Cone-silent substitution influences spatial contrast sensitivities of cone signals in the luminance pathway

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ABSTRACT

We investigated how transient changes of a background colour influence the spatial contrast sensitivities of cone signals in the luminance pathway. Previous studies have shown that 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 as a function of spatial frequency in background substitutions at which the background colour altered from orange to yellow and from green to yellow. It was found that the M-cone signals were suppressed at spatial frequencies less than 1 cycle deg^{-1} by orange to yellow background substitution, and the L-cone signals were suppressed at spatial frequencies less than 1 cycle deg^{-1} by green to yellow background substitution. These results indicated that chromatic mechanisms in the luminance pathway suppress cone signals particularly at low spatial frequencies less than 1 cycle deg^{-1}.

1. INTRODUCTION

In retino-cortical visual pathway, it is generally agreed that there are two distinct principal pathways, one mediates the information of luminance and the other mediates the information of colour. These pathways are separate processing steams of major functional significance. The luminance pathway mostly conveys luminance signals for perceptions of luminance, texture and motion, while the chromatic pathway conveys chromatic signals for perceptions of the colour (*e.g.* Cavanagh, 1988). However, a number of studies have shown that the luminance pathway conveys chromatic signals as well as luminance signals (*e.g.* de Vries, 1948; Ikeda & Urakubo, 1968; Eisner & MacLeod, 1981; Stromeyer, Cole & Kronauer, 1987). Stockman, MacLeod, and Vivien (1993) showed that the L-cone signal was suppressed by changing the background colour with the mean L-cone quantal catch kept constant. They found that the L-cone signal was suppressed when a bright blue background was substituted by a bright red one and, similarly that the M-cone signal was suppressed when a bright red background was substituted by a bright blue one. These results suggest the existence of chromatic suppression in the luminance pathway. Recently, Tsujimura, Shioiri, Hirai and Yaguchi (1999) measured thresholds on a yellow background following the orange and green background substitutions. Since the background colour was fixed to the yellow, this allowed them to isolate the effect of suppression produced by background substitution from effects of the steady background adaptation. They found that the increment of the L-cone excitation and decrement of the M-cone excitation of the background, (*i.e.* L^+M^-), suppress the L-cone signals and the decrement of the L-cone excitation and that the increment of the M-cone excitation of the background, (*i.e.* L^-M^+), suppress the M-cone signals. However, to date, very little is known about the effect of spatial frequency on cone signals by the background substitutions. The aim of this paper was to investigate the effect of spatial frequency on cone signals suppressed by coloured background substitutions, which could be used to reveal neural substrates regarding the chromatic suppression in the luminance pathway.

2. METHOD

Stimuli were generated by a video controller (Cambridge Research Systems) 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.

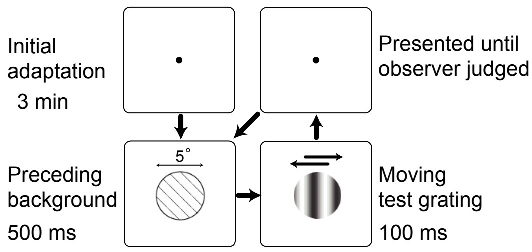

Figure 1: Spatial and temporal configuration of the stimulus in the experiment.

Spatial and temporal configuration of stimulus is shown in Figure 1. Three preceding colours (yellow, green and orange) were used in the experiment, which were represented in L and M cone-excitation space. 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 decrement of L-cone excitation and with an increment of M-cone excitation, respectively (*e.g.* Stockman *et al.*, 1993; Tsujimura *et al.*, 1997). 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.

A mixture of sinusoidally modulated L- and M-cone signals was used as a test grating. It was displayed in a circular region with 5-degree diameter at 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.

We represent the test grating as a vector in L, M cone-contrast space. In L, M cone-contrast space, the gratings along the L-cone axis represent the gratings that modulate 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: $C' = C/C_{BGN}$, where C represents a difference in cone excitation between the background and the amplitude of the test grating and CBGN 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.

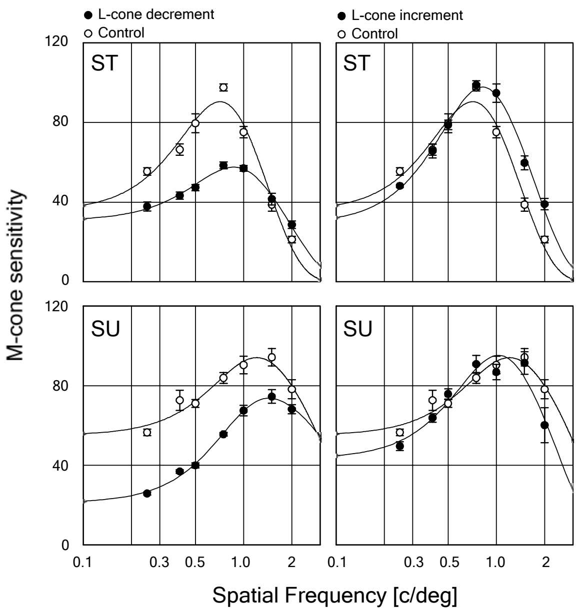

Figure 2: M-cone contrast sensitivities as a function of spatial frequency. Open circles represent the sensitivities in the steady background condition (control), and filled circles represent the sensitivities in L-cone decrement condition (left panels) and in L-cone increment condition (right panels). The error bar represents a standard error of means.

3. RESULTS & DISCUSSION

Figure 2 shows M-cone contrast sensitivities in the luminance pathway as a function of spatial frequency. The left panels represent the M-cone 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 M-cone 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. The sensitivities were obtained from subject ST (upper panels) and from subject SU (lower panels), respectively.

In the control condition the peak frequencies were found at around 0.7-1.2 cycle deg^{-1} for both subjects 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. In the L-cone increment condition (right panels), on the other hand, a small difference in sensitivity was found for both subjects. Although there was no difference in M-cone excitation between the background substitutions (only increment 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; Stockman *et al.*, 1993; Stromeyer *et al.*, 1987; 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}.

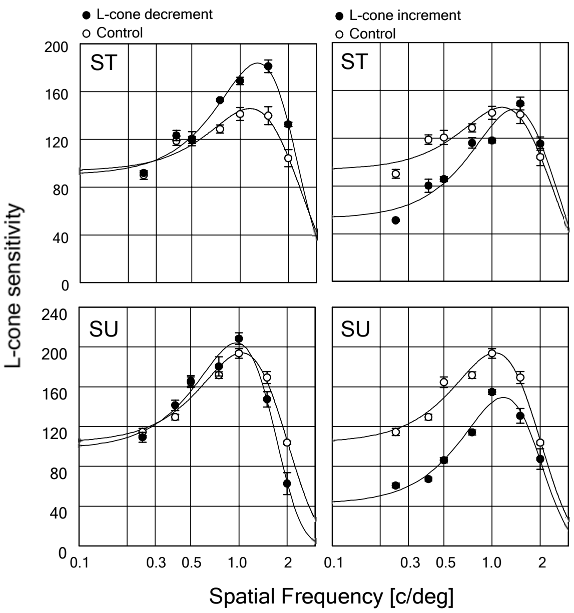

Figure 3: L- and M-cone contrast sensitivity as a function of spatial frequency. Other details are the same as those in Fig.2.

Figure 3 shows L-cone sensitivities as a function of spatial frequency. The arrangement of the panels was the same as the M-cone sensitivities in Fig. 2. Open circles represent sensitivities in the control condition with steady background. In the control condition the peak frequencies were found at around 1.0-1.2 cycle deg^{-1} and the sensitivity monotonically decreased away from the peak frequency. As we mentioned previously, several studies have shown that the L-cone sensitivities were suppressed by L-cone increment substitution. In the L-cone increment condition (right panels), when the background altered from green to yellow, the L-cone sensitivities were suppressed at lower spatial frequencies less than 1 cycle deg^{-1}. In the L-cone decrement condition (left panels), when the background altered from orange to yellow, the small difference in L-cone sensitivity was found at lower spatial frequencies less than 0.5 cycle deg^{-1}. The L-cone sensitivities were facilitated at frequencies more than 1 cycle deg^{-1} for subject ST, but the effect was not evident for subject SU.

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.

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

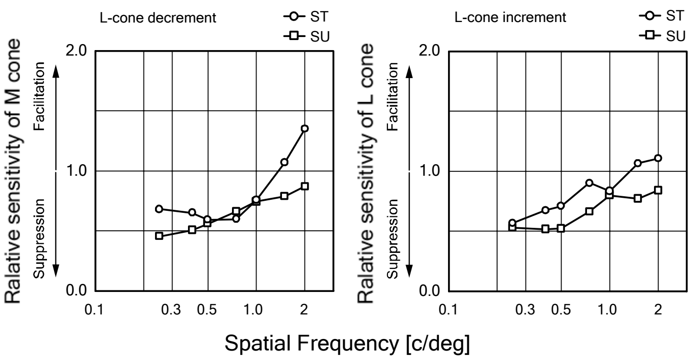

Figure 4: Relative contrast sensitivity of M and L cones as a function of spatial frequency. The sensitivity at each spatial frequency was normalised with that in the control condition. The sensitivities less than 1.0 represent that sensitivity was suppressed relative to that in the control condition.

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 (*e.g.* Chaparro *et al.*, 1993). We confirmed that cone thresholds measured in the experiment were solely determined by the |L+M| luminance mechanism. The iso-response contours in cone-contrast space were determined (Tsujimura *et al.*, 1999) to examine whether the luminance mechanism was solely responsible for detecting thresholds. Figure 5 showed threshold contours in L, M cone-contrast space for subjects ST and SU at spatial frequency of 1.0 cycle deg^{-1}. In cone-contrast space, a horizontal axis represents a stimulus modulating L cone alone, and a vertical axis represents a stimulus modulating M cone alone. The origin in cone-contrast space represents a background field colour (*i.e.* yellow in this experiment). The vector length defines the contrast of the stimulus. It was found to be linear in the first and fourth quadrants, indicating that the |L+M| mechanism solely determined the thresholds. The correlation coefficients at all frequencies ranged from 0.96 to 1.00 for ST and from 0.88 to 0.98 for SU, and averages were 0.99 and 0.94, respectively. These results indicated that the L- and M-cone thresholds in the experiment were solely determined by |L+M| luminance mechanism.

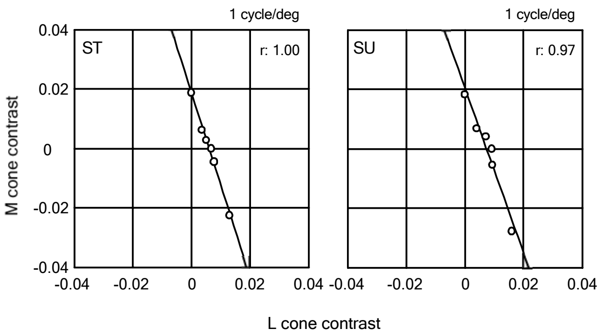

Figure 5: Threshold contour in L, M cone-contrast space for subjects ST and SU at spatial frequency of 1.0 cycle deg^{-1}.

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