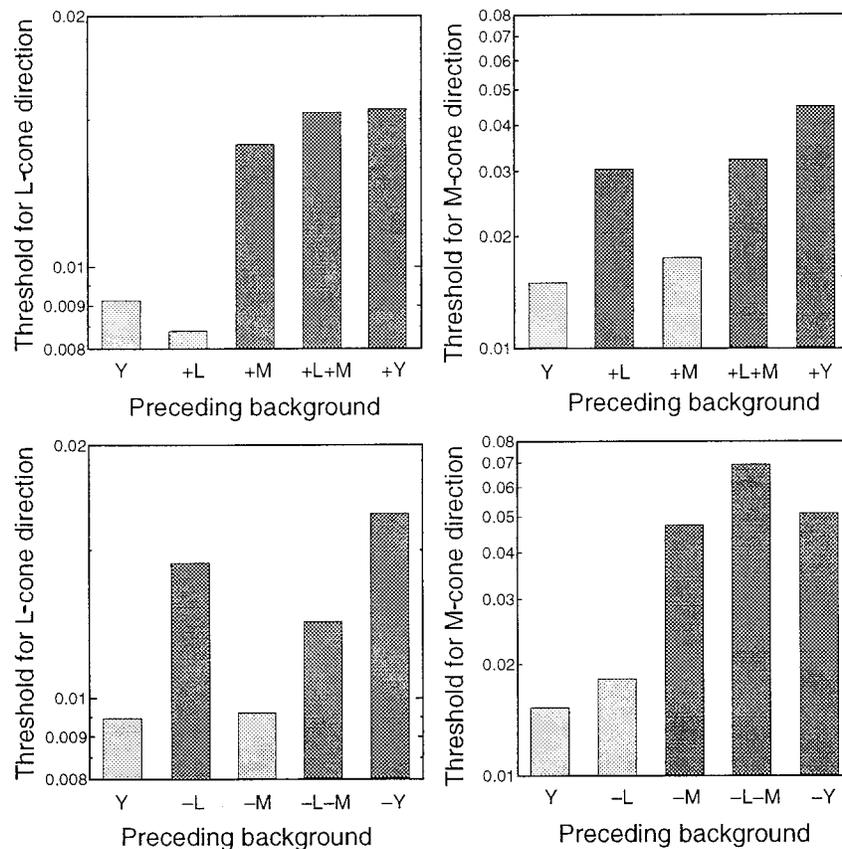


Fig. 11. Thresholds for L- and M-cone direction in the four luminance conditions. The thresholds in the Y , $+L$ to Y , $+M$ to Y , $-L$ to Y , and $-M$ to Y conditions of experiment 1 are also shown for comparison. The upper panels show the L-cone and the M-cone thresholds in the $+L+M$ to Y and $+Y$ to Y conditions. The lower panels show the L-cone and the M-cone thresholds in the $-L-M$ to Y and $-Y$ to Y conditions. In all conditions the L- and M-cone thresholds are elevated. In the $+L+M$ to Y and $+Y$ to Y conditions, the amount of L-cone threshold elevation is similar to that produced by the $+M$ preceding background. In the $-L-M$ to Y and $-Y$ to Y conditions, the amount of M-cone threshold elevation is similar to that produced by the $-L$ preceding background. See text.

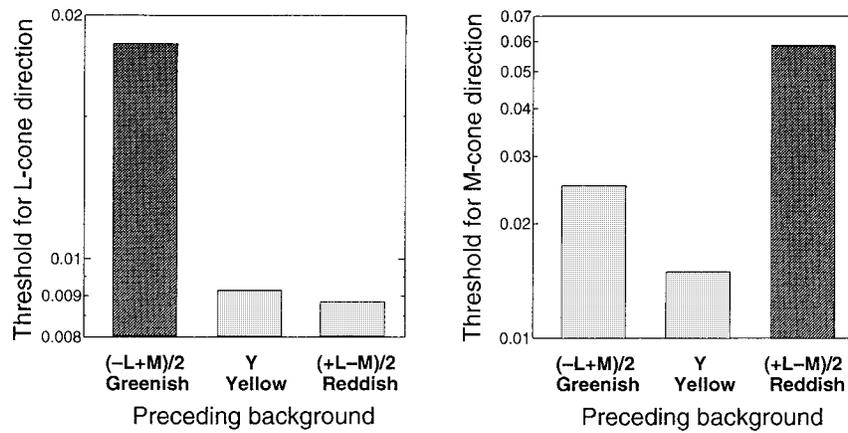


Fig. 12. Threshold for L- and M-cone direction in two equiluminant conditions. The threshold in the Y condition of experiment 1 is also shown for comparison. The panel on the left represents the thresholds for the L-cone direction (L-cone thresholds) and the panel on the right represents the thresholds for the M-cone direction (M-cone thresholds). The results show that the L-cone threshold is elevated only by the $(-L+M)/2$ preceding background and the M-cone threshold is elevated only by the $(+L-M)/2$ preceding background.

between L-on and M-on signals and between L-off and M-off signals. Our model predicts these results, since L-on and M-off signals activate L^+M^- cells that suppress L-cone signals and L-off and M-on signals activate L^-M^+ cells that suppress M-cone signals separately. The $+L+M$ to Y background substitution (L-off and M-off) mechanism activates both L^+M^- cells and M^+L^- cells. There is no cancellation of signals of the cone-opponent cells by the substitution.

Second, the previous models assumed independence of L- and M-cone signals from the luminance mechanism. That is, the center and the surround of the L-cone (or M-cone) signals are summed independently of the M-cone (or L-cone) signals. This type of manipulation cannot predict the threshold elevation in the L-cone direction by a background substitution along the M-cone axis and that in the M-cone direction by a background substitution along the L-cone axis. The signals from opponent cells that control the weights of L- and M-cone inputs to the luminance cell separately realize different suppression across cone types.

Third, in our model the cone-opponent cells modulate the L- and M-cone signals by controlling the gain of L- and M-cone inputs to the luminance cell. This separate control of L- and M-cone signals is critical for explaining the selective elevation of L- and M-cone thresholds. This phenomenon is difficult to explain with models that produce the threshold elevation by subtraction. Since the luminance cell adds the signals of the L and M cones, reduction of the signal from either cone by a preceding background would elevate the threshold in both L- and M-cone directions. The selective control of L- and M-cone inputs implies that the opponent cells suppress the signals of the receptive-field center of the luminance cell. This implication is inconsistent with the previous models, in which the suppressive signals come from the receptive-field surround. Since the suppression from the surround in the previous models is based on the physiological evidence, our model might be physiologically implausible. However, our model and the previous models are based on different empirical evidence. Our model explains selective suppression by use of background substitutions,

whereas the previous models explain suppression by use of steady background colors. Since our model cannot explain suppression with steady background and previous models cannot explain suppression with background substitution, it is suggested that the effect of background substitution is different from that of steady background and that different mechanisms contribute to these effects.

6. CONCLUSION

We found that L- and M-cone signals to the luminance mechanism were selectively suppressed by substitutions of the background color: The background substitution that incremented the activity of the L^+M^- opponent mechanism suppressed the L-cone signals with little effect on the M-cone signals, and the substitution that incremented the excitation of M^+L^- opponent mechanism suppressed the M-cone signals with little effect on the L-cone signals.

APPENDIX A

If the luminance mechanism linearly sums L- and M-cone signals, the motion identification thresholds will be arranged on a straight line with a negative slope in the cone contrast space. In this case, the threshold contour of the luminance mechanism in cone contrast space is expressed as

$$D = aL' + bM', \quad (\text{A1})$$

where L' and M' denote contrasts along the L- and M-cone axes and a and b are relative weights of the L- and M-cone signals, respectively ($a, b > 0$). D is the amplitude of the signals in the luminance mechanism above which motion can be identified.

When the threshold is determined by a luminance mechanism that has a temporal phase shift or delay between L- and M-cone signals, it forms an ellipse in cone contrast space, described as follows:

$$D^2 = (aL')^2 + (bM')^2 + 2ab \cos(\varphi)L'M', \quad (\text{A2})$$

where ϕ is relative phase shift between L- and M-cone signals. The principal axis of the ellipse contour, Sl , is given by

$$Sl(\phi, a_i) = \frac{2a_i \cos(\phi)}{a_i^2 - 1 - [a_i^4 - 2a_i^2 + 1 + 4a_i^2 \cos^2(\phi)]^{1/2}}, \quad (\text{A3})$$

with

$$a_i = a/b, \quad (\text{A4})$$

where a_i denotes the contribution ratio between L- and M-cone contrasts.

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