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## Curvature Detectors in Human Vision?

McCollough (*1*) showed that a striking aftereffect was produced by adaptation for several minutes to a vertical grating of black and orange stripes alternating with a horizontal grating of black and blue stripes. Black and white test gratings with retinal orientations similar to those of the adapting patterns were tinged with colors opposite to the adapting colors. She ascribed these effects to "color adaptation of orientation-specific edge-detectors."

Riggs (*2*) has observed similar effects with patterns of curved lines. Fig. 1, A and B, shows his stimuli. The observer views lines that are concave up in green light and lines that are concave down in red light, always keeping his gaze near the center of each pattern (Fig. 1A). The test pattern (Fig. 1B) then appears pink on concave-up lines and green on concave-down lines. Adaptation to weakly curved lines produces aftereffects that are most vivid on patterns with sharper curvature. Riggs postulates curvature detectors, which prefer strong curvature.

McCollough's simpler idea (the oriented-line hypothesis) can explain these effects. While looking at the center of the adapting patterns, the retina to the right of gaze is exposed to green lines of positive slope and red lines of negative slope; the retina to the left of gaze is adapted to the opposite condition. The McCollough effect is, in fact, specific to retinal locus (*3, 4*). Now, with gaze at the center of the test pattern (Fig. 1B), concave-up lines appear pink due to adaptation to green lines of positive slope to the right of gaze and negative slope to the left of gaze. Similarly, concave-down lines appear green. The experiments I describe here show that this hypothesis accounts for Riggs' observations.

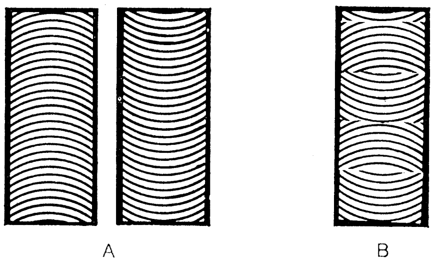

Fig. 1. (A) Adapting patterns viewed in magenta light and green light. These patterns have a radius of curvature of 4.5° when the patterns subtend about 5.5° across. (B) Test pattern with a radius of curvature of 4.5°. [Courtesy of L. A. Riggs]

High-contrast adapting patterns (Fig. 1A) were projected from the rear on a diffusing screen in magenta light (Wratten 34a filter) and green light (Wratten 53 filter). These colors (*4*) produce very strong McCollough effects. The mean luminance was approximately 140 millilamberts. The test patterns were high-contrast prints viewed in white fluorescent room light. All patterns were about 5.5° wide, as were Riggs'.

Three observers adapted for 20 minutes to the concave-up pattern in green and the concave-down one in magenta; the patterns were interchanged every 10 seconds. The observer scanned up and down the vertical midline of each pattern. With gaze at the center of the test pattern (Fig. 1B), concave-up lines appeared pink and concave-down lines green. But, with gaze about 1° beyond the left or right edge, the colors definitely reversed—concave-up lines now appeared green and concave-down lines pink. Riggs observed that the colors did not reverse when gaze was moved somewhat off the midline. The oriented-line hypothesis predicts that the colors will appear weaker as gaze moves off the midline, but the clearest color reversal will occur only when gaze falls about 1° beyond the edges of the pattern. No reversal is expected even when gaze is as much as 1.5° from the midline. The concave-up lines will still predominantly stimulate regions to the right of gaze with lines of positive slope and regions to the left of gaze with lines of negative slope, and the concave-down lines will have the opposite effect. (These properties may be seen by sliding a tracing of Fig. 1A across Fig. 1B.)

Riggs observed that each panel of the test pattern (concave-up or concave-down lines) appeared pink or green throughout. This spread of color along contours within each panel, especially to the horizontal tangents of the curves, reflects a general property of the McCollough effect (*4*), and does not support the curvature detector hypothesis in particular, contrary to Riggs' argument.

Truly curvature-specific adaptation was not observed here. Three observers adapted for 20 minutes as described above while fixating a single point on a horizontal train of lighted points that moved leftward across the adapting patterns at approximately 1.5° per second. The train subtended 20° centered on each pattern, and the observer tracked repeatedly from far right to far left. Two other observers adapted for 1 hour to the opposite color condition, and the patterns were interchanged between each track from right to left. No aftereffects were seen. Every retinal area affected by the test pattern (with gaze anywhere within the test contours) is exposed equally to each orientation in both green and complementary magenta. This presumably cancels out orientation-specific adaptation. (The patterns are symmetric, and thus the tangents to the green and magenta lines are identical.) To produce this control condition, the train of lights must be at least three times the width of the adapting pattern. However, if gaze is confined strictly to the midline of the test pattern (an unlikely condition), the train must be twice the width of the adapting pattern. MacKay and MacKay (*5*) also observed no aftereffects with large movements of the adapting pattern left and right past a stationary fixation point.

Riggs' color effects can be produced by adapting to straight lines. High-contrast square-wave gratings of 2 cycles per degree were presented in fields 12° wide and 6° high. The entire grating in one field was tilted 6° counterclockwise from horizontal and was green on the right half and magenta on the left. The grating in the second field was tilted 6° clockwise from horizontal with the colors reversed. Three observers scanned the vertical line that divided each field for 20 minutes, as the fields were alternated every 10 seconds. Concave-up lines on the test pattern (Fig. 1B) appeared strongly pink and concave-down lines appeared strongly green. The aftereffects were progressively stronger on patterns of greater curvature: the colors were weak when the radius of curvature was 24°, and strongest when it was 4.5° [see figure 3 in (*2*)]. Thus, adaptation to patterns tilted only slightly off horizontal produced maximum aftereffects on test patterns curved strongly away from horizontal. This is explained by the oriented-line hypothesis, as shown by the next experiment.

The adapting fields were similar to those in the preceding experiment, but the entire 6° counterclockwise grating was green and the entire 6° clockwise grating was magenta. The test pattern was a bipartite field in which gratings (2 cycles per degree) in the upper and lower halves were tilted symmetrically to either side of horizontal by various amounts. After 3 minutes of color adaptation, six observers reported that the pattern with the same tilt as the adapting pattern, 6°, was not the most vividly colored. The pattern with the maximum color was observed between 12° and 21° for five of the six observers. This might be explained as follows. Each adapting pattern produces a distribution of adaptation over a wide range of orientations. The orientation distributions produced by the two adapting patterns will overlap considerably because the patterns are similar in orientation. A test pattern whose orientation falls near the peaks of the distributions will strongly elicit both aftereffects, but little color will be seen because the two aftereffects are complementary in color. The distributions may overlap less away from the peaks. Thus, a test grating in this region will appear more vividly colored. These arguments provide a very simple explanation for the observation that adaptation to weak curvature produces the best aftereffects on test lines of sharper curvature.

The oriented-line hypothesis is thus quite sufficient to explain all the curvature effects observed by Riggs. Furthermore, truly curvature-specific adaptation could not be demonstrated by using a moving fixation point.

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Stromeyer and I have come to opposite conclusions about explaining aftereffects of curvature in terms of an oriented-line hypothesis. My view (*1*) is that "these effects, strongly dependent on radius of curvature, cannot be attributed to tilt or orientation." Stromeyer and I disagree not so much on the effects observed (contingent aftereffects, or CAE's) but on the interpretation of them. Indeed, we have been sharing information about techniques, stimulus patterns, and other technical aspects of the work.

Certainly, line orientation is a major factor in generating the CAE with straight-line arrays (*2*). Nor is there any doubt that the CAE is specific to retinal locus (*3*). However, it is also well established that the CAE can be produced without any differences of line orientation. As an example, patterns in which all the lines are vertical have been used to produce differential CAE's dependent on spatial frequency of the lines (*4*). Also, the inspection of lines of one color moving to the left and lines of the opposite color but the same orientation moving to the right produces a vigorous CAE in which opposite colors appear on moving achromatic test lines having the same orientation but opposite directions of motion (*5*).

The first point of real disagreement is with respect to paragraphs 2 to 6 in Stromeyer's comment. I do not believe that the oriented-line hypothesis can explain the effects observed. Given the inspection conditions described in paragraph 3, it is true that "with gaze at the center of the test pattern (Fig. 1B), concave-up lines appear pink . . . [and] concave-down lines appear green." But the most interesting point is that this color specificity is retained when the subject moves his gaze as much as 1.5° to either the left or the right of the center of the pattern. To realize the implication of this, imagine that a circle 2° in diameter is placed anywhere within the lowermost test panel of Fig. 1B. Such a circle, fixated at the center, is imaged on the fovea centralis, the retinal region subserving the clearest vision for the test lines. Placing the 2° circle with its center 1.5° to the right of the center of the 5.5° test panel has the effect that the fovea views positively sloping portions of test curves that are concave up; placing it 1.5° to the right of the center has the fovea looking at negatively sloping portions of the same curves. In both locations, however, the CAE is seen as pink in the curves concave up, following the procedures outlined above by Stromeyer. Now repeat the same left and right tests in the test panel just above, in which the lines are of opposite curvature. This time the positively and negatively sloping portions of the curves are seen throughout as green. The dependence of the observed colors on direction of curvature and line orientation is shown in Table 1.

If Stromeyer objects that, despite the known specificity of the McCollough effect to retinal locus, regions outside the fovea somehow are involved, or that there may be a "spread of color . . . within each panel, especially to the horizontal tangents of the curves," I invite him to view the test panels through a mask that exposes only a vertical strip 2° wide. He will find that the same color is seen within a strip that is placed either to the right or to the left of center, even though the mask then covers all the horizontal and the oppositely sloping portions of the curves in each panel. Within these limits the color of the CAE is determined not by line orientation but by direction of curvature. So what is curvature? It is rate of change of slope or orientation of line. That feature, present all along the test curves, seems to govern their color. Lines that are concave up have a constantly increasing slope going from left to right in each panel. Concave down means constantly decreasing slope. The visual system is presumably responding, then, to the direction in which orientations are changing.

It is interesting that no color reversal occurs as fixation is moved from the center to the edge of the test panel. While the edge is fixated, the half of the fovea that still lies within the test panel is stimulated by strongly sloping lines, yet neither hue predominates in the CAE. Perhaps the factors of curvature and line orientation are opposing one another almost equally at this point, and it is only after the fovea moves entirely outside the test area, with fixation 1° or more away, that the curvature factor becomes so weak that color reversal can occur.

I regard the moving-lights experiment described by Stromeyer in paragraph 7 as something of a red herring (or should I say a green and magenta herring?) dragged across the trail of the CAE. Granted that the 20° eye movements made during inspection do control for the factor of the line orientation by equally exposing each point on the retina with the two colors, the relative time of effective exposure to curvature is very short. An outside estimate is that the fovea occupies a favorable position (that is, centered within 1.5° of the centers of the inspection patterns) during 15 percent of the inspection time. Add to that the possible smearing of the lines on the retina, the possibility that detectors for motion may generate competing responses, and the likelihood that the 85 percent ineffective exposure time may permit the CAE to decay as fast as it is built up, and the prediction must be that if any CAE is obtained under these conditions it will indeed be minimal. The MacKays and Stromeyer report zero CAE's. White and I (*6*), using different experimental conditions (with steady fixation and patterns moving all the way across a restricted aperture) have obtained small but reliable CAE's after long periods of inspection. Inasmuch as a null hypothesis can never be proved, we regard even slight amounts of CAE as evidence that curvature can be effective in these difficult experiments in which the line orientation factor is canceled out. But we rely more heavily on the evidence (see above) of experiments in which stronger CAE's are obtained.

Table 1. Hues of pattern-contingent aftereffects of color.

| Direction of curvature | Slope of line | |
|---|---|---|
| | Positive | Negative |
| Concave up | Pink | Pink |
| Concave down | Green | Green |

The most interesting experiments are reported in paragraphs 8 and 9. Stromeyer verifies my finding (*1*) that "the most vivid aftereffects are seen on test patterns having a stronger curvature" than those used for inspection. His procedure, however, is one in which straight lines are used to build up the effects. In some experiments he tests also with straight-line patterns inclined at various angles to one another. These experiments may be leading in the same direction as those of White and Riggs (*7*). We show that a CAE can be produced by inspection of either curves or angles and tested with either angles or curves, and also that the inspection of nearly straight curves or angles leads to larger CAE's when tested with sharp curves or with angles near 90° than when tested with the ones used for inspection. A reasonable interpretation would seem to be that there are cortical units that receive inputs from more than one set of line orientation units, and that lines at right angles to one another (and curves of radius 3° or less) are particularly effective stimuli for such units. Our tentative hypothesis is that the visual system has some units that respond selectively to direction of change of slope, whether this be an abrupt change as in angles or a continuous one as in curves. We do not hesitate to invoke such constructs in view of present reports that they exist as hypercomplex cells in the cortex of cat and monkey (*8*). We doubt that the Stromeyer hypothesis about the overlapping sensitivities of separate line orientation units over a wide range of orientations is applicable here, since widths up to about ± 15° are characteristic of line orientation channels (*9*), while orientation differences near 90° are required for arousing CAE's of optimal strength.

In summary, McCollough's experiments and many succeeding ones show that CAE's can be established on the basis of line orientation. However, certain other CAE's are based on spatial frequency, direction of motion, and curvature under conditions in which the line orientation hypothesis is not applicable. Admittedly, we cannot yet take the leap of dealing with the perception of little green apples and pink cheeks, but we do wish to take one step in that direction. We maintain, as a working hypothesis, that there are visual units specialized both for color and for the changes in line orientation that define angles and curves.

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## Eye-Tracking Patterns in Schizophrenia

The report of saccadic interruptions during ocular pursuit in patients with schizophrenia by Holzman *et al.* (*1*) confirms and replicates a 1908 study by Diefendorf and Dodge (*2*) in which the authors graphically demonstrated similar saccades during ocular pursuit in patients with dementia praecox and compared them with individuals with mania, epilepsy, and dementia paralytica and normal controls. They used the beam of an "electric arc" reflected from the cornea onto a vertically sliding photographic plate (the rate of fall of which was ingeniously contrived by a hydrostatic device) to record re-