

INTEROCULAR TRANSFER OF A CHROMATIC FREQUENCY SHIFT: TEMPORAL CONSTRAINTS

OLGA EIZNER FAVREAU and PATRICK CAVANAGH

Department of Psychology, University of Montreal, Case Postale 6128 Succursale "A", Montreal, P.Q.
Canada H3C 3J7

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Abstract—Interocular transfer of a chromatic version of the Blakemore and Sutton (1969) [*Science* 166, 245-247] spatial frequency shift is not obtained with long steady (3000 msec) test presentation, but does occur when the test is brief (400 msec) or flickering. By contrast, interocular transfer of achromatic spatial frequency adaptation occurs with long steady tests as well as with brief or flickering tests.

Interocular transfer Equiluminous chromatic gratings Spatial frequency shift Temporal
properties Duration Flicker

INTRODUCTION

It has often been reported that color-related adaptation effects do not normally transfer interocularly (see, e.g. Coltheart, 1973; Stromeyer, 1978 and Favreau and Cavanagh, 1981). More recently, however, we have succeeded in obtaining interocular transfer of one aftereffect of this type (Favreau and Cavanagh, 1983). In that paper we reported that a chromatic version of the Blakemore and Sutton (1969) spatial frequency shift can transfer interocularly when the colors of the inducing stimulus are equiluminous. We describe here some additional constraints involving temporal properties of the test stimulus.

As noted above, interocular transfer of color-related effects does not occur in a normal direct way, unlike many achromatic figural aftereffects. Thus, for example, the McCollough effect (McCollough, 1965) when induced in one eye cannot be obtained in the unadapted eye. By contrast, there are many instances of adaptation to achromatic stimuli transferring interocularly. Wohlgenuth (1911) showed this 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.

Although interocular transfer of color-related adaptation does not appear to occur in an ordinary straightforward fashion, there have been reports in the literature which indicate that there can be some interaction between color inputs to the two eyes. For example, Mackay and Mackay (1973) presented alternating red and green color fields to one eye paired with alternating achromatic vertical and horizontal gratings to the other eye. When each eye was tested separately with achromatic vertical and horizontal gratings, the eye that had seen the color fields saw a typical McCollough effect in complementary colors,

but the eye that had seen the gratings saw positive color aftereffects associated with the gratings—i.e. the gratings that had been paired with red in the other eye appeared reddish, while the grating that had been paired with green appeared greenish. Murch (1974) found a similar result for color-contingent motion aftereffects. Vidyasagar (1976), using the McCollough effect, adapted observers to one orientation-color contingency monocularly for each eye separately, and to the inverse orientation-color contingency binocularly. Observers subsequently reported seeing the appropriate contingency for monocular or binocular testing, respectively. All of these data indicate that there must be some kind of sharing of color information between the two eyes.

More recently we have reported that color-contingent spatial frequency adaptation can transfer interocularly when the colored gratings are equiluminous (Favreau and Cavanagh, 1983). This transfer seemed to occur best with a brief test stimulus. In the experiments described below we report on a more systematic exploration of the temporal parameters of test stimuli that potentiate interocular transfer of color adaptation. Specifically, we investigate the effects of test duration (Experiment 1) and of a flickering test stimulus (Experiment 2).

EXPERIMENT 1: TEST DURATION AND DELAY

In this experiment we report on the effects of manipulating test duration and test delay. If interocular transfer does occur with a brief test stimulus but not with a long one, it could be because the interocularly transferred component of the aftereffect is so brief that it is not available for more than a short period after adaptation, or it could be because the mechanism that mediates interocular transfer prefers transient to sustained stimulation, regardless of when

it occurs. In order to test for these different possibilities we used three levels of test delay following the offset of the adapting stimulus. If the effect is only briefly available then it should decrease or even disappear with increased test delay. We used two values of test duration: 400 and 3000 msec.

We did not vary the temporal properties of the adapting stimuli. Drifting gratings were used for adaptation in order to avoid the formation of after-images.

Method

Observers. Eight paid naive observers participated in this experiment. They had normal or corrected vision and were screened for color defects and stereopsis.

Procedure. The adapting and test stimuli were 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. These adapting gratings differ from each other in spatial frequency by at least one octave. Following an adaptation period there is a test with a pair of gratings of intermediate equal spatial frequency. To the adapted observer these gratings have an apparent shift in the perceived spatial frequencies such that the test grating that occupies the position previously occupied by the higher frequency adapting grating appears to be of lower spatial frequency than it actually is and the grating that occupies the position of the lower frequency adapting grating seems to have a higher frequency.

We modified this paradigm to induce opposing aftereffects of chromatic and achromatic gratings (Favreau and Cavanagh, 1981). Observers were adapted to alternating exposures of pairs of red/green and black/white gratings which induced opposite directions of spatial frequency shift (see Fig. 1). The gratings were arranged vertically, one above the other, with a fixation point in the space between them. For one of the pairs of gratings the higher frequency appeared in the upper position, whereas for the other pair the higher frequency was at the bottom. These positions were counter-balanced across observers for the chromatic and achromatic gratings.

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 $0.5^\circ \times 0.5^\circ$ 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 were 1 c/deg.

Flicker photometry was used to equate the luminance of the red and green portions of the chromatic gratings. Although this procedure may not establish

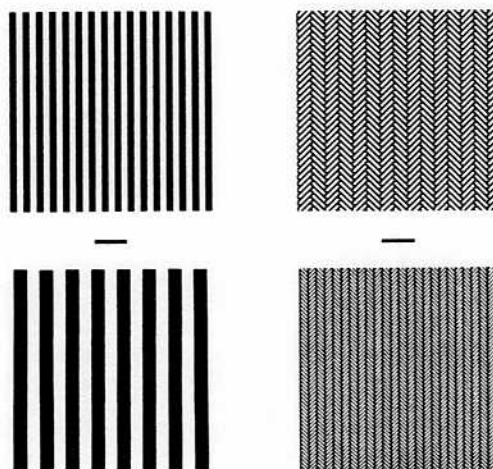


Fig. 1. Schematic representation of the adapting stimuli used in Experiments 1 and 2. The black-white gratings are represented on the left, and the red-green gratings on the right. The relative locations of high and low spatial frequencies are reversed. The test gratings were of intermediate equal frequencies, similarly arranged above and below a central fixation point.

colors that are perfectly equiluminous, the use of the opposing chromatic and achromatic adaptation described above should compensate for any remaining residual luminance differences. If there is any residual luminance difference in the chromatic gratings 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 while also obtaining an indication of whether there is independent processing of chromatic and achromatic spatial frequency information.

At the beginning of each session the observers' 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 alternately. 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 until the observer reported seeing minimum flicker simultaneously in all three areas. The flicker rate was 30 Hz. Although varying somewhat among observers and sessions, the resulting mean luminance was about 25 cd/m^2 . Similarly the overall mean luminance for the black/white gratings was also approximately 25 cd/m^2 (white $\approx 50 \text{ cd/m}^2$, black $\approx 0 \text{ cd/m}^2$).

Following the luminance matching, adaptation was begun. Adaptation was monocular to the non-dominant eye (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 source.

In this way both eyes were maintained at equivalent levels of light adaptation.

An adapt-test session consisted of 24 alternating adapting and test periods. The initial adaptation period consisted of alternating 8 sec presentations of the red/green and black/white gratings, respectively, for a total of 4.25 min. Each of the subsequent adaptation periods lasted for 48 sec. The order of presentation of test type (red/green or black/white) was varied so that on half the trials a test followed adaptation to gratings of the same type (e.g. achromatic after chromatic) and on the other half a test followed adaptation to gratings of the opposite type (e.g. chromatic after achromatic).

There were 2 levels of test duration: 400 msec and 3000 msec, and 3 levels of test delay: 1000, 2000 and 5000 msec. The levels of test duration were chosen empirically—preliminary experimentation indicated that they were appropriate. Each of the 6 possible combinations of test duration and test delay was presented to each observer 4 times within a session. For each test the pair of gratings that was presented were of identical spatial frequency. The observer was required to adjust a knob that controlled the position of a marker on the screen which provided a magnitude estimation of the apparent size and direction of any difference between the two test gratings. In order to enable them to do this observers were given some preliminary practice sessions during which they were instructed in the use of the magnitude estimation procedure. They were shown upper and lower pairs of gratings which were either of equal spatial frequency or in which there was a 2:1 difference. A narrow horizontal bar was located between the two gratings and a movable marker on it was controlled by a joystick. The observers were told to position the marker in the center of the bar if the gratings were equal, at the extreme right when the 2:1 grating appeared at the top, and at the extreme left when the 2:1 grating was on the bottom. They were told that during the actual test sessions they were to position the marker to the right when the upper grating appeared larger and to the left when the lower grating appeared larger, and to scale the positions in accord-

ance with the magnitude of the apparent difference, considering the center to represent equality and the extremes to represent a 2:1 difference. The results were registered as arbitrary units proportional to the distance of the setting from the center. During the actual response period the marker appeared on the screen alone—the rest of the screen was of uniform luminance, equal to the mean adaptation luminance.

Each observer participated in two test sessions—during one the adapted eye was tested and during the other the unadapted eye was tested. The order of these two sessions was counterbalanced among observers.

Results

The results are shown graphically in Fig. 2. Since, as will be seen, there was no effect of test delay, the results are shown averaged across all three values of test delay. Visual inspection shows that there was a substantial aftereffect of spatial frequency adaptation for all conditions for the adapted eye and for the unadapted eye in all conditions except for the long duration chromatic gratings. While there is no significant interocularly-transferred color aftereffect for the long test ($t = 0.55$, ns), there is a corresponding aftereffect with the brief test ($t = 5.8$, $P < 0.01$). These results confirm the hypothesis that a short but not a long test will permit interocular transfer of the color adaptation.

An analysis of variance (see Table 1 for summary of results) revealed that the effect of test delay was not significant, either as a main effect or as an interaction. This implies that the short test duration was not more effective simply because of the rapid decay of the interocularly transferred chromatic spatial frequency shift. Test duration, however, did have a significant effect, the chromatic aftereffect was stronger for short duration tests than for longer tests; however, both test durations gave similar aftereffects for the achromatic condition (chromaticity by duration interaction). Overall, the interocularly transferred chromatic effects are weaker than the interocularly transferred achromatic effects. Reference to Fig. 2 shows that this is mostly due to the virtual

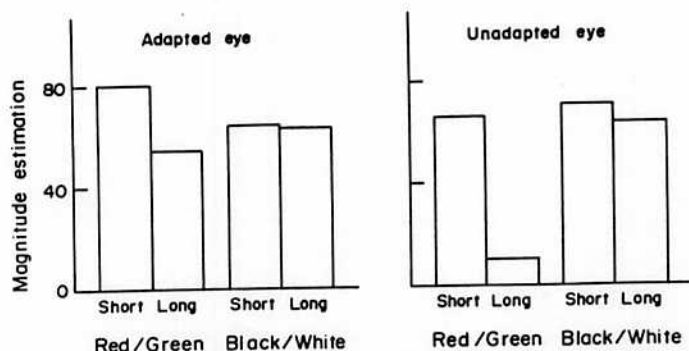


Fig. 2. Magnitude estimations of the amount of spatial frequency shift for the adapted and unadapted eyes in relation to the two test durations (400 and 3000 msec) and test chromaticity (red/green and black/white).

Table 1. Summary of results of analysis of variance for Experiment 1

Source	d.f.	Mean square	F
Eye	1	8842.76	1.90
Chromaticity	1	8125.01	0.97
Duration	1	24865.76	8.91*
Delay	2	110.85	0.70
Eye × chromaticity	1	11954.30	7.90*
Eye × duration	1	4024.17	1.65
Eye × delay	2	3649.85	3.71
Chromaticity × duration	1	16151.67	6.73*
Chromaticity × delay	2	5331.15	2.97
Duration × delay	2	1049.85	0.50
Eye × chromaticity × duration	1	2100.13	0.75
Eye × chromaticity × delay	2	4975.17	1.63
Eye × duration × delay	2	4223.08	1.78
Chromaticity × duration × delay	2	486.42	0.40
Eye × chromaticity × duration × delay	2	178.82	0.06

* $P < 0.05$.

absence of interocular transfer for long duration chromatic tests. In the adapted eye, however, chromatic and achromatic aftereffects are quite similar in magnitude (eye by chromaticity interaction).

EXPERIMENT 2: FLICKERING TEST

The results of Experiment 1 confirm that a brief test is more effective than a longer test for showing interocular transfer of the chromatic spatial frequency shift, and also that test delay is not a critical factor. These results therefore show that the effect is stored at least until it is called forth by an appropriate test, thus indicating that the effectiveness of the brief test is not because it "catches" the effect before it has had time to decay, but rather that there is something about the test onset which can evoke the aftereffect, whereas continuation seems to suppress it.

This leads us to ask whether it is the onset of one single test stimulus that abolishes the interocularly transferred effect or whether the relevant aspect of the appropriate test stimulation is that it be transient or dynamic rather than sustained. To answer this question we did a second experiment in which the test stimulus was presented in counterphase flicker for the same duration as the long test in the preceding experiment.

Method

Observers. Twelve paid, naive observers par-

ticipated in this experiment. They were screened according to the same criteria that were applied to observers in Experiment 1.

Procedure. In general the procedure was identical to that used in Experiment 1, except that test delay and duration were held fixed, and the test was either a flickering or a steady stimulus. For the flicker tests the gratings was flickered in counterphase at 2.5 Hz. Both the flickering and the steady test stimuli were exposed for 3000 msec following a 400 msec delay. Half of the tests following any adaptation presentation were of a flickering stimulus and for the other half the test stimulus was steady.

Results

The results are shown graphically in Fig. 3. It can be seen, as predicted, that interocular transfer did occur for the color gratings with the flickering test but not with the steady test. Significant aftereffects also occurred for all the other conditions. This observation is confirmed by the analysis of variance, the results of which are summarized in Table 2. The adapted eye gave overall significantly larger effects than the unadapted eye. Flickering tests gave stronger aftereffects than steady tests for colored stimuli, but not for black/white stimuli.

Interocular transfer for the steady chromatic test did not differ significantly from zero ($\bar{X} = 5.8$, $t = 0.75$, NS). For the corresponding flickering test

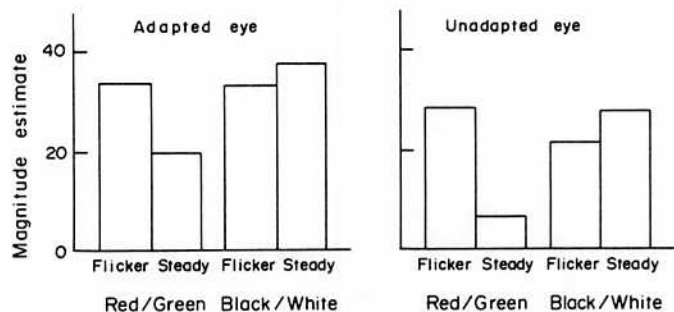


Fig. 3. Magnitude estimations of the amount of spatial frequency shift for the adapted and unadapted eyes in relation to flickering or steady tests and test chromaticity.

Table 2. Summary of results of analysis of variance for Experiment 2

Source	d.f.	Mean square	F
Eye	1	2450.26	7.55*
Chromaticity	1	1625.26	1.29
Eye \times chromaticity	1	3.76	0.01
Eye \times flicker	1	61.76	0.18
Eye \times chromaticity \times flicker	1	162.76	0.30
Flicker w chromaticity (R/G)†	1	3870.02	16.37**
Flicker w chromaticity (B/W)‡	1	261.33	0.45

* $P < 0.05$.** $P < 0.01$.

†These effects refer to the effect of flicker versus steady test presentation for red/green (R/G) and black/white (B/W) respectively.

the effect does differ significantly from zero ($\bar{X} = 27.9$, $t = 2.73$, $P < 0.05$).

DISCUSSION

The results of the experiments described in this paper show that chromatic spatial frequency adaptation can be transferred interocularly under appropriate conditions. We found that the temporal characteristics of the test stimulus can be a critical factor in obtaining interocular transfer. In a previous paper (Favreau and Cavanagh, 1983) we showed that the chromatic properties are also an important factor. These results can thus be added to those cited in the introduction which show that interocular transfer of color related effects can be obtained under certain circumstances.

Coltheart (1973), noting that the color-coded cells in monkey visual cortex that were described by Hubel and Wiesel (1968) were all monocularly driven, pointed out that this could explain the failure to obtain interocular transfer of color adaptation. Since then, however, binocular color cells have been found in monkey cortex (Michael, 1978; Van Essen and Zeki, 1978). Cells such as these may mediate in the transfer of color effects between eyes. Michael described a type of cell in area 17 that is of particular interest in the present context. These are binocular complex cells which often respond best to equiluminous color stimuli. Complex cells, moreover, respond best to moving or transient stimuli. These cells may possibly provide the physiological basis for interocular transfer of a color-related effect. The test stimuli that we used in the present research and previously (Favreau and Cavanagh, 1983) conform to the properties of these binocular cells. They are transient and equiluminous. Unfortunately, it is not feasible to further test this possible connection by comparing the relative effectiveness of stationary versus moving gratings during adaptation, since adaptation to stationary gratings would lead to the formation of afterimages. We may, however, note that Ono *et al.* (1971) found that dichoptic color fusion occurs with shorter stimuli, whereas rivalry is more likely with longer lasting stimuli, showing also

the superiority of brief stimulation for the combination of color information from both eyes.

Our conclusion, that dynamic or transient properties are preferred by a chromatic channel, appears to be in contradiction with the conclusions arrived at by a number of other researchers (e.g. Bowen *et al.*, 1977; King-Smith and Carden, 1976; Lovegrove and Evans, 1980; Nissen and Pokorny, 1977; Schwartz and Loop, 1982, 1983). These authors have all postulated that there is a sustained chromatic channel and an achromatic transient channel. In general, their conclusions have been based on reaction time or on threshold measures which are quite different from adaptation and which may thus be tapping different aspects of the sustained and transient mechanisms.

A more relevant difference, however, between our work and that of the above authors is that they all used either monocular or simultaneous binocular stimulation, and did not, therefore, investigate specifically interocular connections. Our results on interocular transfer provided evidence for the existence of a binocularly driven color channel that requires transient stimulation, as is shown by the results for interocular transfer. By contrast, the results we obtained for chromatic tests in the adapted eye, where we found that both sustained and transient tests can induce aftereffects, show that there are monocular chromatic channels with sustained and possibly also with transient characteristics.

Blake *et al.* (1981) have argued that, when an aftereffect is induced monocularly and then transferred to the other eye, the effect in the unadapted eye is mediated by binocularly driven units and in the adapted eye by either a mixture of monocular and binocular units or only binocular units. In our experiment, the fact that with sustained stimulation the chromatic aftereffect occurs in the adapted but not the unadapted eye implies that only monocular color units are sustained. This is consistent with Michael's findings that simple color coded cells, in area 17, were predominantly monocular. The relative similarity in magnitude of the chromatic aftereffect for the transient stimulation in both eyes implies either that all units with transient characteristics are binocular, or that a ceiling of adaptation has been reached (see Blake *et al.*, 1981). The authors mentioned previously, who had argued that the chromatic channel is sustained, used either monocular or binocular stimulation alone and did not test for interocular transfer. Their results therefore probably pertain to the functioning of a monocular sustained channel and do not address the issue of a binocular chromatic channel.

A recent article by Smith (1983) that was published subsequent to the completion of this research provides some psychophysical data that are at least partly in accord with the present results. Smith found that threshold elevation for the perception of a green or red rotating spiral following color-contingent adaptation to a rotating green or red spiral can transfer

interocularly when the test is a moving spiral. Smith claimed that the motion of the test spiral was critical for obtaining interocular transfer and that previous failures to obtain interocular transfer were due to the use of stationary test figures. He did not, however, himself provide comparison tests with stationary spirals. If it is the case that motion of the test spiral is the critical factor, then this is another case in which dynamic stimulation, like the rapid and flickering stimuli that were used in the present research, has promoted interocular transfer of color-related adaptation. There are however some possibly critical differences between our research and Smith's. Smith obtained interocular transfer with spirals that were defined by both color and luminance i.e. red/black and green/black spirals. As noted earlier, we have reported (Favreau and Cavanagh, 1983) that chromatic spatial frequency adaptation can be obtained when the stimulus is composed of equiluminous colors, and is not demonstrable with red/black and green/black stimuli like those used by Smith. Smith, however, used threshold elevation rather than negative aftereffects as the dependent variable. As he pointed out, this may be measuring a quite different aspect of adaptation since threshold elevation effects are of much shorter persistence (a few minutes) than contingent aftereffects which may last up to months (e.g. Jones and Holding, 1975). While we did not test for persistence of our aftereffects, both the adaptation and test procedures were like those that are used for contingent aftereffects.

We found no differential effect of sustained and transient stimulation for achromatic adaptation, for either the adapted eye or for interocular transfer. This suggests that there are achromatic channels with sustained and transient characteristics and that these are at least binocular and possibly also monocular. Held and Wolfe (1983), on the other hand, have reported a differential effect for short and long stimulation for an achromatic effect. Specifically, the tilt aftereffect appears stronger for shorter test exposure time. We have no way, at the present time, to resolve this apparent difference other than to speculate that it might be due to the different effects being tested—spatial frequency in our case, and orientation in the work of Held and Wolfe.

In a similar vein, Green *et al.* (1983) have recently reported that the motion aftereffect, when tested with a flickering test field, had properties that were distinct from those of a steady test field. Among other differences, these authors found no interocular transfer with the flickering test stimulus. These data seem to be in direct contrast with the results reported in the present article, as we found that a flickering test permitted interocular transfer to occur. However, it should be remembered that in the present experiment, the facilitation provided by flicker was specifically for the equiluminous colored stimuli, whereas Green *et al.* (1983) used stimuli that did contain luminance contrast. What all of these results, taken together,

seem to indicate is that the channels that convey monocular and binocular information may function according to different principles and that these principles may differ according to the kind of information they are conveying.

In conclusion, we have found that interocular transfer of chromatic spatial frequency adaptation cannot be detected with a long, steadily presented test stimulus, but that it does become evident when a brief or a flickering test stimulus is used. We have hypothesized that the mediating units correspond to the binocular color cells that were described by Michael (1978). While a psychophysical technique cannot directly show whether certain physiological processes are at work, there is nevertheless a correspondence between the temporal restrictions in the interocular transfer of chromatic adaptation reported there, and the chromatic requirements reported earlier (Favreau and Cavanagh, 1983) and the characteristics of complex binocular cells described by Michael.

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