McCollough Effects: Experimental Findings and Theoretical Accounts

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McCollough effects, a group of visual contingent aftereffects involving color and contour, have been the subject of a recent body of literature. While a number of investigations have simply reported variations of the original phenomenon, others have closely examined characteristics of these effects and the conditions under which they can be optimally produced. Indications that their spatial specificity is similar to that of single cortical cells investigated electrophysiologically in animals have inspired several models; however, the extraordinary persistence of the effects is difficult to explain at a single-unit level. Findings which suggest that McCollough effects have characteristics like those of learned responses may help to resolve this paradox.

In 1965 McCollough reported a color aftereffect which was dependent on the orientation of lines and could persist for an hour or more. It was produced by exposing subjects to a grating of vertical black stripes on an orange background, which alternated every few seconds with a horizontal grating on a blue ground. After 2 to 4 minutes, when subjects viewed a test display of black and white vertical and horizontal gratings side by side, most of them reported seeing a desaturated blue green on the background of the vertical lines and orange on the horizontal portion. These colors would exchange places on the gratings if the test stimuli or the subject's head were rotated 90 degrees, disappearing altogether at approximately 45 degrees.

Since McCollough's article, several variants of the original phenomenon have been reported. These chromatic aftereffects can be made contingent on a variety of spatial patterns, most of which have been found in contour-masking experiments to have selective threshold-elevating properties. It has been suggested that these contour-masking effects reflect the activity of neural pattern analyzers (Weisstein, 1969), and there has been some speculation that McCollough effects indicate a relationship between form and color vision at a single-cell level.

Characteristics of these effects and the conditions under which they appear have been described in a substantial and rapidly accumulating body of experimental literature. The first part of this article is a survey of these data as well as a description of the reasoning behind designs and interpretations of the experiments. The second part is a more detailed review of theoretical attempts to account for the data.

SURVEY OF RESEARCH

The Dependent Variable

A major problem facing researchers who investigate this phenomenon is one of finding a satisfactory dependent variable. Although it is relatively easy to demonstrate these effects, it is rather more difficult to quantify them adequately. In many published reports, the data are simply whether or not subjects give the appropriate color response when viewing the achromatic test patterns. Under conditions in which color naming is unrestricted, not all naive subjects report the effect (e.g., McCollough, 1965), possibly because the colors are quite desaturated. If a forcedchoice procedure is used, some subjects who do not report seeing colors on test patterns will nevertheless give the appropriate color response when forced to guess (Harris & Gibson, 1968). Magnitude estimation has been

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used to determine relative strengths of the aftereffects (Stromeyer, 1969), but the small range in magnitude over which McCollough effects occur makes the use of such a technique difficult.

Several different procedures may be classified as cancellation of effects; here, some aspect of the test pattern is varied until the aftereffects disappear. Since McCollough effects are strongly dependent on spatial dimensions of adaptation and test stimuli, some investigators have chosen as their dependent variable the amount of change in test pattern orientation (Teft & Clark, 1968) or in test pattern spatial frequency (Harris, Note 1) required to make the apparent color disappear. Care should be taken in interpreting data of this type as an indication of magnitude of the effect since the variable actually being measured is bandwidth (i.e., the range of orientations (or spatial frequencies) over which the effects remain visible).

A color-cancellation technique, achieved by varying the colorimetric purity of the light bars of test gratings, is a more direct measure of strength. Variable amounts of desaturated lights which are complementary to the color of the aftereffect are added to test patterns until the gratings appear achromatic. The colorimetric purity required to cancel the effects can then be used as an index of the effect's magnitude (Riggs, White, & Eimas, 1974).

Hue matching has been used by several experimenters. Stromeyer (1969) had subjects use Munsell colored papers to match the color of aftereffects. In another of Stromeyer's studies (1972b), subjects adjusted a rotating polarizer until the saturation of a projected field (similar in color to the effects) matched the strength of effects seen on a test display. Other investigators (Hirsch & Murch, 1972; Murch & Hirsch, 1972; Skowbo, Gentry, Timney, & Morant, 1974; Timney, Gentry, Skowbo, & Morant, 1974) have used a projection colorimeter to match McCollough effects. With the use of such instruments, strength of the effects can be expressed in terms of CIE chromaticity coordinates.

Spatial Parameters

Many articles in the literature have focused on spatial features of the inducing and test stimuli. Here, the variables of interest have been (a) the kinds of spatial patterns that can be paired with color during adaptation to produce these effects or (b) the characteristics of achromatic test patterns which are necessary for the effects to appear.

McCollough's (1965) finding that the orientation of the test gratings determined the color of the aftereffect led her to suggest that color adaptation of orientation-specific "edgedetector mechanisms" was a possible explanation for the effect. Fidell (1968, 1970) pursued this idea. With reference to findings that neurons selective to orientation in cats and monkeys had high degrees of angular specificity (e.g., Campbell, Cleland, Cooper, & Enroth-Cugell, 1968), she reasoned that McCollough's effect might depend on the excitation of different populations of cortical neurons by the adapting patterns. Fidell found that pairing red and green with various adaptation gratings whose angular separation was 90 degrees produced the effect quite readily. However, for divergences of 45 and 22 degrees, subjects reported seeing hues on the test patterns less frequently; and at 11 degrees of separation in orientation (which would presumably stimulate the same population of edge-detecting units), hue responses were rare.

The importance of the "density," as well as the orientation, of stripes in adaptation and test gratings was first pointed out by Teft and Clark in 1968. Taking as their dependent variable the degree of rotation of test gratings at which the aftereffect disappeared (a choice which emphasized the necessary correspondence between adaptation and test orientation), they found that less rotation was possible as the spatial frequency of the test grating departed from that used in adaptation. Stromeyer (1972b) reported that effects appeared strongest when test gratings had the same spatial frequency as adaptation grids. Results of a study by Harris (Note 2) underscored the importance of similarity between the retinal spatial frequencies of adaptation and test gratings. Uhlarick and Osgood (Note 3), in an experiment designed to separate the influences of black bar width, slit width, and spatial frequency, found similarities in bar widths to be the critical variable.

Other investigators have been able to produce differentially colored aftereffects using adaptation gratings of the same orientation but different spatial frequencies. Harris (Note 1) reported obtaining such an effect by pairing green with a vertical 5-cycles-per-degree grating and red with a vertical 10-cycles-perdegree grating. The aftereffect in this paradigm is, then, red appearing on achromatic gratings having the lower frequency and green, on the higher. A more parametric study was done by Breitmeyer and Cooper (1972). These authors based their reasoning on findings in animals of cells sensitive to spatial frequency (Campbell, Cooper, & Enroth-Cugell, 1969) and also on psychophysical evidence which suggested that in humans, neural elements exist which are maximally sensitive to some given range of spatial frequencies and less sensitive to higher or lower spatial frequencies (Blakemore & Campbell, 1969). Again using red and green, they combined a vertical 3.3-cycles-per-degree grating with gratings of various other frequencies. No subjects reported seeing an effect when the difference in adaptation frequencies was 15%, and all subjects saw effects when they differed by two octaves (a factor of 4). Lovegrove and Over (1972) also produced a spatial-frequency McCollough effect with stimulus configurations designed on the basis of psychophysical data. Working from the suggestion of Blakemore and Campbell (1969) that a single class of detectors processes all frequencies below 3 cycles per degree and that those sensitive to higher frequencies are tuned within a one-octave range on either side of preferred frequency, these authors predicted and did find that a spatial-frequency McCollough effect could be obtained only when the frequencies of the adapting gratings differed by at least one octave and when at least one grating was higher in frequency than 3 cycles per degree.

Leppmann (1973) has reported that color aftereffects induced with horizontal gratings of different spatial frequencies could also be seen on vertical test gratings. For both orientations, effects appeared strongest on the portion of a variable-frequency test grid which corresponded to induction frequency. Leppmann has suggested that his findings require postulation of units which are spatially tuned but not orientation selective.

While most studies of spatial frequency and orientation effects have used square-wave gratings, Stromeyer, Lange, and Ganz (Note 4) attempted to generate McCollough effects with complex sine wave gratings having identical spatial frequencies but which differed in the phase angles between their frequency components. They reported that Mc-Collough effects could be produced using leftand right-facing sawtooth gratings or gratings composed of the sum of the first and second harmonics; however, effects were weak with first-plus-third harmonic patterns, and almost absent with first-plus-fourth harmonic gratings.

Viola (Note 5) hypothesized that a Mc-Collough effect should not be inducible with sets of oppositely curved lines since they would be processed by edge detectors tuned to all tangents on the curves-in other words, the same population of detectors would respond to both sets. As predicted, she was not able to obtain aftereffects with curved patterns, although sets of orthogonally oriented straight lines presented under the same conditions did produce effects. More recently, however, Riggs (1973) has reported obtaining McCollough effects following adaptation to sets of oppositely curved lines. He found that stronger degrees of curvature produced effects more readily than weaker ones; Viola's use of relatively weak curves may account for her negative results. Similar findings were reported by White and Riggs (1974), who were able to induce McCollough effects with oppositely pointing chevron patterns most easily when the angles were 90 degrees. A finding in both these studies was that unlike McCollough effects built up with adaptation to straight lines, these effects were not necessarily strongest on test patterns having the same curvature or angle as the adaptation stimuli. Rather, all effects were seen best on test configurations with strong degrees of curvature or 90-degree angles. In addition, effects built up with inspection of angles could be seen on test patterns of curves, and vice versa. White and Riggs have speculated that both effects may be mediated by a mechanism which is broadly tuned for departures from straight lines and which responds best to stimuli that contain right angles or strong curvatures. They have related their hypothetical mechanism to descriptions of hypercomplex cells by Hubel and Wiesel (1965).

Leppmann (1973) found that differential color aftereffects could be made contingent on concentric circle patterns having different spatial frequencies. More complex pairs of spatial patterns, such as concentric circles alternating with radiating lines, were found by Fidell (1968) not to produce McCollough effects.

McCollough effects have also been produced by adaptation to colors paired with moving stimuli. Hepler (1968) had her subjects view green and magenta patterns of horizontal stripes moving up and down. After adaptation, white stripes moving up or down appeared to be tinted with the complement of the hue with which they had been paired during adaptation. No colors were reported when test grids remained stationary. Similar findings were described by Stromeyer and Mansfield (1970), though with a somewhat different paradigm. Their subjects fixated between two belts which moved in opposite directions (up or down) and were paired with different colors (red or green); the belts alternated in direction of movement and color. After adaptation, when the stripes moved in white light, subjects reported the predicted color associated with each direction of movement; the effects appeared to be most saturated at movement speeds near those used during adaptation. Stromeyer and Mansfield were also able to produce differentially colored aftereffects with a rotating spiral, by illuminating it with bipartite chromatic fieldsgreen on one side and red on the other when it rotated in one direction, and the reverse color arrangement when it moved in the other. When the spiral was rotated in white light, colors were reported in positions opposite to those with which the direction of rotation had been paired. Several control conditions produced results which indicated that aftereffects required adaptation to different colors paired with different directions of motion.

Color-Contingent Spatial Aftereffects

A few articles have reported "reverse" Mc-Collough effects—that is, spatial aftereffects

which are contingent on color. Held and Shattuck (1971) reported that the direction of a tilt aftereffect could be made color dependent: After scanning red and green stripes tilted, respectively, clockwise and counterclockwise off the vertical, a test pattern of vertical lines appeared tilted counterclockwise when red and clockwise when green. The magnitude of the effects was a good deal smaller than that usually found in tilt-aftereffect experi-(e.g., Campbell & Maffei, 1971; ments Morant & Harris, 1965), and the effects were not significant when subjects were tested 24 hours after adaptation. Some color specificity in tilt aftereffect has also been reported by Lovegrove and Over (1973).

Virsu and Haapasalo (1973) have reported evidence for a shift in apparent spatial frequency that is color dependent. For example, following adaptation to narrow red alternating with wide green gratings, subjects presented with red and green grids of an intermediate density judged the spatial frequency of the red grating to be lower than that of the green. A similar effect was reported by Wyatt (Note 6).

Color-contingent spiral aftereffects have been reported by two groups of investigators. One of these, Favreau, Emerson, and Corballis (1972), had subjects adapt to a rotating spiral which was either red while expanding and green while contracting, or vice versa. Both motion-contingent color aftereffects and color-contingent motion aftereffects were found after adaptation, and both kinds of effects were present after a 24-hour interval. Mayhew and Anstis (1972) have reported that spiral aftereffects can be made contingent on illuminants of red alternating with yellow and on yellow alternating with green. They believed that these effects were dependent on the relative changes in color of the stationary test spiral. For example, adaptation to red clockwise alternating with yellow counterclockwise produced counterclockwise effects on a red test spiral and clockwise effects on a yellow test spiral; however, if the test spiral was illuminated as yellow alternating with green, the motion associated with yellow became counterclockwise, and clockwise motion was reported when the spiral was green.

Hue Parameters

In studies in which the adaptation hue has not been manipulated as the independent variable, inducing hues have been usually red and green (Kodak Wratten filters # 26 and 55 were common choices). Stromeyer (1972a) has remarked that magenta and yellow-green adaptation colors (Wratten #34A and 53) produce particularly strong effects, and a few other investigators have used similar hues. McCollough (1965) had her subjects adapt to orange and blue colors, but in subsequent studies, these hues have been found not to induce effects as readily as others. Fidell (1968), for example, found little evidence for aftereffects resulting from blue and yellow adaptation colors, though red and green readily produced McCollough effects when paired with appropriate spatial patterns.

An investigation in which adaptation hue was systematically varied was undertaken by Stromeyer (1969), who had his subjects adapt to gratings projected through a variety of interference filters, report the color of the aftereffect for each filter, and estimate its saturation. Aftereffects produced by filters with transmission peaks from approximately 490 to 620 nm were found to be predominately red and green, with greenish adaptation colors producing red effects and vice versa. Filters with peak transmissions in the region of 405 to 486 nm produced aftereffects that were "weak and ambiguous," but generally violets produced green effects and the blue greens, red effects. Adaptation colors near pure yellow or pure blue frequently did not produce aftereffects; when they did, the effects were usually weak pinks or greens, depending on the redness or greenness of the adapting color. In a later article, Stromeyer (1972b) found that the strength of the aftereffect for a given adaptation hue seemed to vary with the spatial frequency of the adapting grating and that aftereffects following exposure to orange and blue could be produced if these colors were paired with the appropriate spatial frequencies. Aftereffects resulting from red, green, and blue adaptation hues were strongest around 5 cycles per degree and those produced by orange, around 10 cycles per degree; all effects declined in strength at low frequencies.

7) obtained colorimetric (Note Yood matches to aftereffects produced by red, violet, green, and yellow-green adaptation hues presented singly and in pairs. Reddish effects produced by adaptation to green had dominant wavelengths that were somewhat displaced toward the short end of the spectrum as compared to those produced by yellowgreen adaptation. Correspondingly, exposure to violet resulted in greenish aftereffects with longer peak wavelengths than those following adaptation to red. Dominant wavelength was essentially the same whether the aftereffects resulted from exposure to a single chromatic grating or resulted from an adaptation sequence also containing an orthogonally oriented, differently colored grating.

Murch and Hirsch (1972) felt that they were able to demonstrate that an afterimage could serve as the chromatic stimulus for a McCollough effect. Their subjects adapted either to a homogeneous red field alternating with a vertical achromatic grating or to green alternating with horizontal. The predicted aftereffect was based on the assumption that the "effective" stimulus for, say, green alternating with horizontal was actually green alternating with red horizontal (red being considered the afterimage of green). In this case, then, a green effect would be expected to appear on a horizontal test pattern. A few subjects did report such an effect; many saw effects on the orientation of test field not present during adaptation (e.g., adaptation to green alternating with horizontal produced mainly red effects on vertical test lines). Since testing was apparently carried out directly after adaptation, exposure to a single hue, for example green, could have resulted in a successive-contrast appearance of red on both halves of the test grating. Perhaps, if the predicted green-on-horizontal effect were present, it was obscured by the successivecontrast effect, leaving only an appearance of red on vertical lines.

Murch and Hirsch felt that these findings ran counter to McCollough's (1965) explanation of the effect in terms of chromatic adaptation of edge detectors since, in their experiment, orientation-dependent effects were produced when the colors and contours were

presented separately. Another attempt to differentiate color adaptation from orientation processing came from these authors in the same vear (Hirsch & Murch, 1972), McCollough and Clark (Note 8) had reported to them some evidence of shifts in the color of aftereffects produced by a particular adaptation hue dependent on the other hue present during adaptation. Hirsch and Murch reasoned that if such shifts could be produced by introducing unlined colored fields into the adaptation sequence, it would indicate that different neural populations were processing colors and orientations. They obtained colorimetric matches for aftereffects produced by adaptation to vertical orange alternating with horizontal blue green. They also obtained matches to effects resulting from a sequence in which a homogeneous yellow field preceded the orange vertical grating and blue homogeneous preceded the blue-green horizontal. The matches to aftereffects produced by the two sequences were significantly different, with the vertical matches changing perceptually from bluish to greenish and the horizontals from vellow orange to reddish. In the second sequence, the authors felt that the "'effective' color component of the lined stimulus pattern would be that portion of the spectrum not stimulated by the preceding color field," and the color of the aftereffect was, as predicted, the approximate complement to the "nonadapted portion of color receptors stimulated by the lined inspection pattern" (p. 406). Hirsch and Murch concluded that the McCollough effect may be produced in two levels of the visual system, with color analyzers being able to work independently of edge detectors.

A few investigators have illuminated test patterns with monochromatic light and found that McCollough effects remain visible. Mc-Collough first observed this phenomenon, reporting that after adapting to orange vertical and blue horizontal stripes, horizontal lines illuminated with green, yellow, or orange appeared yellow green or orange; in the same lights, the vertical portion looked green or blue. Stromeyer (1969) commented that when test patterns were projected through interference filters, aftereffects appeared as though they were being viewed through colored glasses. Leppmann and Allen (Note 9) have reported that red and green McCollough effects remain visible under sodium illumination.

Luminance Parameters

Adaptation stimuli, Information concerning the role of luminance in generating McCollough effects is scarce. The range of adaptation luminances used in different experiments has varied widely, suggesting that the effects are not dependent on absolute luminance levels. Stromeyer and Mansfield (1970) reported that a two log unit decrease in adapting luminance did not produce a marked change in a motion-contingent aftereffect. However, in a study by White (Note 10), use of a colorcancellation technique to assess McCollough effects did reveal differences among effects generated by various adaptation luminances. High luminances (up to approximately 100 cd/m^2) were found to build up stronger effects than lower luminances inspected for the same duration. Harris and Barkow (Note 11) showed that the strength of an effect was diminished when the contrast between colored stripes and black bars of the adapting gratings was reduced.

In their article on color-contingent motion aftereffects, Mayhew and Anstis (1972) reported that marked differences in the brightness of adaptation colors did not influence the color dependency of these effects. These investigators did claim, however, to have produced motion aftereffects contingent on differential achromatic brightness; they also mentioned having been able to demonstrate a "brightness analogue" of the chromatic Mc-Collough effects using stationary gratings. Whether such an effect can in fact be considered as an analogue is unclear, however. Inspection of high-contrast gratings has been found in selective adaptation studies to result in a "contrast reduction" effect on subsegratings (Blakemore, quently presented Muncey, & Ridley, 1973).

Test stimuli. The luminance and contrast of test gratings also seem to influence McCollough effects. Stromeyer (1971) found that he could produce a variety of aftereffect colors with red vertical and green horizontal adaptation by using a test matrix of gratings which varied in lightness and contrast, viewed at the mesopic level. Munsell matches to each cell of the matrix after adaptation indicated the following tendencies: Red colors appeared on high contrast vertical gratings, green on high contrast horizontal; yellow and orange were seen on light vertical lines, blue and violet on dark horizontals; intermediate hues could be found for lightnesses and contrasts between these extremes.

In the study by White (Note 10), strength of McCollough effects was measured on test gratings that could be varied in luminance. Results suggested that a low-luminance test pattern (approximately 2 cd/m²) would assess stronger effects than ones of higher luminance, regardless of inspection luminance. Skowbo et al. (1974) have also commented that McCollough effects tend to be seen best on rather dim test gratings.

Interocular Transfer and Binocular Interaction

In the first description of these effects, Mc-Collough reported that if adaptation to the inducing stimuli were monocular, the chromatic aftereffects would appear only when test patterns were viewed with the adapted eye. This finding has been challenged only once (Mikaelian, Note 12); in this study, the transferred effect was occasionally the opposite of that seen with the adapted eye. All other investigations of this characteristic have supported McCollough's original contention, even under conditions designed to enhance the probability of transfer. For example, aftereffects contingent on the direction of rotation of a spiral do not transfer either with central fixation (Stromeyer & Mansfield, 1970) or with side fixation (Smith, Note 13), although the latter maneuver seems to promote transfer of spiral aftereffects themselves (Walls, 1953). Mayhew and Anstis (1972), in their study of color-contingent spiral aftereffects, were not able to obtain motion aftereffects when the unstimulated eye was used to view stationary colored test spirals, though these effects were consistently reported with use of the ipsilateral eye. Favreau (1973), however, has reported that although the usual "negative" color-contingent motion aftereffects do not transfer interocularly, there is a tendency for the unadapted eye to see "positive" color-contingent effects (i.e., the direction of motion associated with a color is the same in the aftereffect as in adaptation). Held and Shattuck (Note 14) have found that their color-contingent tilt aftereffect fails to transfer interocularly.

Color aftereffects have not been found to transfer even when they are made to depend on a spatial aftereffect known to show transfer. Stromeyer (1972b) made color aftereffects contingent on the "perceived spatialfrequency shift" (Blakemore & Sutton, 1969); although the size aftereffect transferred, no color differences could be detected with the unadapted eye. Murch (1972) found transfer of the spatial-frequency effect in the absence of McCollough effect transfer.

MacKay and MacKay (1973) have reported binocular interaction during adaptation to form McCollough effects. Subjects in their experiment viewed alternating homogeneous red and green fields with one eye and alternating horizontal and vertical gratings with the other. When subsequently examining test patterns with the eye that had viewed gratings, subjects reported seeing the same color as had been associated with each orientation during adaptation. When viewed with the eye that had been exposed to chromatic fields, lines in the test patterns appeared weakly tinted with the hue complementary to that originally paired with each orientation.

In an experiment by Over, Long, and Lovegrove (1973), a condition similar to that in the MacKays' study was run. In an additional condition, colorless gratings and unpatterned colors were "mixed" (i.e., red to left together with vertical to right were alternated with horizontal to left plus green to right). In this study, however, little evidence for binocular interaction was found.

There is some evidence that binocular interaction can occur when the stimulus presented to each eye is both chromatic and lined, but by itself is incapable of generating particular McCollough effects. White and Riggs (1974) had subjects view half an angle pattern with one eye and the other half of the pattern with the other eye. Although no angles were apparent to either eye alone, the binocularly fused stimulus was a chromatic angle pattern which could induce angle-dependent effects.

Retinal Specificity

Several studies have been directed toward determining the extent to which McCollough effects are specific to adapted portions of the retina. Harris (Note 15) reported that differential aftereffects could be produced simultaneously on different retinal regions, so that, for example, vertical lines on one part of the retina could appear red, but verticals on a different area could appear green.

Murch (1968, 1969) reported that the effect was seen to cover a test grating no matter what its size relative to the size of the adapting field; his interpretation of this result was that McCollough effects do not follow Emmert's law of afterimages. However, since fixation was not used during either adaptation or testing, it could not have been known whether the test pattern was or was not actually falling on adapted areas of the retina. An experiment in which this could be determined was done by Stromeyer and Mansfield (1970) in work with the spiral effect. Their subjects adapted to the following patterns projected on rotating spirals: red square with green surround, contracting, alternating with green square with red surround, expanding (or vice versa). During testing, subjects maintained central fixation and instructed the experimenter to move adjustable rods until they coincided with the borders of the square; this was repeated at several viewing distances. With the use of this procedure, the image of the square did appear to follow Emmert's law.

Additional evidence for the importance of retinal localization has been provided by Stromeyer (1972a). He had his observers adapt to a grating located just to one side of a fixation point; he found that the saturation of the colored aftereffects was greatest when the test grating was in approximately the same retinal location as the adapting grating had been. The effects disappeared when the test grid was moved about .5 degrees away from the adapted area and reappeared when the pattern was brought to within about .3 degrees of the adapted portion. Smith (Note 13) had subjects adapt monocularly to spiral patterns with bipartite chromatic illumination (i.e., green on one side and red on the other as the spiral rotated in one direction, and the reverse color arrangement during rotation in the opposite direction), with fixation either at the center or to one side of the spiral. During testing, fixation at the same point as during adaptation produced the expected pattern of color effects, but shifting fixation caused a reversal in the pattern, with colors on the half of the spiral falling on the unadapted portion of the retina either diminished or absent.

Piggins and Leppmann (1973) have reported that when inspection stimuli are viewed as stabilized images, McCollough effects are not reported either when the test stimuli are freely scanned or when they are also stabilized.

Temporal Characteristics

The rate at which the adapting patterns alternate does not seem to be of crucial importance for stationary grating effects. Stromeyer (1969, 1972b) has shown that prolonged observation of a single chromatic grating, either continuously or with periodic dark intervals, will produce a colored aftereffect on a test grid at the adapting orientation. At the other extreme, Harris and Gibson (1968) were able to produce an aftereffect by means of an adaptation sequence in which each grating was presented for only 80 msec at a time. Effects were seen by some subjects after total adaptation times of less than 1 min. Favreau et al. (1972) varied the alternation rate of rotating spirals and found that more reports of colored aftereffects were obtained when the alternation rate was slow (60 and 150 sec per presentation) than when it was rapid (10 or 30 sec). Even with the more rapid rates, however, subjects did report seeing the aftereffects. Smith (Note 13) was able to generate quite strong effects with a spiral that alternated in its direction of rotation every 10 sec.

Perhaps the most striking aspect of the McCollough effects is their extraordinary persistence. On one occasion, Stromeyer and Mansfield (1970) found an aftereffect to last as long as 6 wk after a 20-min adaptation to

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red and green moving gratings. A duration of this length is somewhat unusual, but it is quite common for subjects to observe some color in achromatic patterns for more than a day following adaptation. Hepler (1968) found that 3-5 hr of adaptation to moving belts produced effects lasting 20-27 hr; Smith (Note 13) reported effects with spirals that lasted up to 10 days after 20 min of adaptation. As regards stationary effects, McCollough (1965) mentioned that the appearance of color could last 1 hr or more after approximately 4 min of adaptation. Effects persisting for 3 days were found by Stromeyer (1969) following "prolonged viewing." In another article, Stromeyer (1971) noted that after 2 hr of exposure, effects were visible for 2 wk; he also reported that increasing the adaptation time appeared to strengthen the saturation of the effects up to approximately 90 min of adaptation.

Riggs et al. (1974) have shown, however, that the magnitude of the effects can continue to increase with inspection times of up to 150 min. The effects declined in strength with time after adaptation; weak effects were measurable for a few hours, and strong effects persisted for a week or more. Riggs et al. described the decay over time as "not quite linear" either on semilog or on log-log coordinates.

It is possible to "neutralize" spatially contingent color aftereffects by brief exposures to the hue orientation combination opposite to that which was used during adaptation. Stromeyer (1969) reported that it took approximately 3 min to neutralize effects resulting from a 10-min adaptation; Fidell (1968) found 2 min to be sufficient for neutralization of 8 min of adaptation. Skowbo et al. (1974) found that exposure to a neutralization configuration for a time equal to that used for acquiring an effect could reverse the original effect. The influence of other kinds of visual stimulation following induction of McCollough effects was also explored by these investigators. They found postadaptation exposure to achromatic gratings to be associated with a fairly rapid decay of McCollough effects, while exposures to homogeneous chromatic fields, "natural" visual stimulation, or complete darkness diminished the strengths of the effects only slightly.

THEORETICAL FORMULATIONS

Afterimages

One of the first articles to appear following McCollough's report was a study by Harris and Gibson (1968) to test the possibility that her effect could be explained in terms of afterimages. These investigators arranged an adaptation sequence in which each of the two gratings appeared randomly in one of two locations such that the colored portions of one position coincided spatially with the black portions of the other; also, the gratings were alternated too rapidly for any systematic eye movements to occur. This procedure insured homogeneous exposure of the retina, so that patterned afterimages could not be formed. Nevertheless, the appropriate colored aftereffects appeared on test patterns, and it was generally accepted from these results that the phenomenon was not itself an afterimage.

Dipoles

Harris and Gibson (Note 16) felt that edge detectors, such as those described by Hubel and Wiesel (1962), were more specialized than necessary to account for the McCollough effect. Their hypothetical sensory construct, called the dipole, was defined by its feature of receiving input from two nonconcentric locations on the retina, with the additional specifications that there be (a) a variety of different spatial arrangements of the dipoles' two receptive areas, (b) variation in the wavelengths dipoles are most sensitive to, and (c) the possibility of fatiguing a dipole by prolonged stimulation. However, a curvaturespecific effect, which Harris and Gibson have stated could not be accounted for by a dipole model, has recently been reported (Riggs, 1973).

Edge-Detector Models

Support for the idea that edge-detecting units, such as those described by Hubel and Wiesel (1962, 1965, 1968), are implicated in McCollough effects comes partly from a comparison of the spatial characteristics of Mc-Collough effects and those of receptive fields of single cortical cells in animals. In addition, the spatial specificity of McCollough effects seems to correspond with that observed in contour-masking experiments; Weisstein (1969) suggested that selective threshold elevation might reflect the activity of neural units or pattern analyzers.

In order to induce an orientation-dependent effect, adapting gratings must differ from each other by at least 20 degrees (Fidell, 1970), with a 90-degree separation being optimum. As Fidell suggested, this finding may indicate that it is necessary to stimulate two separate populations of edge detectors. Hubel and Wiesel (1965) reported that in the cat, the range of orientations which evoke a response from a particular edge-detecting cell is not more than 30 degrees; Campbell et al. (1968) found cortical cells whose responses fall to 50% at 14-26 degrees from preferred orientation. In a contour-masking paradigm, the amount of threshold elevation has been estimated to drop to 50% at 12-15 degrees from adapting orientation and to be zero 90 degrees away from adapting orientation (Campbell & Kulikowski, 1966). Blakemore and Nachmias (1971) found that threshold-elevation effects are reduced by a factor of 2 at only 6.75 degrees away from adapting orientation. The disappearance of the effects when test gratings are rotated 24-27 degrees (Teft & Clark, 1968) may indicate that effects are limited to the population of cells stimulated during adaptation.

Analogous specificity is found for the spatial-frequency McCollough effects. The amount of separation necessary between adaptation gratings—minimally one octave (Lovegrove & Over, 1972), optimally two octaves (Breitmeyer & Cooper, 1972)—is similar to the range over which spatialfrequency threshold elevation extends (Blakemore & Campbell, 1969). In this case also, the test gratings must be close in spatial frequency to the adapting frequency (Teft & Clark, 1968).

White and Riggs (1974) have quantitatively related their angle and curvature effects to characteristics of higher order edge detectors (hypercomplex cells) described by Hubel and Wiesel (1965). As yet, data on angle- or curvature-specific masking have not appeared in the literature.

Possibly because many of the psychophysical and neurophysiological studies were being carried out contemporaneously, most references to edge detectors in the McCollough effect literature have not included detailed comparisons with these other kinds of data.

Single-unit models. McCollough (1965) postulated simply that "edge-detector mechanisms in the visual system are subject to color adaptation, responding with decreased sensitivity to those wavelengths with which they have been most recently stimulated" (p. 1115). This point of view has been adopted by Fidell (1968, 1970) and Teft and Clark (1968); similarly, Hepler (1968) suggested that color adaptation of motion detectors might account for the effect she described. In this kind of model, no assumption seems to have been made that the mechanism is color selective. Rather, the cells envisioned by these authors presumably need possess only spatial selectivity and the capability of responding to a broad band of wavelengths. Such cells have been found in the striate cortex of Rhesus monkeys (Gouras, 1972); selective chromatic adaptation experiments indicated that they received input from red and green (and occasionally blue) cone mechanisms, and most were driven well only by spatial stimuli.

Adaptation of a mechanism which is specific for orientation and wavelength has been suggested by Held and Shattuck (1971), Breitmeyer and Cooper (1972), Favreau et al. (1972), and Lovegrove and Over (1972). Cells which respond to only a narrow range of wavelengths as well as possessing spatial specificity have been found in monkey cortex (Hubel & Wiesel, 1968), but the proportion of cells which was selective for both features seemed to be small. Other investigators (Dow & Gouras, 1973; Gouras, 1972) have obtained single-cell recordings which suggested that most cortical cells were selective for either form or color, but not both. There is, in addition, some doubt as to whether orientation-specific threshold-elevation effects have any chromatic specificity (Gentry, Timney, Skowbo, & Morant, Note 17).

Sequential or multiple-unit models. Riggs et al. (1974) have found that there is no simple function which describes the time courses of acquisition and decay of McCollough effects; they felt that a "two-stage" process, in which analysis is carried out sequentially by color-sensitive and later orientation-sensitive cells, would be consistent with their findings. These authors have also pointed out that the failure of McCollough effects to transfer interocularly, considered in contrast to the transfer of spatial aftereffects, may indicate the presence of a separate color component.

Murch's findings (Hirsch & Murch, 1972; Murch & Hirsch, 1972) indicated that color and line configurations presented separately could interact to form spatially differentiated color aftereffects. He suggested that his results reflect color and contour processing occurring in different parts of the visual system and that "color adaptation in conjunction with a specific line orientation" (Murch, 1972, pp. 30-31) might be an appropriate way to describe physiological correlates of the McCollough effect. According to Murch's model, fatigued opponent-process color receptors in the lateral geniculate nucleus would "feed into" cortical units having orientation sensitivity. Achromatic spatial patterns would appear colored because the lines were processed through fatigued color units on their way to the orientation detectors.

Murch (1972) also suggested that the McCollough effect "probably does not involve a fatiguing of orientation-sensitive units" (p. 33) which, he believes, are involved only to the extent that they "convey" the effect. This idea is consistent with the results of a study by Timney et al. (1974). Observers in this experiment were tested for threshold detection of chromatic and achromatic gratings before and one-half hour after 90 min of adaptation to alternating red vertical and green horizontal gratings. No threshold elevation was found in the posttest, though a colornaming technique and matches to the effects with a projection colorimeter indicated presence of color effects throughout postadaptation testing.

Although at least one aspect of Murch's model has some empirical support, his ac-

count nevertheless failed to explain satisfactorily how exposure to chromatic gratings could produce no long-lasting fatigue of the orientation-detecting mechanism and yet, at the same time, would fatigue color units for a period of weeks. Indeed, it is difficult to accept any model based on simple neural fatigue as the cause of an aftereffect of such persistence.

Associative learning models. Mayhew and Anstis (1972) have commented that colorcontingent spiral aftereffects have characteristics which "resemble those of conditioning and extinction more than those of physiological adaptation" (p. 84). Recently, several other investigators have expressed similar opinions about the spatially contingent color aftereffects. Skowbo et al. (1974) felt that their finding of rapid decay of McCollough effects resulting from exposure to achromatic gratings would not have been predicted by models based on either chromatic adaptation of edge detectors or wavelength-selective receptors, or adaptation in channels specific to both stimulus attributes. Rather, they suggested that the firing of units associated with a particular orientation might act as a conditioned stimulus which has become associated with adaptation in color units. According to this line of thought, decay of McCollough effects could be regarded as the extinction of conditioned responses. Traditional models of conditioning would require that the same colors be associated with the spatial stimuli during and after exposure to the patterns. To account for the reversal in association, their model assumes that the firing of colorsensitive cells, in response to colored patterns, can itself be considered a stimulusone which eventually leads to a "fatigue" response of depression in firing rate. Leppmann (1973), who also suggested a model based on classical conditioning, accounted for the reversed association by postulating the involvement of an opponent-color response. Physiologically, chromatic information would be relayed to cortical centers via opponentprocess lateral geniculate units; the coloropponent response would then become associated with contour information which had been processed through cortical units.

Perhaps these contingencies would be analogous to an idea expressed by Hebb (1949)—that the firing of neurones in a "cell assembly" can affect the probability that other cells will fire. There is some evidence that changes in firing rates of cells in the visual areas of rabbits can be observed after prolonged stimulation or after various programs of paired stimulation (e.g., Sokolov, Polyansky, & Bagdonas, 1971; Vinogradova & Lindsley, 1964).

Without expressing their ideas in neurophysiological terms, a few other writers have suggested that certain characteristics of McCollough effects could be interpreted in terms of learning or memory. Leppmann and Allen (Note 9) have reported that when test patterns are presented for brief periods, the exposure time required to identify the form of the pattern is less than that required for subjects to identify the colored aftereffects. To account for this finding, they have proposed that McCollough effects are built up by an associative learning process, following which the subjective color is elicited by the corresponding stimulus configuration. Riggs et al. (1974) have concluded that the build-up and decay of McCollough effects show some time characteristics like those associated with "central adaptability rather than sensory adaptation." Harris (Note 17), in a paper reviewing various models which have been proposed to account for McCollough effects, has concluded that some sort of associative learning framework is probably the most suitable.

CONCLUSIONS

Most recent work on McCollough effects suggests, then, that some kind of learning mechanism may be involved in the production and maintenance of the effects. It is difficult to account for the persistence of McCollough effects without postulating that such a process occurs in addition to that of neural adaptation. Unfortunately, it seems possible to say little more than that McCollough effects have characteristics like those of learned responses. Neurophysiological models to account for modifications in connections between color- and contour-detecting mechanisms are particularly difficult since the con-

nections themselves are not well understood. DeValois (Note 19) has recently remarked that two major unknowns in the physiological basis for color vision are how color and luminance information are separated at the cortical level and the nature of the relationship between luminance and color information in the shape-detecting mechanisms in the cortex. It would seem most reasonable, for the present, for researchers to avoid complex neurophysiological model building and to concentrate instead on using quantifiable dependent variables to examine the effects themselves more closely. Perhaps a thorough description of their characteristics will permit McCollough effects to be regarded as "missing links" between perception and learning.

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