

Luminance dependency of perceived color shift after color contrast adaptation caused by higher-order color channels

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Color adaptation is a phenomenon in which, after prolonged exposure to a specific color (i.e. adaptation color), the perceived color shifts to approximately the opposite color direction of the adaptation color. Color adaptation is strongly related to sensitivity changes in photoreceptors, such as von Kries adaptation and cone-opponent mechanisms. On the other hand, the perceptual contrast of colors (e.g. perceptual saturation of the red-green direction) decreases after adaptation to a stimulus with spatial and/or temporal color modulation along the color direction. This phenomenon is referred to as color contrast adaptation. Color contrast adaptation has been used to investigate the representation of colors in the visual system. In the present study, we measured color perception after color contrast adaptation to stimuli with temporal color modulations along complicated color loci in a luminance-chromaticity plane. We found that, after the observers adapted to color modulations with different chromaticities at higher, medium, and lower luminance (e.g. temporal alternations among red, green, and red, each at a different luminance level), the chromaticity corresponding to perceptual achromaticity (the achromatic point) shifted to the same color direction as the adaptation chromaticity in each test stimulus luminance. In contrast, this luminance dependence of the achromatic point shift was not observed after adaptation to color modulations with more complex luminance-chromaticity correspondences (e.g. alternating red, green, red, green, and red, at five luminance levels, respectively). In addition, the occurrence or nonoccurrence of the luminance-dependent achromatic point shift was qualitatively predicted using a noncardinal model composed of channels preferring intermediate color directions between the cardinal chromaticity and luminance axes. These results suggest that the

noncardinal channels are involved in the luminance-dependent perceived color shift after adaptation.

Introduction

Human vision adjusts its sensitivity to the visual environment through a process known as adaptation. Adaptation occurs in a variety of visual features, including brightness (Reuter, 2011), motion (Anstis, Verstraten, & Mather, 1998), and spatial frequency (Blakemore & Campbell, 1969). Adaptation also occurs for color (see Webster, 1996 for review). Color adaptation is a phenomenon in which, after prolonged observation of a specific color (an adaptation color), the perceived color shifts in the opposite color direction to that of the adaptation color. Color adaptation involves adjusting the relative sensitivities of different classes of cones, as modeled by the von Kries adaptation (Chichilnisky & Wandell, 1995), and adjusting the sensitivities of the post-receptoral cone-opponent mechanisms (Pugh & Mollon, 1979; Stromeyer, Cole, & Kronauer, 1985). Color adaptation has a significant impact on various everyday color perception. For example, color adaptation is regarded as one of the main factors supporting color constancy (Foster, 2011); under reddish illumination, the light reflected from objects should be predominantly long-wavelength, but color adaptation suppresses reddish components from the perceived color by decreasing the responses of the L-cone and post-receptoral L–M channel. This type of color adaptation is primarily caused by the mean color of a scene (Webster, 1996).

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However, the mean color of a scene is not the only cause for adaptation to color. After adapting to a visual stimulus, including spatiotemporal modulations in chromaticity and luminance, the perceptual contrast of colors (e.g. perceptual saturation of red-green) is known to decrease along the modulation color direction of the adaptation stimulus (Krauskopf, Williams, Mandler, & Brown, 1986; Webster & Mollon, 1991). This adaptation is called color contrast adaptation (Webster, 1996) and is distinguished from the typical color adaptation described above. Because our visual environments have large spatiotemporal variations in luminance and chromaticity, color contrast adaptation should also significantly affect daily color perception. For instance, it has been reported that color aftereffects seemingly occur contingent on specular and diffuse reflection components (Nagai, Yamagishi, Tani, Koida, Kitazaki, & Nakauchi, 2013). In their experiments, the observers adapted to an object image created by adding high-luminance specular components and low-luminance diffuse components with different chromaticities (e.g. red specular and green diffuse components). In this adaptation stimulus, chromaticity-luminance relations were spatially variegated and differed between these two reflection components. After the adaptation, they were presented with a test achromatic image with only diffuse or specular components and perceived the opposite color to the corresponding adaptation component (e.g. after they adapted to an image with red specular and green diffuse components, they perceived greenish colors on an achromatic image with only specular components and reddish colors on an image with only diffuse components). This phenomenon cannot be explained by color adaptation to the mean color but may be partly due to adaptation mechanisms sensitive to combinations of luminance and chromaticity. This phenomenon provides us the motivation for investigating adaptation to complex chromaticity-luminance combinations.

What mechanisms are involved in this seemingly complex adaptation phenomenon? One candidate is the noncardinal channels of color representations in the visual cortex (Gegenfurtner, 2003; Webster & Mollon, 1991). A series of experiments by Webster and colleagues (Mizokami, Paras, & Webster, 2004; Webster & Mollon, 1991; Webster & Mollon, 1994; Webster & Wilson, 2000) have shown that the attenuation of perceptual contrast after color contrast adaptation occurs not only in the cardinal directions corresponding to the cone-opponent channels (Derrington, Krauskopf, & Lennie, 1984; L–M and S directions) but also in intermediate color directions. This result cannot be explained by the cardinal mechanism model and has been interpreted as involving higher-order mechanisms composed of channels sensitive to intermediate (noncardinal) color directions (Webster, 1996). Such higher-order mechanisms have also been suggested by

color discrimination experiments using noise-masking paradigms (Gegenfurtner & Kiper, 1992; Goda & Fujii, 2001; Hansen & Gegenfurtner, 2006; Li & Lennie, 1997). Furthermore, physiological studies on color tuning characteristics in V1 and V2 (Kiper, Fenstemaker, & Gegenfurtner, 1997; Lennie, Krauskopf, & Sclar, 1990; Wachtler, Sejnowski, & Albright, 2003), and functional neuroimaging studies (Kuriki, Sun, Ueno, Tanaka, & Cheng, 2015) have supported the existence of cells tuned to the intermediate color directions rather than the cardinal directions.

However, the experimental conditions for investigating the noncardinal mechanisms may be insufficient. In earlier experiments on contrast adaptation, the colors in adaptation stimuli were defined in luminance-chromaticity planes, and the locus of the spatiotemporal color modulation in adaptation stimuli was often one-dimensional (Webster & Mollon, 1991; Webster & Mollon, 1994). Their results showed a decrease in perceived color contrast along the adaptation direction after adaptation. In addition, when focusing only on the chromaticity direction, the perceived color seems to shift in the opposite direction of the adaptation stimulus between higher and lower luminance levels (e.g. figure 17 in Webster & Mollon, 1994). For instance, after the observer adapts to a stimulus whose color modulates along the red-bright/green-dark direction, the perceived color shifts to the greenish direction at a high luminance level and the reddish direction at a low luminance level. Therefore, in stimuli whose specular and diffuse components differ in their luminance-chromaticity distributions, as described earlier, this type of luminance-dependent perceived color shift is likely to be one of the causes of color adaptation, seemingly contingent on specular and diffuse reflections. However, there is naturally some overlap in the luminance distributions of the specular and diffuse reflections. Therefore, the chromaticities are not neatly separated between low and high luminance levels but are somewhat complicated. Few studies have examined how the visual system adapts to stimuli with complex luminance-chromaticity distributions.

In the present study, we investigated the characteristics of color contrast adaptation to stimuli with temporal color modulations along complex chromaticity-luminance loci. We aimed to infer the color representations contributing to color contrast adaptation throughout the psychophysical experiments. Specifically, by increasing the complexity of the luminance-chromaticity relationship, we examined whether perceived color shift after adaptation occurs differently across different luminance levels (e.g. adaptation to diffuse and specular reflections, as described above). In the results, when lower, medium, and higher luminance levels have different chromaticities in an adaptation stimulus, such as red, green, and red at the three luminance levels, color

contrast adaptation induced shifts in chromaticities corresponding to perceptual achromaticity (so-called achromatic points) in the color directions at these three luminance levels. In contrast, no such luminance-dependent achromatic point shift occurred after adaptation to color modulations along more complex luminance-chromaticity loci, such as red, green, red, green, and red, at five luminance levels. These results support the idea that noncardinal color mechanisms, whose neutral point exists at the adaptation mean color, contribute to luminance-contingent color shift after color contrast adaptation, as well as in previous studies.

Experiment 1: Adaptation to simpler color loci

In [Experiment 1](#), the observers adapted to two types of adaptation stimuli whose color modulation trajectory on the luminance-chromaticity plane was the “>” or “<” shape. We then measured the perceptual achromatic points at different luminance levels using an adaptive staircase method. In this experiment, we examined the existence of an adaptation mechanism that can follow complex luminance-chromaticity temporal modulations by measuring the difference in achromatic points across luminance levels.

Method

Observers

Four graduate students at Yamagata University (three men and one woman, all in their 20s) participated in the experiment. All observers had normal or corrected-to-normal visual acuity. All the observers passed the Ishihara color vision test. The experiment was approved by the Ethical Review Committee of the Faculty of Engineering, Yamagata University, and followed the Code of Ethics of the World Medical Association (Declaration of Helsinki). Written informed consent was obtained from all observers.

Apparatus

The experiment was conducted in an otherwise dark room with a liquid crystal display (ColorEdge CX241, EIZO, Japan), trackball mouse, and chin rest for stimulus presentation. The resolution of the display was 1920×1080 pixels, and the refresh rate was 60 Hz. The color depth of the red, green, blue (RGB) channels was 8 bit. The display was connected to a personal computer (OptiPlex3040, DELL, USA), which controlled the experiment using MATLAB 2014a (MathWorks, USA) and Psychtoolbox ([Brainard, 1997](#); [Kleiner, Brainard, &](#)

[Pelli, 2007](#)) on Ubuntu 16.04 LTS. Observers’ responses were captured using a USB-connected trackball. The observer’s head was approximately fixed with a chin rest during the experiment, and the viewing distance to the monitor was 67 cm.

To accurately reproduce the desired luminance and chromaticity on the monitor, the spectral distribution of each of the RGB primaries was measured with a spectroradiometer (SR3-AR, Topcon, Japan), and their gamma characteristics were measured using a colorimeter (ColorCAL II, Cambridge Research Systems, UK). In addition, the noisy-bit method was applied to the presented stimulus to improve the luminance and chromaticity resolution ([Allard & Faubert, 2008](#)), which is a software technique that probabilistically presents the continuous intensities of RGB primaries by superimposing weak pixel-by-pixel noise on the stimulus.

Stimulus

The colors of the stimuli were defined in a three-dimensional color space spanned by the MacLeod-Boynton chromaticity diagram ([MacLeod & Boynton, 1979](#)) and luminance, both of which were calculated based on the cone fundamentals proposed by [Stockman and Sharpe \(2000\)](#). The origin of the color space was set to be metameric to equal-energy white of 15 cd/m^2 for Stockman and Sharpe cone fundamentals, and the L–M axis (the r axis in [MacLeod and Boynton, 1979](#)) was linearly scaled so that the gamut limit of the display in the L–M negative direction became -1 . [Figure 1](#) shows the scaled L–M axis plotted in the CIE2006 xy chromaticity diagram. The luminance axis was used in the log scale, considering that luminance perception is approximately logarithmic, as in the Weber-Fechner law. The value of the S axis (the b axis) was fixed at the origin, and thus, all changes in stimulus colors were defined only in the L–M versus log-luminance plane (referred to simply as the chromaticity-luminance plane). It should be noted that this does not mean that the S-cone excitation was not changed in our stimulus; that is, stimulus colors were not defined on the L- and M-cone contrast plane. Instead, the chromaticity was maintained constant along the luminance axis, and thus, the S-cone excitation was also altered to maintain a constant chromaticity during luminance modulations. In addition, the S-axis direction was not adjusted for individual observers, but the direction for the standard observer was directly used.

We used two types of stimuli: adaptation and test. The adaptation stimulus was a uniformly colored circle with a black edge on a gray background. The luminance and chromaticity of the background were those at the origin of the color space. The radius of the circular stimulus was 1.5 degrees (68 pixels) at

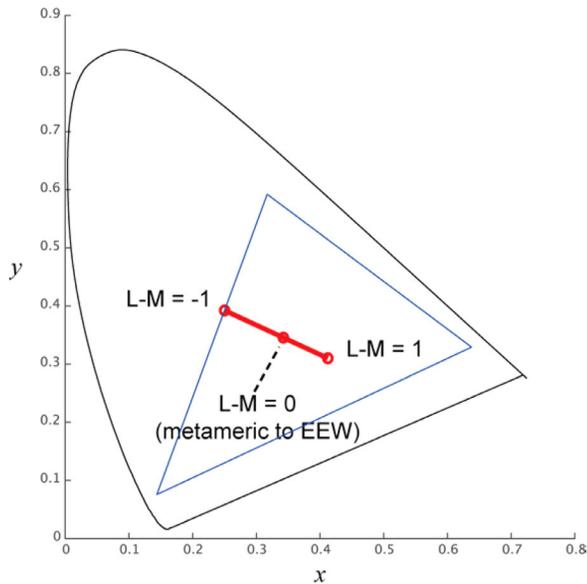


Figure 1. L–M colors used in the experiment in the CIE 2006 xy chromaticity diagram. The red and blue lines indicate the colors on the L–M axis from -1 to 1 and the color gamut of the monitor used in the experiment, respectively.

the visual angle. The width of the black edge was one pixel. This edge was used to denote the position and timing of the stimulus isoluminant with the background and help the observer judge the stimulus color by fulfilling the color appearance within the luminance edges (e.g. Anstis, Verger, & van Lier, 2012). The luminance and chromaticity of the stimuli varied temporally along a locus with the “>” or “<” shape on the chromaticity-luminance plane. Figure 2a shows these loci on the chromaticity-luminance plane; the red and blue lines show the “>” and “<” shapes, respectively. Figure 2b shows the luminance and chromaticity of the “<” adaptation stimulus as functions of time. The luminance changed sinusoidally at 1 Hz ranged from 3.75 to 60 cd/m^2 . The L–M value was automatically determined according to the locus in Figure 2a and stimulus luminance; it ranged from -1 to 0.579 for the “<” shape and from -0.579 to 1 for the “>” shape. These values were determined such that the mean chromaticity was zero across the chromaticity and luminance variations. The appearances of the “<” and “>” adaptation stimuli can be found in the Supplementary Material Movies S1 and S2, respectively. It should be noted that the luminance sinusoidally changed along the log luminance scale, not linear luminance scale. The adaptation color loci on the L- and M-cone contrast plane on a linear scale are shown in Figure 2c. Although the S-cone contrast was modulated along the luminance axis in the adaptation stimulus, the S-cone change is not represented in this figure. As shown in this figure, the luminance

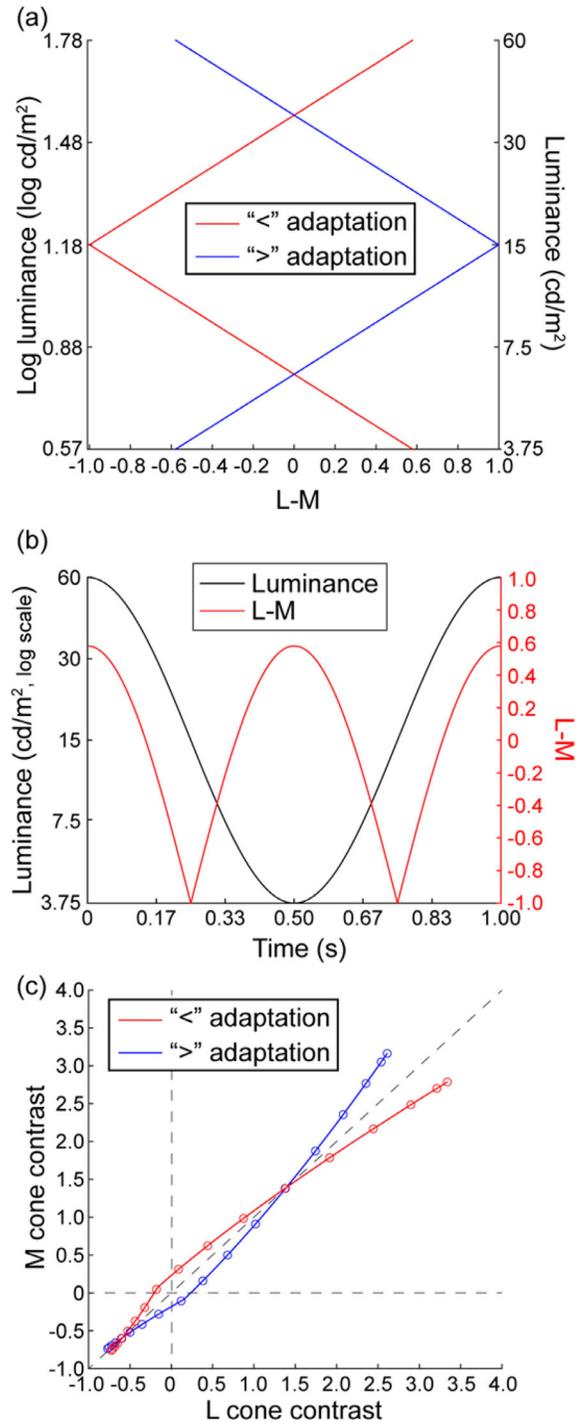


Figure 2. Properties of adaptation color. (a) Loci of adaptation color on the chromaticity-luminance plane in Experiment 1. The red and blue lines represent “<” and “>” adaptation loci, respectively. (b) Luminance (black line) and L–M (red line) of “<” adaptation color as a function of time. (c) Loci of adaptation color on L- and M-cone contrast plane. No log transform is applied to the axes. Although S-cone contrast was modulated along the luminance axis, it is ignored in this figure.

change during adaptation was much larger in the positive (bright) direction than in the negative (dark) direction. In addition, Hansen and Gegenfurtner (2013) suggested that perceptually variegated color noise near the 45 to 225 degree axis in the cone-contrast space is adequate to detect the effects of higher-order color mechanisms. Figure 2c shows that the color modulations in our adaptation stimuli were situated near 45 to 225 degrees, indicating that the adaptation color modulation may capture the involvement of the higher-order channels.

The spatial configuration of the test stimulus was the same as that of the adaptation stimulus, whereas the color of the circular uniform patch was different. The color of the test stimulus was temporally stationary. In each trial, the luminance was one of five equal logarithmic intervals from 3.75 to 60 cd/m² (3.75, 7.50, 15.00, 30.00, and 60.00 cd/m²). The L–M value was determined based on the observer’s response history using the Psi (ψ) adaptive staircase method (Kontsevich & Tyler, 1999). The L–M value range in the Psi staircase method was -0.3 to 0.3. Although the background luminance (15 cd/m²) might allow slight rod intrusion into the test color appearance (Zele & Cao, 2015), we believe that the rod effects on the results should be subtle, considering that the adaptation and test stimuli were primarily projected on the central retina.

Procedure

At the beginning of each experimental session, the observer adapted to the adaptation stimulus for 1 minute, during which the observer kept fixating on the central circle of the adaption stimulus. The trials began after adaptation. In each trial, a uniform gray (the origin of the color space) background without the circular patch was first presented for 300 ms, and then the test stimulus was presented for 500 ms. The observer judged whether the circular patch of the test stimulus appeared reddish or greenish and responded using the trackball button in a two-alternative forced-choice manner. A beep sound indicated to the observer that the response had been recorded. After the response, the background was presented for 300 ms, and then the observer re-adapted to the adaptation stimulus for 6000 ms. These trials and re-adaptations were repeated during each session.

Each session comprised 200 trials. The trials for the two adaptation conditions (“>” and “<”) were performed in separate sessions. Each observer performed five sessions for each adaptation condition, resulting in 10 sessions.

Control condition: Adaptation to static background

In addition to the main experiment, we conducted a control experiment in which the observer adapted

to a static gray background instead of a temporal modulation adaptation stimulus. The color of the adaptation stimulus was constantly neutral gray of the color space origin. The remaining procedures were the same as in the main experiment and were conducted in a separate session after the main experiment.

Analysis

The ratios of the “reddish” to “greenish” responses were measured for each test L–M value in the experiment. Then, the psychometric function, response ratios as a function of L–M values, were analyzed by fitting a logistic function with the Palamedes Toolbox (Prins & Kingdom, 2018). Finally, the L–M value corresponding to a response probability of 50% was defined as the achromatic point. This achromatic point was calculated for each observer and for each of the five test luminance levels.

Results: Achromatic points

Figure 3a shows the achromatic points, L–M values that appeared achromatic after adaptation at each test luminance level. The bold lines show the results averaged across observers, and the thin lines show the results of individual observers. The individual data for the control condition is not shown in Figure 3 but the Supplementary Material Figure S1. The line colors indicate adaptation conditions: red plots show the “<” adaptation, the blue plots show the “>” adaptation, and the black plots show the control condition.

These graphs show that, for most observers, the achromatic points shifted toward red (in the positive direction on L–M) after the “>” adaptation, as compared with the control condition, and shifted toward green (in the negative direction on L–M) after the “<” adaptation in general. These results appear to indicate a phenomenon in which color adaptation is induced more strongly based on higher luminance components in the adaptation stimulus. This can be inferred from von Kries adaptation in the photoreceptors; a higher luminance color can induce stronger responses of the photoreceptors than a lower luminance color, and therefore, higher luminance colors govern the adaptation state. For instance, in the case of “<” adaptation, the chromaticity corresponding to high luminance was positive (reddish); therefore, the overall strength of color adaptation was strongly affected by the reddish component. This adaptation made the test stimulus appear greenish, which induced a shift of the achromatic point in the positive direction.

However, the line shapes created by connecting the achromatic points were more intriguing. The achromatic points did not reach L–M = 0 and were slightly different across the luminance levels. Therefore,

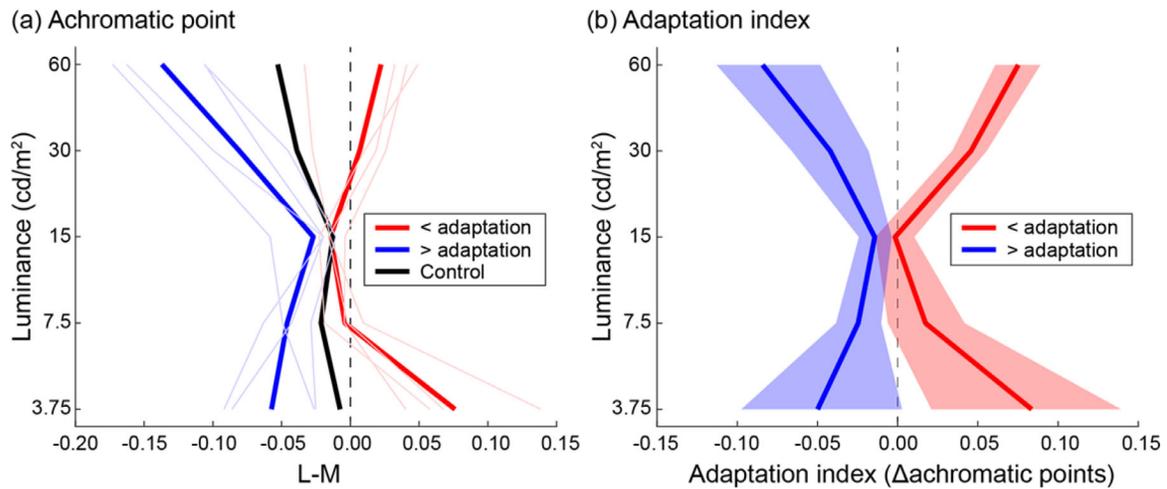


Figure 3. (a) Achromatic points after adaptation in Experiment 1. The thin lines show individual observers' results, and the bold lines show the results averaged across the observers. The line colors indicate the adaptation conditions. (b) Differences between the “<” or “>” adaptation and the control condition averaged across the observers. The shaded zones show 95% confidence intervals calculated using a parametric bootstrap method with 10,000 repetitions.

to visualize the effects of color modulation components in “<” and “>” adaptation stimuli, the differences of achromatic points between the “<” or “>” adaptation (AP_a) and those in the control conditions (AP_c) are shown in Figure 3b (i.e. $AP_a - AP_c$). Subtraction was performed for every observer's result, and the subtracted values were averaged across the observers. This achromatic point difference is referred to as the adaptation index in this study. The shaded zones represent 95% confidence intervals calculated using the parametric bootstrap method with 10,000 repetitions. In the case of the “<” adaptation, for instance, the shift of the adaptation index to the positive direction was particularly larger in the higher and the lower luminance levels than in the medium luminance level (15 cd/m^2), resulting in the “<” shape of the adaptation effect. In contrast, in the case of the “>” adaptation, the adaptation effect drew an “>” shape. Although these trends are obvious in the averaged chart, the individual achromatic points exhibited a similar trend.

To clarify the effects of the temporal modulation components in the adaptation stimuli, we subtracted the achromatic points in the “>” condition from those in the “<” condition. The results are shown in Figure 4. As expected from Figures 3a and b, the differences formed clear “<” shapes, as expected. We statistically tested the differences between zero and the subtracted achromatic point at each luminance level based on a parametric bootstrap procedure with 10,000 repetitions, in which the Bonferroni correction adjusted the significance level. The test found significant differences from zero ($p < 0.01$ after Bonferroni correction) for all luminance levels, except 15 cd/m^2 . In addition, we statistically tested the differences in the subtracted achromatic points between the luminance levels based on multiple comparisons. The results showed that all the differences

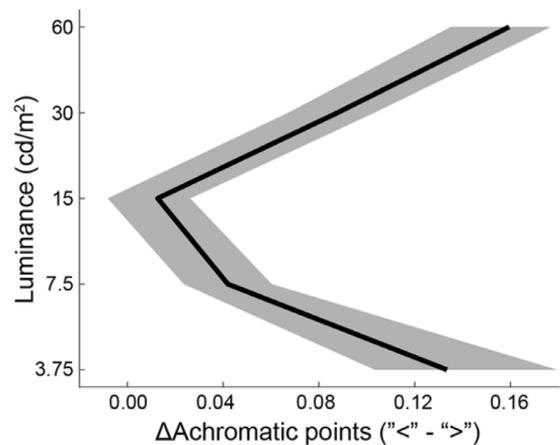


Figure 4. Differences in achromatic points between “<” and “>” adaptation conditions averaged across observers. The shaded zone shows 95% confidence intervals calculated using a parametric bootstrap procedure with 10,000 repetitions.

in the luminance-level combinations other than $3.75\text{-}30$ and $3.75\text{-}60$ were statistically significant ($p < 0.05$ after Bonferroni correction). These statistical tests indicate that the temporal modulation components in the adaptation stimuli induced differences in achromatic point shapes between the “<” and “>” adaptations.

Discussion

The results showed that the lines created by connecting the achromatic points were similar to the adaptation color loci. These results suggest that the visual system has mechanisms of color contrast adaptation that induce different perceived color shifts among higher, medium, and lower luminance levels.

What mechanisms support this type of adaptation? Previous neurophysiological and functional brain imaging studies have shown that cone-opponent channels represent color information in the retinal ganglion cells and the LGN (Gegenfurtner, 2003). On the other hand, in visual cortical areas, such as V1, there are cells sensitive to various color directions, not only to the cardinal directions (Gegenfurtner, 2003; Kuriki, Sun, Ueno, Tanaka, & Cheng, 2015). However, the characteristics of these cortical cells have not been fully elucidated. In psychophysics, many studies have shown that noise-masking properties in color discrimination and color contrast adaptation suggest the involvement of noncardinal mechanisms (Kuriki, 2007; Hansen & Gegenfurtner, 2006; Li & Lennie, 1997; Webster & Mollon, 1991; but see Eskew, 2009). Considering these results, it is highly likely that the (seemingly) luminance-dependent color adaptation phenomenon, as measured in this study, may involve the noncardinal mechanisms. In the following subsections, we test the possibility of the involvement of noncardinal mechanisms in our adaptation results using a model analysis.

Prediction by noncardinal model

In this section, we examine the correspondence between the noncardinal model and current results. The model used here represents color information based on the response balance between the eight channels ($k = 1$ to 8). The response of each channel to a stimulus is assumed to change linearly with its contrast in the chromaticity-luminance plane (i.e. the distance from the origin). Importantly, in color contrast adaptation, response sensitivity decreases linearly with the magnitude of the channel response change to the adaptation stimulus over time. Therefore, the response balance across channels changes after adaptation, depending on the color locus of the adaptation stimulus. Finally, the channel response balance was used to predict perceived color shift after adaptation.

Figure 5 shows the response sensitivities of the channels before and after the “<” adaptation to different color directions on the chromaticity-luminance plane (L–M versus scaled log-luminance plane) in our noncardinal model. Here, the log-luminance from 7.5 to 60 cd/m^2 is scaled from -1 to -1 on the vertical axis (defined as “normalized log luminance”), and the L–M value was directly displayed on the horizontal axis (defined as “normalized L–M”). The relative magnitudes of normalized L–M and luminance were used to determine the stimulus color direction. Each line color represents the response sensitivity of each channel, from $k = 1$ (maximum sensitivity to 0 degrees, the L–M positive direction) to 8 (maximum sensitivity to 315°), whose k values were defined in

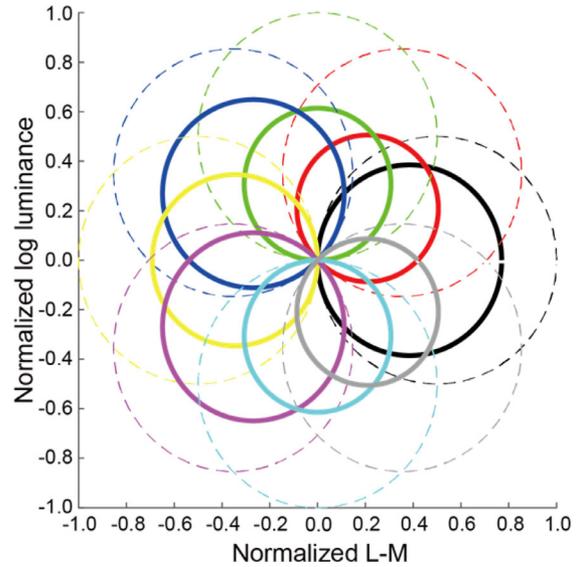


Figure 5. Relative sensitivities of channels to different color directions before and after “<” adaptation in our 8-channel model. Each line color corresponds to the sensitivity of each channel, and the distance between the origin and the line indicates the relative sensitivity to different color directions. Dotted and bold lines show the sensitivities before and after adaptation, respectively.

counterclockwise order. The distance from the origin to each point of the line indicates sensitivity to the color direction. The dotted and bold lines in this chart show the sensitivities before and after “<” adaptation, respectively. The details are described in the following paragraphs:

First, we define the baseline (or pre-adaptation) channel-response properties. Because they were defined for the color directions on this plane, the stimulus color (the normalized log L–M and luminance) was transformed into amplitude s and phase θ using Equations 1 and 2:

$$s = \sqrt{LM^2 + Lum^2} \quad (1)$$

$$\theta = \tan^{-1} \left(\frac{Lum}{LM} \right), \quad (2)$$

where LM is the normalized L–M and Lum is the normalized log luminance. The baseline response of each channel $r(k)$ to a visual stimulus (s, θ) was then calculated using Equation 3:

$$r(k) = \max \left(s \times \cos \left(\theta - \frac{k-1}{4} \pi \right), 0 \right). \quad (3)$$

As shown in Equation 3, the channel response is defined as $\max(\cos(\theta - \frac{k-1}{4}\pi), 0)$, assuming that the channel responses exhibit unidirectional broadband response characteristics obtained by linearly

transforming the cone response to stimuli (Hansen & Gegenfurtner, 2006). Every dotted line in Figure 5 shows $r(k)$ for the stimuli with $s = 1$ and different θ .

Next, we formulated the response sensitivity after color contrast adaptation. The degree of sensitivity attenuation after adaptation, SA , was formulated for each channel as follows:

$$SA(k) = a \times \sqrt{\frac{1}{n} \sum_{t=1}^n (r_{kt} - \bar{r}_k)^2}, \quad (4)$$

where n is the total number of display frames during the adaptation period, r_{kt} is the response of channel k calculated using Equations 1, 2, and 3 from $LM(t)$ and $Lum(t)$ of the adaptation stimulus at each frame t , and \bar{r}_k is the mean of the responses during the adaptation period. In addition, a is the coefficient used to adjust the overall strength of adaptation; we arbitrarily used $a = 2$ because this value yields predictions similar to the experimental results. As shown in Equation 4, SA is assumed to be determined by the standard deviation (or contrast) of the channel response over the adaptation period.

The channel responses to the test stimulus after adaptation were calculated considering SAs according to Equation 5, based on the assumption that SA multiplicatively attenuates channel responses:

$$r_a(k) = \left(\left\{ s \times \cos \left(\theta - \frac{k-1}{4} \pi \right) \right\} / (SA(k) + 1) \right). \quad (5)$$

The channel response $r_a(k)$ is obtained by dividing Equation 3 by $(SA(k) + 1)$. The bold lines in Figure 5 show the channel response $r_a(k)$ to the stimulus with $s = 1$ and different θ values calculated using Equation 5 after “<” adaptation. One can see that the channel responses of $k = 2$ (red line), 3 (green line), 7 (sky blue line), and 8 (gray line) are significantly attenuated. These unbalanced responses predict a shift in the color appearance after adaptation. Please note that this adaptation effect is simpler than previous suggestions that sensitivity attenuation by adaptations is composed of both subtractive and multiplicative processes (Webster & Mollon, 1994).

Finally, the predicted values of the perceived normalized L–M, LM_p , and luminance, Lum_p , were calculated from $r_a(k)$ according to Equations 6 and 7, respectively:

$$LM_p = \frac{1}{2} \sum_{k=1}^8 \left[r_a(k) \times \cos \left(\frac{k-1}{4} \pi \right) \right] \quad (6)$$

$$Lum_p = \frac{1}{2} \sum_{k=1}^8 \left[r_a(k) \times \sin \left(\frac{k-1}{4} \pi \right) \right] \quad (7)$$

These equations assume that each channel response is divided into L–M and luminance components and that the perceived L–M and luminance are determined by summing these components across the channels. In these equations, the color saturation s_p calculated from LM_p and Lum_p for $SA = 0$ coincides with the saturation s of the stimulus.

In Experiment 1, we measured the achromatic points at the five luminance levels after adaptation. Thus, we searched for the LM value corresponding to LM_p of 0 for “<” and “>” adaptation to predict the achromatic point at each luminance level with a brute force search, in which LM_p range searched was -1 to 1 with a 0.001 interval. The results are shown in Figure 6a. The red and blue plots show the predicted achromatic points after “<” and “>” adaptation, respectively. For the “<” adaptation, the achromatic points at high and low luminance levels largely shifted to the red side, forming a “<” shape similar to the measured achromatic points in Figure 2. This result indicates that the perceived color shift induced by color contrast adaptation can be qualitatively predicted by assuming a noncardinal model.

Similar color representation models have been frequently used in previous studies of higher-order color representations underlying color contrast adaptation (Kuriki, 2007; Webster & Mollon, 1994) and noise masking in color detection (Hansen & Gegenfurtner, 2006). In these models, color perception is determined based on summations of the channel responses, as shown in Equations 6 and 7. In addition, the sensitivities of the channels are adjusted by adaptation or noise masking based on the stimulus contrast, as shown in Equations 4 and 5. Although these features are shared by our model and previous models, our model has some arbitrary parameters such as the channel number and tuning width. It remains debatable whether noncardinal channels have a broad or narrow tuning width to color directions (Eskew, 2009) and whether the channel number and tuning width affect the fine properties in predicting color perception by the models. However, the choice of the channel number and the tuning width should not have significant impacts on our conclusions because the purpose of our model analysis is to qualitatively determine if the model can represent the critical property of the contrast adaptation (a “<” or “>” shaped line of achromatic points), not quantitatively predict the achromatic points.

Prediction by cardinal model

We performed a similar prediction of achromatic points using the cardinal model. Our cardinal model is almost identical to the noncardinal model above but consists of only four channels corresponding to $k = 1, 3, 5,$ and 7 of the noncardinal model. These four channels have the maximum sensitivity in the

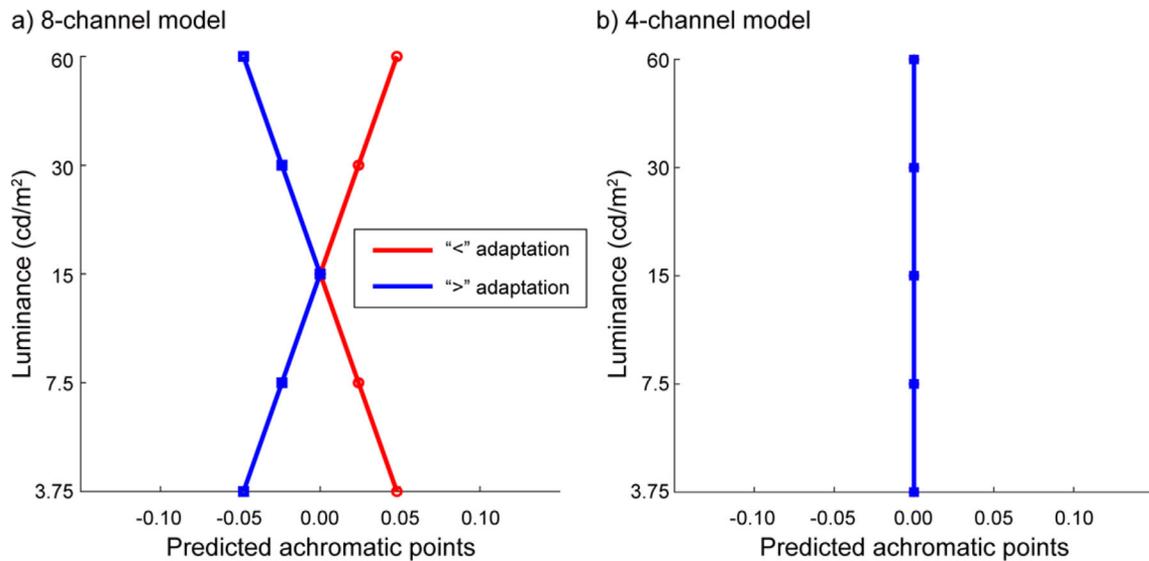


Figure 6. Achromatic points predicted by color representation models. (a) Noncardinal (8-channel) model. (b) Cardinal (4-channel) model.

cardinal directions. Figure 6b shows the achromatic points predicted by the cardinal model. Evidently, the cardinal model does not reproduce any differences in perceptual achromatic points across luminance levels. This result was expected because the stimulus L–M and luminance information were represented independently in the cardinal model. In other words, to explain the perceived color shift across different luminance levels, as confirmed in Experiment 1, it is essential to have channels that simultaneously represent L–M and luminance information, such as the channels of $k = 2, 4, 6,$ and 8 in our noncardinal model. This suggests that the luminance-dependent color shift due to adaptation cannot be explained by the cardinal processing but involves the noncardinal mechanisms in the visual cortex. Notably, the color channels preferring intermediate (noncardinal) directions, not the number of channels, are essential. In another model analysis, we confirmed that the model with only four channels preferring intermediate color directions (composed of channels $k = 2, 4, 6,$ and 8) also predicts the “<” shape formed by the achromatic points after the “<” adaptation, as in the noncardinal model. The results are shown in the Supplementary Material Figure S2.

Effects of nonlinearity of luminance axis: An additional model analysis

In previous studies, color representation models used to analyze behavioral data in color noise masking and adaptation used the luminance axis with a linear scale (e.g. Gegenfurtner & Kiper, 1992; Giulianini & Eskew, 1998; Webster & Malkoc, 2000; Webster & Mollon, 1994). Therefore, the log-scale luminance axis used in our experiment makes it difficult to directly compare

the models in these previous studies and our study. In addition, it may seem strange to use the log luminance axis, as the L–M axis was constructed by subtracting the linear L- and M-cone responses. Therefore, we conducted an additional model analysis using a linear luminance axis to address these problems.

The model was identical to the noncardinal model in the previous section, except that the luminance was represented on a linear scale, where luminance from 0 to 30 cd/m² was scaled from -1 to 1. Although this scaling was arbitrary, we verified that it did not qualitatively affect the model behavior. In this linear model, the effects of the adaptation stimuli in Experiment 1 become much stronger for channels corresponding to higher luminance levels because the linear luminance contrast in the adaptation stimulus was much stronger in the bright direction than in the dark direction. The achromatic points predicted by the linear luminance model are shown in Figure 7. As expected, the achromatic point shift was substantially larger for higher luminance levels than for lower luminance levels because the channels preferring higher luminance were more strongly adapted. This difference in the achromatic point shift between lower and higher luminance levels was not observed in the experimental results. In addition, we tested an extended version of this linear model, in which the log-transform to the luminance axis was applied only in the adaptation but not in the color appearance calculation. However, the estimated achromatic points were rarely affected by the log-transform in the adaptation.

Another alternative model with a linear luminance representation is the model with noncardinal channels in the cone-contrast space proposed by Shepard, Swanson, McCarthy, and Eskew (2016). They reported

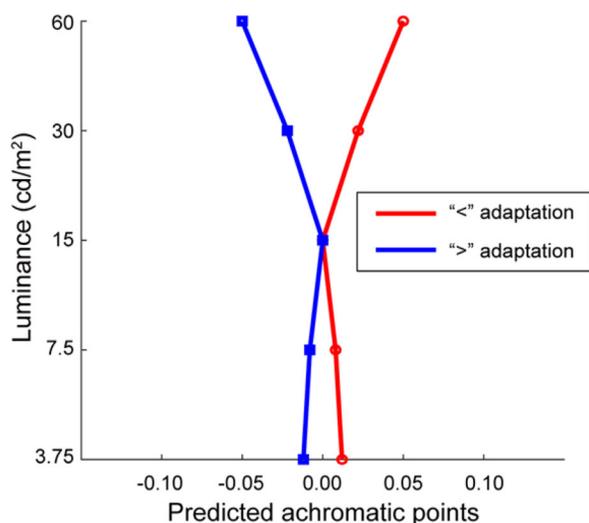


Figure 7. Achromatic points predicted by color representation model with eight channels and linear luminance representation.

that a model with only six channels could explain noise masking in color detection along various color directions, which had been considered as evidence for higher-order color mechanisms. Furthermore, they claimed that noncardinal channels near the L–M direction are essential for this model to be effective. Thus, we also tested the prediction of achromatic point shifts due to adaptation of the six-channel model in the cone-contrast space, similar to that of Shepard et al. (2016). The results were nearly identical to those in Figure 7 (the details of the model analysis are described in Supplementary Material Figure S3). This suggests that the channels preferring intermediate color directions between luminance and chromaticity are crucial for explaining our adaptation effects. However, our results do not indicate which of the models in the chromaticity-luminance and cone-contrast planes are more plausible.

These additional models with linear luminance representations revealed strong asymmetry in the achromatic point shifts between low- and high-luminance levels. This asymmetry raises the possibility that a nonlinear transform similar to the logarithm could mediate the adaptation effects. This possibility is further examined in an additional experiment, as described in the following subsection.

Effects of nonlinearity of luminance axis: An additional experiment

To further examine the effects of log-scale luminance on adaptation effects, we conducted an additional experiment using the linear-scale luminance axis instead of the log-scale luminance axis. Three newly employed observers, including the author T.N., participated in the experiment. The luminance modulation in the

adaptation stimuli ranged from 5 to 25 cd/m^2 on a linear scale (in contrast, the modulation range was 3.75 to 60 cd/m^2 on the log scale in Experiment 1). The adaptation loci in the additional experiment are shown in Figure 8a, whereas those in Experiment 1 are shown in Figure 8b. It should be noted that the luminance axis is shown on a linear scale differently from that in Figure 2a. The test luminance was also selected on a linear scale: 5, 10, 15, 20, or 25 cd/m^2 . The other experimental methods were identical to those used in Experiment 1. According to the noncardinal model with log luminance scale (see Figure 6a), the achromatic point shifts were expected to be smaller for the higher-luminance test stimuli than for the lower-luminance test stimuli in this additional experiment. In contrast, the model with a linear luminance scale (see Figure 7) predicted comparable achromatic point shifts between the higher- and lower-luminance levels.

The measured achromatic points are shown in Figure 9a. The thin lines show the achromatic

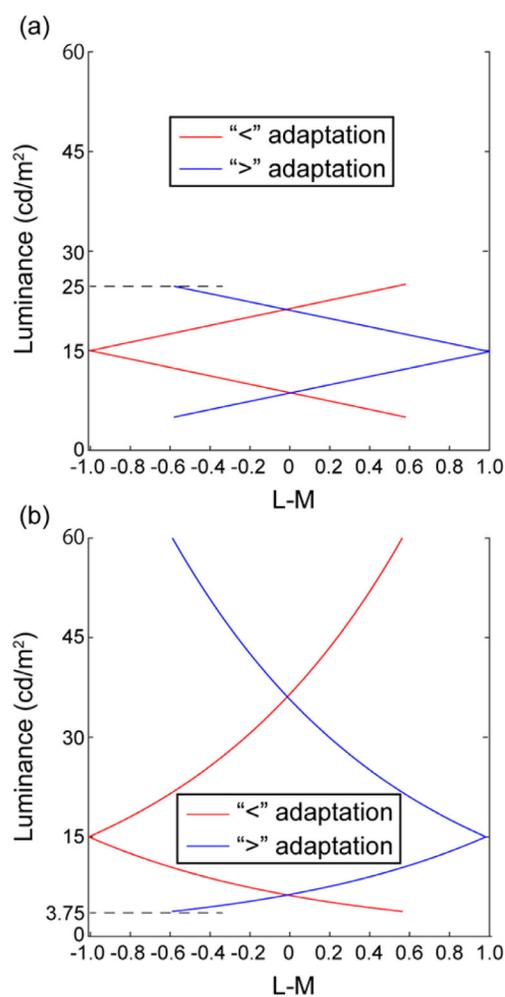


Figure 8. Loci of adaptation color in the chromaticity-luminance plane with linear luminance scale for (a) the additional experiment and (b) Experiment 1.

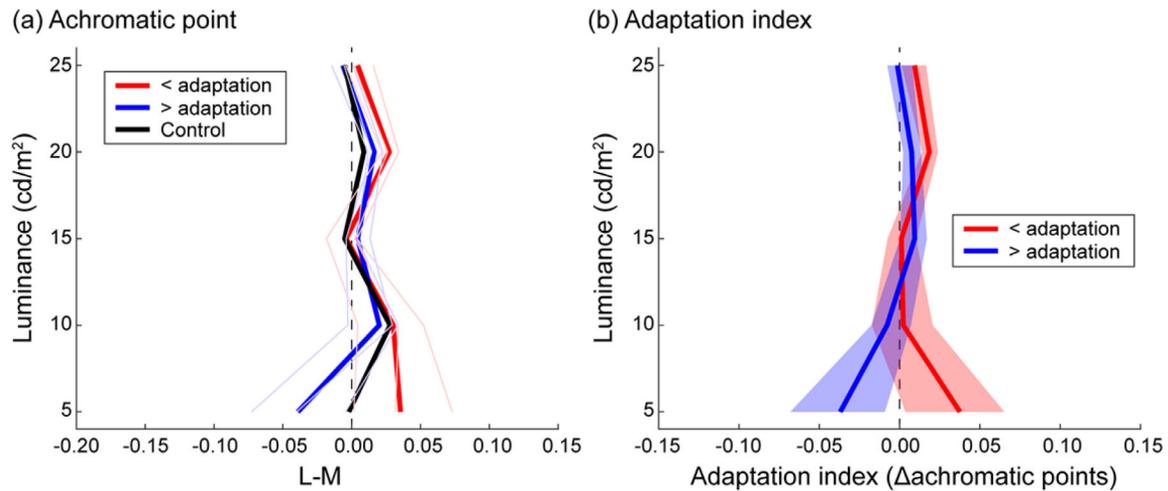


Figure 9. (a) Achromatic points after adaptation in the additional experiment. (b) Differences between the “<” or “>” adaptation and the control condition averaged across the observers. The formats are identical to those in Figure 3, except that the luminance axis is depicted on a linear scale.

points of individual observers, and the bold lines show the achromatic points averaged across the observers. Figure 9b shows the differences in achromatic points between the “<” or “>” adaptation (AP_a) and those in the control conditions (AP_c ; i.e. $AP_a - AP_c$, adaptation index) averaged across all observers and their confidence intervals. The overall trend seems similar to that of Experiment 1: the achromatic point locus formed a weak “<” (“>”) shape after adapting to the “<” (“>”) adaptation stimulus. However, the results indicated that the magnitude of the adaptation effects were different from those in Experiment 1. For lower test luminance (e.g. 5 cd/m^2), the adaptation effects (differences between the “<” and “>” conditions) were comparable between the experiments. In contrast, the adaptation effects for higher luminance were much weaker than those in Experiment 1, in accordance with the prediction by the log-luminance model. Although the higher and lower luminance in the stimuli of the additional experiment were symmetric to the background luminance in the linear scale, the adaptation effects were vastly different between the luminance levels. On the other hand, the adaptation effects in Experiment 1 were closer between the higher and lower luminance levels regardless of the asymmetric luminance setting on a linear scale.

In the additional model analysis and experiment, the results suggest that the color mechanisms for color contrast adaptation represent luminance information in a nonlinear fashion, similar to the log scale representation. However, to the best of our knowledge, few studies have directly supported nonlinear luminance coding in psychophysical color mechanisms for noise masking or adaptation. For instance, the magnitude of color contrast adaptation was comparable between higher- and lower-luminance levels (Webster & Mollon,

1994). Although the causes of this discrepancy are unknown, the luminance ranges used in adaptation or noise masking may be related to it because the effects of nonlinearity should increase with the width of stimulus luminance ranges. In addition, our experimental conditions were severely limited to obtaining clear conclusions regarding this luminance nonlinearity issue. Therefore, further studies with additional experimental conditions and quantitative analyses are necessary.

Experiment 2: Adaptation to more complex color loci

Experiment 1 demonstrated that the visual system has adaptation mechanisms that cause perceived color shifts after color contrast adaptation differently at lower, medium, and higher luminance levels. In addition, the model analysis suggested that one of the plausible underlying mechanisms is the noncardinal mechanism. We conducted Experiment 2 to further examine the involvement of the noncardinal mechanism in this type of color-contrast adaptation. In Experiment 2, we used adaptation stimuli with more complex color-modulation loci on the chromaticity-luminance plane that the noncardinal model cannot capture. Our hypothesis was that if the noncardinal mechanism is involved in color contrast adaptation, the luminance-dependent perceived color shift should disappear in Experiment 2.

Method

The same observers as those in Experiment 1 participated in Experiment 2. The apparatus was

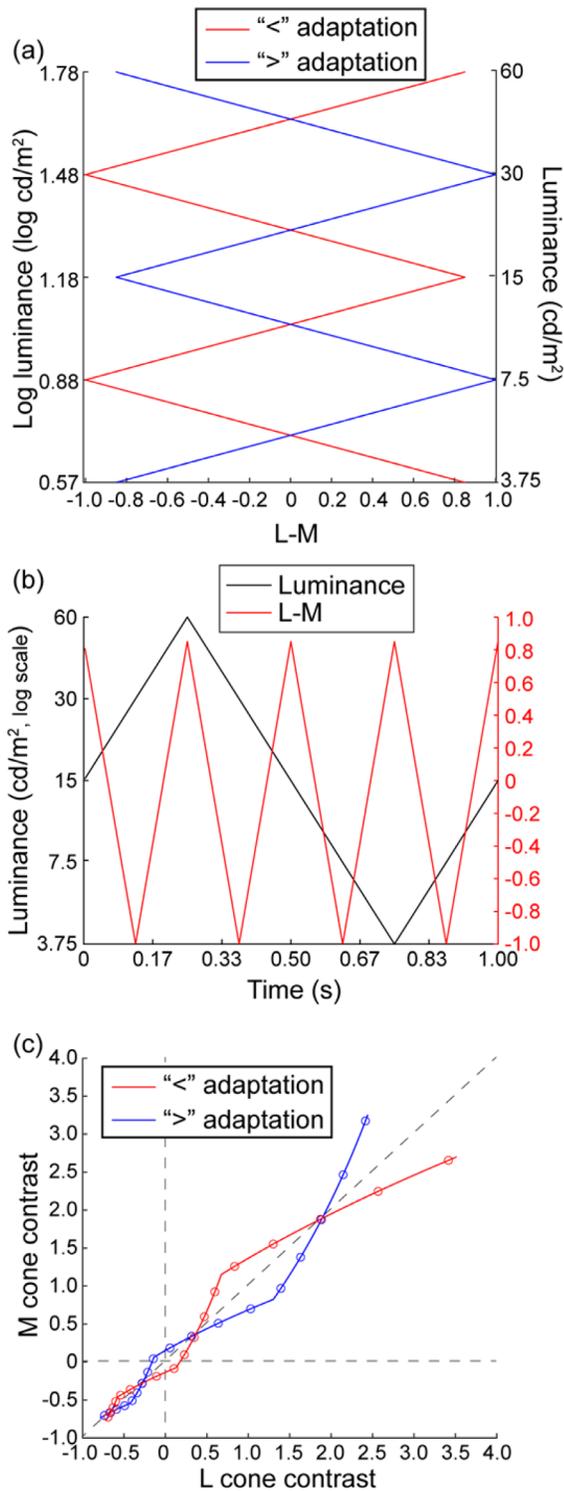


Figure 10. Properties of adaptation color in Experiment 2. The formats are the same as Figure 2.

identical to that used in Experiment 1. The procedure was the same as that in Experiment 1, except for the color loci of the adaptation stimulus. The properties of the two adaptation stimuli in Experiment 2, such as color loci and temporal profiles, are shown in Figure 10.

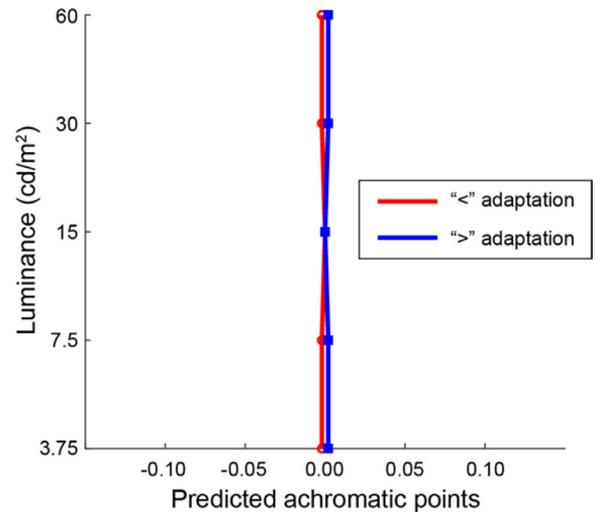


Figure 11. Achromatic points after the double “<” and “>” adaptation predicted by the noncardinal model.

The shape of the locus was either a “double <” or a “double >” shape on the chromaticity-luminance plane. The log luminance changed linearly at a fixed speed, not along the sinusoidal profile used in Experiment 1, and the chromaticity was automatically determined based on the locus. The temporal frequency of luminance modulation was 1 Hz. The initial phase of luminance (starting luminance) was set randomly for each trial. The luminance ranged from 3.75 to 60 cd/m², as in Experiment 1. The L–M value ranged from -1.00 to 0.85 for the “double <” adaptation and from -0.85 to 1.00 for the “double >” adaptation. These values were determined so that the mean chromaticity during adaptation was zero. The appearances of the “double <” and “double >” adaptation stimuli can be found in the Supplementary Material, Movies S3 and S4, respectively.

To check the relations between the adaptation stimuli in Experiment 2 and the noncardinal model, we predicted the achromatic points after adaptation to the “double <” and “double >” stimuli using the noncardinal model introduced in the previous section. The achromatic points after the “double <” adaptation predicted by the noncardinal model are shown in Figure 11. In contrast to Experiment 1, the predicted achromatic points formed an approximately straight line. The reason for this prediction is that this model represents stimulus chromaticity differently only between the lower, medium, and higher luminance levels. For instance, in the “double <” adaptation stimulus, colors on the L–M side at the highest luminance level and those on the M–L side at the second-highest luminance level are represented by separate channels in the first and second quadrants in the chromaticity-luminance plane. In addition, the perception of higher-luminance colors is determined

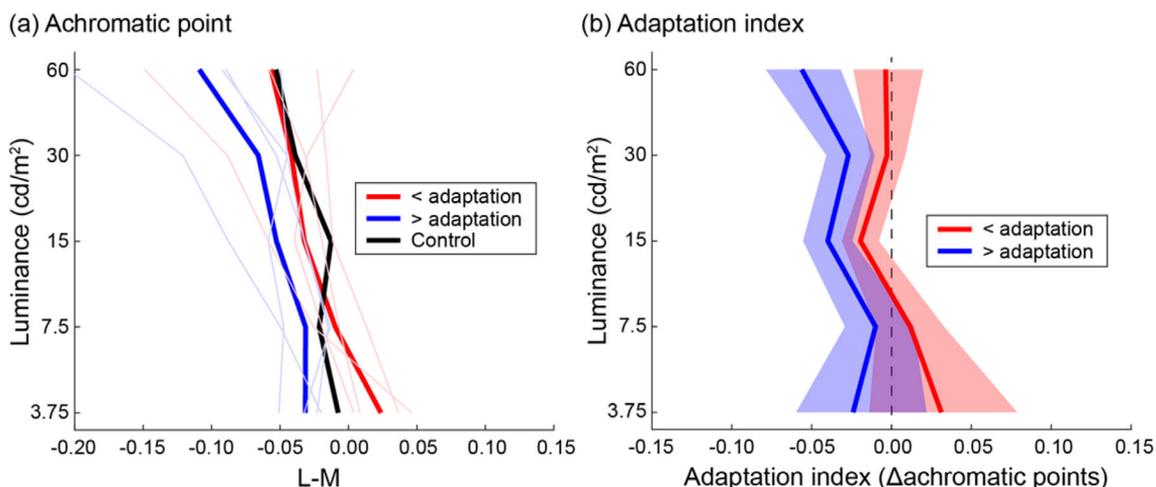


Figure 12. (a) Achromatic points after adaptation in Experiment 2. The thin lines show individual observers’ results, and the bold lines show the results averaged across the observers. The line colors show the adaptation conditions. The results of the control conditions are the same as Figure 3a. (b) Differences between the “<” or “>” adaptation and the control condition averaged across the observers. The shaded zones show 95% confidence intervals calculated using a parametric bootstrap method with 10,000 repetitions.

by the balance of the channel responses in the first and second quadrants. Therefore, the adaptation to the “double <” adaptation stimulus, which affects channels in both quadrants, may induce only the decrease in perceptual saturation due to weakened channel responses but not perceptual color shift.

Results and discussion

The achromatic points for each luminance are shown in Figure 12a. As shown in Figure 3 (a), the thin lines show the individual observer results, and the bold line shows the average results. Additionally, the differences between achromatic points in the contrast adaptation condition (AP_a) and those in the control condition (AP_c) measured in Experiment 1 are plotted (i.e. $AP_a - AP_c$, which represents the effects of adaptation color modulation is plotted) in Figure 12b. The red plots show the results for the “double <” adaptation, the blue plots show those for the “double >” adaptation. Figures 12a and b show that the achromatic points generally shift to the reddish and greenish sides after the “double <” and “double >” adaptation, respectively, in general. However, it is difficult to find shapes similar to the adaptation loci; the subtracted achromatic points seem to fluctuate across luminance levels, but the shapes are unclear and similar between the two adaptation conditions.

To emphasize the shape difference between the “double <” and “double >” adaptation conditions, Figure 13 shows the difference in the achromatic points between them (Δ achromatic points). The graph shape was entirely different from

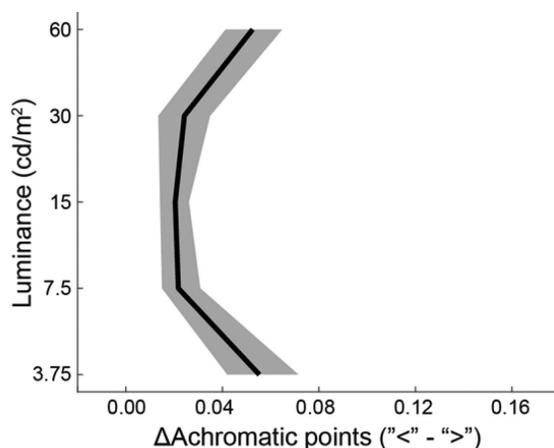


Figure 13. Differences in achromatic points between “double <” and “double >” adaptation conditions averaged across observers. The shaded zone shows 95% confidence intervals calculated using a parametric bootstrap procedure with 10,000 repetitions.

the adaptation locus; instead, it formed a simple “(“ shape, somewhat similar to Experiment 1. Parametric bootstrap testing with 10,000 repetitions showed significant differences in all achromatic point differences from 0 ($p < 0.01$ after Bonferroni correction). In addition, the differences in Δ achromatic points between the luminance levels were tested using a bootstrap test with Bonferroni correction. The results are presented in the Table 1. This trend is consistent with the idea that the respective mechanisms for lower, medium, and higher luminance are involved in the adaptation effects. This result suggests that the visual system does

Luminance (cd/m ²)	30	15	7.5	3.75
60	**	**	**	n.s.
30		n.s.	n.s.	**
15			n.s.	**
7.5				**

Table 1. Results of bootstrap test on differences in Δ achromatic points (Figure 13) between luminance levels. ** Indicates $p < 0.01$, and the “n.s.” indicates no significant difference. The significance level was adjusted based on Bonferroni correction.

not have adaptation mechanisms that induce perceived color shifts differently across luminance levels after the “double <” shaped adaptation.

Some aspects of the results should be addressed. The first is the temporal frequency of the adaptation stimuli. The temporal frequencies of the chromaticity modulations in the adaptation stimuli differed between Experiments 1 (2 Hz) and 2 (4 Hz). Although we determined the temporal frequency of our adaptation stimulus based on previous findings that a 2–4 Hz frequency induced similar strength of the color contrast adaptation (figure 3 in Webster & Wilson, 2000), it is unclear whether the doubled temporal frequency induced the absence of the luminance-dependent achromatic point shift in Experiment 2. To address this issue, we performed an additional experiment that used an adaptation stimulus with half the temporal frequency of that used Experiment 2. In the results, the achromatic points were nearly identical between the two temporal frequencies, indicating that the doubled temporal frequency did not cause the absence of luminance-dependent achromatic point shift. The details of this additional experiment are described in Supplementary Material Figure S4.

The second aspect is the dissociations between the model prediction and experimental results. The results (see Figures 12a, 13) exhibited modestly different features from the model prediction (see Figure 11): “(“or”)” shapes of lines connecting achromatic points and overall shifts of the achromatic points to the left and right. The former was predicted by the model but only weakly, as shown in Figure 11, although the strength of the “(“or “<” shape in the model prediction moderately depends on the model parameters, such as the tuning widths of the channels. Thus, these shapes are considered qualitatively consistent between the model and the results in Experiments 1 and 2. Moreover, the most crucial finding in Experiment 2 is that neither the model prediction nor the results exhibit double “<” or “double >” shapes in the achromatic point contours. For the latter, we suspect that adaptation at the cone-opponent level to the mean color of the adaptation stimuli was involved. Although the mean chromaticity of the adaptation

stimulus was set achromatic, the mean response during the adaptation period was unlikely achromatic because of temporal chromaticity-luminance variation. As our model did not incorporate the adaptation to the mean color, it seems natural that the model could not predict the overall shift of the achromatic points.

General discussion

This study measured color contrast adaptation to stimuli with temporal color modulations along a complex locus on the chromaticity-luminance plane. The results of Experiment 1, in which “<” and “>” adaptation loci were used, showed that color shifts due to adaptation occurred differently to the higher, medium, and lower luminance levels; that is, the measured achromatic points formed “<” or “>” shapes similar to the adaptation locus. This result suggests the existence of a mechanism that encodes chromaticity information separately for the three luminance levels. Furthermore, this adaptation effect was predicted qualitatively using a noncardinal color representation model. In Experiment 2, we measured color contrast adaptation to stimuli with more complex “double <” and “double >” color loci. The noncardinal model described above does not predict different perceptual color shifts between the luminance levels after adaptation. Consistent with this model prediction, the psychophysical results showed no noticeable differences in the color shift among the luminance levels. Taken together, these results suggest that color representation mechanisms composed of channels tuned to noncardinal color directions from a mean color are one of the most likely candidates that induce luminance-contingent color shifts after adaptation.

The current results do not necessarily reveal any novel properties of noncardinal mechanisms, but rather reconfirm the properties suggested by previous studies. Physiologically, the preferred color directions of V1 and V2 cells are not biased toward the cardinal directions (e.g. Gegenfurtner, 2003). Similarly, functional brain imaging studies have shown large individual differences in the preferred color direction of V1 and V2 voxels (e.g. Kuriki et al., 2015), whereas the cardinal directions are not explicitly preferred. The present results reiterate that these neural response properties, preferring different color directions, significantly affect color perception. In addition, our results suggest the directionality of color channels. In previous psychophysical studies, stimuli whose colors were symmetric to the color space origin (i.e. mean of adaptation color) were frequently used in color adaptation and noise-masking experiments (Hansen & Gegenfurtner, 2006; Webster 1991; Webster, 1994; but there are some exceptions, such as

Kuriki, 2007). In our results, perceived color shifted in the same direction only for higher- and lower-luminance levels, but not for medium luminance. This asymmetric pattern of luminance-dependent color shift suggests that unidirectional channels, rather than origin-symmetric bidirectional channels, are involved in color contrast adaptation. Several studies have already supported the existence of such unidirectional mechanisms at both the cone-opponent level (Beer & MacLeod, 2000) and higher-order levels (Webster & Malkoc, 2000). There is a complex correspondence between luminance and chromaticity in natural scenes, such as the blue sky and brown ground (Burton & Moorhead, 1987; Webster & Mollon, 1997). We speculate that such unidirectional mechanisms can be beneficial in terms of adjusting color sensitivity depending on different luminance levels in daily life.

The model used in our analysis was insufficient to quantitatively reproduce the adaptation effects. First, our model considered only the effects of higher-order color channels in predicting the perceived color shift. Because the mean chromaticity of our adaptation stimulus was achromatic, the adaptation at the photoreceptor and cone-opponent levels, which are induced based on the mean of adaptation color (e.g. Chichilnisky & Wandell, 1995), were not incorporated in our model. In our results, however, the overall achromatic point shifted in the L–M negative direction in Experiment 1, which may reflect adaptations at the photoreceptor and cone-opponent levels. To quantitatively understand the relative contributions of color adaptation and color contrast adaptation to color perception, it is necessary to model the adaptation effects in the photoreceptor and the cone-opponent channels, as well as those in the higher-order level. Second, the model can explain our results only qualitatively, but cannot explain some properties in our results. For instance, the perceived color shift due to adaptation was smaller on the lower-luminance side than on the higher-luminance side. In addition, the results of Experiment 2 show a pattern that is slightly double “>” for both “<” and “>” adaptations. However, our model could not reproduce these properties quantitatively. In future studies, it may be necessary to consider detailed channel characteristics, such as the number of channels and their nonlinearities.

Furthermore, in daily stimuli, such as those created by combining the diffuse and specular components with different chromaticities described in the Introduction, spatial features such as orientation and spatial frequency vastly differ between these reflection components. Thus, color adaptation contingent on such spatial patterns should also occur for these stimuli (e.g. McCollough Effect; McCollough, 1965; Lovegrove & Over, 1972). Although we ignored all the effects of these spatial parameters in the current study, it is crucial to examine

the characteristics of the adaptation mechanisms contingent on different spatial patterns to understand everyday color perception.

Conclusions

In the current study, we investigated the effect of color contrast adaptation to stimuli with temporal modulation along the “<” or “>”-shaped locus on the chromaticity-luminance plane. The perceived achromatic points (L–M values) were measured at various luminance levels after adaptation. The results showed a line connecting achromatic points with a “<” or “>” shape, similar to that of the adaptation stimulus. Furthermore, the adaptation effects can be qualitatively explained using a noncardinal model. In contrast, the more complex double “<” and “>” adaptation stimuli, which were expected not to induce a luminance-dependent color shift by the noncardinal model, did not induce the lines connecting achromatic points similar to that of the adaptation locus in the additional experiment, but instead induced only weak “<” and “>” shapes, similar to the main experiment. These results suggest that unidirectional noncardinal channels are involved in color contrast adaptation, which yields a luminance-dependent perceived color shift.

Keywords: color vision, color contrast adaptation, psychophysics

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