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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.

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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 interocularly¹. 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).

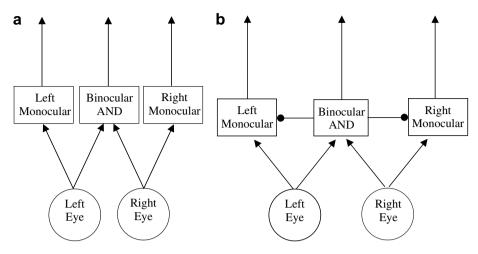


Fig. 1. Schematic representation of a model based on the logical gate theory for color perception (a) and that of its modification (b). In (a), binocular color perception is assumed to be mediated via two monocular (right and left) systems and a binocular AND system. In (b), binocular color perception 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 conditions² (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

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.

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