Is Orientation-Specific Color Adaptation in Human Vision Due to Edge Detectors, Afterimages, or "Dipoles"?

Abstract. *After one looks alternately at red vertical and green horizontal stripes, vertical and horizontal white stripes appear greenish and pink, respectively. This color aftereffect might imply that contour-detecting cells participate in human vision, or might simply be due to afterimages. A procedure that precludes afterimages still yields aftereffects, but sensory units less complex than edge detectors could be responsible.*

After a person looks alternately at grids of red vertical and green horizontal stripes for several minutes, vertical white stripes appear greenish and horizontal stripes appear pink (*1*). McCollough attributed this aftereffect to color adaptation of edge detectors in the visual system, citing neurophysiological evidence that some sensory cells respond well only to contours in a particular orientation on the retina (see *2*).

McCollough had several good reasons for assuming that the aftereffect was not due to ordinary negative afterimages (*3*). Three of the most salient were: (i) the McCollough effect is linked to the orientation of the white test stripes, whereas an afterimage can be seen best on a homogeneous surface; (ii) the McCollough effect appears even after equal exposure to complementary colors; and (iii) the classical afterimage requires either fixation of the colored adapting stimulus or a very intense stimulus, whereas the McCollough effect requires neither.

However, these facts, as well as others that suggested that afterimages are not responsible for the McCollough effect (*1, 4*), can in fact be explained in terms of afterimages, given one plausible assumption (*5*). The assumption is that observers tend to look predominantly at some part of the colored adapting grids. Suppose, for example, that observers see black areas as background and tend to fixate on colored bars during adaptation and on white ones during tests. Red vertical bars will then build up a greenish vertically striped afterimage, and green horizontals will yield a pink horizontally striped one. The alternate exposures, instead of cancelling each other out, will build up a plaid afterimage.

If the observer now fixates on a white bar in a black-and-white test grid, the parts of the afterimage that are visible against vertical white bars will be mostly green; those against horizontals will be mostly pink.

Several observations do indicate that McCollough's adaptation procedure may produce striped afterimages. For example, while the adapting grids are alternating, many subjects notice afterimage stripes running perpendicular to whichever colored grid is being displayed at the time (*6*). The existence of such afterimages suggests that fixations are not random.

However, other informal observations (*5*), suggesting that there is more to the McCollough effect than afterimages, led us to the following experiments.

Each of our adapting grids consisted of 11 red or green bars (0.4 by 10.5°, visual angle) spaced 0.4° apart on a black background (*7*). The luminances of the red, green, and black bars were 8, 6, and 0.3 millilamberts, respectively. The adaptation procedure was like McCollough's (alternately presenting a red and a green grid, one horizontal and one vertical), with two differences. (i) Each grid was flashed for only 80 msec each time (as compared to a few seconds in McCollough's experiment), too short a time to permit systematic eye movements (*8*). The interval between successive flashes was about 170 msec. (ii) Each grid appeared randomly in one of two locations on the screen. In one position, the colored bars fell where the black bars fell in the other position. The observers were told to fixate a luminous spot 0.04° in diameter, which remained lit throughout the experiment and which fell on the edge of a bar in the center of each colored grid. But no matter where the observers fixated and no matter what eye movements they made, they were unlikely to build up a systematic striped afterimage of either grid.

The test pattern (Fig. 1, inset), with luminances of 16 and 0.2 mlam on the white and black bars (each 0.4° wide), was shown to each subject after successive periods of adaptation—0.5, 1, 2, 4, and 4 minutes in the first experiment; and 0.25, 0.25, 0.5, 1, and 4 minutes in the second experiment. The test pattern was displayed for 45 seconds each time, preceded and followed by 5 seconds of darkness (*9*).

On each test trial, the subject used a printed checklist to answer five questions asked by the experimenter, who was unable to see what answers were given: "Do you see any color on the center diamond?" "If you had to pick a color for the center diamond, would you call it green, or pink? You must answer this question, even if you don't see any color." Next, these two questions were asked about the diamond surrounding the center one. Finally, the subject was asked whether the color that he saw (if any) looked weaker, the same, or stronger than on the immediately preceding test trial. After the last test trial, subjects were asked to

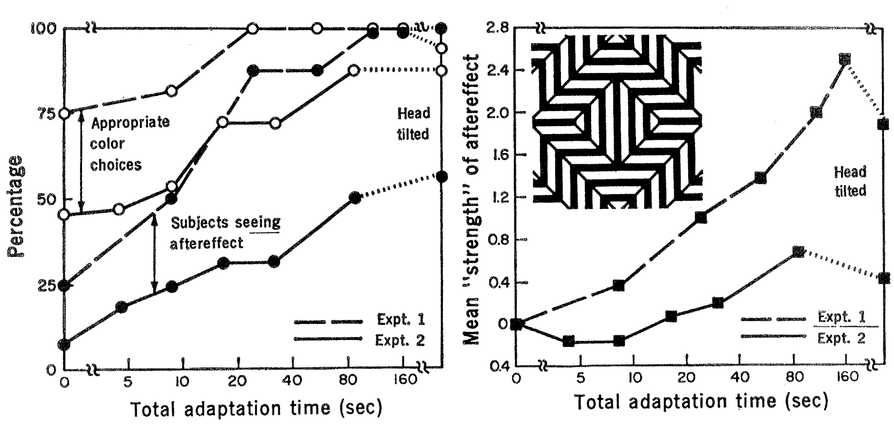

Fig. 1. Growth of the aftereffect produced by randomly located adapting flashes. ●, Percentage of subjects who reported that they saw some color in at least one part of the test figure and then named the appropriate color for that part (*10*); ○, percentage of color choices that were appropriate, regardless of whether the subject said he saw color or not (chance level = 50 percent); and ■, mean "strength index." A subject's "strength index" was calculated by adding 1 each time he judged the aftereffect color to be stronger than on the preceding trial, and subtracting 1 each time he judged it to be weaker. A judgment of "same" left the index unchanged. Thus the index could reach +6 (if a subject said "stronger" on all trials) or −6 (if he always said "weaker"). [Inset, test pattern (based on a painting by Reginald Neal)]

tip their heads 90° to one side (so that the physically vertical test stripes were retinally horizontal) and then answer the same five questions. All subjects had earlier been given practice filling out the checklists in response to four sample stimuli, three of which were actually tinted.

All eight subjects in the first experiment had previously seen the McCollough effect on a variety of test patterns. None of the 16 subjects in the second experiment had ever seen the effect or heard about its direction.

The main finding was that most subjects saw a McCollough aftereffect. On the last trial, 16 of the 24 subjects reported that they saw an appropriate aftereffect color on at least one part of the test figure, and six of the remaining eight named both appropriate colors when forced to "guess."

Thus, the McCollough effect occurs even when striped afterimages are precluded by flashing the colored grids randomly in two different locations. The phenomenon must therefore depend (as McCollough assumed) on neural units more complex than the individual retinal receptors that could (in principle) yield an ordinary afterimage.

Several possible objections to this conclusion are countered by various aspects of the procedure and results. For example, it is conceivable that striped afterimages could be produced by certain sorts of eye movements, by a preponderance of colored grids in one location, or by optical imperfections in the slides, the projectors, or the subjects' eyes. Most such objections would lead one to expect that the aftereffect would be at least as likely to be seen after a short adaptation period as after a long one, that it would wax and wane irregularly as adaptation time increased, and that subjects would often see the "wrong" colors on the test figure (whenever the afterimage overlapped the test pattern in an inappropriate way).

However, as total adaptation time increased, there was a steady growth in the strength of the aftereffect (Fig. 1). Only one subject ever did report, after seeing an aftereffect color on one trial, that the color looked weaker on any subsequent trial with head upright. And only one subject reported seeing an inappropriate color on the test pattern after being exposed to the colored grids.

Our findings show that afterimages cannot account for the McCollough effect. Must we then attribute it to color adaptation of edge detectors in the visual system? Although that inference is attractive, especially in view of the recent discovery of cells in the monkey's visual cortex that are differentially sensitive to both wavelength and orientation of a contour (*11*), the psychological data do not yet demand such a conclusion.

The perceptual phenomena observed to date could be ascribed to hypothetical sensory units much less highly structured than edge detectors are commonly thought to be—units that could not even report accurately on a contour's orientation, and thus could not individually yield a perception of an edge. The simplest such unit [Gibson and Harris (*5*) called it a "dipole"] would receive inputs from two nonconcentric areas of the retina. Given a population of fatiguable dipoles with some variation in spectral sensitivity and in spatial relation of receptive areas, very few additional assumptions are necessary to deal with all data on the McCollough effect (*12*). For example, if the dipoles responded to differences between light intensities on their two receptive areas, they would fire when a light-dark boundary fell between the two areas. This rudimentary model may help clarify which of the presumed properties of edge detectors and which physiological findings are actually relevant to the psychological data.

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References and Notes

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5. A. Gibson and C. S. Harris, paper read at convention of the Eastern Psychological Association (1968).
6. Hajos's subjects reported seeing aftereffect bars during dark intervals between presentations of adapting grids (*4*).
7. The colors were produced by gelatin filters that give a strong McCollough effect: Edmund Scientific Co. No. 818 for the red, and No. 471 combined with "cyan" for the green.
8. M. G. Saslow, *J. Opt. Soc. Amer.* **57**, 1030 (1967).
9. A shaded incandescent light, permitting the subject to read the answer sheet, remained on during the entire session. The luminance of the answer sheet was less than 0.1 mlam and was negligible elsewhere.
10. The bias in responses that preceded exposure to the colored grids in the first experiment was eliminated in the second by counterbalancing conditions: half the subjects saw green vertical and red horizontal adapting grids, and half saw the reverse; for half, the center test diamond was vertically striped, and for half, horizontally.
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13. We thank S. Sternberg and J. Krauskopf for suggestions and R. A. Payne for aid in designing the randomizing circuit.
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Potassium Feldspar in Weekeroo Station, Kodaikanal, and Colomera Iron Meteorites

In a recent paper (*1*), a reference was made to our "erroneously [reporting] a feldspar of composition $Ab_{64}An_9$-Or_{27} in Weekeroo Station as potassium feldspar" (*2*). No explanation or alternative nomenclature was offered by these authors; however, they apparently meant that, since the feldspar in question has an Ab : Or molecular ratio of 2:1, it should correctly be referred to as alkali feldspar.

The electron microprobe analysis of this feldspar, as given in our paper, is an average of 5 to 15 spot analyses on each of ten very small grains. The K_2O content ranges from 0.90 to 11.5 percent by weight with a corresponding reciprocal Na_2O content of 9.8 to 3.1 by percent weight; the average is 4.9 percent K_2O and 7.6 percent Na_2O. Potassium-rich areas were too small ($<10\ \mu$) to obtain a complete analysis without interference from the host material. X-ray diffraction studies indicate a possible antiperthitic intergrowth of sodic plagioclase and potassium feldspar. Unfortunately, the extremely small grain size and scarcity of material did not allow us to obtain precise x-ray data.

Potassium-rich areas are small in volume compared to the much larger sodic plagioclase host. The important point is that potassium feldspar is present in the Weekeroo Station meteorite. We chose to refer to the average of all analyses of these particular grains as potassium feldspar simply to distinguish between potassium feldspar and plagioclase and in keeping with the