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Science, New Series, Vol. 149, No. 3688 (Sep. 3, 1965), 1115-1116.

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Color Adaptation of Edge-Detectors in the Human Visual System

Abstract. *An aftereffect of color which depends on the orientation of lines in the test field may be obtained by presenting a horizontal grating of one color alternately with a vertical grating of a different color. Like the aftereffect of adaptation to chromatic fringes produced by prismatic spectacles, this aftereffect is visible in monochromatic light and fails to show interocular transfer. It is suggested that both effects are to be understood in terms of color adaptation of orientation-specific edge-detectors.*

Negative aftereffects of color stimulation which resemble the familiar negative afterimage but which are not bound to a specific visual field area can be demonstrated by the following procedure. Let a grating of vertical black stripes on an orange ground be projected on a screen for a few seconds, alternating with an identical grating of horizontal stripes on a blue ground. An observer with normal color vision, after watching this alternation for 2 to 4 minutes, will report an orange aftereffect in the right half of Fig. 1 and a blue-green aftereffect in the left half. Although the colors are not as saturated as ordinary negative afterimages, the two halves are of clearly different hue. These colors remain stationary as the observer shifts visual fixation from point to point within the figure. Rotation of the figure 90° clockwise leads to a report of blue-green in the lower half and orange in the upper half. Turning the head 90° on one side causes the colors to exchange places. After somewhat longer adaptation periods, patterns of concentric circles, spirals, or radiating lines show interesting arrangements of color, orange appearing wherever the lines in the pattern are predominantly horizontal and blue-green where they are predominantly vertical. The colored aftereffects can also be seen in patterns of chalk lines drawn on a blackboard. These aftereffects may persist for an hour or more before fading completely.

Evidently these aftereffects are determined by the orientation of stripes in the test pattern. They indicate that edge-detector mechanisms in the visual system are subject to color adapta-

tion, responding with decreased sensitivity to those wavelengths with which they have recently been most strongly stimulated. On the basis of neurophysiological evidence obtained from cats and monkeys, it has generally been presumed that the human visual system does contain edge-detector mechanisms; perceptual demonstrations, such as those discussed by MacKay (1), support this assumption. Until now, however, no suggestion has been made that these detectors show color adaptation.

A phenomenon already reported, however, seems to require such a suggestion. The occurrence of "phantom" fringes as negative aftereffects of prolonged adaptation to strong base-left (or base-right) prisms makes it highly probable that edge-detectors are subject to color adaptation. Such prisms produce vivid yellow and blue fringes on all vertical boundaries of objects, the yellow appearing when the lighter side of the boundary is to the right and blue appearing when the lighter side is to the left (for base-left prisms). Most observers who wear such prisms for 3 to 6 days report "phantom" colors after the prisms are removed. These "phantoms" are complementary to the prismatic fringes, a "phantom" blue appearing when the lighter side is to the right (2). It is known from the study of Hay, Pick, and Rosser (3) that the magnitude of the adaptation observed in such cases is dependent upon relative contrast rather than upon absolute brightness of the striped test pattern, and therefore the phenomenon must be connected with the edge-detecting process.

It is known further (4) that interocular transfer of the chromatic fringe adaptation does not occur. Monocular wearing of a prism produces changes in the adapted eye alone, and "phantoms" are observed only with that eye. Some of Hajos' observers wore oppositely oriented prisms (base-left before the left eye, base-right before the right eye), and in such observers he was able to measure an independent adaptation of each eye to its specific chromatic fringes. Hence, if such adaptation is a process that occurs in edge-detectors, these detectors must be located at a stage in the visual system below the convergence of inputs from the two eyes.

Neurophysiological work shows that edge-detector systems are orienta-

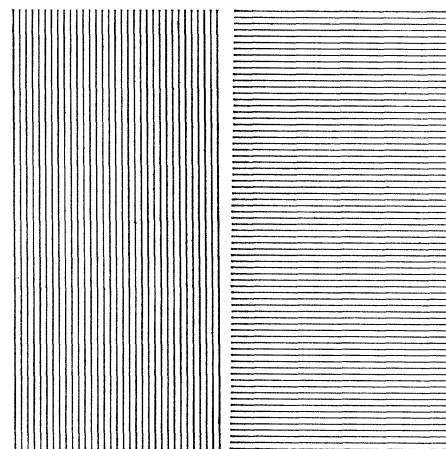


Fig. 1. Test pattern used in four orientations. After adaptation to orange-vertical and blue-horizontal, the left half appears blue-green and the right half appears orange when the pattern is shown in the orientation above.

tion-specific: a vertical boundary with the light side to the right is detected by one system, while another vertical boundary with the light side to the left is detected by another. It seems not unlikely that the "phantoms" are to be explained by the adaptation of the one system to yellow, the other system to blue. However, edge-detector systems differ not only in orientation; they also differ in direction. If they are indeed subject to color adaptation, it should be possible to demonstrate differential adaptation of horizontal and vertical edge-detector mechanisms. In an effort to determine whether such adaptation could be demonstrated, we performed the experiment described at the beginning of this report.

Gratings of 70 lines to the inch were projected from 2- by 2-inch (5-by 5-cm) slides on a 4-foot-square screen 15 feet (5 m) from the two projectors. Color filters were placed in front of the projector lenses, and a timing circuit was set to switch the projectors on and off alternately (5 seconds first projector, 1 second dark interval, 5 seconds second projector, 1 second dark interval, and so on). Corning filters 2-73 (orange) and 5-56 (blue) work very well, since each has a high transmission of wavelengths at the long or short wavelength end of the spectrum, with very little overlap in the yellow. Wratten filters 25 and 44A have similar properties. However, the choice of filters is not critical; distinguishable though unsaturated aftereffects can be obtained with most

pairs of filters which clearly differ in their transmission characteristics.

Twenty-six naive observers were tested in two groups to verify the interocular independence of the adaptation. These observers were first shown the test pattern (Fig. 1, projected on the screen by a third projector) and asked to indicate any differences in color, however faint, which they could detect between the two halves. They then watched for 2 minutes while the orange and blue fields without grating patterns were presented alternately, and they indicated afterward in writing the color appearance of the test pattern for each eye. No color aftereffects were consistently reported at this stage. All observers then covered the right eye and observed orange-vertical and blue-horizontal with the left eye for 4 minutes, giving test pattern responses with the left eye after 2 and 4 minutes. Then they covered the left eye, gave responses with the right eye alone, and then observed orange-horizontal and blue-vertical with the right eye for 4 minutes, giving test pattern responses after 2 and 4 minutes with the right eye. They were finally asked to compare the appearance of the test pattern to the left and right eyes, by opening and closing the eyes alternately. The test pattern was varied in position by rotation between and during all tests.

Twenty-two of the 26 observers reported at least 12 of the 16 possible color aftereffects in the series. Of these 22 observers, 20 reported colors seen with the left eye which were consistently the reverse of those seen with the right eye. One of the 22 reported seeing colors with the right eye before adaptation of that eye, and the colors reported were the same as those just obtained by adaptation of the left eye. Most observers also reported that all color disappeared when the test pattern was rotated 45° into an oblique position.

Chromatic fringe adaptation and the "phantom" aftereffects are visible in monochromatic light. Hay, Pick, and Rosser have accordingly pointed out that wherever adaptation of the same kind takes place, "it should manifest itself in ineradicable color fringes along high contrast borders in monochromatic illumination." Observations made with the test pattern shown in nearly monochromatic light (Corning narrow-band-pass filters 4-102, 3-110, or 2-77 held in front of the projector) con-

firm the expectation that the color-adaptation of edge-detectors is visible in such light. After adaptation to orange-vertical and blue-horizontal, the right half of Fig. 1 appears yellow-green or orange in green, yellow, or orange light, and the left half appears green or blue in such colored light. These observations strengthen the supposition that chromatic fringe adaptation, as seen in experiments with prismatic spectacles, is explainable as color adaptation of oppositely oriented, vertical edge-detector systems.

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References and Notes

1. D. M. MacKay, in *Sensory Communication*, W. A. Rosenblith, Ed. (Wiley, New York, 1961), pp. 339-355. MacKay's figures 1 to 3 are excellent patterns for observing these color aftereffects.
 2. I. Kohler, *Oester. Akad. Wiss. Phil. Hist. Kl.* **227**, 1 (1951); *Sci. Am.* **206**, 62 (May 1962).
 3. J. C. Hay, H. L. Pick, E. Rosser, *Science* **141**, 167 (1963).
 4. A. Hajos and M. Ritter, *Acta Psychol.* **24**, 81 (1965); A. Hajos, unpublished report on research contract 91-591-EUC-2917, 1 July 1964.
 5. These experiments were carried out under grant 04898-02 from the National Institute of Neurological Diseases and Blindness.
- 7 June 1965

A Brief Temporal Gradient of Retrograde Amnesia Independent of Situational Change

Abstract. Rats were given a single electroconvulsive shock at varying intervals after receiving a punishing shock to the feet immediately after stepping into a compartment. Significant amounts of retrograde amnesia for the memory of the punishment was shown when electroconvulsive shock was administered up to and including 30 seconds after the punishment but not at 60 seconds. This brief temporal gradient cannot be explained in terms of changed stimulus cues or learned interference analogous to retroactive inhibition.

Previous studies have shown that electroconvulsive shock (ECS) given shortly after a learning experience can interfere with the learning. This interference typically has been interpreted as a disruption of a consolidation of the memory trace (1). Two other interpretations, however, are possible: (i) that ECS reduces the amount of learning by

removing the subject from the stimulus situation, and thus preventing him from adequately noticing it, and possibly from rehearsing in it, after the reinforcement has indicated its biological significance, or (ii) that ECS conditions many random brain impulses to the cues involved in the immediately preceding learning and hence produces a learned interference analogous to retroactive inhibition. The purpose of this study was to secure additional information on the effects of the interval between the learning experience and ECS, and to test hypothesis (i) by substituting sudden removal for ECS, and hypothesis (ii) by administering ECS after subject had been removed from the situation, a procedure which should reduce the chances for retroactive inhibition.

Subjects were 310 male rats of the Holtzman strain, 90 to 150 days old, housed in individual wire-mesh cages and having free access to food and water. An equal number of rats from each shipment was assigned to the various groups to cancel out shipment effects. The apparatus, a modification of that described by Jarvik and Essman (2), was a compartment 38 by 38 by 44 cm, with a vertical slot cut into one end, into which fitted a start box (19 by 15 by 15 cm) which could be raised and lowered by means of a lever. A guillotine door separated the two compartments. The entire apparatus was constructed of ¼-inch (0.6-cm) Plexiglas, except for the floors, which were made of stainless steel rods 3/32 inch (0.24 cm) in diameter, spaced 1.25 cm on centers. The interior was illuminated from above by a 100-watt bulb. A 60-cy a-c grid shock (GS) of 1.0-ma intensity was delivered for 2.0 seconds to the grid floor of the large compartment through a 820,000-ohm resistor connected in series with the rat. An ECS (100 ma for 0.3 second) was delivered through small padded alligator clips, soaked in saline, attached to the animal's ears before the animal was placed in the start box. Subjects that did not exhibit tonic flexion or tonic extension in response to ECS were discarded. Durations of GS and ECS, as well as time intervals between GS and ECS, were automatically triggered and timed by a system of relays and timers. Actual intensities of GS and ECS were monitored on milliammeters.

A rat was placed in the start box and