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Temporal integration of the chromatic channels in peripheral vision

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ABSTRACT

We measured the temporal summation properties of paired flashes to investigate the temporal responses of the chromatic channel in peripheral vision in comparison with those of the luminance channel. The size of the stimulus was scaled according to the cortical magnification factor. The temporal response was biphasic to complementary-chromatic pulse pairs, and was accelerated in peripheral vision in the same way as luminance pulse pairs. On the other hand, the temporal response was monophasic to same-chromatic pulse pairs, and was decelerated in the periphery. We proposed a model of the chromatic channel in which biphasic and monophasic internal channels were arranged in parallel. The sensitivity of the biphasic channel at high temporal frequency in the periphery was comparable to that in the fovea, whereas the sensitivity of the monophasic channel at low temporal frequency in the periphery matched that in the fovea. Similar results were obtained with pairs of flashed chromatic Gabor patches with their spatial frequencies scaled according to the cortical magnification factor. The inhibition phase of the biphasic channel was degraded with the spatial carrier frequency of the Gabor patch. The properties of the biphasic channel were consistent with the double duty hypothesis, while those of the monophasic channel were consistent with the two-channel hypothesis. The biphasic channel may correspond to the parvocellular pathway and the monophasic channel may reflect the properties of the koniocellular pathway.

1. Introduction

Our ability to see color and fine spatial detail deteriorates in the peripheral visual field (Boynton, Schafer, & Neun, 1964; Gordon & Abramov, 1977; Stabell & Stabell, 1984; Wertheim, 1891). However, most deterioration of visual function in the periphery can be compensated by spatially scaling the stimuli at each retinal eccentricity so that their representations in the primary visual cortex are equivalent (M-scaling). For example, the spatial contrast sensitivity functions at various retinal eccentricities overlap each other by scaling the size and the spatial frequency of the sinusoidal grating stimuli based on M-scaling (Rovamo, Virsu, & Näsänen, 1978). Similar results were obtained for color vision such that color appearance (Abramov, Gordon, & Chan, 1991) and spectral sensitivity of red–green opponent response (Hibino, 1992) in the periphery were recovered by M-scaling of the stimuli.

As for the temporal properties, by M-scaling the stimulus size at each eccentricity, the peak contrast sensitivity of the luminance channel in the periphery can be equated. The temporal response in the periphery, however, is faster than that in the fovea (Tyler, 1985). The acceleration of the luminance channel in the periphery is consistent with the elevation of the critical flicker frequency in the periphery (Rovamo & Raninen, 1984). On the other hand, little is known about the spatiotemporal characteristics of the chromatic channel in the periphery. Noorlander, Koenderink, den Ouden, and Edens (1983) found that chromatic contrast sensitivity in the periphery was compensated by M-scaling, but their experimental condition was limited to only 1 Hz in the temporal frequency and 2 cycles in the spatial property.

Wiesel and Hubel (1966) found several distinct cell groups in the lateral geniculate nuculeus. The type I cells show both spatial and spectral opponency. On the other hand, the type II cells show only spectral opponency. The same properties were found also in the retinal ganglion cells (DeMonasterio, 1978; DeMonasterio & Gouras, 1975). The double duty hypothesis that the type I cells in the parvocellular pathway (PC cells) convey both luminance and color information has been widely accepted as a model for the color vision mechanism (Boycott & Wässle, 1999), whereas the two-channel hypothesis that the PC cells are only for fine spatial details, and that color vision is mediated by type II cells in the koniocellular pathway, has been proposed recently (Calkins & Sterling, 1999; Rodieck, 1991). Based on the double duty hypothesis, the deterioration of color vision in the periphery can be attributed to the random wiring between cones and retinal ganglion cells (Shapley & Perry, 1986). However, the residual color sensitivity to proper

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stimulus conditions in the far periphery (Noorlander et al., 1983) is inconsistent with the random wiring hypothesis.

The results of direct electrophysiological recordings of the macaque retina remain controversial. Martin, Lee, White, Solomon, and Rüttiger (2001) showed that the PC cells in the periphery still respond well to isoluminant chromatic modulation. They rejected the random wiring hypothesis and insisted that PC cells are the origin of the red–green channel in color vision. However, Dacey (1996) showed that the PC cells in the periphery codes the sum of L and M cone responses and their color opponencies are lost, which is consistent with the random wiring hypothesis. Solomon, Lee, White, Ruttiger, and Martin (2005) recently reported that about a quarter of peripheral PC cells were non-opponent even at low temporal frequencies.

As noted above, there remains controversy about the mechanisms of peripheral color vision. In particular, the effects of retinal eccentricity and spatial scale on temporal characteristics are yet unknown. Here we can present a working hypothesis that if a single mechanism mediates both the luminance and chromatic channels, the effects of eccentricity on the temporal responses of the luminance and chromatic channels will be consistent. On the other hand, if the mechanisms of the luminance and chromatic channels are separated in the early stage, the temporal responses of the luminance and chromatic channels may not necessarily vary consistently with eccentricity. The purpose of the present study is to reveal the mechanisms of color vision by investigating the temporal characteristics of the chromatic channel in the periphery, and their relationship with spatial scale.

In experiment 1, we measured the temporal responses to luminance and chromatic modulations both in the fovea and in the periphery, and found two modes of response to chromatic stimuli. A model to explain the difference in chromatic response is proposed. The possibility of luminance artifacts in experiment 1 is examined in experiment 2. A result in experiment 1 is reconfirmed by another method in experiment 3. To test the generality of the results in experiment 1, we investigated the temporal responses of the chromatic channel with spatial patterns of various spatial frequencies in experiment 4.

2. General methods

2.1. Apparatus

Subjects observed the test stimuli presented on a CRT (Nanao FlexScan T766; 100 Hz; 1024 × 768 pixels) through an aperture opened on a white screen. The screen was a hemispherical dome made of styrene foam in experiments 1, 2 and 3, and a hemicylindrical dome made of white paper in experiment 4. The inner surfaces of the screens were illuminated brightly and almost uniformly to saturate the rods with four or eight approximated D65 fluorescent lamps (FL20S D-EDL-D65, Toshiba Lightech, Tokyo, Japan; CIE 1931 (x, y)-chromaticity coordinates (0.315, 0.335)). The CRT was controlled by a video card (VSG2/4, Cambridge Research Systems, Kent, UK) and a PC (Dimension V350, Dell, Texas, USA).

2.2. Stimuli

The test stimuli were two brief (10–60 ms) flashes modulating in either luminance or chromaticity. The stimulus onset asynchrony (SOA) of the two flashes ranged from 10 to 2000 ms. In experiments 1, 2 and 3, the test stimulus was a spatially uniform disk, whose diameter was scaled with eccentricity according to the cortical magnification factor (Rovamo & Virsu, 1979). In experiment 4, the test stimulus was 10° in diameter and spatially modulated as a Gabor patch of various spatial carrier frequencies (0.38–3.79 cpd). The surround of the test stimulus was bright (>120 cd/m^2) white for the entire visual field. The eccentricities tested were 30° in the temporal visual field for experiments 1, 2 and 3, or 10° in the nasal visual field for experiment 4.

2.3. Temporal double-pulse method

Many previous studies have measured contrast sensitivity to flicker with various temporal frequencies in the investigation of temporal vision. However, a temporal modulation transfer function (tMTF) provides information only about the amplitude, not about the phase of the visual channel under investigation. To estimate a temporal impulse response function (tIRF) from a tMTF, most previous studies assumed that the channel was minimum phase (Stork & Falk, 1987; Swanson, Ueno, Smith, & Pokorny, 1987 e.g.). If a filter is known to be minimum phase, you can derive the phase of the filter from its amplitude using the Hilbert transform. However, the assumption of minimum phase is not necessarily justified for visual systems (Victor, 1989). Here we can show two tIRFs that have exactly the same tMTF (Fig. 1). One is minimum phase and monophasic, but the other is non-minimum phase and biphasic. It cannot be determined whether a tIRF is monophasic or biphasic even if its tMTF is known, unless its phase information is given.

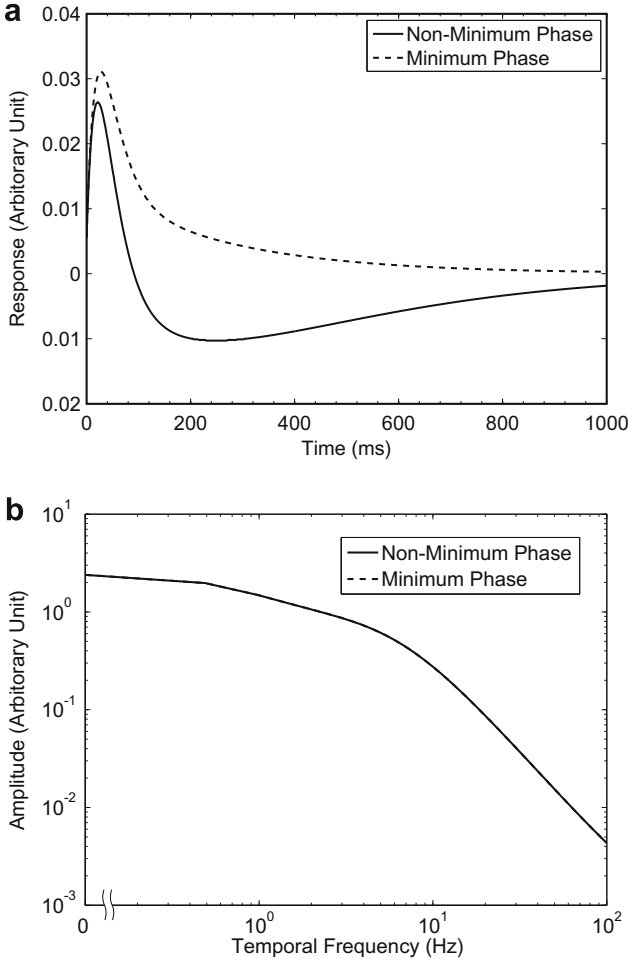

Fig. 1. Monophasic and biphasic IRFs that have exactly the same tMTF. (a) IRFs. The solid curve is non-minimum phase and biphasic, and the dashed curve is minimum phase and monophasic. (b) The tMTFs of the IRFs in (a). The two curves are perfectly overlapping with each other and only one of them is seen on the figure.

In addition, the stimuli in the peripheral visual field with strict fixation fade out in a short time (Troxler, 1804). Troxler's effect is widely known for stationary stimuli, but even flickers are subject to this effect when they are presented with a constant temporal frequency (Anstis, 1996). Applying a temporal window to the flicker might prevent Troxler's effect, but such a solution deteriorates the temporal frequency selectivity of the flicker.

In the present study, we measured the temporal summation of double flashes (Burr & Morrone, 1993; Granit & Davis, 1931; Ikeda, 1965; Shinomori & Werner, 2003; Uchikawa & Yoshizawa, 1993) to investigate the temporal characteristics of the luminance and chromatic channels. Pulses are inherently transient, and therefore expected to be invulnerable to Troxler's effect in the periphery.

We can estimate the tIRFs from the data in temporal summation directly in the temporal domain, and then take the Fourier transform to calculate the tMTFs in the frequency domain. We measured detection thresholds in temporal summation, and it is thought to be valid to assume small-signal linearity to the data obtained in threshold level.

Minimum phase has been assumed for the sake of convenience in calculating tIRFs from tMTFs, and has little empirical validity. On the other hand, the assumptions that we used in the present study to derive IRFs from the summation data have been validated by many previous empirical studies.

2.4. Procedure

Subjects were first dark adapted for 5 min, then light adapted to the stimulus for 3 min. Two sessions of experiments were conducted in succession. The subject voluntarily started each trial by pressing a button. A pair of pulses was presented with a certain SOA (10–2000 ms) between two beeps separated by 3000 ms (experiment 1) or 2500 ms (experiments 2–4). The subject answered whether he had seen any flash between the beeps. The intensity of the pulses in each trial was controlled by a multiple-series yes/no staircase method. Each staircase series of an SOA condition was continued until the reversal of the series exceeded 3. All the series were randomly interwoven in a session. After each

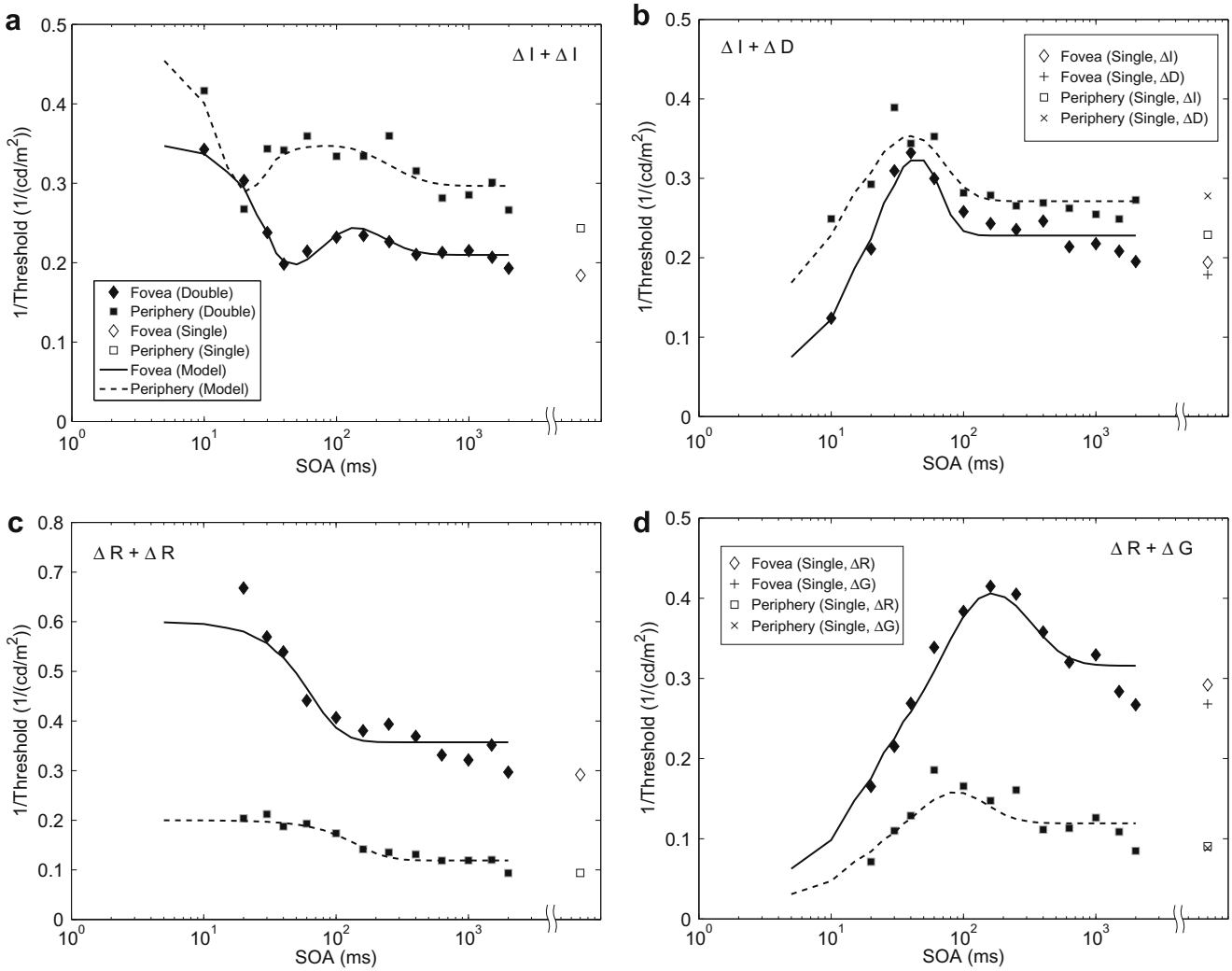

Fig. 2. Temporal summation of double flashes in the case of subject OM. The ordinate represents the reciprocal of the threshold (rTH) and the abscissa represents the SOA between the two pulses. The filled and open symbols represent results of double-pulse and single-pulse summation, respectively. The diamond and square symbols represent results in the fovea and in the periphery, respectively. The solid and dotted lines represent the prediction by a model described later. (a) Incremental and incremental pulse pair ($\Delta I + \Delta I$). (b) Incremental and decremental pulse pair ($\Delta I + \Delta D$). (c) Red and red pulse pair ($\Delta R + \Delta R$). (d) Red and green pulse pair ($\Delta R + \Delta G$). In (b), the square and diamond symbols correspond to incremental (ΔI) single pulse thresholds and the '×' and '+' symbols correspond to decremental (ΔD) single pulse thresholds. In (d), The square and diamond symbols correspond to red (ΔR) single pulse thresholds and the '×' and '+' symbols correspond to green (ΔG) single pulse thresholds. In (b) and (d), the square and '×' symbols correspond to the foveal condition and the diamond and '+' symbols correspond to the peripheral condition.

experiment, the responses from all sessions were put together and the 50% response threshold intensity was estimated for each SOA with Probit analysis (Finney, 1971). All the experiments were undertaken with the understanding and written consent of each subject.

3. Experiment 1: the temporal responses of the luminance and chromatic channels in the peripheral visual field

3.1. Methods

Subjects observed the test stimuli through an aperture placed at the center of a hemispherical dome (radius 40 cm) with their right eyes. The CRT was placed 50 cm behind the aperture. The inner surface of the dome was illuminated by 4 fluorescent lamps and its luminance and CIE 1931 (x, y)-chromaticity coordinates were 120 cd/m^2 and (0.318, 0.339), respectively. The diameter of the aperture was 1° in the foveal condition or 10° in the peripheral condition. In the foveal condition, the subject fixated at the center of the test stimulus, and accommodated to the edge of the aperture. In the peripheral condition, the subject fixated at a black disk placed 30° to the left of the center of the test stimulus.

The background color of the test stimulus was (0.420, 0.503) in CIE 1931 (x, y)-chromaticity coordinates, and 50 cd/m^2 in luminance. A luminance flash was either an increase (ΔI) or decrease (ΔD) in luminance with the modulation ratio of the R primary to the G primary kept constant. A chromaticity flash was made by shifting the chromaticity with the total luminance kept constant. For a red pulse (ΔR), the luminance of the R primary was increased and that of the G primary was decreased at the same time. A green pulse (ΔG) was made in the same way but in the opposite direction. The modulation ratio of the R and G primaries were adjusted for each subject and for each eccentricity based on flicker photometry, performed in advance. The thresholds for single flashes of each type were also measured in the main sessions.

The paired flashes were combined in four different ways: (i) $\Delta I + \Delta I$: the luminance of both flashes were increased. (ii) $\Delta I + \Delta D$: the luminance of the first pulse was increased, but that of the second was decreased. (iii) $\Delta R + \Delta R$: the chromaticity of both flashes was modulated to red. (iv) $\Delta R + \Delta G$: the chromaticity of the first pulse was modulated to red, and the second to green. When the types of the first and the second pulses were different (in the cases of $\Delta I + \Delta D$ and $\Delta R + \Delta G$), the modulation ratio of the first to the second was scaled according to the preliminarily measured threshold for single flashes of the same type. The pulse duration of a flash was 10 ms for a luminance flash in both the foveal and peripheral conditions. The pulse duration of a chromaticity flash in the foveal condition was 20 ms for all subjects, but that in the peripheral condition was 20 ms for subject OM and 40 ms for the other two subjects.

Three subjects, OM (one of the authors, 32 years old), TN (23 years old), KK (22 years old); who participated in the experiment and were male with color-normal vision and normal or corrected-to-normal acuity. TN and KK were naive to the purpose of the experiment.

3.2. Results

The results for the subject OM are shown in Fig. 2. Similar results were obtained for the other subjects. The ordinate represents the reciprocal of the threshold (rTH) of a flash. The threshold was defined as the amount of luminance change for the first pulse in a pair that caused 50% response on the subject. For a luminance pulse, the amount of luminance change was the sum of the luminance changes for the R and G primaries. For a chromaticity pulse, the threshold was expressed in terms of the luminance change of the R primary, and the G primary was changed in the opposite direction so that there was no net luminance change. The abscissa represents the SOA between the two flashes. The filled symbols correspond to double flashes, and the open symbols to single flashes. The symbols '+' and '×' correspond to the single pulses of the same type as the second pulse in the double flashes. The single flashes were plotted at the rightmost position of each graph. The diamond and '+' symbols represent the results in the foveal condition, and the square and '×' symbols in the peripheral condition. The solid and dotted curves represent the fit of a model described later for each condition.

The rTHs for pulse pairs $\Delta I + \Delta I$ and $\Delta R + \Delta R$ were higher at shorter SOA, which means that the internal responses elicited by these pulses were summed to evoke a strong total response in the visual system. At the shortest SOA, the rTHs for $\Delta I + \Delta I$ and $\Delta R + \Delta R$ were almost twice that of the corresponding single pulses (perfect summation). On the other hand, the rTHs of the pairs of the opposite pulses ($\Delta I + \Delta D$ and $\Delta G + \Delta G$) were small at shorter SOAs, which means that the internal response elicited by these opposite pulses canceled each other and the total response became weak.

At longer SOAs, the rTHs tended to approach an asymptotic constant level, which means that the two pulses were independent of each other and had no actual interaction (probability summation). At the middle SOA (40 ms for the foveal and 20 ms

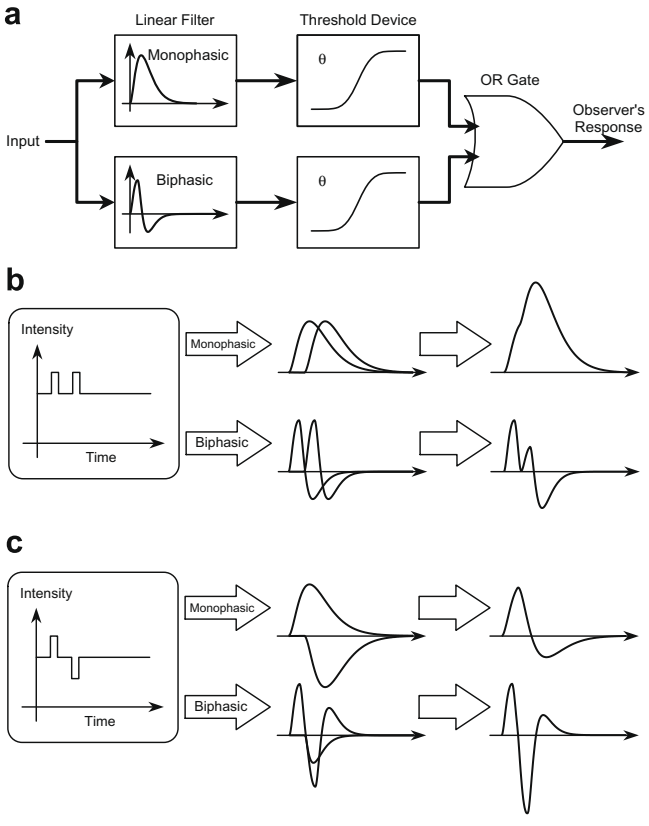

Fig. 3. Parallel two-channel color vision model. (a) Block diagram. The sensory input is forked into two parallel internal channels. Each inner channel has a linear filter followed by a threshold device. The observer's response is the logical "or" of the outputs of the two threshold devices. (b) In this case, an in-phase pulse pair is input. In the monophasic internal filter, two pulses are always combined, but in the biphasic internal filter, two pulses cancel each other at a certain SOA. (c) In this case, an out-of-phase pulse pair is input. In the monophasic internal filter, the two pulses always cancel each other, but in the biphasic internal filter, two pulses are combined at a certain SOA.

for the peripheral condition) in $\Delta I + \Delta I$, the rTHs became lower, which means that the internal responses to the two pulses canceled each other. The rTHs became higher for $\Delta I + \Delta D$ at the SOA of 40–60 ms for the foveal and 30 ms for the peripheral condition, which means that the internal responses to the two pulses summed together.

These results mean that the response to a luminance pulse has a negative or inhibitory lobe. The result of $\Delta R + \Delta R$ shows monotonous shift with SOA from perfect summation to probability summation, which means that the response to these chromatic pulses was monophasic and had no negative or inhibitory phase. The result of $\Delta R + \Delta G$ resembles that of $\Delta I + \Delta I$, which means that the response to these chromatic pulses had a negative or inhibitory phase.

3.3. Discussion

In the result of $\Delta I + \Delta I$, the trough in the rTH appears earlier for the peripheral condition (20 ms) than for the foveal condition (40 ms). A similar result was obtained for $\Delta I + \Delta D$. The peak in the rTH for the peripheral condition (30 ms) appears earlier than for the foveal condition (40–60 ms). These results suggest that the response of the luminance channel is faster in the periphery than in the fovea.

The temporal integration of the same-chromatic pulse pair ($\Delta R + \Delta R$) did not show an inhibitory phase but that of the complementary-chromatic pulse pairs ($\Delta R + \Delta G$) did. This discrepancy has been reported by Uchikawa and Yoshizawa (1993). Here we found it again, even in the periphery. The temporal response to a chromatic pulse in the periphery lasts longer than that in the fovea as shown in Fig. 2c. On the other hand, the peak in the temporal response to complementary-chromatic pulse pairs in the periphery appears earlier than that in the fovea (Fig. 2d). The convergence of the temporal response to the asymptotic probability summation level is earlier for the peripheral condition than for the foveal condition. These results suggest that the temporal response of the chromatic channel in the periphery is slower for same-chromatic pulse pairs, but faster for complementary-chromatic pulse pairs. It seems reasonable to deduce that these disagreements may reflect the responses of two different internal channels in the chromatic mechanism.

3.3.1. Parallel two-channel color vision model

Here we propose a model shown in Fig. 3. In this model, there are two internal channels; one is temporally monophasic and the other biphasic. When either of the responses from these channels reaches a threshold level, the observer detects the stimulus. When a same-chromatic pulse pair comes to these channels the responses to each pulse in the monophasic channel always sum together and the total response is larger than that to a single pulse. On the other hand, those in the biphasic channel cancel each other at a certain SOA and the total response in the biphasic channel is smaller to that in the monophasic channel. Thus only monophasic characteristics are observed.

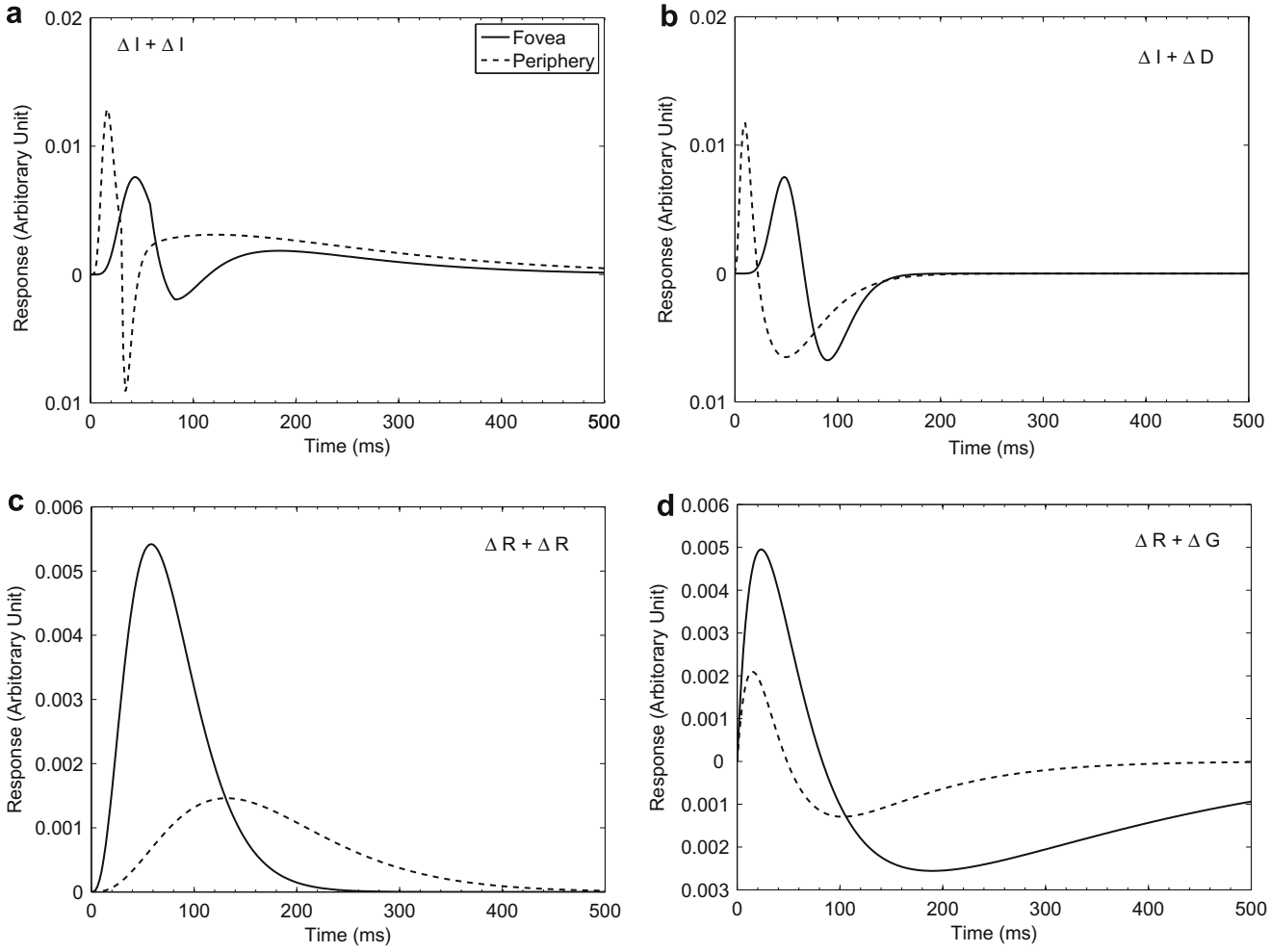

Fig. 4. Estimated impulse responses of subject OM. (a) $\Delta I + \Delta I$. (b) $\Delta I + \Delta D$. (c) $\Delta R + \Delta R$. (d) $\Delta R + \Delta G$. In luminance conditions, (a) and (b), the IRFs in the periphery are both accelerated regardless of the combination of the pulse pair. In contrast, in chromatic conditions, the IRFs in the periphery are either decelerated (c) or accelerated (d).

When a complementary-chromatic pulse pair comes to these channels, the responses to each pulse in the monophasic channel always cancel each other, and the total response is smaller than that to a single pulse. However, those in the biphasic channel sum together at a certain SOA, and the total response in the biphasic channel is larger than that to a single pulse. Thus, only biphasic characteristics are observed.

3.3.2. Impulse responses

The impulse response functions (IRFs) of each channel were estimated as shown in Fig. 4 with a method based on Uchikawa and Yoshizawa (1993). An IRF $h(t)$ is assumed to be a train of n-stage low pass filters (LPFs) $H_i(t)$

$$h(t) = k\sum_i U(t-d_i)H_i(t-d_i), \quad (1)$$

where $U(t)$ is Heaviside's unit step function and

$$H_i(t) = A_i/\tau_i(t/\tau_i)^{n_i-1}\exp\left[-(t/\tau_i)\right]/(n_i-1)!.$$

The total response $R(t)$ by the input stimulus $I(t)$ is the convolution of the input with the IRF $h(t)$

$$R(t) = \int_0^t h(t-t')I(t')dt'.$$

The observer's detection probability P is determined by Watson (1979)'s model of probability summation over time

$$P = 1 - \exp\left[-\int_0^T |R(t)|^\beta dt\right].$$

The parameters in the model were determined to minimize the sum of the squared errors between the measured and the estimated thresholds at each SOA using simulated annealing (Kirkpatrick, Gelatt, & Vecchi, 1983). The parameter k in $h(t)$ is determined as the mean of the values that make the detection probability (P) 50% at each SOA. Based on the model described in Fig. 3, a monophasic internal channel is assumed for the $\Delta R + \Delta R$ condition, and a biphasic internal channel is assumed for the $\Delta R + \Delta G$ condition. A biphasic channel is also assumed for the $\Delta I + \Delta D$ condition. On the other hand, for the $\Delta I + \Delta I$ condition, a biphasic channel was not suitable enough to fit the small peak following the trough in the summation data. A triphasic channel was assumed for the $\Delta I + \Delta I$ condition, and a small excitatory lobe was followed by the inhibitory lobe in the same way as Uchikawa and Yoshizawa (1993).

In the estimated IRFs of the luminance channel (Fig. 4a and b), the peaks and troughs appear at earlier times in the periphery than in the fovea, which means that the luminance channel becomes faster in the periphery. The IRF to a same-chromatic pair ($\Delta R + \Delta R$) is slower in the periphery than in the fovea (Fig. 4c). However the

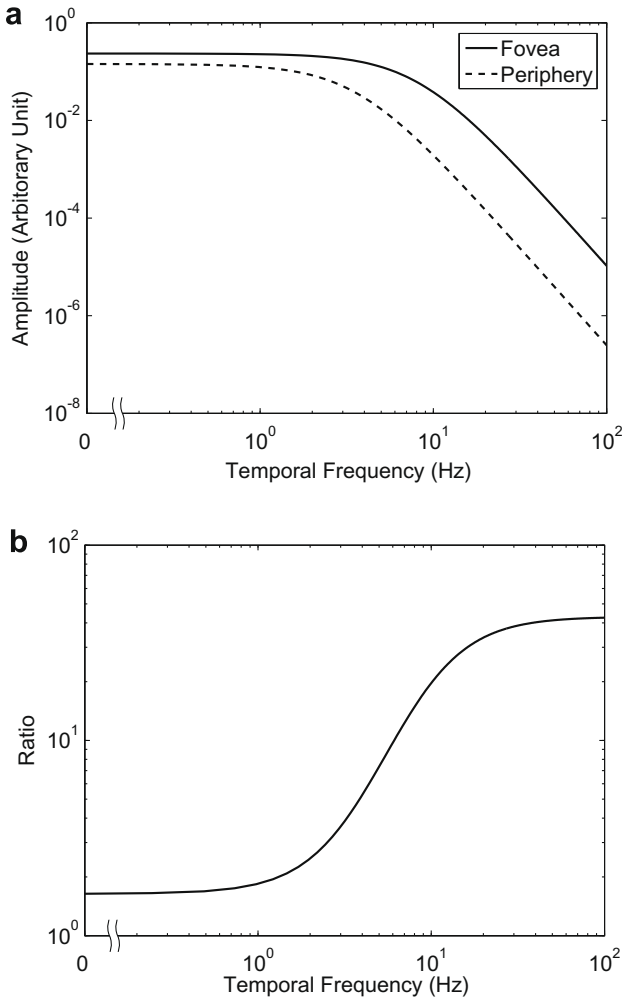

Fig. 5. Frequency analysis of the IRFs to $\Delta R + \Delta R$. (a) The amplitudes of the IRFs in Fig. 4 obtained by Fourier transform. (b) The ratio of the amplitude of the IRF in the fovea to that in the periphery. At lower frequencies, the difference between the fovea and the periphery is small, but at higher frequencies, the amplitude in the fovea is much higher than that in the periphery.

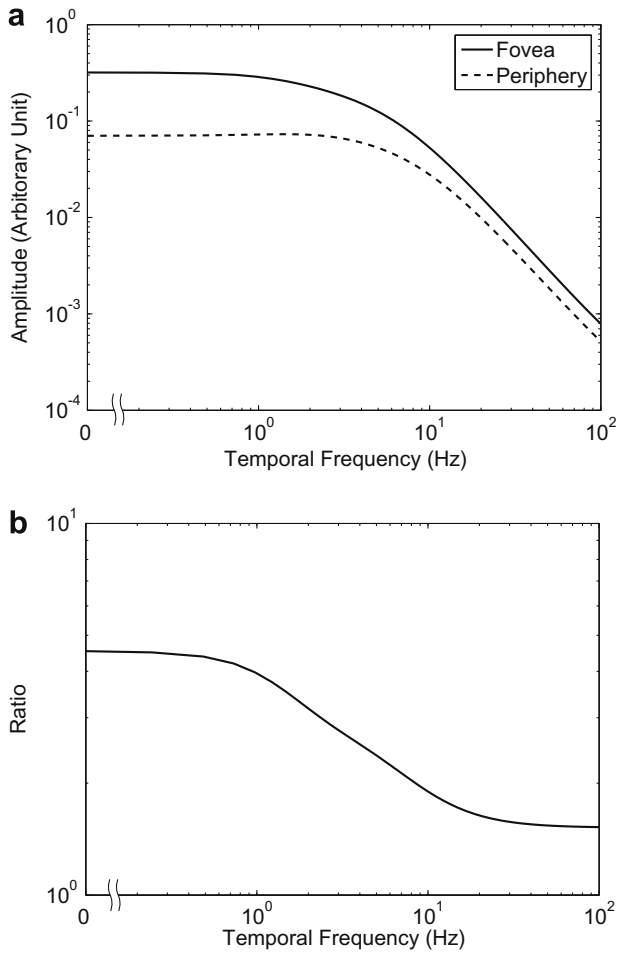

Fig. 6. Frequency analysis of the IRFs to $\Delta R + \Delta G$. (a) The amplitudes of the IRFs in Fig. 4 obtained by Fourier transform. (b) The ratio of the amplitude of IRF in the fovea to that in the periphery. At lower frequencies, the difference between the fovea and the periphery is large, but at higher frequencies, the amplitude in the fovea is close to that in the periphery.

IRF to a complementary-chromatic pair ($\Delta R + \Delta G$) is faster in the periphery than that in the fovea (Fig. 4d). Both responses of monophasic and biphasic IRFs in the chromatic channels were smaller in the periphery than those in the fovea, which suggests that the chromatic channel in the periphery is deteriorated despite the enlargement of stimulus size with M-scaling.

The IRF to $\Delta R + \Delta R$ lasts longer in the periphery than in the fovea, which suggests that the response of the channel in the periphery is less deteriorated at lower temporal frequencies. To test this idea, Fourier analysis was applied to the IRFs of $\Delta R + \Delta R$ to obtain the temporal modulation transfer function (tMTF) as shown in Fig. 5a. The overall tMTF in the periphery is lower than that in the fovea, but the difference between the two tMTFs is not constant across temporal frequency. The peripheral tMTF is much lower at higher temporal frequencies, but the difference at lower temporal frequencies is smaller. The ratio of the foveal and peripheral amplitudes is plotted with temporal frequency in Fig. 5b.

Similar analysis was applied to the IRFs of $\Delta R + \Delta G$ as shown in Fig. 6. The result was opposite of the case of $\Delta R + \Delta R$. The decline of amplitude in $\Delta R + \Delta G$ was larger at lower temporal frequency and smaller at higher temporal frequency. Such differences in the effects of eccentricity on frequency characteristics in $\Delta R + \Delta R$ and $\Delta R + \Delta G$ support the model mentioned above: that the chromatic mechanism has two channels that differ in temporal characteristics.

We also estimated different IRFs for the luminance channel depending on the polarity combination of the pulses. Triphasic IRFs were estimated for $\Delta I + \Delta I$, and biphasic ones for $\Delta I + \Delta D$. This is consistent with Uchikawa and Yoshizawa (1993), and might be explained by assuming two internal channels in the luminance mechanism. In both cases, the luminance channels are faster in the periphery than in the fovea.

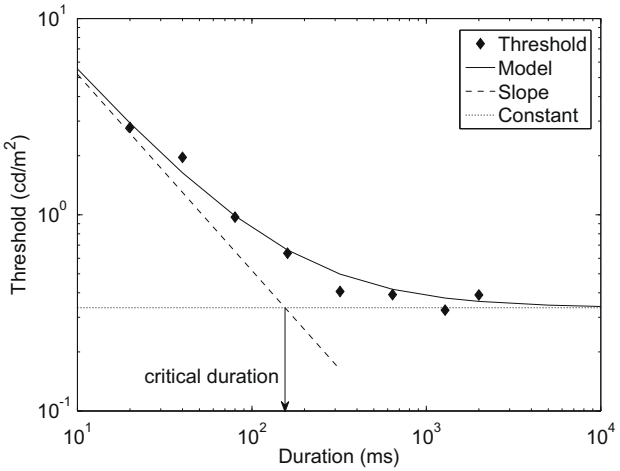

Fig. 8. Temporal summation of a single chromatic pulse. The detection thresholds are plotted as a function of the duration of the pulse. At short duration, perfect summation holds and the plot lies on the slope of −1. At long duration, the plot lies on a constant asymptotic level. Subject OM. Foveal condition.

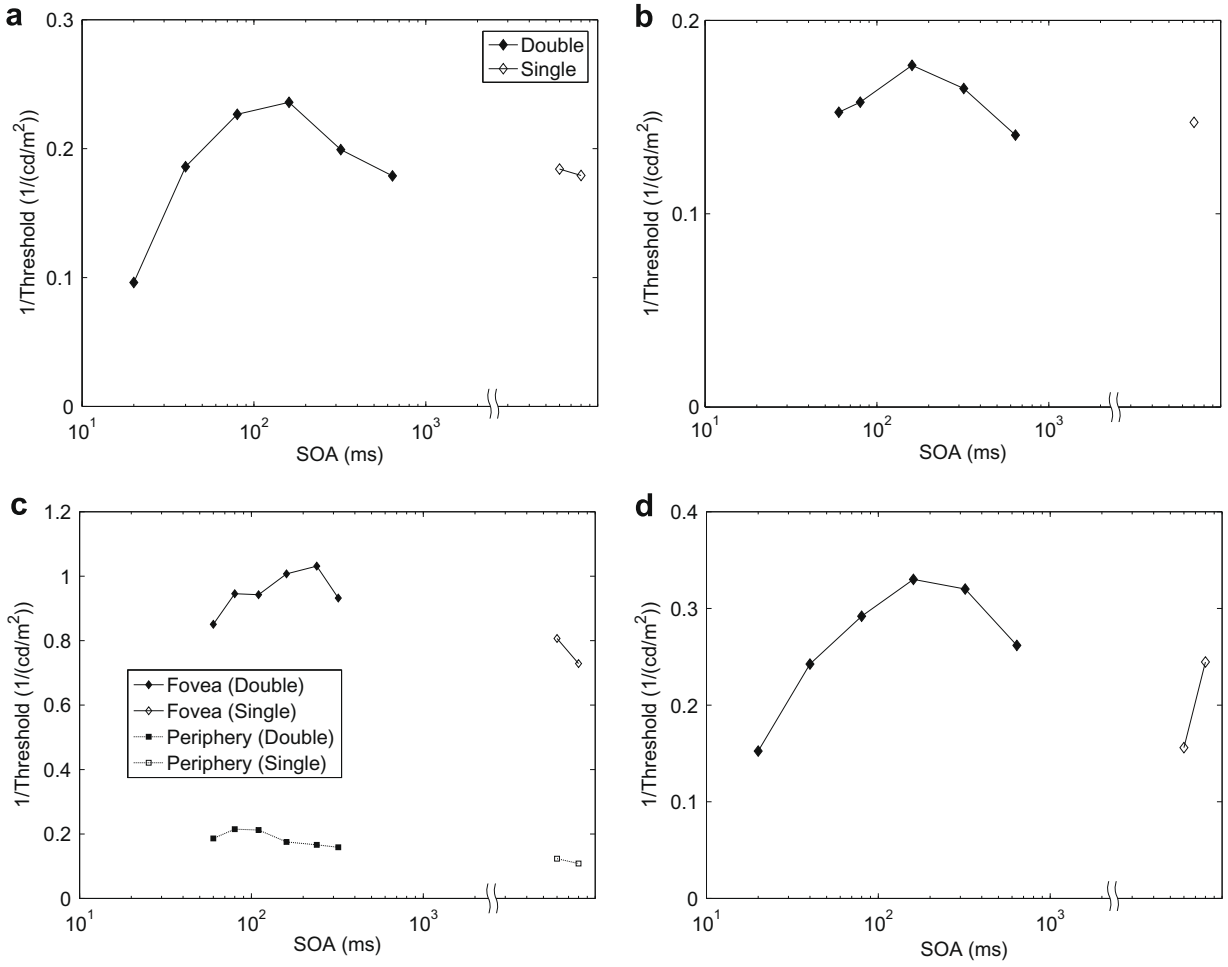

Fig. 7. The peak in temporal summation of complementary-chromatic pulse pairs appeared again even after the detection criterion is changed and the subjects adapted to luminance flicker. (a) Subject OM. (b) Subject MS. (c) Subject OM. Effects of eccentricity. (d) Subject OM, after adaptation to temporal white noise.

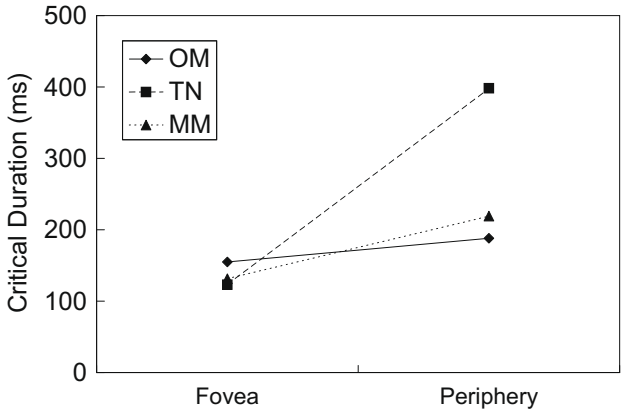

Fig. 9. Critical durations were longer in the periphery than in the fovea. The critical durations were estimated as the duration at which the slope of −1 and the constant asymptotic level intersect each other in Fig. 8. Each symbol represents a subject.

3.3.3. Threshold elevation at long SOA

At long SOA, the two pulses should be independent of each other, and the detection threshold of the pulse pair should asymptotically approach the probability summation level. However in Fig. 2, the rTHs declined at SOAs longer than 1500 ms. This phenomenon was found in almost all conditions regardless of the pulse polarity combination or of eccentricity. Such a phenomenon has not been observed in previous studies using the temporal double flashes technique. It seems unlikely that inhibitory interaction occurred between two flashes with such a long SOA.

Masuda and Uchikawa (2005) found that this phenomenon was caused by Ganzfeld stimulation in the peripheral visual field and intentional tight fixation. This phenomenon was found to be diminished with a salient luminance edge surrounding the test field. We drew a circular luminance edge around the test stimulus in the following experiments to reduce this Ganzfeld-like appearance of the stimuli.

3.3.4. Luminance artifact

It was found in the results of the $\Delta R + \Delta G$ stimuli that there was a peak of the response function that could not be explained if the chromatic response was monophasic. This peak appeared at shorter SOA in the periphery than in the fovea. If the chromatic response to $\Delta R + \Delta G$ was accelerated in the periphery, it would contradicts the result of $\Delta R + \Delta R$ stimuli, which showed that the chromatic response was decelerated in the periphery. The luminance responses were found to be faster in the periphery than in the fovea regardless of the polarity combination of the stimulus pulses.

The peak SOA in the $\Delta R + \Delta G$ response seemed to coincide with the third peak SOA in $\Delta I + \Delta I$ for each subject and for each eccentricity as shown by Uchikawa and Yoshizawa (1993). In Fig. 2 the peak in the $\Delta R + \Delta G$ response appeared at SOAs of 160 ms (fovea) or of 60 ms (periphery), which coincides with the SOA of the third peak (160 ms in the fovea, or 60 ms in the periphery) in the $\Delta I + \Delta I$ response. With these results, there remains the possibility that the peak in $\Delta R + \Delta G$ response might be an artifact caused by some luminance response. We confirmed that the peak in the $\Delta R + \Delta G$ response reflected the chromatic response, and is not a luminance artifact, as shown in experiment 2.

3.3.5. The deceleration of the chromatic response in the periphery

It seems inconsistent that the IRF to $\Delta R + \Delta R$ is decelerated while the IRF to $\Delta R + \Delta G$ is accelerated in the periphery. The fact that the IRF is accelerated in all other three conditions ($\Delta I + \Delta I$, $\Delta I + \Delta D$, $\Delta R + \Delta G$) makes it doubtful that only the IRF to $\Delta R + \Delta R$ is decelerated in the periphery. However, we confirmed it in experiment 3 by comparing the critical durations for the detection of single chromatic pulses in the periphery to those in the fovea.

3.3.6. Spatial pattern

In this experiment, we used only one pair of stimulus sizes according to the M-scaling with no spatial pattern. We confirmed the generality of the result with patterned stimuli of various spatial frequencies in experiment 4.

4. Experiment 2: possibility of luminance artifacts in the response to complementary-chromatic pulse pairs

4.1. Methods

The same apparatus as in experiment 1 was used in this experiment, and a 10° diameter ring was added around the test stimulus to avoid a Ganzfeld-like appearance. The response criterion here was whether any chromatic change was detectable. In addition, to reduce the influence of the luminance response, the subject adapted to luminance flicker during the initial light adaptation (3 min) and during every intermission between trials (at least 5 s). The adaptation stimulus was flickered in its luminance contrast between 10% and 90% at a frequency of 12.5 Hz, which was the frequency of flicker photometry used to set isoluminance. In this adaptational condition, only a sub channel around this temporal frequency may be adapted. In the other condition, the adaptational stimulus was modulated randomly at the frame rate of

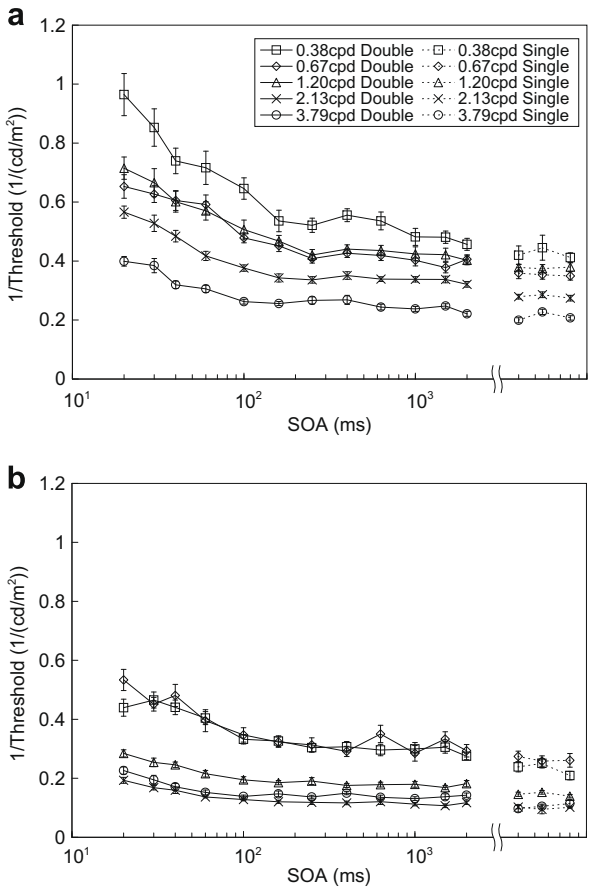

Fig. 10. Temporal summation of same-chromatic Gabor patch double flashes. (a) Foveal condition. (b) Peripheral condition. The rTHs became monotonically smaller with SOA and with spatial frequency, which suggests that the response to a same-chromatic pulse pair is monophasic both temporally and spatially.

100 Hz to make temporal white noise. In each trial (2500 ms), the test stimulus stayed constant, except during pulse pair presentation. Two male subjects, OM and MS of 35 and 22 years old, respectively, with normal color vision and normal or corrected-to-normal acuity participated in the experiment. The subject MS was naive to the purpose of the experiment.

4.2. Results and discussion

The results are shown in Fig. 7. The peak in the response to a complimentary-chromatic pulse pair appeared again even after the criterion was changed and the subject adapted to luminance flicker (a, b). The peak SOA was also earlier in the periphery than in the fovea in this experimental condition (c). The peak in $\Delta R + \Delta G$ response appeared again even after adaptation to temporal white noise (d). These results suggest that the peak in complementary-chromatic $\Delta R + \Delta G$ response is not an artifact caused by a luminance response but a genuine chromatic response.

The chromatic channel has been thought to have a monophasic IRF, and its tMTF to be LPF in many studies using flicker stimuli. The peak in the response to a complementary-chromatic pulse pair has also been found in previous studies (Eskew, Stromeyer, & Kronauer, 1994; Uchikawa & Yoshizawa, 1993) at the fovea. The present study confirmed this also in the periphery. Burr and Morrone (1993) concluded that the chromatic response was monophasic, even to a complementary-chromatic pulse pair. However, their model (Fig. 1D) failed to agree with the data at the intermediate SOA range (around 100 ms). Effectively, their model had only three free parameters. If they had used a more flexible model to fit the data more closely, the resultant IRFs would have been biphasic.

5. Experiment 3: the deceleration of the chromatic response in the periphery

5.1. Methods

The same apparatus was used as in experiment 2. We measured the detection thresholds of single chromatic pulses (ΔR) with various durations (20–2000 ms). Subjects OM, TN and MM (35, 22 and 22 years old male, respectively, color normal, and normal or corrected-to-normal acuity) were tested. The subjects TN and MM were naive to the purpose of the experiment.

5.2. Results and discussion

A model with two asymptotic lines was fitted to the data. Fig. 8 shows that complete temporal summation holds with shorter duration and the threshold gets close to the asymptote of slope −1. When the duration is long, the threshold is constant. We defined the critical duration of temporal summation as the duration at the crossing point of these two lines (Fig. 8). As shown in Fig. 9, the critical durations in the periphery were longer than that in the fovea for all subjects.

A long single chromatic pulse can be interpreted as two short same-chromatic pulses with zero SOA. In this experiment we confirmed that the response to a single chromatic pulse integrated longer in the periphery than in the fovea, which is consistent with the idea that the response to a same-chromatic pulse pair decelerates in the periphery. The temporal response to a same-chromatic pair is fundamentally different from that to a complementary-chromatic pair. One is monophasic and the other biphasic. In

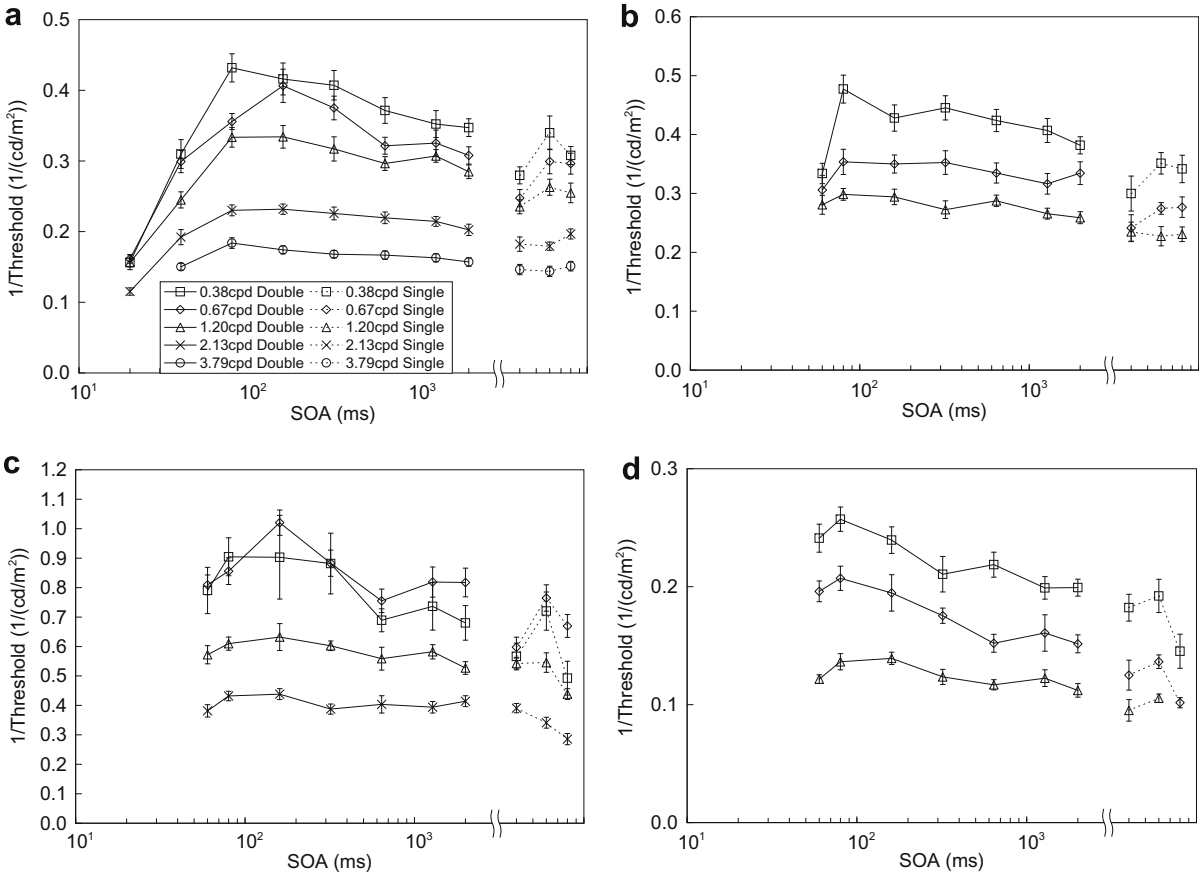

Fig. 11. Temporal summation of complementary-chromatic Gabor patch double flashes. (a) Subject OM, foveal condition. (b) Subject OM, peripheral condition. (c) Subject JT, foveal condition. (d) Subject JT, peripheral condition. The response to a complementary-chromatic Gabor flash pair was biphasic again, and the peak appeared earlier in the periphery than in the fovea.

addition, eccentricity has opposite effect on the speed of each response. These results are consistent with the parallel two-channel color vision model we proposed in experiment 1.

6. Experiment 4: the effects of spatial frequency on the chromatic responses

6.1. Methods

At each trial the test stimulus was modulated twice with an SOA (20–2000 ms); spatially, as an isoluminant chromatic Gabor patch (carrier spatial frequency 0.38–3.79 cpd) and temporally, as a brief rectangular pulse (20–40 ms). In the same-chromatic condition, the two patches were spatially in phase, thus the same spatial position in the test field was stimulated by two flashes of the same intensity. In the complementary-chromatic condition, the two patches were spatially counter-phased, so that a point in the test field was modulated by a complementary-chromatic pulse pair.

In the same-chromatic condition, the subject observed the test stimuli presented on the CRT through an aperture ($14^\circ \times 14^\circ$) placed in the center of a semi-cylindrical dome screen (radius: 90 cm) with his right eye only. The inner surface of the dome was made of a white paper and was illuminated by eight D65 fluorescent lamps. The height of the screen was 180 cm. The luminance of the screen was approximately 120 cd/m^2. The CRT was placed just behind the aperture so giving a surface reflection of 20 cd/m^2.

The test stimulus was a yellow disk of 10° in diameter surrounded by a black ring. The CIE 1931 (x, y)-chromaticity coordinates of the disk were (0.497, 0.439) and the luminance was 25 cd/m^2 without the surface reflection. The thickness of the black ring was 0.2°. In the foveal condition, the subject fixated at the center of this ring. The surround of the disk was a uniform white ((x, y) = (0.320, 0.339), 100 cd/m^2) without the surface reflection. In the peripheral condition, a white paper fixation disk of 10° in diameter with a black ring was put in the right side of the test stimulus. The subject fixated at the center of this disk, and the test stimulus appeared at 10° nasal visual field. The subject reported whether he observed any flash during the test. Thresholds of single pulses were also measured for each spatial frequency condition. The onset time of the single pulse was either 500, 1250, or 2000 ms from the beginning of a trial.

Three male subjects, OM, TF, KN who were 33, 22 and 37 years old, respectively, with normal color vision and normal or corrected-to-normal acuity participated in the experiment. The subjects TF and KN were naive to the purpose of the experiment. The CRT primary ratio for equiluminance was adjusted based on flicker photometry for each subject and for each eccentricity. The ratio was not adjusted for each spatial frequency, but was confirmed to be almost the same for all the spatial frequencies tested. The luminance artifacts caused by ocular chromatic aberrations are not thought to be severe in these spatial frequencies (Bradley, Zhang, & Thibos, 1992).

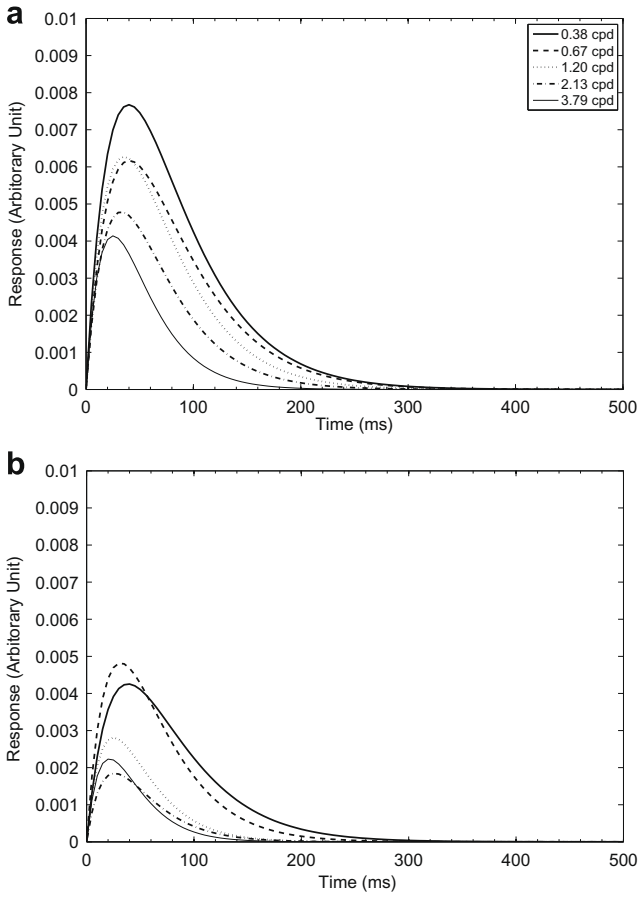

Fig. 12. Estimated IRFs in the same-chromatic condition. (a) Foveal condition. (b) Peripheral condition. The IRF model was assumed to be a single LPF.

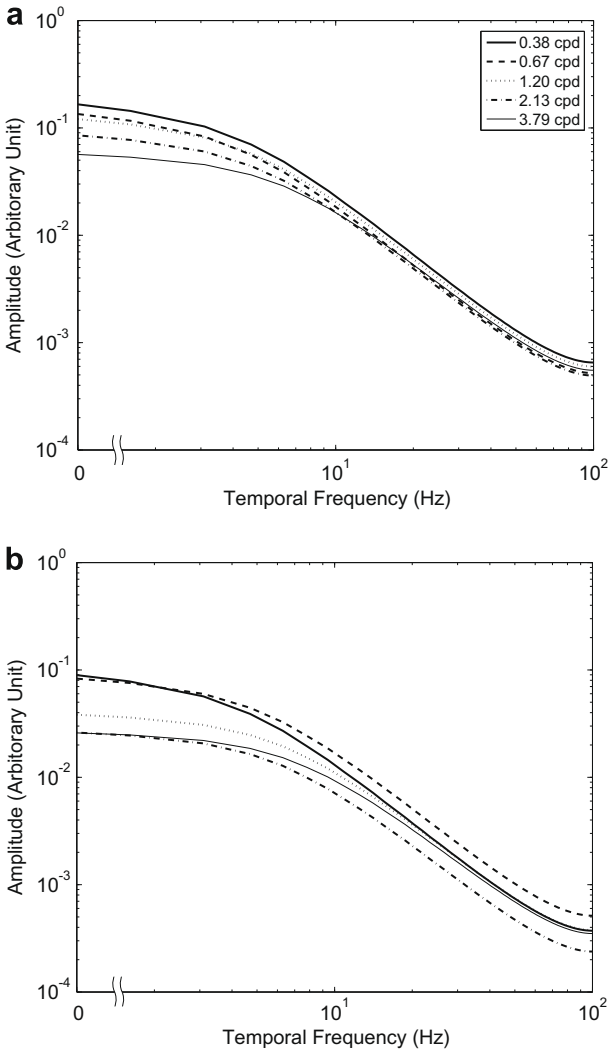

Fig. 13. Frequency analysis of the IRFs in the same-chromatic condition. The amplitudes of tMTFs were obtained by Fourier transform from the IRFs in Fig. 12. (a) Foveal condition. (b) Peripheral condition.

In the complementary-chromatic condition, the radius of the semi-cylindrical dome was decreased to 45 cm to reduce the light intensity to the CRT surface from the fluorescent lamp illumination. The aperture was a disk of diameter 10°. The CRT was placed 45 cm behind the aperture, thus the viewing distance of the test stimulus was the same as that in the same-chromatic condition (90 cm). The inner surface of the dome was illuminated by four fluorescent lamps and its luminance was about 200 cd/m^2. The edge of the test stimulus was surrounded by eight small black notches to help observer's accommodation. Subjects OM and JT were male and 35 and 26 years old, respectively, and they had normal color vision and corrected-to-normal acuity. The subject JT was naive to the purpose of the experiment. The subject reported whether he observed any chromatic flash during the test. The CRT primary ratio for equiluminance was adjusted based on flicker photometry for each subject, each eccentricity, and each spatial frequency.

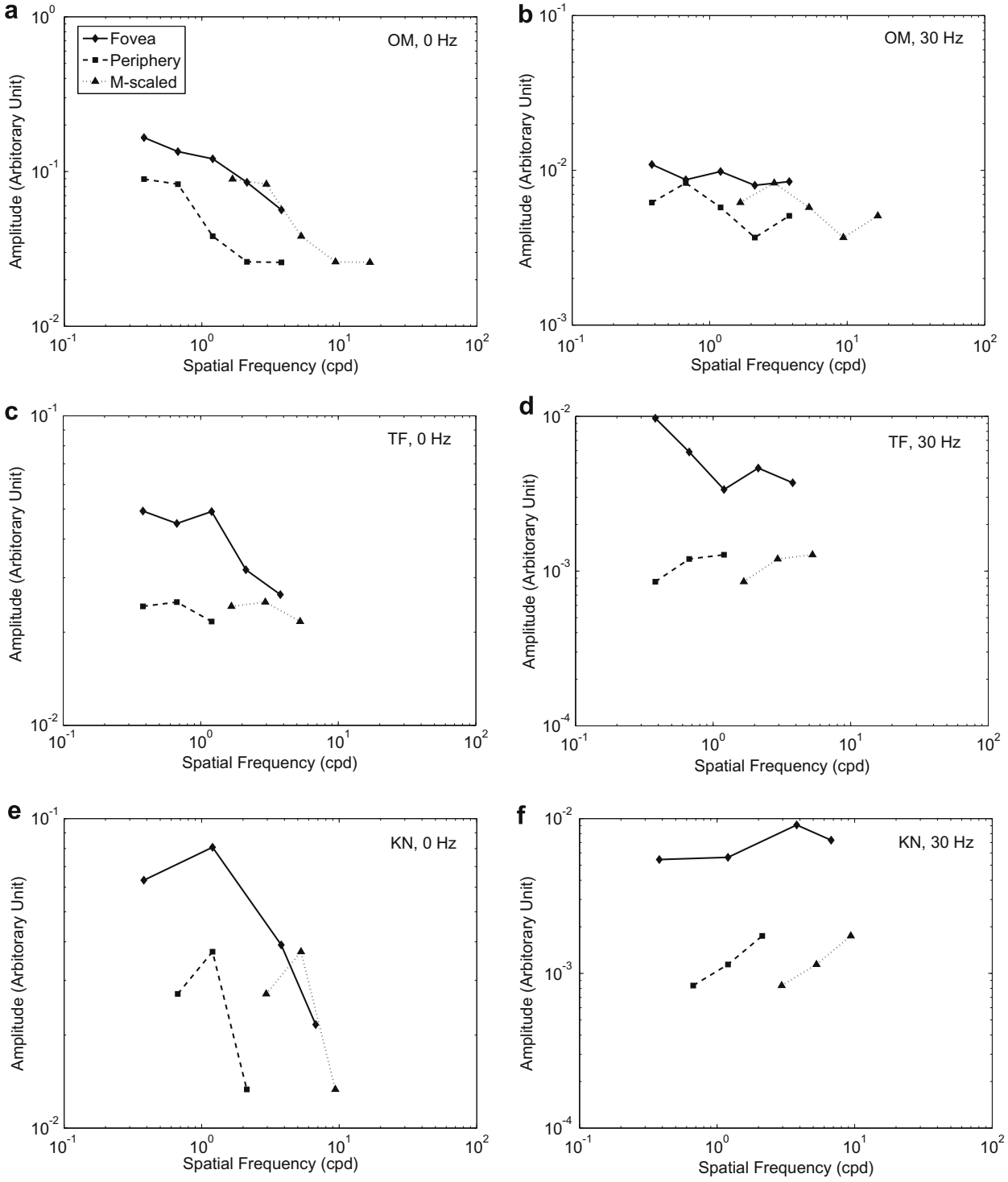

Fig. 14. sMTFs in the same-chromatic condition. (a) OM. 0 Hz. The foveal (diamond) and the peripheral (square) curves are far away from each other, but the M-scaled peripheral (triangle) curve overlaps well with the foveal curve. (b) OM. 30 Hz. The peripheral curve does not overlap well with the foveal one even after M-scaling. (c) TN. 0 Hz. (d) TN. 30 Hz. (e) KN. 0 Hz. (f) KN. 30 Hz.

6.2. Results

The results of the same-chromatic condition for the subject OM are shown in Fig. 10. The ordinate represents the rTH and the abscissa represents the SOA between the two pulses. Results of three single pulses were plotted on the right. The rTH became smaller monotonically with longer SOAs, which means that the temporal response to a same-chromatic pulse pair was monophasic. The rTH became smaller monotonically with spatial frequency, which means that the spatial response was also monophasic. The rTHs in the peripheral condition are lower than those in the foveal condition of the same spatial frequency. The other subjects showed similar results.

The results of the complementary-chromatic condition are shown in Fig. 11. The peaks in inhibition phase were observed for all the spatial frequencies tested, but became less prominent as the spatial frequency increased. The overall rTHs decreased with spatial frequency.

6.3. Discussion

The IRFs for the same-chromatic condition were shown for each spatial frequency in Fig. 12. They were estimated with the method described in the previous section. We assumed that the IRF was a monophasic LPF. The tMTFs of these IRFs were calculated using Fourier transform as in Fig. 13. Next, spatial modulation transfer functions (sMTFs) were obtained by slicing the tMTFs at each temporal frequency. The sMTFs for two temporal frequencies, 0 Hz and 30 Hz, are shown in Fig. 14.

In Fig. 14, the diamond symbols represent the sMTF in the foveal condition and square symbols that in the peripheral condition. The trianglular symbols are the sMTF for the peripheral condition, laterally shifted according to the cortical magnification scale (factor of 4.4) for the 10° nasal visual field. In the result at 0 Hz, the foveal sMTF and the peripheral sMTF are far apart from each other, but the M-scaled peripheral sMTF overlaps well with the foveal sMTF. On the other hand, in the result at 30 Hz, the peripheral sMTF does not overlap well with the foveal sMTF even after M-scaling.

The mean of the squared error of the M-scaled peripheral sMTF relative to the foveal sMTF at each overlapping point of spatial frequency is shown in Fig. 15. The error is larger at higher temporal frequencies than at lower temporal frequencies, which confirms

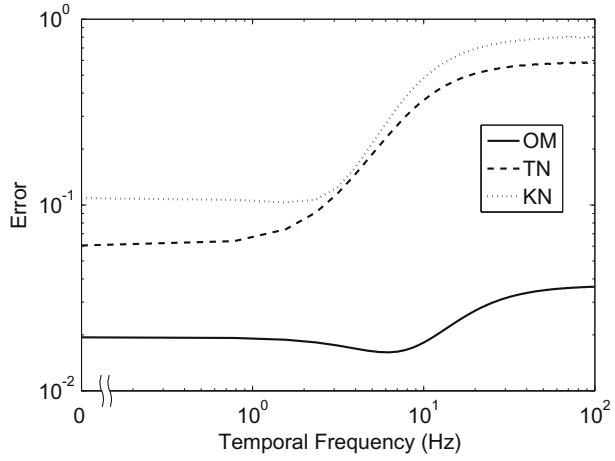

Fig. 15. Squared relative error of the M-scaled peripheral sMTF compared to the foveal sMTF in the same-chromatic condition. The error was smaller at lower temporal frequencies, but became larger with temporal frequency. Each curve represents a subject.

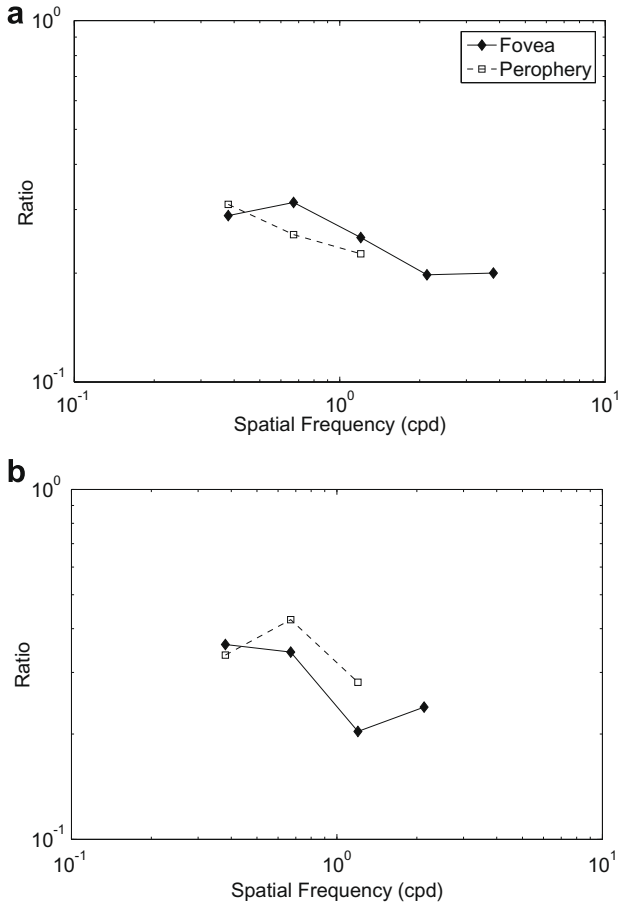

Fig. 16. The relative height of the peaks of the temporal integration curves in the complementary-chromatic condition compared to the average height of the single pulses plotted as a function of spatial frequency. At higher spatial frequencies, the peak became weaker. (a) Subject OM. (b) Subject JT.

that the response of the peripheral chromatic channel to the same-chromatic pulse pair deteriorates at higher temporal frequencies even though the stimulus size was compensated in the periphery. On the other hand, the response at lower temporal frequencies was not deteriorated when the spatial scale was properly compensated. This result is consistent with that for same-chromatic pairs in experiment 1.

We derived the IRFs in Fig. 12 using only one LPF based on the model from Eq. (1), which means that the estimated IRFs are restricted to be minimum phase. We repeated the analysis using the IRF model by Burr and Morrone (1993), which is not restricted to minimum phase. We obtained the same results with both IRF models.

If the inhibition phase, found in the temporal response to a complementary-chromatic pair (Fig. 11), is caused by lateral inhibition within a mechanism with a fixed spatial scale (e.g. a receptive field), deterioration of the inhibition phase is expected at higher spatial frequencies. The height of the peak in the rTH for the double pulse is plotted relative to that for the single pulse as a function of spatial frequency in Fig. 16. The peak tend to be weaker at higher spatial frequencies, which suggests that the inhibition phase is caused by lateral inhibition in the center-surround organization of a receptive field. This result is consistent with previous studies. Uchikawa and Yoshizawa (1993) and Eskew et al. (1994) found biphasic response to complementary-chromatic pairs using spatially uniform stimuli with no pattern. On the other hand, Burr and Morrone (1993) used a one cycles per deg sinusoidal pattern and reported no inhibition phase.

The sMTFs of the complementary-chromatic condition for two temporal frequencies, 0 Hz and at 20 Hz, are shown in Fig. 17. At 0 Hz, the peripheral MTFs (square and triangle) overlap poorly with the foveal MTF (diamond) both before and even after M-scaling. On the other hand at 20 Hz, the M-scaled MTF overlaps well with the foveal one. The squared error of the M-scaled peripheral sMTF relative to the foveal sMTF was plotted against temporal frequency in Fig. 18. The error tended to be higher at lower temporal frequencies and is lower at higher temporal frequencies. This result is consistent with that for complementary-chromatic pairs in experiment 1. The sensitivity of the biphasic channel to a complementary-chromatic pair is preserved in the periphery at higher temporal frequencies with its spatial frequencies scaled by M-scaling.

The findings in experiment 1 were confirmed consistently among various spatial scales in general. The fact that the chromatic responses are very different depending on the polarity combination of a pulse pair stimulus suggests that these reflect two distinct internal mechanisms in the chromatic channel.

7. General discussion

7.1. Psychophysical mechanisms

In the present study we tested the spatiotemporal properties of the chromatic channel in the peripheral visual field by measuring temporal summation of double flashes. The response of the chromatic channel to a same-chromatic pulse pair in the periphery is comparable to that in the fovea at lower temporal frequencies. The chromatic response to a complementary-chromatic pulse pair at higher temporal frequencies was not degraded in the periphery.

The previous studies have shown that the temporal response is either monophasic or biphasic depending on the polarity combination of a stimulus pulse pair, same-chromatic or complementary-chromatic (Eskew et al., 1994; Uchikawa & Yoshizawa, 1993). The present study found that the same temporal properties exist even in the peripheral visual field, and that the effect of eccentricity on these temporal properties are also different depending on the combination of pulses. It seems reasonable to consider that these very different properties reflect two distinct mechanisms rather being different profiles of a single mechanism. The parallel two-channel color vision model, proposed in experiment 1, could account for the results in the present study.

7.2. Physiological correlates

In the primate visual system, two distinct pathways, the parvocellular pathway and the magnocellular pathway, are known to pass from the retina through the LGN to the primary visual cortex (V1). It has been widely accepted that the cells in the parvocellular pathway (P cells), which have type I center-surround spatially antagonistic receptive fields, convey both luminance and

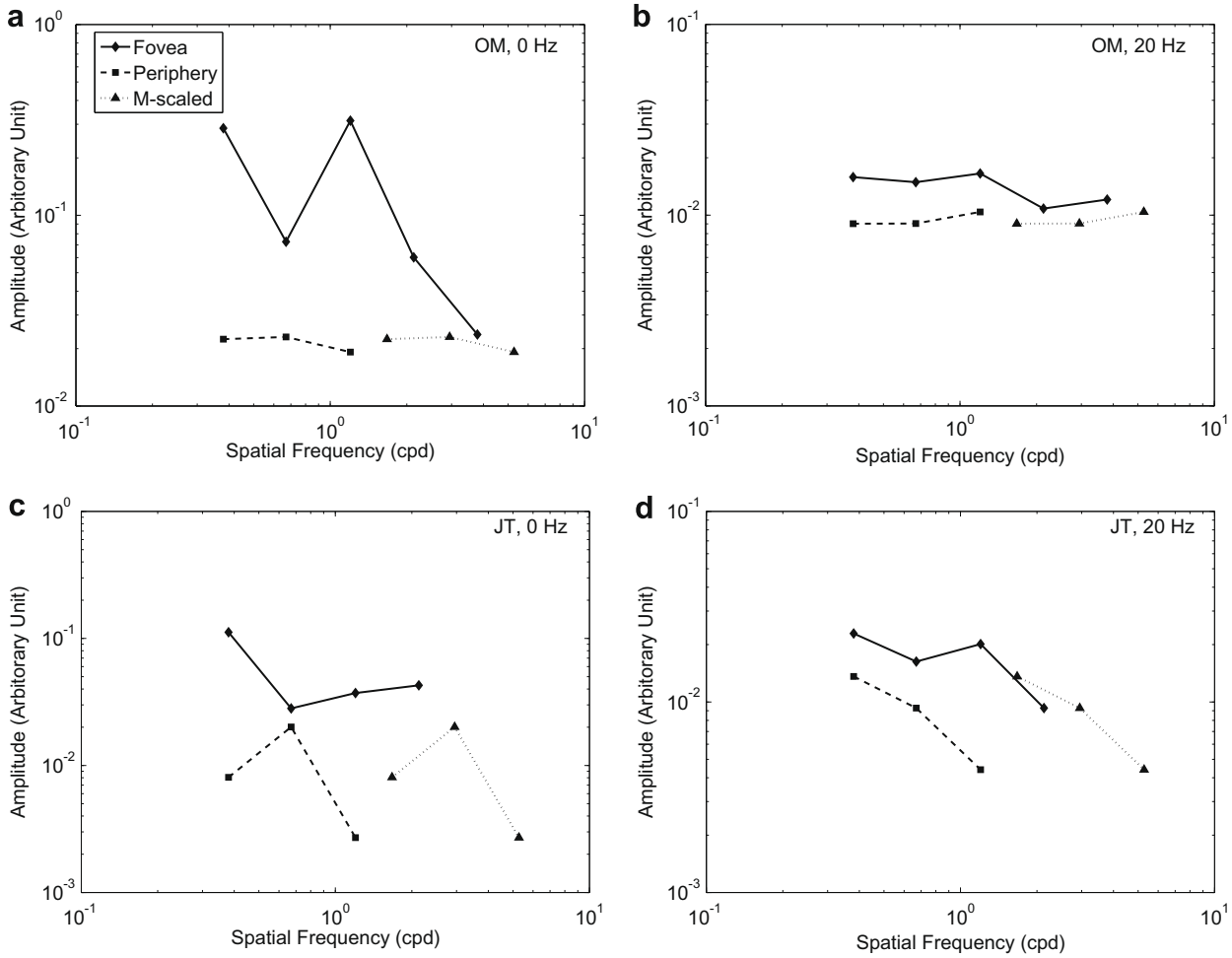

Fig. 17. sMTFs in the complementary-chromatic condition. (a) OM. 0 Hz. The peripheral (square) curve does not overlap with the foveal (diamond) one even after M-scaling (triangle). (b) OM. 20 Hz. The peripheral curve does not overlap well with the foveal one, but the M-scaled one does. (c) JT. 0 Hz. (d) JT. 20 Hz.

chromatic information (double duty hypothesis). However, a third pathway, the koniocellular pathway, was recently found to mediate chromatic information. The cells in the koniocellular pathway (K cells) have type II spatially non-antagonistic receptive fields and convey only chromatic and not luminance information. There are 6 layers (K1, K2, ⋯, K6) of K cells in the LGN. All 6 layers have innervation to the CO-rich blob in V1. The cells in the K3 and K4 layers are known to be S–ON cells (Hendry & Reid, 2000), but the function of the other cells must still be investigated. It is known that there is more variability in the response properties among K cells compared to the other two classes (White, Solomon, & Martin, 2001).

The two-channel hypothesis insists that the role of P cells is to convey luminance information, and that chromatic information is conveyed by K cells. Here we propose a hybrid model that the biphasic chromatic response to complementary-chromatic pairs is taken by type I cells in the parvocellular pathway. The monophasic chromatic response to same-chromatic pairs is taken by type II cells in the koniocellular pathway as shown in Fig. 19. The results that the inhibition phase of the biphasic response to a complementary-chromatic pair is diminished at higher spatial frequencies is consistent with the center-surround receptive field organization of type I cells in the parvocellular pathway. The result that the temporal response to a complementary-chromatic pair have the same tendency with eccentricity as that to a luminance pair is consistent with the double duty hypothesis that chromatic and luminance information are conveyed in a single channel.

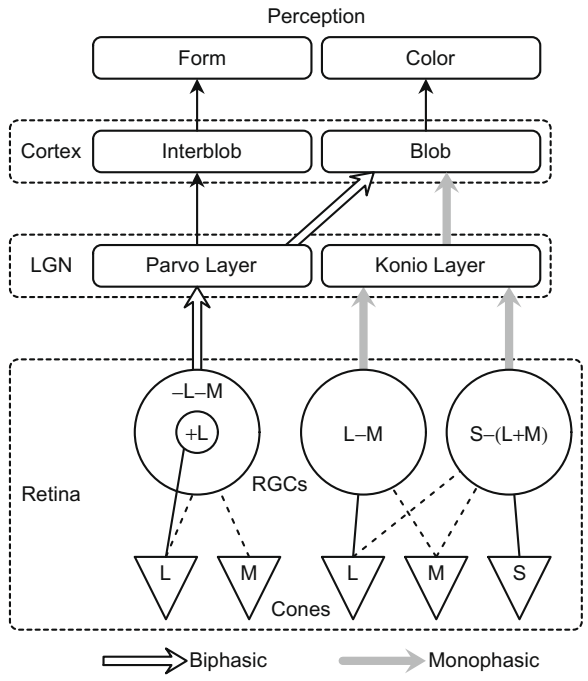

Fig. 19. The schematic model of the color vision mechanism that integrates the double duty hypothesis and the two-channel hypothesis. The type I retinal ganglion cells (RGCs) are temporally biphasic and innervate to the parvocellular layers (P layers) in the lateral genuculate nucleus (LGN). The type II RGCs are temporally monophasic and innervate to the koniocellular layers (K layers) in the LGN. The interblob in the primary visual cortex (V1) accepts input from only the P layers, and contributes to the perception of form. The blob in the V1 accepts input from both P and K layers and mediates the perception of color. In this diagram, the RGCs of opposite polarity (type I – L/+L + M and type II – L + M) are omitted.

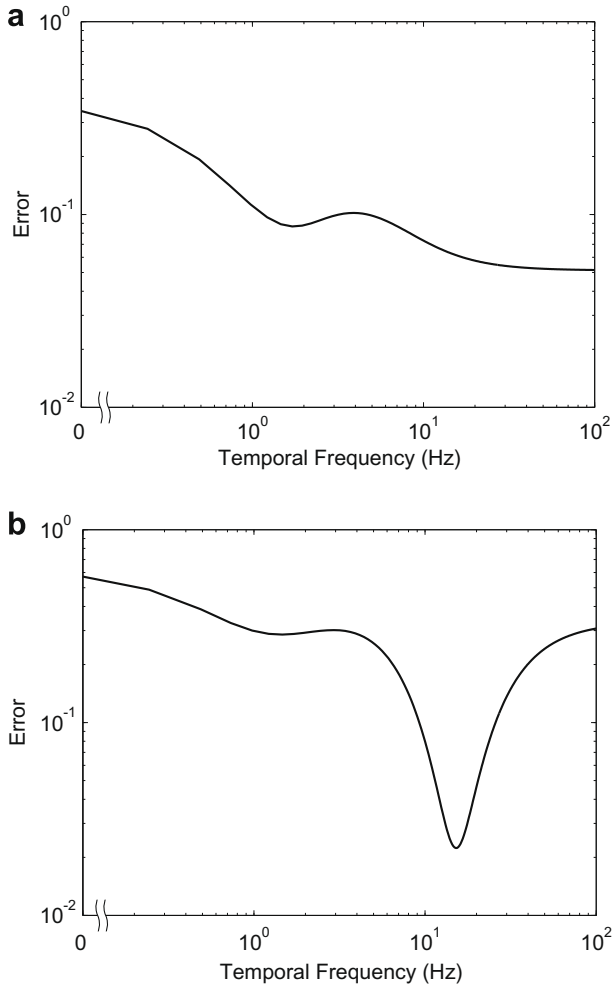

Fig. 18. Squared relative error of the M-scaled peripheral sMTF compared to the foveal sMTF in the complementary-chromatic condition. The error was larger at lower temporal frequencies, but smaller at higher temporal frequencies. (a) Subject OM. (b) Subject JT.

On the other hand, the monophasic response to a same-chromatic pair was decelerated in the periphery, which is consistent with the two-channel hypothesis that chromatic and luminance information are conveyed in distinct channels. The S–ON K cells in the K3 and K4 layers accept input from small-bistratified ganglion cells in the retina. The L–M type II cells have been reported physiologically in the LGN (Dreher, Fukada, & Rodieck, 1976; Wiesel & Hubel, 1966) and in the retina (DeMonasterio, 1978; DeMonasterio & Gouras, 1975). These cells are thought to have bistratified morphology (Rodieck, 1991). Dacey, Peterson, Robinson, and Gamlin (2003) also recently found at least 8 new morphologically distinct ganglion cell classes other than the well-known magnocellular, parvocellular and small-bistratified cells, and their physiological functions have yet to be investigated.

It is known that cells in the magnocellular pathway (M cells) are not silenced by isoluminant chromatic flicker, but have frequency doubled responses (Lee, Martin, & Velberg, 1989). The inhibition phase of the biphasic response to a complementary-chromatic pulse pair might be caused by the frequency doubled responses of the M cells. However, the biphasic response appeared even after adaptation to luminance flicker, and even when the detection criterion was whether any chromatic change was observed. It does not seem plausible to refer the biphasic response we found to the M pathway. Directly recorded, the temporal response of the P cells to isoluminant chromatic modulation is biphasic and can be modeled by linear combination of the responses to cone-isolating stimuli (Benardete & Kaplan, 1999), which is consistent with our model.

8. Conclusions

We have measured the temporal summation of double flashes. The temporal response was found to be accelerated both to a luminance pulse pair and to a complementary-chromatic pulse pair, while the response to a same-chromatic pair was decelerated in the peripheral visual field. By spatial compensation of the stimulus based on M-scaling, the response to a same-chromatic pair at lower temporal frequencies in the periphery shows sensitivity comparable to that in the fovea. The response in the periphery also shows sensitivity to complementary-chromatic pairs at higher temporal frequencies comparable to that in the fovea. The fact that the effect of eccentricity on the temporal chromatic response depends on the combination of a pulse pair suggests that two distinct internal channels are arranged in parallel in the chromatic mechanism. The peak in the summation of a complementary-chromatic pair declined with spatial frequency, which suggests that the inhibition phase in that response is caused by the lateral inhibition of the center-surround receptive field. The double duty hypothesis and two-channel hypothesis could be integrated by attributing the monophasic response to the koniocellular pathway and the biphasic response to the parvocellular pathway.

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