Spatial contribution of colour signals to the luminance pathway

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We measured M- and L-cone thresholds as a function of spatial frequency in background substitutions at which the background colour altered from orange to yellow and from green to yellow. These background substitutions correspond to a decrement of the L-cone excitation of the background and an increment of the L-cone excitation, respectively. The results showed that the M-cone signals were selectively suppressed at spatial frequencies less than 1 cycle deg^{-1} by orange to yellow background substitution, and that the L-cone signals were selectively suppressed at spatial frequencies less than 1 cycle deg^{-1} by green to yellow background substitution. These results indicated that chromatic signals selectively suppress the M- and L-cone signals in the luminance pathway particularly at low spatial frequencies, suggesting that these selective suppressions of cone signals influence the spatial profile of the receptive field in the luminance pathway.

Key words: *Luminance pathway, Threshold, Cone-contrast space, Spatial frequency*

Introduction

In the early visual pathway, it is generally agreed that there are two functionally distinct principal pathways, one mediates the information of luminance and the other mediates the information of colour. These pathways are independent processing steams of major functional significance. The luminance pathway mostly conveys luminance signals for perceptions of luminance while the chromatic pathway conveys chromatic signals for perceptions of the colour. Although luminance and chromatic signals were processed separately in the early visual pathway several studies have shown that the luminance pathway conveys chromatic signals as well as luminance signals. Thresholds in the luminance pathway vary dramatically depending on colour of background. For example, a substitution of background colour from orange to yellow suppressed signals of Middle-wavelength-sensitive cones (M cones) in the luminance pathway and a substitution of background from green to yellow suppressed signals of Long-wavelength-sensitive cones (L cones).

Here, we measured M- and L-cone thresholds in the luminance pathway as a function of spatial frequency in background substitutions at which the background colour altered from orange to yellow and from green to yellow. These background substitutions correspond to a decrement of the L-cone excitation of the background and an increment of the L-cone excitation, respectively. The spatial frequency characteristics regarding the suppression may reflect a spatial profile of the mechanism, such as a shape of the receptive field.

Methods

Stimuli were generated by a video controller (Cambridge Research Systems, Visage) and displayed on a colour monitor. Each phosphor was driven by a 15-bit Digital to Analog converter. The CIE coordinates of each phosphor were measured by a spectroradiometer (Minolta, CS-1000), using three cone fundamentals obtained by Smith and Pokorny (1975). The monitor was gamma corrected and tested for linearity by using the OPTICAL device provided with Cambridge Research

Systems.

Spatial and temporal configuration of stimulus is shown in Figure 1. A mixture of sinusoidally modulated M- and L-cone signals was used as a test grating. It was displayed in a circular region with 5-degree diameter at

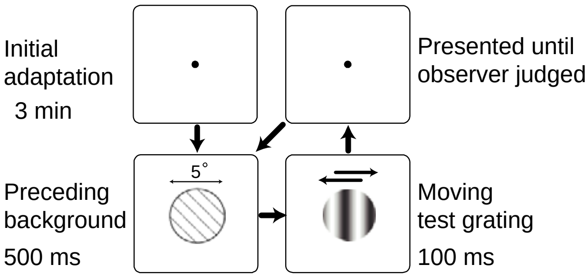

Figure 1: Spatial and temporal configuration of the stimulus in the experiment.

the centre of the screen on the background and moved either rightward or leftward at 12 Hz. Observers had to report whether the grating drifted rightward or leftward after each stimulus presentation and ran at least five sessions for each condition. Two-alternative staircase procedure was used to determine the contrast threshold at which the direction of motion was identified correctly 79 % of the time.

Three preceding colours (yellow, green and orange) were used in the experiment, which were represented in M and L cone-excitation space (Fig.2). Cone-excitation space uses three fundamentals which correspond to the excitation of the three kinds of cones in retina (Smith & Pokorny, 1975). The cone excitations of yellow background was, 18 cd m^{-2} for L-cone excitation 9 cd m^{-2} for M-cone excitation and 12.5 cd m^{-2} for S-cone excitation (18, 9, 12.5). The orange preceding background was (23, 9, 12.5) and the green background was (14, 9, 12.5), respectively. The M- and S- cone excitations of the preceding background were kept constant throughout (*i.e.* L-cone substitution). We used an L cone-silent substitution paradigm since previous studies have shown that the M-cone signals were suppressed by coloured background substitutions with a

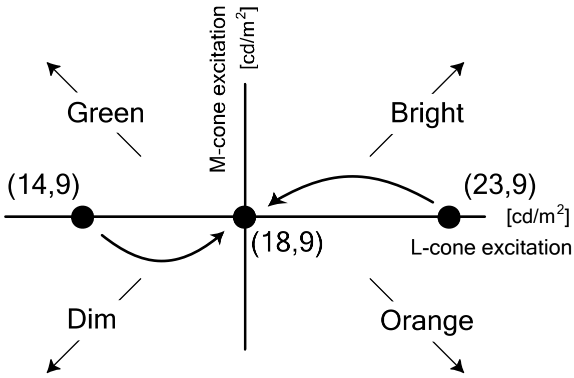

Figure 2: Three colours of preceding backgrounds used in the experiment represented in M- and L-cone excitation space.

decrement of L-cone excitation and with an increment of M-cone excitation, respectively (*e.g.* Stockman *et al*., 1993; Tsujimura *et al*., 1999). The ratio of the L- and M-cone excitation of the yellow background was 2.0 that was identical to that for 570 nm monochromatic light. In the control condition, since a colour of the preceding background was the same as background (*i.e.* yellow background), the condition corresponded to a steady background condition.

We represent the test grating as a vector in M, L cone-contrast space. In M, L cone-contrast space, the gratings along the M-cone axis represent the gratings that modulate M cone alone (M-cone grating); similarly, the gratings along the L-cone axis represent gratings that modulate the L cone alone (L-cone grating). A contrast in cone-contrast space along each cone axis was defined as: $C' = C/C_{BGN}$, where C represents a difference in cone excitation between the background and the amplitude of the test grating and C_{BGN} represents the cone excitation of the background. Therefore, the origin in cone-contrast space represents a background field colour. Thresholds were measured along M-cone axis (*i.e.* 90° vector direction in the space), along L-cone axis (0° vector direction) and along luminance axis (45° vector direction). Test gratings at seven spatial frequencies (0.25, 0.4, 0.5, 0.75, 1.0, 1.5 and 2.0 cycle deg^{-1}) were measured in the same session using interleaved staircases.

Test gratings along six different vector directions (0° to 165° in a 30° steps) were also measured in the control condition to obtain threshold contours in cone-contrast space.

Results and Discussion

Figure 3 shows M- and L-cone contrast sensitivities in the luminance pathway as a function of spatial frequency. The upper panels represent the M-cone sensitivities and the lower panels represent the L-cone sensitivities. The left panels represent sensitivities in the L-cone decrement condition, when the background altered from orange to yellow at which L-cone excitation of the background decreased. The right panels represent sensitivities in the L-cone increment condition, when the background altered from green to yellow at which L-cone excitation of the background increased. Note that the M-cone and S-cone excitations of the background in two conditions were the same and kept constant throughout. Open circles represent sensitivities in the steady background (*i.e.* control condition). We used the difference-of-Gaussians (DOG) model to fit the data (solid curve) to quantitatively examine a receptive-field centre/surround organization.

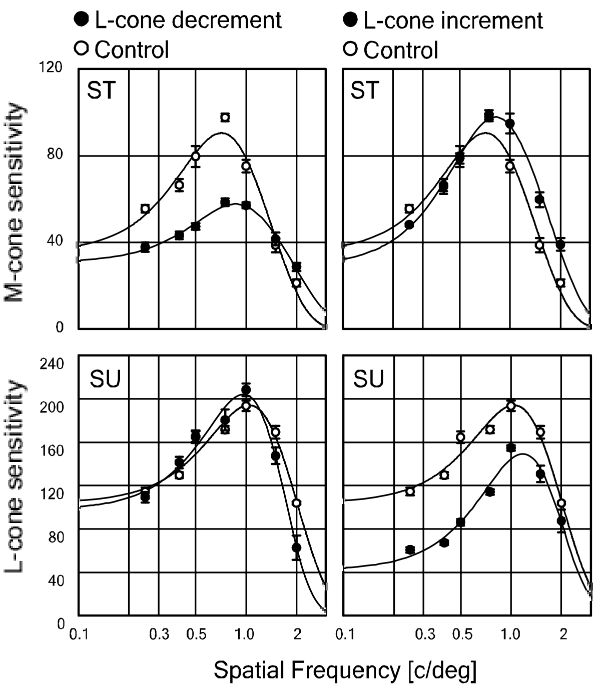

Figure 3: M- and L-cone contrast sensitivities as a function of spatial frequency. The error bar represents a standard error of means (N=5).

In the control condition the peak frequencies were found at around 0.7-1.2 cycle deg^{-1} and the sensitivity monotonically decreased away from the peak frequency. In the L-cone decrement condition (left panels), when the background altered from orange to yellow, M-cone sensitivities were smaller than those in the control condition at frequencies less than 1 cycle deg^{-1}, while small difference was found at higher frequencies. The small difference in L-cone sensitivity was found at lower spatial frequencies less than 0.5 cycle deg^{-1}. Although there was no difference in M-cone excitation between the background substitutions (only decrement of L-cone excitation) the change in M-cone sensitivity was evident in the L-cone decrement condition, indicating inputs from L-cone signals to M-cone signals in the luminance pathway, probably through chromatic mechanisms suggested by several researchers (Eisner & MacLeod, 1981; Stromeyer *et al.*, 1987; Stockman *et al.*, 1993; Tsujimura *et al.*, 1999). Furthermore, we have shown here that the suppression was evident particularly at lower spatial frequencies less than 1 cycle deg^{-1}.

In the L-cone increment condition (right panels), when the background altered from green to yellow, on the other hand, a small difference was found in M-cone sensitivity, while the L-cone sensitivities were remarkably suppressed at lower spatial frequencies less than 1 cycle deg^{-1}. We have shown that the M-cone sensitivity was selectively suppressed in the L-cone decrement condition, and L-cone sensitivity was suppressed in the L-cone increment condition. Interestingly, these sensitivities were suppressed particularly at lower spatial frequencies less than 1 cycle deg^{-1}. To clarify the effect of suppression as a function of spatial frequency, M- and L-cone contrast sensitivities were compared with those in the control condition (Fig. 4). The left panel represents a relative sensitivity of M cones and the right panel represent a relative sensitivity of L cones. The relative sensitivities less than 1.0 represent a suppression of cone signals at which the cone sensitivity in the substitution condition was lower than that in the control condition.

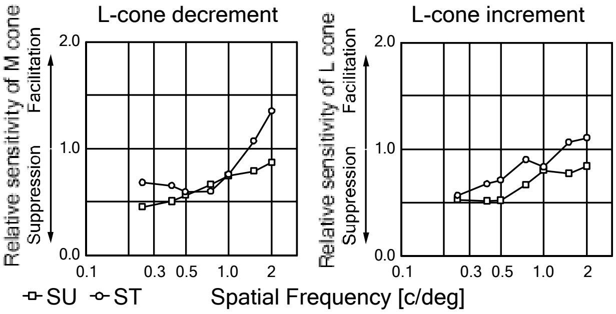

Figure 4: Relative contrast sensitivity of M and L cones as a function of spatial frequency. The sensitivity at each spatial frequency was normalised with that in the control condition.

In the L-cone decrement condition (left panel) the relative sensitivities of M cones were lower than 1.0 at lower frequencies, indicating that the M-cone signals were suppressed at lower spatial frequencies less than 1.0 cycle deg^{-1}. The relative sensitivity of M cones increased as spatial frequency increased, indicating an amount of suppression decreased as spatial frequency increased. In the L-cone increment condition (right panel) the relative sensitivities of L cones were lowest at the spatial frequency of 0.25 cycle deg^{-1} and increased as spatial frequency increased for both subjects. Consistently for two subjects, the suppression was evident at lower frequencies, indicating that the L-cone signals were suppressed at these spatial frequencies.

We have assumed that the cone sensitivities measured in the experiment were determined by the |L+M| luminance mechanism. The M- and L-cone sensitivities, however, could be influenced when |L-M| cone-opponent mechanism determined the thresholds. We confirmed that cone thresholds measured in the experiment were solely determined by the |L+M| luminance mechanism. When M- and L-cone thresholds were solely determined by the |L+M| luminance mechanism, luminance thresholds could be a simple linear sum of these thresholds. Figure 5 shows the relationship between the actual luminance thresholds and estimated luminance thresholds calculated from M- and L-cone thresholds. The estimated luminance thresholds calculated from M- and L-cone thresholds were well correlated with the actual luminance thresholds, indicating that the M- and L-cone thresholds were solely determined by the luminance mechanism.

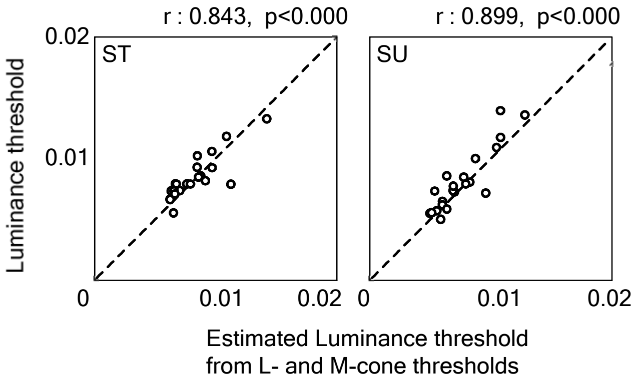

Figure 5: The relationship between the luminance thresholds and the estimated luminance thresholds calculated from M- and L-cone thresholds.

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