plant precursors; (iii) "induction" of pheromone biosynthesis (possibly over multiple generations); (iv) de novo biosynthesis; and (v) production by microorganisms associated with the plant or insect. We believe it is unlikely that all insects will use the same method or methods for procuring pheromone. Schneider *et al.* (*27*) reported the degradation of dietary compounds (alkaloids) in plants to pheromones in danaid butterflies, and Pliske (*28*) discussed the reproductive importance of the attraction of danaids and other Lepidoptera to alkaloid-containing plants. Cardé *et al.* (*29*) found that males of the Oriental fruit moth, an apple-feeding tortricid moth related to the OLR, respond sexually (precopulatory behavior) to a compound which is not a tetradecenyl acetate, namely, dodecanol. We have found that dodecanol is a significant component of apple leaves, a food source of the Oriental fruit moth (*9*). Twelve-carbon compounds of varying functionality have been reported as components of the sexual communication system of other tortricids, including the fruit tree leaf roller (*30*), a member of the same genus as the OLR. The biological activity of the male OLR (*2*) in response to oak leaves could partly involve responses to 12-carbon compounds (*31*) in the plant. [Whether the reported correlation in the Tortricidae of the success of pheromone trapping with the amount of foliage per acre (*32*) is due in part to the behavior mediated by such host plant chemicals remains to be elucidated.]

Whatever mechanisms are involved in the ultimate production of pheromones, investigations such as those by Miller *et al.* are likely to provide insight into the general importance of nutritional chemicals in biological processes.

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Spatial Frequency–Contingent Color Aftereffects

Abstract. *Two-dimensional Fourier analysis of checkerboards reveals that major components are at a 45° angle to the check edges. After adapting to chromatic checkerboards, subjects who viewed achromatic grating stimuli reported that complementary color aftereffects are aligned with spatial frequency components rather than with the edges in the pattern.*

McCollough attributed orientation-contingent color aftereffects to chromatic adaptation of edge detectors (*1*). Implicit in this interpretation is the assumption that human pattern perception involves a relatively simple feature-extraction mechanism (*2*). Other studies have suggested that spatial properties of visual stimuli are processed by spatial frequency analysis (*3*). There is evidence that the visual system responds to the spatial period rather than to the bar width of grating stimuli (*4*). Our study is an extension of these findings, and emphasizes the importance of frequency analysis in visual perception. We used checkerboard adapting stimuli and square-wave test stimuli (or vice versa) to assess the relative importance of edges and spatial frequency components in the production of contingent color aftereffects. Kelly (*5*) pointed out that checkerboards contain Fourier components oriented at 45° angles to the edges of individual checks. Our results indicate that color aftereffects contingent on pattern involve the orientation of the major two-dimensional Fourier components rather than the orientation of the edges.

The four patterns used in this study were labeled "squares," "diamonds," "verticals," and "obliques" (Fig. 1). The square pattern was a checkerboard with the edges of individual squares oriented vertically and horizontally. The diamond pattern was identical to the square except that the checks were rotated 45° (edges of squares were on the diagonals). Vertical and oblique patterns were square-wave gratings oriented appropriately. The grating spatial frequency was 2.5 cycles per degree of visual angle, and the sides of the checks were 12′ of visual angle (*6*). All stimuli

Table 1. Color aftereffect responses to achromatic test stimuli before and after adaptation. Responses to the forced-choice questions were coded as complete (both red and green aftereffects with the predicted test orientations), partial (either red or green aftereffects in a predicted direction), or no predicted color aftereffect.

Response	Frequency of response			
	Complete	Partial	Neither	Total
Experiment 1: Adaptation to red squares and green diamonds				
Green squares and red diamonds				63
Before adaptation	0	6	57	
After adaptation	11	24	28	
Red horizontal and green oblique stripes				63
Before adaptation	0	6	57	
After adaptation	9	20	34	
Experiment 2: Adaptation to red vertical and green oblique stripes				
Vertical green and oblique red stripes				39
Before adaptation	0	5	34	
After adaptation	14	10	15	
Red squares and green diamonds				39
Before adaptation	0	4	35	
After adaptation	11	12	16	

were Kodalith negatives (96 percent contrast) transilluminated in a tachistoscope (Scientific Protoype model 800-F). Test stimuli were presented at a luminance of 5.14 cd/m^2, averaged across the entire field. The luminances of the red and green adapting stimuli were 12.7 and 27.5 cd/m^2, respectively, and each rectangular stimulus field subtended 9.0° of visual angle on a side.

In the first experiment, the test stimuli were two compound test patterns; one contained squares and diamonds, the other horizontal and oblique stripes (Fig. 1A). Subjects (N = 63) were asked to compare the two panels of a test pattern presented in white light and report their perceptions on written questionnaires. The observers were shown both grating and checkerboard patterns in counterbalanced order both before and after adaptation. They were forced to choose a color (red, orange, yellow, green, blue, or purple) which best described the right panel. This forced-choice procedure was repeated for the left panel. All observers then adapted for 10 minutes to alternating 3-second presentations of a pattern of squares in red light (Wratten filter No. 26, dominant wavelength of 630 nm) and diamonds in green light (Wratten filter No. 55, dominant wavelength of 525 nm). Three minutes elapsed between adaptation and final testing. During this time, subjects gazed around the dimly illuminated room and conversed with the experimenter.

If edges are the prepotent aspect of these stimuli, then contingent color aftereffects of text patterns with horizontal and vertical edges should be green and those with oblique edges should be red.

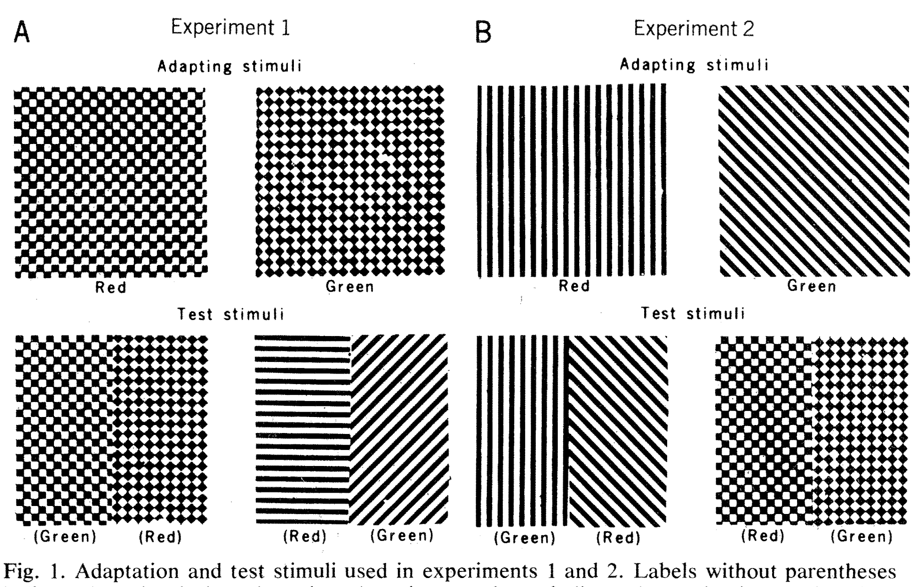

Fig. 1. Adaptation and test stimuli used in experiments 1 and 2. Labels without parentheses indicate the color during adaptation; those in parentheses indicate the predominant color aftereffects after adaptation.

If the orientation of major Fourier components is the more important characteristic, then test stimuli with such components oriented vertically and horizontally (diamonds and horizontal stripes) would be expected to appear red, while those with oblique components (squares and oblique stripes) would appear green. Both hypotheses predict that the checkerboard test patterns would elicit the appearance of red diamonds and green squares since both Fourier components and edges are in the same orientation in test and adapting stimuli. The test pattern with horizontal and oblique gratings would discriminate between the hypotheses, since the square adapting stimulus contains horizontal and vertical edges, but the largest Fourier components are on the diagonals.

With the achromatic checkerboard test stimuli, almost half of the subjects reported that squares appeared green and diamonds appeared red (Table 1). The increase of partial and complete responses after adaptation was statistically significant ($\chi^2 = 28.51$, d.f. = 2, $P < .001$) (*7*). This result shows only that a contingent color aftereffect can be obtained with checkerboard test and adapting stimuli, since the aftereffects could have been due to either edges or Fourier components of the test stimuli. With grating test stimuli, the subjects reported that oblique gratings appeared green and horizontal gratings appeared red (Table 1). The increase of partial and complete reports of aftereffects was statistically significant ($\chi^2 = 15.33$, d.f. = 2, $P < .001$). Since the aftereffects occurred in the same orientations as the major Fourier components of checkerboard adapting stimuli, contingent color aftereffects result from major Fourier components rather than the edges of the adapting stimuli. Of the 35 subjects who reported partial or complete aftereffects after adaptation to checkerboard stimuli, 30 also reported partial or complete aftereffects with gratings.

The second experiment was conducted to see if the same contingent aftereffects could be obtained with square-wave gratings as adapting stimuli (Fig. 1B). All procedural details were identical to those of experiment 1 (N = 39). After adapting to gratings, the subjects reported that vertical stripes appeared green and oblique stripes appeared red (Table 1). The increase of partial and complete aftereffects after adaptation was statistically significant ($\chi^2 = 16.98$, d.f. = 2, $P < .001$). This is a McCollough effect with the two adapting orientations 45° apart, since reported colors of achromatic 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 checker-