Technique to investigate the temporal phase shift between L- and M-cone inputs to the luminance mechanism

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We describe a technique to estimate the intrinsic phase shift between long-wavelength-cone (L-cone) and middle-wavelength-cone (M-cone) signals in the luminance mechanism with minimal contamination by chromatic mechanism(s). The technique can also estimate, simultaneously with the phase shift, the weight ratio of L and M cones for the luminance mechanism. We measured motion identification thresholds for a 1.0 cycle/deg, 12.0-Hz sinusoidal grating representing different vector directions in L- and M-cone contrast space. The physical phase of the L- and M-cone signals was varied over a broad range between −150 deg and +150 deg to investigate the effect on the threshold contours. The slope of the threshold contour in cone contrast space varied as a function of the physical phase. Estimates of the intrinsic phase shift between L and M cones are based on the change in slope of the threshold contour. The estimates are consistent with previous reports and show that whereas the L-cone signal lags behind the M-cone signal by ~35 deg for an orange background, the M-cone signal lags behind the L-cone signal by ~8 deg for a green background. © 2000 Optical Society of America [S0740-3232(00)00705-5]

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1. INTRODUCTION

Lindsey *et al.*[1] reported evidence of phase shifts between the middle-wavelength cone (M cone) and the long-wavelength cone (L cone). They measured amplitude thresholds at 6 Hz for a pair of equiluminant red and green lights summed in different temporal phases and found that the threshold was highest when a relative physical phase between two lights was 20 deg. This showed that the red light leads the green light by ~20 deg. Subsequently, Swanson *et al.*[2,3] showed that both the sign and the magnitude of the phase shifts (i.e., whether the M-cone signal leads the L-cone signal or vice versa) are dependent on the state of luminance and chromatic adaptation. Although these studies clearly showed that phase shifts between the L- and M-cone signals occur, Swanson[4] and Stromeyer *et al.*[5] noted that phase measurements that use the red and the green lights do not directly estimate the phase shifts between L and M cones. The phase shifts measured in these later studies are dependent on the choice of red and green lights and on the weight ratio of the L- and M-cone inputs. For direct measurements of the cone phase shifts, it is necessary therefore to stimulate L and M cones independently.

Stromeyer *et al.*[6] developed a motion quadrature protocol to measure the intrinsic phase shift in the luminance mechanism directly. The technique is a variation of the minimum motion technique developed by Anstis and Cavanagh[7] and is used to isolate the luminance mechanism from the chromatic mechanism(s). They showed that the M-cone signal leads the L-cone signal by 30 deg for a yellow background (577 nm) for temporal frequencies between 4 and 9 Hz. The method of Stromeyer *et al.*[6] is clearly applicable to lower temporal frequencies, at which chromatic mechanism(s) contribute more to visual processing. However, the phase shift derived by the technique may be influenced by the use of a pedestal stimulus for isolation of luminance signals for motion. Indeed, Webster and Mollon[8] showed that the null direction depended on the pedestal contrast unless purely achromatic or equiluminant pedestals were used. This represents a limitation of the method, although Stromeyer *et al.*[6] carefully chose achromatic pedestals to minimize

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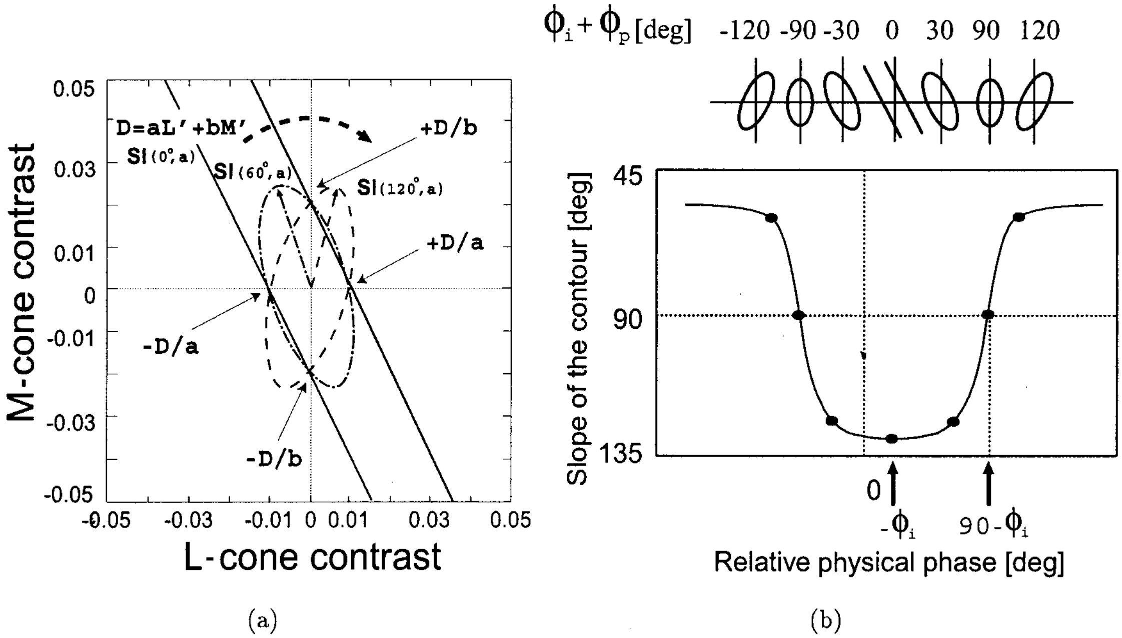

Fig. 1. (a) Predicted threshold contours with no intrinsic phase shift between L and M cones for a relative physical phase of 0 deg (solid line), 60 deg (dotted–dashed curve), and 120 deg (dashed curve). With the increase of the physical phase, the slope of the contour, $S1(\phi_p, a)$ rotates about the origin. (b) The slope of the contour as a function of relative physical phase with the intrinsic phase shift of ϕ_i. The ellipses above the panel represent threshold contours for several physical phases. The slope is 90 deg at the physical phase of $90 - \phi_i$.

the effect of pedestals on their measurements. Pedestal stimuli can also give rise to the problem of transient signals. Furthermore, when temporal interactions between stimuli (such as the transient effect of background substitutions) are measured, a temporally modulating pedestal can generate unwanted signals.

We propose a different method that estimates the intrinsic phase shift directly with a simple motion identification paradigm. Although this method is similar to the methods of Lindsey *et al.*[1] and Swanson *et al.*,[3] there are four critical differences. First, the present method used two gratings modulated along L- and M-cone axes (L- and M-cone grating), instead of red and green lights; the use of the L- and M-cone gratings can access the phase shift between L and M cones directly.

Second, the intrinsic phase shift is measured without previous knowledge of the weight ratio of the L- and M-cone signals to luminance; as described later, the phase shift and the weight ratio are estimated simultaneously, which eliminates the need to measure the equiluminant point before the experiment. The phase shift could also be estimated without any estimation of the weight ratio (described later in experiment 3).

Third, we used the change in the slope of the threshold contour in cone contrast space to estimate the phase shift between L and M cones. Swanson *et al.*[3] measured amplitude thresholds for a pair of equiluminant red and green lights as a function of relative temporal phase between two lights. Then they determined the relative phase with the highest threshold, which corresponds to $180 - \phi_i$, where ϕ_i is the intrinsic phase shift. In contrast, we measured thresholds along the various vector directions in cone contrast space to determine the slope of the threshold contours. Use of the slope to estimate the phase shift should reduce the contamination by chromatic mechanism(s) in comparison with previous methods,[4,5] since the slope is determined mostly by the data in the region of high sensitivity.

Finally, our method essentially measures the point of the relative phase of $90 - \phi_i$ instead of $180 - \phi_i$. This corresponds to the greatest rate of change in slope near the physical phase of $90 - \phi_i$, as shown in Fig. 1.

In experiment 1, we showed that threshold ellipses can be obtained and that their slopes can be used to estimate intrinsic phase differences and weight ratios of L-cone and M-cone contrast. In experiment 2 we confirmed that the slopes are not contaminated by the chromatic mechanism(s). In experiment 3 we introduced a faster method for phase-shift estimation.

2. METHODS

The stimulus consists of two sinusoidal heterochromatic gratings: One modulates along the L-cone axis, and the other modulates along the M-cone axis. The threshold contours in L- and M-cone contrast space for motion identification are obtained for variable relative spatial phases between the two gratings. With the change in relative phase, it is predicted that the orientation of the slope of the ellipse that approximates the threshold contour (the threshold ellipse) will rotate about the origin in the L, M cone contrast coordinates. The orientation change of the threshold ellipse contains information about both the phase shift and the relative weight between the L- and M-cone inputs to the luminance mechanism.

A. Principle

In cone contrast space the amplitudes of the stimulus gratings for L- and M-cone directions are normalized by the mean field stimulation of each respective cone. The stimulus is a composite grating produced by adding the two heterochromatic gratings. Cone contrast space is calculated with the Smith and Pokorny cone fundamentals.[9] The cone contrast was defined as: $C' = (C_{\max} - C_{\min})/(C_{\max} + C_{\min})$, where $C_{\max}$ and $C_{\min}$ represent the maximum and minimum, respectively, of the response of the L cone or M cone to the stimulus grating. The luminance profile of the L- and M-cone gratings are represented by

$$\mathrm{L}(x, t) = \mathrm{L}_m[1 + \mathrm{L}' \sin(\omega_s x + \omega_t t)], \tag{1}$$

$$\mathrm{M}(x, t) = \mathrm{M}_m[1 + \mathrm{M}' \sin(\omega_s x + \omega_t t)], \tag{2}$$

where $\mathrm{L}(x, t)$ represents the spatiotemporal variation along the L-cone direction and $\mathrm{M}(x, t)$ represents that along the M-cone direction, L_m and M_m are the mean luminance, L' and M' denote contrasts along the respective cones, ω_s is the spatial angular frequency, x is the horizontal position of the grating, ω_t is the temporal angular frequency, and t is time. Figures 1(a) and 1(b) show how the slope of the threshold ellipse (or line in special cases) changes with the relative phase between L- and M-cone signals. Consider first the case in which no intrinsic phase shift occurs between L and M cones. We assume here that thresholds are determined solely by the luminance mechanism and that the luminance is determined by a linear sum of L- and M-cone signals. In this case the threshold contour of the luminance mechanism for constant L_m and M_m in cone contrast space is expressed as

$$D = a\mathrm{L}' + b\mathrm{M}', \tag{3}$$

where a and b represent the L- and M-cone contrast weights to the luminance, respectively ($a, b > 0$), and D represents the criterion for the threshold (motion direction can be distinguished correctly when the amplitude of the summed grating exceeds D in our case). The equation describes a line with a negative slope when plotted in cone contrast space [Fig. 1(a), solid lines].

Next, consider the intrinsic phase shift of ϕ_i between L and M cones. Then threshold contours would be expected to form an ellipse as

$$D^2 = (a\mathrm{L}')^2 + (b\mathrm{M}')^2 + 2ab\cos(\phi_i)\mathrm{L}'\mathrm{M}'. \tag{4}$$

When we vary the relative physical phase of ϕ_p between the L- and the M-cone gratings, the slope of this contour rotates about the origin [positive values of ϕ_p corresponding to $\mathrm{M}(x, t)$ preceding $\mathrm{L}(x, t)$]. Then $\mathrm{L}(x, t)$ is expressed as

$$\mathrm{L}(x, t) = \mathrm{L}_m[1 + \mathrm{L}' \sin(\omega_s x + \omega_t t - \phi_p)]. \tag{5}$$

After adding the physical phase, the threshold contours are expressed as

$$D^2 = (a\mathrm{L}')^2 + (b\mathrm{M}')^2 + 2ab\cos(\phi_p + \phi_i)\mathrm{L}'\mathrm{M}'. \tag{6}$$

For the sum of the physical and intrinsic phases, $\phi_p + \phi_i$, the slope of the threshold contour, $\mathrm{Sl}(\phi_p + \phi_i, a_i)$, becomes

$$\mathrm{Sl}(\phi_p + \phi_i, a_i) = \frac{2a_i\cos(\phi_p + \phi_i)}{a_i^2 - 1 - [a_i^4 - 2a_i^2 + 1 + 4a_i^2\cos^2(\phi_p + \phi_i)]^{1/2}}, \tag{7}$$

where $a_i = a/b$ denotes the weight ratio between L- and M-cone contrast (see Appendix A). Equation (7) shows that the slope changes depend on both the relative phase, $\phi_p + \phi_i$, and the weight ratio, a_i. Figure 1(b) shows the predicted ellipse contours and the curve at several physical phases. The contour rotates in a clockwise direction with the increase or decrease of the phase parameter, $\phi_p + \phi_i$. We can estimate the intrinsic phase shift, ϕ_i, with the weight ratio, a_i, from the experimental data.

Since the rate of change in slope is greatest near the phase of $90 - \phi_i$ [Fig. 1(b)], the estimation of this function corresponds essentially to finding the phase with which the slope crosses 90 deg. This indicates that the data in this region provide critical information on phase estimation. This can be recognized by considering the special case in which the weight ratio of L and M cones is one. The slope of the threshold contour changes only when the phase crosses 90 deg. The shape of the threshold contour becomes an ellipse with orientation of either 45 deg or 135 deg for all $\phi_p + \phi_i$ but for 0, 90, and 180 deg. When $\phi_p + \phi_i$ is 0 or 180 deg, the threshold contour is a pair of parallel lines oriented at 45 or 135 deg, respectively, and when it is 90 deg the threshold contour becomes a circle. For the phases between 0 and 90 deg, the orientation of the ellipse is 45 deg, whereas the orientation is 135 deg for the phases between 90 and 180 deg. Therefore the slope changes from 45 to 135 deg abruptly when the phase crosses 90 deg in this special case. In general, however, the change of the slope is rather gradual, and the slope data from various phases can contribute to the estimate of the phase with a slope of 90 deg.

The physical meaning of the change in slope at 90 deg of the phase is related to the sign of the L- and M-cone signals. If they have the same sign, the threshold is highest in the vector direction of 45 deg, since the sum of the signals is the largest in this direction. On the other hand, the threshold is highest in the vector direction of 135 deg if the signs are opposite. This is because the contrast of either of the two gratings is reversed in the stimulus and the L- and M-cone signals are additive in the vector direction. The L- and M-cone signals are subtractive in the direction of 45 deg in this case. In general, for the stimulus in the 45-deg vector direction, the additive summation produces a slope of 45 deg and the subtractive summation produces a slope of 135 deg. Since the L- and M-cone signals are additive for the phases between 0 and 90 deg and subtractive for the phases between 90 and 180 deg, our method determined principally the phase for which the slope of the threshold contour crosses 90 deg.

B. Apparatus

The stimulus gratings were displayed on a color monitor (Sony Multiscan 17seII), which was controlled by a video controller (Cambridge Research Systems VSG2/3). The resolution of the monitor was 640 × 480 pixels and the frame rate was 120 Hz. Each phosphor was driven by a 12-bit digital-to-analog converter. The CIE coordinates of each phosphor were measured by a spectroradiometer (Minolta, CS1000). Two observers participated in the experiments. They were seated 64 cm in front of the monitor, and the screen size was 19 deg × 25 deg.

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. Test 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 eight to twelve reversals in one session. Thresholds were measured for twelve different vector directions in cone contrast space. The thresholds for all vector directions with a given physical phase were measured in the same session by interleaving staircases.

3. EXPERIMENT 1

A. Stimulus

The L- and M-cone gratings, each of which was a vertical sinusoid of 1.0 cycle per degree (cycle/deg), were displayed in a circular aperture of diameter of 2 deg. The grating drifted leftward or rightward at 12.0 Hz for 83 ms. This high temporal frequency, short-duration, stimulation was used to isolate the luminance mechanism from the chromatic mechanism(s).[10] A spatial phase shift was added into the L-cone grating to provide relative physical phase between the two gratings. The grating was presented on a uniform background extending across the whole of the display. We used two backgrounds: orange, with CIE coordinates of (0.48, 0.44), and green, with CIE coordinates of (0.33, 0.57). The gratings were modulated with an average of the background luminance and chromaticity. The fraction of the background luminance for the L cone (i.e., r in the cone-excitation diagram proposed by MacLeod and Boynton[11]) was 0.71 for orange and 0.63 for green. The two backgrounds were chosen to stimulate selectively either L and M cones without any concurrent change in the stimulation of the short-wavelength-sensitive cones. The orange and the green backgrounds had identical luminance level (55.0 cd m^{-2}), which corresponded, for natural pupils, to a retinal illuminance of 650 td for observer ST and 1080 td for observer YT.

The size of the test grating was chosen so that the results could be directly compared with the results of Lindsey *et al.*[1] and Swanson *et al.*[3] We employed a motion identification task because from preliminary observation we found that it was easier than flicker detection. It has been shown that the threshold for motion identification and that for flicker detection are essentially the same in foveal vision,[12] and we assumed that both processes would access the luminance mechanism.

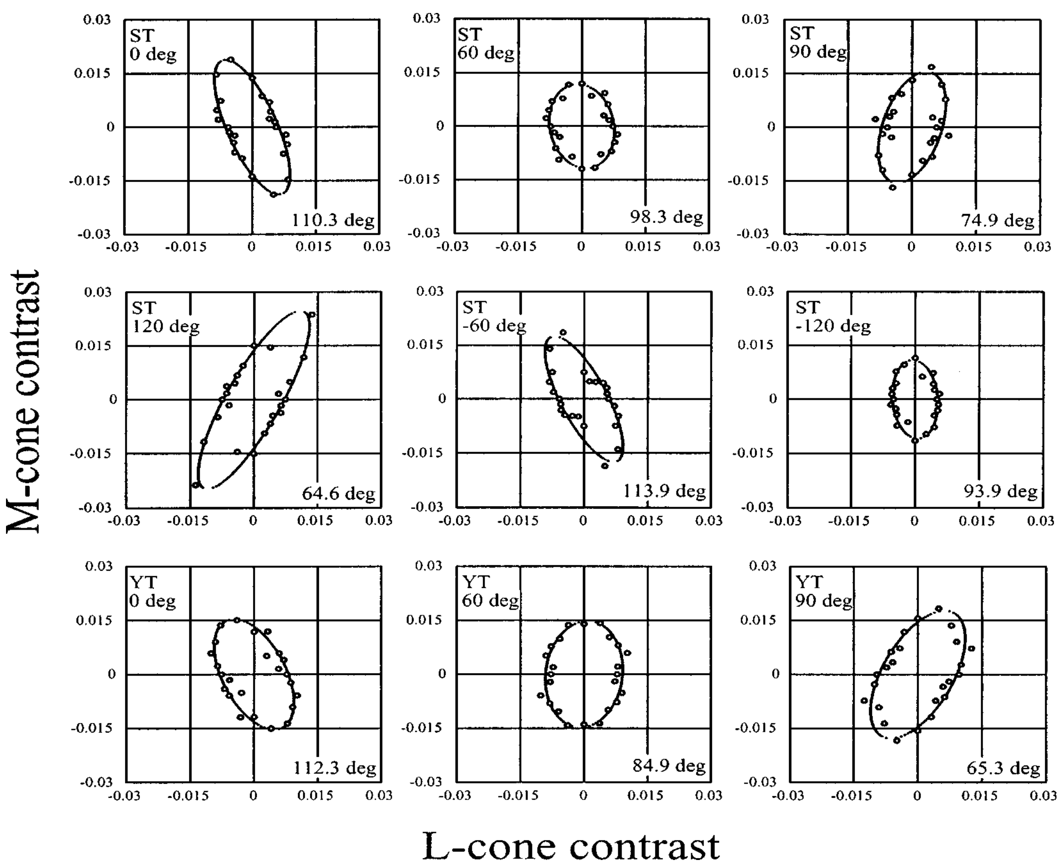

Fig. 2. Threshold contours for motion identification for the orange background. The solid curve represents the ellipse fitted to the threshold data (circles) by a least-squares method. The value at the lower-right corner in each panel represents the slope of the ellipse contour, and the value at the upper-left corner represents the physical phase condition (not all phase conditions are shown).

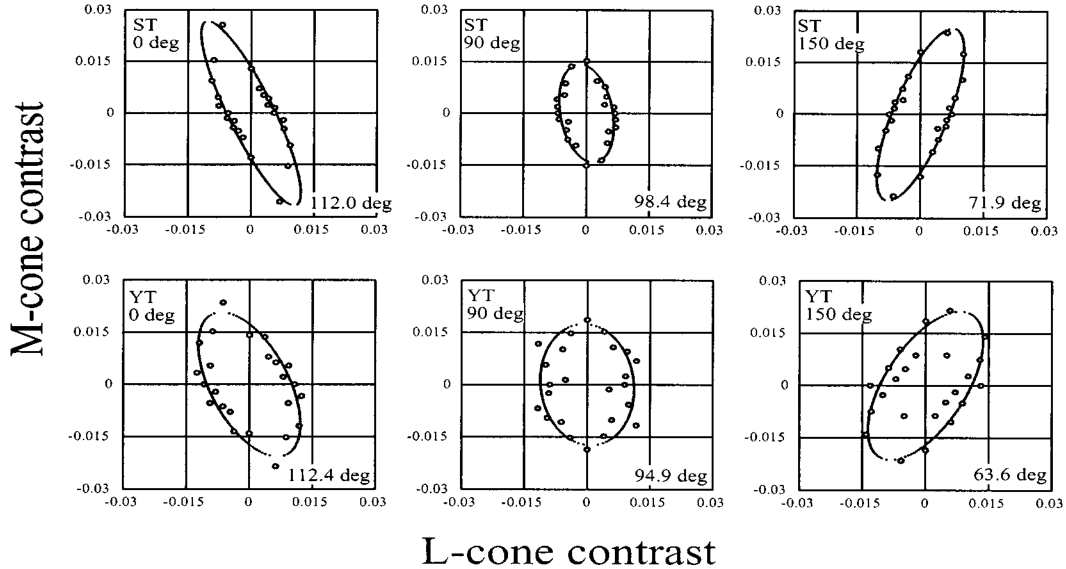

Fig. 3. Threshold contour for motion identification for the green background. All other details are as in Fig. 2.

B. Procedure

The observer adapted to the uniform background for five min before each experimental session and reported whether the grating drifted rightward or leftward after each stimulus presentation. Thresholds for twelve vector directions were measured for each of eleven physical phases ranging from −150 to +150 deg in 30-deg steps for observer ST and six positive phases from 0 to +150 deg for observer YT.

C. Results

The threshold data for motion identification for the orange and the green backgrounds are shown in Figs. 2 and 3. The ellipse in each panel represents the best-fit function for the data points with a least-squares method. The observer's initial and physical phases are shown in the upper-left corner, and the slope of the fitted ellipse is shown in the lower-right corner.

If the luminance mechanism linearly sums L- and M-cone signals without any phase shift, the motion identification thresholds will form a straight line with a negative slope in the cone contrast space. However, the results with a physical phase of zero show that they are fitted well by an ellipse. This suggests that there is a temporal phase shift or delay between L- and M-cone signals for the luminance mechanism. An alternative explanation is that the threshold near the direction of the principal axis of the ellipse may be determined by chromatic mechanism(s). Although the temporal conditions of the experiment were chosen to isolate the luminance mechanism, the chromatic mechanism(s) may have contributed to the threshold when the sensitivity of the luminance mechanism was low. This, however, does not significantly affect the estimation of the phase shift from the slope change, because the slope of the principal axis is determined mostly by data in the high-sensitivity region. It can be seen in the figures that the slope of the principal axis of the ellipse would also be a good estimate of the slope of the data array in the first and third quadrants.

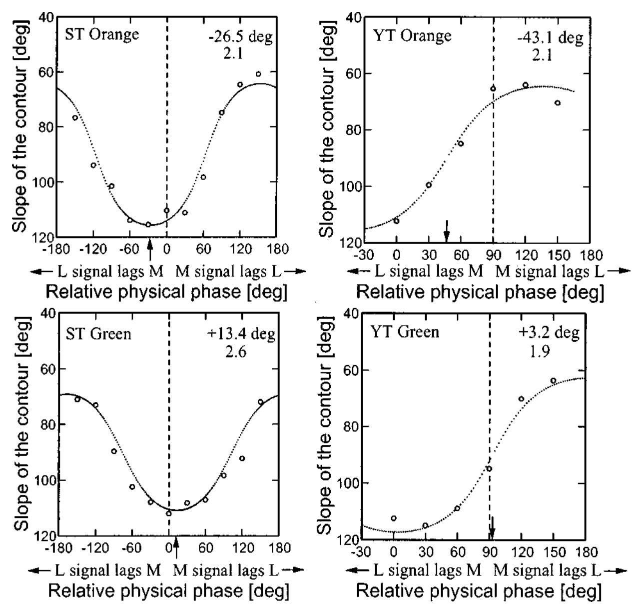

Fig. 4. Relationship between the slope of the contour and the relative physical phase for the orange and the green backgrounds. The dotted curve indicates the function shown in Eq. (7) fitted to the data (circles). To fit the data, the two variable parameters were (1) the intrinsic phase shift, ϕ_i[deg], and (2) the weight ratio of the L-cone and M-cone contrast to luminance mechanism, a_i (shown at upper-right corner).

The possible effect of chromatic mechanism(s) are considered further in experiment 2.

Comparison across the panels in Fig. 2 indicates that the slope rotates clockwise about the origin with the increase of the relative physical phase from 0 deg as Eq. (7) predicts. When the physical phase is 90 deg, the slope of the ellipse should be 90 deg if there is no intrinsic phase shift. The measured slopes are less than 90 deg for the orange background and greater than 90 deg for the green background for both observers. These results indicate that there is an intrinsic phase shift between L- and M-cone signals and that the shift depends on the background colors.

The relationship between the slope and the relative physical phase is shown in Fig. 4. The dotted curve is the fitted function for Eq. (7), estimating the unknown parameters of ϕ_i and a_i (shown at the upper-right corner in each panel). The data fit the predicted curve well and thus support the assumptions made. The phase shifts for the orange background were found to be negative, indicating that the L-cone signal lags behind the M-cone signal. In contrast, the phase shifts for the green background were found to be positive, indicating that the M-cone signal lags slightly behind the L-cone signal. The estimated value of a_i is greater than 1.0, independent of background color, which indicates that, in terms of cone contrast, the L cone contributes to the luminance mechanism more than the M cone for either background. These results are consistent with previous reports (see Section 6).

4. EXPERIMENT 2. QUADRATURE PROTOCOL

A. Method

The technique developed here requires that the estimated slope of the threshold contour is determined by the luminance mechanism. We conducted experiment 2 to verify that the estimation of slopes in experiment 1 was not contaminated by the chromatic mechanism(s). The quadrature protocol was used to measure slopes that isolated the luminance mechanism.[6]

The stimulus for the quadrature protocol consisted of a pair of flickering sinusoidal gratings with the same spatiotemporal frequency: One was the test whose contrast varied, and the other was a luminance pedestal of fixed contrast. The two superimposed flickering gratings were shifted in relative spatial and temporal phase by 90 deg. Neither of the gratings alone produced any net motion, but motion arose from an interaction of the two gratings. In the quadrature paradigm, motion for the luminance component is evident when there is a luminance variation in the test grating. The sensitivity of the luminance mechanisms can be measured by varying the contrast of the test grating. Since there is no color difference in the pedestal grating, there is no net color component motion for the test grating for any vector direction. Because motion signals from chromatic mechanism(s) do not contribute to motion identification, the luminance mechanism can be isolated even for conditions in which the color in the test grating might determine the threshold in a simple detection threshold experiment.

In the present experiment the vector direction of the test grating was variable (as in experiment 1) and no physical phase was added. The vector direction of the pedestal grating was set to the direction of the short axis of the ellipse contour obtained in experiment 1. Although the slope of the threshold contour assessed by the quadrature protocol varies with the intrinsic phase shift and vector direction of the pedestal grating, it should correspond to the slope of the ellipse estimated in experiment 1 if the luminance mechanism determines the slope in both cases.[6] It has been shown that the slope of the lines measured with the quadrature protocol is tangential to the ellipse contour at the point where the pedestal vector intersects the arc.[6] In this experiment the vector direction of the pedestal grating was set to the direction of the short axis of the ellipse contour with no physical phase, and therefore the slope measured with the quadrature protocol should correspond to that of the ellipse contour with no physical phase.

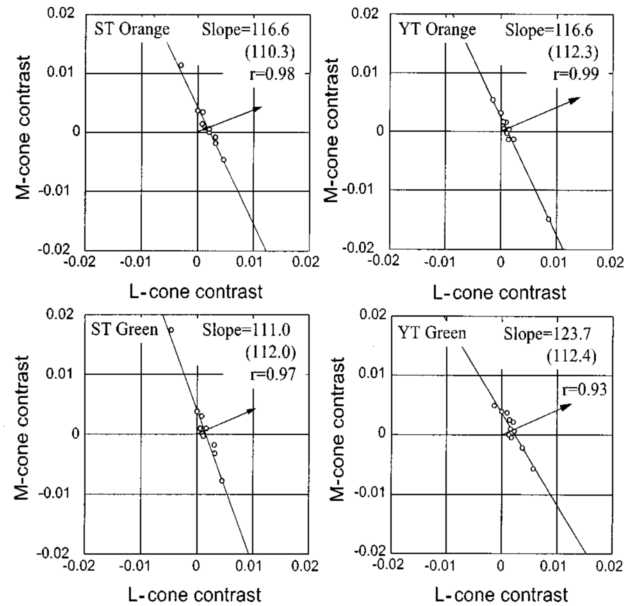

Fig. 5. Motion identification contours assessed by the quadrature protocol for observer ST (left column) and observer YT (right column). The values at the upper-right corner in each panel represent the slope of the fitted line and the correlation coefficient, respectively. The arrow represents the direction and the amplitude of the pedestal grating used.

The contrasts of the pedestal gratings were approximately twice the threshold of the simple moving grating. The spatial frequency was 1 cycle/deg, and the presentation duration was 83 ms with a temporal frequency of 12 Hz as in experiment 1.

B. Results

The threshold contours assessed by the quadrature protocol are shown in Fig. 5. The contour resembles a straight line for all conditions. To estimate the slope of the threshold contour, we fitted straight lines to the data (the solid line in each panel). The slopes and correlation coefficients are shown in the upper right of each panel and, for comparison, those obtained in experiment 1 are shown in parentheses. The slopes for the two estimates are similar, with the greatest difference (10%) for the green background for observer YT (lower-right panel). These results confirm that there was minimal contamination of the slope measurements in experiment 1 by the chromatic mechanism(s).

5. EXPERIMENT 3. ABBREVIATION METHOD

A. Method

We measured the threshold data for a number of conditions to estimate the phase shift in experiment 1. However, the number of conditions can be reduced when only the intrinsic phase shift is measured. For an extreme case, the number of vector directions for threshold measurements can be as small as two if an abbreviation method is used. The method measures the ratio between thresholds in two vector directions for each physical phase to find the physical phase that gives a ratio of one. Figure 6 shows hypothetical threshold contours for physical phases of 60, 90, and 120 deg for the intrinsic phase of zero. If a threshold is measured for 60- and 120-deg vector directions, the ratio of thresholds for the two directions becomes one when the sum of the physical and intrinsic phases is 90 deg. This corresponds to the case in which the slope of the threshold contour is 90 deg in the original method.

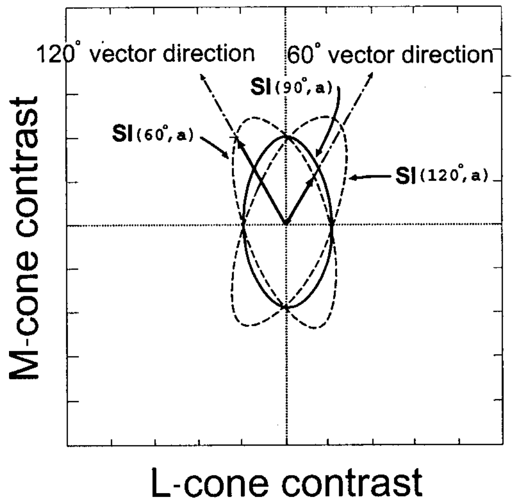

Fig. 6. Schematic diagram to show how the abbreviation method relates to the slope of the threshold ellipse. The diagram illustrates the change in shape of the threshold contour with the increase of physical phase (intrinsic phase is assumed to be zero in this case). The threshold in the 60-deg vector direction increases with the increase in physical phase from 60 to 120 deg, whereas that in the 120-deg direction decreases. The ratio of the threshold for the 60-deg direction to that for the 120-deg direction is 1.0 at the physical phase where the slope of the threshold contour is 90 deg (the physical phase is 90 deg in this case). If the intrinsic phase shift is ϕ_i, the ratio is 1.0 when the phase shift is $90 - \phi_i$.

Mathematically, the use of two vector directions of $\pm\tan^{-1} a_i$ (a_i is the ratio of L- and M-cone weight to the luminance) provides the greatest change in the ratio of two thresholds near the phase of $90 - \phi_i$ (see Appendix C) and thus provides the most reliable estimate of the phase shift. This indicates that knowledge of the L- and M-cone weights is useful to estimate the intrinsic phase shift. However, this is not essential, as any pair of vector directions that roughly corresponds to L + M and L − M directions would suffice. We applied this method to estimate the phase shift from the data of experiment 1.

B. Results

The ratio of threshold values for 60- and 120-deg directions are shown as a function of relative physical phase in Fig. 7. The panels in the left column represent the results for observer ST and those in the right column for observer YT. The physical phase for a ratio of one was determined from a linear regression line and is indicated by the white arrow in Fig. 7. We used a linear fit, since fitting the template of Eq. (C4) of Appendix C is a quasi-

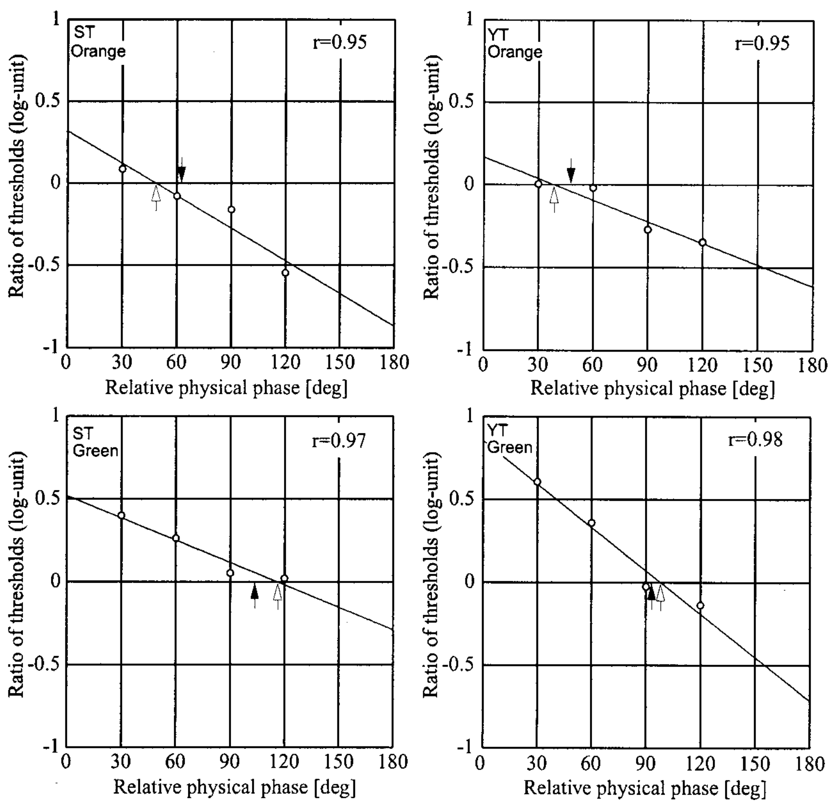

Fig. 7. Estimate of phase by the abbreviation method. The physical phase for a ratio of 1 was determined from a linear regression line and is indicated by the white arrow. The black arrow indicates the phase where the slope is rotated 90 deg from that obtained in experiment 1.

linear function near the phase of $90 - \phi_i$. The correlation coefficient is shown at the upper-right corner for each condition. The black arrow indicates the phase at which the slope is rotated 90 deg from that obtained in experiment 1. The points indicated by the white and black arrows are very close, which demonstrates the reliability of the abbreviation method.

6. DISCUSSION

A. Comparison with Previous Studies

We found that the sign of phase shift for the orange background is negative (i.e., the L-cone signal lags behind the M-cone signal by ~35 deg), whereas the sign of the phase shift on the green background is positive (i.e., the M-cone signal lags behind the L-cone signal by ~8 deg). These results are consistent with the results of Stromeyer *et al.*[5] obtained under similar conditions: They found, for a 1-cycle/deg grating at 9 Hz and 600 td, that the L-cone signal lagged behind the M-cone signal for the orange background by 10 and 30 deg for two observers and that the M-cone signal lagged behind the L-cone signal for the green background by ~20 deg for three observers. The effect of the background color reported in previous studies is also in the same direction.[3,13] The estimation of the weight ratio of L-cone and M-cone contrast for the luminance mechanism ranges from 1.9 to 2.6. The value of a_i greater than 1.0 indicates that the L cone contributes to the luminance mechanism more than the M cone. The larger contribution of the L cone to the luminance mechanism is consistent with previous reports[5,6,14,15] and suggests that our method is appropriate for the measurement of the phase shift and weight ratio.

The effect of background color on the phase shift is consistent with the model proposed by Stromeyer *et al.*[5] In their model, phase shift is explained by the delay of an inhibitory signal from the surround of the receptive field of the luminance mechanism. Since the surround organization of the receptive field is different for different background colors, the sign of phase shift depends on the background colors. Their model predicted that the L-cone signal would lag behind the M-cone signal by ~50 deg for the red background (596 nm) at 12 Hz, whereas the M-cone signal would lag behind the L-cone signal by ~50 deg for the green background (505 nm). Since the present study used backgrounds similar to these two conditions, these predictions are relevant to our results. The difference of the sign of phase shift for the two background colors in our experiments is consistent with the model. The amounts of phase shift, on the other hand, are smaller than the model predictions, possibly because the saturation and luminance of our backgrounds are lower than those assumed in the Stromeyer *et al.* model.

B. Comparison with Other Techniques

Two methods have been previously used to estimate the phase shift between L- and M-cone signals by measuring simple contrast thresholds.[2,5] Both use a template for the threshold function with physical phase shift between L- and M-cone gratings. To examine how these methods relate to our measurements, Fig. 8 shows our threshold data for the vector direction of 60 deg with a template that uses the parameters estimated in experiment 1 [Eq. (B4) of Appendix B]. Data for 60 degrees are selected because this direction is close to the luminance axis. The template predicts that the threshold is highest (infinity) for the sum of the physical and intrinsic phases of 180 deg because the L- and M-cone signals are added in-counterphase (i.e., one subtracts from the other). It also predicts that the threshold is lowest when the sum of the physical and intrinsic phases is 0 deg, because the signals add when in-phase.

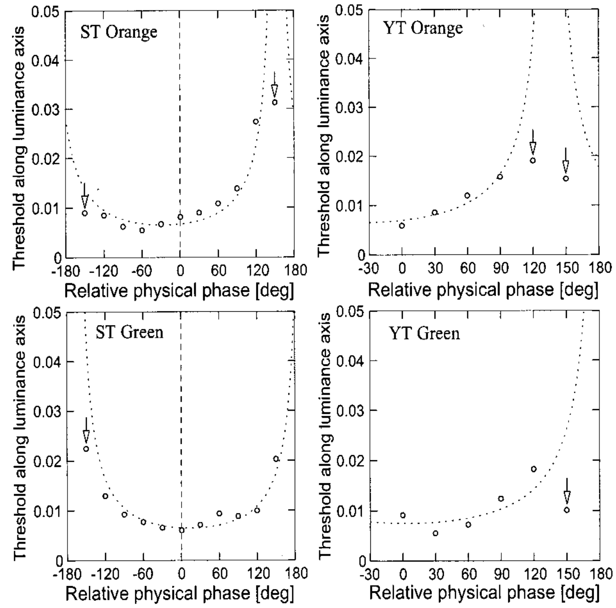

Fig. 8. Thresholds along the luminance axis as a function of relative physical phase. Data (circles) are from thresholds along a 60-deg vector direction in Figs. 2 and 3. The dotted curves represent the theoretical curve in Eq. (C4) of Appendix C with parameters obtained in the main experiment. The threshold data near $180 - \phi_i$ (indicated by arrows) might be contaminated by chromatic mechanism(s).

The first method to assess the intrinsic phase shift determines the physical phase that gives the highest threshold.[1,2] The change of threshold with relative physical phase is greatest near the phase of least sensitivity ($180 - \phi_i$). The data in this region should fit the template most effectively. However, the threshold for these phases is likely to be contaminated by the chromatic mechanism(s) because the sensitivity along the luminance axis is very low in these conditions. Our data show deviation from the template in the region of high threshold that is due to contamination by the chromatic mechanism(s) (white arrow). This indicates the difficulty in matching the template with threshold data that have least sensitivity.

The second method to assess the intrinsic phase shift determines the physical phase that gives the lowest threshold.[5] Since the threshold is expected to be the lowest when the L- and M-cone signals add in-phase, the physical phase with the lowest threshold can be regarded as the phase shift that is required to cancel the intrinsic phase shift ($-\phi_i$). The lowest threshold is found by use of the central part of the *U*-shaped template, where the threshold of luminance is low enough to prevent any influence from chromatic mechanism(s). However, the change in the threshold in the region with relative phase is very small, which makes it difficult to fit the template to the data reliably. Figure 8 clearly shows that these methods cannot provide good estimates of phase shift, at least under our experimental conditions.

In contrast to the above methods, our method mainly depends on the threshold data near the phase of $90 - \phi_i$. Slope data are less likely to be contaminated by the chromatic mechanism(s) than threshold data with a phase near $180 - \phi_i$. The experiment can provide good estimates of phase shift, because the change in slope at the phase of $90 - \phi_i$ is greater than the change in threshold at the phase of zero.

C. Contamination of Chromatic Mechanism

In experiment 2 we showed, using the quadrature protocol, that the slope is determined solely by the luminance mechanism, and in an earlier section we also showed a substantial effect of chromatic mechanism(s) on thresh-

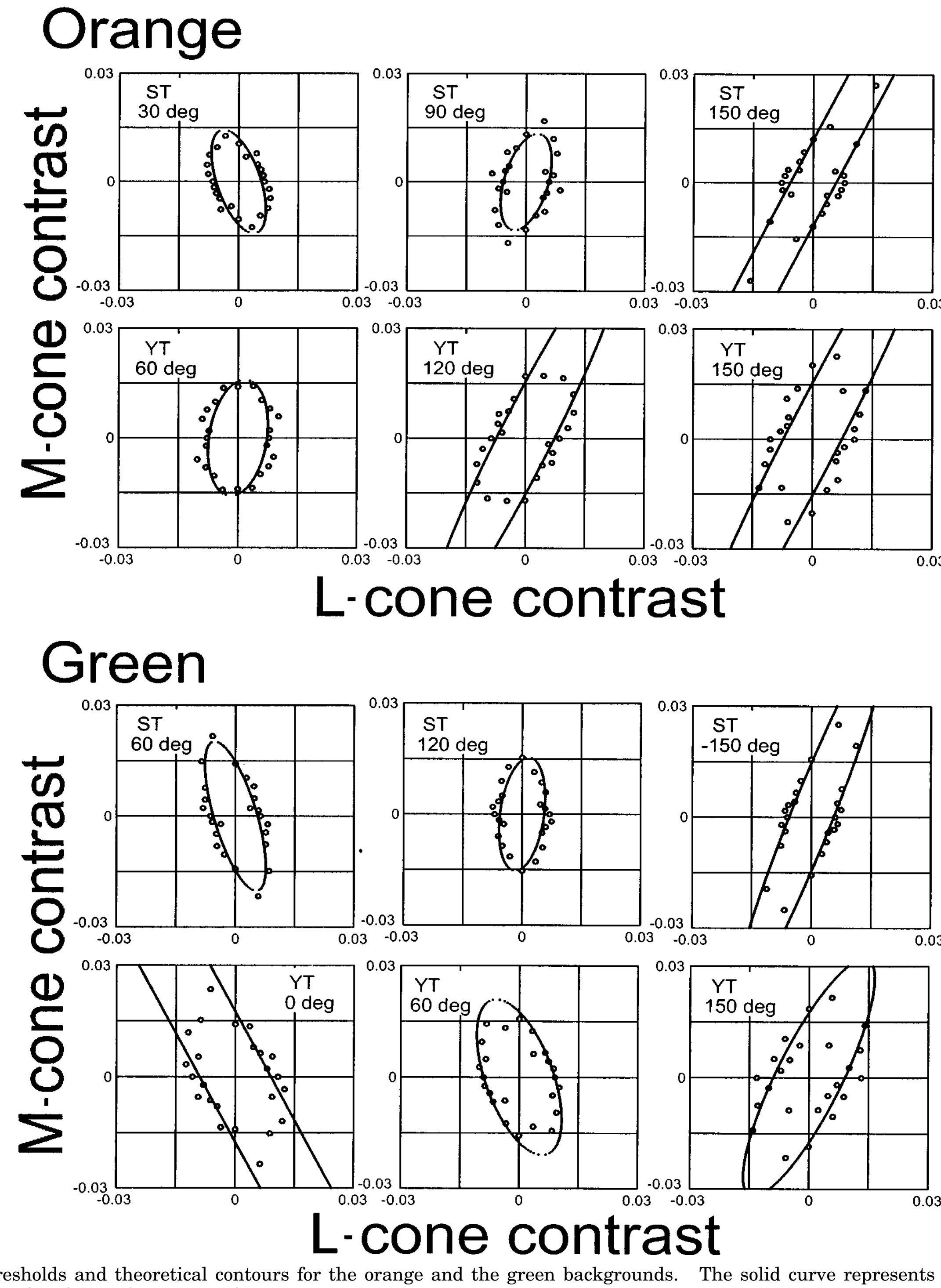

Fig. 9. Thresholds and theoretical contours for the orange and the green backgrounds. The solid curve represents the theoretical curve. Other details are the same as for Fig. 2.

olds for the phase of least sensitivity. We discuss below how chromatic mechanism(s) contribute to the thresholds in cone contrast space at various physical phases.

To investigate whether chromatic mechanism(s) affect the thresholds in cone contrast space, we calculated theoretical threshold contours from the results obtained in experiment 1. If all thresholds were determined solely by the luminance mechanism, they would show good agreement with the theoretical contours. To calculate the theoretical contour, absolute sensitivity is required, in addition to the intrinsic phase shift and the weight ratio. We obtained this information from sensitivities of the L- and M-cone thresholds averaged over all physical phases.

The empirical thresholds and theoretical contours for the orange and the green backgrounds are shown in Fig. 9. The solid curve represents the theoretical curve, and the circles represent experimental data. Other details are the same as in Fig. 2. For all plots, it is evident that the theoretical contours match experimental data when the sensitivity is high. Most important, it is proposed that the thresholds are solely determined by the luminance mechanism when the slope is ~90 deg, that is, where the sum of the physical and intrinsic phases is 90 deg. The theoretical contour matches approximately the threshold data in the high-sensitivity region, which is proof that our method is not affected by chromatic mechanism(s), since the slope is determined mostly by data in this region.

Conversely, there is a clear discrepancy between the experimental data and the theoretical contours for certain conditions. For example, the results with the physical phase of 120 deg for the orange background show that thresholds for vector directions of 60 and 75 deg are much lower than the theoretical predictions. The empirical thresholds are more likely to be determined by a chromatic mechanism(s) in these cases. This indicates that the threshold measurements have been significantly contaminated by chromatic mechanism(s). However, the comparison between the empirical and the theoretical thresholds shows that the discrepancy has little effect on the estimation of the slope when ellipses are fitted to the threshold data even in those cases in which large discrepancies have occurred. This confirms the robustness of the method with regard to the potential for contamination by chromatic mechanism(s).

The results also show that it is difficult to estimate the phase shift from a single threshold contour when chromatic mechanism(s) contribute to the thresholds. Equation (6) implied that the single threshold contour contains information on the amount of phase shift. Kremers *et al.* also estimated the phase shifts from a single threshold contour in cone contrast space.[16] To investigate the effect of chromatic mechanism(s) on the phase estimation from a single threshold contour, we calculated the phase shifts from fitting parameters of ellipses with no physical phase shown in Figs. 2 and 3. The results showed that for the orange background the phase shifts are 45.2 deg for ST and 59.6 deg for YT and for the green background they are 29.8 deg and 56.5 deg for ST and for YT, respectively. All phase shifts from a single threshold contour are greater than those obtained in the main experiments. These phase differences are due to contamination by the chromatic mechanism(s). When part of the arc of the contour is determined by the chromatic mechanism(s), the resultant phase shift should be different (see lower-left panel for YT for the green background).

CONCLUSION

We measured intrinsic phase shift with L- and M-cone weights in the luminance pathway by a new method that is more robust with respect to the potential contamination by chromatic mechanism(s) than previous methods. The effect of background colors on phase shift and estimates of L- and M-cone weights are similar to those found for similar experimental conditions in previous reports and support the utility of the proposed technique.

APPENDIX A: SLOPE OF THE THRESHOLD CONTOUR

Figure 1 shows that the slope of the threshold contour changes with physical phase added to the L-cone grating. The slope change with physical phase is modeled as follows. Since the equation of the threshold ellipse is a quadratic form, the direction can be determined by the direction of an eigenvector of a component matrix of Eq. (6). The component matrix, F, is given by

$$F = \begin{bmatrix} a^2 & ab\cos(\phi_p + \phi_i) \\ ab\cos(\phi_p + \phi_i) & b^2 \end{bmatrix}. \quad \text{(A1)}$$

Two eigenvectors of the matrix, $\mathbf{p}_1$, and $\mathbf{p}_2$, indicate the principal directions of the threshold contour as follows:

$$\mathbf{p}_{1,2} = \left\{ \frac{a^2 - b^2 \mp [a^4 - 2a^2b^2 + b^4 + 4a^2b^2\cos^2(\phi_p + \phi_i)]^{1/2}}{2ab\cos(\phi_p + \phi_i)}, 1 \right\}. \quad \text{(A2)}$$

One of the eigenvectors, $\mathbf{p}_1$, indicates the slope of the threshold contour. To simplify the description, a ratio of L′ to M′ weight for luminance mechanism, a_i, is set by

$$a_i = a/b \quad \text{(A3)}$$

in the following equations. Therefore the vector direction of the threshold contour, $Sl(\phi_p + \phi_i, a_i)$, is given by

$$Sl(\phi_p + \phi_i, a_i) = \frac{2a_i\cos(\phi_p + \phi_i)}{a_i^2 - 1 - [a_i^4 - 2a_i^2 + 1 + 4a_i^2\cos^2(\phi_p + \phi_i)]^{1/2}}. \quad \text{(A4)}$$

APPENDIX B: PHASE TEMPLATES USED BY LINDSEY *et al.* AND STROMEYER *et al.*

First, we mathematically express the template for phase estimates proposed previously by Lindsey *et al.*[1] and Swanson *et al.*[2,3] They measured the sensitivity in the direction of equiluminance in cone contrast space. The direction of the equiluminance represents aL' equated to bM' in Eq. (6). In that situation, L' and M' are represented as

$$L'^2 = \frac{D^2}{2a^2[1 + \cos(\phi_p + \phi_i)]}, \quad \text{(B1)}$$

$$M'^2 = \frac{D^2}{2b^2[1 + \cos(\phi_p + \phi_i)]}. \quad \text{(B2)}$$

When stimulus–response is processed by a single channel and the criterion is not changed by the variation of the physical phase, threshold, $T(\phi_p + \phi_i)$, is represented as

$$T(\phi_p + \phi_i) = \sqrt{L'^2 + M'^2} \quad \text{(B3)}$$

$$= \left| \frac{D}{2\cos[(\phi_p + \phi_i)/2]} \left(\frac{1}{a^2} + \frac{1}{b^2} \right)^{1/2} \right|. \quad \text{(B4)}$$

Sensitivity is defined as the reciprocal of the threshold, so it is proportional to the $\cos(\phi_p + \phi_i/2)$.

Second, we show that the template used by Stromeyer *et al.*[5] is essentially the same as that used by Lindsey *et al.* The threshold at the vector direction of θ, $T(\theta, \phi_p + \phi_i)$, in Eq. (6) is represented by

$$T^2(\theta, \phi_p + \phi_i) = \frac{D^2}{b^2\cos^2(\theta)} \times \frac{1}{a_i^2 + \tan^2(\theta) + 2a_i\tan(\theta)\cos(\phi_p + \phi_i)}. \quad \text{(B5)}$$

Stromeyer *et al.* measured contrast thresholds of the summed grating along the fixed vector direction of $\theta_0 = \tan^{-1} a/b = \tan^{-1} a_i$. In this case the thresholds of the summed grating along the L- and the M-cone axis, C_L and C_M, are represented as

$$C_L^2(\theta_0, \phi_p + \phi_i) = \frac{D^2}{2a_i^2b^2[1 + \cos(\phi_p + \phi_i)]}, \quad \text{(B6)}$$

$$C_M^2(\theta_0, \phi_p + \phi_i) = \frac{D^2\tan^2(\theta)}{2a_i^2b^2[1 + \cos(\phi_p + \phi_i)]}. \quad \text{(B7)}$$

After the normalization by the L- and M-cone thresholds, they are represented by

$$\frac{C_L^2}{T_L^2}(\phi_p + \phi_i) = \frac{1}{2\cos[(\phi_p + \phi_i)/2]}, \quad \text{(B8)}$$

$$\frac{C_M^2}{T_M^2}(\phi_p + \phi_i) = \frac{1}{2\cos[(\phi_p + \phi_i)/2]}, \quad \text{(B9)}$$

with

$$T_L^2(0°, \phi_p + \phi_i) = \frac{D^2}{a_i^2b^2}, \quad \text{(B10)}$$

$$T_M^2(90°, \phi_p + \phi_i) = \frac{a_i^2D^2}{a^2}. \quad \text{(B11)}$$

T_L and T_M are given by Eq. (B5) and represent thresholds for the L- and M-cone gratings. Therefore the summed threshold, T_{sum}, for vector direction of $\tan^{-1} a_i$ is represented as

$$T_{\text{sum}} = \left(\frac{C_L^2}{T_L^2} + \frac{C_M^2}{T_M^2} \right)^{1/2} \quad \text{(B12)}$$

$$= \left| \frac{1}{\cos[(\phi_p + \phi_i)/2]} \right|. \quad \text{(B13)}$$

This template is the same as that used by Lindsey *et al.* [Eq. (B4)] except for the coefficients *a, b*, and *D*, which scale the threshold but do not change the shape of the template.

APPENDIX C: ABBREVIATION METHOD

Two thresholds, which are symmetrical at the M-cone axis, is given by Eq. (B5) of Appendix B, and the ratio of two thresholds is represented by

$$f(\theta, \phi_p + \phi_i) = \left[\frac{a_i^2 + \tan^2(\theta) + 2a_i\tan(\theta)\cos(\phi_p + \phi_i)}{a_i^2 + \tan^2(\theta) - 2a_i\tan(\theta)\cos(\phi_p + \phi_i)} \right]^{1/2}. \quad \text{(C1)}$$

This equation shows that the ratio of two thresholds monotonically decreases with the increase in relative physical phase when the phase, $\phi_p + \phi_i$, is $\pi/2$. The gradient of $f(\theta, \phi_p + \phi_i)$ as a function of $\phi_p + \phi_i$ is represented by

$$\frac{\partial}{\partial(\phi_p + \phi_i)} f(\theta, \phi_p + \phi_i) = \frac{-2[a_i^2 + \tan^2(\theta)]a_i\tan(\theta)\sin(\phi_p + \phi_i)}{[a_i^2 + \tan^2(\theta) - 2a_i\tan(\theta)\cos(\phi_p + \phi_i)]^2} \times \frac{1}{f(\theta, \phi_p + \phi_i)}. \quad \text{(C2)}$$

In the abbreviation method we assess the phase, $\phi_p + \phi_i$, at which two thresholds are the same (i.e., $\phi_p + \phi_i = \pi/2$). In this case the equation becomes

$$\frac{\partial}{\partial(\phi_p + \phi_i)} f(\theta, \pi/2) = \frac{-2a_i\tan(\theta)}{a_i^2 + \tan^2(\theta)}. \quad \text{(C3)}$$

This shows that the gradient is maximum at $\theta_0 = \tan^{-1}(a_i)$: In this case the ratio of two thresholds represented by Eq. (C1) becomes

$$df(\theta_0, \phi_p + \phi_i) = \left| \frac{1 + \cos(\phi_p + \phi_i)}{\sin(\phi_p + \phi_i)} \right|. \quad \text{(C4)}$$

The relative phase, $\phi_p + \phi_i$, for $f(\theta_0, \phi_p + \phi_i) = 1$, can be estimated by fitting Eq. (C4) to the data. A linear fit was used in Fig. 7 because Eq. (C4) is a quasi-linear function near the phase of $90 - \phi_i$.

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