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Psychophysical evidence for a purely binocular color system

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ABSTRACT

Two adaptation experiments were conducted to examine a hypothesis for a purely binocular color system that responds only to simultaneous inputs from the two eyes and that inhibits the activities of a pair of monocular color systems with each receiving input from their respective eye. In the first experiment, after a red or green stimulus was presented to both eyes to adapt the hypothesized binocular system, its compensatory color was presented alternately to each eye to nullify the adaptation effect of the hypothesized monocular systems. Results showed that after adaptation, the color appearance of a test stimulus shifted more to that of the compensatory color in binocular viewing than in monocular viewing. In the second experiment, a red or green stimulus was presented either to both eyes or to the left eye, and then its compensatory color was presented only to the left eye. Comparison was made to the adaptation effect between the binocular presentation of the color stimulus and its monocular presentation. Results showed that the color appearance viewed with the left eye shifted toward the compensatory color for the binocular adaptation and was constant for the monocular adaptation. These results are consistent with the idea of a "purely" binocular color system inhibiting the activity of a pair of monocular systems.

1. Introduction

When we observe a three dimensional scene, binocularly disparate and non-disparate colored images are projected into our two eyes. In 1838, Wheatstone reported that the binocular disparate images can give rise to a vivid three dimensional impression of objects in space, and since then a large number of studies has been conducted on binocular stereopsis (e.g., Howard & Rogers, 2002). In contrast, until recently, relatively less attention has been paid to how color information is processed in binocular perception. This may be the case because the cortical system(s) that mediates color perception is thought to be monocular (e.g., Coltheart, 1973; Hubel & Livingstone, 1987). In line with this thought, some studies have shown that stereoscopic performance is poor under isoluminant conditions (e.g., Kingdom & Simmons, 1996; Krauskopf & Forte, 2002). However, some studies have reported that stereoscopic depth perception is still possible even at isoluminance (e.g., Grinberg & Williams, 1985; Kingdom & Simmons, 1996) and it can also be influenced by color information (e.g., den Ouden, van Ee, & de Haan, 2005; Domini, Blaser, & Cicerone, 2000). These latter studies suggest that the system mediating chromatic perception interacts with that mediating stereoscopic depth perception.

Although stereopsis can be affected by chromatic information, it is not well known whether colors experienced during binocular viewing are mediated by only monocular systems, or also by a binocular system. It is clear from evidence for the color aftereffect that the right and left monocular systems, which are assumed to respond only to the input from their respective eye, play a role in binocular color perception (e. g., Coltheart, 1973). The color aftereffect, while it can be obtained readily with one eye, does not transfer interocularly[1]. An interocular transfer of an aftereffect is often thought to be mediated by a system which responds to inputs from either eye or both eyes (e.g., Anstis & Duncan, 1983; Blake, Overton, & Lema-stern, 1981; Moulden, 1980; Wolf & Held, 1981). The absence of evidence for interocular transfer in color perception suggests that the color aftereffect is not mediated through a binocular system that responds to inputs from either eye or both eyes.

In this study we examined whether or not a "purely" binocular system that responds only to simultaneous inputs from both eyes is involved in color perception. In the literature, it has been shown that purely binocular systems are involved in several types of perceptual experience, such as depth (e.g., Julesz, 1971), motion (e.g., Anstis & Duncan, 1983; van Kruysbergen & de Weert, 1994), mo-

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[1] When it comes to the color-contingent aftereffect, some studies claim that interocular transfer can occur (Delmore, 1994; Domini et al., 2000; Favreau, 1978; Sheth & Shimojo, 2008; White, Petry, Riggs, & Miller, 1978), although other studies claimed that it is difficult to verify that interocular transfer has occurred (Harris & Potts, 1980; Stromeyer, 1972).

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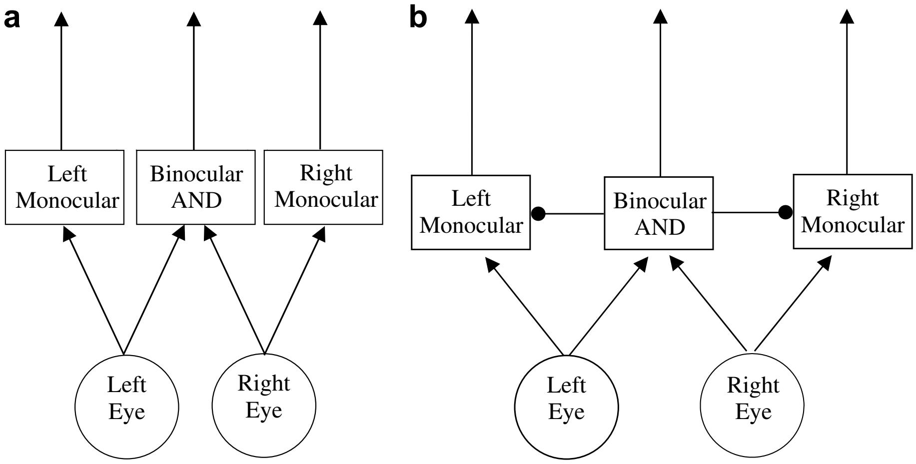

Fig. 1. Schematic representation of a model based on the logical gate theory for color perception (a) and that of its modification (b). In (a), binocular color perception is assumed to be mediated via two monocular (right and left) systems and a binocular AND system. In (b), binocular color perception is assumed to be mediated via monocular (right and left) and inhibitory binocular AND systems. Please refer to the main text for details.

tion in depth (e.g., Shioiri, Saisho, & Yaguchi, 2000), and the tilt aftereffect (e. g., Wolf & Held, 1981). However, it is yet to be firmly established that the colors experienced during binocular viewing of a visual scene are mediated in part by such a system. Reports in the literature that are suggestive of a purely binocular system in color perception actually relate to a phenomenon called binocular color mixture or color fusion (e.g., Hovis, 1989; Ikeda & Sagawa, 1979; Ono, Komoda, & Mueller, 1981). Under some conditions[2] (see Howard & Rogers, 2002 for a discussion), when a color stimulus is presented to one eye and a stimulus with a different hue is presented to the other eye, the binocularly fused stimulus is perceived to have a hue that is intermediate between those perceived monocularly. This binocular color mixture cannot be easily explained without assuming such a purely binocular system responding to simultaneous inputs from the two eyes. However, empirical evidence for the existence of a purely binocular system is not known and it is still an open question whether a purely binocular system plays a role in the final color percept particularly when the same color stimulus is presented simultaneously to both eyes.

To examine whether the purely binocular color system mediates color perception, we designed an experiment to measure adaptation effects of the binocular and monocular systems, separating the color aftereffect of the binocular system from that of the monocular system. In designing the experiment, we assumed that binocular color perception can be described by the logical gate theory. In the logical gate theory, a set of cortical neurons are assumed to be classified into three distinct subsystems; two monocular (right and left), a binocular OR, and a binocular AND (Blake et al., 1981; Moulden, 1980; Wolf & Held, 1981). A monocular system is assumed to only respond to inputs from one eye. Acting as a logical OR gate, a binocular OR system is assumed to respond to inputs from either eye or both eyes, and a binocular AND system (i.e., a purely binocular system) is assumed to act as a logical AND gate, responding only to simultaneous inputs from both eyes. In our model, depicted in Fig. 1, color perception is based on a binocular AND system and two monocular systems (right and left). In the model, the binocular OR system is not included, taking into consideration the absence of evidence of interocular transfer in color perception. On the other hand, it is clear from the color aftereffect that the right and left monocular systems play a role in binocular color perception.

Vimal and Shevell (1987) explored this issue more than two decades ago. They searched for experimental evidence of "central mechanisms that respond only to corresponding neural signals from both eyes" in color perception (p. 429). They found that (1) the chromatic adaptation effect was larger for a condition in which the two eyes were adapted simultaneously than for a condition in which the eyes were adapted through alternate stimulation of the eyes, and (2) the chromatic adaptation effect for binocular viewing is not larger than that for monocular viewing. They explained these findings by assuming that there is a binocular system that does not respond to simultaneous inputs from both eyes, but responds only when there is an input from one eye but no input from the other eye (i. e., exclusive OR system). Recently, Erkelens and van Ee (2002) proposed a similar mechanism that reduces color differences between the color appearances of two monocular stimuli. These studies suggest that the mechanism to compensate for differences in appearances of stimuli between two eyes plays a role in binocular color perception.

In this study, we revisited the issue studied by Vimaland Shevell (1987) using a selective cancelation method to isolate the hypothesized pure binocular system. In our method, the hypothesized pure binocular system was adapted by presenting either a red or a green stimulus to both eyes simultaneously and the hypothesized right and left monocular systems were adapted by presenting the compensatory green or red stimulus sequentially in each eye. Through cycles of these simultaneous and sequential presentations the adaptation effects for the monocular systems were canceled while leaving the adaptation effects intact for the binocular system. Experiment 1 examined the prediction from our model that consists of the right monocular, the left monocular and the binocular AND system (Fig. 1a). Results showed that as predicted from the model, the perceived color was closer to that of a compensatory color when a test stimulus was seen with two eyes (binocular viewing) than when seen with one eye (monocular viewing). However, the difference in the perceived color between the two viewing conditions appeared to be mostly due to a shift of the color appearance in the monocular viewing, rather than that in the binocular viewing. To explain these results, we modified our model so that the binocular AND system inhibits the activity of the monocular systems (Fig. 1b) and examined the prediction from the modified model in Experiment 2. Results showed that adaptation

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[2] It is also known that under other conditions, only one of the two colors is seen at any one time and is as if the colors "compete" with each other (see, for example, Fig. 1d in de Weert & Wade, 1988). This phenomenon is called binocular color rivalry and it suggests that, even when both eyes are stimulated simultaneously, the binocular AND system does not respond all the time.

effects for the eye that was adapted in monocular adaptation conditions were “weaker” than those for the same eye in binocular adaptation conditions. The results of Experiments 1 and 2 are discussed as indicting the existence of a purely binocular color system that responds only to simultaneous inputs from both eyes and inhibits the activity of the monocular systems.

2. Experiment 1: Adaptation of the hypothetical binocular AND system

Predictions from our model are summarized in Fig. 2a in which the level of the adaptation and the predicted color appearance of a test stimulus are depicted. If the binocular AND system, in addition to the monocular systems, is involved in color perception as assumed in the model (Fig. 1a), the adaptation effect obtained with either the right or the left eye alone could differ from that obtained with both eyes. For example, when a red stimulus is presented to both eyes for a period of time and immediately later a green stimulus is presented alternately to each eye for another period of time, effectively only the AND system would be adapted by the red stimulus. This is because the adaptation effect of the monocular systems by the binocular red stimulus will be nullified by the monocular green stimulus. In this example, the color appearance of a test stimulus as indicated by a binocular matching task will appear to be more greenish to observers than that indicated by a monocular matching task. Similarly, when a green stimulus is presented to both eyes simultaneously and a red stimulus is presented alternately to each eye, the color appearance of the test stimulus matched with both eyes will appear to be more reddish than that matched with one eye. [Note that Fig. 2a is depicted under the assumption that there is no ocular difference in the adaptation effect between the right and left monocular systems. Even if there is an ocular difference, the adaptation effect of the monocular system would be less than that of the binocular AND system, provided that an averaging of color signals from the left monocular, the right monocular and the AND systems determines color perception in binocular vision.]

To examine the predictions, we presented an adaptation color stimulus (red or green) and its compensatory color stimulus (green or red) to each eye of observers using a method similar to that of Vidyasagar (1976). The adaptation color was presented to both eyes simultaneously to adapt the hypothesized binocular AND system. To nullify the adaptation effect of the monocular systems, after the simultaneous presentation of the adaptation color the compensatory color was presented alternately to each eye (Fig 3a). At the end of the presentation of cycles of the adaptation and compensatory colors, we used a hue matching method to estimate the perceived hue of a test stimulus.

2.1. Method

2.1.1. Observers

Six observers (HN, KM, SI, JH, YM, and RM,) participated in the experiment. All had normal or corrected to normal visual acuity and normal color vision.

2.1.2. Stimuli and apparatus

The stimuli were generated with a personal computer (Macintosh II fx) and were displayed on a CRT screen (Apple Color High-Resolution RGB monitor). The red and green phosphors of the CRT were used to produce the color stimuli for adaptation but its blue phosphor was not. The yellow stimulus was generated by a mixture of the red and green phosphors. The CIE *xy* coordinates for the red stimulus was 0.63 and 0.34, the green stimulus was 0.27 and 0.60, and the yellow stimulus was 0.47 and 0.46. For each observer, the luminance of the green and the yellow stimuli was adjusted so as to be subjectively equal to the red stimulus at 19.4 cd/m^2 by using heterochromatic flicker photometry. Each color stimulus was viewed through a mirror stereoscope. The CRT screen was divided into two half-fields, with the right half-

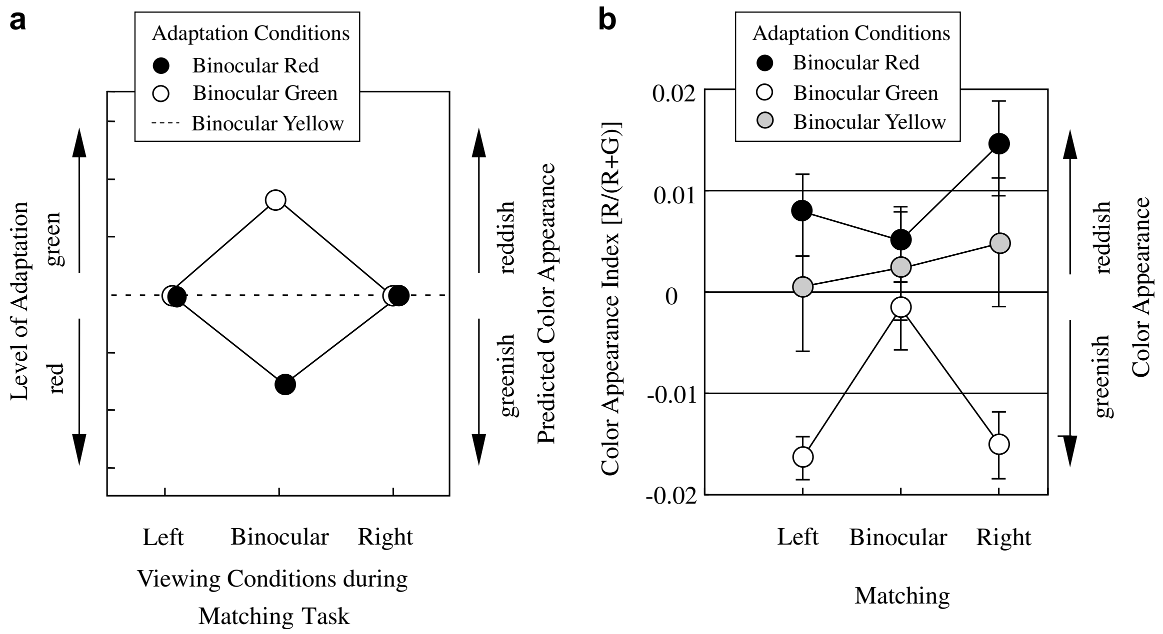

Fig. 2. (a) Schematic representation of color appearance of a test stimulus after adaptation, which is predicted from a model depicted in Fig. 1a. The solid and open circles indicate the predicted color appearance for the adaptation conditions with the binocular red and binocular green stimuli, respectively. (b) Mean of the color appearance index for each of the three matching conditions (left monocular, binocular, and right monocular). The solid, open, and gray circles indicate the results for the adaptation conditions with the binocular red, binocular green, and control yellow stimuli, respectively. The vertical lines attached to the data points indicate the standard errors. Please refer to the main text for the procedure to compute the color appearance index.

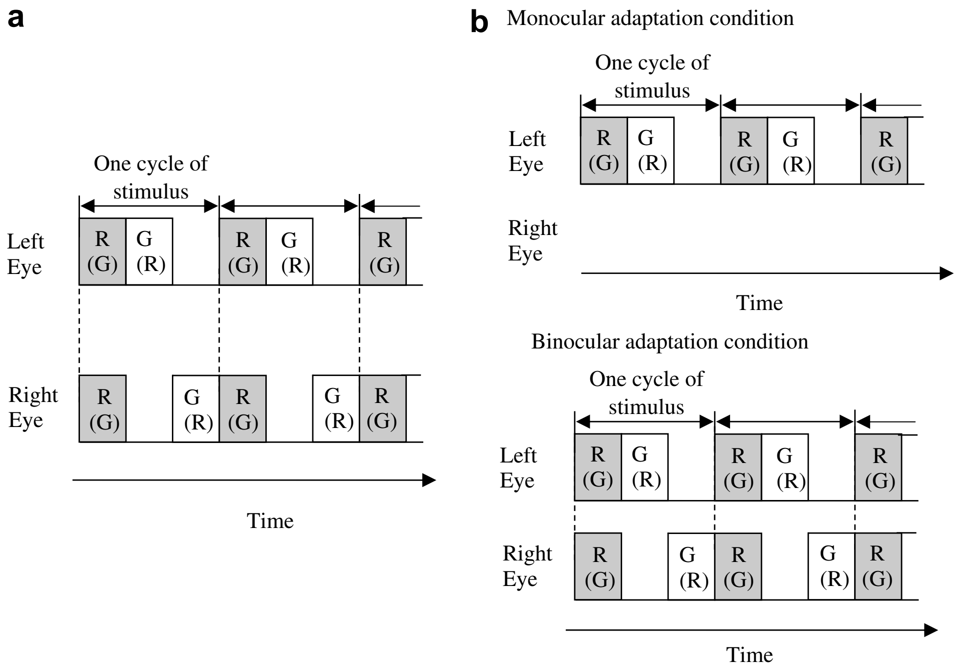

Fig. 3. Schematic representation of the stimulus presentation used in Experiment 1 (a) and that used in Experiment 2 (b). Each box represents the presentation of a color stimulus (R, red stimulus; G, green stimulus). Gray boxes indicate that the stimulus was presented to both eyes at the same time and open boxes indicate that the stimulus was presented to only one eye.

field visible to the right eye and the left half-field visible to the left eye. Each half-field was divided into upper and lower fields (2.0×2.0 degree of arc). The upper field was used to display the adaptation and test stimuli, and the lower field was used to display the matching stimulus so that observers could adjust it to the apparent hue of the test stimulus. We refer to the upper and lower fields as the test field and the matching field, respectively. When the color stimulus was shown in the test field during adaptation and matching, a yellow stimulus was presented in the matching field so that luminance adaptation was equated in the two fields. The vertical separation between the centers of the two fields was 4°. Optical distance from the eyes to the screen was 60 cm. Outside the stimulus field was blank in dark (<0.01 cd/m^2).

2.1.3. Procedure

After about 10 min of dark adaptation, observers undertook a session consisting of adaptation and matching periods. There were three adaptation conditions: with the binocular red stimulus, the binocular green stimulus and the binocular yellow stimulus that was used as a control condition. Only one of the three adaptation conditions was used in any given session. For the binocular red and green adaptation conditions, the adaptation color (either red or green) was presented to both eyes simultaneously for 1 s. Following the binocular stimulation, its compensatory color was presented alternately to the left eye and the right eye for 1 s (Fig. 3a). When one eye saw a compensatory stimulus, the other eye saw a blank field (no color stimulus). There were 90 cycles of the presentation of the color stimuli in the adaptation period, and it took 4.5 min in total to complete the cycles. In the control condition, the yellow stimulus instead of the red and green stimuli was presented in the same manner as in the red and green conditions. All the color stimuli were always on a dark blank screen (<0.01 cd/m^2).

Following a 0.5 s blank period after the adaptation, the matching period was initiated with a beep. During the blank period, the observer viewed the dark blank screen. In the matching period, the yellow stimulus was presented in the test field and a mixture of the red and green stimuli was presented in the matching field. Observers controlled the ratio of the red and green mixture in the matching field by manipulating a computer mouse, so that the hue in the matching field appeared to be the same as that in the test field. Observers clicked the mouse button when they were satisfied that they found a match. Observers were also asked to finish one match within 3 s. If the observer was unable to finish the match during the three-second interval, a top-up adaptation period was introduced. The top-up adaptation period consisted of two cycles of the presentation of the two color stimuli. Following a 0.5 s blank period after the top-up adaptation, observers continued their attempt to find a match. The matching was made three times for each of the three matching conditions, in which viewing was either left monocular, binocular, or right monocular. Thus, each observer made 9 matches within one matching period for a given session. [Note that our pilot experiment showed that the hue shift due to adaptation was approximately constant for the duration of the period in which the 10 matches were made, suggesting that the adaptation effect of the color stimulus can be constant throughout, at least, the set of ten matches.]

During matching, the luminance of the mixture in the matching field was maintained the same as that of the test field and the color changed between the red and green used during the adaptation. In that sense, the task was hue matching rather than color matching which includes the matching in saturation and lightness. The hue matching in the present experiment, however, was virtually identical to color matching because observers reported that the color of the test field and that of the matching field appeared to be the same including the lightness and the saturation when the criterion for a hue match was satisfied.

Three observers (HN, KM, and SI) completed four sessions for each of the three adaptation color conditions (binocular red, binocular green and binocular yellow) and the other three observers (JH, YM and RM) completed four sessions for each of the two adaptation color conditions (binocular red and binocular green). The order of the adaptation conditions was randomized among observers. In each session, there were three trials for each one of the three matching conditions (left monocular, binocular, and right monocular). The order of the three matching conditions in each session was randomized among observers. Usually observers were not aware of whether the matching was made with the right eye, the left eye or both eyes. There was an interval of at least two hours between sessions.

2.2. Results and discussion

As an index of color appearance, we used the ratio of luminance[3] of the red stimulus in the color mixture, which matched the test stimulus, to the total luminance of the mixture. To eliminate individual differences from the obtained data, the ratio was further subtracted from the index of color appearance without adaptation (that of the yellow stimulus). Thus, when the value is zero, it indicates no effect of adaptation. The difference in the ratio of luminance was calculated for each trial and was averaged for each observer. The averaged value of the difference was used for further analysis.

Fig. 2b shows the averaged difference of the six observers for either the binocular red adaptation or the binocular green adaptation and the averaged difference of the three observers for the binocular yellow control condition. As can be seen in Fig. 2b, the color appearance index between the binocular and monocular matching conditions differed from each other in both the binocular red adaptation condition and the binocular green adaptation condition. The color matched in the binocular condition had a larger value than that in the monocular condition after adaptation with the binocular green stimulus; the color matched in the binocular condition had smaller value than that in the monocular condition after adaptation with the binocular red stimulus. In contrast, in the binocular yellow condition the color appearance index was relatively constant among the three matching conditions. These results are consistent with the predictions from the model.

The results from a statistical analysis is also consistent with the predictions. A two-way ANOVA, [2 adaptation conditions (red and green) × 3 matching conditions (left monocular, binocular, and right monocular)] on the averaged values of the color appearance index, showed that the main effects of adaptation conditions and matching conditions and their interaction were statistically significant, $F(1,5) = 53.81$, $p < .001$, $F(2,10) = 4.31$, $p < .05$, and $F(2,10) = 59.72$, $p < .001$, respectively. Furthermore, a multiple-pairwise Tukey HSD test revealed that the color appearance index between the binocular matching condition and either monocular matching conditions was statistically significant ($p < .05$) for the binocular green adaptation case. As well, the difference in color appearance index between the binocular matching and the right monocular matching conditions was statistically significant ($p < .05$), although that between the binocular matching and the left monocular conditions was not ($p > .5$) for the binocular red adaptation case. These statistical results generally support the idea that the binocular AND system contributes to binocular color perception.

Nevertheless, there is a clear difference between the predicted results from our model (Fig. 2a) and the results obtained from the present experiment (Fig. 2b); the mean value of the color appearance index for the binocular red adaptation condition was larger than that for the binocular green adaptation condition (Fig. 2b) and the model predicted the opposite (Fig. 2a). It appears that the apparent difference between the predicted and the obtained results for the two adaptation conditions is mostly due to a shift of the color appearance in the monocular matching conditions, rather than a shift of the color appearance in the binocular matching condition. Specifically, the color matched under monocular viewing appears to have shifted towards the color of the binocular adaptation stimulus (Fig. 2b).

There are two possible explanations for the shifts of the color appearance in the monocular matching conditions. The first explanation is based upon the assumption that when the color stimulus is presented binocularly, the binocular AND system inhibits the activity of the monocular systems. This "inhibition" hypothesis predicts that in the adaptation condition with the binocular green stimulus, the color appearance of the test stimulus would be more greenish than that predicted without the inhibition in both the binocular matching and the monocular matching conditions. If the monocular system shows opponent responses and its activity is inhibited by the AND system from adaptation with a binocular green stimulus, the monocular system would be less adapted to the green than to the red. Thus, the color aftereffect in the monocular system would be in the green direction, and would shift the color appearance in that direction in the monocular matching conditions. Furthermore, the color aftereffect in the monocular system would shift the final color appearance toward the green direction even in the binocular matching condition, provided that averaging the color signals from the left monocular, the right monocular and the AND systems would determine the binocular color perception. Similarly, the inhibition hypothesis predicts that in the adaptation condition with the binocular red stimulus, the color appearance of the test stimulus would be more reddish than that predicted without the inhibition in all the matching conditions. The color aftereffect of the monocular system would be in the direction towards more red, which would shift the final color appearance in that direction in all matching conditions. In Experiment 2 we examined whether or not the activity of the binocular AND system can inhibit that of the monocular system.

The second explanation is based upon the assumption that the adaptation effect is mainly determined by the color stimulus presented right before the matching stimulus. In our procedure, the color stimulus that was presented right before the matching was green in the adaptation condition with the binocular red stimulus and red in the adaptation condition with the binocular green stimulus (Fig. 3a). If the color appearance of the test stimulus were affected mainly by the color stimulus presented right before matching, the color appearance of the test stimulus in the adaptation condition with the red stimulus would be more reddish than that with the green stimulus in any matching condition. Results of Experiment 2, described next, are not consistent with this explanation; they showed no systematic effect of the color stimulus presented right before the matching.

3. Experiment 2: Binocular AND system and the inhibition hypothesis

We modified our initial model depicted in Fig. 1a so that it can explain the results obtained in Experiment 1. Fig. 1b illustrates our modified model that contains a left monocular system, a right monocular system and a binocular AND system that is assumed to provide inhibitory inputs to the left and right monocular systems.

To verify the modified model (Fig. 1b), we compared the color aftereffect obtained in a condition in which a color stimulus (red or green) and its compensatory color stimulus (green or red) were presented alternately to the left eye (Fig. 3b1) against that in which a color stimulus (red or green) was presented to the two eyes simultaneously and its compensatory color stimulus (green or red) was presented only to the left eye (Fig. 3b2). If the activity of the binocular AND system inhibits that of the monocular system, the activity of the left monocular system in a condition in which the same color stimulus is presented to both eyes, would be less

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[3] In the scale of the ratio of the luminance, the color resolution of the system used in the present study was approximately 0.003, which was about one third of the standard deviation of the matching data.

than that in a condition in which the color stimulus is presented only to the left eye. Thus, the adaptation effect of the compensatory stimulus would be larger in the binocular adaptation condition than in the monocular adaptation condition. Consequently, when the color appearance of the compensatory stimulus is green, the appearance of the color seen in the left eye after adaptation would be more reddish for the binocular adaptation condition than for the monocular adaptation condition. Similarly, when the color of the compensatory stimulus is red, the appearance of the color after adaptation would be more greenish for the binocular adaptation condition than for the monocular adaptation condition (Fig. 4a).

3.1. Method

3.1.1. Observers

Six observers (JH, RM, and HN from Experiment 1, and TM, HNN, and YK) participated in this experiment. All six observers had normal or corrected to normal visual acuity and normal color vision.

3.1.2. Stimuli and apparatus

The stimuli and apparatus for the three observers (TM, HNN, and YK) were generated with a personal computer (Apple iBook) and were displayed on a CRT screen (Sony G520). As in Experiment 1, the red and green phosphors of the CRT were used but its blue phosphor was not to produce the color stimuli for adaptation. The CIE *xy* coordinates for the red stimulus was 0.63 and 0.34, the green stimulus was 0.32 and 0.36. We used unique yellow for these three observers as the yellow stimulus instead of a fixed color. For each observer, the luminance of the green and the yellow stimuli was adjusted so as to be subjectively equal to the red stimulus at 19.3 cd/m^2 by using heterochromatic flicker photometry. The stimuli and apparatus for the other three observers (JH, RH, and HN) were those used in Experiment 1. Stimulus presentation in this experiment was the same as that used in Experiment 1 except for the changes required for the adaptation conditions for this experiment.

3.1.3. Procedure

The procedure was similar to that used in Experiment 1. After about 10 minutes of dark adaptation, observers undertook a session consisting of periods of adaptation and matching. For adaptation, there were two monocular and two binocular adaptation conditions. Adaptation consisted of presentation of either the red stimulus or the green stimulus first. Specifically, in the red–green (green–red) monocular adaptation condition, the red (green) stimulus was presented first for 1 s to the left eye, followed by the green (red) stimulus presented for 1 s to the same eye (Fig. 3b1). The presentations were repeated with a blank field (no color stimulus) between presentations such that the period of one cycle was the same as that in Experiment 1. For the red–green (green–red) binocular adaptation condition, the red (green) stimulus was presented to both eyes for 1 s simultaneously, followed by the green (red) stimulus presented for 1 s only to the left eye and the blank field presented for 1 s to both eyes (Fig. 3b2). In the adaptation period, there were 90 cycles of the presentation of the two colors and the blank field, which took a total of 4.5 min to complete.

After the adaptation, there was a blank (no color stimulus) of 0.5 s followed by a beep that indicated the start of the matching period. The observer's task was the same as in Experiment 1, but the matching task was carried out only with the left eye. Three observers (JH, RM, and HN) from Experiment 1 and three new observers (TM, HNN, and YK) participated in two and three sessions, respectively, for each of the four conditions (two adaptation color conditions and two adaptation ocularity conditions). There were six matches in each session, with an interval of at least two hours between sessions. The order of the conditions was randomized for each observer.

3.2. Results and discussion

As in Experiment 1, we used the difference in the ratio of the luminance in the red stimulus between the matched color and the yellow stimulus as an index of the color appearance. [The yellow stimulus was the fixed color with *xy* coordinate of 0.47 and

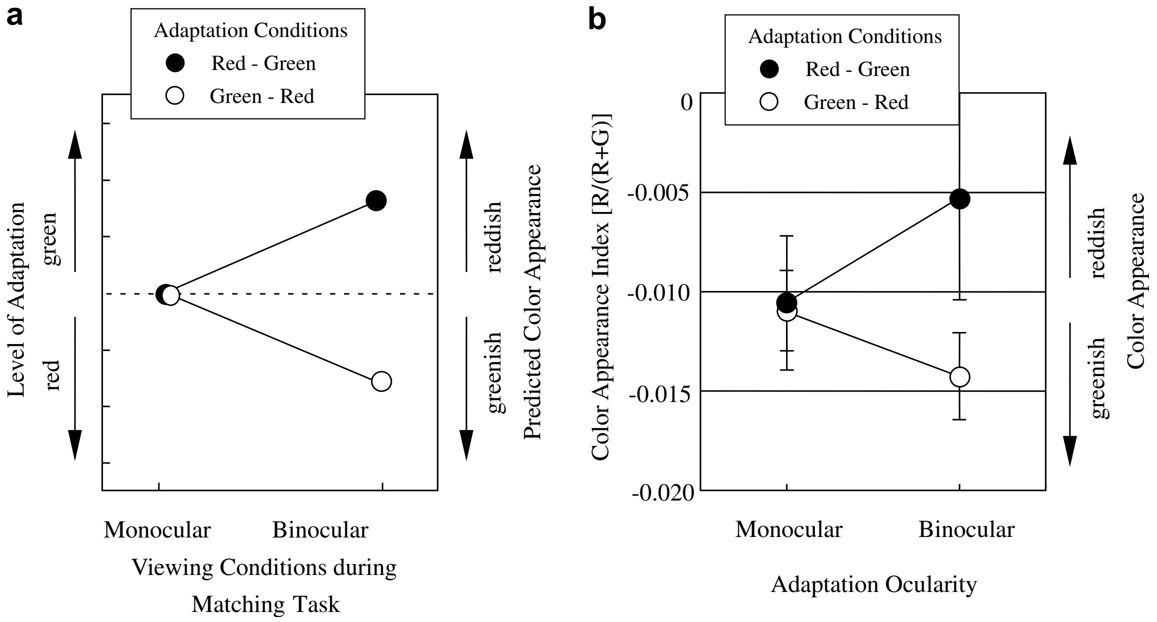

Fig. 4. (a) Schematic representation of color appearance of a test stimulus after adaptation, which is predicted from a modified model depicted in Fig. 1b. The solid and open circles indicate the predicted color appearance in the red–green and green–red adaptation conditions, respectively. (b) Mean of the color appearance index for each of the two adaptation ocularity conditions (monocular adaptation and binocular adaptation). The solid and open circles indicate the results in the red–green and green–red adaptation conditions, respectively. The vertical lines attached to the data points indicate the standard errors. Please refer to the main text for the procedure to compute the color appearance index.

0.46 for the three observers (JH, RH, and HN) and the unique yellow measured individually for the other three observers (TM, HNN, and YK).] The difference in the ratio of luminance was calculated for each trial and was averaged for each observer. The average difference was used for further analysis. Fig. 4b shows the mean based on the average of the six observers.[4]

As can be seen in Fig. 4b, the mean value of the color appearance index in the binocular adaptation case differed between the two adaptation color (red–green and green–red) conditions while that in the monocular adaptation case is almost the same; the mean value of the color appearance index for the binocular adaptation case is larger than that for the monocular adaptation case in the red–green adaptation condition and the mean value for the binocular adaptation case is smaller than that for the monocular adaptation case in the green–red adaptation condition. This pattern of results is consistent with the prediction from the inhibition hypothesis, depicted in Fig. 4a.

Further, the results of a statistical analysis are also consistent with predictions. A two-way ANOVA [2 adaptation color (red–green and green–red) × 2 adaptation ocularity (monocular and binocular)] was performed on the color appearance index. An analysis of the simple main effect revealed that (a) the difference in the color appearance index between the red–green and green–red conditions was significantly different for binocular adaptation, $F(1,10) = 10.21$, $p < .01$ but not for monocular adaptation, $F(1,10) = 0.02$, $p > .05$, and (b) the difference in the color appearance index between monocular adaptation and binocular adaptation was significantly different in the red–green adaptation condition, $F(1,10) = 5.30$, $p < .05$, but not in the green–red adaptation condition, $F(1,10) = 2.05$, $p > .05$. The significant difference in binocular adaptation between the two adaptation color conditions is consistent with the expectations from the inhibition hypothesis, although the color appearance index in the binocular adaptation is not always significantly different from that in the monocular adaptation. The present result, in general, supports the idea that an inhibitory binocular AND system contributes to binocular color perception.

As mentioned in the discussion of the results of Experiment 1, the present results are not consistent with the notion that the color presented right before the matching task determines the final matched color appearance. If this were the case, the color appearance of the test stimulus in the red–green adaptation condition should be more reddish than that in the green–red adaptation condition for each of the binocular and monocular adaptation cases. This is so, because the color presented right before the matching task was green in the red–green adaptation condition and was red in the green–red adaptation condition. However, as can be seen in Fig. 4b, there is no such difference in the color appearance index for the monocular adaptation between the two adaptation color conditions. The color presented right before the monocular matching task seems to have no systematic effect on the final color percept in the monocular matching condition. Thus, it is difficult to attribute the difference in the color appearance index in the monocular matching task between the two binocular adaptation conditions in Experiment 1 to any effect of the color presented right before the matching task.

4. General discussion

The results of the two experiments support the idea that when the same color is presented to both eyes simultaneously, perceived color is mediated through a purely binocular color system that inhibits the activity of the monocular color systems. Experiment 1 showed that after the hypothesized binocular system (but not the hypothesized monocular systems) were selectively adapted by a red or green stimulus, the perceived color of a test stimulus viewed with both eyes shifted more to that of the compensatory color (green or red) than that viewed with one eye. Experiment 2 showed that the perceived color of a test stimulus viewed with one eye (the left eye) shifted in the direction that is opposite to the monocular adaptation color after adaptation to an alternation of a red (or green) monocular (the left eye) adaptation and green (or red) binocular adaptation. These results are consistent with the predictions from our model of an inhibitory binocular AND system, and a left and a right monocular system (Fig. 1b).

Are the results of Vimal and Shevell (1987) consistent with predictions from our model? They have reported that the adaptation effect in a binocular viewing condition was larger than that of either the right or left monocular viewing condition in Experiment 1, in which the adaptation effect was measured with both eyes. According to our model, both the binocular and monocular systems were involved during binocular adaptation, only the monocular systems were adapted in the monocular viewing conditions, and the binocular and monocular systems were involved in the binocularly test in their Experiment 1. Thus, if we do not consider the inhibition of the monocular systems by the binocular system, the total activity in the binocular viewing is more than that of either of the left monocular or the right monocular viewing conditions. Our model predicts a larger adaptation effect in the binocular adaptation condition, which is consistent with their results. Even when we consider the effect of inhibition, a larger effect of binocular adaptation is predicted as long as the inhibitory effect is smaller than the additional effect of the binocular system. Vimal and Shevell (1987) have also reported that in Experiment 2, the amount of the adaptation effect with both eyes was not larger than that measured with either the left or the right eye. This result can be explained by our model by assuming that the final percept during binocular viewing is determined by the average of the signals from the binocular system and those from the left and right monocular systems, which have inhibitory inputs from the binocular system. Our model, therefore, can explain the results of Vimal and Shevell (1987), although there may be other models that can also do.

A binocular system with inhibition has also been proposed by Erkelens and van Ee (2002) to explain a phenomenon they found (binocular color induction). They found that when a chromatic stimulus having a small monocular gray patch is presented to one eye and a stimulus with a different hue is presented to the other eye, the color appearance of the monocular patch shifts to that of the other eye's stimulus. They propose a binocular system, which acts as if it reduces differences between the color appearances of the two monocular views, and the system can explain the results of Experiment 1 of Vimal and Shevell (1987). However, it is difficult for their color induction system to explain our results. Because their system reduces color differences, it should not be active during binocular stimulation with the same color in the two eyes as in our stimulus. On the contrary, our binocular AND system, if it can operate locally, predicts binocular color induction but in the opposite direction to what Erkelens and van Ee (2002) reported. If the AND system mixes the hues of the right and left eyes (say, red and gray in a monocular region) and inhibit the monocular systems, the monocular gray will become greenish because of inhibition of the desaturated red. Thus, either their model or

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[4] Fig. 4b also shows that the color appearance index has a negative value for each of the four conditions (two adaptation color and two adaptation ocularity), indicating that the color appearance of the matched stimulus shifted to be more greenish than that of the yellow stimulus in all the conditions in Experiment 2. We do not know yet what caused the shift of the color appearance. However, the relative value (or the difference) in the color appearance index is more important than its absolute value to examine the prediction from the inhibition hypothesis. Thus, we discuss the difference hereafter in the text.

ours have difficulty in explaining all the experimental results. This problem may be solved if one assumes a two-stage model of color processing as proposed by Erkelens and van Ee (2002): the first stage processing the binocular color induction and the second processing the binocular color mixture. The processing of the second stage can be regarded as a binocular AND gate, which is broadly consistent with the idea of a binocular AND system.

The multi-stage model is worth further discussion. In the literature, several different types of binocular interaction have been reported in color vision (e.g., Medina, 2006; Shevell & Wei, 2000; Simmons, 2005). Simmons (2005) reported that the binocular chromatic-contrast threshold is lower than the monocular chromatic-contrast threshold, and suggested that there is linear summation of chromatic-contrast between the two eyes at threshold condition. Medina (2006) argued, based on reaction time data to changes in color appearance at isoluminance, that there are binocular excitatory and inhibitory interactions at suprathreshold conditions. Furthermore, Shevell and Wei (2000) reported that the color appearance of a stimulus surrounded by chromatic stimuli with different hues in one eye can be altered by introducing chromatic variation of a remote region outside the surrounding color stimulus in the other eye; they proposed a binocular system of chromatic-contrast gain control, which regulates a neural representation of chromatic-contrast at edges. These psychophysical studies suggest that binocular color vision can be mediated through several binocular systems, potentially in multiple stages. How these binocular color systems co-work in the multiple stages is to be determined, and a binocular inhibitory AND system should be taken into account as one of important components of the stages.

What role, then, a binocular inhibitory AND system would play in the multiple stages? Its possible role is to reduce the differences in ocular medias and/or adaptation states. When the same color is seen by the two eyes with different optical medias or it is seen after the eyes are differentially adapted, the AND system would inhibit the outputs of the monocular systems so that the difference between the two eyes may be eliminated or at least become smaller. That is, the AND system may control the monocular outputs to be relatively constant at the stage in which outputs from the monocular systems and the AND system are combined, irrespective of differences in ocular medias and/or adaptation states. Furthermore, the AND system may also make it easier for color images seen by eyes, with differences in ocular medias and/or adaptation states, to be fused.

Neurophysiologically, however, cortical neurons which respond only to simultaneous binocular inputs (exclusively binocular neurons) have been reported less commonly (e.g., Timney, Wilcox, & St. John, 1989). In color vision, Peirce, Solomon, Forte, and Lennie (2008) found that in early visual cortex (V1 or V2), binocular color-specific neurons, which respond well to uniform isoluminance color fields, are well-matched in their color preferences. While these neurons can be a “candidate” for the binocular inhibitory AND system, the neurons “can very often be driven by either eye” (Peirce et al., 2008, p. 8). That is, they act as if they were binocular OR gate. Provided that the activity of the neurons in the early visual cortex correlates with the final percept, the property of the color-specific neurons is inconsistent with the psychophysical fact that there is no interocular transfer in “non-contingent” color aftereffect. One interpretation is that “awareness” of color aftereffect is not determined only by the neural activity in the early visual cortex. Meanwhile, in a study on binocular rivalry (Logothetis, 1998), it has been reported that the neurons affected by suppression are almost exclusively binocular in V2, V4, V5, TPO, TEm, and TEa, and their population increases as processing stages of the visual system becomes higher. Erkelens and van Ee (2002) have argued that the binocular rivalry occurs at the level of binocular color mixing based on their psychophysical study and Logothetis’, 1998 physiological study. If they are right and if the phenomenon reported in the present study is mediated at the same level of binocular mixture, then the binocular inhibitory AND system is implemented at V2 or higher.

In conclusion, we found that a binocular color stimulus selectively influences binocular vision, which suggests the existence of a pure binocular color system in the visual system. We also showed experimental results that suggest that the pure binocular color system inhibits the activity of monocular color systems.

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