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Color-specific depth mechanisms revealed by a color-contingent depth aftereffect

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Abstract

Models of stereoscopic depth perception for both natural and random-dot images have focused mainly on the matching of achromatic features of binocular images. Recently, a growing body of research has investigated whether chromatic features can also contribute to the construction of stereoscopic depth. Here we present experiments yielding color-contingent depth aftereffects comparable in magnitude to those measured after adaptation to achromatic stimuli as evidence of neural mechanisms tuned to both color and depth. Furthermore, we report that the locus of the combined processing of color and depth is likely to lie beyond the site of binocular matching. © 1999 Published by Elsevier Science Ltd. All rights reserved.

Keywords: Adaptation; Aftereffect; Color; Depth perception

1. Introduction

Human vision depends on the existence of mechanisms sensitive not only to particular features of visual stimuli, such as color, depth, orientation, or motion, but also to the conjunction of such features. Some of the most compelling psychophysical evidence for such conjunctive mechanisms comes from studies based on selective adaptation, for example orientation-contingent color aftereffects (McCollough, 1965), color-contingent motion aftereffects (Favreau, Emerson & Corballis, 1972) and depth-contingent motion aftereffects (Regan & Beverley, 1972; Anstis & Harris, 1974). In the McCollough effect (McCollough, 1965), for example, after adaptation to, say, alternating red and black vertical stripes and alternating green and black horizontal stripes, the white stripes in a subsequently viewed black-and-white, striped pattern appear to be tinged green if the pattern is viewed vertically and appear to be tinged red if viewed horizontally. Here we report that simultaneous adaptation to different depth planes, each composed of dots of a single chromaticity, either red or green, results in a modification of depth perception, linked to chromaticity, in subsequently viewed stimuli. We argue that this 'color-contingent depth aftereffect' reveals depth mechanisms specific to chromaticity.

Models of stereoscopic depth perception for both natural (Wheatstone, 1838) and random-dot images (Julesz, 1971) have focused mainly on the matching of achromatic features of binocular images. Recently, a growing body of research has investigated whether chromatic features can also contribute to the construction of stereoscopic depth (Lu & Fender, 1972; Nakayama & Silverman, 1986; Tyler & Cavanagh, 1991; Simmons & Kingdom, 1994; Chau & Yei-Yu, 1995). Depth mechanisms can be identified by using adaptation (Blakemore & Julesz, 1971; Long & Over, 1973). Indeed, it has been previously established that adaptation to an achromatic surface lying in depth

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produces an aftereffect: After adaptation, a test stimulus lying in the fixation plane is perceived to be located not at the fixation plane but either nearer or farther in depth, the reverse of the perceived depth of the adapting stimulus (Blakemore & Julesz, 1971). In a similar fashion, we reasoned that if depth segregation is aided by multiple, independent, color channels (Akerstrom & Todd, 1988), then two overlapping, transparent surfaces of different chromaticities should selectively stimulate near depth mechanisms in one color-coded channel and far depth mechanisms in the other. Furthermore, it should be possible to selectively reduce the sensitivity of these chromaticity-specific depth mechanisms by means of prolonged exposure to such surfaces. Accordingly, we predicted that adaptation to a surface of a particular chromaticity seen as lying in front of the fixation plane should tend to influence the perceived depth of a similar surface in a subsequent test to appear 'pushed back' relative to the fixation plane, whereas adaptation to a surface of that chromaticity seen as lying behind the fixation plane should have the opposite effect (Fig. 1).

2. Methods

In order to test our hypothesis, novel stimuli were designed that (1) required the merging of information from the two eyes in order to make depth judgments possible and (2) minimized achromatic cues as to the distribution of chromatic features. The first requirement was satisfied by using random-dot stereograms (Julesz, 1971). The second requirement was met by creating a stimulus in which the distribution of chromatic features in depth could be manipulated without significant change to the distribution of achromatic features in depth. Accordingly, stimuli were composed of red and green dots with one gaussian distribution in depth for the red dots and a different but overlapping second gaussian distribution in depth for the green dots (Fig. 2). The red and green dots were matched in luminance using the method of heterochromatic flicker photometry. As Fig. 2 illustrates, stimulus elements fall into two distinct, overlapping depth distributions on the basis of chromaticity and a single unimodal, symmetric distribution on the basis of luminance. Hence chromaticity was potentially useful to discriminate depth but the achromatic information, luminance, was uninformative.

2.1. Observers

Four color normal observers, with normal or corrected to normal vision, participated in these experiments. Of the four observers, two were naïve and two were authors. Informed consent was obtained prior to participation.

2.2. Stimuli, apparatus and procedure

The stimuli were presented on a high-resolution color monitor (1280 × 1024 addressable locations), under the control of a Silicon Graphics Indigo 2 workstation. The screen had a 120 Hz refresh rate. The stimuli were presented stereoscopically by using LCD (liquid crystal) shuttered glasses that were synchronized with the monitor refresh rate. When, say, the right eye was occluded by the glasses and the left eye was not, the left image was presented on the screen. Therefore, the refresh rate of the stereo image was 60 Hz. The observer sat at 53 cm from the screen. The basic stimulus consisted of 1600 high luminance random dots on a low luminance background and each dot subtended 1.73 arcmin of visual angle. 800 dots were red and 800 dots were green. Luminosity matches for red (approximately 2.08 cd m^{-2}) and green (approximately 2.01 cd m^{-2}) were obtained with a minimum flicker technique. Although the glasses may not be completely reliable for higher luminances, for these levels of luminance the shuttered glasses completely occluded the green as well as the red dots when the polarized lens was in the off setting. The disparity of each dot was randomly selected in order to obtain two overlapping distributions in depth of red and green dots (see Fig. 2). The standard deviation of the red and green dot distributions was kept constant (1.73 arcmin), whereas location in depth was varied by adjusting the means of the distributions. The achromatic distribution, defined as the distribution of all red and green dots, was a unimodal distribution whose mean did not change when the means of the red and green distributions were varied. Fused stimuli subtended 11.5 × 11.5 degrees of visual angle and they appeared to observers as two intermingled distributions of dots, typically with one distribution appearing slightly closer (i.e. 'in front').

The separations between the means of the two distributions, determined in a pilot experiment, (GIF as positive and RIF as negative values) were −1.38, −0.92, −0.46, 0, 0.46, 0.92, 1.38 for observers C.F., S.H., F.D. in experiment 1 and for observer E.B. in experiments 1 and 2, and −2.07, −1.38, −0.69, 0, 0.69, 1.38, 2.07 arcmin for observers C.F., S.H., F.D. in experiment 2.

Each experimental session consisted of a block of pre-adaptation test trials, followed by a block of adaptation trials, and ending with a block of post-adaptation test trials. During test trials, observers indicated which distribution of dots, red or green, was in front. During adaptation trials, observers viewed distributions whose means were separated by 9.5 arcmin or 8.5 arcmin (forming two distinct distributions of points, both chromatically and achromatically) and were asked to classify stimuli into 'large separation' or 'small separation.' This classification task was designed to ensure
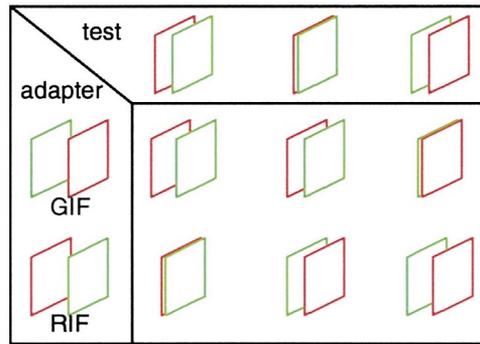
Fig. 1. Predicted depth relationships after adaptation. Schematic description of the predictions made by a model that assumes the existence of color-specific mechanisms for stereoscopic depth perception. Predicted perceived depth relationships are shown, after exposure to green-in-front (GIF) and red-in-front (RIF) adapting stimuli, for three types of test stimuli: GIF, no difference, and RIF.

that the observers were attending to the depth information during adaptation. During both adaptation and test, fixation was not controlled — observers freely viewed the stimuli. There were 160 trials in adaptation blocks, with each trial lasting 1000 ms; and there were 91 trials in test blocks, each lasting 1000 ms. Each
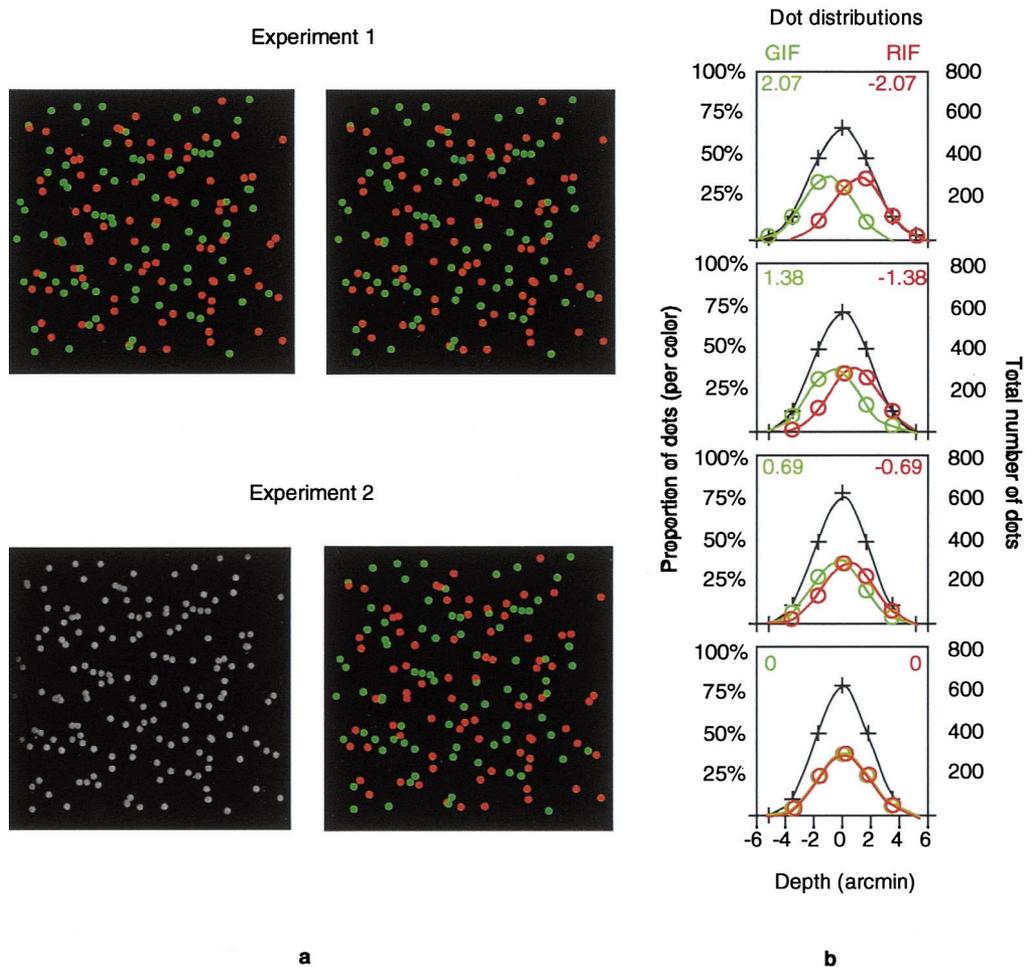
Fig. 2. Description of stimuli. (a) A representation of the random-dot stimuli used in experiment 1 (top stereogram) and experiment 2 (bottom stereogram). Actual stimuli differed in size, dot density, and chromaticity. (b) Distributions of dots in depth. Red and green circles indicate, respectively, the proportions of red and green dots per depth plane (left *y*-axis) and the number of dots per depth plane (right *y*-axis). Red and green curves illustrate the gaussian distribution of dots in depth. Black crosses indicate the total number of dots (without respect to chromaticity) at each depth plane. The black curve illustrates the unimodal property of this distribution. Separations, in arcmin, are indicated on the *x*-axis for both RIF and GIF test stimuli.
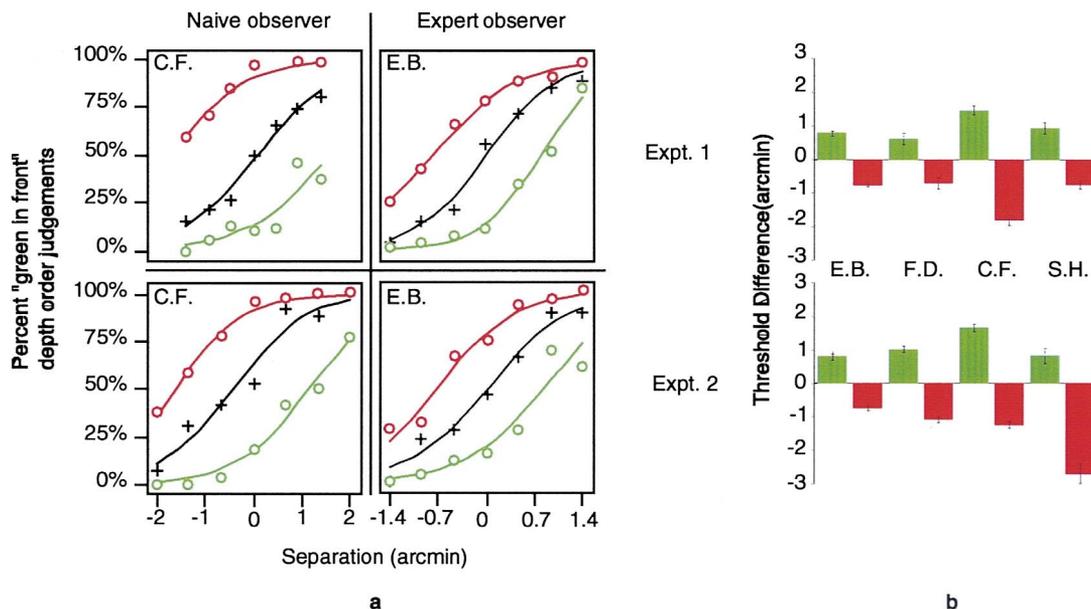
Fig. 3. Results. (a) Psychometric functions for experiments 1 and 2 for an expert and naive observer. Percent 'green-in-front' depth-order judgments vs. the difference between the means of the green and red dot distributions ('separation') are plotted (40 observations per datum point). The curves drawn through the data are the best-fitting cumulative normal functions. After RIF adaptation (red circles), psychometric functions shifted leftward with respect to pre-adaptation (black crosses), indicating that the threshold for responding 'green-in-front' decreased. Complementarily, after GIF adaptation (green circles), psychometric functions shifted rightward, indicating that the threshold for responding 'green-in-front' increased. (b) Summary of the adaptation effect sizes for all observers. Adaptation effects were determined by the difference between post- and pre-adaptation thresholds in the GIF condition (green boxes) and RIF condition (red boxes). Error bars indicate 95% confidence intervals.

session consisted of a block of pre-adaptation test trials followed by two additional blocks of adaptation/test pairs.

3. Results

As illustrated in Fig. 3, when observers adapted to a green-in-front (GIF) stimulus, there was a subsequent bias to see the red distribution as lying nearer as compared to pre-adaptation values. Similarly, when observers adapted to a red-in-front (RIF) stimulus, there was a subsequent bias to see the green distribution as lying nearer. The magnitudes of the aftereffects in experiment 1 are comparable to those measured with achromatic stimuli (Long & Over, 1973).

If small luminance artifacts remained in the adapting stimuli, then dots of one chromaticity may be perceived as brighter or dimmer than those of the other. This is unlikely to be the basis of our results because luminance was equated separately for each observer by flicker photometry. Nonetheless, we ran an additional control experiment in which luminance was decorrelated from color and depth. To accomplish this, in the adapting stimulus the luminance of the red dots was chosen randomly as greater than or less than the luminance of the green dots. Hence, the observer saw what appeared to be the brighter distribution as nearer on

half the trials and farther on the other half, but chromaticity remained consistently linked to near or far depth. If the adaptation effects found in experiment 1 had been luminance-based, then the effects should disappear; instead the results of this control experiment were indistinguishable from those of experiment 1.

These results are compatible with the hypothesis that separate color-specific depth mechanisms exist. The locus of the effect, however, remains unspecified. Can the same results be obtained with a stimulus whose chromatic properties are not available to binocular matching processes? Indeed, previous experiments suggest that higher level mechanisms are likely to be involved in stereoscopic depth aftereffects for achromatic stimuli (Rogers & Graham, 1984). Experiment 2 was designed to test whether depth aftereffects linked to chromaticity, like the ones found in experiment 1, could be obtained by adapting only higher-level mechanisms, beyond binocular matching. We used a display, for both adaptation and test stimuli, in which the monocular images were matched in luminance contrast but not in chromaticity (Fig. 2). The display was identical to that in the previous experiment, except that one eye's image was achromatic, while the other eye's image contained chromatic information. Thus, the information provided by chromaticity could not be used during the stereo matching process. Nevertheless, observers easily fused the two images, although the colors in the

fused image appeared desaturated (Hering, 1861) as compared with the fused images of experiment 1. Additionally, during post-adaptation testing the achromatic stimulus was presented to the opposite eye so that the eye viewing the chromatically differentiated test had viewed an adapting stimulus devoid of chromatic information and vice versa. Thus, the chromatic information in the adapting stimulus, carried by one monocular stream, and the chromatic information in the test stimulus, carried by the other monocular stream, must combine at a point beyond binocular matching to produce any adaptation effect. Each of the same four observers from experiment 1 shows a clear effect of adaptation in experiment 2, and the magnitudes of biases in perceived depth due to adaptation are indistinguishable from those of experiment 1 (Fig. 3).

4. Discussion

The search for mechanisms that combine different signals is important for understanding how the visual system uses different sources of information to solve perceptual problems. Motion mechanisms and stereo mechanisms, for example, contribute at some stage to the process involved in depth perception (Nawrot & Blake, 1989). But why should color be involved in depth perception? Indeed previous attempts to demonstrate color-contingent depth aftereffects have failed. In fact, Over, Long and Lovegrove (1973) failed to find any chromatic influence on binocular depth aftereffects and therefore concluded that binocularly-driven spatial detectors in human vision are insensitive to chromaticity. This apparent inconsistency between their results and ours may be explained by the substantial differences between our stimuli and Over's stimuli. These differences can be summarized as follow: (1) their adapting stimulus was a central square at a different depth from a background; we used two transparent layers. (2) Over's adapting and test stimuli were uniformly colored, e.g. the chromaticity of a central square was the same as the chromaticity of the background; our adapting and test stimuli contained both chromaticities. It is important to note that color played a fundamental role in defining the depth segregation of the two transparent layers in our stimuli, whereas color did not add useful information that could be used by the perceptual system to segregate the central square from the background in Over et al.'s stimuli. Indeed, when disparity differences between two achromatic transparent surfaces are increased, it becomes more difficult for human observers to see depth transparency. However, there is empirical evidence that when chromaticity is added to luminance-based stereoscopic stimuli, the perceptual segregation of two overlapping transparent surfaces is enhanced (Akerstrom & Todd,

1988). This finding suggests either that (1) stereo matching of features is facilitated by adding color information, with color reducing the possible matches or (2) color may be used as a cue for 3D object segmentation. Either hypothesis would imply the existence of visual pathways where depth and color are processed together. In this case it would be reasonable to consider that there may be multiple color channels involved in stereopsis (Blakemore & Julesz, 1971). The goal of the present research was to provide evidence for such color-specific depth mechanisms.

Our results, based on selective adaptation, provide compelling evidence for color-specific depth mechanisms. However, the results of experiment 1 do not specify the locus of adaptation. The failure to find interocular transfer for the McCollough effect, for example, has been attributed to the fact that it involves only monocular mechanisms. Mackay and Mackay (1975), however, found that when one eye is stimulated with the achromatic pattern and the other eye is stimulated with an unpatterned red or green field the McCollough effect can be reproduced. Moreover, the sign of the effect is the same as McCollough's only when the eye that sees the colored field is tested. This suggests the involvement of binocular mechanisms, as has been confirmed by Vidiasagar (1976) who found evidence for separate monocular and binocular McCullough effects. Other researchers have found that the color-contingent motion aftereffect is the byproduct of a monocular color mechanism and a binocular motion mechanism (Murch, 1974; Potts & Harris, 1979). To investigate whether the nature of the color-contingent depth aftereffect found in experiment 1 of the present study is purely binocular we designed an additional experiment in which only one eye was exposed to the chromatic information during adaptation and only the opposite eye was exposed to chromatic information during test: The results of experiment 2 indicate that the locus of the effect lies beyond binocular matching. The fact that the magnitude of the effect in experiment 2 is the same as in experiment 1 suggests that the color-contingent aftereffect is not linked to the adapted eye. The finding that the results of experiment 1 and 2 are comparable is consistent with the idea that in our experiments color is linked to depth information at a point beyond binocular matching. Certainly, it appears that for the stimuli of experiment 2, matching of left and right eye images is carried out mainly on the basis of luminance information. Nonetheless, the adaptation effect in experiment 2 is clearly linked to color.

These findings are consistent with the proposal that color may constitute important information for object segregation in 3D space at higher levels of visual processing. In line with this idea, a recent study showed that visual search can be facilitated when the target is defined by both color and depth, even if only depth

information is sufficient to identify the target among the distractors (Chau & Yei-Yu, 1995). We suggest that the results of the present study provide even more compelling evidence that color and depth may be processed together at a higher site.

Furthermore, the results of experiment 2 suggest that the putative neural stream processing combined chromatic and depth information, although sensitive to hue, may be blind to saturation, which was substantially reduced in experiment 2 as compared with experiment 1. If so, then the site of combination of chromatic and depth information is likely to lie beyond V1 (Derrington, Krauskopf & Lennie, 1985) and may involve processing independent of or beyond any human homologue (Howard, Ffytche, Barnes, McKeefry, Ha, Woodruff et al., 1998; McKeefry & Zeki, 1997) of a structure such as V4 which is believed to be sensitive to hue and saturation on the basis of neurophysiological (Zeki, 1977) and post-ablation behavioral testing (Heywood & Cowey, 1987).

Finally, an intriguing speculation, which we are currently investigating, is that this color-contingent depth effect is just one of many feature-contingent depth effects. If this turns out to be the case, then a model in which particular features serve to distinguish depth levels as separate 'objects' becomes plausible. Such a model is reminiscent of recent proposals of salience-based mechanisms (Koch & Ullman, 1985; Lu & Sperling, 1995) to account for interattribute (Cavanagh, Arguin & von Grunau, 1989), alternating-feature, and attention-generated motion (Cavanagh, 1992; Lu & Sperling, 1995; Blaser, Sperling & Lu, in press), where higher-level representations are abstracted from those based on particular features.

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