tic gratings were complementary to the adapting color presented with the same stripe orientation. With checkerboard test stimuli, squares appeared red and diamonds appeared green ($\chi^2 = 18.12$, d.f. = 2, $P < .001$). Since contingent aftereffects were obtained when Fourier components of the checkerboard test stimuli were oriented in the same direction as corresponding grating adapting stimuli, Fourier components of the test stimuli rather than their edges are critical for contingent color aftereffects. The observed frequencies of complete and partial aftereffects were essentially the same with checkerboard tests as with grating test stimuli, so the effects are of approximately equal magnitude.

As far as we know, these data are the first to indicate that color is coded with frequency-specific (as opposed to feature-specific) information. This is important, since it extends the predictions concerning Fourier-like mechanisms which have been suggested by data obtained with threshold measures (*3*, *5*) or rating procedures (*4*). Consequently, these data bear on various color aftereffects contingent on pattern (*1*, *8*) by suggesting a fundamental process under which human perceptual responses to diverse figural stimuli may be unified. Some consideration (*9*) has been given to the idea that color aftereffects contingent on pattern derive from higher order association between simple color mechanisms and pattern-specific processes. If such an associational process is involved in these aftereffects, our procedure is an indirect way of studying frequency analysis mechanisms. The results reported here are probably limited to medium and high spatial frequencies. As Kelly (*5*) has pointed out, if the fundamental frequencies of gratings and checkerboards are lowered, bars and checks become logically indistinguishable, and there should be no difference between the adaptational effects of each.

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A Comparison of Fourier Analysis and Feature Analysis in Pattern-Specific Color Aftereffects

Abstract. *Subjects were adapted to alternating upright red and oblique green checkerboards. After adaptation, vertical and horizontal gratings appeared pink and oblique gratings appeared green. The results show an orientation and spatial frequency selectivity predicted by two-dimensional Fourier analysis.*

McCollough (*1*) was the first to note that colored aftereffects could be made contingent on the pattern of adapting stimuli. The aftereffects are produced by adapting subjects to pairs of chromatic patterns which are alternated every few seconds. Subjects subsequently view achromatic versions of the same patterns. If subjects report each achromatic pattern to be tinged with the complement of the color contained in the pattern during adaptation, the patterns were processed by different color- and pattern-sensitive neural channels. If no color is seen, the patterns are presumed to have been processed by the same channel and to have cancelled each other. In McCollough's original paper, the adapting stimuli were identical gratings of different orientation. The discovery of chromatic aftereffects in her experiment was, therefore, evidence of orientation selectivity in the visual system. More recently, pattern-specific color aftereffects have been used to demonstrate channels sensitive to spatial frequency (*2*, *3*) and motion (*4*). Similar channels have been found in studies in which a variety of other psychophysical techniques were used (*5*). Although disputed (*6*), pattern-specific color aftereffects based on visual features such as curves (*7*) and angles (*8*) have been reported.

McCollough originally attributed orientation-specific effects to edge-sensitive neural units of the type discovered by Hubel and Wiesel (*9*). Most subsequent researchers have continued to ascribe the aftereffects to edge detectors (*10*). In most studies, square- or rectangular-wave gratings with edges and fundamental Fourier components in the same orientation have been used. The purpose of our experiment is to demonstrate that Fourier analysis (*11*) can better account for the processing of patterns than an analysis which treats spatial stimuli as collections of visual features.

The adapting patterns were chosen so that the edges and fundamental Fourier components lay in different orientations; the predictions of Fourier and feature analyses were thus in conflict. Three experienced and two naive subjects adapted for 15 minutes to high-contrast chromatic checkerboards projected onto a white screen by a slide projector. Three of the subjects viewed a red upright checkerboard (edges at 0° and 90°) alternating every 10 seconds with a green oblique (edges at 45° and 135°). The other two subjects adapted to the reversed pairing of color and orientation.

One cycle of light and dark check elements subtended a visual angle of 0.18° along the edge axis. This corresponds to one period of a square-wave grating with a spatial frequency of 5.6 cycles per degree of visual angle. Frequency specified in this way was used to characterize checkerboard patterns of a given check size.

After adaptation, subjects viewed the achromatic test patterns (Fig. 1). Subjects were tested on nine similar patterns which varied only in the spatial frequency of the component gratings. An analysis which treats patterns as a collection of edges predicts that the aftereffects of red upright and green oblique checkerboard pairings should be green in the 0° and 90° gratings, and red in the 45° and 135° gratings. Kelly (*12*) has pointed out that the fundamental Fourier components of an upright checkerboard are oriented at 45° and 135°. Therefore, Fourier analysis predicts that the red upright checkerboard should produce a green aftereffect in the 45° and the 135° gratings. Conversely, green oblique checkerboards have their fundamental Fourier components oriented at 0° and 90°, so that red aftereffects should be seen in these orientations. All five subjects confidently reported chromatic aftereffects congruent with Fourier analysis rather than with edge analysis. Subjects who adapted to the reverse pairing of color and orientation reported the opposite color aftereffects. The colors of the sectors could be reversed by tilting the head 45°, and a second reversal could be caused by further tilting to 90°.

All subjects reported aftereffects with all nine test patterns. Subjects were then asked to rank the nine test patterns according to the strength of the aftereffect, from 1, the most saturated, to 9, the least. Individual subject rankings are shown in Fig. 2A. The strongest aftereffects were found by most subjects for gratings with a fundamental spatial frequency a factor of 1.5 (+ 0.5 octave) above the frequency of the adapting checkerboards. This result agrees well with Kelly's (*12*) demonstration that the spatial frequency of the fundamental Fourier components of a checkerboard lie a factor of 1.41 (that is, $\sqrt{2}$) above the check size. The aftereffects, therefore, exhibit not only an orientational but also a spatial frequency selectivity predicted by the two-dimensional Fourier spectra of the adapting patterns. The tuning of the spatial frequency selectivity appears to have a fairly broad bandwidth. This would appear to argue against a Fourier model, since narrow bandwidths seem necessary for a Fourier analysis to be performed. However, rankings have only ordinal scale properties. That is, the change in aftereffect strength corresponding to a difference between rankings of 1 and 2 is not necessarily the same as that corresponding to the difference between rankings of 2 and 3. Therefore, no strong conclusion about the bandwidth of the aftereffect can be made, and the conflict may be more apparent than real. However, subjects reported that color had almost entirely disappeared in patterns ranked 8 and 9.

In order to confirm the spatial frequency selectivity of the aftereffect, the experiment was repeated for adapting patterns of lower spatial frequency. Two experienced and one naive subject adapted to checkerboards of 1.7 cycles per degree of visual angle. The results of this experiment are similar to those of the previous experiment (Fig. 2B).

It could be argued that the length of individual edges in the checkerboards might have been too short to elicit a response from edge detector units. To test this possibility, three subjects were adapted to checkerboards of 0.85 cycle per degree of visual angle and three more to those of 0.425 cycle per degree. In both cases, weak aftereffects, in accord with Fourier analysis, were reported by all subjects. The failure to obtain strong color aftereffects following adaptation to low spatial frequency patterns has previously been noted (*2*). However, the weak aftereffects found here might have been due to the low luminance of the adapting stimuli (*13*). The 0.425 cycle per degree checkerboard contained edges longer than 1°. These edges seemed long enough to excite possible feature detectors since acuity has been shown to reach an asymptote for features of this length (*14*).

Although the results of this experiment conflict with the predictions of a feature model of pattern vision (*15*), they do not rule out the possibility that chromatic aftereffects can be made contingent on features under other conditions. There is considerable evidence from electrical recording work (*16*) for the existence of neurons sensitive to a number of specific visual features. This fact does not prove that these units directly mediate pattern vision in humans, however. It is possible that a group of feature-sensitive neurons might indirectly mediate pattern vision by projecting to higher order units which act as Fourier analyzers.

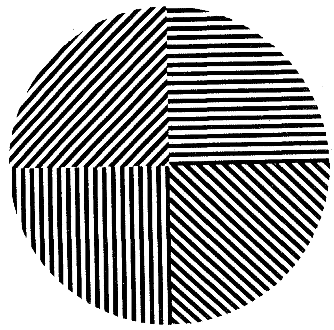

Fig. 1. Example of achromatic patterns used to test for color aftereffects. Each pattern was composed of four gratings of the same spatial frequency.

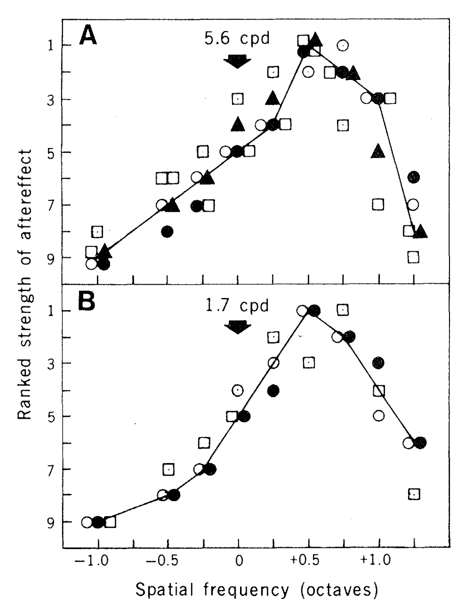

Fig. 2. Individual subject ranking of the nine test patterns after adaptation to checkerboards with a spatial frequency of 5.6 cycles per degree (*cpd*) of visual angle (A) and 1.7 cycles per degree of visual angle (B). Lines are drawn through the median rankings for each spatial frequency test pattern.

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13. Red and green patterns were produced by projecting slides through Wratten 25a and 61 filters. In the first two experiments, luminance of the red patterns was 13.6 cd/m², the green patterns, 23.8 cd/m², and achromatic patterns, 187 cd/m². In the third and fourth adapting conditions, red patterns were 1.87 cd/m², green patterns, 2.89 cd/m², and achromatic patterns, 6.8 cd/m². The size of the visual field was 4.4° in the first two experiments, 14.9° in the third, and 29.8° in the fourth.
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