

Two distinct cone-opponent processes in the L+M luminance pathway

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ABSTRACT

We measured phase shifts between Long-wavelength cone (L-cone) and Middle-wavelength cone (M-cone) signals as well as sensitivity in the luminance pathway either following a cone-silent substitution of colored background or on a steady colored background. In background substitution, the phase shifts between L- and M-cone signals varied only slightly depending on the substituted color, whereas marked elevation of the threshold following the substitution of colored background was found. In contrast, the phase shifts, as well as threshold, varied largely, depending on the background color in the steady background. These facts suggest that suppression by the cone-opponent process for background color substitution is different from the one for a steady colored background.

Keywords: cone-silent substitution, luminance mechanism, chromatic adaptation, phase shift between cones

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INTRODUCTION

Psychophysical and physiological experiments have revealed that there are differences in process between luminance and color signals in spatiotemporal properties and also in contributions to pattern, motion and stereo perception (*e.g.* Cavanagh, 1988, Livingstone & Hubel, 1984, 1988, Shioiri & Cavanagh, 1992). These results suggest that color and luminance signals are processed separately in early visual perception as the two stage color vision models represent. However, they are not completely independent and chromatic stimulation often influences the luminance process. Thresholds in the luminance pathway vary dramatically depending on the color of the background (*e.g.* de Vries, 1948; Ikeda & Urakubo, 1968; King-Smith & Web, 1974; Eisner & MacLeod, 1981; Stromeyer, Cole & Kronauer, 1987; Stockman, MacLeod & Vivien, 1993). For example, de Vries (1948) showed that the isoluminant point of red and green obtained by flicker photometry, which is assumed to be determined by the luminance mechanism, is strongly affected when an intense red or blue background is used. Ikeda and Urakubo (1968) observed that there is a cone-selective suppression in the luminance pathway with heterochromatic flicker photometry on an intense chromatic adapting field. Eisner and MacLeod (1981) suggested that such an effect can be interpreted by the suppression of Long-wavelength cone (L-cone) or Middle-wavelength cone (M-cone) input to the luminance pathway.

Some of these results could be interpreted as the results of photoreceptor specific adaptation, which is not inconsistent with the separate processing of luminance and color. However, photoreceptor specific adaptation cannot interpret the whole influence of a color background on the sensitivity change. For example, Stromeyer, Cole, and Kronauer (1987) measured flicker detection thresholds for red and blue-green backgrounds, both of which had identical L-cone excitations, and found that the L-cone signal was suppressed by the red background (Stromeyer, Cole & Kronauer, 1987). These results indicate that the suppression

is related to the background color rather than to the mean quantal catch of each cone, suggesting that there is a chromatic post-receptoral mechanism which selectively suppresses each cone signal in the luminance pathway. There have been reports that color opponent processes, in addition to cones, influence the luminance pathway (Smith, Lee, Pokorny, Martin & Valberg, 1992; Stromeyer, Chaparro, Tolia & Kronauer, 1997; Tsujimura, Shioiri, & Hirai, 1997; Tsujimura, Shioiri, Hirai & Yaguchi, 2000a; Stockman & Plummer, 2005ab; Stockman, Plummer & Montag, 2005c). In physiology, the magno- and parvo-cellular pathways have been proposed as physiological substrates for the luminance, defined by flicker photometry, and chromatic pathways (*e.g.* Livingstone & Hubel, 1988; Merigan & Maunsell, 1990). Smith, Lee, Pokorny, Martin and Valberg (1992) have shown that the magno-cellular ganglion cells (MC cells) in monkey retina, receive chromatically opponent signals. They measured phase shifts between L- and M-cone signals input to MC cells and showed that MC cells have a large phase shift on the red background. They concluded that the phase shifts are produced at a post-receptoral site since such a large difference in response latency among different cones had not been observed physiologically and since phase shifts are found only when both the center and the surround of the receptive field was stimulated. Subsequently, in psychophysics Stromeyer, Chaparro, Tolia and Kronauer (1997) investigated the phase shift between L- and M-cone signals in the luminance pathway and showed that the L-cone signal lags behind the M-cone signal on the orange background, and the M-cone signal lags the L-cone signals on the green field. Stockman and Plummer (2005ab) measured spectral sensitivity, modulation sensitivity and phase delays on the steady red background and found cone selective suppression and phase shifts.

Smith et al. (1992) proposed a model of the MC cell, in which the center of the receptive field receives luminance signals (+L+M), while the surround receives a linear difference of L- and M-cone signals (+L-M). Stockman and Plummer proposed a similar model of the

psychophysical luminance channel that has fast non-opponent, L- and M-cone inputs (+fL and +fM), and slow, spectrally opponent cone input signals (-sL and +sM). These fast and slow signals contribute to achromatic perception regarding the flicker nulls. The interference between slow and fast signals could account for sensitivity changes and phase shifts according to the stimulus changes (see also Stromeyer et al., 1997; Stockman & Plummer, 2005ab; Stockman, Plummer & Montag, 2005c). These results strongly support the MC-cell model of Smith et al., in which the surround of the receptive field receives the cone-opponent chromatic signals (*i.e.* +L-M or -L+M).

The studies mentioned above have shown that the color of a steady background affects the thresholds in the luminance pathway and that the influence can be explained by models of the luminance channel with influence from the cone-opponent processes (*i.e.* the background suppression). An abrupt exchange of the background color is also known to elevate the luminance thresholds and the threshold elevation is cone selective (King-Smith & Webb, 1974; Stockman, MacLeod & Vivien, 1993; Tsujimura, Shioiri, Hirai & Yaguchi, 1999). The amount of threshold elevation by the abrupt exchange of the background color is greater than that of the steady background (Stockman et al., 1993). King-Smith and Webb (1974) achieved isolation of cones using the abrupt exchange of background color. They set the intensities of two colored backgrounds so that the background exchange was a silent substitution for one cone type (*i.e.*, no change in terms of the mean quantal catch) while it caused an abrupt increase of stimulation to the other types of cones. Using a similar technique, Stockman et al. (1993) showed that flicker detection can be suppressed cone-selectively. Tsujimura, Shioiri, Hirai and Yaguchi (1999), further found that the onset of the L-cone excitation and offset of the M-cone excitation on the background, suppress the L-cone signals and that the offset of the L-cone excitation and the onset of the M-cone excitation suppress the M-cone signals.

A question to be asked to understand the adaptation and suppression mechanisms in color vision is whether the suppression process activated by abrupt exchanges of the background color is the same process activated by steady background adaptations. Chromatic signals at a post-receptoral site suppress each cone signal selectively in both cases. However, the suppression by abrupt changes of the background color is not related to the color of the background. The abrupt change of the preceding color which is presented for as brief a time as 0.5 sec could influence thresholds even in the same concurrent color background conditions. The suppression processes sensitive to steady backgrounds perhaps respond either to cone signals (L- and M-cone excitations) of the background or to a linear difference of L- and M-cone excitations (*i.e.* +L-M and -L+M), while the suppression processes sensitive to abrupt background exchanges respond to onset and offset of the L- and M-cone excitations of the background (we refer to them as L^+M^- and L^-M^+). These differences may be due to different aspects of the same process or they may be related to different processes and the purpose of the present study was to investigate this issue.

In this study we measured phase shifts between L- and M-cone signals and the amount of cone-selective suppression in the luminance pathway following the background substitution. The phase shifts vary strongly depending on the color of the steady background. If the suppression process for the background substitution is the same process for the steady background, one expects that the phase shifts would also vary strongly depending on the background substitution. Our results showed that phase shifts depended little on the amount of background color changes, even when the threshold variation was clearly dependent on it. These results suggest that the suppression process for the background substitution is different from the process for the steady background adaptation. To explain the influence of color adaptation in the luminance pathway, two different types of cone-opponent processes are required (see Discussion).

Methods

Stimulus generation

All stimuli were generated by a video controller (Cambridge Research Systems VSG2/3) and displayed on a color monitor (Totoku CV821X). The resolution of the display was set to 640 x 480 pixels and the frame rate was set to 150 Hz. Each phosphor was driven by a 15-bit Digital to Analog converter. The CIE coordinates of each phosphor were measured by a spectroradiometer (Photo Research, PR650), using three cone fundamentals obtained by Smith and Pokorny (1975). The monitor was gamma corrected for linearity by an optical device (Cambridge Research Systems, OPTICAL).

General Procedure

Spatial and temporal configuration of stimulus is shown in [Figure 1](#). Before each session, each observer was adapted to a concurrent background field with full screen size for 3 minutes. The luminance was 40.0 cd/m² for the green background and 48.0 cd/m² for the orange background. The pupil size was approximately 4.0 mm for both subjects in the luminance levels. Color changes cause pupil responses which varies retinal illuminance (Tsujimura, Wolffsohn & Gilmartin, 2001, 2003). Considering the estimated pupillary responses of about 0.4 mm, the retinal illuminance was between 2.7 and 2.9 log troland in our experiment. After the initial adaptation, the observer initiated the session by pressing a mouse button. In each trial, a preceding background was presented for 500 ms, the moving test grating was presented for 100 ms in a circular region with a 2-degree diameter at the center of the screen on the concurrent background, and then presentation of a concurrent background which lasted until the judgment of the direction of motion of the test grating was

reported. In each session, trials were repeated until the observer's judgments converge in a staircase method.

Figure 1

We used a two-alternative staircase procedure to determine the contrast threshold at which the direction of motion was identified correctly 79 % of the time. The test contrast was lowered by 0.1 log unit after three successive correct responses and increased by the same amount after each error. We discarded the first three contrast reversals and estimated the thresholds from the average of the last twelve reversals in one session to minimize a bias of threshold caused by initial errors. Three observers (including the first author) with normal color vision (Ishihara plates) participated in the experiment and one of them (DO) participated in a subset of experiments.

Background Stimuli

Figure 2 shows the preceding colors for the green concurrent background (left panel) and for the orange concurrent background (right panel) used in the experiment, which are represented in cone-excitation space. Cone-excitation space uses three fundamentals which correspond to the excitation of the three kinds of retinal cones. The fundamentals were designed so that the total amount of excitation of Long-wavelength cones and Middle-wavelength cones is the same as Judd's modified photopic luminosity function $V(\lambda)$ (Smith & Pokorny, 1975). Pokorny and Smith (1975) did not specify the coefficient by which the color-matching function of $z(\lambda)$ is to be multiplied to obtain the S-cone excitation of $s(\lambda)$. We have chosen the value 1.0 such that the cone fundamental of the short wavelength is the same as the Judd's modified color matching functions (1951), $\bar{z}'(\lambda)$. This is proportional to the unit

(blue troland) used by Boynton and Kambe (1980). In the space, the horizontal axis represents the L-cone excitation and the vertical axis represents the M-cone excitation. The top axis specifies the field wavelength corresponding to the ratio of the L- and M-cone excitation of the stimulus for comparison. The M- and S- cone excitations of the stimulus were kept constant, indicating that backgrounds modulated the L cone alone (M- and S-cones silent substitution). There were four preceding colors (open circles) in each concurrent background along the L-cone axis. We also used the concurrent background as a preceding background (i.e., no background substitution) in the control condition (filled circles). In the control condition, since the color of the preceding background was the same as the concurrent background, the condition corresponded to a steady background condition. The L-cone excitations of these preceding colors were 35.0, 32.5, 30.0, 27.5 and 25.0 cd/m^2 for the green background and 24, 25, 28, 30 and 33 cd/m^2 for the orange background, respectively. The M- and S-cone excitations, which were 15.0 and 12.5 cd/m^2 , were kept constant throughout the experiment. The CIE coordinates of these preceding colors were (0.31, 0.52), (0.36, 0.49), (0.40, 0.47), (0.43, 0.45), and (0.46, 0.43) for the green background, and (0.29, 0.54), (0.31, 0.52), (0.37, 0.49), (0.40, 0.47), and (0.44, 0.45) for the orange background, respectively. These preceding colors were chosen to have as large a change of L cone excitation as possible within the limitation of our apparatus.

The phase shifts were measured also in the steady background condition with several L-cone excitations to compare with those in the background substitution condition. The L-cone excitations of the steady backgrounds were 25.0 cd/m^2 , 26.5 cd/m^2 , 28.0 cd/m^2 , 30.0 cd/m^2 , 31.5 cd/m^2 and 33.0 cd/m^2 and M- and S-cone excitations were the same as those in the background substitution. The ratio of the L- and M-cone excitation of yellow background with L-cone excitation of 30 cd/m^2 was 2.0, being identical to that for 570 nm isochromatic light.

Figure 2

Experiment 1: Threshold elevation following the background substitution

Test gratings and threshold measurements

A mixture of sinusoidally modulated L- and M-cone signals was used as a test grating whose spatial frequency was set to $1.0 \text{ cycle deg}^{-1}$. It was displayed in a circular region with a 2-degree diameter at the center of the screen on the concurrent background and moved either rightward or leftward at 10 Hz. Observers had to report whether the grating drifted rightward or leftward after each stimulus presentation and we ran at least three sessions for each condition. We represent the test grating as a vector in an L, M cone-contrast space. In the L, M cone-contrast space, the gratings along the L-cone axis represent the gratings that modulate the L cone alone (L-cone grating); similarly, the gratings along the M-cone axis represent gratings that modulate the M cone alone (M-cone grating). A contrast in cone-contrast space along each cone axis was defined as: $C' = \Delta C / C_{\text{BGN}}$, where ΔC represents the amplitude of the test grating and C_{BGN} represents the cone excitation of the concurrent background. Therefore, the origin in cone-contrast space represents a background field color. We measured thresholds for six different vector directions in cone-contrast space in the same session using interleaved staircases (0° to 150° in a 30° steps).

The size, stimulus duration, spatial and temporal frequencies of the test grating were chosen (Tsujimura et al., 1999, 2000a). We employed a motion identification task because we felt that it makes the observer's task easier than flicker detection tasks do. It has been shown that both the threshold and the phase shift are similar between motion identification and for flicker detection tasks, at least in foveal vision (Derrington & Henning, 1993; Stromeyer et al. 1997). We assumed that both processes access the same luminance mechanism.

Isolation of the luminance mechanism

We confirmed before the experiment that M- and L-cone stimuli used in the experiments were solely determined by the luminance mechanism, by measuring threshold contours in cone-contrast space. The shape of the threshold contour consists of thresholds in various vector directions, providing information that confirms the isolation of the luminance mechanism. The threshold contour has a negative slope, if the luminance mechanism determined the threshold. Conversely, the threshold contour has a positive slope if the chromatic mechanism determines the threshold (Chaparro, Stromeyer, Chen & Kronauer, 1995; Stromeyer et al., 1997; Tsujimura et al., 1999, 2000a).

The left panels in [Fig. 3](#) represent contours on the green background and the right panels represent those on the orange background. Open circles represent thresholds in the steady background, and filled circles represent those in the background substitution (bottom panels of the figure). The left bottom panel showed a selective suppression of M-cone signals in the L-cone decrement condition in which the orange background was substituted with green (L-cone excitation varied from 35 cd/m² to 25 cd/m²). The right bottom panel showed a selective suppression of L-cone signals in the L-cone increment condition in which the green background was substituted with orange (L-cone excitation varied from 24 cd/m² to 33 cd/m²). For all conditions the slopes of the contour in the first and third quadrants were negative, suggesting that the luminance mechanism determined the thresholds.

These results were consistent with those in our previous paper (Tsujimura et al., 1999, 2000a) in which we measured threshold contours in several background substitution conditions at the same spatio-temporal frequency (Tsujimura et al., 1999) and in a similar condition, where the same spatial frequency was used, but the temporal frequency was 12 Hz rather than 10 Hz (Tsujimura et al., 2000a). A quadrature protocol was employed to

confirm the isolation of the luminance mechanism in these papers. The quadrature protocol was proposed by Stromeyer et al. (Stromeyer et al., 1995) who modified the minimum-motion paradigm that had been developed by Anstis and Cavanagh (1983). Regarding the isolation of the luminance mechanism in terms of phase estimation, our phase method can provide good estimates of phase shift particularly at mid-temporal frequencies where the chromatic mechanism often contaminates the thresholds (described later).

Figure 3

RESULTS

L- and M-cone thresholds as a function of L-cone excitation of the preceding background

Figure 4 shows thresholds in cone contrast along the L- and M-cone axes as a function of L-cone excitation of the preceding background. The left panels represent thresholds for the green background and right panels for the orange background. The top panels represent L-cone thresholds and the bottom ones represent M-cone thresholds. The horizontal axis represents a change in the L-cone excitation of the preceding background. The top axis specifies the L-cone excitation of the preceding background. Note that only L-cone excitation varied so that the axes specify the color of the preceding background. The vertical axis represents thresholds of color change along the L- or M-cone direction. Error bars indicate the standard error of the mean of each data point. The dashed curves correspond to the straight lines fitted to the data in log-log plot (Fig. 5). The arrow in each panel indicates thresholds in the control condition.

Figure 4

When the background altered from orange to green (left panels), both the L- and M-cone thresholds systematically increased according to the decrease in L-cone excitation of the preceding background. The background substitution elevated both L- and M-cone thresholds. However, the M-cone threshold elevation was larger than the L-cone threshold elevation despite the substitution being silent for the M cone (only a decrement of the L-cone excitation). When the background altered from green to orange, at which the L-cone excitation of the preceding background increased (right panels), L- cone thresholds increased while the M-cone threshold showed little change. These results are consistent with previous results of cone-silent substitution experiments (Tsujimura et al., 1999). The results, in general, support the model that incrementing L-cone excitation and decrementing M-cone excitation (L^+M^-) selectively suppress L-cone signals, and that decrementing L-cone excitation and incrementing M-cone excitation (L^-M^+) selectively suppress M-cone signals.

Next, we evaluated the strength of the suppression in terms of Weber exponent, which corresponds to the slope of t.v.i. (threshold vs. intensity) function. Figure 5 showed the \log_{10} cone thresholds in cone-contrast space as a function of \log_{10} L-cone excitation (cone threshold vs intensity, t.v.i, function) for the green and orange backgrounds. The arrangement of the four panels at the top is the same as Fig.4 and the two panels at the bottom represent a log M/L contrast weight ratio to the luminance mechanism. Note that the horizontal axis of t.v.i. function represents the log L-cone excitation of the preceding background, instead of the intensity of the concurrent background as in conventional t.v.i. function. The solid line represents a linear fit to each data set. The slope of the fitting lines allowed us to evaluate the strength of suppression in comparison with previous results.

Figure 5

In the green background conditions, the slope of the fitting line for the L-cone threshold was 1.2 for ST and 1.5 for TM, whereas the slope for the M-cone threshold was 1.9 for both subjects. Larger loss in sensitivity (increase in threshold) for the M-cone threshold is clear evidence of suppression of a post-receptoral mechanism. It is interesting to note that the M-cone suppression in the green background substantially exceeded Weber's law of slope of 1.0. Several studies reported Weber's law of slope of approximately 1.0 in steady backgrounds (Ikeda & Urakubo, 1968; Eisner & MacLeod, 1981; Stromeyer et al., 1987) and also in a background substitution (Stockman et al., 1993).

In the orange background conditions, the slope of the fitting line for the L-cone threshold was 1.1 for ST and 1.7 for TM, whereas the slope for the M-cone threshold was -0.2 for ST and 0.5 for TM. Larger loss in sensitivity (increase in threshold) for the L-cone threshold is clear evidence of suppression. The two panels at the bottom showed the change in M/L contrast weight ratio by the background substitution on the green background (left panel) and on the orange background (right panel). The slope was positive (reflecting the larger sensitivity loss for the M-cone threshold) for the green background and negative (reflecting the larger sensitivity loss for the L-cone threshold) for the orange background, indicating the selective cone suppression in each condition. These results suggest post-receptoral processes suppress luminance signals selectively in each type of cone.

Experiment 2: Phase shifts following the background substitution

In the first experiment, we showed evidence of cone-selective suppression by background substitution, where the decrement of L-cone excitation of the preceding background selectively increased M-cone thresholds and where the increment of L-cone excitation increased L-cone thresholds. In the second experiment we measured phase shifts between L- and M-cone signals for green/orange backgrounds as L-cone excitation of preceding stimulus

decreases/increases. As mentioned in the Introduction, recent studies have shown that the phase shifts between L- and M-cone signals in the luminance pathway varied depending on adaptation to the steady colored background (Smith et al., 1992; Stromeyer et al., 1997; Tsujimura et al., 1997, 2000a). If a common mechanism suppresses luminance signals both in background substitutions and in steady backgrounds, similar phase shifts as in steady backgrounds should result in background substitutions. We measured phase shift in background substitutions to compare with that in steady backgrounds.

The observer's task was the same as in the first experiment. After an initial adaptation of three minutes to the uniform concurrent background field, following the presentation of the preceding background the observer responded alternatively to the direction of a drifting sinusoidal grating on the concurrent background. We employed a technique proposed by Tsujimura et al (2000a) to measure the phase shifts

This technique uses two stimuli which are "same-sign" and "opposite-sign" stimuli. Both of them consist of L- and M-cone gratings with a relative temporal phase shift. The L- and M-cone gratings are summed in phase for the same-sign stimulus and are summed in opposite phase for the opposite-sign stimulus. Thresholds for these stimuli will vary when the visual system adds a relative temporal phase shift between L- and M-cone gratings. If the relative phase is zero the threshold for the same-sign stimulus will be the minimum. Thresholds will increase after adding the relative temporal phase. On the other hand, the threshold for the opposite-sign stimulus is the maximum at the relative phase of zero. Thresholds will decrease as relative temporal phase shifts are added.

Figure 6 shows a schematic diagram of the measurement. The upper panel represents thresholds for the same-sign and opposite-sign stimuli as a function of the relative temporal phase between the L- and M-cone gratings. The temporal phase shift was added into the L-cone grating to provide a relative physical phase between two stimuli. The solid curve

specifies thresholds for the same-sign stimuli and the dashed curve specifies thresholds for the opposite-sign stimuli. These two U-shaped curves cross at the relative temporal phase of 90° when there was no intrinsic phase shift. The middle panel represents an enlargement of the panel around the relative phase of 90° . Open circles represent thresholds for the same-sign stimuli and filled circles represent those for the opposite-sign stimuli. If there is an intrinsic phase shift between L- and M-cone signals these U-shaped curves shifted to right or left according to the amount of the intrinsic phase shift. Therefore, we measured thresholds for the same-sign and the opposite-sign stimuli around a relative temporal phase of 90° , then estimated the intrinsic phase shifts.

Figure 6

Regarding the isolation of the luminance mechanism in terms of phase estimation, our phase method can provide good estimates of phase shift particularly at mid-temporal frequencies where the chromatic mechanism often contaminates the thresholds. Swanson et al. (1987) measured phase shift with a U-shaped template to estimate the phase shift. They measured amplitude thresholds for a pair of isoluminant red and green lights as a function of the relative temporal phase between two lights. They determined the relative phase with the highest thresholds, which corresponds to the relative physical phase of $180-\phi$, where ϕ is the intrinsic phase shift. The bottom panel in Fig. 6 shows a schematic diagram of their phase template. Their phase template is essentially the same as our template for the same-sign stimuli (Tsuji-mura et al., 2000a). The threshold is largest at the phase of $180-\phi$ and the data in this region should provide the most reliable information to estimate the U-shaped template. However, the threshold for phases around $180-\phi$ is likely to be contaminated by the chromatic mechanism because the sensitivity of the luminance mechanism is very low. The

threshold could be determined by the chromatic mechanisms at the phases (broken curve in the panel). The data in Tsujimura et al (2000a) suggested that deviation of the thresholds from the template at around $180-\phi$ is due to contamination by the chromatic mechanism. At the phases where the luminance mechanism is assumed to be insensitive, it is not appropriate to compare the thresholds with those at other phases. Similar contamination from chromatic mechanism can be seen in Swanson et al's data at low temporal frequency (Swanson et al., 1987). In general, at mid-temporal frequencies it is difficult to match the template with the largest threshold data because the threshold in such conditions is often contaminated by the chromatic mechanism. In contrast to their phase estimation technique, our method mainly uses the threshold data around the phase of $90-\phi$ in which threshold data are much less likely to be contaminated by the chromatic mechanism than at phases around $180-\phi$ (see upper panel in Fig.6). To avoid possible contamination around the phase of $180-\phi$, one could use an alternative method that uses only lower thresholds (*i.e.* higher sensitivities) around the central part of the U-shaped template. However, the change in the threshold with phase is small around the center of the template, which makes it difficult to fit the template to the data reliably (see also Stromeyer et al., 1995). Our measurements using phases around $90-\phi$ obtain data with larger change and little contamination of the chromatic mechanism.

Figures 7 and 8 show phase estimation in the steady background and for the background substitution conditions with the largest color changes (35 cd/m^2 for the green background and 24 cd/m^2 for the orange background). Thresholds for the same-sign and the opposite-sign stimuli are shown as a function of the relative temporal phase between L- and M-cone gratings, which correspond to the middle panel in Fig. 6. The panels in the left column represent thresholds for the green background and panels in the right column for the orange. The horizontal axis represents a relative temporal phase between L- and M-cone gratings and the vertical axis represents \log_{10} -thresholds for the same-sign stimuli (open circle) and for the

opposite-sign stimuli (filled circle). The error bar represents the standard error of mean obtained from 5 measurements. We used a linear fit to estimate the phase shift since the U-shaped curve forms a quasi-linear function around 90° (Tsujimura et al., 2000a). The dash-dotted lines specify the relative temporal phase at which two fitting lines crossed. Intrinsic phase shifts between L- and M-cone signals were obtained from a difference in phase between the dash-dotted line and the relative temporal phase of 90° . The values in the upper right in the panel represent the intrinsic phase shift estimated. The positive values of phase shifts indicate that the L-cone signal lags behind the M-cone signal, and the negative phase shifts indicates that M-cone signal lags behind the L-cone signal.

Figure 7

Figure 8

As shown in Figs. 7 and 8, thresholds for the same-sign stimuli (open circle) increased as the relative temporal phase increased, while thresholds for the opposite-sign stimuli (filled circle) decreased. If there were no intrinsic phase shift between L- and M-cone signals in the luminance pathway, the threshold functions would cross at the relative temporal phase of 90° . Figures 7 and 8, however, shows the intersection of the two functions is at a phase larger than 90° in the green background condition and at a phase smaller than 90° in the orange background condition. These results indicate that the direction of the phase shift varies according to the background color, being consistent with previous studies (Tsujimura et al., 1997, 2000a; Stromeyer et al., 1997).

Figure 9 shows the intrinsic phase shift between L- and M-cone signals estimated from the threshold measurements (Figs. 7 and 8) in the background substitution (left panel) and in the

steady background (right panel) conditions. The horizontal axis represents \log_{10} L-cone excitation of the preceding background. The vertical axis represents an intrinsic phase shift between L- and M-cone signals and the top axis represents a wavelength corresponding to the ratio of L- and M-cone excitation of the backgrounds for comparison. The open circles in the left panel represent the data for the green background and filled circles represent the data for the orange background. The error bar represents the standard error of means estimated by the bootstrap method using a statistical analysis computer program (R Development Core Team, 2006). In the right panel the phase shifts in the control condition were plotted in addition to the phase shifts measured on steady backgrounds with different L-cone excitations.

In the steady background condition, the phase shifts strongly depend on the color of the background. The phase shifts are positive in the green background, decrease as L-cone excitation increases, and become negative in the orange background. The phase shift is approximately +15 deg on the green background, null on the yellow background and -20 deg on the orange background. These results are consistent with previous results (Tsujiura et al., 1997, Stromeyer et al., 1997). Stromeyer et al. (1997) measuring the phase shifts in the steady background in a similar condition. They showed that the phase shifts vary depending on the color of the background. They were approximately +20 deg at 555 nm, null at 570 nm and -10 deg at 575 nm.

The results in the background substitutions are very different. All phase shifts of both observers were positive for green backgrounds and negative for orange backgrounds. Contrary to steady background conditions, no reversal of shift direction was found with the change in the preceding color. Phase shift varies unsystematically around approximately plus or minus 20 deg, which roughly corresponds to the phase shifts in the steady background condition (see the right panel). It is likely that the concurrent background determined the

phase shifts. This contrasts with a clear change in the sensitivity reduction with change in the preceding color (see [Figs.4 and 5](#)).

Figure 9

We fitted a line to the average of the phase shifts in each condition. The correlation coefficients between the phase shift and L-cone excitation of the background were 0.10 for the green background and 0.05 for the orange background in the background substitution, whereas it was 0.99 in the steady background. The slopes were 12.3 and -4.8 for the green and orange backgrounds in the background substitutions and -267.9 for the steady background. The low correlation coefficients suggest that the background substitutions do not produce the phase shift between L and M cone inputs. The phase shift independent of substitution colour can be attributed to the effect of the concurrent background. The steep slope and the high correlation in the steady background showed that the color of the steady backgrounds produces the phase shift. These results indicate that the process for the background substitution is different from that for the steady background.

One may think that the background substitution did not change the direction and amount of the phase shift as in the steady background because the background change was too small. However, this is not the case. We found the cone selective suppressions in each substitution condition in [Figs 4 and 5](#), indicating that the change in chromatic background was large enough to induce the L- and M-cone selective suppressions. Moreover, the difference in L-cone excitation of the preceding background was 10 cd/m^2 for the green background, and 9 cd/m^2 for the orange background in the background substitution. This is indeed larger than the difference in L-cone excitation between the orange and green backgrounds of 8 cd/m^2 in the steady background. Although the difference in L-cone excitation was larger in the

background substitution than in the steady background, the background substitution changed the phase shift less than the steady background. This strongly supports the presumption that the background substitution does not cause the phase shift between L and M-cone input to the luminance.

Stockman et al. (1993) measured phase shifts between L and M cones to cancel a residual flicker at isoluminance by adjusting the relative phase between two monochromatic lights so that the flicker sensation became minimum. They showed that there were substantial phase shifts in the steady background condition. In the background substitution, the measured relative phases for the task were smaller and close to null when a signal from the unwanted cone was completely suppressed. Our results showed, however, that there were substantial intrinsic phase shifts in the background substitution. The intrinsic phase shifts were similar to those in the steady background condition, indicating that they were minimally influenced by the background substitution. The difference between the two experiments is probably caused by the difference in the degree of cone isolation by the background substitution. The relative phase between two monochromatic lights measured in Stockman et al should be zero when the signal of the unwanted cone is completely suppressed because only one type of cone inputs to the luminance.

The present experiment has shown that the phase shift is negative in the orange concurrent background and positive in the green concurrent background both in background substitution and steady background conditions. In other words, the background substitution does not affect the phase shifts while the color of the steady background remarkably affects them. To explain these results we suggest that a spectrally opponent process that is sensitive to transient color changes suppresses L- and M-cone signals selectively without causing phase shifts between L- and M-cone signals. This is different from the process that suppresses cone signals with phase shifts in the steady background.

DISCUSSION

We showed that the relative phase between L- and M-cone signals in the luminance pathway had little influence from background substitution, whereas background substitution caused anomalous cone selective threshold elevation. In the steady background, on the other hand, the phase shifts varied depending on the color of the background. Phase shifts were positive (L-cone signal precedes M-cone signal) for the green background and negative (M-cone signal precedes L-cone signal) for the orange background. Results in both background conditions suggest that opponent processes influence the luminance detection. These differences may be due to different aspects of the same process while they may also be related to different processes. We shall discuss the possibility of two different processes in the luminance mechanism in detail below.

Before entering into a detailed discussion, we briefly summarize the similarities and differences between the effects of a steady colored background and a background color substitution. First, it was clearly shown that both a steady color background and a background substitution suppress the cone inputs in the L+M luminance pathway (Eisner & MacLeod, 1981; Stromeyer et al., 1987; King-Smith & Webb, 1974; Stockman et al., 1993; Tsujimura et al., 1999). Second, both a steady background and a background substitution are suggested to receive post-receptoral opponent signals. In other words, L-cone signals could contribute to the suppression of M-cone signals and *vice versa*. Cone silent substitution experiments showed that M-cone (or L-cone) signals to the luminance were suppressed solely by the change of L-cone (or M-cone) signals (Stromeyer et al., 1987; Stockman et al., 1993; Tsujimura et al., 1999). Third, both a steady adaptation and a background substitution selectively suppress each cone signal. If the threshold is measured along the L- or M- cone axis, a certain type of background color or color substitution selectively elevates the

threshold along the L- or M- cone axis. (Ikeda & Urakubo, 1968; Eisner & MacLeod, 1981; Stromeyer et al., 1987; King-Smith & Webb, 1974; Stockman et al., 1993; Tsujimura et al., 1999)

Although these three facts show similarity between the steady background and the background substitution, there are also differences. First, in the steady background condition there is little suppression at around 570 nm, which could be a neutral point for L-M and M-L cone-opponent processes, while in the background substitution the suppression is observed even with a background substitution along the achromatic axis. The yellow steady background of 570-nm light minimized the variation of sensitivity of the luminance mechanism when the mean luminance level, temporal frequency or spatial frequency of the test stimulus was changed (Pokorny, Jin & Smith, 1993; Stromeyer, Chaparro, Tolia & Kronauer, 1997). Pokorny et al. (1993) indicated that the variation of spectral-luminosity function is caused primarily by chromatic adaptation which is null at 570 nm background. On the other hand, in the background substitution condition, Tsujimura et al. (1999) showed that the simultaneous increment/decrement of both the L- and M-cone excitations, which correspond to the increment/decrement of the achromatic stimuli (L^+M^+ and L^-M^-), suppressed both L- and M-cone signals.

Second, the amount of suppression by a steady background is usually less than that by a background substitution (Stockman et al., 1993). Third, the present experiments provided an additional difference between the two suppression paradigms: steady backgrounds produce phase shifts between L- and M-cone inputs to the luminance, while background substitutions do not. These three facts indicate that a single mechanism has difficulty in interpreting all of the suppression effects in the luminance due to chromatic backgrounds. We, therefore, consider the possibility that there are two distinct opponent processes that suppress the luminance pathway.

We start by examining whether models proposed in the literature can explain these empirical results. First, Smith et al. (1992) proposed a model of the MC cell, in which the center of the receptive field receives luminance signals (+L+M), while the surround receives a linear difference of L- and M-cone signals (+L-M). In the MC-ganglion cell model, the cell has spectrally opponent inputs in the receptive field surround and the L-cone signal lags M-cone signal on an orange background, and M-cone signal lags L-cone signals on a green field. Assuming that MC cell determines the luminance threshold, this model predicts the influence of background color on threshold elevations and phase shifts. Stromeyer et al. (1997) also proposed a similar model based on the results of psychophysical experiment.

Second, Stockman, Montag and Plummer (2006) proposed a psychophysical model in luminance channel that has fast non-opponent, L- and M-cone inputs (+fL and +fM), and slow, spectrally opponent cone inputs signals (sM-sL and +sL-sM) (see also Stockman & Plummer, 2005ab; Stockman, Plummer & Montag, 2005c). The interference between slow and fast signals could account for both cone selective suppression and phase shift. In their model, the sM-sL pair is suppressed on the orange field, while the sL-sM pair is suppressed on the green field. The difference in time between the fast L+M and the slow +sL-sM or +sM-sL causes phase shift when these signals are integrated.

In both of the models, the phase shifts are produced by a subtraction of L-M cone-opponent signals (probably from a surround of the receptive field) from the L+M achromatic signals (probably from the center of the receptive field) with temporal delays between both signals. The subtraction produces a change in relative weights of L and M cone signals (M/L contrast weight ratio) as well as the phase shift. When the M/L ratio differs largely from the standard condition, a large phase shift is expected due to delayed cone-opponent signals. Our results are inconsistent with the model prediction. [Figure 10](#) shows a relationship between log M/L contrast ratio and the intrinsic phase shift between cones obtained in Experiment 2.

Open and filled circles represent the M/L contrast ratio for the green and the orange backgrounds. For the large range of the M/L contrast ratio (more than 0.3 log unit), no systematic change is seen in the phase shifts with M/L ratio, suggesting that background substitution has little effect on the phase shifts.

Figure 10

These considerations lead us to propose a new model for the color suppression mechanism in the luminance, in which we assume two different suppression mechanisms (Figure 11). We assumed that both mechanisms coexist and contribute to the luminance. The suppression mechanism in the left column is essentially the same as the models proposed in the literature. (Smith et al., 1992; Stromeyer et al., 1997; Stockman et al., 2005abc, Stockman, Montag & Plummer, 2006). The luminance mechanism receives $+L+M$ and $+L-M/+M-L$ signals, respectively. The luminance response is the result of subtraction between the $+L-M/+M-L$ and $L+M$ signals. The subtraction provides threshold elevation with a phase shift because of the temporal delays between the two signals. For brevity, we call the model “the chromatic subtraction model”. The direction and the amount of phase shift vary depending on the color of the background. The suppression mechanism in the right column is a model that we proposed previously (Tsujimura et al., 1999), that onset of L-cone excitation and offset of M-cone excitation (L^+M^-) selectively decreases the gain of the L-cone input, and offset of L-cone excitation and onset of M-cone excitation (L^-M^+) selectively decreases the gain of the M-cone signals. The selectivity of the suppression is dependent on the change in cone excitation of the background substitution, but not on the background color itself. The mechanism does not affect the phase shifts between L- and M-cone signals in the luminance pathway because the outputs of L^+M^- and L^-M^+ are assumed to control the weights of each

cone signal to the luminance mechanism, which explains our results of cone selective suppression. We call this model “the gain control model”. The crucial difference between the two models is how chromatic signals contribute to the luminance. Phase shift and threshold elevation are expected to occur together in the subtraction model whereas no phase shift is expected in the gain control model.

We assumed that both mechanisms coexist and contribute to luminance to explain our finding that phase shift was constant in the background substitution even in conditions in which large sensitivity changes were obtained. According to the models, the chromatic subtraction generates the phase shifts dependent on the current background and the gain control mechanism produces the cone-selective suppressions in the background suppression.

The subtraction model can be a model of a MC ganglion cell as Smith et al proposed. However, we have no information of the possible site of the gain control model proposed here. This should be at a site prior to the stage of the L+M since it would be difficult to suppress each cone signal after the summation of L and M cone signals.

One may think that constant phase shift in the background substitution may be explained by a subtraction model. The threshold elevation is explained by the suppression of +sM-sL (or +sL-sM) on the orange (or green field) in the model of Stockman et al. If cone opponent signals are suppressed, L+M non opponent signals would determine the threshold, leaving constant phase shift between L and M inputs. Although this explanation is not perfect since the phase shift due to L+M mechanisms are assumed to be zero in the models, we should not rule out this possibility because the phase shift of the L+M mechanism without cone opponent inputs has not been fully investigated.

However, we do not think that this explanation is probable. The selectivity of the suppression is dependent on the change in cone-excitation caused by the background substitution, but not on the background chromaticity. Tsujimura, Shioiri, Hira and Yaguchi

(1998) showed that a change in M/L threshold ratio is in the same direction if the direction of background substitution is the same, independently of the color of the current background (either orange or green). The subtraction model has trouble explaining this fact because the activities of the cone-opponent processes depend on the concurrent background. We therefore claim that different types of suppression or adaptation processes are active between the stationary background and the background substitutions. Assuming a single mechanism for suppression and/or detection in the two background conditions is not sufficient to explain the data.

The present results suggest that the cone-opponent process in the luminance pathway for steady background and that for background substitution are different. Testing this hypothesis in future experiments will provide an important step in understanding the relationship between chromatic and achromatic signals and processing in early visual pathways.

Figure 11

FIGURE CAPTIONS

Figure 1.

Spatial and temporal configuration of the stimuli in the experiment. The grating and concurrent background are substituted for a preceding background. The test grating moving either left- or rightward at 10 Hz is presented for 100 ms.

Figure 2.

Preceding colors in the green background (left panel) and in the orange (right panel) background used in the experiment, represented in the cone-excitation space. Four of the preceding colors (open circles) were away from the green and the orange backgrounds (filled circles) along the L-cone axis.

Figure 3.

Threshold contours for the green background (left panels) and for the orange background (right panels). The open circles represent thresholds in the steady background condition and filled circles in the background substitution (bottom panels).

Figure 4.

L- and M-cone thresholds in the luminance pathway with a change in L-cone excitation of the preceding background. The left panels represent thresholds for the green background and right panels for the orange background. The top panels represent L-cone thresholds and bottom panels M-cone thresholds. The horizontal axis represents a change in L-cone excitation of the preceding background. The vertical axis represents thresholds along the L- and M-cone axes. The top axis specifies L-cone excitation of the preceding background for comparison. Error bars indicate the standard error of mean of each data point. The dashed curves show the fit of a model of the cone-selective suppression. The arrow in each panel indicates thresholds in the steady background.

Figure 5.

Log₁₀ cone threshold as a function of log₁₀ L-cone excitation (top and middle panels) for green background (left panels) and for orange background (right panels). The solid line represents a linear fit of each data set. The values in the panel represent a slope of the fitting line. The two panels at the bottom showed a change in M/L contrast weight ratio as a function of log₁₀ L-cone excitation for the green and for the orange backgrounds, respectively.

Figure 6.

Schematic diagram to show how our technique estimates the phase shift. The upper panel represents thresholds for the same-sign and the opposite-sign stimuli as a function of relative temporal phase. The solid curve specifies thresholds for the same-sign stimuli and dashed curve for the opposite-sign stimuli. The middle panel represents an enlargement of the panel around the relative phase of 90°. Open circles represent thresholds for the same-sign stimuli and filled circles represent those for the opposite-sign stimuli. The solid and dashed lines represent a linear fit of the thresholds. The arrows specified a relative temporal phase at which two lines crossed. In the bottom panel we stated a difference in our phase estimation from those in previous studies (see text for details).

Figure 7.

Measurements of the phase shifts in the steady background: The left panels represent log₁₀ thresholds for the green background and right panels for the orange background as a function of the relative temporal phase, which correspond to the middle panel in [Fig.6](#). Open circles represent thresholds for the same-sign stimuli and filled circles represent those for the opposite-sign stimuli. The error bar represents the standard error of mean obtained from 5 measurements. The arrows in the panel represent a relative temporal phase at which two

fitting lines crossed. The values in the panel represent an intrinsic phase shift estimated from thresholds.

Figure 8.

Measurements of the phase shifts in the background substitution: other details are the same as

Fig.7.

Figure 9.

Intrinsic phase shift between L- and M-cone signals for the cone-silent substitution (left panel) and for the steady background (right panel). The horizontal axis represents \log_{10} L-cone excitation of the preceding background. The vertical axis represents an intrinsic phase shift between L- and M-cone signals. The positive values of phase shifts indicates that the L-cone signal lags behind the M-cone signal, and the negative values indicates that the M-cone signal lags behind the L-cone signal. The top axis represents a wavelength corresponding to the ratio of L- and M-cone excitation of the preceding backgrounds for comparison. The open circles in the left panel represent the data for the green background and filled circles represent the data for the orange background. In the right panel the three different symbols represent phase shifts for three observers in the steady background condition. The solid lines specified a linear fit of the data. The values in the panels represent a correlation coefficient, r , obtained from the fitting.

Figure 10.

Relationship between the log M/L contrast ratio and the intrinsic phase shift between cones in the luminance pathway. Open and filled circles represent the M/L contrast ratio and the phase shifts at several background substitution conditions.

Figure 11.

Hypothetical two distinct color suppression mechanisms both of which operate in the luminance pathway. The right column shows the suppression mechanism with a gain control

of each cone signal (the gain control model) and the left column represents a mechanism with a subtraction of chromatic opponent signal from L+M achromatic signals (the chromatic subtraction model). The gain control model consists of the L^+M^- and L^-M^+ . They selectively suppress the L- and M-cone signals, respectively. The subtraction model selectively suppresses L- and M-cone signals, while it responds to a linear difference of L- and M-cone excitations (+L-M and +M-L) in the L+M luminance pathway.

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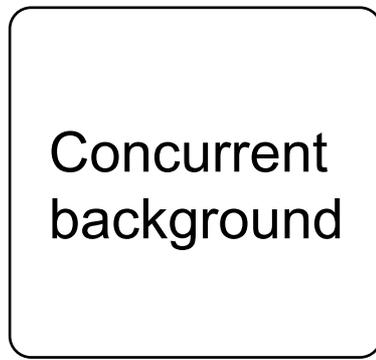
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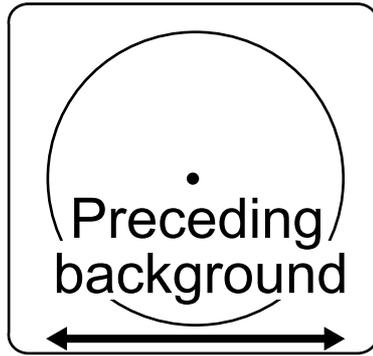
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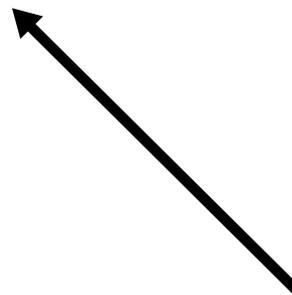
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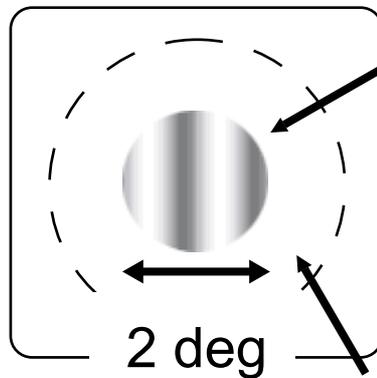
3 min of initial adaptation



500 ms presentation



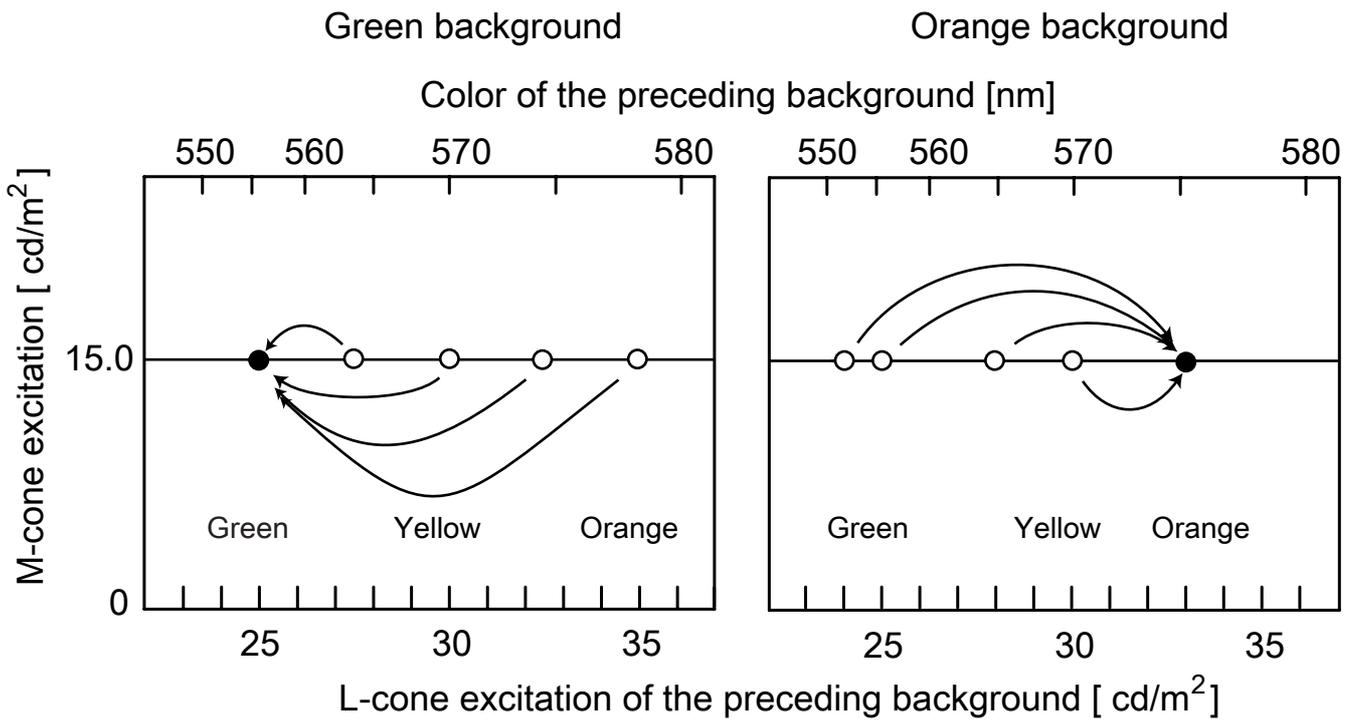
100 ms presentation



moving grating

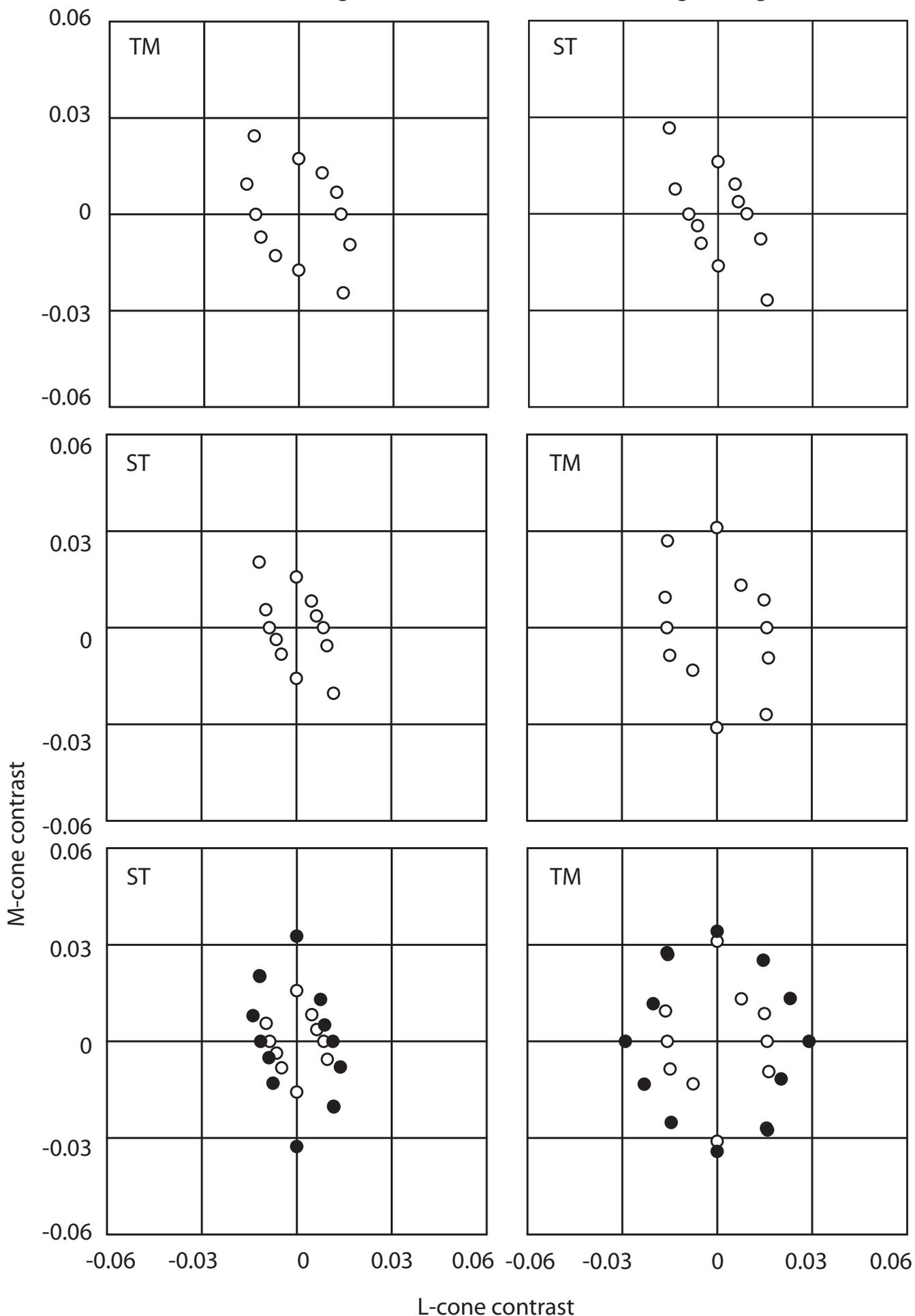


Presented until observer judged



Green background

Orange background



○ Thresholds with steady green background

● Thresholds with background substitution
(Orange to Green: L-cone excitation=35 cd/m²)

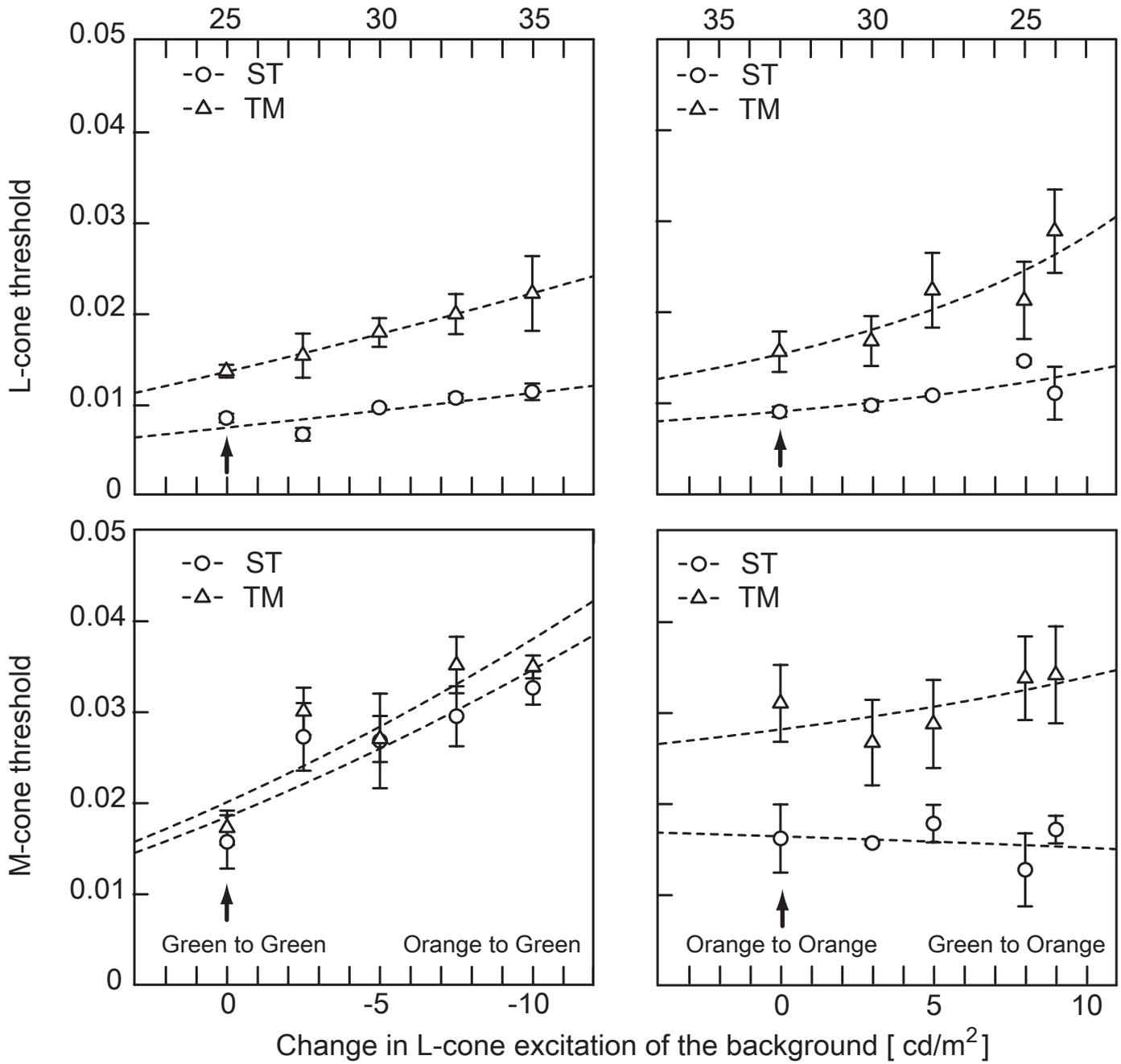
○ Thresholds with steady orange background

● Thresholds with background substitution
(Green to Orange: L-cone excitation=24 cd/m²)

Green background

Orange background

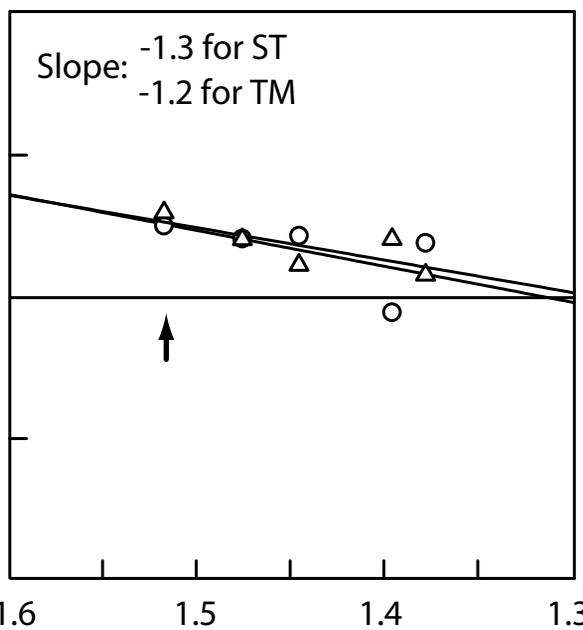
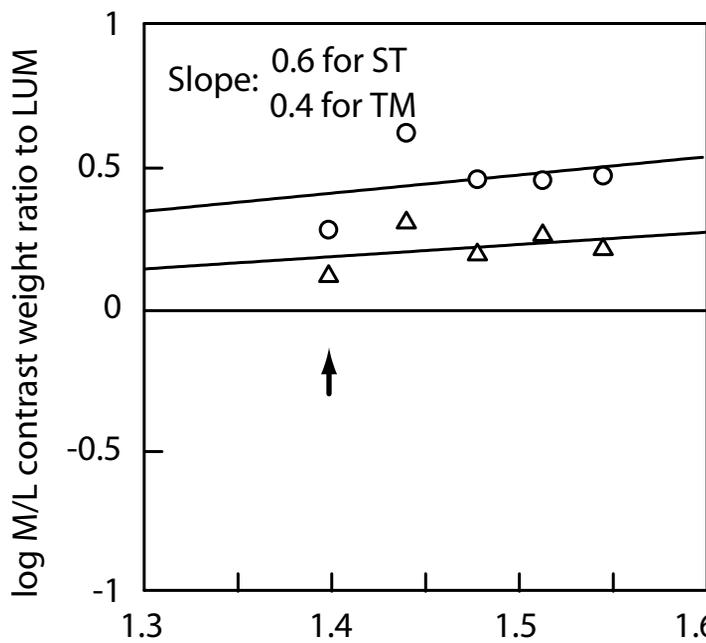
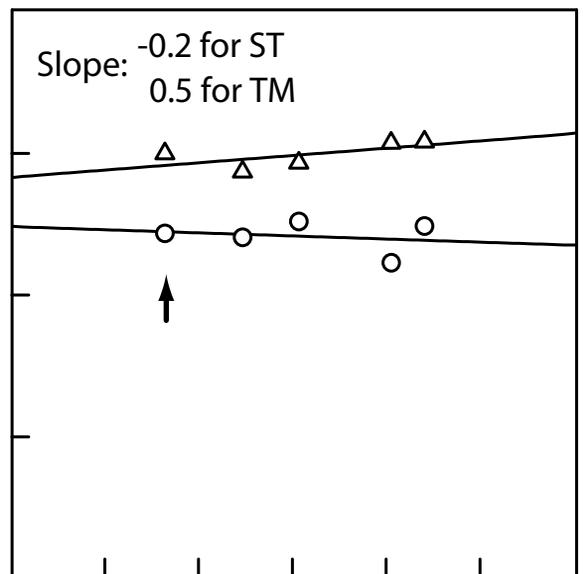
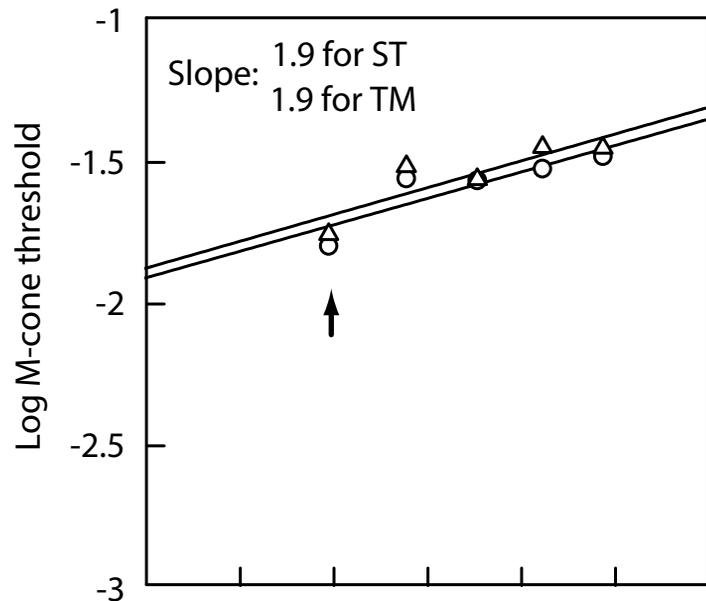
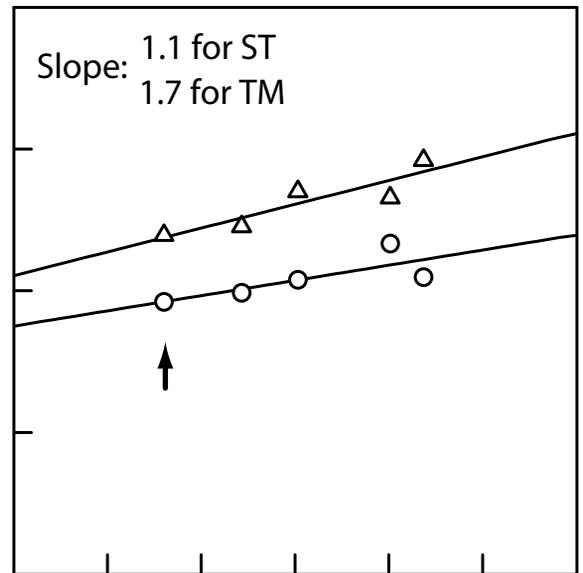
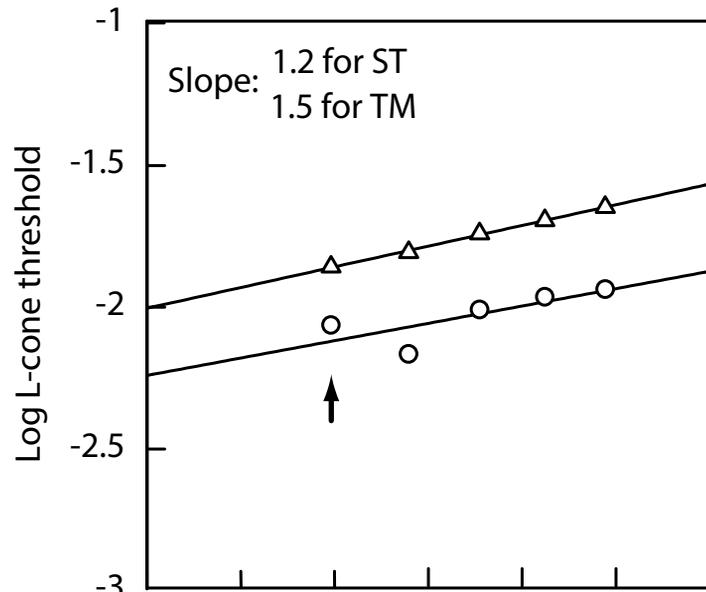
L-cone excitation of the preceding background [cd/m^2]



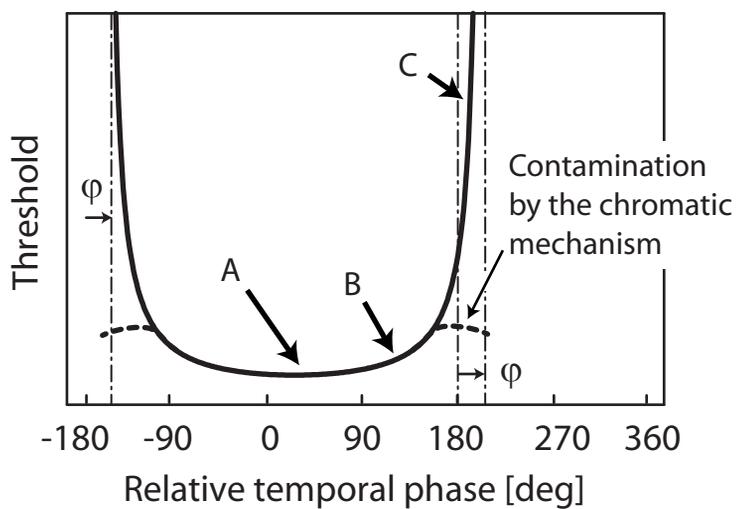
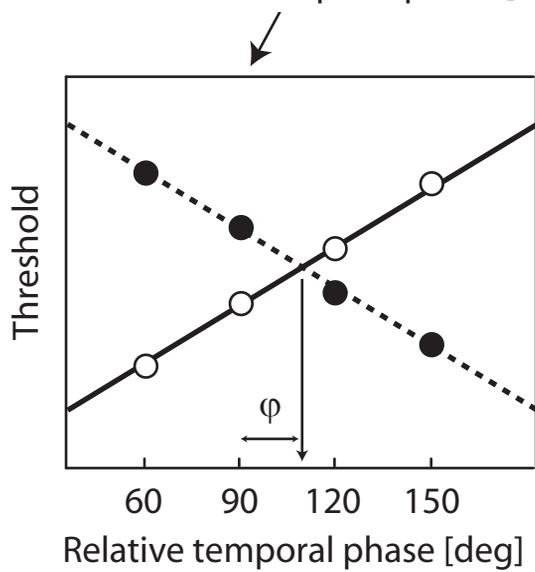
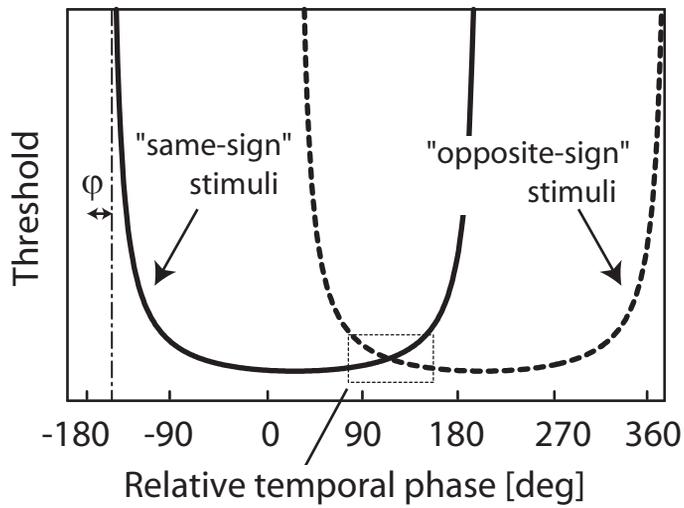
-o- ST
-Δ- TM

Green background

Orange background



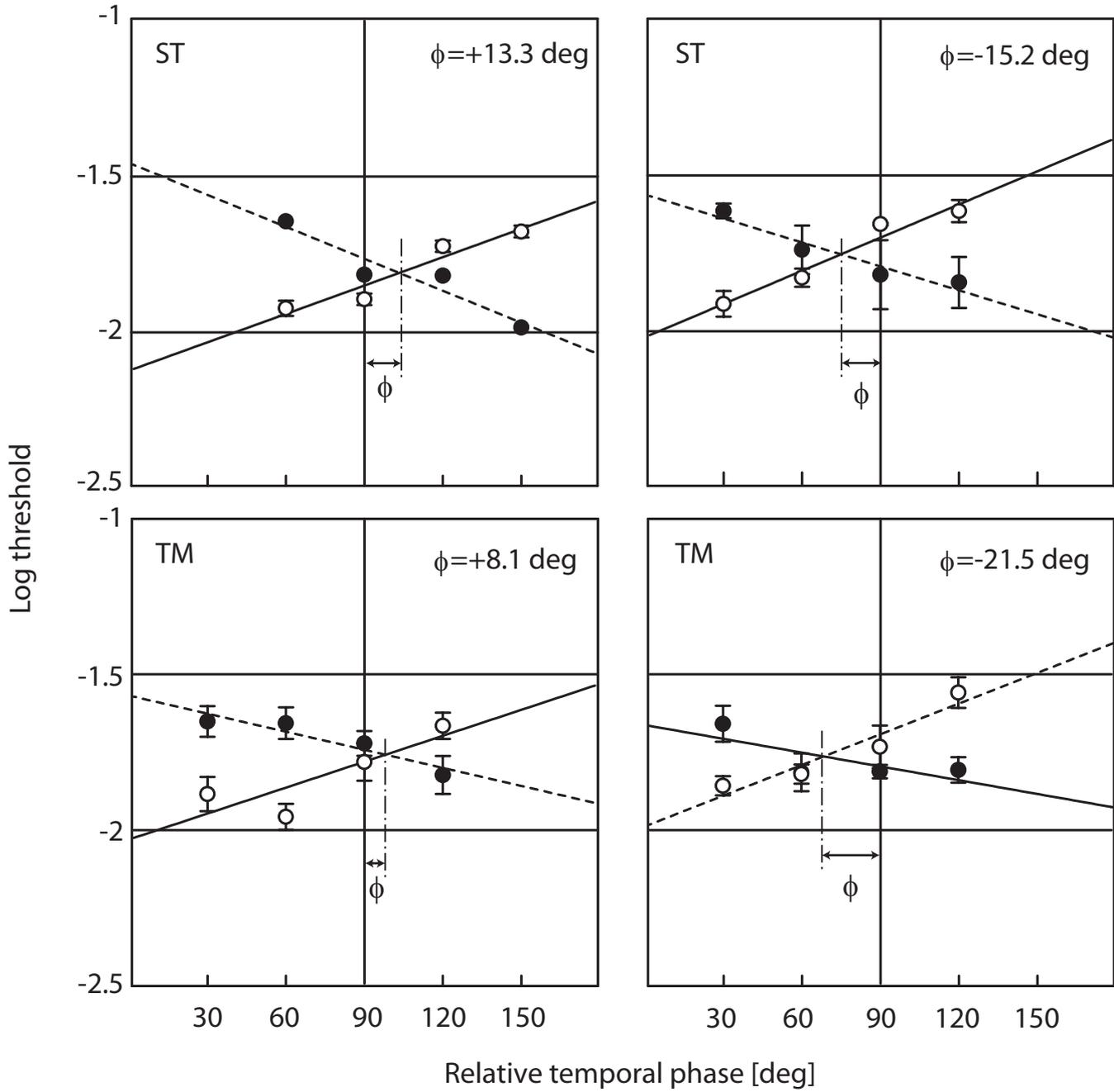
Log L-cone excitation of the concurrent background



- A
 - gentle slope
 - high sensitivity
- B
 - moderate slope
 - moderate sensitivity
- C
 - steep slope
 - low sensitivity

Green background

Orange background

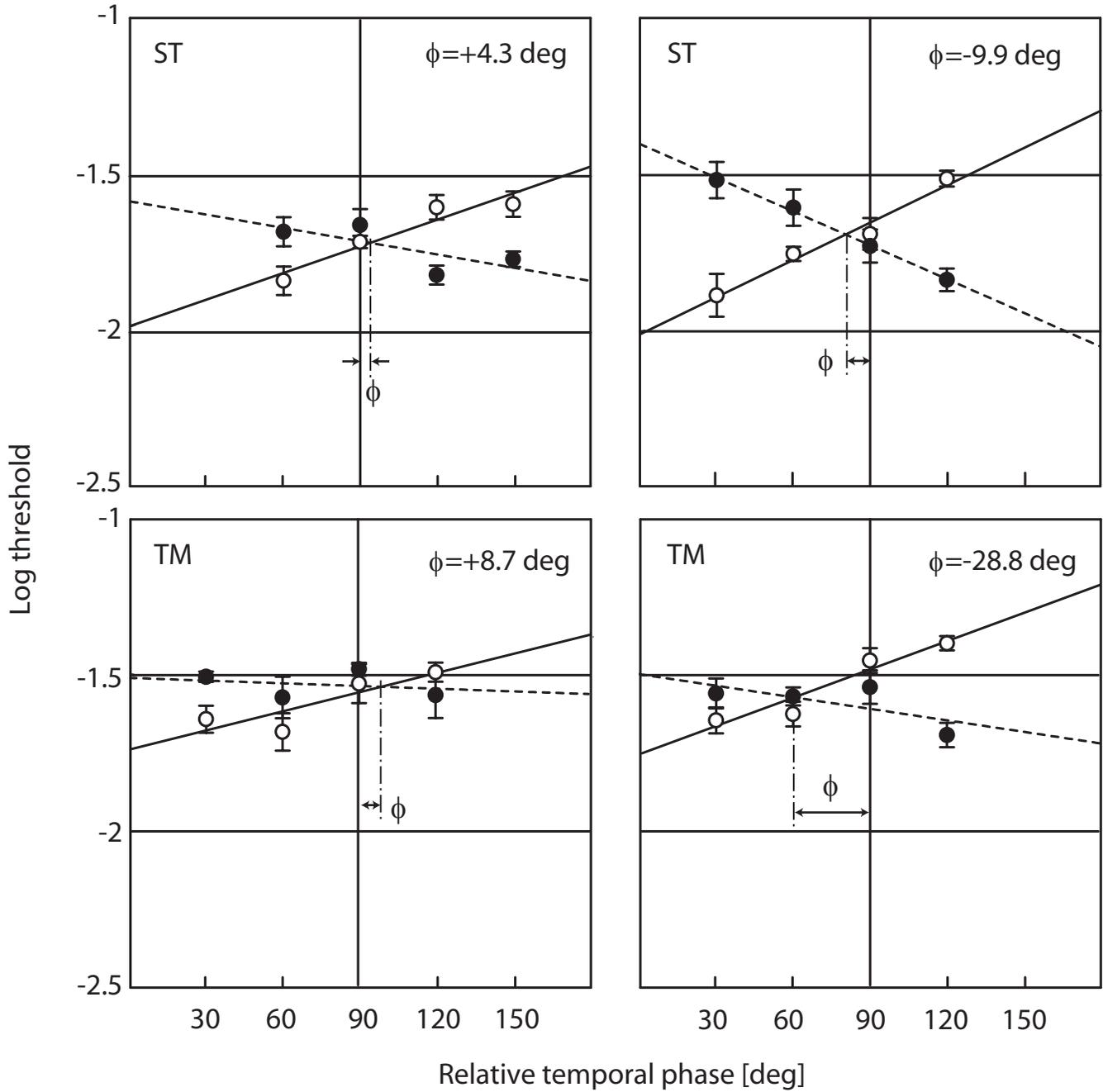


○ Thresholds for the same-sign stimuli

● Thresholds for the opposite-sign stimuli

Green background

Orange background



○ Thresholds for the same-sign stimuli

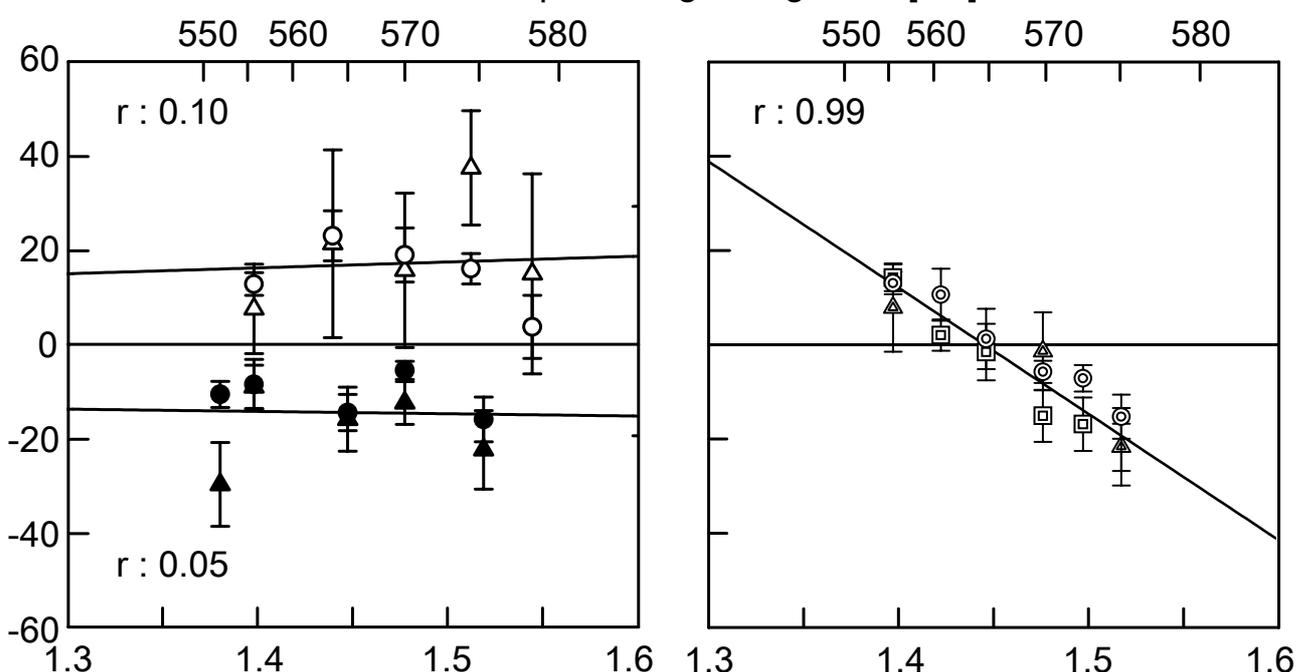
● Thresholds for the opposite-sign stimuli

Intrinsic phase shift between L- and M-cone signals [deg]

Cone-silent substitution

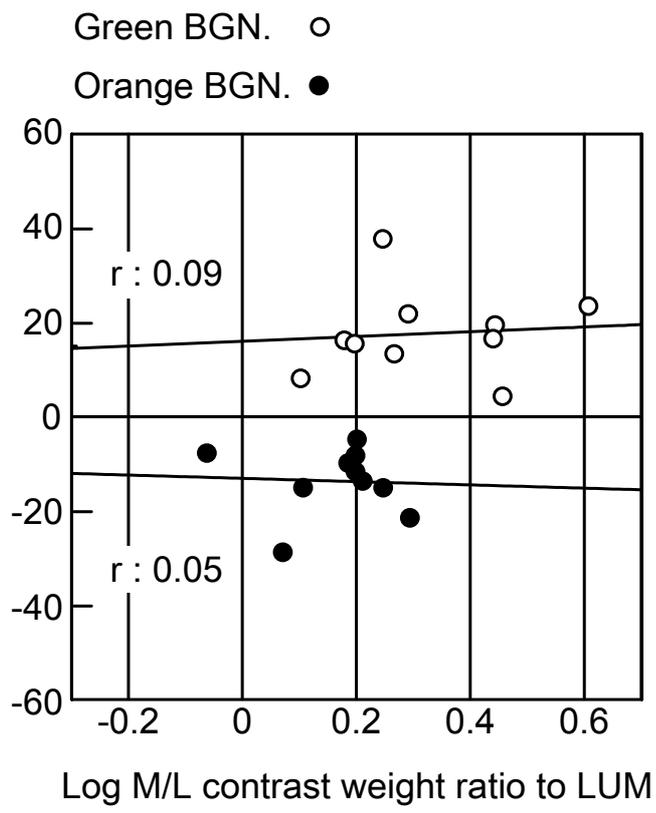
Steady background

Color of the preceding background [nm]



- | | | | | |
|-------------|---|----|---|----|
| Green BGN. | ○ | ST | ⊙ | ST |
| | △ | TM | △ | TM |
| Orange BGN. | ● | ST | □ | DO |
| | ▲ | TM | | |

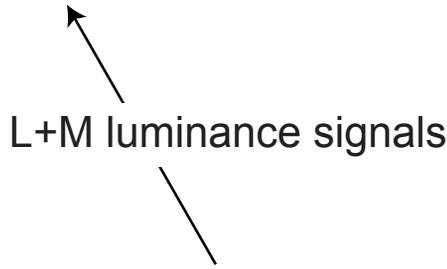
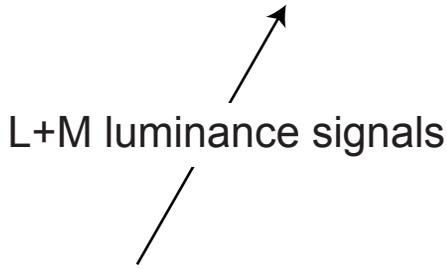
Intrinsic phase shift between L- and M-cone signals [deg]



The chromatic subtraction model

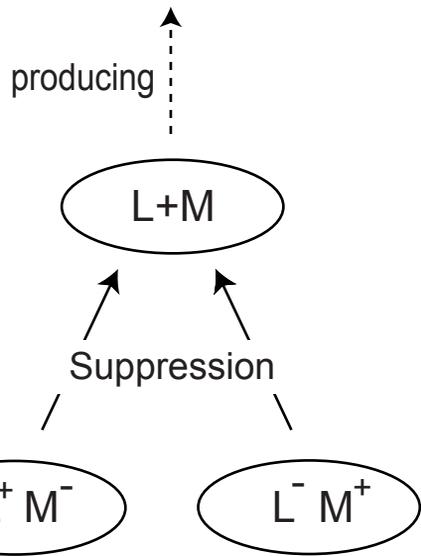
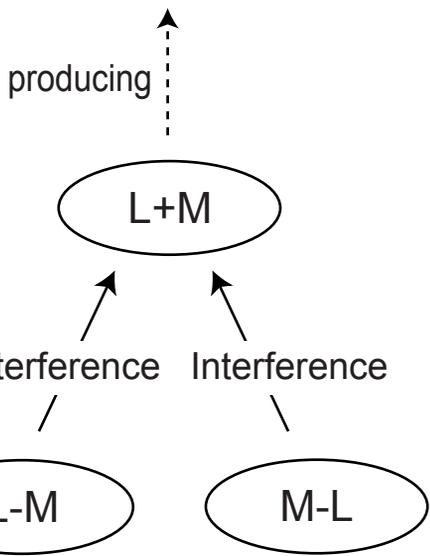
The gain control model

Decision mechanism
in cortical module



- Suppression of L- and M-cone signals
- Temporal phase shift between cones

- Suppression of L- and M-cone signals
- No phase shift between cones



Subtraction of M cone from L cone

Subtraction of L cone from M cone

Onset of L cone & Offset of M cone

Offset of L cone & Onset of M cone

Orange background

Green background

Green to orange substitution

Orange to green substitution