The effects of differential adaptation on spatial frequency-contingent color aftereffects

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The magnitude of color aftereffects was measured with a color-cancellation technique after subjects adapted to oblique checkerboards in magenta light and square-wave gratings of various orientations in green light. Test stimuli were composed of achromatic patterns of an oblique checkerboard and an appropriately oriented grating. Two different spatial frequencies were used: 0.8 and 3.0 c/deg. With 3.0-c/deg stimuli, the largest color aftereffects occurred when fundamental Fourier components of adapting stimuli were oriented at 45° angles to one another. At the lower spatial frequency (0.8 c/deg), the greatest color aftereffects occurred when fundamental Fourier components of adapting stimuli were in the same orientation. These findings agreed with previous color aftereffect studies which involved adapting to checkerboards and testing with gratings. They offer further support for the notion that the human visual system responds to spatial frequency content of such stimuli as it is described by two-dimensional Fourier analysis.

A number of reports have suggested that the human visual system processes spatial information by performing some sort of spatial frequency analysis (Carter & Henning, 1971; Pollen, Lee, & Taylor, 1971; Sullivan, Georgeson, & Oatley, 1972; Weisstein & Bisaha, 1972). Since Kelly (1976) reported that a two-dimensional Fourier analysis shows that the fundamental Fourier components of a checkerboard stimulus are oriented at 45° angles to the edges of individual checks, checkerboard stimuli have been used in conjunction with rectilinear gratings to assess the importance of various aspects of spatial frequency. Kelly's study of counterphase flicker sensitivity indicated that pattern detection depends on the sensitivity of the visual system to the maximum magnitude of the fundamental Fourier components of spatial stimuli. May and Matteson (1976) and Green, Corwin, and Zemon (1976) found that orientation-contingent color aftereffects are associated with the fundamental components of checkerboard stimuli, and May, Agamy, and Matteson (1978) found that this effect occurs only with spatial frequencies above 1.0 c/deg. At 0.8 c/deg, color aftereffects were found to be

associated with the edges of individual checks.

If fundamental Fourier components are prepotent when high fundamental spatial frequencies are presented to the human visual system, but the higher harmonics (edges) of the stimuli are the important pattern elements when low fundamental frequencies are used, then the results of contingent color aftereffect experiments with checkerboard vs. grating adapting stimuli should be predictable. The present study used test stimuli which were spatially identical to the adapting stimuli and compared the magnitude of contingent color aftereffects across adaptation conditions. It was expected that with 3.0-c/deg stimuli, maximum color aftereffects would be obtained when the fundamental Fourier components in the checkerboard adapting stimuli were oriented 45° from the orientation of the fundamental components of the grating adapting stimuli. With 0.8-c/deg stimuli, the largest color aftereffects were predicted when the edges of individual checks were oriented 45° from the edges of stripes (the fundamental Fourier components having the same orientation).

Two-dimensional Fourier transforms of checkerboard patterns have two fundamental components oriented 90° apart (45° from the edges of individual checks) as well as high-frequency components oriented in various meridians. Adapting with a checkerboard and a single rectilinear grating would allow cancella-

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tion of aftereffects due to only one of the two fundamental components of the checkerboard, so some color aftereffect would remain. Alternating adaptation to a checkerboard and two gratings 90° apart would allow cancellation of fundamental components in both directions. For this reason, adaptation conditions involving both partial (one grating) and complete (two orthogonal gratings) adaptation were included.

METHOD

The subjects were 18 student volunteers. All had normal color vision, as measured by HRR Pseudoisochromatic plates and were either emmetropic or corrected to 20/20 acuity. Subjects of each sex were randomly assigned to one of two spatial frequency conditions. These two spatial frequency groups were each composed of four females and five males. The subjects ranged in age from 21 to 33 years and all were experimentally naive.

The stimuli were Thermofax copies of Kodalith negatives and had a contrast of 65%. The checkerboard and square-wave gratings were matched in terms of their fundamental spatial frequency. Thus, the edge of an individual check was 1.4 times wider than a bar in a grating of equal fundamental spatial frequency. Sets of adapting stimuli and test stimuli of two different spatial frequencies (0.8 and 3.0 c/deg) were used. Four adaptation-test conditions were run at each spatial frequency (see Figure 1): (1) adaptation to magenta "diamonds" (oblique checkerboard rotated such that the edges of individual checks were oriented 45° from vertical) and green vertical gratings—test with a bipartite field of achromatic "diamonds" (left panel) and an achromatic vertical grating (right panel); (2) adaptation to magenta "diamonds" and green oblique (45°) gratings—test with achromatic diamonds and oblique (45°) gratings; (3) adaptation to magenta "diamonds" and green vertical and horizontal gratings—test with achromatic "diamonds" and vertical gratings; and (4) adaptation to magenta "diamonds" and green oblique (45° and 135°) gratings—test with achromatic "diamonds" and oblique 45° gratings.

Conditions 1 and 3 were designed to assess the effects of adaptation stimuli in which at least one of the fundamental two-dimensional Fourier components of checkerboards and gratings were in the same orientation. Conditions 2 and 4 involved adaptation stimuli in which at least one of the fundamental two-dimensional Fourier components were at 45° angles to those represented in the "diamond" pattern. Condition 1 involved green adaptation to only one of the two orientations represented in the "diamond" pattern and can be considered to be a condition involving partial cross-adaptation. Condition 2 involved green adaptation to one orientation which was rotated 45° from the orientation of the fundamental Fourier components in the "diamond" pattern; therefore, it also involved only partial cross-adaptation. Conditions 3 and 4 involved adaptation to two orientations in each pattern. Condition 3 was such that all fundamental Fourier components were of the same orientation; Condition 4 assured that horizontal and vertical orientations were adapted to magenta, and oblique orientations were adapted to green.

Stimulus Presentation

Adaptation stimuli were presented at a distance of 47.5 cm in a two-channel tachistoscope (Scientific Prototype Model 800). The "diamond" patterns were always viewed through a magenta filter (Wratten No. 32); the gratings were always viewed through a green filter (Wratten No. 53). The subjects adapted for 15 min, to alternating 5-sec periods in which the magenta and green patterns were presented. For Conditions 3 and 4, the grating pattern in the green channel was oriented 90° from the orientation used in the previous green adaptation period.

Test stimuli were rear-projected on a ground-glass screen with a lantern slide projector (Beseler Model 3620). Each test slide was composed of pairs of patterns (see Figure 1) which were sandwiched with orthogonal Polaroids. Test stimuli were projected through (1) a color compensating filter and (2) two daylight filters (Wratten 80A and 82A), which rendered the coloration of the test stimulus pair at its neutral position as close as possible to the coloration of the daylight fluorescent lights used to illuminate the adapting patterns. The space-averaged luminance of all test stimuli was 10.2 cd/m^2 .

The apparatus for projecting test stimuli was patterned closely after one described by White (1976) which allows the observer to cancel out aftereffect colors with complementary colors added to the two halves of the test field. A color-compensating filter, composed of 12.5-mm squares of magenta (Wratten CC20M) and green (CC30G) gelatin filters sandwiched with orthogonally polarized squares in a checkerboard pattern, was positioned between the projector lens and the projection screen and could be rotated with a single knob. The crossed Polaroids in the color-balancing filter in conjunction with the crossed Polaroids in the test slide made it possible to add magenta to one side of the test stimulus and green to the other half.

The data were collected in four sessions for each subject with one adaptation condition per session. At least 1 week elapsed between sessions. The order of presentation of conditions was randomized. At the beginning of each session, the subject adjusted the color-compensating filter with instructions to match the left and right panels in chromaticity, as closely as possible. They were also instructed to fixate a point in the exact middle of the pattern. Ten such matches were made on either side of the match point. The direction in which the knob had to be turned to achieve a match was randomized.

Upon completion of the initial matches, the subjects adapted for 15 min to one of the conditions described above. To prevent the formation of afterimages, they were instructed to allow their fixation to move across the middle two-thirds of the pattern. After adaptation, the subjects were given 2 min to align themselves with the test apparatus and again make 10 matches, following the same procedures used during preadaptation testing. A measure of the magnitude of color aftereffects was obtained by subtracting each subject's mean preadaptation match from his (her) mean post-adaptation match. The magnitude of the score indicated the before-after difference in the amount of green that was added to stripes (to cancel out magenta aftereffects) and the amount of magenta added to "diamonds" (to cancel out green aftereffects).

Figure 1. Conditions of differential adaptation (G = green, M = magenta). Data were collected with 0.8- and 3.0-c/deg stimuli under each condition, and the adaptation and test stimuli within a condition were equated for fundamental spatial frequency.

RESULTS

Mean difference scores obtained by subtracting the mean preadaptation match point from the mean postadaptation match point for each subject were analyzed with a two-way mixed analysis of variance (Spatial Frequency by Adaptation Condition). Both main effects (spatial frequency: $F = 5.01$, $df = 1,16$; adaptation conditions: $F = 9.28$, $df = 3,48$) and the interaction ($F = 37.87$, $df = 3,48$) were significant at the .05 level. High spatial frequency stimuli resulted in greater aftereffects than did low spatial frequency stimuli (43.07 and 28.80, respectively). Conditions 1, 2, and 4 resulted in greater aftereffects than Condition 3. (Condition means: 1 = 40.75, 2 = 33.09, 3 = 22.85, 4 = 47.07). Mean aftereffect magnitude and the standard error of the means are presented in Figure 2. With low spatial frequency stimuli, the greatest aftereffect magnitude occurs in adaptation conditions which have one or more of the fundamental Fourier components aligned in the same orientation; the smallest aftereffects are observed when the edges of the individual checks and stripes are aligned. By contrast, high spatial frequency stimuli resulted in maximal aftereffects under conditions which match the orientation of edges of the individual diamonds and stripes, but minimal aftereffects occurred when the orientation of one or more of the fundamental Fourier components were matched during adaptation. In other words, when the spatial frequency was low, edges 45° apart resulted in the largest aftereffects, but with high spatial frequencies, nonalignment of the fundamental Fourier components lead to the greatest aftereffects.

Figure 2. Mean aftereffect magnitude following the four adaptation conditions for two different fundamental spatial frequencies. Unfilled bars represent conditions in which the fundamental Fourier components in the adapting stimuli had the same orientation; filled bars represent conditions in which the edges of the adapting stimuli had the same orientation. Vertical marks indicate ± 1.0 SE.

Aftereffect magnitude was significantly different from zero ($p < .05$, using a two-tailed t test) in all conditions except 4 with 0.8-c/deg stimuli and 3 with 3.0-c/deg stimuli. These conditions involved almost complete cancellation of pattern-contingent color aftereffects. Conditions 1 and 2 (adaptation with only a single grating) resulted in greater aftereffects than Conditions 3 and 4 (adaptation with two gratings 90° apart). This is evident from a comparison of aftereffect strengths within a spatial frequency condition (i.e., compare 1 to 3 and 2 to 4). This result might be expected for two reasons: (1) Total adaptation time for a given grating in Conditions 3 and 4 was half that for the gratings used in Conditions 1 and 2; and (2) Conditions 1 and 2 allowed more meridional features (fundamental Fourier components for 3.0-c/deg stimuli and higher harmonics for 0.8-c/deg stimuli) to be associated with color than Conditions 3 and 4. This second point can be better appreciated by considering that adaptation to 3.0-c/deg green vertical stripes and 3.0-c/deg magenta diamonds (Condition 1) would be expected to result in a cancellation of aftereffects deriving from the vertical meridian, but the horizontal meridian would still give rise to a green aftereffect. By contrast, adaptation to 3.0-c/deg vertical and horizontal green stripes and 3.0-c/deg magenta diamonds results in much smaller aftereffects, because the green aftereffects produced on the vertical and horizontal meridians by the diamonds are more completely cancelled by magenta aftereffects produced by the stripes in these same meridians.

DISCUSSION

These results agree with previous studies of pattern-contingent color aftereffects. The finding that high spatial frequency stimuli result in greater color aftereffects has been reported before (Stromeyer, 1972). The major difference between the adaptation conditions is reflected in the relative attenuation of aftereffects observed when the orientations of the relevant features (edges or fundamental Fourier components) in the two types of adapting patterns (checks and stripes) were in the same orientation.

The significant interaction between spatial frequency (0.8 vs. 3.0 c/deg) and adaptation condition supports previous findings (May et al., 1978) regarding the range of color aftereffects contingent upon the fundamental Fourier components of such patterns. That study showed that, while color aftereffects were associated with the fundamental spatial frequency of patterns of high spatial frequency, at low spatial frequencies the aftereffects were mediated by the edges (i.e., higher harmonics) of such patterns. In the present study, the largest color aftereffects occurred when the orientation of the fundamental Fourier

components were at 45° angles to each other and high spatial frequency stimuli were used (3.0 c/deg). When low spatial frequency stimuli were used, the greatest aftereffect magnitude occurred when the fundamental Fourier components were in the same orientation.

The present study shows that the difference between the adaptational effects of checkerboards and gratings, which is evident at high spatial frequencies, is not present at low spatial frequencies. This can be understood by assuming that the mechanism which mediates pattern perception in this situation involves an optimal functional receptive field size which is most sensitive to 3.0-c/deg stimuli. Checkerboards with a 3.0-c/deg fundamental spatial frequency result in the greatest adaptational effect and the magnitude of color aftereffects is diminished as the fundamental frequency of adapting stimuli is increased or decreased. At about 1.5 c/deg, the period of the fundamental Fourier components exceeds functional receptive field size and the pattern-contingent aftereffects are effectively absent. As the adapting stimuli are further reduced in spatial frequency, the higher harmonics of these low spatial frequency targets fall near the optimal center frequency of a neuronal filter (or network of filters). At this point, however, the receptive field subtends only about one cycle of the checkerboard (i.e., the effective stimulus is one black square adjacent to one white square) and treats the energy distribution as if it were a rectilinear grating (i.e., contains the fundamental and the higher harmonics in the same orientation). Thus, the color aftereffects appear to be associated with the edges as opposed to the fundamental Fourier components.

A less parsimonious view would postulate that a low-frequency mechanism, tuned to the fundamental of low-frequency patterns mediates the "reversed" color aftereffects when low spatial frequencies are used. With this explanation, it would be necessary to

postulate some sort of antagonistic interaction between such mechanisms to account for the lack of after-effects which occur when stimuli of about 1.5 c/deg are used. While this position is not precluded by the present data, it seems unlikely. Future investigations of pattern-contingent color aftereffects (or masking) which compare the magnitude of cross-adaptational effects of checkerboards upon the perception of simple and complex sine-wave gratings should disassociate these two views.

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