INTEROCULAR TRANSFER OF A CHROMATIC FREQUENCY SHIFT

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Abstract—Interocular transfer of a spatial frequency shift was obtained with equiluminous color gratings. Gratings which combined both color and luminance contrast yielded small aftereffects and no interocular transfer. Recent electrophysiological work has uncovered color-sensitive binocularly driven cells in visual cortex. These cells are transient and often respond to color contrast in the absence of luminance contrast. The stimulus parameters associated with successful interocular transfer, equiluminous colors and brief test, matched the properties of these cells. Previous failure to induce interocular transfer of color effects may be explained by inappropriate stimulus parameters.

Color vision   Spatial frequency   Interocular transfer

INTRODUCTION

When an effect of visual adaptation that has been induced by monocular inspection can be seen by the nonexposed eye, it is inferred that the units which mediate the transfer receive input from both eyes. Recently Blake *et al.* (1981) pointed out that assumptions of this kind have never been directly tested. Usually an effect that shows interocular transfer is weaker in the unadapted eye than in the adapted eye, and it has been assumed that the greater strength in the adapted eye implies that in this eye the effect is mediated by both monocular and binocular units, whereas the weaker effect in the unadapted eye reflects the involvement of binocular units only. Blake *et al.* (1981) found evidence to support this view. They also pointed out that absence of interocular transfer does not necessarily imply that the effect is mediated uniquely by monocular units but that other conditions, such as the postadaptation state of responsiveness, may come into play.

Many negative aftereffects of visual adaptation transfer interocularly. Wohlgemuth (1911) showed this to be true for the motion aftereffect, Gibson (1933) for curvature, Köhler and Wallach (1944) for size, Blakemore and Campbell (1969) for spatial frequency, and Ware and Mitchell (1974) for orientation. All of these effects were based on stimuli whose contours were defined by luminance contrast alone.

Color-related aftereffects, by contrast, constitute a class of aftereffects for which direct interocular transfer has not previously been successful. For example, Lovegrove *et al.* (1972) reported that the color specificity of the motion aftereffect does not transfer from the adapted to the unadapted eye. Similarly, contingent aftereffects that involve color do not show straightforward interocular transfer (McCollough, 1965;

Hepler, 1968; Kavadellas and Held, 1977; Murch, 1972; Stromeyer and Mansfield, 1970).

Coltheart (1973), noting the repeated failures to obtain interocular transfer of color-related effects, pointed out that all of the color-coded cortical cells identified by Hubel and Wiesel (1968) were predominantly monocularly driven. If color cells are indeed driven by only one eye, then that could explain why color-related effects do not transfer from one eye to the other.

More recent psychophysical research has provided some evidence which indicates that there can be some degree of interaction of chromatic information from both eyes. For example, if an observer looks at inducing stimulus gratings with one eye while the other eye is exposed to a homogeneous field of the same color, then the effect will transfer (Murch, 1974; White *et al.*, 1978). Vidyasagar (1976) has shown that one contingency for the McCollough effect can be induced independently in each eye and that, simultaneously, the opposite contingency can be maintained binocularly, thus also showing that there must be some kind of interaction of color information from both eyes. De Weert and Levelt (1976) showed that dichoptic fusion of stimuli depended on their relative wavelengths, thereby implying that there can be chromatically based interocular interaction. Conversely, Rogers and Hollins (1982) have found that in a binocular rivalry situation, exclusive visibility time (the time during which either the right or the left eye stimulus is seen alone) increases as a function of the color difference between the targets, thus providing further evidence of binocular interaction between color channels. For a more extensive review of the question of chromatic binocular interactions, see Stromeyer (1978). In summary, while it has not yet been possible to obtain

direct interocular transfer of a chromatic aftereffect, there is psychophysical evidence showing that interocular interaction of chromatic information can occur.

In addition to the psychophysical work, we now have some electrophysiological evidence that shows, contrary to the data reviewed by Coltheart, that there are binocular color coded cells. Zeki (1977) and Van Essen and Zeki (1978) reported that rhesus monkey visual cortex, especially area V_4, contains many such units. Similarly, Michael (1978) found binocular complex color-coded cells in area 17. He also found that these cells had transient response properties and often responded best to color contrast in the absence of luminance contrast. These discoveries make it puzzling that interocular transfer of color aftereffects has not been achieved and raises the possibility that transfer might occur if stimulus parameters appropriate to these binocular color-coded cells were used.

Specifically, Michael's (1978) work suggests that there may be two critical stimulus properties which could facilitate interocular transfer of color adaptation effects. First, contours should be defined by color contrast alone without concomitant luminance contrast. Previously reported failures to obtain interocular transfer have involved stimuli that were defined by both color and luminance contrast, for example red and black gratings paired with green and black gratings. Second, in view of the transient response characteristics of Michael's (1978) cells, both the adapting and the test stimuli should be adjusted appropriately. Here we report the results of tests of the importance of equiluminous chromatic stimuli. We have made a preliminary report elsewhere of a systematic examination of the temporal requirements for interocular transfer (Favreau and Cavanagh, 1982).

Specifically, the main purpose of the research described in this paper was to determine whether interocular transfer of spatial frequency adaptation can be obtained with equiluminous colored gratings as compared with gratings in which luminance and chrominance information is combined. In order to do this we used an experimental paradigm in which opposite spatial frequency shifts are established simultaneously.

The basic experimental procedure employed was derived from the spatial frequency shift paradigm that was introduced by Blakemore and Sutton (1969). In this paradigm an observer is exposed to a pair of gratings located above and below a central fixation bar. The adapting gratings differ in spatial frequency by at least one octave. On a subsequent test with a pair of gratings of equal intermediate spatial frequency there is an apparent negative shift in the perceived spatial frequencies of the equal test gratings such that the test grating that occupies the position previously occupied by the higher frequency adapting gratings appears to have a lower spatial frequency and vice versa.

Using this paradigm, Virsu and Haapsalo (1973) have shown that *opposite* adaptations can be induced

with pairs of red/black and green/black gratings, so that the direction of the adaptation is contingent on the color of the gratings. In the present research we used the opposing aftereffects paradigm with red/green and black/white gratings in one condition, and with red/black and green/black gratings in another condition. The purpose of the red/green vs black/white opposition was twofold: (a) the black/white adaptation could compensate for any residual luminance differences in the red/green gratings (see Method section for detailed explanation), and (b) this adaptation permits one to estimate whether there is independent processing of color and luminance. Red/black and green/black gratings were opposed in order to see whether having equiluminous colors is a necessary condition for interocular transfer or whether transfer can also occur when chromatic and achromatic information is mixed. We have previously used a similar strategy to show that independent opposite spatial frequency adaptation can be maintained with chromatic (red/green) and achromatic (black/white) gratings. In the present research we attempt to induce interocular transfer with, in one condition, red/green and black/white gratings, and in another condition red/black and green/black gratings.

Our data also allow us to evaluate whether there is any difference in the amount of interocular transfer when observers are adapted only to chromatic or only to achromatic gratings as compared to the magnitude of the effects when simultaneous opposite adaptations are induced. Previous research (Favreau and Cavanagh, 1981) indicated that there is no substantial difference for the adapted eye, implying that the chromatic and achromatic channels may be substantially independent at the level at which adaptation occurs.

METHODS

Observers

Two practised observers (R.B. and C.G.) participated in conditions I, II, and III, and three practised observers (R.B., C.G. and P.C.) were run in Condition IV. All had normal color vision.

Procedure

In Conditions I and IV of the present experiment, observers were adapted simultaneously, by alternating exposures, to two pairs of gratings which induced opposite directions of spatial frequency shift. That is, for one pair of gratings the higher frequency occupied the upper position, whereas for the other pair the higher frequency was at the bottom. In Condition I, opposing chromatic and achromatic, they saw presentations of red/green gratings alternating with black/white gratings. In Condition IV, mixed chromatic and achromatic red/black and green/black gratings were alternated. In Conditions II (simple chromatic) and III (simple achromatic) adaptation was to only one grating pair at a time—red/green in the former and black/
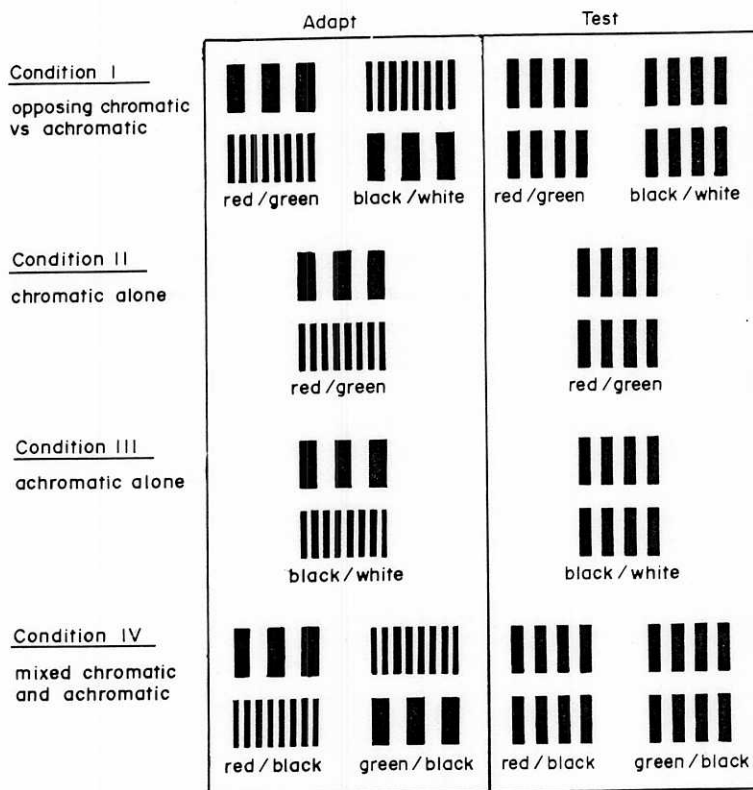
Fig. 1. Schematic representation of the adaptation and test phases of the four experimental conditions. See text for explanation. For Conditions I and IV the two pairs of gratings alternated within each adaptation period, and each pair of test gratings was seen on every other test period. For Conditions II and III only one kind of test grating was seen.

white in the latter. See Fig. 1 for a summary of these experimental conditions.

The stimuli were generated by computer on a color television monitor (see Cavanagh and Anstis, 1981; Favreau and Cavanagh, 1981, for further technical information). The entire display was 7 wide and 9 high. Each member of a grating pair was 7 wide and 4.1 high. The distance between the upper and lower gratings was 0.7 and a 0.5 × 0.5 fixation point was located in the centre. During adaptation the low and high frequency gratings were 0.75 and 1.50 c/deg. respectively. The test gratings at equal setting were 1 c/deg.

Since part of our procedure required adaptation to equiluminous red/green gratings, it was necessary to choose a way in which to equate the red and the green. Equating the luminance of chromatic stimuli is problematic. A number of different techniques have been used to establish equality and they do not all yield the same results (see e.g. Ingling *et al.*, 1978; Wagner and Boynton, 1972). Flicker photometry was used to approximately match luminance, and an additional adaptation manipulation was introduced in order to compensate for any residual luminance differences that may remain. Specifically, as mentioned above, chromatic and achromatic adaptation were opposed, so that observers were adapted to alternating pairs of chromatic and achromatic gratings which induced opposite directions of spatial frequency shift as

we have described elsewhere (Favreau and Cavanagh, 1981). If there is any residual luminance difference in the chromatic gratings then it is possible that a frequency shift would be mediated by luminance contrast rather than by the chromatic gradient. By inducing a simultaneous luminance based shift in the opposite direction we eliminate this possibility and also obtain an indication of whether there is independent processing of chromatic and achromatic information.

At the beginning of each session the observer's red/green luminance match was established with flicker photometry. Flicker photometry was also used to equate the overall mean luminance of the chromatic and achromatic (black/white) gratings. In order to do this the screen was divided into three equal areas. In one area red and green were flickered alternatively. In the other two areas very fine stripes of black and white that appeared gray were flickered in alternation with red in one case and green in the other. The color monitor was then adjusted to give minimum flicker simultaneously in all three areas. The flicker rate was 30 Hz. Although varying somewhat among observers and sessions, the resulting mean luminance of both the red and the green was about 25 cd/m². Similarly the overall mean luminance for the black/white gratings was also approximately 25 cd/m² (white $\simeq$50 cd/m², black $\simeq$0.6 cd/m².

Following the luminance matching, adaptation and testing were commenced for the condition that was

to be run on that session. Adaptation was monocular with the nondominant eye being adapted. Eye dominance was determined by a sighting test. The observer shielded the unexposed eye by holding a piece of cardboard at an oblique angle, in order to reflect light from a nearby light source. Thus vision of the screen was obscured for the unadapted eye while both eyes were exposed to the same level of light.

An adapt-test session consisted of 28 alternating adapting and test periods; the initial adaptation period was substantially longer than the following refresher adaptation periods. The protocol was identical for Conditions I and IV, which both involved opposing directions of adaptation. During the initial adaptation period, alternating 8 sec. presentations of the opposing adapting gratings (red/green vs black/white in Condition I and red/black vs green/black in Condition IV) were presented for $3\frac{1}{2}$ min; each of the subsequent adaptation periods lasted for 32 sec.

The last seen adaptation field was alternated between the two opposing types on each trial. In addition, the order of presentation of test type (red/green vs black/white in Condition I or red/black vs green/black in Condition IV) was varied so that on half the trails a test followed exposure to the same adaptation type and on the other half a test followed exposure to the opposing adaptation type.

Adaptation and test procedures for Conditions II and III were similar to those for Conditions I and IV. Adaptation took half the time because only one grating type was used in each of these conditions (chromatic in Condition II and achromatic in Condition III).

The observers were instructed to gaze steadily at the central fixation point. In order to avoid the formation of afterimages the gratings were drifted back and forth at 0.5 /sec. changing directions every 8 sec. This also ensured that the adapting stimulus favored transient, as opposed to sustained channels, in accord with the properties of Michael's (1978) binocular color cells (see above). At the end of this initial adaptation period a double beep signalled the start of a 2 sec blank period which preceded the first test. During this interval the luminance of the screen was the same as the mean luminance of the gratings.

The testing procedure was as follows. On the first test following adaptation there was a 100 msec presentation of any one of three randomly selected pairs of gratings. They were either both of the same spatial frequency (1 c/deg) or differed by 8% in either direction (upper or lower grating larger). The observer was required to adjust a knob that controlled the position of a marker on the screen in order to give a magnitude estimation of the size and direction of the apparent difference between the two test gratings. The setting also indicated whether it was the upper or the lower grating that appeared larger (i.e. to have a lower spatial frequency). During the response period the marker appeared on the screen alone—the rest of the screen was of uniform luminance, equal to the mean of the adapting luminance.

For the second and subsequent tests the relative sizes of the upper and lower test gratings was determined by the response on the previous test with that grating type. If the observer had estimated that the upper grating, for example, appeared larger than the lower grating, then on the following test the upper grating was made relatively smaller by a step of 8%. When a grating pair had been judged equal, then on the subsequent trial there was a randomly selected upward or downward step of 8% of one of the gratings.

The size of the frequency shift was defined as the frequency difference in the test gratings that elicited a magnitude estimate of zero. When none of the tests elicited a response of zero, the zero point was determined by interpolating between the frequency differences of the two tests for which the estimates had crossed from positive to negative.

During an entire session each observer went through the procedure described above twice for any given condition—on one round the adapted eye was tested and on the other round the unadapted eye was tested. Each observer had 6 sessions for each condition. The locations of the grating pairs relative to each other were reversed on half of the sessions, so that a given high frequency grating which had appeared in the upper position on 3 of the 6 sessions, was located on the bottom for the remaining 3 sessions.

RESULTS

The results are shown graphically in Figs 2, 3 and 4 where the frequency shifts (the difference of the frequencies of the gratings judged equal) are shown as a
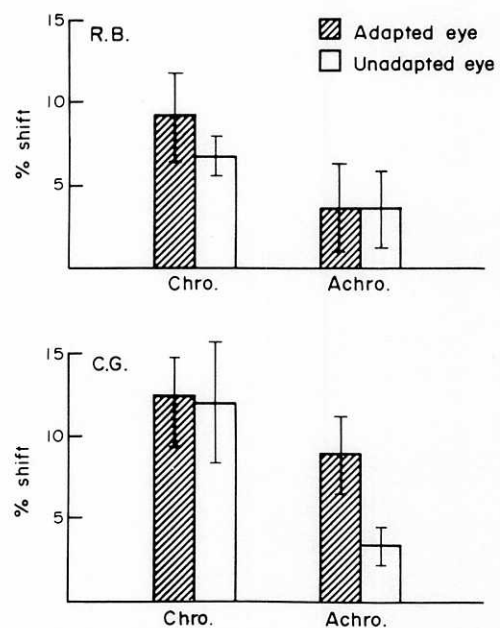
Fig. 2. Percent spatial frequency shift in the adapted and unadapted eyes of observers R.B. and C.G. following alternating adaptation to red/green (Chro.) and black/white (Achro.) gratings which induced simultaneous and opposite directions of spatial frequency shift. Vertical bars indicate ± 1 SE.
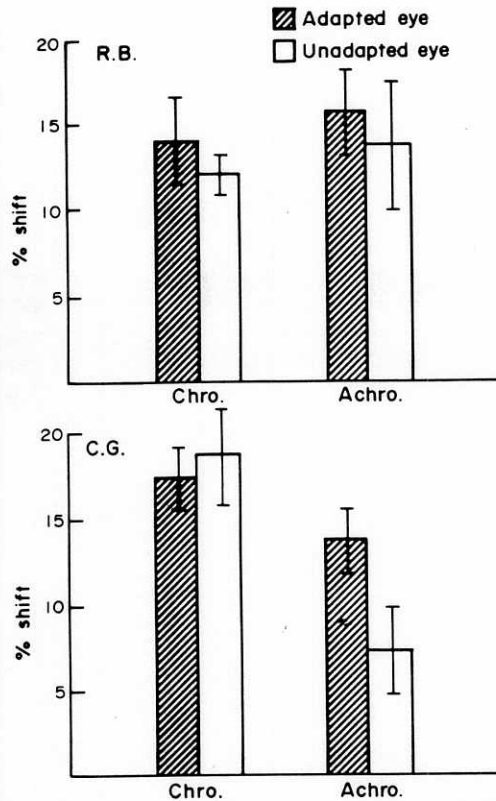
Fig. 3. Percent spatial frequency shift in the adapted and unadapted eyes of observers R.B. and C.G. following simple adaptation to red/green (Chro.) or to black/white (Achro.) gratings. Vertical bars indicate ± 1 SE.

percentage of the test frequency. The criterion for appropriate frequency shifts was the same for both the adapted and unadapted eyes.
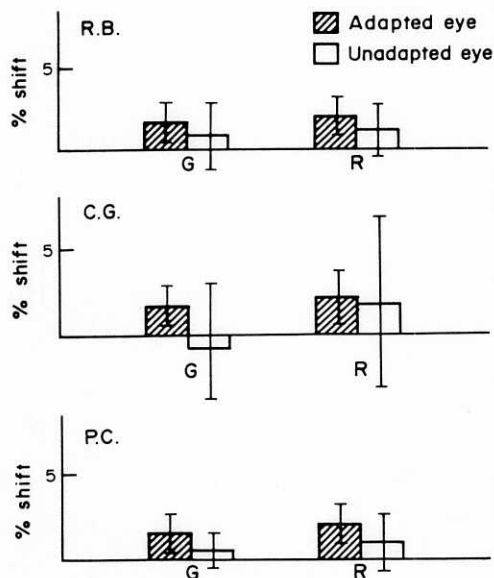

Fig. 4. Percent spatial frequency shift in the adapted and unadapted eyes of observers R.B., C.G. and P.C. following alternating adaptation to red/black (R) and green/black (G) gratings which induced simultaneous and opposite directions of spatial frequency shift. Vertical bars indicate ± 1 SE. The negative value for C.G. denotes aftereffects in the inappropriate direction.

Consider first the results obtained in Condition I, in which observers were adapted to opposing red/green and black/white gratings (see Fig. 2). Both observers obtained significant chromatic spatial frequency shifts for the adapted eye (for observer R.B., $\bar{X} = 9.4$, $t = 4.68$, $P < 0.01$; for observer C.G., $\bar{X} = 12.7$, $t = 6.89$, $P < 0.01$, d.f. = 5 in all the tests reported here) as well as for the unadapted eye (R.B., $\bar{X} = 6.8$, $t = 7.31$, $P < 0.01$; C.G., $\bar{X} = 11.9$, $t = 3.94$, $P < 0.05$). There was no significant difference in the magnitude of frequency shift in the adapted and unadapted eyes (R.B., $t = 2.04$, NS; C.G., $t = 0.03$, NS). The achromatic shift was successfully induced in the adapted eye for only one of the two observers (R.B., $\bar{X} = 3.8$, $t = 1.69$, NS; C.G., $\bar{X} = 9.1$, $t = 5.98$, $P < 0.01$). This observer showed successful interocular transfer (unadapted eye $\bar{X} = 3.8$, $t = 4.73$, $P < 0.01$), but the size of the effect was less in the unadapted eye than in the adapted eye ($t = 4.39$, $P < 0.01$).

In Conditions II and III (Fig. 3), simple chromatic (red/green) and simple achromatic (black/white) adaptation, the results were similar but somewhat stronger. Again both observers showed interocular transfer of the chromatic shift to the unadapted eye (R.B., $\bar{X} = 12.2$, $t = 11.92$, $P < 0.01$; C.G., $\bar{X} = 19.2$, $t = 7.03$, $P < 0.01$). In Condition III both observers had significant achromatic shifts (R.B., $\bar{X} = 16.2$, $t = 8.10$, $P < 0.01$; C.G., $\bar{X} = 13.9$, $t = 8.99$, $P < 0.01$) that transferred interocularly (R.B., $\bar{X} = 14.4$, $t = 4.95$, $P < 0.01$; C.G., $\bar{X} = 7.0$, $t = 3.47$, $P < 0.05$). The significant reduction of the achromatic aftereffect in the unadapted eye, compared to that in the adapted eye, shown by observer C.G. in Condition I was not confirmed in Condition III with either of the two observers (R.B., $t = 0.31$, NS; C.G., $t = 1.48$, NS).

For Condition IV (Fig. 4) using mixed chromatic and achromatic stimuli (red/black and green/black gratings), significant effects were obtained only for the adapted eye. In the red/black condition, the results for the adapted eye were as follows: for observer R.B., $\bar{X} = 3.9$, $t = 3.72$, $P < 0.05$; for observer C.G., $\bar{X} = 4.6$, $t = 3.00$, $P < 0.05$; for observer P.C., $\bar{X} = 4.5$, $t = 5.27$, $P < 0.01$. In the green/black condition, the following results were obtained for the adapted eye: for observer R.B., $\bar{X} = 2.8$, $t = 3.06$, $P < 0.05$; for observer C.G., $\bar{X} = 2.9$, $t = 2.85$, $P < 0.05$; for observer P.C., $\bar{X} = 3.0$, $t = 4.03$, $P < 0.05$. On the other hand there was no evidence of interocular transfer for either the red/black or the green/black condition. The results for the unadapted eye in the red/black condition were as follows: R.B., $\bar{X} = 1.9$, $t = 1.27$, NS; C.G., $\bar{X} = 4.3$, $t = 0.86$, NS; P.C., $\bar{X} = 1.5$, $t = 1.49$, NS. For the green/black condition, the following results were obtained for the unadapted eye: R.B., $\bar{X} = 0.9$, $t = 0.52$, NS; C.G., $\bar{X} = 0.7$, $t = 0.03$, NS; P.C., $\bar{X} = 0.1$, $t = 0.19$, NS. Furthermore the size of the shift was generally much smaller than in Conditions I, II and III, being in most cases under 2% whereas it had been around 10% or greater in the previous conditions.

The results of Condition I on the one hand can be

compared with those of Conditions II and III, on the other hand to see whether the aftereffects obtained in the combined condition are smaller than those obtained in the simple conditions. This comparison can give an indication as to whether there is some degree of overlap between the chromatic and achromatic channels. When this was done five out of the eight *t*-tests confirmed that the aftereffects in the simple condition were larger.

DISCUSSION

The results demonstrate interocular transfer of a chromatic spatial frequency shift. Interocular transfer of the chrominance based shift occurred only when the stimuli were composed of equiluminous colors with no concomitant luminance information (or, at least, as nearly equiluminous as they could be made by heterochromatic flicker photometry). When the stimuli contained mixed chrominance and luminance information (red/black and green/black) there was no interocular transfer. Most previously reported failures to obtain interocular transfer of chromatic adaptation have involved stimuli in which chrominance and luminance information has been combined. Thus it seems that one necessary condition for interocular transfer of chromatic adaptation is that the stimuli be composed of equiluminous colors. We have, however, previously reported that interocular transfer did not occur with equiluminous gratings (Favreau and Cavanagh, 1981). In that research we used long (5 sec) test presentations whereas in the present experiments the test presentations were very brief (100 msec). We have reported elsewhere that short test duration (Favreau and Cavanagh, 1982) is a critical factor and a fuller report is in preparation. In the present report we concentrate on the relative chromatic and achromatic properties of the stimuli.

Our results are congruent with the properties of color sensitive cells that were discovered by Michael (1978). The interocular transfer implies the existence of units receiving information from both eyes. The superiority of the color-only gratings to the color-plus luminance gratings implies that the units involved require color gradients and do not respond well to a luminance gradient. The apparent efficacy of the brief test is in accord with the transient firing properties of Michael's cells.

Although interocular transfer did not occur in Condition IV where luminance and chrominance information was combined, it should be noted that the effect in the adapted eye was very small (approximately 2% compared with chromatic effects ranging from about 10–20%). Thus one reason for the absence of transfer may be because the effects in the adapted eye were quite small in the first place. However, the fact that these effects were small may indicate that there is a substantial amount of overlap between channels carrying red/black and green/black size information. The channels carrying such information would prob-

ably include luminance channels which do not convey differential color information but which do react to the luminance gradient in these stimuli. The gratings used in Condition IV would stimulate these luminance channels in opposite directions, thereby producing size shifts that would cancel each other. The remaining color information is then apparently insufficient to sustain a large effect. A similar phenomenon has been reported by one of us (Favreau, 1976) with regard to color contingent motion aftereffects which are best induced with equiluminous stimuli, but are rather weak when induced with stimuli combining both luminance and chrominance information.

Another finding obtained in the present study should be noted. In a recent paper on interocular transfer of adaptation effects Blake *et al*. (1981) pointed out that interocularly transferred effects were generally smaller than those obtained in the adapted eye. They inferred that this was because the test stimulus affects both adapted binocular units as well as unadapted monocular units. In this study we found that the strength of the chromatic shift in the unadapted eye was no different from the strength of the shift in the adapted eye (see Figs 1 and 2). This was true in Conditions I and II for both observers. By contrast, the results for the achromatic stimuli were more variable. In one of four instances the interocularly transferred effect was smaller than the original, in two cases they were approximately equal, and in the last case, neither the original nor the interocularly transferred effect was statistically significant. The fact that the chromatic shift does not diminish significantly when transferred to the unadapted eye may imply that all or at least a large majority of the units involved receive information from both eyes. However, it should be noted that Blake *et al*. (1981) have argued that, before this inference can safely be made, it is important to measure the equivalence of direct and interocularly transferred effects at different levels of strength.

Our previous work (Favreau and Cavanagh, 1981) and the results of Condition I in the present experiment establish that there is substantial independent processing of chromatic and achromatic spatial frequency information. The question remains as to whether there is any overlap between these channels. That there is can be seen by comparing the results of Condition I (opposing aftereffects) on the one hand, with those of Conditions II and III (simple aftereffects) on the other hand. In most cases the frequency shift is greater for the simple aftereffect than for the opposing aftereffect, implying that there is some overlap between chromatic and achromatic channels. This overlap might be attributed to the multicolor cells described by DeValois and DeValois (1975). These cells respond to both pure color or pure luminance contrast as well as any combination of the two. They could act, according to DeValois and DeValois, as generalized contour extraction mechanisms. Michael (1978) also recorded cells of this type.

In summary, we have obtained interocular transfer

of a chromatic aftereffect which we believe is due to mediation by transient color cells (Michael, 1978). It appears that there are two conditions sufficient to optimally stimulate these cells: one is chromatic contrast in the absence of luminance contrast, and the other is brief test presentation. We are currently investigating other parametric conditions such as spatial frequency in order to determine more fully what other factors may limit interocular transfer that do not limit monocular effects.

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