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MOTION-CONTINGENT COLOR AFTEREFFECTS:
A LASTING MODIFICATION OF PERCEPTION

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Let an observer view red stripes moving up and green stripes moving down. When he sees white stripes later, those moving up appear green and those moving down appear pink. After several cumulative hours of viewing, similar motion-contingent color aftereffects persist for days. Their localization to a limited area of the visual system and their specificity to spatial features of the stripe display suggest that these color aftereffects involve motion-sensitive cortical neurons. Their persistence may reflect habituation which prolongs the effects of chromatic adaptation within such cortical cells.

MOTION-CONTINGENT COLOR AFTEREFFECTS:
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by

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"I have not made any attempt to account for the more feeble colors exhibited by the two intermediate groups of lines in Benham's top, nor for the changes which occur when the speed of rotation is increased. These effects no doubt result, at least in part, from modifications of the phenomena already discussed. But for the present I am compelled to discontinue the experiments on account of the disagreeable and probably injurious effects which they produce upon the eyes."

— S. Bidwell

"On subjective color phenomena attending
sudden changes of illumination." (1897)

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Introduction

An observer who sees red stripes moving up and green stripes moving down in a dark room later finds that his perception of moving stripes has changed in an interesting way. He notices that stripes which looked white before he saw the colored display now appear green when they move up and pink when they move down. One might describe this change in the observer's perception of moving stripes as a "motion-contingent color aftereffect". In a preliminary report (Hepler, 1968), we emphasized the important fact that motion-contingent color aftereffects persist for at least 20 hours after the observer sees the display of moving, colored stripes.

An investigator might study motion-contingent color aftereffects for two reasons. He may be interested, initially, in using color aftereffects to reveal the presence of neurons in human vision which share the response properties of cat and monkey cortical cells. One of the first researchers to argue for the existence of orientation detectors in human vision used this strategy. McCollough (1965a) discovered color aftereffects that were contingent upon the orientation of colored adapting stripes. Observers in her experiment saw a blue-green color on vertical white stripes that were orange during adaptation. At the same time, they saw an orange color on horizontal white stripes that were blue during adaptation. McCollough reasoned that these aftereffects resulted from chromatic adaptation of human visual neurons which, like cat and monkey cortical cells, respond to stripes placed in particular orientations. The investigator of motion-contingent color aftereffects sees that the direction of stripe movement determines which aftereffect color an observer reports. He may conclude that there are neurons in the human visual system which, like those in cat and monkey cortex, restrict their response to particular directions of stripe motion. Motion-contingent aftereffects put a color "tracer" on these neurons, giving the investigator a convenient index of their response restrictions.

Or an investigator may choose to study motion-contingent color aftereffects because they persist. Their presence, hours after adaptation, is interesting because it may reflect a learned change in visual perception. Perhaps learning occurs when neurons in human vision, sensitive to moving stripes, develop a new mode of response with repeated chromatic stimulation --a mode which persists for hours after stimulation stops. Experiments described in this thesis study the development, specificity and persistence of motion-contingent color aftereffects.

Our experiments are related to recent studies of neurons that serve as feature detectors in animal and human visual systems. It will be useful to review these studies, stressing their evidence of a compatible relation between neurophysiological and psychophysical descriptions of neurons in primate vision. This review will consider neurons that detect spatial and chromatic features of visual displays.

Neurophysiological and Psychophysical Studies of Feature Detectors

This review organizes information about single cells and human observers into three sections. The first section discusses evidence for opponent-spatial organization in the visual system. It describes how visual neurons function to detect black-and-white contours. The second section reviews evidence for opponent-chromatic organization in vision. It describes what we know about visual mechanisms that code the brightness, hue and saturation of colors. The third section describes visual neurons that combine opponent-spatial and opponent-chromatic organization. These neurons detect colored contours. They are the cells, we will argue later, that develop and store color aftereffects.

Opponent-Spatial Organization

Reviews by several authors (Bishop, 1967; Goldberg and Lavine, 1968; Creutzfeldt and Sakmann, 1969; Jacobs, 1969; Weisstein, 1969; Brindley, 1970; Thomas, 1970; Bishop and Henry, 1971; Pick and Ryan, 1971; Over, 1971) offer information relevant to our discussion of opponent-spatial organization in the mammalian visual system.

Kuffler (1953) was the first investigator to show that ganglion cells in the mammalian retina respond to the spatial organization of a visual display. He noticed that a spot of light illuminating a small area of the cat's retina excited a ganglion cell whose response he was monitoring. Light placed in an annular surrounding area on the cat's retina inhibited the cell. He concluded that such cells have concentric receptive fields. Since their receptive fields are comprised of two antagonistic areas, these cells have opponent-spatial organization.

Neurons whose receptive fields have opponent-spatial organization populate all levels of the mammalian visual system. However, at any given level along the primary visual pathway from retina through cortex, one finds cells with distinctive spatial properties. Cells with concentric receptive fields, similar to those just described in the cat retina (Kuffler, 1953; Barlow, Fitzhugh and Kuffler, 1957; Wiesel, 1960; Rodieck, 1965; Rodieck and Stone, 1965; Stone and Fabian, 1966; Spinelli, 1967), are common in the retina of the monkey (Gouras, 1967) and in the lateral geniculate body of the cat (Hubel, 1960; Hubel and Wiesel, 1961; McIlwain, 1964; Kozak, Rodieck and Bishop, 1965) and the monkey (Wiesel and Hubel, 1966). These neurons respond to contrasting light and dark areas of a visual display. Studies of single cells in the cat cortex (Hubel and Wiesel, 1959, 1962, 1963, 1965) describe neurons whose receptive fields have more complicated opponent-spatial organization. The receptive field of a simple cortical cell has an elongated excitatory center surrounded by inhibitory flanks. This type of opponent-spatial organization would arise of several geniculate cells with concentric fields arrayed in a straight line on the retina all projected to the simple cortical cell. Simple cells respond to properly positioned and oriented edges, slits or bars. They make only transitory responses to moving edges. A properly oriented edge will excite a complex cortical cell, regardless of its position within the cell's receptive field. The organization of a complex receptive field may reflect converging input from several simple cells whose aligned excitatory-inhibitory boundaries are scattered on the retina. Complex cells respond to properly oriented moving edges with sustained excitation. They often restrict their response to a particular direction of motion. The receptive field of a lower-order hypercomplex cell has adjacent antagonistic regions. Evidently one half of the field receives excitatory input from complex cells sensitive to contours placed in a particular orientation and the other half of the field receives inhibitory input from similar cells. A properly oriented corner, placed so that one edge falls within the excitatory region of the receptive field while the other edge falls along the border separating excitatory and inhibitory regions, excites the cell. The corner, in this case, is a display with a "stopped" edge. Lower-order hypercomplex cells respond to moving edges. They restrict their response to particular directions of edge motion within one or both of their antagonistic receptive field regions. A "double-stopped" edge that falls in proper position within the receptive field of a <u>higher-order hypercomplex</u> cell will excite the cell. These cells probably receive converging input from a large number of lower-order hypercomplex cells. They respond to contours placed in two orientations separated by 90^o and they restrict their response to contours moving in particular directions. Neurons whose receptive fields have simple and complex opponent-spatial organization populate area 17 of the cat's visual cortex (Hubel and Wiesel, 1959, 1962, 1963). Cells whose receptive fields have complex and hypercomplex opponent-spatial organization occupy higher visual projection areas. They are found in cortical areas 18 and 19 (Hubel and Wiesel, 1965), in the suprasylvian gyrus or Clare-Bishop area (Dow and Dubner, 1969; Hubel and Wiesel, 1969) and in the suprasylvian sulcus (Wright, 1969).

Information most relevant to speculation about neurons that serve as feature detectors in human vision comes from studies of cells located in the visual cortex of a fellow primate, the monkey. Monkey cortical cells, like their feline counterparts, have receptive fields with simple, complex and hypercomplex opponent-spatial organization. Simple, complex and hypercomplex cells populate area 17 of the macaque monkey's visual cortex (Hubel and Wiesel, 1968). Complex and hypercomplex cells occupy monkey cortical area 18 (Hubel and Wiesel, 1968) and monkey inferotemporal cortex (Gross, Bender and Rocha-Miranda, 1969).

The receptive field of a cortical cell has opponent-spatial organization which clearly restricts the cell's response to particular features of a visual display. It is important to discover how stringent this restriction is when the cell responds to display features such as size, orientation, direction and velocity of motion, and location in depth.

<u>Size</u>. Consider a display of black-and-white stripes of equal width. One cycle of the display includes a black stripe and a white stripe. The number of cycles subtending one degree of visual angle on the observer's retina specifies the spatial frequency of the display. Campbell, Cooper and Enroth-Cugell (1969) studied the response of cat cortical cells to moving stripe displays of various spatial frequencies. They determined the stripe contrast required to excite a cell each time the spatial frequency of the display changed. These researchers succeeded in fitting an exponential function to the cells' responses. The spatial frequency at which this exponential function drops by one log unit defines the "characteristic frequency" of a cell--the spatial frequency to which the cell is most sensitive. Cat cortical cells have "characteristic frequencies" that occupy positions scattered over four octaves of the frequency spectrum, from 0.18 to 3.80 cycles/degree visual angle. Each cortical cell responds to a narrow, select, band of spatial frequencies centered on its "characteristic frequency".

Lateral geniculate neurons in both the monkey (Campbell, Cooper, Robson and Sachs, 1969) and the cat (Campbell, Cooper and Enroth-Cugell, 1969) restrict their responses to particular spatial frequencies. Monkey cells respond to higher spatial frequencies than cat cells, giving the monkey's visual system greater resolving power. Since monkey cortical neurons have smaller receptive field diameters than cat cortical cells (Hubel and Weisel, 1962, 1968), it is possible that they, too, respond selectively to spatial frequencies that correspond to narrower stripes.

Recent neurophysiological evidence (Campbell and Maffei, 1970) demonstrates the presence of neurons in human vision that respond to stripe displays of particular spatial frequencies. Let an observer view a stripe display of a given spatial frequency with one eye and an identical display with his other eye. While the observer does this, the experimenter measures the amplitude of the potential which he records from the observer's occipital cortex. Now let the observer view a stripe display of a given spatial frequency with one eye and a display of a different spatial frequency with his other eye. When the stripe displays have different spatial frequencies, the amplitude of the observer's visual evoked potential increases. If the spatial frequencies of the stripe displays differ by more than an octave, no increase in the amplitude of the evoked potential occurs. Given these results, Campbell and Maffei conclude that neurons in human foveal vision restrict their response to a select band of spatial frequencies that ranges about an octave above and an octave below their "characteristic frequency".

Another neurophysiological study (Blakemore and Campbell, 1969) confirms their conclusion. After an observer views a display of moving stripes, he requires increased stripe contrast to detect the presence of a display whose stripes have the same orientation and spatial frequency. In short, his contrast threshold for the display is elevated. This threshold elevation, indexed by reduced evoked potential amplitudes, spreads to stripes whose spatial frequencies range an octave above and an octave below the frequency of the adapting stripe display. Neurons whose "characteristic frequencies" occupy positions along the spectrum from 3 to 14 cycles/degree visual angle, restrict their response to this two-octave band centered on the adapting spatial frequency. Neurons sensitive to stripe displays of higher spatial frequencies are a bit more selective. The threshold elevation that occurs in this experiment is specific to the orientation of stripes in the adapting display as well as to their spatial frequency. It is also true that the threshold elevation produced in one eye transfers to the observer's other eye. These facts mean that the neurons which serve as size detectors in human vision must be cortical cells. These cortical cells process stripe displays whose spatial frequencies are higher than 3 cycles/degree visual angle: they obviously have greater resolving power than the cat cortical cells studied by Campbell, Cooper and Enroth-Cugell (1969).

Orientation. A quantitative study (Campbell, Cleland, Cooper and Enroth-Cugell, 1968) reports that most neurons in the cat's cortex decrease their firing rate by half when a contour tilts $14-26^{\circ}$ away from the orientation that excites their maximal response. Studies with other purposes mention that cat cortical neurons, whose receptive fields have simple opponent-spatial organization, stop firing when a contour tilts $5-10^{\circ}$ away from optimal orientation (Hubel and Weisel, 1962; Pettigrew, Nikara and Bishop, 1968) while complex and hypercomplex cells fail to respond when deviations approach $10-20^{\circ}$ (Hubel and Wiesel, 1962, 1965; Ganz, Fitch and Satterberg, 1967). Evidently, complex cortical cells in the monkey make finer angular discriminations than those in the cat: they tolerate only $5-10^{\circ}$ deviations from the orientation that excites their maximal response (Hubel and Wiesel, 1968).

Campbell and Maffei (1970) have used a neurophysiological technique, with which we are already familiar, to study neurons in human vision that respond to stripes placed in particular orientations. Let an observer view two displays of stripes, those of orientation A with his left eye and those of orientation B with his right eye. When the orientations of the two stripe displays differ, the amplitude of the observer's visual evoked potential increases. No amplitude increase occurs if the orientations of stripes in the two displays differ by more than 15-20°. Campbell and Maffei conclude that human cortical neurons tolerate deviations up to about 15° from the stripe orientation that elicits their maximal response. This estimate is somewhat less stringent than the 5-10° angular selectivity displayed by complex neurons in the cortex of another primate, the monkey (Hubel and Wiesel, 1968).

<u>Direction</u>. In area 17 of the cat's visual cortex, both simple cells (Hubel, 1959) and complex cells (Hubel and Wiesel, 1962; Baumgartner, Brown and Schulz, 1964, 1965; Spinelli and Barrett, 1969) respond only to contours moving in one direction. Pettigrew, Nikara and Bishop (1968) report that 35 percent of the simple cells and 48 percent of the complex cells in this cortical area produce direction-specific responses. Complex and hypercomplex cells with similar response restrictions are common in areas 18 and 19 of the cat's cortex (Hubel and Wiesel, 1965) and in the Clare-Bishop cortical area (Hubel and Wiesel, 1969). In the latter area of the cat's cortex, neurons that respond only to contours moving in one direction are about three times as numerous as those with less stringent response restrictions.

Complex cells in visual area 17 of the anesthetized monkey's cortex respond to movement, and about half of them are excited by contours moving in a particular direction (Hubel and Wiesel, 1968). Both complex and hypercomplex cells in visual area 18 of the monkey's cortex have similar response constraints (Hubel and Wiesel, 1970). Wurtz (1969b) has studied complex cortical cells in awake monkeys. He finds that these neurons, like those in anesthetized animals, restrict their response to contours moving in particular directions. The mechanism of directional selectivity proposed by Barlow and Levick (1965) for units in the rabbit's retina may also function at this higher level in the monkey. In their model, inhibition cancels cell response to motion in the "non-preferred" direction.

Velocity. A given neuron in area 17 of the cat's visual cortex is sensitive to a particular velocity of movement that may fall anywhere between 1°/second and 10°/second (Hubel and Wiesel, 1962). If one considers all the velocities to which different neurons are sensitive, the average velocity is 4°/second (Pettigrew, Nikara and Bishop, 1968). Complex cells in areas 18 and 19 of the cat's cortex respond to velocities of movement ranging from 0.1°/second to 20°/second (Hubel and Wiesel, 1965). Apparently, cat cortical cells do not change their firing rates to mirror changes in contour velocity. Instead, a different cell population begins to respond when the velocity of the moving contour changes (Pettigrew, Nikara and Bishop, 1968). Some of the complex cortical cells studied in awake monkeys (Wurtz, 1969b) also restrict their response to particular velocities of contour motion.

Depth. Sixty-two (Nikara, Bishop and Pettigrew, 1968) to 80 percent (Hubel and Wiesel, 1962) of cells present in the cat's striate cortex respond to independent stimulation from either eye. Appropriate stimulation arriving simultaneously from both eyes facilitates their response. Similar binocular neurons are found in areas 18 and 19 of the cat's cortex (Hubel and Wiesel, 1965). A binocular cell receives input from two receptive fields which share the same opponent-spatial organization but occupy slightly disparate positions on the two retinae. A given cell is influenced by receptive fields that occupy positions on the two retinae which are separated by a particular horizontal disparity. Different cells respond to different horizontal disparities (Barlow, Blakemore and Pettigrew, 1967; Nikara, Bishop and Pettigrew, 1968; Blakemore, 1969; Blakemore and Pettigrew, 1970). This arrangement insures that, when the eyes maintain fixed convergence, objects located at different depths will stimulate different cells. Thus, the optimal location of a contour in depth for a binocular cell is determined by the horizontal disparity of its receptive fields. For both simple and complex binocular neurons, the optimal location of a contour in depth is quite specific: a significant reduction in binocular response accompanies 2 min arc adjustments which move contours out of receptive fields placed at the appropriate horizontal disparity on the retinae (Pettigrew, Nikara and Bishop, 1968).

Binocular cells, which respond only to simultaneous stimulation from both eyes, dominate visual area 18 of the monkey's cortex. A monkey binocular neuron strictly limits its response to a properly oriented contour which falls at a given horizontal disparity on the two retinae (Hubel and Wiesel, 1970). Since that disparity indicates the contour's location in depth, it is reasonable to say that binocular cells in the monkey's visual cortex restrict their response to contours located at a particular depth.

Two recent studies have used visual evoked potential recordings to demonstrate the presence of neurons in man's visual cortex that are sensitive to select horizontal disparities. Let us return to the familiar situation in which an observer views one stripe display with his left eye and another stripe display with his right eye. Suppose that the observer always sees a stripe display with his left eye that has a spatial frequency of 1.33 cycles/degree visual angle. At the same time, he views a stripe display with his right eye whose spatial frequency may differ from that of the left display by 0-12 percent. When the stripe displays projecting to either eye have slightly different spatial frequencies, the observer sees a fused set of stripes that incline in depth (Fiorentini and Maffei, 1970). As the spatial frequency difference between the two displays increases from 0-12 percent, the amplitude of the evoked potential recorded from the observer's visual cortex also increases. If the spatial frequencies of the left and right eye displays differ by more than 25 percent, no increase in the amplitude of the evoked potential occurs. The stripe displays in this experiment may fuse to become a single display of stripes inclined in depth because they stimulate human cortical neurons which respond to select horizontal disparities. Those disparities correspond to particular locations of contours in depth. Obviously, the range of horizontal disparities available in the human visual system is small.

Another display, which creates impressions of location in depth by providing only horizontal disparity cues, also changes the electrical response evoked from an observer's visual cortex. Random dot stereograms (Julesz, 1964), arranged so that a center square which fluctuates between recessed and raised location in depth, produces positive potential waves each time the observer's percept changes (Regan and Spekreijse, 1970). The same stereograms, rotated so that the disparities are vertical instead of horizontal, do not produce impressions of location in depth or changes in the visual evoked potential. Since recordings of electrical activity in the retina do not reflect depth shifts produced by rearranging the random dot stereograms, it is likely that higher visual mechanisms--possibly cortical neurons excited by particular horizontal disparities--are responding to these displays.

We have reviewed neurophysiological studies which describe neurons in cat, monkey and human visual systems whose receptive fields have opponent-spatial organization that restricts the cells' response to particular features of visual displays. Several investigators have studied neurons in human vision, whose receptive fields have opponent-spatial organization, by using psychophysical methods. Keeping information from neurophysiological studies in mind, we turn to their research.

Size. In his paper on shape discrimination and receptive fields, Sutherland (1963, p. 122) suggested that neurons might operate as size-detecting mechanisms in human vision: "It may be that there are receptive fields of different sizes and the size actually used can be altered with the size of the shape under analysis." Richards' (1967) model of size constancy requires similar mechanisms. It employs sets of spatial filters tuned to retinal image areas of different sizes; the visual system selects a filter set appropriate to its state of accommodation and convergence.

To establish the presence of neurons in human vision that might serve as size detectors, Pantle and Sekuler (1968a) designed a psychophysical experiment. Each observer, on a given trial in their experiment, adapts to a display of stationary stripes. Stripes on the adapting display have one spatial frequency selected from a set of 10 frequencies. These 10 frequencies range from 0.18 cycles/degree visual angle (wide stripes) to

22 cycles/degree visual angle (narrow stripes). The observer, adapted to a stripe display of one spatial frequency, tries to detect the presence of three separate test displays. Stripes on the test displays have spatial frequencies of 0.35, 1.05 or 3.50 cycles/degree visual angle. One predicts that observers will have difficulty detecting the presence of a test display when its stripes have the same spatial frequency as stripes on the adapting display. To test this prediction, Pantle and Sekuler plotted observers' detection thresholds for test displays against the spatial frequencies of stripes on the adapting displays. Their plot shows that the threshold curves for both test displays with wide stripes (1.05 and 3.50 cycles/degree visual angle) have similar shapes and peak in the region of adapting displays with wide stripes. The threshold curve for the test display with narrow stripes (0.35 cycles/degree visual angle) has a different shape and peaks in the region of adapting displays with narrow stripes. These data show that an observer's visual sensitivity to stripes of one spatial frequency decreases when he has experience viewing stripes of the same spatial frequency. Evidently, there are neurons in the human visual system that restrict their response, within rough limits, to stripes of a particular spatial frequency.

Other studies (Blakemore and Sutton, 1969; Blakemore, Nachmias and Sutton, 1970) define these limits more precisely. Observers in these studies, adapted to a stripe display of one spatial frequency, view test displays of wider or narrower stripes. They report a size adaptation aftereffect: narrow test stripes look even narrower than they really are and wide test stripes look even wider than they really are. This size adaptation aftereffect generalizes to displays of stripes whose spatial frequencies range about 1 1/2 octaves above and 1 1/2 octaves below the spatial frequency of stripes in the adapting display. These data, then, picture neurons in the human visual system that respond to a stripe display of a particular spatial frequency and restrict their response to displays whose frequencies bracket that of the original display by about 2 octaves. They confirm the results obtained by Campbell and Blakemore (1969) in their neurophysiological study of neurons in human vision sensitive to the spatial frequency of stripe displays.

A final psychophysical study (Campbell, Nachmias and Jukes, 1970) shows that, on 75 percent of all trials, observers correctly discriminate stripe displays whose spatial frequencies differ by 4 percent. Correct discrimination between the two displays in this study depends upon the ratio of their spatial frequencies, not upon the absolute values of the spatial frequencies chosen. This means that observers discriminate between two displays of wide stripes whose spatial frequencies differ by 4 percent as easily as they discriminate between two displays of medium stripes whose spatial frequencies differ by the same ratio. The authors conclude that, in order to accomplish discrimination with such regularity across the spatial frequency spectrum, the human visual system must contain many populations of neurons, each of which is sensitive to a limited range of spatial frequencies.

Orientation. MacKay (1957) thought that the human visual system might contain neurons sensitive to the orientation in which contours are placed. He suggested that orientation detecting mechanisms could become "satiated" after prolonged inspection of repetitive contour patterns. An observer with "satiated" orientation detectors would see "complementary after-images" and experience subjective impressions of contour motion. Sutherland (1961) also thought that the human visual system might contain neurons that serve as orientation detectors; he proposed adaptation of such detectors to explain visual tilt aftereffects.

Early psychophysical experiments (Backus, 1966; Gilinsky, 1967, 1968; Gilinsky, Boyko and Baras, 1967) support the notion that orientation detectors exist in human vision. In these experiments, observers adapt to a display of stripes placed in a particular orientation. Then they try to identify (a) a test display whose stripes are placed in the same orientation as those of the adapting display and (b) a test display whose stripes are rotated 90°. Observers take more time to identify test display (a) than to identify rotated test display (b).

More recent studies have examined not only the presence, but also the response restrictions, of neurons in human vision sensitive to the orientation of contours in visual displays. Let an observer view a masking display of stripes immediately before he views a test display of stripes whose presence he must detect. This is a forward masking paradigm. Or let an observer view a test display of stripes, whose presence he must detect, just before he sees a masking display of stripes. This is a backward masking paradigm. Masking is most efficient when the orientations of stripes on masking and test displays match. Studies that employ masking paradigms (Sekuler, 1965; Houlihan and Sekuler, 1968; Mayo, Gilinsky and Jochnowitz, 1968; Sekuler, Rubin and Cushman, 1968; Gilinsky and Doherty, 1969; Parlee, 1969) show that, as stripes on the masking display tilt $15 \pm 10^{\circ}$ from the orientation of stripes on the test display, masking efficiency drops to half its maximal value. This means that an observer is twice as likely to detect a test display when its stripes tilt about 15° from the orientation of masking display stripes than when its stripes are placed in an orientation which matches that of masking display stripes. It seems that neurons in human vision restrict their response to contours placed in one orientation. They may generalize that response to other contours if those contours are placed in orientations which closely flank that of the display which elicits their maximal response.

A careful test of this hypothesis (Campbell and Kulikowski, 1966) shows that masking efficiency drops to half its maximal value when the orientation of test display stripes deviates 12° from vertical masking stripes and 15° from oblique masking stripes. The reader will recall that neurons in the cat's visual cortex decrease their firing rate by half when a contour tilts $14\text{-}26^{\circ}$ away from the orientation that excites their maximal response (Campbell, Cleland, Cooper and Enroth-Cugell, 1968). Neurons in the human visual system, sensitive to contours placed in a particular orientation, clearly are more selective in their response than cat cortical cells.

It is important to note that the studies we have just discussed specify the angular separation between stripes on masking and test displays that decrease masking efficiency by <u>half</u>. One supposes that masking occurs in these studies because there is overlap between the response range of cells sensitive to the orientation of masking stripes and the response range of cells sensitive to the orientation of test stripes. Presumably, one would have to increase the angular separation between masking display stripes and test display stripes to $30 \pm 15^{\circ}$ in order to eliminate masking. These values are comparable to the 15° angular tolerance of human cortical neurons revealed by neurophysiological recording in a test situation where there was overlap between the response ranges of two cell populations (Campbell and Maffei, 1970).

Direction. The idea that there are neurons in the human visual system which serve as motion detectors occurred to MacKay (1961). Sutherland (1961, p. 227) endowed these neurons with direction preferences and used their response to explain aftereffects of seen motion: "The direction in which something is seen to move might depend upon the ratios of firing in cells sensitive to movement in different directions, and after prolonged movement in one direction a stationary image would produce less firing in the cells which had just been stimulated than normally, hence apparent movement in the opposite direction would be seen to occur."

Let an observer view a display, stabilized on his retina, which presents stripes moving in one direction. Then ask the adapted observer to detect the presence of test stripes moving in the same direction. We want to compare his performance on this task with his performance on the task which requires him to detect the presence of test stripes moving in the opposite direction. Observers require higher luminance to detect test stripes moving in the adapting direction than to detect test stripes moving in the opposite direction. Sekuler and Ganz (1963) attribute this result to "direction-specific adaptation" and advertise that it demonstrates the presence, in human vision, of neurons which restrict their response to contours moving in one direction. The same authors suggest that, since luminance detection thresholds for moving test stripes are highest and motion aftereffects are strongest at about the same adapting velocity, adaptation of direction-specific cortical neurons may explain both phenomena.

Adaptation to stripes moving in one direction raises an observer's luminance detection threshold for test stripes moving in the same direction above pre-adaptation value. After adaptation, the observer's luminance detection threshold for test stripes moving in the opposite direction remains unchanged (Mathias, 1968). This means that changes in perception resulting from direction-specific adaptation reflect decreased firing of neurons sensitive to the adapting direction of contour motion, not increased firing of neurons sensitive to contours moving in the opposite direction. A study (Barlow and Hill, 1963) which recorded the activity of neurons in the rabbit's retinal ganglion during and immediately after adaptation to moving stripes confirms this conclusion.

An observer's perception, in the experiments we have just considered, may be modified by the contrast and orientation of adapting stripes as well as by the direction in which they move. We need experiments that account for the separate effect that each of these display features may have. A recent study (Pantle and Sekuler, 1969) moves in this direction: it compares the contrast sensitivity of neurons that serve as orientation detectors with the contrast sensitivity of cells that function as motion detectors. The study shows that the amount of contrast on an adapting display of stationary stripes determines the amount of adaptation that orientation detectors sustain. This is true over a wide range of contrast values. On the other hand, the amount of contrast on an adapting display of moving stripes determines the amount of adaptation that motion detectors sustain only at low contrast values. It is clear that orientation detetectors have a wider range of contrast sensitivity than motion detectors.

A psychophysical experiment may easily confound the effects of orientation and direction by using test stripes that share both the orientation and the direction of adapting stripes. In this situation, when an observer has difficulty detecting the presence of the test display, his performance may reflect (a) the adaptation of orientation detectors (b) the adaptation of direction detectors or (c) the combined effects of adaptation in both populations of cells. As a general rule, when adapting and test display stripes share the same orientation, orientation detectors carry the burden of adaptation, even though one or both of the displays may be moving. For example, Antelman, Olson and Orbach (1969) show that, when adapting and test stripes share the same orientation, either stationary or moving adapting stripes raise the adapted observer's luminance detection threshold for stationary test stripes. Pantle and Sekuler (1969) demonstrate a rise in the observer's luminance detection threshold for test stripes that move in the direction <u>opposite</u> to that of moving adapting stripes when adapting and test stripes share the same orientation. On the other hand, moving adapting stripes do not alter the observer's luminance detection threshold for stationary test stripes when adapting and test stripe orientations differ by 90° (Pantle and Sekuler, 1969). Of course, one may remove the effects of adaptation among orientation detectors to reveal changes in the observer's perception due solely to adaptation among direction detectors. This is accomplished by subtracting the observer's detection threshold value for test stripes of the adapting orientation from his detection threshold value for test stripes of <u>both</u> the adapting orientation <u>and</u> the adapting direction (Pantle and Sekuler, 1969). This procedure usually reveals a significant direction effect.

The angular tolerance of motion detectors seems to be broader than that of orientation detectors. Sekuler, Rubin and Cushman (1968) find that masking efficiency drops to half its maximal value when stationary adapting and test contours have orientations that differ from one another by 15-25°. Moving adapting and test contours, in comparison, must have orientations separated by about 45° to produce the same drop in masking efficiency. One may wish to conclude that orientation detectors make finer angular discriminations than motion detectors. This conclusion must remain tentative since the present study confounds the effects of contour orientation and direction of motion.

Velocity. One may, of course, use psychophysical methods to discover neurons in the human visual system that serve as velocity detectors. Let an observer adapt, on any given trial, to contours moving at a particular velocity (Pantle and Sekuler, 1968b). The adapting velocity that he sees is chosen from a set of adapting velocities that range from 0.50°/second to 45°/second. Then ask the observer to detect the presence of three separate test displays of moving stripes. One test display has stripes moving at a velocity a 2°/second, another at 5°/second and the third at 9°/second. Test stripes may move in the same direction as adapting stripes, or in the opposite direction. Of course, the observer requires higher luminance to detect the presence of test stripes moving in the adapting direction than to detect the presence of test stripes moving in the opposite direction. This result is a product of the "direction-specific adaptation" with which we are already familiar. To assess the effects of adapting velocity, independent of adapting direction, Pantle and Sekuler computed a measure of the relative elevation of luminance detection thresholds. This computation subtracts the log luminance threshold values that

that of orientation detectors. Sekuler, Rubin and Cushman (1968) find that masking efficiency drops to half its maximal value when stationary adapting and test contours have orientations that differ from one another by 15-25°. Moving adapting and test contours, in comparison, must have orientations separated by about 45° to produce the same drop in masking efficiency. One may wish to conclude that orientation detectors make finer angular discriminations than motion detectors. This conclusion must remain tentative since the present study confounds the effects of contour orientation and direction of motion.

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We recall the suggestion of Sekuler and Ganz (1963) that neurons in the human visual system, sensitive to direction of contour motion, sustain aftereffects of seen movement. It is plausible to suppose that neurons with velocity constraints might sustain motion aftereffects of particular velocities. However, Sekuler and Pantle (1967) find that adapting velocity, duration and retinal area all interact to determine the velocity of the motion aftereffect. Weisstein (1969, p. 164), in reviewing their experiment, concludes that: "...at most, then, the aftereffect tells us that direction selectivities exist."

Velocity effects may depend, at least in part, upon neurons that serve as size detectors in human vision. Consider these data. A stationary adapting display with wide stripes elevates detection thresholds for fast moving stripes; an adapting display with narrow stripes elevates detection thresholds for slowly moving stripes (Pantle and Sekuler, 1968b). This means that size detectors tuned to large retinal areas may specialize in screening fast moving targets while those tuned to small retinal areas handle slowly moving displays. If size detectors do respond to contours moving at different velocities, human cortical neurons must be sensitive to slower velocities than cat cortical cells since they have smaller receptive fields with greater powers of spatial resolution (Campbell, Cooper and Enroth-Cugell, 1969; Blakemore and Campbell, 1969).

Depth. Recent psychophysical evidence shows that monkeys, like men, can make depth discriminations solely on the basis of hroizontal disparity cues. This evidence accompanies the discovery of binocular cells in the monkey's cortex that restrict their response to contours placed at a particular horizontal disparity on the two retinae and, hence, at a particular location in depth (Hubel and Wiesel, 1970). Macaque monkeys learn (Bough, 1970), during an operant training procedure, to discriminate between random dot stereograms (Julesz, 1964) whose center squares are raised or recessed in depth. The animals fail to perform above chance level when they use only one eye or view the stereograms with artificial convergent strabismus--conditions which eliminate the relevant horizontal disparity cues.

Monkeys and men, in performing this task, presumably rely upon cortical neurons that detect select horizontal disparities which localize contours in depth.

In this section on opponent-spatial organization, we have reviewed neurophysiological and psychophysical evidence for the existence, in cat, monkey and human vision, of neurons that detect select features of black-and-white visual displays. Those features include display size, orientation, direction and velocity of motion, and location in depth. We have listed an extensive set of correlations between the responses of single cells and the percepts of human observers. These correlations are most convincing (a) when they describe the behavior of cells and observers viewing the same display, and (b) when they emphasize the neural mechanisms shared by fellow primates, monkeys and men. With these data in mind, we turn to studies of opponent-chromatic organization in primate vision.

Opponent-Chromatic Organization

The reader may pursue topics in this section by consulting reviews (Cohen, 1946; Armington and Biersdorf, 1963; MacNichol, 1964; Graham, 1965; De Valois and Abramov, 1966; Ripps and Weale, 1969) and theoretical analyses (Hurvich and Jameson, 1955, 1957, 1960; Jameson and Hurvich, 1955, 1956a, 1956b, 1961) of primate color vision.

A single opponent-color cell responds to one set of wavelengths with excitation and to another set of wavelengths with inhibition. Opponent-color cells, sensitive to diffuse chromatic illumination of the retina, are common in the monkey's lateral geniculate body (De Valois, Smith, Kitai and Karoly, 1958; De Valois, 1960; De Valois and Jones, 1961; De Valois, Jacobs and Jones, 1963; De Valois, Jacobs and Abramov, 1964; Jacobs, 1964;

De Valois, 1965a, 1965b; De Valois, Abramov and Jacobs, 1966; De Valois Abramov and Mead, 1967; De Valois and Jacobs, 1968) and visual cortex (Motokawa, Taira and Okuda, 1962). Obviously, most of our information about opponent-chromatic organization in primate vision comes from studies of lateral geniculate neurons.

Cones in the monkey, and human, retina contain three photopigments which absorb maximal amounts of radiant energy at about 445, 540 and 570 nm (Ripps and Weale, 1963; Brown and Wald, 1964; Marks, Dobelle and MacNichol, 1964). Responses of lateral geniculate neurons reflect the combined influence of these three sets of cones. Lateral geniculate cells with non-opponent-chromatic organization respond to a wide range of colors and to white light: they probably receive excitatory input from all three cone types (De Valois, 1965a). Opponent-color cells, which restrict their response to select colors, receive excitatory input from one set of cones and inhibitory input from a second set: 540 (G) and 570 (R) pigment cones influence +R-G and +G-R opponent cells while 445 (B) and 570 (R) pigment cones influence +B-Y and +Y-B opponent cells (De Valois and Jacobs, 1968).

Because the total amount of activity in retinal cones determines their response, geniculate cells with non-opponent-chromatic organization are very sensitive to intensity changes. They are not responsive to wavelength shifts since these shifts occur without altering total cone output. Geniculate cells with opponent-chromatic organization, on the other hand, detect small wavelength shifts that alter the balance of activity between their two opponent sets of feeder cones. Because intensity changes leave that balance unaltered, opponent-color cells are unresponsive to them (De Valois, Jacobs and Abramov, 1964).

Non-opponent excitatory cells probably signal brightness since their responses fit the CIE (Commission Internationale de l'Eclairage) photopic relative luminous efficiency function (De Valois, 1965a). The CIE photopic function, determined for man (Wyszecki and Stiles, 1967, p. 378) matches the macaque monkey's photopic luminosity curve (Sidley and Sperling, 1967). Evidently non-opponent cells respond like macaque monkeys and macaque monkeys perform like men in detecting brightness.

Opponent cells probably signal hue since they are sensitive to wavelength changes (De Valois, Jacobs and Abramov, 1964). They discriminate wavelengths that produce different balances between their opponent receptors (De Valois, Abramov and Mead, 1967). Opponent cells, macaque monkeys and men with normal trichromatic color vision all discriminate best between hues located in the blue-green (490 nm) or yellow-orange (590 nm) regions of the spectrum (De Valois, 1965a; De Valois and Jacobs, 1968). However, performing primates are more efficient discriminators than single cells (Alpern, 1968). Bright presentation makes short wavelengths appear yellower and long wavelengths appear bluer (the Bezold-Brücke hue shift). If one totals the percentage of spikes which all opponent cell types contribute to all wavelengths, one obtains a function which matches the hue shift curve for human observers (Boynton and Gordon, 1965) in the short wavelength region of the spectrum (De Valois, 1965a).

Opponent and non-opponent cells cooperate to signal the saturation of a color. One may calculate saturation by subtracting the amount of opponent cell activity from the amount of non-opponent cell activity that a color produces. This operation, performed for all wavelengths, yields a curve which shows that all regions of the spectrum, except a narrow yellow (570 nm) band, are highly saturated. Geniculate cells, macaque monkeys (De Valois and Jacobs, 1968) and human observers (Wright, 1947) all produce the same saturation discrimination curve.

In sum, neurons with non-opponent-chromatic organization and those with opponent-chromatic organization function in primate vision to signal the brightness, hue and saturation of colors. Responses of single geniculate cells adequately predict a macaque monkey's performance on color discrimination tasks. On these tasks, macaque monkeys behave like human observers who have normal trichromatic color vision.

The next section considers neurophysiological and psychophysical evidence for the presence of neurons in primate vision whose receptive fields combine opponent-spatial and opponent-chromatic organization.

Combined Opponent-Spatial and Opponent-Chromatic Organization

In their study of macaque monkey lateral geniculate neurons, Wiesel and Hubel (1966) used colored spots to map the spatial organization of each cell's receptive field while assessing its chromatic responsiveness. They found three types of cells, some of which have spatial as well as chromatic response constraints. The receptive fields of Type I cells have opponent-spatial and opponent-chromatic organization: their centers receive input from one set of cones and their antagonistic surrounds receive input from another set of cones (e.g. +R center-G surround). These cells analyze spatial and chromatic features of visual displays. The receptive fields of Type II cells have opponent-chromatic organization: the whole field receives excitatory input from one set of cones and inhibitory input from a second set of cones (e.g. +R-G). These cells analyze chromatic features of visual displays. They resemble the geniculate neurons with opponent-chromatic organization described by De Valois and his colleagues (summarized by De Valois, 1965a). The receptive fields of Type III cells have opponent-spatial organization: their antagonistic centers and surrounds both receive input from all three cone types (e.g. +R,G,B center-R, G,B surround). These cells analyze spatial features of visual displays. Their response to brightness changes would resemble that of De Valois' non-opponent geniculate cells.

The majority of macaque monkey lateral geniculate neurons are Type I cells. In diffuse colored light, these cells limit their analytic talents to hue discrimination--they produce an excitatory response to some wavelengths, an inhibitory response to others, and no response at all to intermediate wavelengths which distribute equal stimulation to their two sets of opponent cones (Wiesel and Hubel, 1966). In short, when confronted with diffuse colored light, Type I geniculate cells behave like those cells with opponent-chromatic organization described by De Valois and his coworkers. Only displays with colors arranged in spatial patterns force Type I cells to use their full analytic powers.

The level at which a Type I cell is located along the geniculo-striate visual pathway determines which spatial arrangement of colors will be its most effective stimulus display. As we have seen, a particular opponent-spatial organization characterizes the receptive fields of cells at a given level along this pathway.

Neurons with <u>concentric</u> receptive fields, which would respond best to a center spot of one color <u>or</u> to a surrounding opponent color annulus, are common in the monkey's retinal ganglion (Gouras, 1968) and optic nerve (Hubel and Wiesel, 1960) as well as in his lateral geniculate body (Wiesel and Hubel, 1966). Simultaneous stimulation with center spot and opponent annulus balances excitatory and inhibitory influences and cancels the cell's response. Type I cells whose receptive fields have simple opponent-spatial organization (e.g. +R center line-B/G flanks) appear in the macaque monkey's visual cortex (Hubel and Wiesel, 1968; Gouras, 1970). Either a properly oriented center line or its opponent color flanks would stimulate this type of cell most effectively. Simple cortical cells with opponent-chromatic organization probably receive input from many Type I geniculate cells whose receptive fields are arrayed in a straight line on the retina (Hubel and Wiesel, 1968). Because the three types of cones pair off in all possible combinations to feed Type I geniculate cells, the responses of cortical cells--which depend upon that geniculate input --may reveal trichromatic interaction (Gouras, 1970). Type I cells with complex and hypercomplex receptive field organization also exist in the macaque monkey's visual cortex (Hubel and Wiesel, 1968). They respond to properly oriented, and colored, moving contours.

The sample of cortical cells whose receptive fields combine opponent-spatial and opponent-chromatic organization is small (Hubel and Wiesel, 1968; Gouras, 1970) and no careful neurophysiological study of their response restrictions exists. If these cortical neurons are like those whose receptive fields have opponent-spatial organization, they probably respond to features of colored visual displays such as contour size, orientation, direction and velocity of motion, and location in depth.

Psychophysical studies of color aftereffects may help us to discover cells in the human visual system with combined opponent response properties. Neurons whose receptive fields combine opponent-spatial and opponent-chromatic organization are ideal candidates among those cells that could sustain color aftereffects. Their opponent-spatial organization allows them to respond to contours on colored displays and their opponent-chromatic organization allows them to adapt to the color of those contours.

Size. Neurons in human vision sensitive to the spatial frequency of stripe displays may participate in the development of color aftereffects. In an earlier part of this review, we mentioned the orientation-contingent color aftereffects discovered by McCollough (1965a): vertical white test stripes look blue-green if they were orange during adaptation and horizontal white test stripes look orange if they were blue-green during adaptation. These aftereffects are strongest when the width of black-and-white test stripes matches the width of the colored adapting stripes (Gibson and Harris, 1968; Fidell, 1968). However, if orientation-contingent color aftereffects involve neurons sensitive to stripes of a particular spatial frequency, it is unclear how restricted the response range of those neurons might be. Aftereffect colors appear on black-and-white test stripes which are considerably wider or narrower than the colored stripes that observers view during adaptation (McCollough, 1965a; Stromeyer, 1969; McCollough and Clark, 1971; McCollough and Gerrein, 1971).

Orientation-contingent color aftereffects typically disappear as test stripes tilt out of the adapting orientation (McCollough, 1965a). Teft and Clark (1968) used this tilt test to measure the response range of neurons, sensitive to stripes of a particular spatial frequency, that sustain orientation-contingent color aftereffects. They found that when stripes on the adapting and test displays share the same spatial frequency, aftereffect colors remain visible as test stripes tilt 24-27°. When stripes on the adapting and test displays have different spatial frequencies, aftereffect colors disappear as test stripes tilt beyond 21-24°. It is clear from this study that orientation-contingent color aftereffects do involve neurons sensitive to the spatial frequency of the adapting stripe display. When stripes of a different spatial frequency appear on the test display, observers see weaker aftereffect colors that fail to generalize over the same range of test stripe orientations.

Orientation. We have already reviewed McCollough's experiment and emphasized that orientation-contingent color aftereffects fade as test stripes tilt out of the adapting orientation. Several experimenters (McCollough, 1965a; Gibson and Harris, 1968; Stromeyer, 1969) find that aftereffect colors associated with vertical and horizontal stripes disappear when test stripes fall in oblique (45° and 135°) orientations on the observer's retina. One may arrange this condition by tilting the test display while the observer's head remains upright or by asking him to tilt his head in relation to the test stripes. We assume that the tilted test display fails to evoke aftereffect colors because it stimulates new populations of unadapted orientation detectors.

A different test of the response range of orientation detectors sustaining color aftereffects varies angular separation between the two adapting stripe displays (Fidell, 1970). Adapting displays whose stripes are separated by 90° produce saturated aftereffect colors. Aftereffect colors are somewhat less saturated when vertical stripes alternate with 45° oblique stripes during adaptation and grow faint or non-existent when adaptation pairs vertical stripes with stripes tilting 22° or 11°. In this experiment, two populations of orientation detectors adapt to colored stripes. Adapting stripes whose orientations are separated by only 11° or 22° stimulate populations of orientation detectors whose response ranges overlap. In the overlap region, red and green aftereffects cancel one another and the observer fails to see colors on the test display. Apparently, to eliminate overlap, one must present displays of adapting stripes whose orientations differ by about 45°. This means that each population of cells sensitive to a particular orientation extends its response to contours tilting away from that orientation 22° clockwise and 22° counter-clockwise. These values are comparable to the 15-20° angular tolerance shown by human visual neurons in another experiment where the response ranges of orientation detectors also overlapped (Campbell and Maffei, 1970).

Direction. Color aftereffects that are contingent upon the direction in which contours move develop when observers view moving colored stripes (Snow, 1966; Hepler, 1968; Stromeyer and Mansfield, 1970) or rotating colored spirals (Stromeyer and Mansfield, 1970). It is apparent that these color aftereffects must involve populations of neurons in the human visual system that restrict their response to contours moving in a particular direction.

If the observer tilts his head while viewing black-and-white moving test stripes, he converts horizontal stripes moving up and down into oblique stripes moving obliquely across his retina. Observers discover during this procedure that aftereffect colors look fully saturated when adapting and test stripes fall in identical orientations on the retina, half-saturated when test stripes tilt 15° and completely faded when they tilt 25° (Stromeyer and Mansfield, 1970). Motion detectors sensitive to colored adapting stripes seem to restrict their response to a range of moving stripe orientations covering 15-20°. This range is more selective than the 45° tolerance range reported for detectors sensitive to moving black-and-white stripes (Sekuler, Rubin and Cushman, 1968).

Velocity. Recent experiments (Stromeyer and Mansfield, 1970) provide some evidence that detectors stimulated by moving, colored stripes restrict their responses to a select range of velocities. Let observers view a rotating spiral whose face has a red center square surrounded by green when it contracts and a green center square surrounded by red when it expands. A clear aftereffect square appears in the center of the spiral viewed in white test light. Its color depends upon the spiral's direction of rotation. Observers viewing the test spiral see best-formed squares at velocities that match or slightly exceed an adapting velocity of 2° 5'/second (2.9 cps). At slower (2.6 cps) and faster (3.4 cps) test velocities the aftereffect square becomes indistinct.

Observers who see color aftereffects on test stripes that move up and down may alter their saturation by adjusting the stripes' velocity. To produce the most saturated aftereffect colors, they choose test stripe velocities that are faster (5° 47'/second to 7° 12'/second) than the adapting stripe velocity of 4° 9'/second. In this situation, aftereffect colors vanish at slower (2° 11'/second) test velocities. We have already seen that, when velocity is not confounded with temporal frequency of stimulation, luminance detection thresholds for moving stripes are highest when adapting and test stripe velocities match (Sekuler, 1967). Likewise, if temporal frequency of stimulation were held constant, we would expect observers to see the most saturated aftereffect colors when test and adapting stripe velocities match.

In this section, we have described neurons in primate vision whose receptive fields combine opponent-spatial and opponent-chromatic organization. These cells can detect contours _and_ adapt to colors. They may be the neurons that sustain color aftereffects which are contingent upon spatial features of colored visual displays.

To conclude our review of neurophysiological and psychophysical studies of feature detectors, it will be useful to summarize those response restrictions that evidently apply to neurons in the human visual system. This summary combines data from studies employing black-and-white displays and displays with colored contours. Masking efficiency drops to half its maximal value when masking and test displays separate contours by slightly more than an octave for size detectors, 12-15^{o} for orientation detectors and 15-45^{o} for motion detectors. The human visual system incorporates detectors that restrict their response to particular directions and velocities of contour motion. No precise measure of the response range of velocity detectors exists. Binocular cells that serve as depth detectors in human vision restrict their response to particular horizontal disparities and probably tolerate displacements away from those disparities of no more than 2 min arc.

Experiments described in this thesis offer observers a visual experience that produces a change in their perception. This change lasts for several days. Our experiments, then, relate directly to a small set of studies that demonstrate lasting modifications of perception resulting from experience with simple visual displays. Let us consider those studies.

Lasting Modifications of Perception Resulting from Simple Visual Experience

In the previous section we learned that neurons populating the geniculo-striate visual pathway detect select features of visual displays. Detecting features, however, is only a preliminary step in recognizing the pattern of a display (Minsky, 1963; Neisser, 1966; Weisstein, 1969). Any experience that modifies the response of feature detectors changes visual perception, not because it revamps complex perceptual and cognitive processes, but because it alters the function of elementary sensory mechanisms (Hebb, 1949). Only a few studies demonstrate lasting modifications of visual perception which might reflect the altered responses of feature detectors operating in the earliest stages of pattern analysis. (The reader who wishes to explore complex perceptual learning may consult reviews by Hebb, 1949; Gibson and Gibson, 1955; Gibson, 1963; Harris, 1965; Wohlwill, 1966; Rock, 1966; Epstein, 1967 and articles by Donderi and Kane, 1965; Tees and More, 1967a, 1967b, 1968.)

Two persisting perceptual changes, apparent to observers who have worn prismatic spectacles (Gibson, 1933), may reflect response alterations among populations of visual neurons tuned to detect contours and colors. An observer who wears prismatic spectacles that displace objects 15° to the right sees vertical lines as curves which are convex to the left. As she continues to wear the spectacles for 45 hours over a period of 4 days, the curvature grows less pronounced. When she removes the spectacles, after this adaptation period, vertical lines look like curves which are convex to the right--an effect which persists for about 2 days. While wearing prismatic spectacles an observer also adapts to another feature of the visual environment: narrow bands of color, red on the right and blue on the left, which flank the edges of dark vertical bars that appear on brighter backgrounds. These bands of color are cumulative half-spectra produced by the prismatic lenses. They grow less prominent during adaptation and reappear in opposite position (red left, blue right) when the observer removes the spectacles. Such "phantom fringes" persist for several hours (Hay, Pick and Rosser, 1963).

McCollough (1965a) thought that "phantom fringes" might result from chromatic adaptation of detectors in the human visual system sensitive to the orientation and facing direction of edges. She succeeded in demonstrating a color aftereffect which is specific to the orientation of stripes with which color is paired. These orientation-contingent color aftereffects, she reports, remain visible for about an hour after adaptation. Subsequent studies show that they may last for up to 3 days (Stromeyer, 1969).

Two recent experiments describe persisting color aftereffects that are associated with the direction in which contours move. Motion-contingent color aftereffects, produced with horizontal moving stripes, persist at least 20 hours after adaptation (Hepler, 1968) while those linked to rotating spiral patterns may last as long as 6 weeks (Stromeyer and Mansfield, 1970).

Another experiment which presents rotating spiral pattern to observers also produces a lasting change in their perception. If an observer fixates the center of a moving spiral pattern for 15 minutes, he sees a negative aftereffect of motion when he returns to view a stationary spiral pattern 20 hours later (Masland, 1969). A spiral pattern which contracted during adaptation appears to expand. To evoke this aftereffect, the stationary spiral must fall on the area of the observer's retina--and the area of topographic projection on his visual cortex--originally stimulated by the moving spiral. Evidently, the motion-sensitive cortical cells which adapt to the moving spiral are also the cells which maintain change in the observer's perception of spiral patterns.

We have seen that, when an observer views a striped display of a given spatial frequency for a few minutes and then shifts his gaze to a display with narrower stripes, those stripes look even narrower than they really are. Wide stripes look different too: they appear to be even wider than they really are. This size-adaptation aftereffect (Blakemore and Sutton, 1969; Blakemore, Nachmias and Sutton, 1970) lasts as long as 4 hours after the observer amasses 45 minutes of adaptation.

It is possible, then, to make rather long-lasting changes in human visual perception that seem to reflect altered responses of neurons which serve as feature detectors and function in the earliest stages of pattern analysis. Our experiments examine, in detail, the lasting change in perception that develops when moving, colored stripes stimulate populations of feature detectors. These experiments assess (a) the kind of change that an observer experiences when he reports motion-contingent color aftereffects (b) the way in which that change develops with experience (c) the specificity of that change to features of the moving, colored stripe display and (d) the form in which that change persists for many hours after the visual experience that creates it.

Section A

The Development and Persistence of Motion-Contingent Color Aftereffects

This research began as a simple demonstration designed to integrate two new ways of modifying human visual perception. The first method (McCollough, 1965a) changes an observer's perception of black-and-white stripes by adapting him to vertical stripes of one color and horizontal stripes of another color. Adapted observers report an aftereffect color on vertical test stripes that differs from the aftereffect color they see on horizontal test stripes. These aftereffect colors last for about an hour after 5-10 minutes of adaptation. The second method (Masland, 1969) changes an observer's perception of a stationary spiral pattern by adapting him to a contracting spiral. After 15 minutes of experience watching the contracting spiral, observers report a negative aftereffect of seen motion when they view the same spiral pattern which is stationary. This aftereffect lasts for at least 24 hours.

Combining contour motion and color, we reasoned, should produce a novel modification of perception. If an observer adapts to moving, colored stripes, he should see aftereffect colors that are contingent upon the direction in which black-and-white test stripes move. And, with enough experience, he should see aftereffect colors on moving test stripes many hours after adaptation.

Experiments in Section A engage observers in a visual task that does produce motion-contingent color aftereffects. These experiments also demonstrate that motion-contingent color aftereffects can persist for at least 20 hours after the visual experience that creates them. Although these experiments are published (Hepler, 1968), it is important to review them here. Their results prompt questions which experiments described in Sections B and C try to answer.

Experiment 1

McCollough (1965a) used chromatic adaptation as a tool to demonstrate the presence of neurons in the human visual system that respond selectively to contours placed in particular orientations. Chromatic adaptation puts a color "tracer" on neurons in human vision and gives the investigator a convenient index of their response restrictions. Experiment 1 employs chromatic adaptation to document the presence of neurons in man's visual system that respond to contours moving in particular directions.

Observers

Six male and two female university students, uninformed about visual aftereffects, participated in this experiment as salaried observers. Each participant had normal color vision and displayed no anomalies of color perception when viewing the AO H-R-R Pseudoisochromatic Plates.

Apparatus

During adaptation in this experiment, observers see horizontal magenta stripes moving in one direction alternate with horizontal yellow-green stripes moving in the opposite direction. It is convenient to arrange this display with simple components.

A loop of translucent white paper carries opaque black Lettraset stripes. Each stripe is 3.0 mm wide and subtends 12 min arc at 83 cm viewing distance. The spatial frequency of the stripe display is 2.50 cycles/degree visual angle.

The paper loop that carries the stripes advances up or down on felt-covered rollers driven by a Bodine Speed Reducer Motor Type NSH-12R. Both sets of stripes move at 2.0°/second.

Kodak Wratten filters 33 (magenta) and 61 (yellow-green), placed in a Kodak Carousel projector located behind the stripe display, transilluminate the moving stripes with color. The luminance of the stripes in white light, provided by the 500 watt tungsten filament projection lamp operating at 3200° K, is 215 ftL. Kodak Wratten filter 33 (magenta) transmits 7.92 percent of the light from the projection lamp. Kodak Wratten filter 61 (yellow-green) transmits 14.44 percent.

Procedure

During adaptation, four observers see magenta stripes moving up alternate with yellow-green stripes moving down. Four different observers see yellow-green stripes moving up alternate with magenta stripes moving down. With his head positioned by a chin rest, each observer fixates the center of the moving stripe display. A timing circuit changes the direction and color of the moving stripes every five seconds. Each observer views moving, colored stripes for 24-33 minutes a session on each of several consecutive days.

Immediately after each adapting session, the observer views horizontal stripes moving up and horizontal stripes moving down in white light from the projection lamp. These are the same stripes that he sees during adaptation, without their color filters. The observer offers his description of moving stripes that are objectively black-and-white.

Results

Table 1 summarizes the results of Experiment 1. Observers require a

Table 1

Summary of Results in Experiments 1 and 2

Adapting condition ↑	 ↓	Cumulative hours of adaptation required to produce motion-contingent color aftereffects visible immediately after the final adapting session*	Cumulative hours of adaptation required to produce motion-contingent color aftereffects visible 20 hours after the final adapting session*
R	G	3.30	3.20
		3.20	8.35
		3.85	6.40
		2.00	.80
G	R	.55	4.80
		.55	5.20
		3.60	3.60
		2.00	3.60
		Mean = 2.38 hours	Mean = 4.50 hours

*n = 8

mean of 2.38 cumulative hours of adaptation to develop motion-contingent color aftereffects that are visible immediately after adaptation. Each observer reports pink on black-and-white stripes moving in the direction traversed by yellow-green adapting stripes and green on black-and-white stripes moving in the direction traversed by magenta adapting stripes. They report no aftereffect colors on horizontal black-and-white stripes that remain stationary.

Each observer tries to offer an accurate description of his perception of moving black-and-white stripes. Although the experimenter does not mention color differences, the astute observer may think that he should report colors on moving test stripes. If he were guessing, the observer's most plausible strategy would be to associate a given color with stripes moving in a particular direction. When confronted with black-and-white test stripes moving up, the observer should report the color that he originally saw on stripes moving up. It is clear that observers do not use this guessing strategy: instead, they report complementary color aftereffects.

A simple association model predicts the guessing strategy that we have just discarded. If the observer sees red stripes moving up during adaptation, the model says that he should associate one feature of the display (red) with another feature of the display (stripes moving up). During testing, presentation of a display that includes one feature should evoke a response that names the second feature. Since this does not happen, a simple association model fails to explain observers' reports. Their reports, naming complementary aftereffect colors, suggest that an adequate explanation must incorporate chromatic adaptation.

Let us examine the way in which chromatic adaptation might work in the present experiment. First, we must decide which neurons adapt. Observers report color aftereffects that are contingent upon the direction in which stripes move. These aftereffects may involve neurons in the human visual system, like those in cat and monkey cortex, that respond to stripes moving in a particular direction. Motion-contingent color aftereffects, visible immediately after an adapting session, could result from chromatic adaptation of motion-detecting neurons in two different cell populations.

Suppose that a neuron which responds to stripes moving in a particular direction has opponent-chromatic organization. This means, we recall, that the neuron is excited by one set of wavelengths and inhibited by another set of wavelengths. When an observer views the adapting display of moving, colored stripes, this neuron responds to stripes moving in one direction and adapts to the set of wavelengths that appears on those stripes. After adaptation, the neuron remains responsive to its opponent set of wavelengths. That opponent set of wavelengths is available in the white light illuminating test stripes which move in the direction that excites the cell's response. The cell, and all others like it, will signal a color for those test stripes that is roughly complementary to the adapting color.

The effects of chromatic adaptation dissipate quickly (Hubel and Wiesel, 1966). If chromatic adaptation were solely responsible for an observer's perception of color aftereffects, one would expect those aftereffects to remain visible for only a short period of time after the end of an adapting session. In the present experiment, observers may see motion-contingent color aftereffects immediately after adaptation that disappear several minutes later.

If we review the results of Experiment 1, we find that observers with a mean of 2.38 cumulative hours of experience watching moving, colored stripes develop motion-contingent color aftereffects that are visible immediately after adaptation. The aftereffect colors that they report are contingent upon the direction in which test stripes move. It is reasonable to suppose that these color aftereffects reflect chromatic adaptation of neurons in the human visual system that respond to particular directions of stripe motion. It is evident that a model, based on known neurophysiology, which incorporates chromatic adaptation offers a more successful explanation of observers' reports in Experiment 1 than a model which describes the experimental situation in terms of associations between stimulus features. Since chromatic adaptation creates transient changes in neural response, color aftereffects due solely to chromatic adaptation should be fleeting phenomena.

Experiment 2 increases the observers' experience with moving, colored stripes. If transient chromatic adaptation is the only process responsible for changing observers' perceptions of moving stripes, increasing their experience should not prolong the visibility of motion-contingent color aftereffects.

Experiment 2

Conventional demonstrations use brief adapting periods to produce aftereffects of seen motion that are visible immediately after adaptation, but quickly decay (Sekuler and Ganz, 1963). Masland (1969) was able to produce a persisting motion aftereffect by giving observers 15 minutes of experience watching a contracting spiral pattern. Experiment 2 allows observers to accumulate as much experience as they need to see motion-contingent color aftereffects 20 hours after an adapting session.

Observers

Five male and three female university students, uninformed about visual aftereffects, participated in this experiment as salaried observers. Each participant had normal vision and displayed no anomalies of color perception when viewing the AO H-R-R Pseudoisochromatic Plates.

Apparatus

The apparatus used in Experiment 1 presents the same stimulus display in Experiment 2.

Procedure

Observers in Experiment 2 follow the adapting procedure of Experiment 1. This time, instead of describing moving black-and-white stripes immediately after each adapting session, these observers return to offer their descriptions 20-27 hours later, just before each adapting session. Their reports are unbiased by experience with aftereffect colors visible immediately after adaptation.

Results

In this experiment, observers require a mean of 4.50 cumulative hours of adaptation to develop motion-contingent color aftereffects that are visible 20-27 hours after their last adapting session. Again, each observer reports pink on black-and-white stripes moving in the direction traversed by yellow-green adapting stripes and green on black-and-white stripes moving in the direction traversed by magenta adapting stripes. They report no aftereffect colors on horizontal black-and-white stripes that remain stationary.

The reader may consult Table 1 to compare the results of Experiments 1 and 2. Consider the experience that observers need to see motion-contingent color aftereffects immediately after adaptation. It is clear that they require about twice as much experience with moving, colored adapting stripes to develop motion-contingent color aftereffects that persist for a day.

Evidently, cumulative experience with moving, colored stripes changes an observer's perception of moving test stripes. That change persists for many hours after the end of an adapting session. Spaced sensory stimulation of the sort provided in Experiment 2 typically produces habituation, the conditioned inhibition of sensory responses. Motion-contingent color aftereffects that persist may be a product of this conditioning process which would prolong the effects of chromatic adaptation in different populations of motion-detecting neurons.

The results of Experiment 2, then, demonstrate that observers develop motion-contingent color aftereffects which persist at least 20 hours if they have enough experience with the adapting display. Establishing a lasting change in their perception of moving stripes takes more time (4.50 cumulative hours) than making a similar change which must persist just long enough to be visible immediately after adaptation (2.38 cumulative hours). Motion-contingent color aftereffects that persist result from cumulative, spaced experience. They must reflect some process, possibly conditioned inhibition, that prolongs the effects of chromatic adaptation within motion-detecting neurons.

Information from Section A tells us that motion-contingent color aftereffects develop and persist. After reading Section A, we have some notion what kind of change produces motion-contingent color aftereffects. We also have ideas about where that change occurs. Experiments in Sections B and C specify (a) precisely what change occurs in the observer's perception, (b) how that change develops and (c) which populations of cells support this change.

Section B

The Localization of Persisting Motion-Contingent Color Aftereffects

We have speculated, on the basis of evidence presented in Section A, that motion-contingent color aftereffects reflect the altered response of cortical neurons with direction preferences. If this spectulation has merit, we should find that color aftereffects are localized to those cells that receive adapting stimulation. One test of this possibility adapts populations of cortical cells that respond to stimulation of adjacent retinal areas to different displays of moving, colored stripes. If we can create "opposite" color aftereffects in cells that respond to neighboring retinal areas, we may be certain that changes which produce those aftereffects occur in the particular cells that are stimulated during adaptation. Experiment 3 tests this possibility.

Experiment 3

Observers

Three men from the Biomedical Engineering research laboratory at the California Institute of Technology participated in this experiment, which was conducted in their laboratory. Each man was a skilled observer in experiments which require him to wear a contact lens with a stalk-mounted mirror in order to view targets in stabilized vision. Two of the men had corrected vision and the contact lenses which they wore during experimentation incorporated their optical corrections. All three men enjoyed normal color vision and had served as observers in a demonstration of the orientation-contingent color aftereffects described by McCollough.

Apparatus

Experiment 3 employs the left-eye channel of the optical system pictured in Figure 1. This system presents stimulus displays in normal or stabilized vision. Fender and Nye (1961) offer a complete description of the apparatus.

The display of moving stripes occupies position T in the left-eye channel of the system. A 35-mm film loop, which traverses a circular path around a vertical guide plate at position T and the mirror M_1, carries opaque and transparent stripes. Each stripe is 1.0 mm wide and subtends 8.4 min arc when imaged on the observer's retina. The spatial frequency of the stripe display is 3.57 cycles/degree visual angle.

The film loop that carries the stripes advances up or down on projector sprockets driven by a Hansen Manufacturing Company Magnatorc DC Motor. Both sets of stripes move at 47 min arc/second.

Figure 2 shows the stripe display that observer S.M. views during adaptation in Experiment 3. The film loop that carries the stripes moves past an aperture in the vertical guide plate at position T. This aperture restricts the area of the stripe display to a circle whose 21 mm diameter subtends 3^{o} visual angle on the observer's retina. A black bar, whose 2 mm width subtends 16.8 min arc, bisects the circular display.

Kodak Wratten filters 33 (magenta) and 61 (yellow-green), placed immediately behind the circular aperture, color the moving stripes during adaptation. The luminance of the stripes in white light, provided by a General Electric Microscope Illuminant 18A/T10/3P-6V operating at 3000^{o} K, is 18 ftL. Kodak Wratten filter 33 (magenta) transmits 8.39 percent of the light from the Microscope Illuminant. Kodak Wratten filter 61 (yellow-green) transmits 14.01 percent.

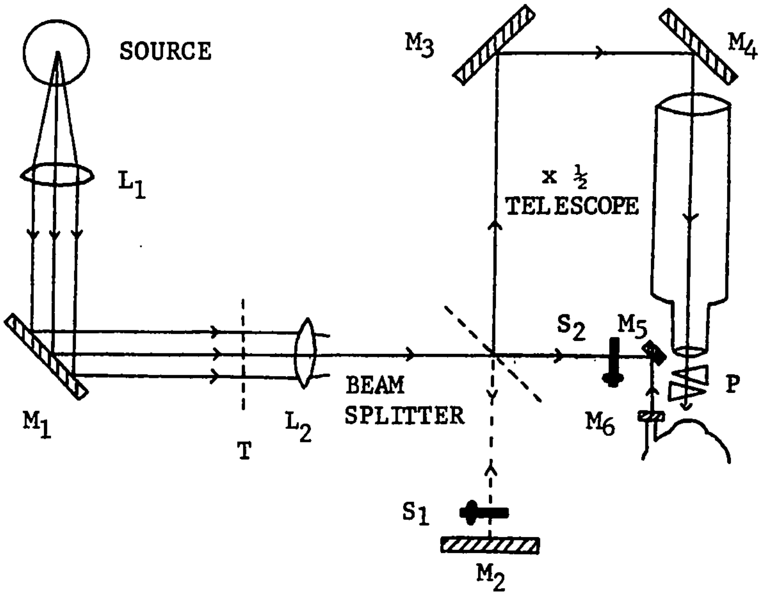

Figure 1. Components in the left-eye channel of the optical system used to stabilize a display of moving stripes on the observer's retina in Experiment 3. The stripe display occupies position T. The observer wears a scleral contact lens which holds a mirror mounted on a stalk. When his eye is aligned before the telescope, the observer sees the stripe display formed by light reflected from his contact lens mirror. The reflected display moves with the observer's eye. With shutter S_1 open and shutter S_2 closed the observer sees the display in normal vision; reversing the shutters presents the display in stabilized vision. The diagram is adapted from Fender and Julesz (1967, p. 821).

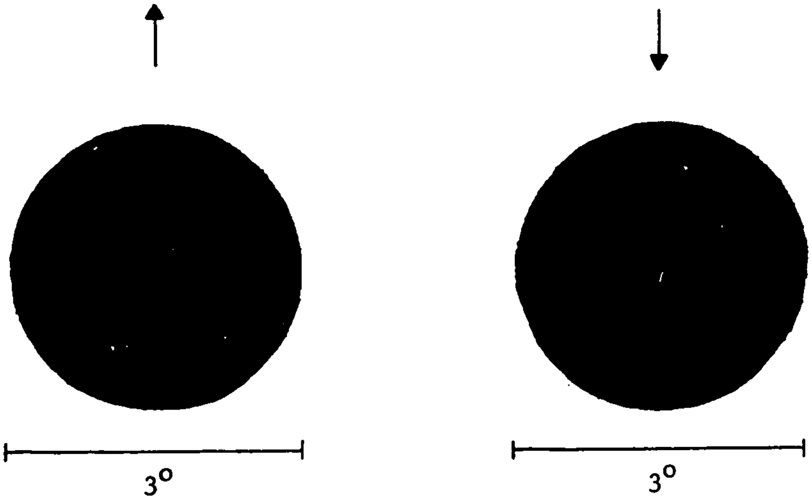

Figure 2. The display of moving colored stripes that observer S.M. views in stabilized vision during adaptation in Experiment 3. Consider the two circular fields in register. They stimulate an area whose diameter is 3° visual angle on the observer's retina. During adaptation, S.M. sees magenta stripes moving up alternating with yellow-green stripes moving down in the left half of his field of view. At the same time, in the right half, he sees yellow-green stripes moving up alternating with magenta stripes moving down.

Procedure

After inserting his left scleral contact lens with its stalk-mounted mirror and occluding his right eye with a patch, the observer sits in an adjustable chair before the optical system. He aligns his left eye with the telescope and fixes the position by gripping a dental mold in his teeth and resting his forehead on a plaster cast. The experimenter adjusts components along the optical bench until the observer sees a cross-hatched alignment pattern clearly imaged on his retina in normal Maxwellian view. Then the experimenter closes shutter S_1 and opens shutter S_2 to present the pattern in stabilized vision. After minor adjustments in stabilized vision, the observer is ready to view the adapting display of moving, colored stripes. A shutter occludes the light source while the experimenter rearranges stimulus displays.

It is crucial in this experiment that the 3^o circular display stimulate the same area of the observer's retina on successive days. To minimize registration error, the optical system remains aligned for a particular observer until his participation in the experiment is complete.

During adaptation, observers see color A on stripes moving up and color B on stripes moving down on the left helf of the circular display. At the same time, on the right half, they see color B on stripes moving up and color A on stripes moving down. Figure 2 shows one adapting display. Observer S.M. sees magenta stripes moving up, yellow-green stripes moving down on the left and yellow-green stripes moving up, magenta stripes moving down on the right. Observers D.F. and P.N. see yellow-green stripes moving up, magenta stripes moving down on the left and magenta stripes moving up, yellow-green stripes moving down on the right. Note that this arrangement tries to produce one set of motion-contingent color aftereffects by stimulating the observer's nasal hemiretina and a second set of motion-contingent color aftereffects by stimulating his temporal hemiretina. The observer should see opposite color aftereffects on white stripes stimulating adjacent regions of his retina.

A timing circuit changes the direction and color of the moving stripes every four seconds, interposing a two second dark interval. Observers view moving, colored stripes for two 15 minute adapting sessions each day. Observer S.M. accumulates 2.5 hours (5 consecutive days) of adaptation while observers D.F. and P.N. accumulate 3.5 hours (7 consecutive days).

Immediately after each adapting session, observers view horizontal stripes moving up and horizontal stripes moving down in white light from the Microscope Illuminant. The display is the same one that they see during adaptation, without its color filters. Each observer offers his description of stripes, moving in either half of the circular field, that are objectively black-and-white.

Observers return 24 hours after their last adapting session to describe the appearance of the same moving black-and-white stripes. Since these observers know the purpose of the experiment and are familiar with color aftereffect research, they are encouraged to use conservative criteria for reporting the presence of colors on moving test stripes.

Results

Table 2 summarizes the results of Experiment 3. Two of the three observers who participate in this experiment develop motion-contingent color aftereffects. After 2.0 cumulative hours of adaptation, observer S.M. reports green on the left of the circular display and pink on the right when black-and-white stripes move up. He sees pink on the left and green on the

Table 2

Summary of Results in Experiment 3

Observer	Adapting condition		Cumulative hours of adaptation	Cumulative hours of adaptation required to produce motion-contingent color aftereffects	Motion-contingent color aftereffects visible 24 hours after the final adapting session
	↓	↑			
S.M.	G R	R G	2.5	2.0	yes
D.F.	R G	G R	3.5	2.5	yes
P.N.	R G	G R	3.5	---	---

right when the same stripes move down. Observer S.M. reports these colors throughout two more adapting sessions.

Observer D.F. develops motion-contingent color aftereffects on the left half of his circular display after 2.5 cumulative hours of adaptation. He reports a clear impression of pink on black-and-white stripes moving up and green on the same stripes moving down. These colors are visible throughout four more adapting sessions. Test stripes on the right half of the circular display remain a neutral color. His failure to develop color aftereffects on the right half of the display is puzzling until one learns that observer D.F. sustained a burn on the temporal hemiretina of his left eye during pioneer experiments with bright stabilized targets. The right half of the circular display falls on the injured area.

Stabilizing the display on the retina does not seem to hasten adaptation. Observers viewing the stabilized display develop motion-contingent color aftereffects after 2.0 to 2.5 cumulative hours of adaptation. Observers in Experiment 1 see similar aftereffects after a mean of 2.38 cumulative hours of adaptation to colored stripes moving in normal vision.

Observer P.N. fails to develop motion-contingent color aftereffects on either half of the circular display. After 3.5 cumulative hours of adaptation, he leaves the experiment. It is interesting to note that, in a previous demonstration of orientation-contingent color aftereffects, both observers S.M. and D.F. saw clear pink and green aftereffect colors. Observer P.N. failed to see aftereffect colors in that demonstration as well as in the present experiment. Since he responds correctly on standard color vision tests, P.N.'s performance does not reflect defective color vision. Research on color aftereffects typically encounters some observers with normal color vision who do not develop the appropriate aftereffects. No satisfactory explanation of their performance is available.

Altering the color of "white" light illuminating the test stripes can enhance the saturation of one aftereffect color and degrade that of its partner. Observers continue to report a difference between the two aftereffect colors but the quality of that difference changes. Suppose, for example, that observer D.F. sees a prominent pink aftereffect on black-and-white stripes moving up and a faint green aftereffect on the same stripes moving down on the left side of the circular display. He makes this report when the stripes are illuminated by the Microscope Illuminant, operating at color temperature 3000° K, which provides rather yellow light. If one places Kodak Wratten color conversion filters 80A and 80D in the light path, they shift the color temperature of the light to approximately 6750° K. Now light illuminating the stripes looks bluer and observer D.F. reports a strong green aftereffect and a much weaker pink one.

One can arrange stripe motion across the retina in two ways. Stripes may move across a stationary retina or the retina may move across stationary stripes. Stabilizing a moving stripe display on the retina establishes condition one. When the observer views the moving, colored stripe display in stabilized vision it continues to stimulate the same region of his retina because the image of the display tracks his eye as it moves. His retina remains in a constant position with reference to the moving stripes. His eye is free to move, but its movements do not determine which direction the stripes move. Under these conditions observers develop motion-contingent color aftereffects that are uncorrelated with voluntary eye movements. Thus, gaze-contingent color conditioning (Kohler, 1964; Harrington, 1965; McCollough, 1956b)--in which specific eye movements cone to evoke particular color percepts--cannot explain the present results.

Stromeyer and Mansfield (1970) established condition two. They adapted observers to colored stripes that moved across the retina because the observer systematically tracked his eyes across a stationary stripe display. Under these conditions, their observers developed appropriate motion-contingent color aftereffects.

It is clear that movement of stripes across the retina, arranged by method one or method two, stimulates neurons that undergo chromatic adaptation. We have suggested that these must be neurons in the visual cortex which have direction preferences. We are encouraged to find that such neurons regard the two conditions of stripe motion as equivalent. Movement of stripes across a stationary retina and movement of the retina across stationary stripes both elicit similar responses from motion-sensitive neurons in the monkey's cortex (Wurtz, 1968, 1969a).

In discussing the results of Experiment 1, we suggested that neurons sensitive to stripes moving in a particular direction may sustain motion-contingent color aftereffects. We explained how this might happen if those neurons have opponent-chromatic organization. Our explanation stressed the fact that chromatic adaptation alters the response of a cell by changing the balance of opponent-chromatic influences _within_ the cell. This model, then, says that there are neurons sensitive to stripes moving up. All of these neurons have opponent-chromatic organization. There are also neurons sensitive to stripes moving down. All of these neurons have opponent-chromatic organization.

There is, however, another possibility. One might suppose that there are neurons that respond to red stripes moving up and other neurons that respond to red stripes moving down. Likewise, there might be neurons that respond to green stripes moving up and other neurons that respond to green stripes moving down. How would chromatic adaptation operate in this model? Consider the case where red appears on adapting stripes moving up. This display would depress the response of neurons sensitive to red stripes moving up. Neurons sensitive to green stripes moving up remain unaffected by the adapting display and their response dominates when the observer views white stripes moving up during testing. Note that this model makes chromatic adaptation a change in the balance of opponent-chromatic influences between two populations of cells.

This model is interesting because it makes a testable prediction. Suppose that there are neurons sensitive to green stripes moving up and other neurons sensitive to green stripes moving down. Let an observer view green stripes moving down during adaptation and let this display alternate with red stripes moving up. The response of green-down cells will be depressed, while that of green-up cells remains unaltered. This is exactly the situation (Sutherland, 1961) that produces an aftereffect of seen motion. We must predict, then, that observers who view stationary green stripes after watching green stripes moving down, will see the stationary stripes appear to move up. In short, observers will experience color-contingent motion aftereffects as well as the motion-contingent color aftereffects that we have already discussed.

Reports of some observers who viewed stationary, colored stripes in normal vision at the end of Experiment 1 seemed to confirm this prediction. They reported that colored stripes did, in fact, appear to move slightly in the direction opposite to the one they had traversed during adaptation. At the end of the present experiment we asked one observer, S.M., to view stationary, colored stripes in stabilized vision. S.M. reports absolutely no movement of the stripes. Since the stripe display is stabilized on his retina, he is not free to move his eyes across the display. Such eye movements might account for the slight motion aftereffect that observers report in normal vision.

Can we elaborate our original model to account for S.M.'s data? Suppose that there are two populations of cells with R/G opponent-chromatic organization. Neurons in one population also have opponent-spatial organization that restricts their response to stripes moving up. Neurons in the second population have opponent-spatial organization that restricts their response to stripes moving down. In the present experiments, observers see stripes moving up and stripes moving down for precisely the same amount of time. Detector populations, all members of which have R/G opponent-chromatic organization, remain in balance and no motion aftereffects occur (Wohlgemuth, 1911).

We recall from Experiment 1 that it is easy, using this model, to account for aftereffect colors that appear on stripes moving in a particular direction. Neurons sensitive to each direction have R/G opponent-chromatic organization. Neurons in one population adapt to yellow-green on stripes moving in their preferred direction and remain sensitive to short wavelengths in the white test light. Their adapted response signals green. Neurons in the second population adapt to magenta on stripes moving in their preferred direction and remain sensitive to long wavelengths in the white test light. Their adapted response signals pink.

Observer S.M.'s reports show that opposite color aftereffects can occupy adjacent retinal areas. Observations by Stromeyer and Mansfield (1970) demonstrate the same point in a different test situation. Their observers saw a well-defined aftereffect square of one color against a complementary color background on the face of a contracting spiral pattern. The aftereffect colors assumed opposite positions when the spiral expanded. Although these color aftereffects occupy adjacent retinal areas, they cannot be localized in the retina. Primate retinal cells are not specialized to detect motion: the only neurons along the primate geniculo-striate pathway that detect moving contours are cortical cells. Since, in primates, the retina projects topographically onto the visual cortex (Daniel and Whitteridge, 1961; Cowey, 1964), these results must mean that neurons in adjacent cortical areas support motion-contingent color aftereffects that are opposites of one another. In our experiment, adjacent retinal areas stimulated project to the visual cortices of either hemisphere. Adjacent retinal areas in the study by Stromeyer and Mansfield project to neighboring cortical cell populations within the same hemisphere.

Suppose that cortical cells in one area adapt to yellow-green stripes moving up and magenta stripes moving down while their neighbors adapt to magenta stripes moving up and yellow-green stripes moving down. If this were the case, each color aftereffect would remain localized to the population of cells originally stimulated. Since the radius of the circular display is 10.5 mm, each half subtends only 1.5° visual angle. Neurons in the left population and neurons in the right population must have small receptive fields in order to sustain independent color aftereffects. Cells with such small receptive field areas--$0.50^{\circ} \times 0.75^{\circ}$ to $1.50^{\circ} \times 1.00^{\circ}$--are common in monkey visual cortex (Hubel and Wiesel, 1968; Wurtz, 1969b).

Observers S.M. and D.F. return to judge moving black-and-white stripes 24 hours after their final adapting sessions. Since they know which colors should appear and are familiar with aftereffect colors visible immediately after adaptation, S.M. and D.F. qualify as critical, but biased, observers. The test display which they see at this 24-hour delay occupies the same retinal area as previous displays. It stimulates the population of cells that originally adapted to moving, colored stripes. Under these conditions, both observers report clear impressions of the appropriate aftereffect colors. Their reports show that those neurons which support the development of motion-contingent color aftereffects are also the neurons which retain them. To completely exclude the possibility that other neurons, as well as those originally adapted, develop and retain color aftereffects, we would have to move the test display away from the original position it occupies on the observer's retina. Since the apparatus limits the observer's field of view to 3^o, this maneuver is impossible. We can conclude, in the present situation, that cells which undergo short-term chromatic adaptation to moving, colored stripes are among those which sustain a long-term change in response to the same stripe display.

We may summarize our analysis of motion-contingent color aftereffects by briefly reviewing the results of Experiment 3. These data show that the change which produces motion-contingent color aftereffects must occur in those cells which receive stimulation during adaptation, since adjacent populations of cortical cells can support "opposite" changes. The educated cells must have opponent-spatial organization that restricts their response to contours moving in particular directions and opponent-chromatic organization that allows them to adapt to one color and signal its complement. Only cells with these properties account for the asymmetrical relation between display features of color and motion. This asymmetrical relation is demonstrated by the fact that observers see motion-contingent color aftereffects but fail to see color-contingent motion aftereffects. The cells that adapt are also the cells that store changes which create persisting motion-contingent color aftereffects. Although we are sure that those cortical cells stimulated by moving, colored stripes are the cells which develop and retain color aftereffects, we cannot completely exclude the possibility that other cells assist them.

With a clear description of cells that develop and retain color aftereffects in hand, we turn to Section C which describes the kind of change that occurs in those cells. Experiments in Section C measure the hue, saturation and specificity of color aftereffects that develop with experience and persist after that experience ceases.

Section C

Colorimetric Measures of the Development, Specificity and Persistence of Color Aftereffects

Observers who participate in experiments described in Sections A and B find their perception of moving black-and-white stripes changed. Their task is to describe that change with color names. Observers have no difficulty indicating that a change has occurred, but they find imprecise color names a handicap when they try to describe the hue and saturation of aftereffect colors. The experimenter who wants to specify the kind of change that an observer's perception sustains also finds color naming unsatisfactory. Section C describes experiments which eliminate this problem by asking the observer to adjust the color of one viewing field to match the aftereffect color he sees on another viewing field. These experiments provide precise measures of the hue and saturation of developing and persisting color aftereffects.

Experiments in Section C study aftereffect colors that are contingent upon the orientation (Experiment 4), direction (Experiment 5) and velocity (Experiment 6) of moving or stationary adapting stripes. These experiments employ techniques of visual colorimetry to measure observers' perceptions. They make quantitative descriptions of (a) the change that occurs when observers adapt to colored stripes (b) the way that change develops over time (c) the specificity of that change to features of the stimulus display and (d) the form in which that change persists. It is convenient to describe the method common to all three experiments before considering each study in detail. The reader who is unfamiliar with the

CIE system of color description may wish to read Appendix A before proceeding.

The Method of Colorimetric Measurement Employed in Experiments 4, 5 and 6

Observers

One female and eleven male university students, uninformed about visual aftereffects, participated in these experiments as salaried observers. Each participant had uncorrected normal vision and displayed no anomalies of color perception when viewing the AO H-R-R Pseudoisochromatic Plates.

Apparatus

Experiments 4, 5 and 6 employ a 4-primary colorimeter whose plan modifies a design suggested by Burnham (1952). Photographs of the colorimeter and technical specifications appear in Figures 1 and 2, Appendix D. Each of the instrument's two channels contain components which are shown in schematic arrangement in Figure 3.

Each channel is illuminated by a General Electric DEB 1000 watt tungsten filament projection lamp. This lamp, located at position A in Figure 3, operates on controlled voltage at a color temperature of 2853° K. Its relative spectral energy distribution approximates that of CIE Standard Source A. A plano-convex lens at position B collimates light from the lamp filament and directs it through a glass filter positioned at C. The glass filter blocks energy at infrared wavelengths which would bleach gelatin filters placed in the light path. Its luminous transmittance is 73.6 percent. The combined characteristics of Source A and the glass filter determine the spectral energy distribution of "white" light which impinges upon the observer's

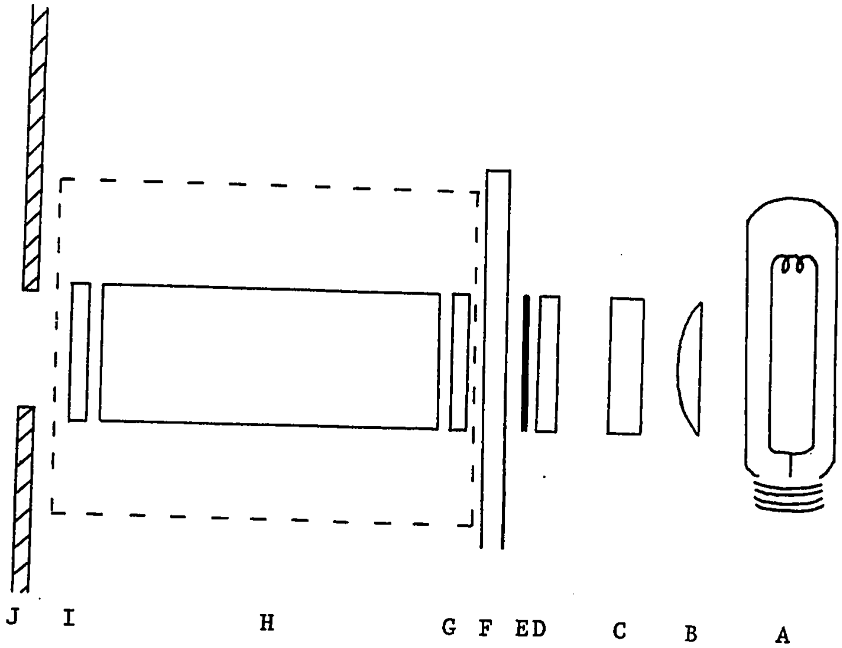

Figure 3. Schematic arrangement of components in each channel of the 4-primary colorimeter used in Experiments 4, 5 and 6. The text describes the components. Technical specifications for each component and photographs of the colorimeter appear in Figures 1 and 2, Appendix D.

retina as he views the channel. A description of the "white" light's color weights this distribution by the 1931 CIE color-matching functions for the Standard Observer. This description places the "white" light at a point defined by chromaticity coordinates x = .4266 and y = .4180 on the CIE x,y-chromaticity diagram illustrated in Figure 4. The information required to calculate these coordinates appears in Table 1, Appendix B. The filter holder at position D accommodates luminance attenuators, cardboard squares with apertures of various diameters, which equalize the brightness of the two channels. A shutter at position E occludes each channel. A plexiglass bar at position H mixes light directed through each channel. Opal glass squares at positions G and I diffuse the light to provide a uniform viewing surface on the circular fields at J, the end of the vision tunnel in which the observer sits.

The standard channel, which the observer sees on his left, has a rectangular filter holder at position F which contains two adapting color filters, A motor drives the filter holder along a horizontal track, alternating the position of each filter in the center of the light path. Kodak Wratten gelatin filters, mounted in optically neutral cover glass, provide the adapting colors. In the "white" light produced by Source A plus the glass filter, Kodak Wratten filter 33 (magenta) has chromaticity coordinates x = .6840, y = .2736 on the CIE x,y-chromaticity diagram in Figure 4. Its luminous transmittance is 5.16 percent. Kodak Wratten filter 61 (yellow-green) has chromaticity coordinates x = .2526 and y = .6980 and its luminous transmittance is 11.52 percent. The information required to make these calculations appears in Tables 6 and 7, Appendix B. A 35-mm film loop, inserted into the standard channel in the position traced by the dashed line, carries

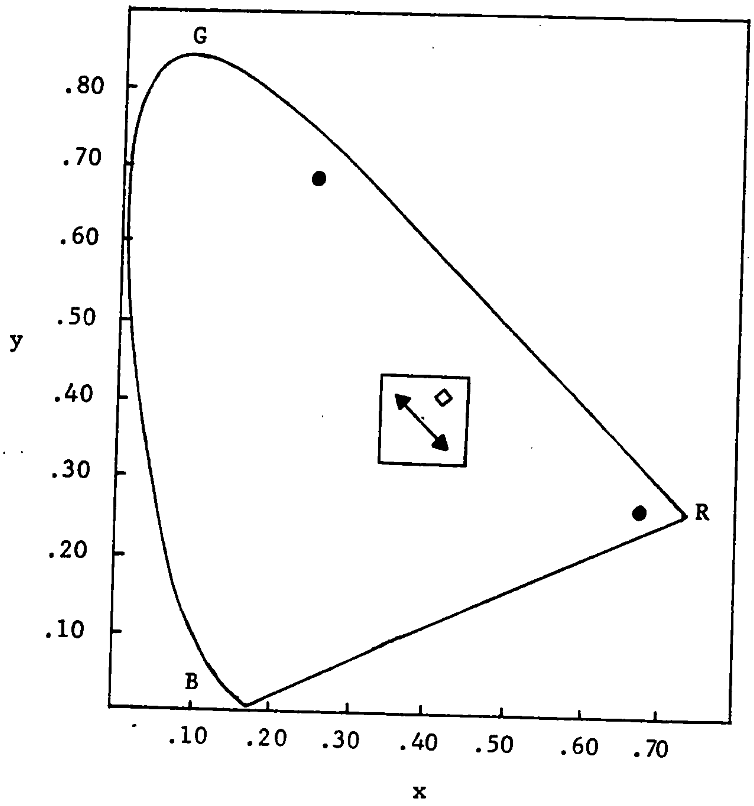

Figure 4. The CIE x,y-chromaticity diagram shows the spectrum locus, purple line, and the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180). Kodak Wratten filter 33 (magenta) ● (x = .6840, y = .2736) and Kodak Wratten filter 61 (yellow-green) ● (x = .2526, y = .6980) viewed in this light provide the adapting colors in Experiments 4, 5 and 6. Color aftereffects that observers see in these experiments occupy loci which diverge from the "white" light toward red or green along the arrow's axis. These loci fall within the area described by the square. Subsequent figures enlarge this area.

the stimulus displays. It advances on projector sprockets driven by a Bodine Speed Reducer Motor Type NSH-12R whose speed and direction are regulated by a Bodine Type ASH 201/DC Motor Control.

The comparison channel, which the observer sees on his right, has a filter holder at position F which contains four primary color filters mounted in optically neutral cover glass. Kodak Wratten gelatin filters provide the four primary colors. In the "white" light produced by Source A plus the glass filter, Kodak Wratten filter 92 (red) has chromaticity coordinates $x = .7223$ and $y = .2776$ on the CIE x,y-chromaticity diagram in Figure 5. Its luminous transmittance is 2.68 percent. Kodak Wratten filter 74 (green) has chromaticity coordinates $x = .2220$ and $y = .7472$. Its luminous transmittance is 3.04 percent. Kodak Wratten filter 75 (cyan) has chromaticity coordinates $x = .0704$ and $y = .3304$. Its luminous transmittance is 0.80 percent. Kodak Wratten filter 47 (blue) has chromaticity coordinates $x = .1394$ and $y = .0624$. Its luminous transmittance is 0.70 percent. The information required to make these calculations appears in Tables 2-5, Appendix B. Figure 6 shows the filter holder, with its arrangement of primary color filters, in place before the face of the plexiglass integrating bar. The filter holder is mounted on the cross-bar of a standard microscope stage with vernier calibration. The observer manipulates two control knobs which move the filter holder horizontally and vertically across the face of the integrating bar. This manipulation controls the area of each primary filter exposed to the light path. The areas exposed determine the color of the mixed light which the observer sees on the circular field at J. The experimenter reads the horizontal and vertical filter holder settings that the observer makes to the nearest 0.1 mm. A computer program converts these

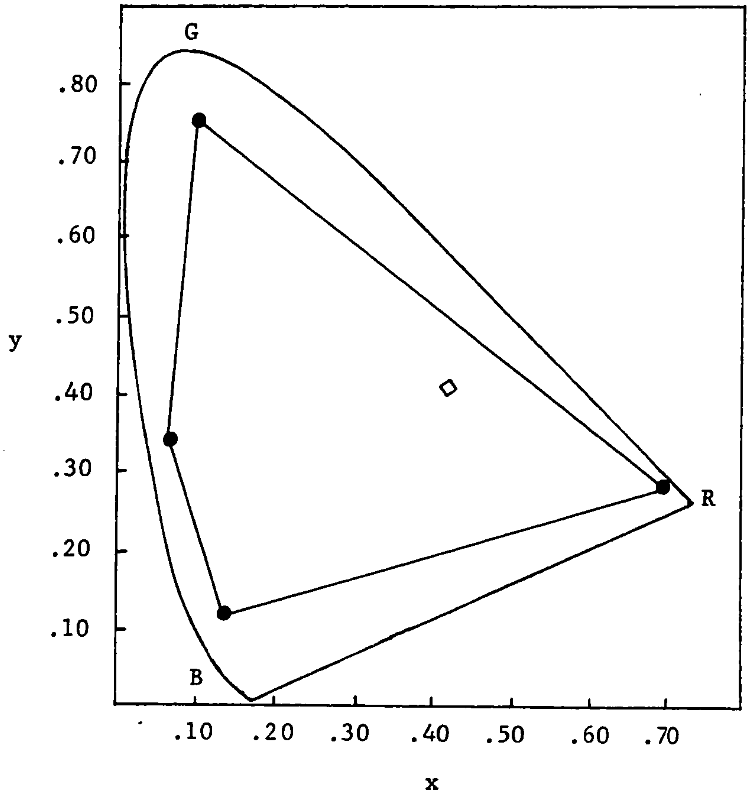

Figure 5. The CIE x,y-chromaticity diagram shows the spectrum locus, purple line, and the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180). Kodak Wratten filter 92 (red) ● (x = .7223, y = .2776), Kodak Wratten filter 74 (green) ● (x = .2220, y = .7472), Kodak Wratten filter 75 (cyan) ● (x = .0704, y = .3304) and Kodak Wratten filter 47 (blue) ● (x = .1394, y = .0624) viewed in this light provide the four primary colors in the comparison channel of the colorimeter used in Experiments 4, 5 and 6. Straight lines connect the primary colors' loci. They enclose an area which defines the gamut of the colorimeter. Using this particular set of primary colors, an observer can match any color whose locus falls within the enclosed area.

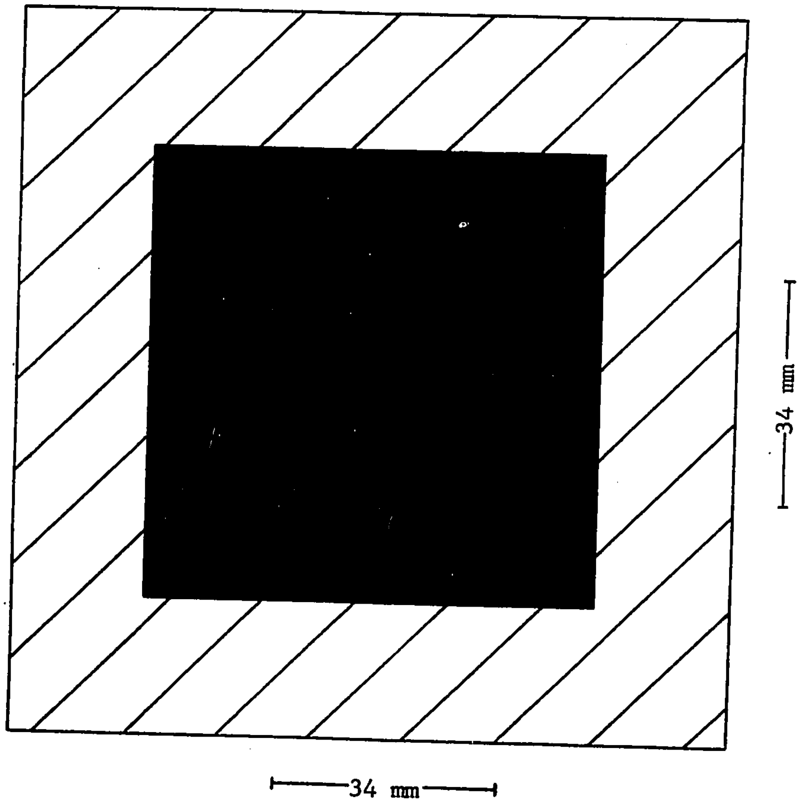

Figure 6. The filter holder, with its arrangement of primary color filters, in place before the face of the plexiglass integrating bar in the comparison channel of the colorimeter used in Experiments 4, 5 and 6. The filter holder moves horizontally and vertically across the 34 x 34 mm square face of the integrating bar. Dots outline the integrating bar's face. Black Lettraset tape lines, 1 mm wide, segregate the primary color filters from one another. Each filter with its black line boundaries occupies an area 34 x 34 mm square. A particular filter holder setting places a given area of each primary filter before the face of the integrating bar. The computer program which uses these areas as weighting factors corrects them by subtracting the small area occupied by black lines at each setting.

settings into exposed areas for each primary filter. It weights the tristimulus values for each filter by its exposed area. Then it sums and X tristimulus values for all four filters. It repeats the summing operation for all Y tristimulus values and all Z tristimulus values. The new X_m, Y_m and Z_m tristimulus values obtained by summing are those for the mixed color. The program computes chromaticity coordinates for the mixed color by calculating the ratio of each tristimulus value to the sum of all tristimulus values. The formulae used to make these calculations appear in Appendix C. The chromaticity coordinates, plotted on the CIE x,y-chromaticity diagram, measure the hue and saturation of the mixed color that the observer sees.

The observer sits at the end of a table enclosed in a vision tunnel. His teeth grip a dental mold, keeping his head in fixed position, as he views the standard field on his left and the comparison field on his right. Each circular field is 20 mm in diameter and subtends 2.3° visual angle at 50 cm viewing distance. A distance of 22 cm, 25.3° visual angle, separates the two fields. The observer changes the color he sees on the comparison field by adjusting the filter holder's vertical position with a control knob in his right hand and its horizontal position with a second control knob in his left hand.

Procedure

The observer's first task is to adjust the color of the comparison field to match white stripes in a black-and-white display which he sees on the standard field. These neutral point matches describe the observer's perception of white stripes before he adapts to stationary or moving stripes that are colored. To make a match, the observer shifts his gaze back and forth between the center of the standard field and the center of the comparison field which he is adjusting. When both fields match, their luminance is 50 ftL. He takes as much time as he needs to make an accurate color match. Then the observer closes his eyes, the experimenter records his setting, and a new matching trial begins. The experimenter adjusts the starting position of the filter holder to bracket the observer's previous settings. Observers make 10 control matches for stripes that will be magenta during adaptation and 10 for stripes that will be yellow-green. They repeat their control matches on successive days until their performance is reliable. The standard deviations along x and y coordinates of the CIE x,y-chromaticity diagram for each set of 10 matches must be less than .008.

After completing his neutral point matches, the observer begins adapting to the colored displays. During adaptation, he fixates the center of the standard field where he sees one display of magenta stripes alternate with a second display of yellow-green stripes. The magenta stripes have a luminance of 25 ftL; the yellow-green stripes, 55 ftL. The colors may appear on stationary vertical and horizontal stripes (Experiment 4), on stripes moving in opposite directions (Experiment 5) or on stripes moving in the same direction at different velocities (Experiment 6). A timing circuit alternates the displays every 25 seconds, interposing a 5 second dark interval between them. The observer views the alternating colored displays for 15 minutes. Then he closes his eyes while the experimenter removes the color filters from the standard channel and illuminates the comparison field which remains occluded during adaptation. When he opens his eyes, the observer sees one of the displays on the standard field. Although the display is black-and-white, he may see a color aftereffect on the white stripes. His task is to adjust the color on the comparison field to match the color he sees on those white stripes. He employs the same procedure that he used to make neutral point matches. When he finds an acceptable match, the observer closes his eyes, the experimenter operates the timing circuit on manual control to present the second display, and another matching trial begins. Observers make five matches for white stripes that were magenta and five matches for white stripes that were yellow-green during adaptation. They complete the 10 matches in about 10 minutes. The standard deviations along the x and y coordinates of the CIE x,y-chromaticity diagram for each set of five matches are less than .008, indicating that the observers perform reliably and that 10 minutes of exposure to white stripes does not erase the aftereffect. At the end of the session, observers describe what they have just seen. They return on successive days to adapt and match until they accumulate a total of 5-6 hours (20-24 days) of adaptation.

By the end of 5-6 cumulative hours of adaptation, aftereffect colors reach stable saturation and observers embark on generalization testing. They continue to adapt for 15 minutes each day but their matching trials now include displays which systematically vary a particular stimulus feature. Matching trials may include stationary stripes of various orientations (Experiment 4) or moving stripes of various velocities (Experiments 5 and 6). Details of generalization testing appear in the description of each experiment.

Observers return 24-96 hours after their last adapting session to make a final set of five matches to each of the original displays. These matches describe the hue and saturation of aftereffect colors which persist beyond the period immediately following adaptation.

Experiment 4

Experiment 4 studies color aftereffects that are contingent upon the orientation of adapting stripes. This experiment serves two purposes. It allows us to check descriptions of observer's perceptions obtained by colorimetric measurement with available data on the aftereffect described by McCollough. And, more importantly, it provides measurements which will serve as useful references when we consider the development and persistence of motion-contingent color aftereffects. The present experiment, then, measures orientation-contingent aftereffect colors as they develop over many adapting sessions. It assesses their specificity to the orientation of adapting stripes, and it measures the strength with which they persist.

Observers

Two students participated in Experiment 4.

Stimulus Display and Procedure

In this experiment the 35-mm film loop carries opaque and transparent stripes whose contrast ratio is 0.89. Each stripe is 1.0 mm wide and subtends 7.2 min arc at 50 cm viewing distance. The spatial frequency of the stripe display is 4.20 cycles/degree visual angle.

During adaptation the observer sees magenta vertical (0°) stripes alternate with yellow-green horizontal (90°) stripes. Both sets of stripes are stationary.

During matching trials the observer sees vertical and horizontal stripes which are objectively black-and-white. They are the same stripes that he sees during adaptation, without their color filters.

In this experiment observers make color matches in two generalization tests. The first generalization test varies the orientation of black-and-white stripes and asks the observer to match the color he sees on each orientation. Observers see stripes of seven different orientations (0°, 15°, 30°, 45°, 60°, 75° and 90°) in random order. They make three matches for each stripe orientation on a given day. Generalization testing continues for five days.

The second generalization test pits stationary horizontal stripes against horizontal stripes moving down at 1.15°/second. Observers make five matches to each stripe display on a given day. Again, generalization testing continues for five days.

Both observers return 48 hours after their last adapting session to match vertical and horizontal stationary stripes.

Results

Figure 7 shows the loci of neutral points for all the observers who participate in Experiments 4, 5 and 6, including those for K.D. and J.D. in the present experiment. It is apparent that the "white" light produced by Standard Source A in combination with the glass filter looks slightly bluer when observers view it through the 35-mm film loop. It is also apparent that observers, all of whom have normal color vision, assign different loci to the white stripes that they see. This fact makes it important to consider individual observers separately when trying to assess the hue and saturation of aftereffect colors that they report.

Figures 8 and 9 display the loci of aftereffect colors that observers K.D. and J.D. see on horizontal and vertical black-and-white stripes after 5 cumulative hours of adaptation. Both observers report clear impressions of green on vertical stripes and red on horizontal stripes. The locus of observer K.D.'s green aftereffect, shown in Figure 8, diverges upward from

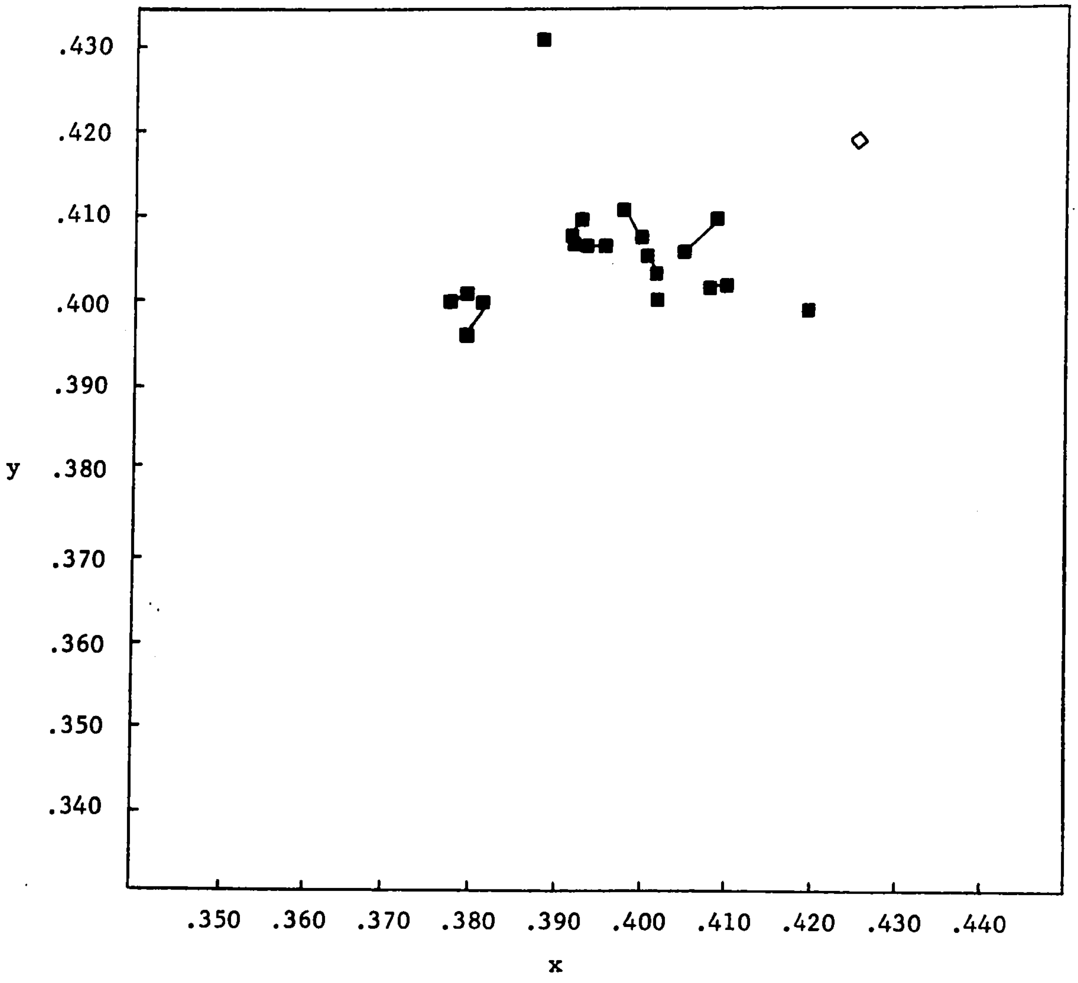

Figure 7. An enlargement of the area described by a square on the CIE x,y-chromaticity diagram in Figure 4. Subsequent CIE x,y-chromaticity diagrams have this format. The present diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180) and the loci of neutral points ■ for 12 observers who participated in Experiments 4, 5 and 6. For some observers, both sets of white stripes look the same: they have only one neutral point. For others, the two sets of white stripes look slightly different: they have two neutral points joined by a straight line. Each point represents a mean of 10 matches. The standard deviation for each set of 10 matches is less than .008.

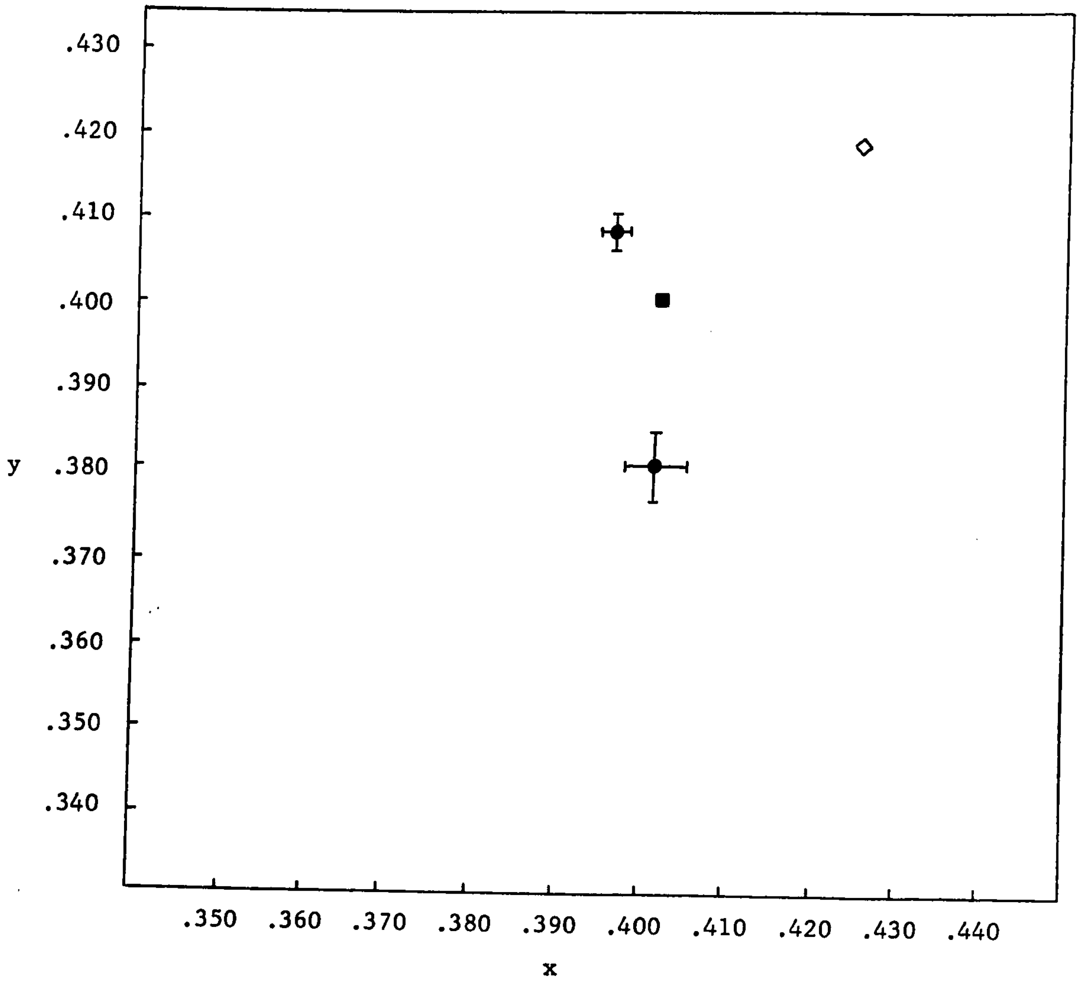

Figure 8. Experiment 4, observer K.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4028, y = .4010) and horizontal white stripes (x = .4019, y = .4009) and the loci of her matches for vertical stripes ● (x = .3970, y = .4088) and horizontal stripes ● (x = .4027, y = .3806) after five cumulative hours of adaptation. Observer K.D. reports a clear impression of green on vertical stripes and red on horizontal stripes. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

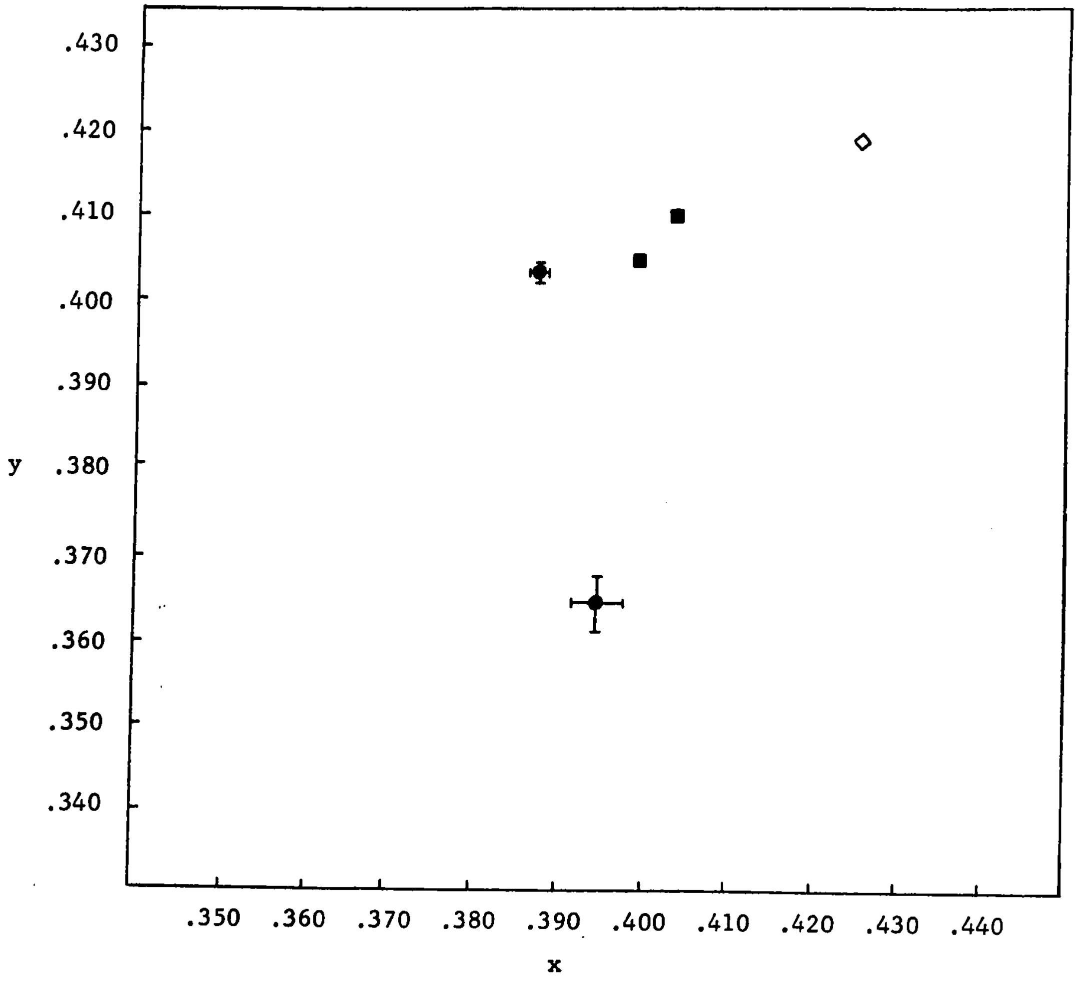

Figure 9. Experiment 4, observer J.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4008, y = .4057) and horizontal white stripes (x = .4043, y = .4100) and the loci of his matches for vertical stripes ● (x = .3883, y = .4032) and horizontal stripes ● (x = .3952, y = .3636) after five cumulative hours of adaptation. Observer J.D. reports a clear impression of green on vertical stripes and red on horizontal stripes. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

her neutral points in the predicted direction. The locus of her red aftereffect diverges downward in the predicted direction. The locus of observer J.D.'s green aftereffect, shown in Figure 9, is close to the loci of his neutral points; only the locus of his red aftereffect diverges downward in the predicted direction. Yet observer J.D. reports clear green as well as red aftereffect colors. Evidently, in making his report, he assesses the hue of the aftereffects in relation to one another, not in relation to some absolute standard provided by the neutral points.

Note that observer J.D.'s aftereffect loci are both slightly displaced toward blue, away from his neutral points. Most observers' matches show this effect, which probably reflects generalized chromatic adaptation to yellow resulting from the additive mixture of yellow-green and magenta adapting colors that alternately stimulate the same area of the observer's retina.

Both observers K.D. and J.D. produce highly reliable aftereffect color matches; standard deviations for red and green matches, shown by brackets in Figures 8 and 9 are small.

Although orientation-contingent aftereffects are clearly visible to the observers and their loci occupy different coordinates on the CIE x,y-chromaticity diagram, their colors are desaturated. As the locus of a color diverges from neutral point loci, the saturation of the color grows. Loci of aftereffect colors in the present experiment do not diverge very far from neutral point loci when one considers the saturation range available on the entire CIE x,y-chromaticity diagram. Aftereffect colors seen by K.D. and J.D. are as saturated as those seen by observers who also made colorimetric matches in McCollough's laboratory at Oberlin College (Snow, 1966; McCollough and Clark, 1971; McCollough and Gerrein, 1971). All of these observers see aftereffect colors which resemble tints on fin de siècle photographs or watercolor washes.

Figures 10 and 11 show the development of orientation-contingent color aftereffects as observers continue to adapt for 15 minutes each day on 20 consecutive days. Both observers report clear impressions of red and green aftereffect colors after 1/2 hour of adaptation. These colors remain visible throughout further adapting sessions. For observer J.D., Figure 11, the difference between the two aftereffect colors grows throughout 2 cumulative hours of adaptation and then maintains stable strength for the remaining sessions. For observer K.D., Figure 10, the difference between the two aftereffect colors grows, decreases, and then returns to original strength. The interim decrease in the strength of K.D.'s aftereffect seems unusual until one discovers that it reflects a change in her matching strategy. At the beginning of the experiment observer K.D. makes her matches according to instruction--she alternates fixation between the center of the standard field and the center of the comparison field, making adjustments until both fields match. After 2 cumulative hours of adaptation she adopts a new strategy: she fixates between the two fields while making her matches. This new strategy can decrease the strength of her aftereffect in two ways. The test display of moving stripes now falls partly outside the cone-rich fovea on an area of retina with relatively impoverished color vision (Polyak, 1957). The display also falls, at least in part, on cells that are not stimulated during adaptation. In this case, decreased differences between aftereffect colors may reflect the area-specificity of color aftereffects discussed in Experiment 3. This explanation seems particularly plausible since Harris (1969) has shown that orientation-contingent color aftereffects

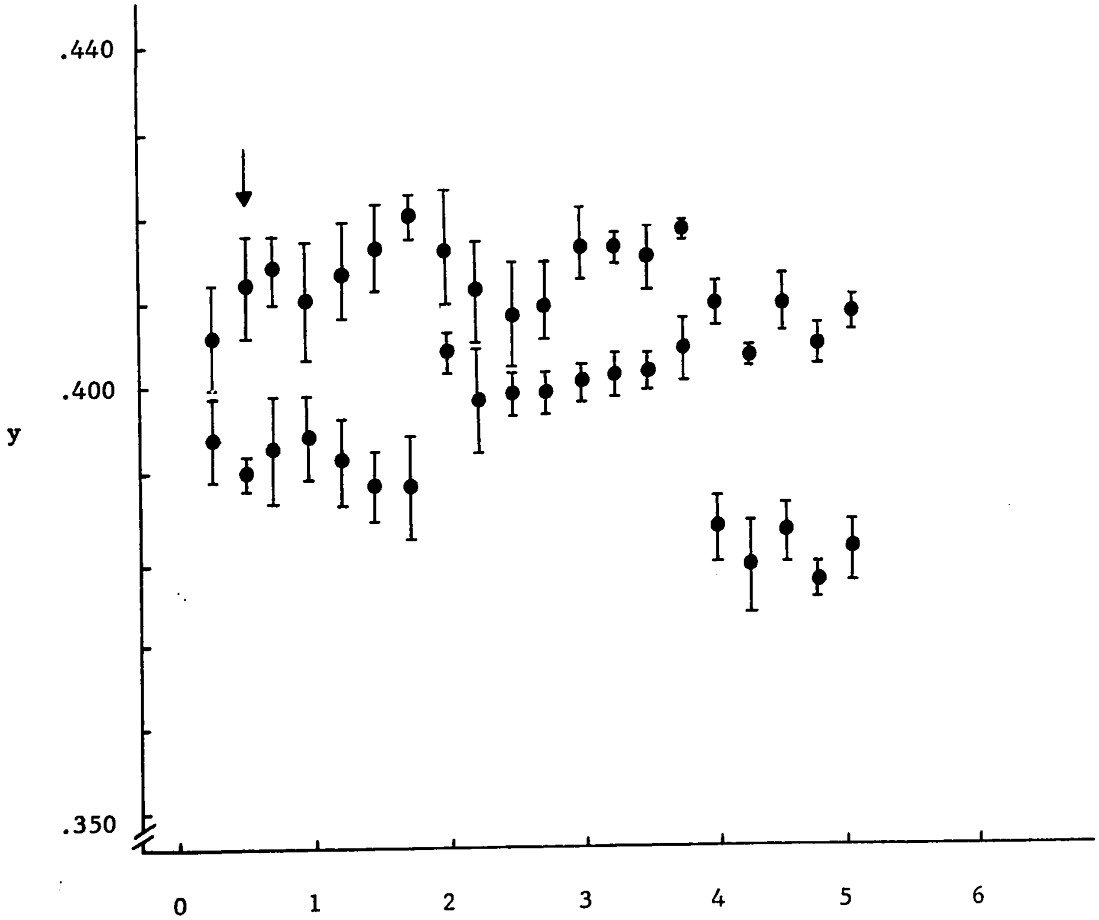

Figure 10. Experiment 4, observer K.D. The development of color aftereffects that are contingent upon the orientation of adapting stripes. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for vertical stripes ● and horizontal stripes ● after each 15 minute adapting session. The observer accumulates five hours (20 consecutive days) of adaptation. Observer K.D. reports a clear impression of green on vertical stripes and red on horizontal stripes after 1/2 hour of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

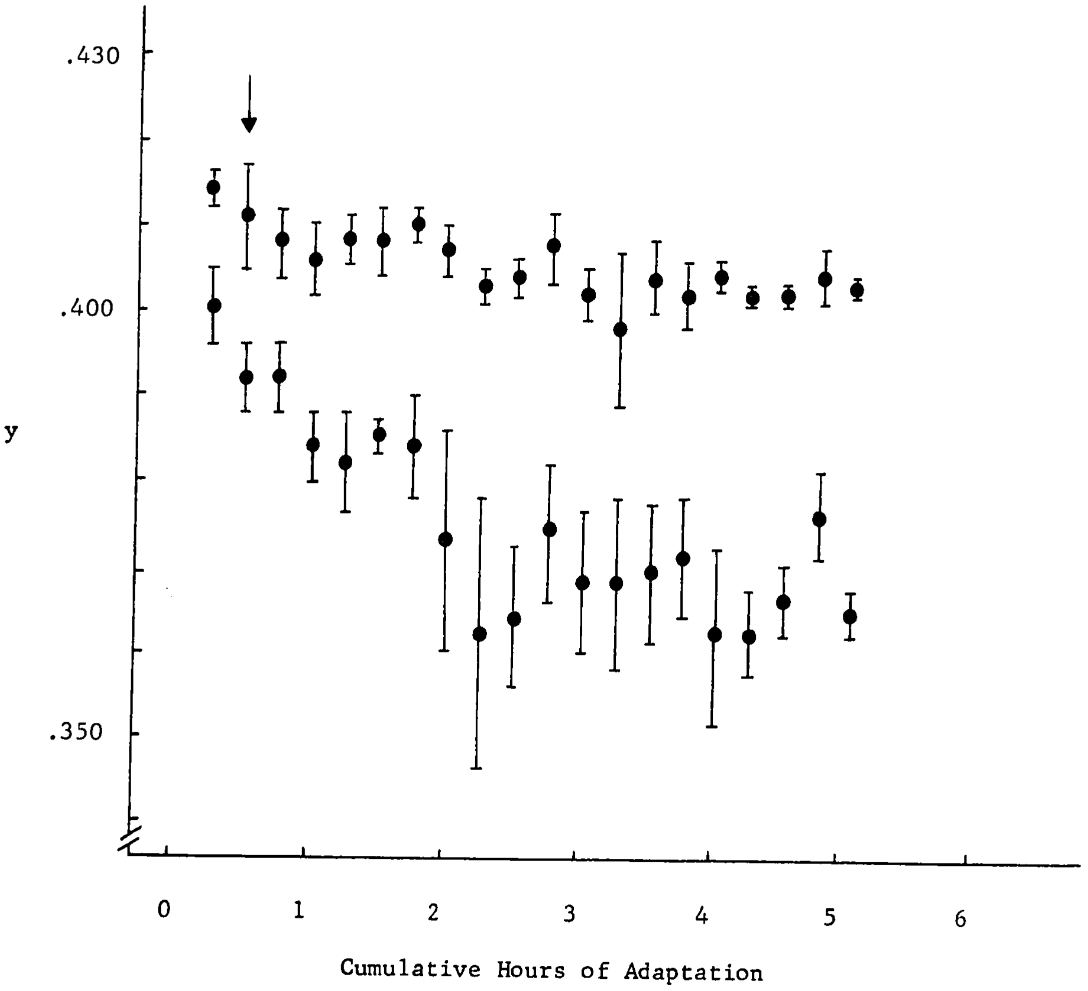

Figure 11. Experiment 4, observer J.D. The development of color aftereffects that are contingent upon the orientation of adapting stripes. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for vertical stripes ● and horizontal stripes ● after each 15 minute adapting session. The observer accumulates five hours (20 consecutive days) of adaptation. Observer J.D. reports a clear impression of green on vertical stripes and red on horizontal stripes after 1/2 hour of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

are specific to the retinal area stimulated during adaptation. When the experimenter discovers this strategy shift after 4 cumulative hours of adaptation and instructs K.D. to follow directions, the original difference between her aftereffect colors returns.

Figures 12 and 13 display the loci of matches that observers make to stationary stripes of various orientations. For both observers, vertical (0^o) stripes appear green and horizontal (90^o) stripes appear red as they have on previous tests. Stripes whose orientation is 45^o look neutral while stripes approaching vertical orientation (30^o and 15^o) become greener and stripes approaching horizontal orientation (60^o and 75^o) become redder. These results confirm reports offered by observers in several other experiments (McCollough, 1965; Gibson and Harris, 1968; Stromeyer, 1969). It is clear from these data that populations of neurons in the human visual system that undergo chromatic adaptation restrict their response to contours placed in preferred orientations. It is tempting to conclude, after inspecting the loci of generalization matches in Figures 12 and 13, that aftereffect colors lose half their saturation when test stripes diverge about 22^o from adapting orientation. Caution must accompany this conclusion because equal distances across the color surface displayed in the CIE x,y-chromaticity diagram do not necessarily correspond to differences in saturation that appear equal to the observer (Wyszecki and Stiles, 1967, p. 511).

In a second generalization test, observers match black-and-white horizontal stripes that remain stationary and similar stripes that move down at 1.15^o/second. Both observers report that horizontal stripes look red when they are stationary, as in previous tests. Horizontal stripes also look red when they move. The loci of the observers' matches for stationary and mov-

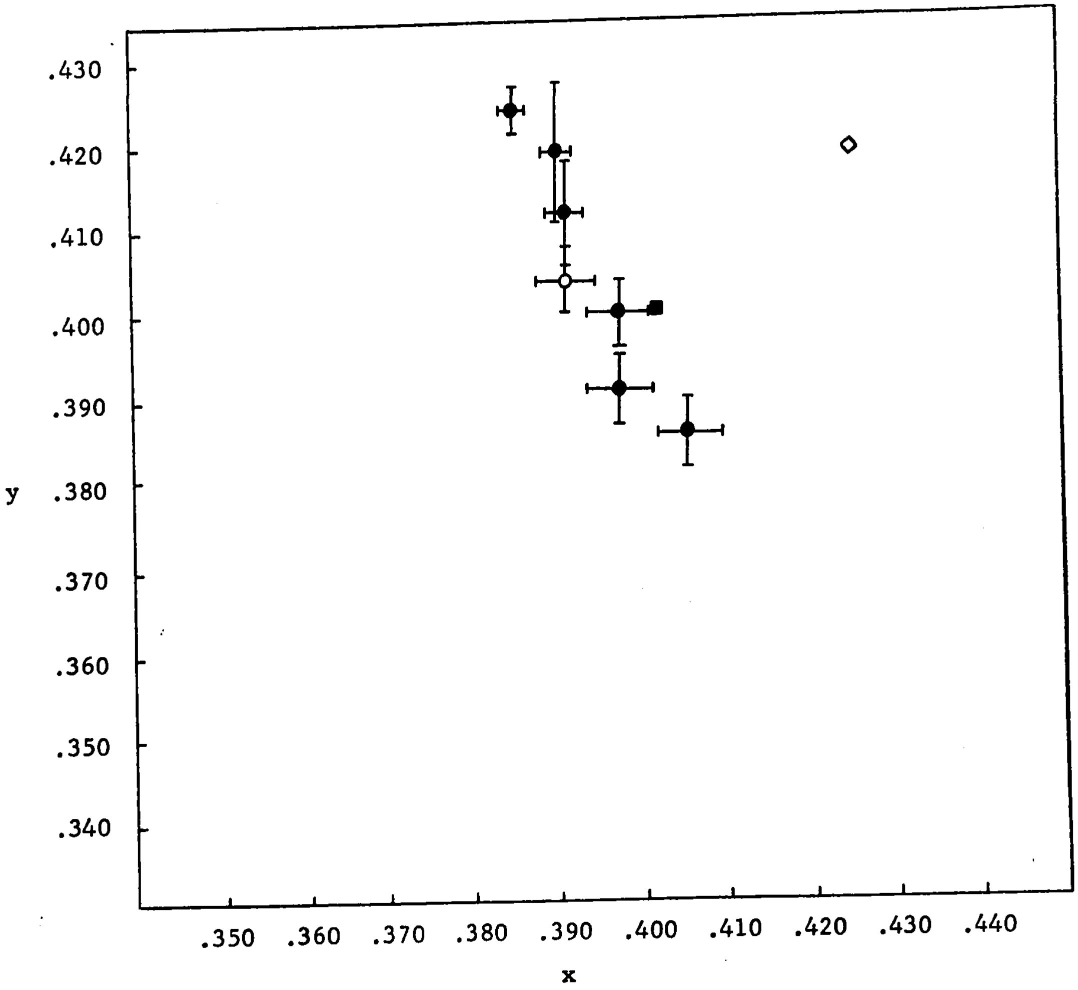

Figure 12. Experiment 4, observer K.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4028, y = .4010) and horizontal white stripes (x = .4019, y = .4009) and the loci of her matches for stripes whose orientations are 0° vertical ● (x = .3866, y = .4245), 15° ● (x = .3912, y = .4193), 30° ● (x = .3922, y = .4116), 45° ○ (x = .3918, y = .4036), 60° ● (x = .3987, y = .4002), 75° ● (x = .3978, y = .3910) and 90° horizontal ● (x = .4006, y = .3859). Observer K.D. reports a neutral color on stripes whose orientation is 45°; stripes become greener as they approach vertical orientation and redder as they approach horizontal orientation. Each point represents a mean of 15 matches. Brackets indicate standard deviations for each set of 15 matches along the x and y axes of the chromaticity diagram.

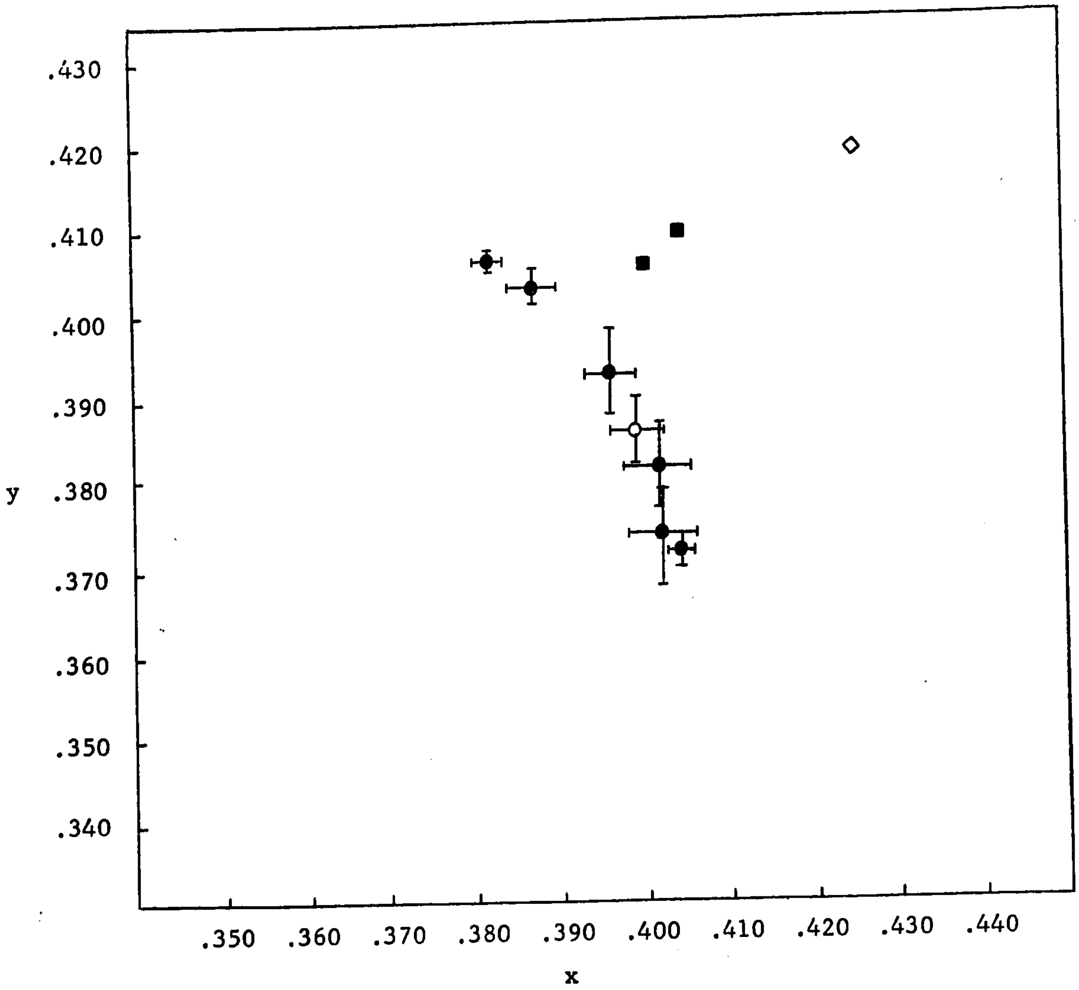

Figure 13. Experiment 4, observer J.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4008, y = .4057) and horizontal white stripes (x = .4043, y = .4100) and the loci of his matches for stripes whose orientations are 0° vertical ● (x = .3861, y = .4067), 15° ● (x = .3874, y = .4032), 30° ● (x = .3957, y = .3933), 45° ○ (x = .3990, y = .3864), 60° ● (x = .4028, y = .3824), 75° ● (x = .4027, y = .3737) and 90° horizontal ● (x = .4032, y = .3716). Observer J.D. reports a neutral color on stripes whose orientation is 45°; stripes become greener as they approach vertical orientation and redder as they approach horizontal orientation. Each point represents a mean of 15 matches. Brackets indicate standard deviations for each set of 15 matches along the x and y axes of the chromaticity diagram.

ing stripes, plotted in Figures 14 and 15, confirm their reports. These data make sense if one assumes, with Hubel and Wiesel (1962, 1965), that simple orientation-sensitive neurons feed complex neurons which serve as motion detectors. In the present situation, orientation-sensitive neurons carry the burden of chromatic adaptation. The red aftereffect color generalizes to horizontal moving stripes because those stripes stimulate adapted horizontal detectors that feed higher-order motion-detecting cells.

Figures 16 and 17 show the saturation of orientation-contingent color aftereffects visible 48 hours after the final adapting session in Experiment 4. Aftereffect colors obviously persist for two days: both observers report clear impressions of green on vertical stripes and red on horizontal stripes. The reader may compare Figure 16 with Figure 8 for observer K.D. Her aftereffect colors, after two days' rest, are as saturated as they were immediately after 5 cumulative hours of adaptation. Although both of her aftereffect loci have shifted toward green in relation to her neutral points, observer K.D. continues to report a definite perception of both red and green aftereffect colors. A comparison of Figures 17 and 9 provides similar information for observer J.D. The loci of his aftereffect colors remain in a stable position with reference to his neutral points, but the colors lose saturation after two days' vacation.

From the results of Experiment 4 we have learned that aftereffect colors roughly complementary to the adapting colors develop after 0.50 cumulative hours of experience. These colors are desaturated, though clearly visible to the observer. The saturation of each color increases, as observers accumulate more experience with the adapting display, until it reaches a stable value that presumably reflects the successful adaptation of all mem-

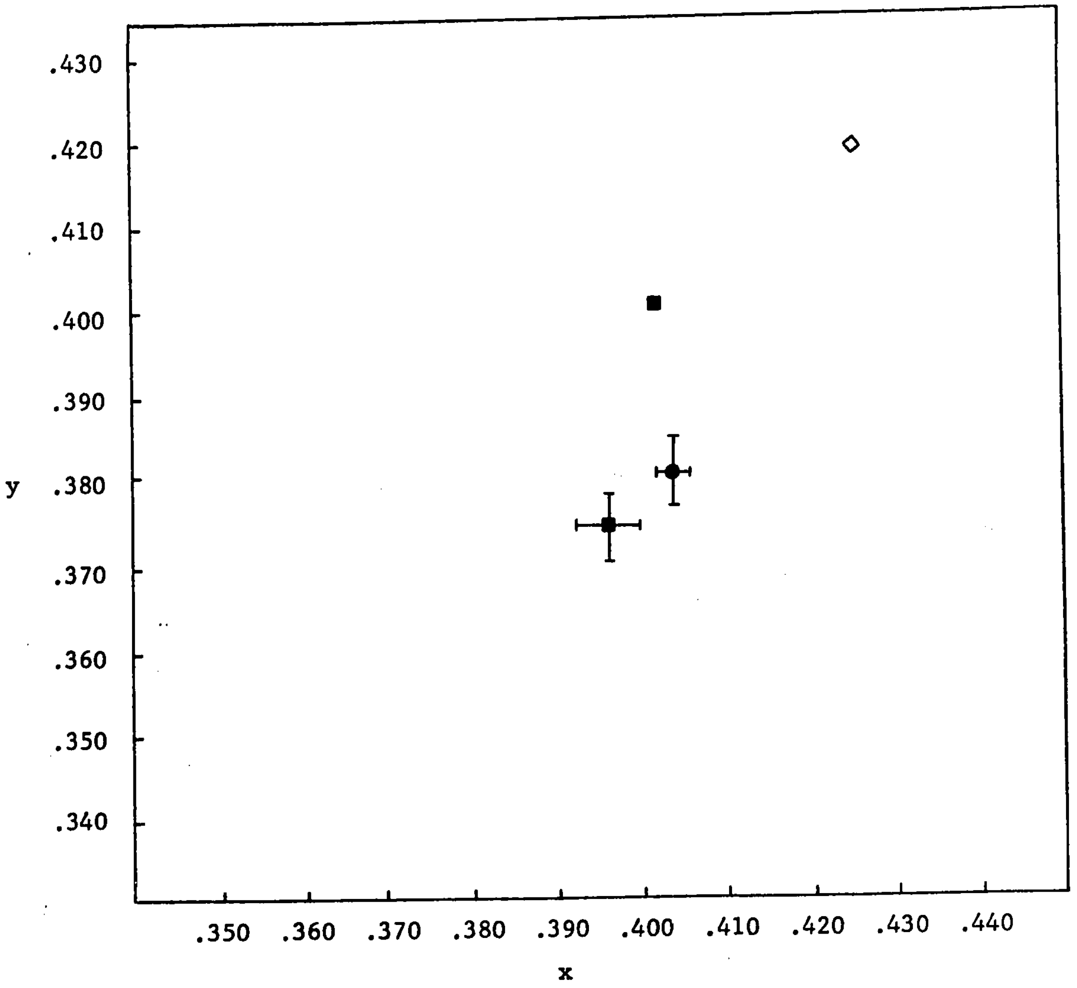

Figure 14. Experiment 4, observer K.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4028, y = .4010) and horizontal white stripes (x = .4019, y = .4009) and the loci of her matches for stationary horizontal stripes ● (x = .4036, y = .3797) and horizontal stripes moving down at 1.15°/second ■ (x = .3965, y = .3738). Observer K.D. reports that moving stripes look slightly bluer than stationary ones but both sets of stripes are clearly red. Each point represents a mean of 25 matches. Brackets indicate standard deviations for each set of 25 matches along the x and y axes of the chromaticity diagram.

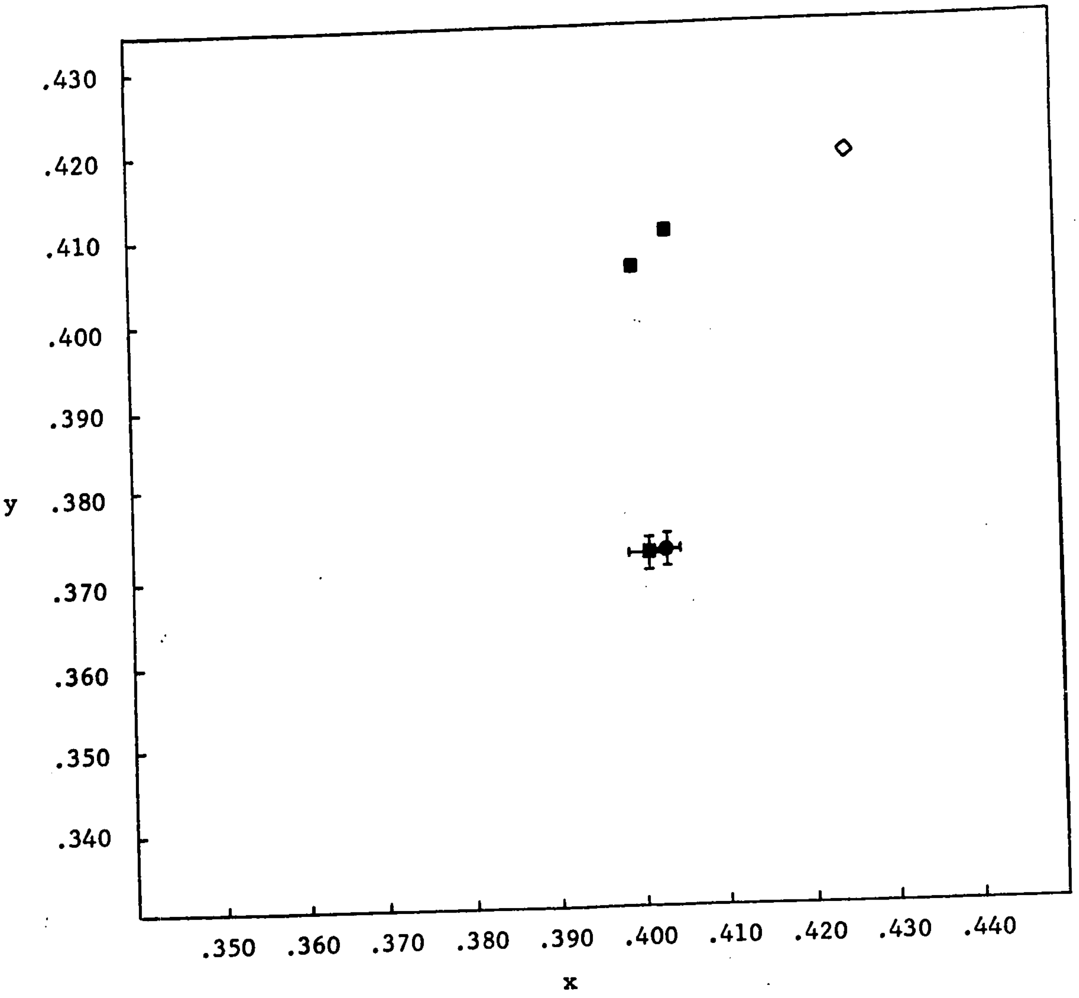

Figure 15. Experiment 4, observer J.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4008, y = .4057) and horizontal white stripes (x = .4043, y = .4100) and the loci of his matches for stationary horizontal stripes ● (x = .4044, y = .3724) and horizontal stripes moving down at 1.15°/second ■ (x = .4025, y = .3720). Observer J.D. reports that both sets of stripes look equally red. Each point represents a mean of 25 matches. Brackets indicate standard deviations for each set of 25 matches along the x and y axes of the chromaticity diagram.

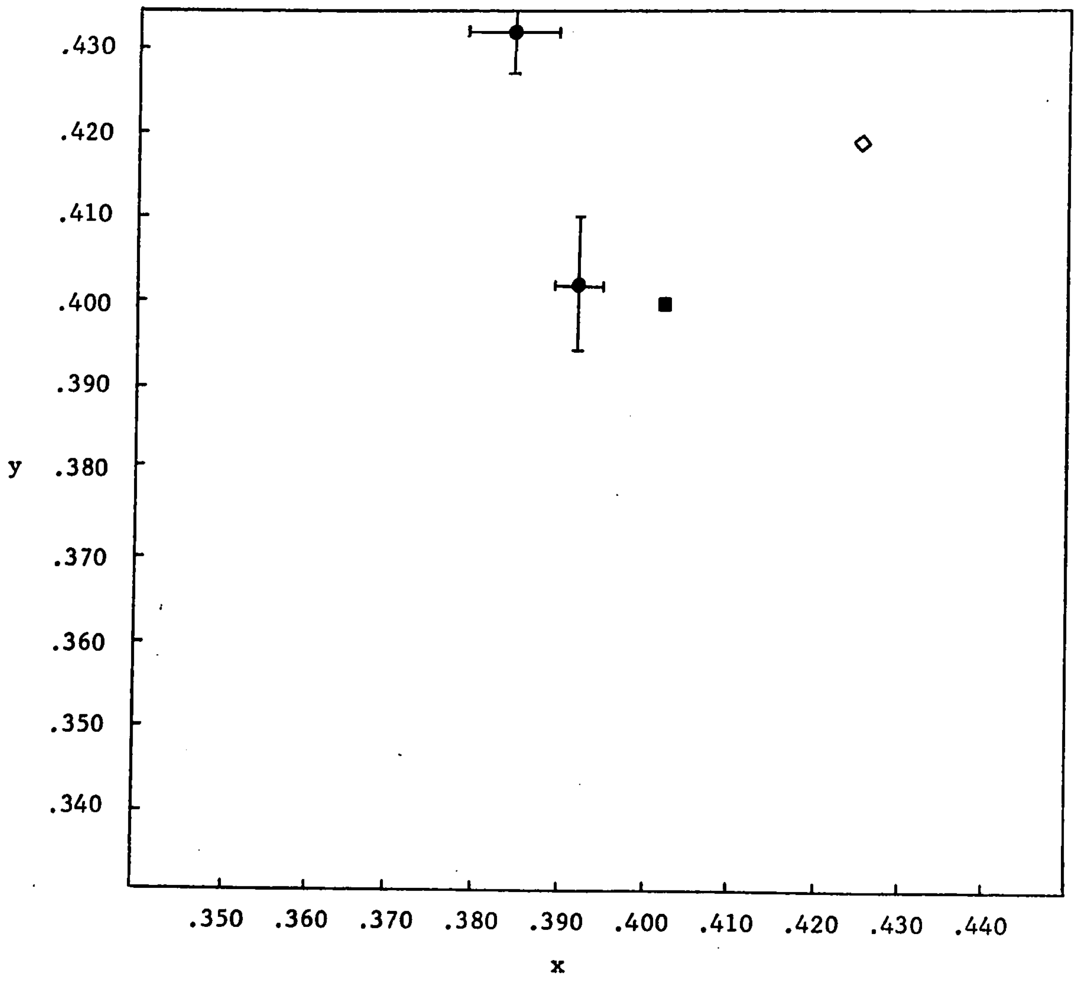

Figure 16. Experiment 4, observer K.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4028, y = .4010) and horizontal white stripes (x = .4019, y = .4009) and the loci of her matches for vertical stripes ● (x = .3836, y = .4324) and horizontal stripes ● (x = .3918, y = .4028) 48 hours after the final adapting session. Observer K.D. reports a clear impression of green on vertical stripes and red on horizontal stripes. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

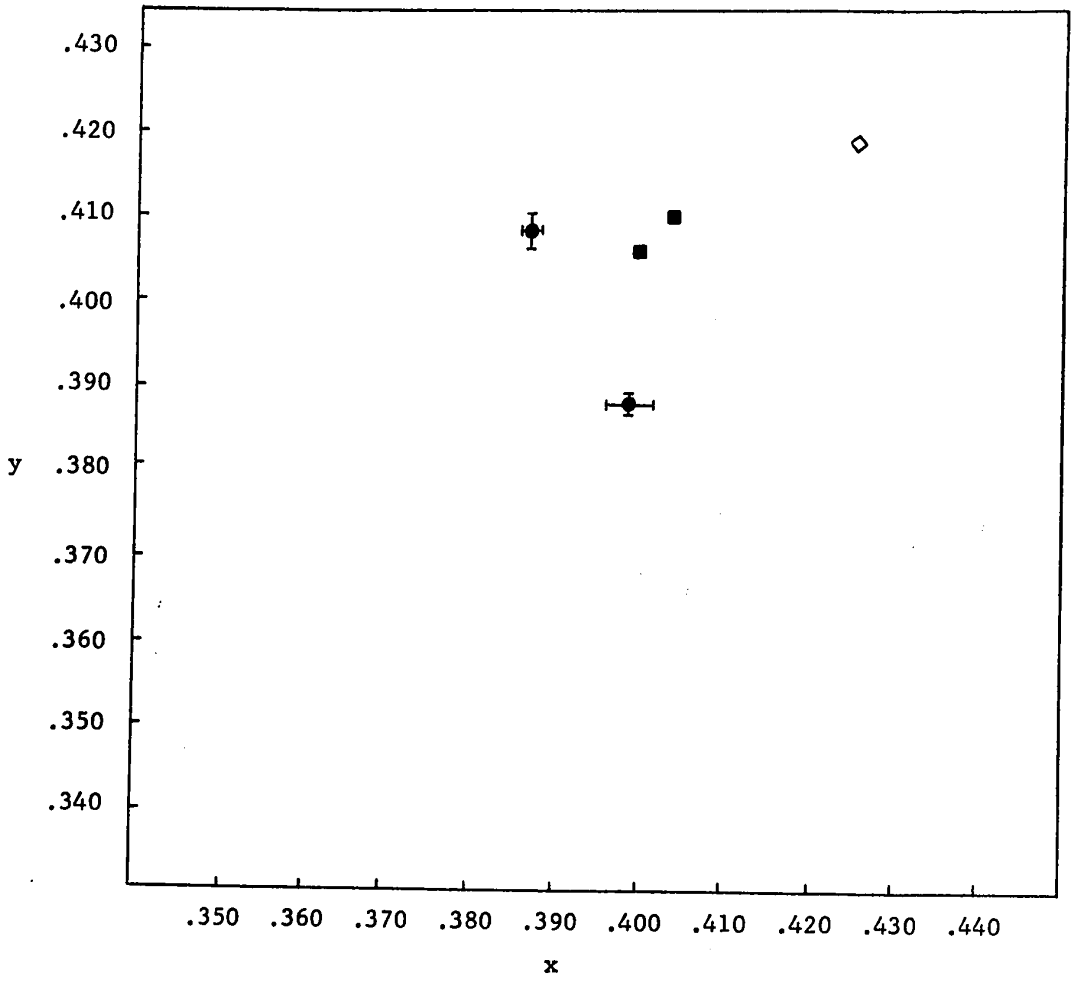

Figure 17. Experiment 4, observer J.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for vertical white stripes (x = .4008, y = .4057) and horizontal white stripes (x = .4043, y = .4100) and the loci of his matches for vertical stripes ● (x = .3872, y = .4079) and horizontal stripes ● (x = .3992, y = .3881) 48 hours after the final adapting session. Observer J.D. reports a clear impression of green on vertical stripes and red on horizontal stripes. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

bers of the stimulated cell populations. Generalization testing shows that each aftereffect color is specific to the orientation of its adapting stripes. The specificity of these colors reflects the response restrictions of human cortical cells. Aftereffect colors generalize to moving stripes of the same orientation; a fact which suggests a hierarchical arrangement of neurons that serve as feature detectors. And, finally, aftereffect colors persist at slightly reduced saturation for at least 48 hours after the final adapting session of the experiment.

It will be useful to keep these results in mind as we turn to Experiments 5 and 6 which make similar measurements of motion-contingent color aftereffects.

Experiment 5

Experiment 5 studies color aftereffects that are contingent upon the direction in which adapting stripes move. These are the familiar motion-contingent color aftereffects of Experiments 1-3. The present study uses techniques of visual colorimetry employed in Experiment 4 to measure direction-contingent aftereffect colors as they develop over many adapting sessions. Since primate cortical cells display velocity as well as direction preferences, it is possible that aftereffect colors in this situation will be specific, not only to the direction in which adapting stripes move, but also to their velocity of motion. Generalization tests assess this possibility. The last matches that observers make in Experiment 5 measure the strength of aftereffect colors that persist many hours after the observers' final experience with moving, colored stripes.

Observers

Five students participated in Experiment 5.

Stimulus Display and Procedure

In this experiment the 35-mm film loop carries opaque and transparent stripes whose contrast ratio is 0.89. Each stripe is 7.0 mm wide and subtends 48 min arc at 50 cm viewing distance. The spatial frequency of the stripe display is 0.62 cycles/degree visual angle.

During adaptation the observer sees horizontal magenta stripes moving up alternate with horizontal yellow-green stripes moving down. Both sets of stripes move at 2.45°/second.

During matching trials the observer sees horizontal stripes moving up and down which are objectively black-and-white. They are the same stripes that he sees during adaptation, without their color filters.

In this experiment observers make color matches in one generalization test. The generalization test varies the velocity of black-and-white stripes and asks the observer to match the color he sees on stripes moving at each velocity. Observers see stripes moving up at five different velocities (1.15°/second, 1.80°/second, 2.45°/second, 3.10°/second and 3.75°/second) in random order. They make two matches for each stripe velocity on a given day. Then they repeat their matches for stripes moving down at the same velocities. Observers begin generalization testing with stripes moving up or stripes moving down on alternate days. Generalization testing continues for five days.

Observers return 24 hours (T.C. and J.W.) and 96 hours (A.R.) after their last adapting session to match horizontal stripes moving up and horizontal stripes moving down at 2.45°/second.

Results

Figures 18, 19 and 20 display the loci of aftereffect colors that observers A.R., J.W. and T.C. view on black-and-white horizontal stripes moving up and similar stripes moving down after 6 cumulative hours of adaptation. Observers A.R. and J.W. report clear impressions of green on stripes moving up and red on stripes moving down. Observer T.C., on the other hand, sees only the red aftereffect on stripes moving down and reports a neutral color on stripes moving up. Inspection of Figures 19 and 20 shows that observers J.W. and T.C., like observer J.D. in Experiment 3, are judging aftereffect colors in relation to one another, not in relation to their neutral reference points.

Consider the saturation of orientation-contingent color aftereffects measured in Experiment 4 and displayed in Figures 8 and 9. Only observer A.R. in the present experiment develops direction-contingent color aftereffects of comparable saturation. Observers J.W. and T.C. see discernible, but much weaker, direction-contingent aftereffect colors.

Figures 21, 22 and 23 show the development of direction-contingent color aftereffects as observers continue to adapt for 15 minutes each day on 24 consecutive days. After 3 1/4 cumulative hours of adaptation for observer A.R. and 1 hour for observer J.W., stripes moving up appear green and stripes moving down appear red. Stripes look neutral when they move up and red when they move down to observer T.C. after 3 cumulative hours of adaptation. Moving stripes retain their colors throughout further adapting sessions for all three observers.

In Experiment 1, observers required a mean of 2.38 cumulative hours of adaptation to develop motion-contingent color aftereffects visible immediate-

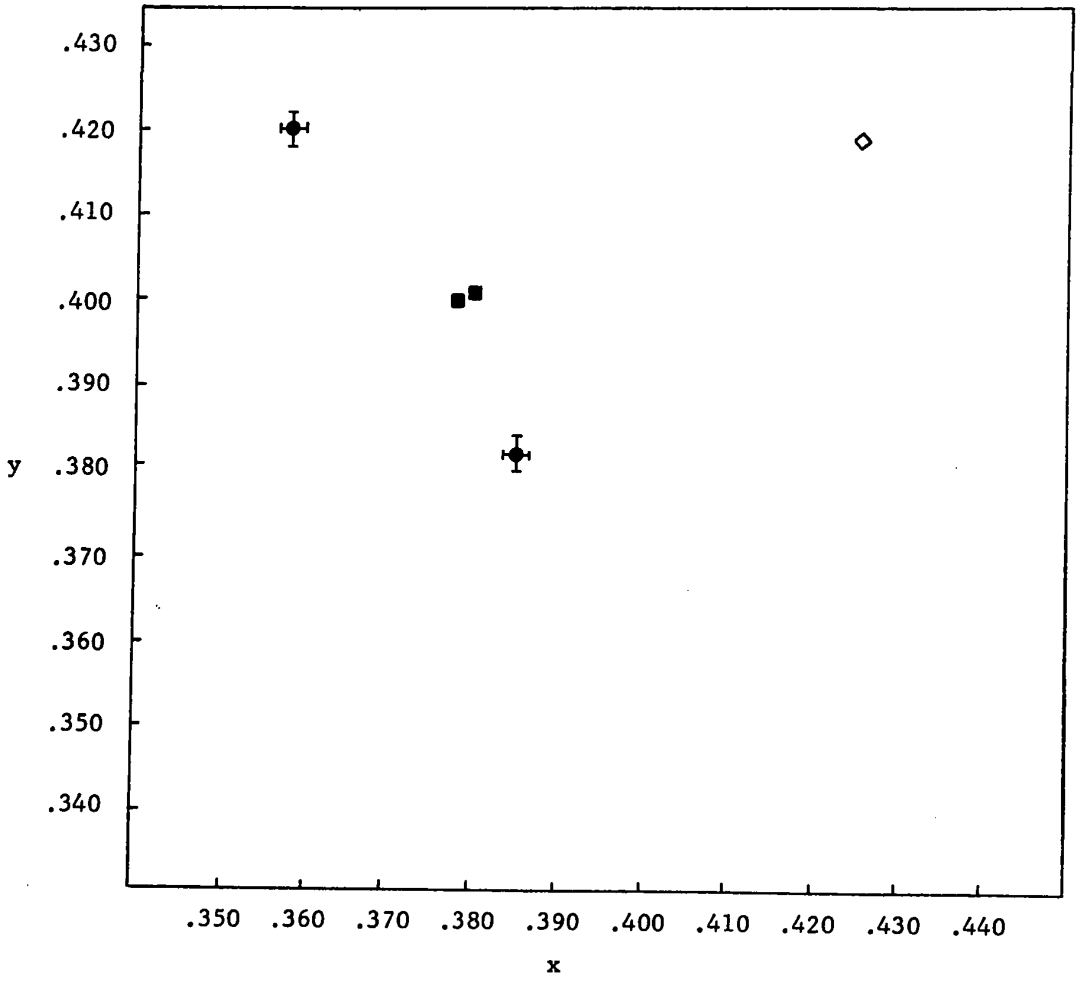

Figure 18. Experiment 5, observer A.R. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3795, y = .4012) and horizontal white stripes moving down (x = .3782, y = .3997) and the loci of his matches for stripes moving up ● (x = .3584, y = .4198) and stripes moving down ● (x = .3850, y = .3828) after six cumulative hours of adaptation. Observer A.R. reports a clear impression of green on stripes moving up and red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

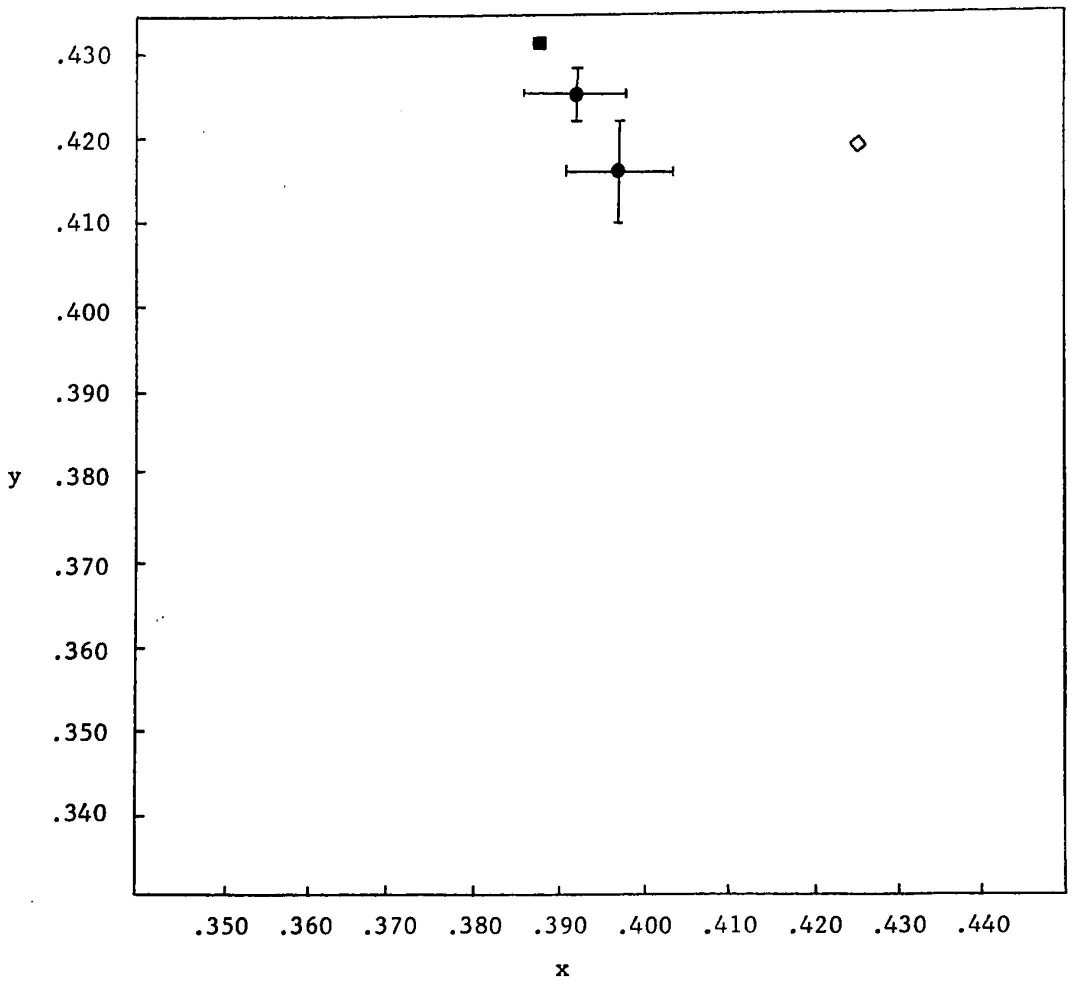

Figure 19. Experiment 5, observer J.W. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3886, y = .4314) and horizontal white stripes moving down (x = .3889, y = .4312) and the loci of his matches for stripes moving up ● (x = .3922, y = .4254) and stripes moving down ● (x = .3970, y = .4162) after six cumulative hours of adaptation. Observer J.W. reports a clear impression of green on stripes moving up and red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

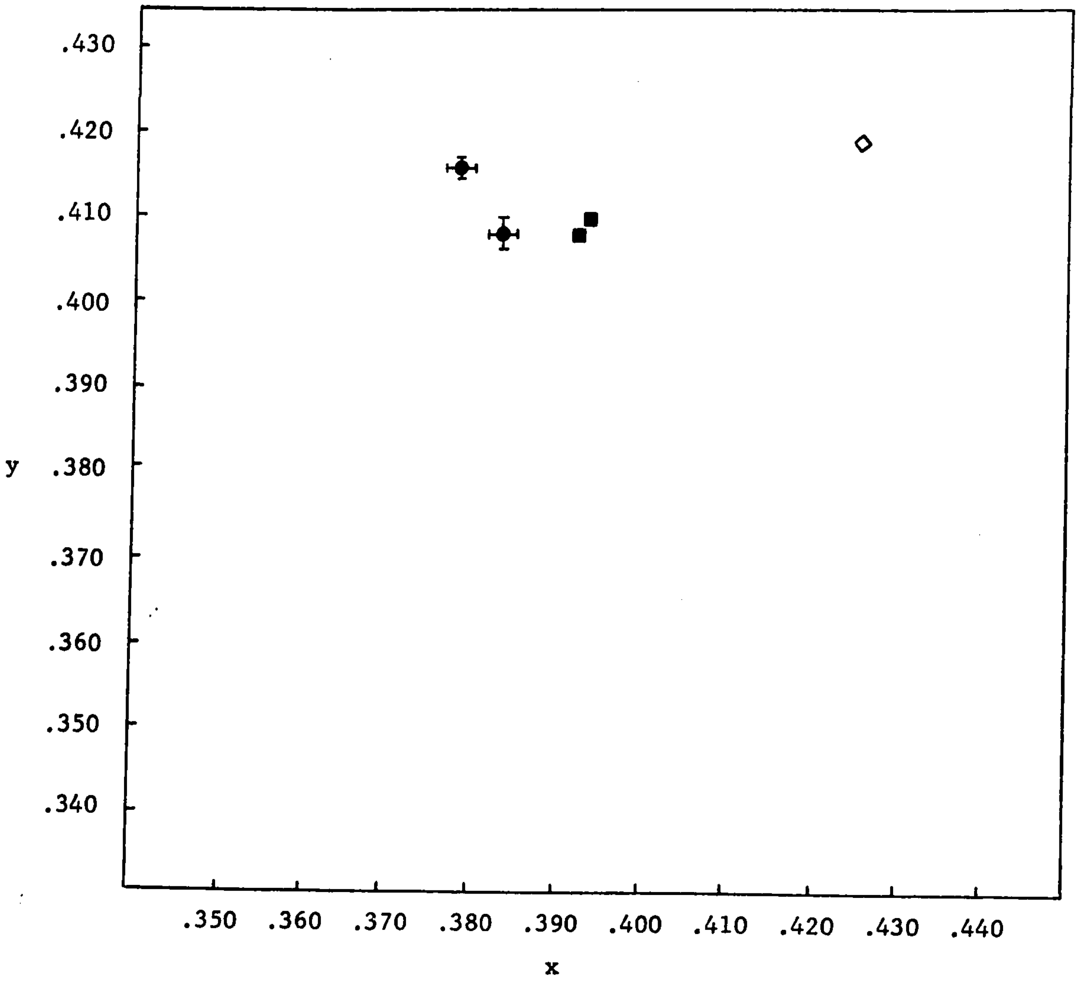

Figure 20. Experiment 5, observer T.C. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3919, y = .4076) and horizontal white stripes moving down (x = .3934, y = .4104) and the loci of his matches for stripes moving up ● (x = .3776, y = .4166) and stripes moving down ● (x = .3838, y = .4083) after six cumulative hours of adaptation. Observer T.C. reports a neutral color on stripes moving up and a clear impression of red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

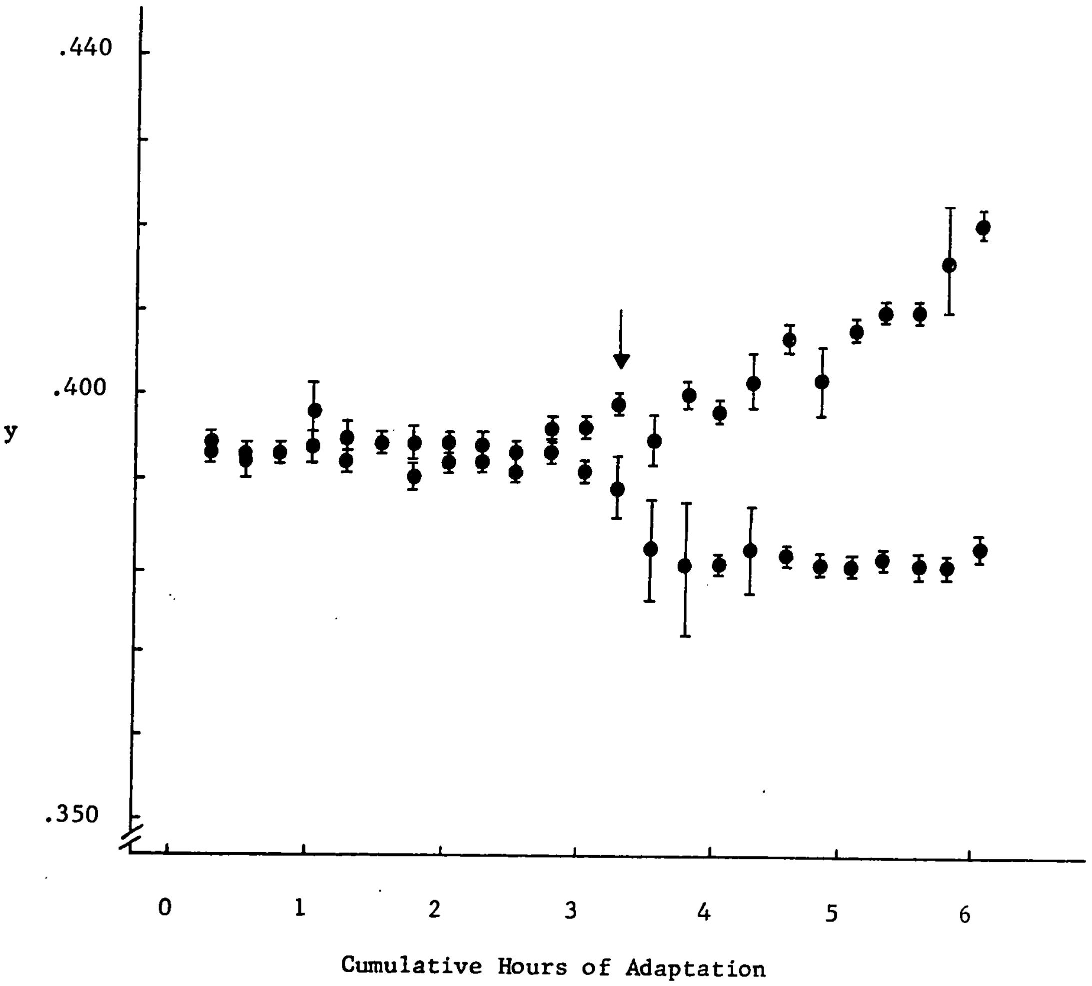

Figure 21. Experiment 5, observer A.R. The development of color aftereffects that are contingent upon the direction in which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving up ● and stripes moving down ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer A.R. reports a clear impression of green on stripes moving up and red on stripes moving down after 3 1/4 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

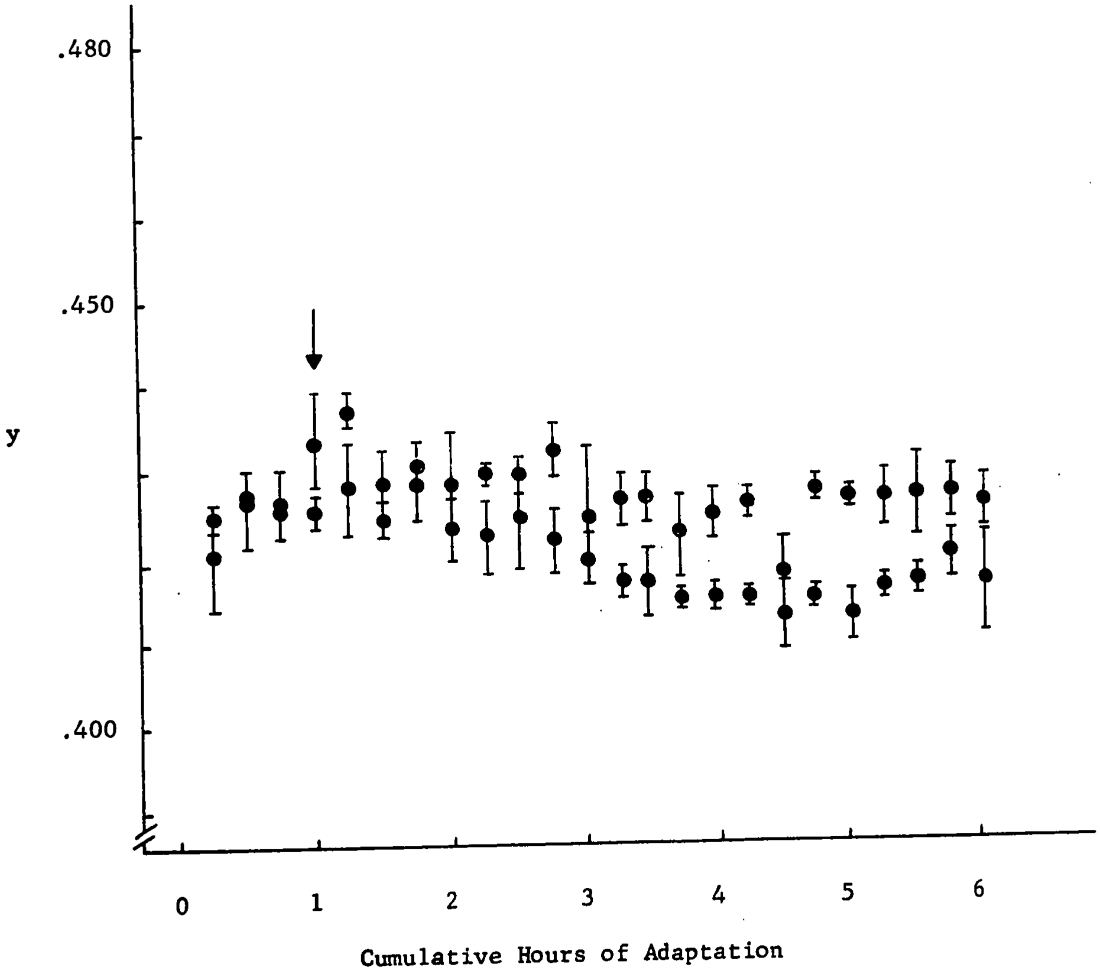

Figure 22. Experiment 5, observer J.W. The development of color aftereffects that are contingent upon the direction in which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving up ● and stripes moving down ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer J.W. reports a clear impression of green on stripes moving up and red on stripes moving down after 1 hour of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

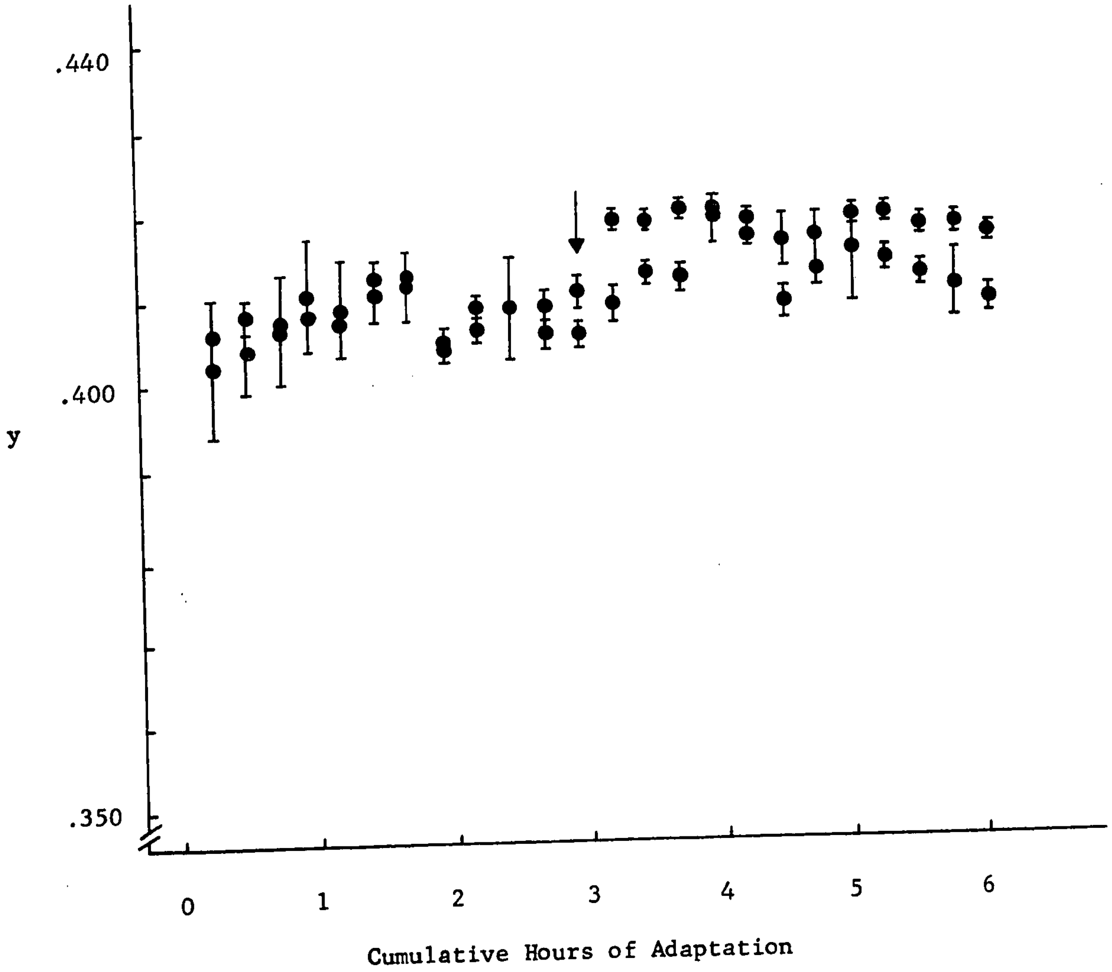

Figure 23. Experiment 5, observer T.C. The development of color aftereffects that are contingent upon the direction in which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving up ● and stripes moving down ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer T.C. reports a neutral color on stripes moving up and a clear impression of red on stripes moving down after 3 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

ly after an adapting session. Observers in the present experiment require a mean of 2.42 cumulative hours of adaptation to see similar aftereffects. Orientation-contingent color aftereffects develop in much less time: observers in Experiment 4 saw appropriate aftereffect colors after only 0.50 cumulative hours of adaptation.

The present experiments employ small adapting and comparison fields that subtend only 2.3° visual angle to meet criteria for valid colorimetric matches. One may hasten the appearance of both orientation-contingent and direction-contingent color aftereffects by increasing the size of the colored adapting patterns. Larger patterns accelerate the development of color aftereffects by incorporating more neurons into the adapting population. This maneuver produces orientation-contingent color aftereffects after 2-5 minutes of adaptation (McCollough, 1965a) and direction-contingent color aftereffects after 10-15 minutes (Stromeyer and Mansfield, 1970). It does not alter the fact that orientation-contingent color aftereffects develop faster than motion-contingent ones.

This fact is easy to understand if one orders neurons sensitive to orientation and those sensitive to motion in a hierarchy extended along cortical pathways in the human visual system. The population of neurons that adapts to colored horizontal stripes includes all cells with opponent-chromatic organization that prefer stripes placed in horizontal orientation. The population of neurons that adapts to colored horizontal stripes moving up includes only those cells with opponent-chromatic organization that restrict their responses to displays which meet both orientation and direction criteria. Moving, colored stripes educate fewer cells. Because fewer cells participate, the probability of having educated enough cells at time *t* to change the observer's perception of moving horizontal stripes is lower than it would be if one were adapting all the neurons sensitive to stripes placed in horizontal orientation.

After direction-contingent color aftereffects appear for observers J.W. and T.C., they stabilize at small, but reliable, values. Color aftereffects for observer A.R., in contrast, continue to grow throughout 3 more cumulative hours of adaptation.

During adaptation in the present experiment, observers view colored stripes moving up and colored stripes moving down at 2.45°/second. Figures 24 and 25 show the loci of matches that observer A.R. makes to black-and-white stripes which move slower or faster than 2.45°/second. Consider Figure 24. Observer A.R. reports the same aftereffect colors--green on stripes moving up at 2.45°/second and red on stripes moving down at 2.45°/second--that he has seen on previous tests. This time, as the velocity of stripes moving up decreases (1.80°/second and 1.15°/second), he sees their green color fade. The same thing happens when stripes move down. As their velocity decreases (1.80°/second and 1.15°/second), A.R. reports that their red color fades. Figure 25 displays similar data for stripes moving faster than 2.45°/second. Again, observer A.R. reports the basic direction-contingent color aftereffects when stripes move up at 2.45°/second and when stripes move down at the same velocity. Stripes moving up at faster velocities (3.10°/second and 3.80°/second) lose some of their green color; stripes moving down at faster velocities (3.10°/second and 3.80°/second) lose some of their red color.

Inspection of standard deviations plotted for loci on both figures shows that observer A.R. makes highly reliable matches for red aftereffect colors and more variable ones for green aftereffect colors. The loci of red aftereffect colors clearly differ from one another when stripes move down at decreasing velocities. They also differ from one another when stripes move down at increasing velocities. The difference between loci of green aftereffect colors under similar circumstances is not as clear.

A comparison of Figures 24 and 25 shows that one may degrade aftereffect colors more by decreasing stripe velocity than by increasing stripe velocity. Stromeyer and Mansfield (1970) report the same result. In both cases, velocity effects are confounded with those produced by temporal frequency of stimulation. If one holds the spatial frequency of the stripe display constant, as we have in the present experiment, and increases the velocity of the moving display, one also increases the frequency with which stripes stimulate a given point on the observer's retina. Likewise, decreases in the frequency with which stripes stimulate a point on the observer's retina accompany decreases in moving stripe velocity. We have observed that decreasing stripe velocity degrades aftereffect colors more than increasing stripe velocity. This result may reflect the fact that the first change provides less frequent stimulation while the second change provides more frequent stimulation for neural elements. On the other hand, it may reflect real differences between slower and faster velocity cut-off points for neurons sensitive to stripes moving at 2.45°/second. A test which separates the effects of velocity from those of stimulation frequency would decide between these alternative interpretations. In the meantime, it is clear from the present data that some velocity selectivity exists in the population of neurons adapted to colored stripes moving at 2.45°/second. If the strength of aftereffect colors depended solely upon frequency of stimulation, their saturation

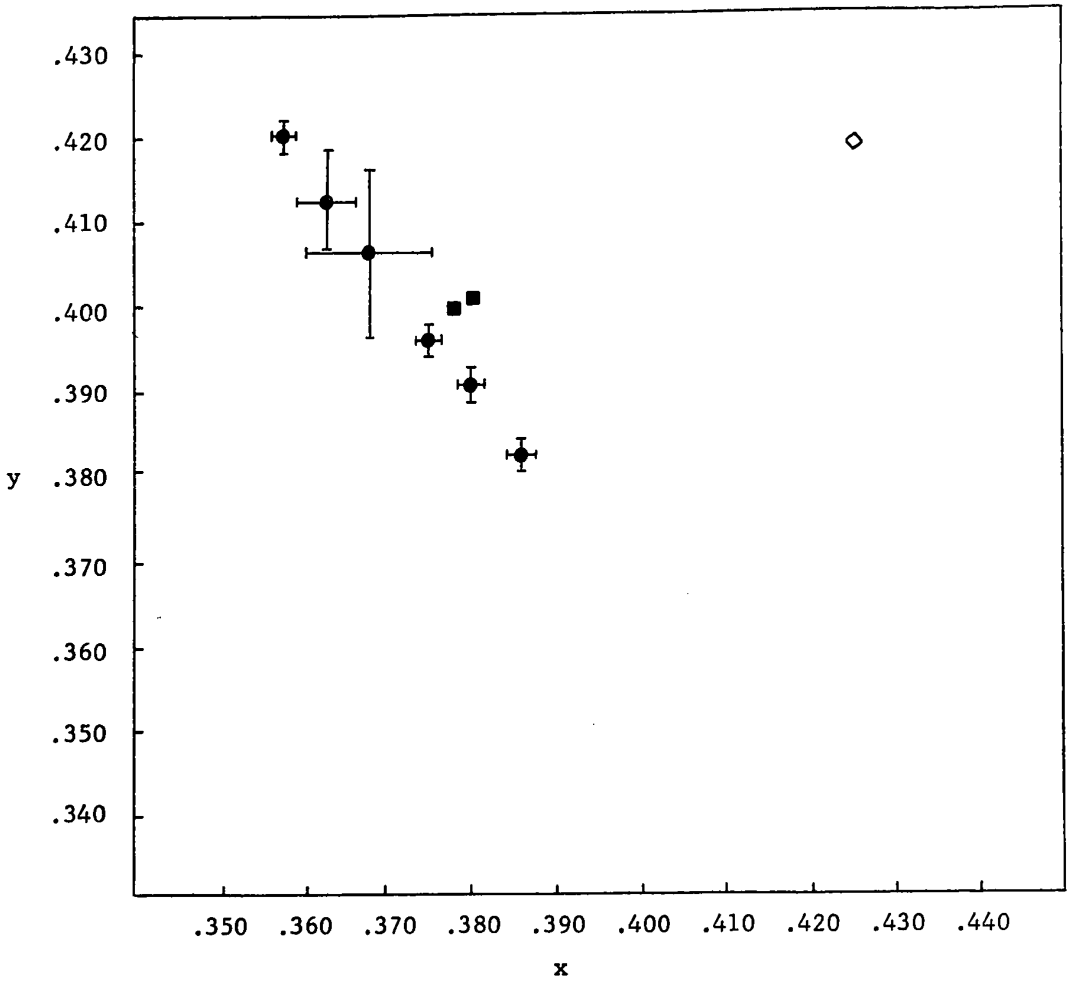

Figure 24. Experiment 5, observer A.R. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3795, y = .4012) and horizontal white stripes moving down (x = .3782, y = .3997) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3578, y = .4204), 1.80°/second ● (x = .3634, y = .4128), 1.15°/second ● (x = .3679, y = .4064) and for stripes moving down whose velocities are 2.45°/second ● (x = .3856, y = .3822), 1.80°/second ● (x = .3800, y = .3896) and 1.15°/second ● (x = .3752, y = .3966). Observer A.R. reports a clear impression of green on stripes moving up at 2.45°/second and red on stripes moving down at 2.45°/second; as velocity decreases, stripes moving in either direction lose their color. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

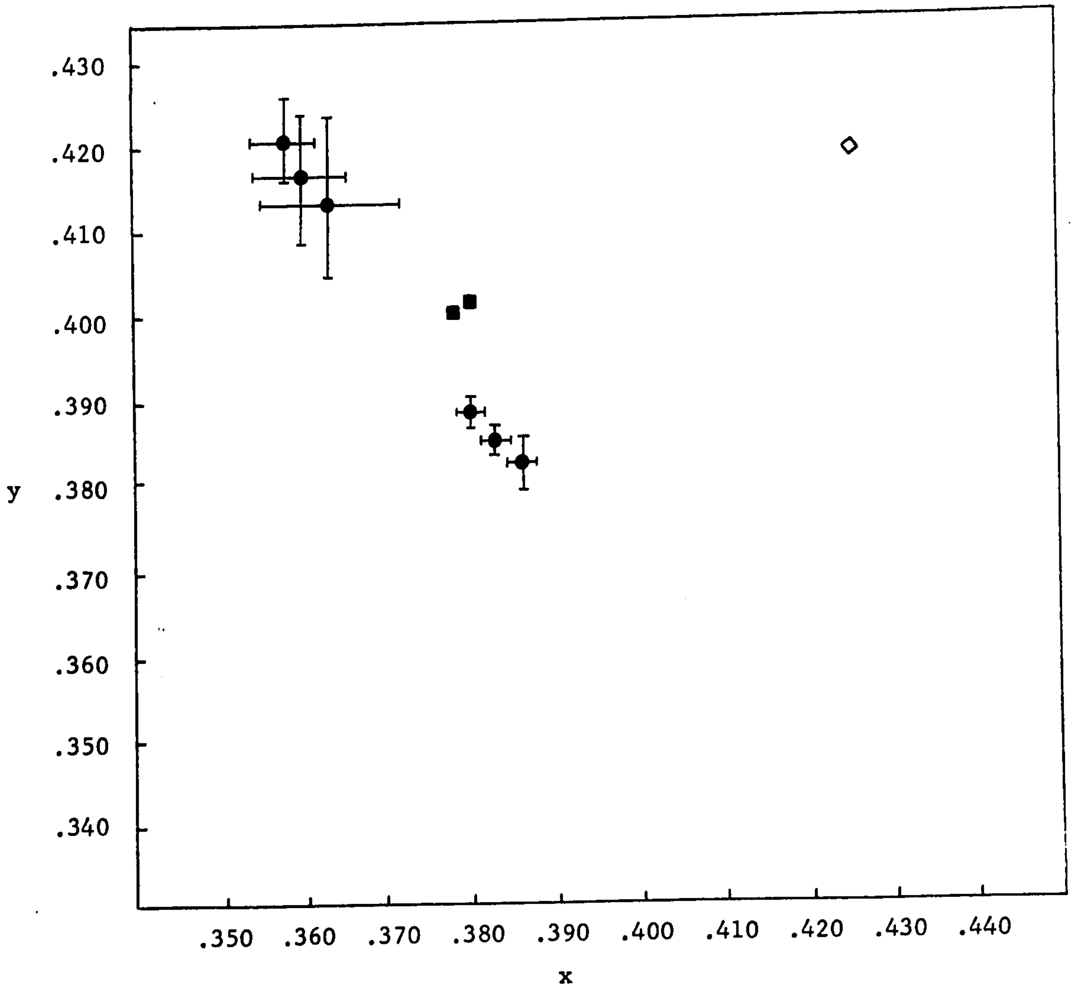

Figure 25. Experiment 5, observer A.R. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3795, y = .4012) and horizontal white stripes moving down (x = .3782, y = .3997) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3578, y = .4204), 3.10°/second ● (x = .3608, y = .4164), 3.80°/second ● (x = .3632, y = .4132) and for stripes moving down whose velocities are 2.45°/second ● (x = .3856, y = .3822), 3.10°/second ● (x = .3832, y = .3854) and 3.80°/second ● (x = .3809, y = .3884). Observer A.R. reports a clear impression of green on stripes moving up at 2.45°/second and red on stripes moving down at 2.45°/second; as velocity increases, stripes moving in either direction lose some of their color. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

should increase, not decrease as we have found, when stripes move faster than the adapting velocity.

Figures 26 and 27 show the loci of matches that observer J.W. makes to black-and-white stripes which move slower or faster than 2.45°/second. Observer J.W. reports a clear impression of green on stripes moving up at all velocities and red on stripes moving down at all velocities. His matches agree with his reports. In Figure 26, the loci of his matches for stripes moving up at slower velocities cluster around the locus of his matches for stripes moving up at 2.45°/second. All velocities appear equally green. Likewise, the loci of his matches for stripes moving down at slower velocities cluster around the locus of his matches for stripes moving down at 2.45°/second. All these velocities appear equally red. The same picture emerges from inspection of Figure 27. Loci for stripes moving up at faster velocities cluster around the locus for stripes moving up at 2.45°/second. All velocities look equally green. Loci for stripes moving down at faster velocities cluster around the locus for stripes moving down at 2.45°/second. All velocities look equally red. Observer J.W. embarked on generalization testing with weak, though reliable, direction-contingent color aftereffects. Evidently weak aftereffect colors generalize readily to a wide range of velocities. The process of strengthening the aftereffects may be one of "sharpening" (von Békésy, 1968)--discarding the participation of neural elements not specifically tuned to both the direction and the velocity of the adapting display.

Figures 28 and 29 show the loci of matches that observer T.C. makes to black-and-white stripes which move slower or faster than 2.45°/second. Observer T.C. starts generalization testing with a well-defined red after-

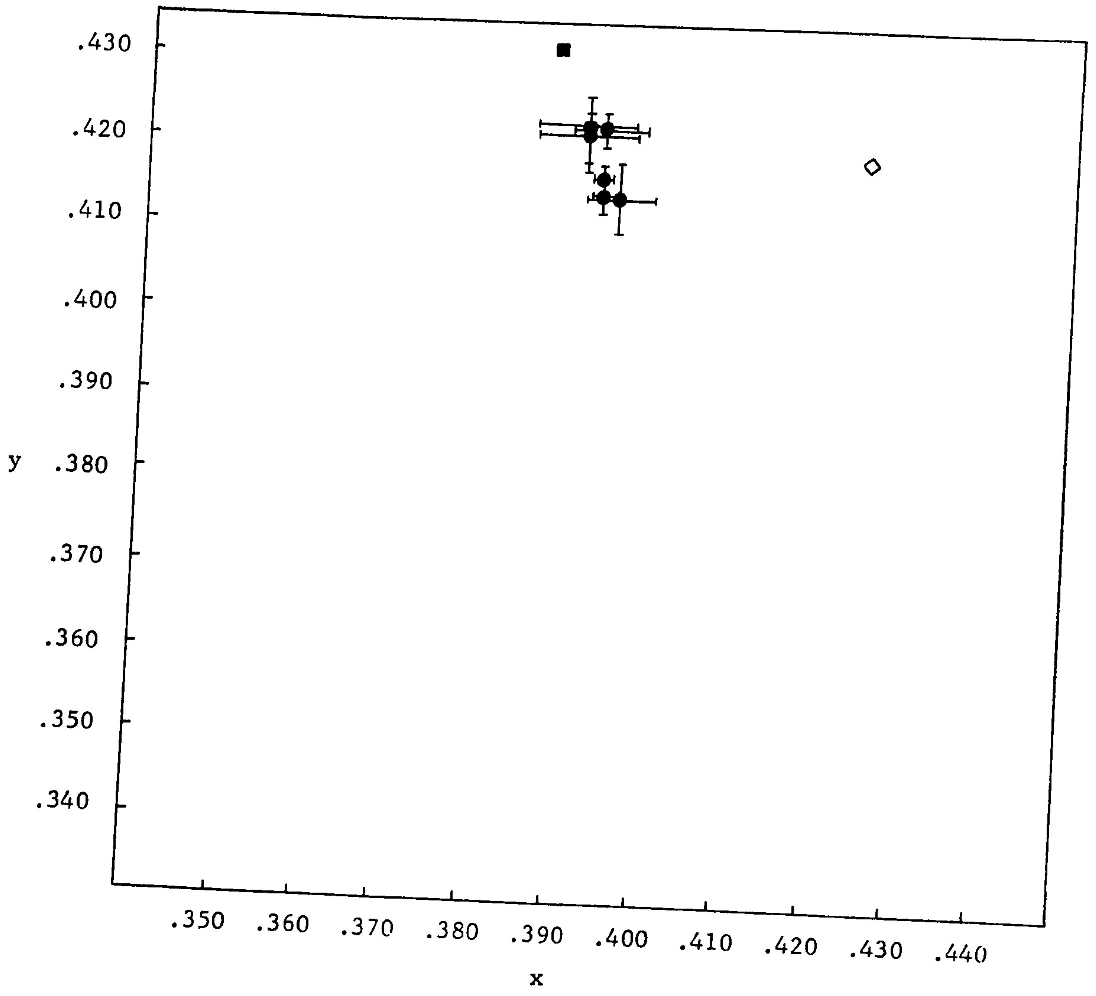

Figure 26. Experiment 5, observer J.W. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3886, y = .4314) and horizontal white stripes moving down (x = .3889, y = .4312) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3928, y = .4228), 1.80°/second ● (x = .3922, y = .4210), 1.15°/second ● (x = .3936, y = .4221) and for stripes moving down whose velocities are 2.45°/second ● (x = .3960, y = .4148), 1.80°/second ● (x = .3944, y = .4146) and 1.15°/second ● (x = .3946, y = .4159). Observer J.W. reports a clear impression of green on stripes moving up and red on stripes moving down at all velocities. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

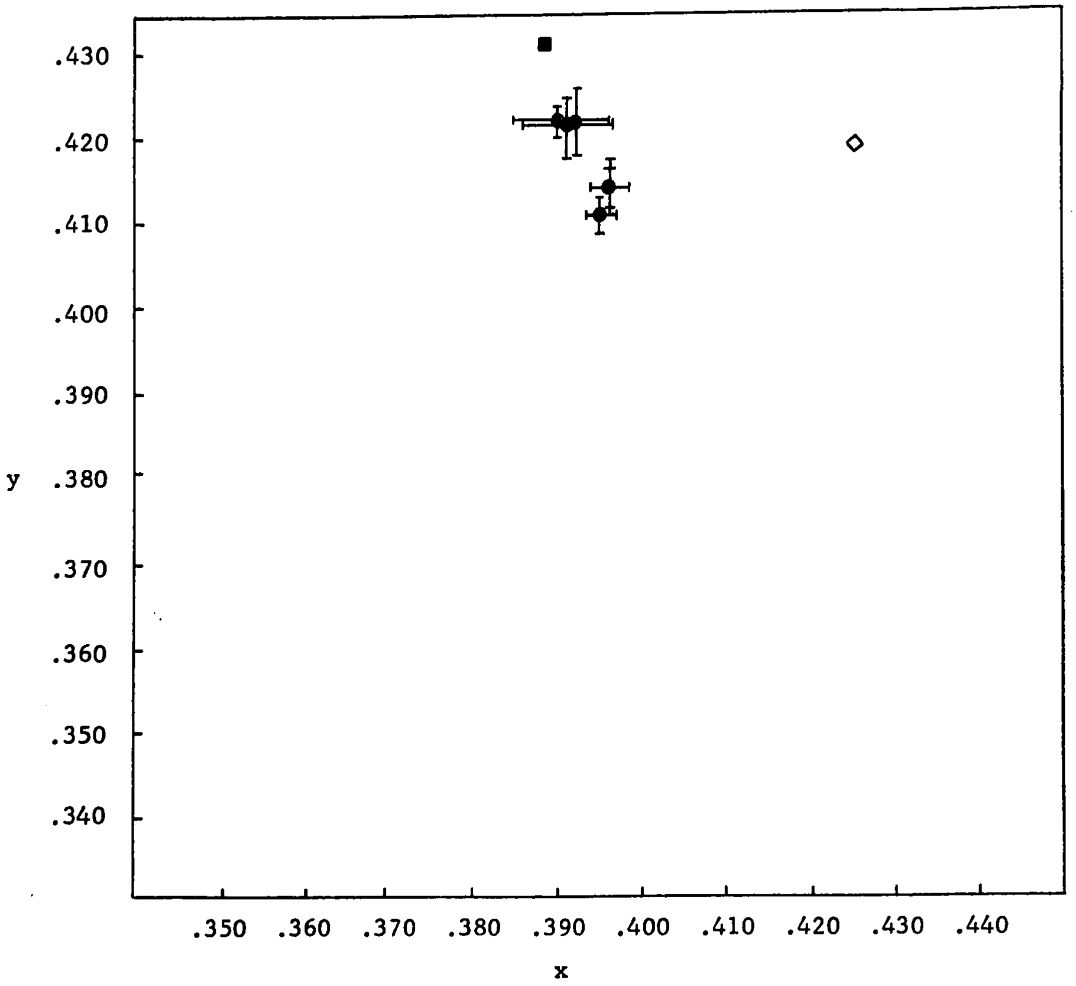

Figure 27. Experiment 5, observer J.W. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3886, y = .4314) and horizontal white stripes moving down (x = .3889, y = .4312) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3928, y = .4228), 3.10°/second ● (x = .3914, y = .4224), 3.80°/second ● (x = .3904, y = .4228) and for stripes moving down whose velocities are 2.45°/second ● (x = .3960, y = .4148), 3.10°/second ● (x = .3956, y = .4139) and 3.80°/second ● (x = .3952, y = .4114). Observer J.W. reports a clear impression of green on stripes moving up and red on stripes moving down at all velocities. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

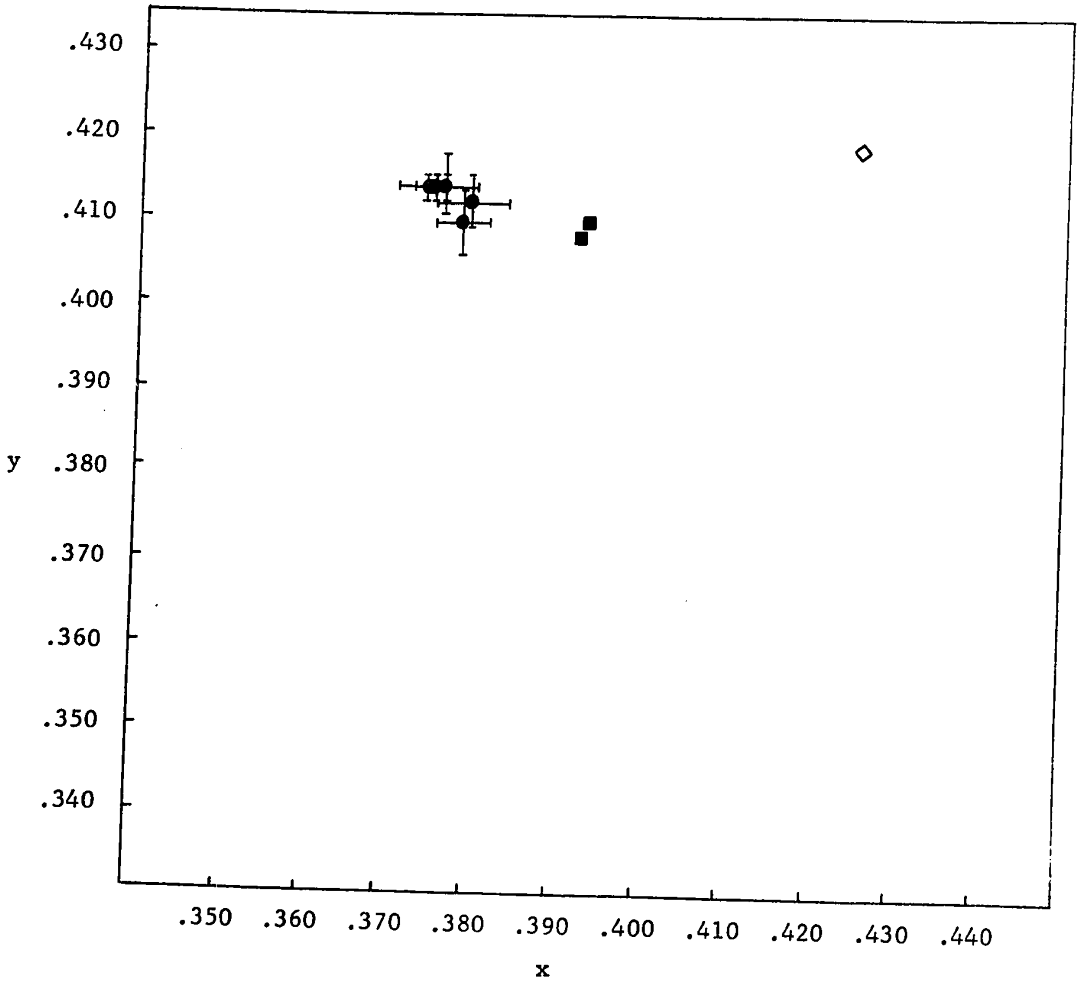

Figure 28. Experiment 5, observer T.C. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3919, y = .4076) and horizontal white stripes moving down (x = .3934, y = .4104) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3750, y = .4144), 1.80°/second ● (x = .3748, y = .4142), 1.15°/second ● (x = .3752, y = .4143) and for stripes moving down whose velocities are 2.45°/second ● (x = .3782, y = .4104), 1.80°/second ● (x = .3792, y = .4122) and 1.15°/second ● (x = .3768, y = .4140). Observer T.C. reports a slight impression of green on stripes moving up at all velocities and a clear impression of red on stripes moving down at 2.45°/second; as velocity decreases, stripes moving down lose their color. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

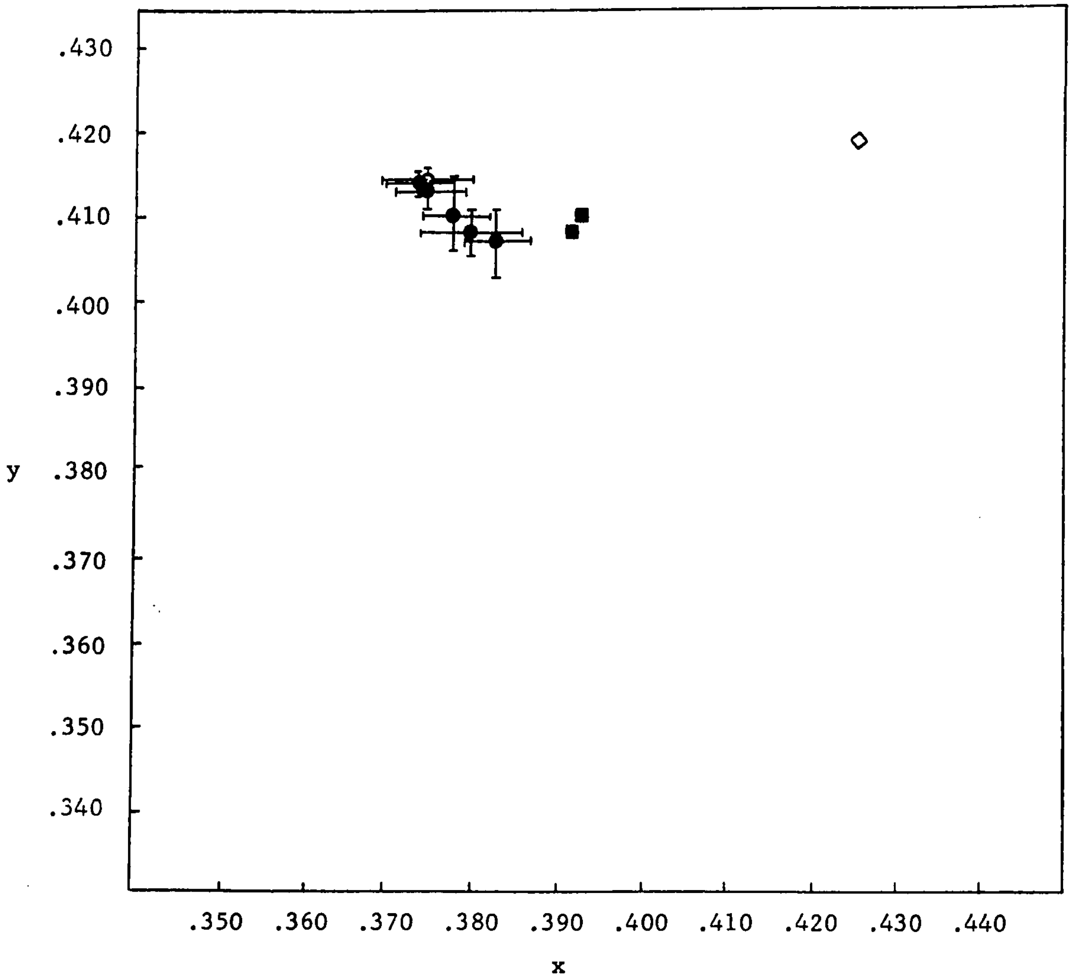

Figure 29. Experiment 5, observer T.C. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3919, y = .4076) and horizontal white stripes moving down (x = .3934, y = .4104) and the loci of his matches for stripes moving up whose velocities are 2.45°/second ● (x = .3750, y = .4144), 3.10°/second ● (x = .3745, y = .4144), 3.80°/second ● (x = .3751, y = .4134) and for stripes moving down whose velocities are 2.45°/second ● (x = .3782, y = .4104), 3.10°/second ● (x = .3804, y = .4086) and 3.80°/second ● (x = .3832, y = .4073). Observer T.C. reports a slight impression of green on stripes moving up and a clear impression of red on stripes moving down at all velocities; as velocity increases, stripes moving down become redder. Each point represents a mean of 10 matches. Brackets indicate standard deviations for each set of 10 matches along the x and y axes of the chromaticity diagram.

effect on stripes moving down and no aftereffect color on stripes moving up. During the course of generalization testing he begins to report a slight impression of green on stripes moving up at all velocities, slower or faster than the adapting velocity of 2.45°/second. Observer T.C. also reports that stripes moving down at velocities slower than the adapting velocity of 2.45°/second (1.80°/second and 1.15°/second) lose their red color while stripes moving down appear redder as their velocity increases (3.10°/second and 3.80°/second) beyond the adapting velocity. Despite observer T.C.'s reports, there is little reason to speculate about the velocity selectivity of neurons storing red aftereffects: the loci of his matches for red aftereffect colors cluster so closely together that their standard deviations overlap. The most that we may saw about observer T.C.'s performance is that direction-contingent aftereffect colors remain visible throughout generalization testing.

Figures 30, 31 and 32 show the saturation of direction-contingent color aftereffects visible 24 to 96 hours after the final adapting session in Experiment 5. The aftereffect colors obviously persist for observer A.R. who reports a clear impression of green on stripes moving up and red on stripes moving down after 96 hours' reprieve from testing. Comparison of Figure 30 with Figure 18 shows that the saturation of A.R.'s aftereffects has declined, although his matches at 96 hours' delay still show a healthy and reliable difference between the loci of green and red aftereffect colors. Observer J.W., Figure 31, also reports a clear difference between green and red aftereffect colors at 24 hours' delayed testing although his matches for the green aftereffect are quite variable. His persisting aftereffects are slightly weaker than the aftereffects that he sees immediately after adapta-

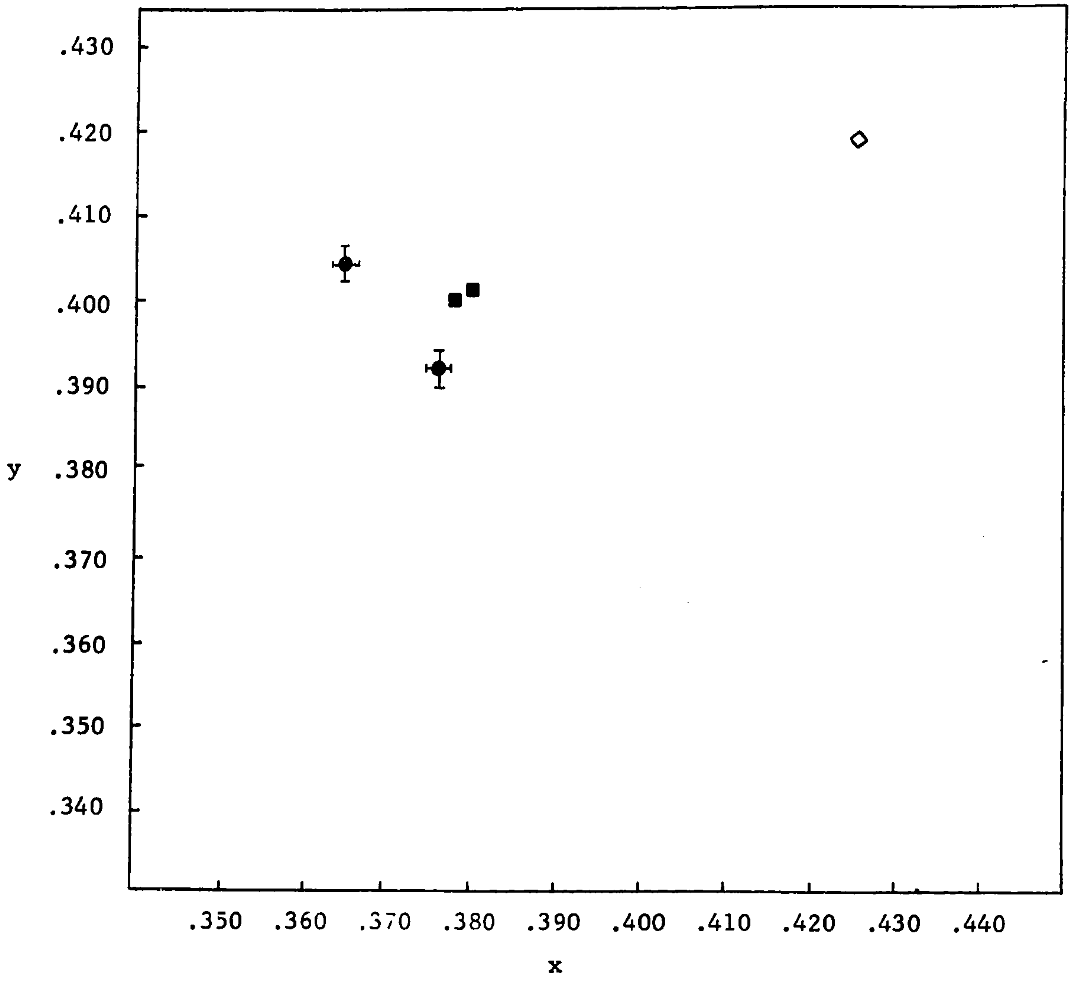

Figure 30. Experiment 5, observer A.R. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3795, y = .4012) and horizontal white stripes moving down (x = .3782, y = .3997) and the loci of his matches for stripes moving up ● (x = .3758, y = .3918) and stripes moving down ● (x = .3656, y = .4094) 96 hours after the final adapting session. Observer A.R. reports a clear impression of green on stripes moving up and red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

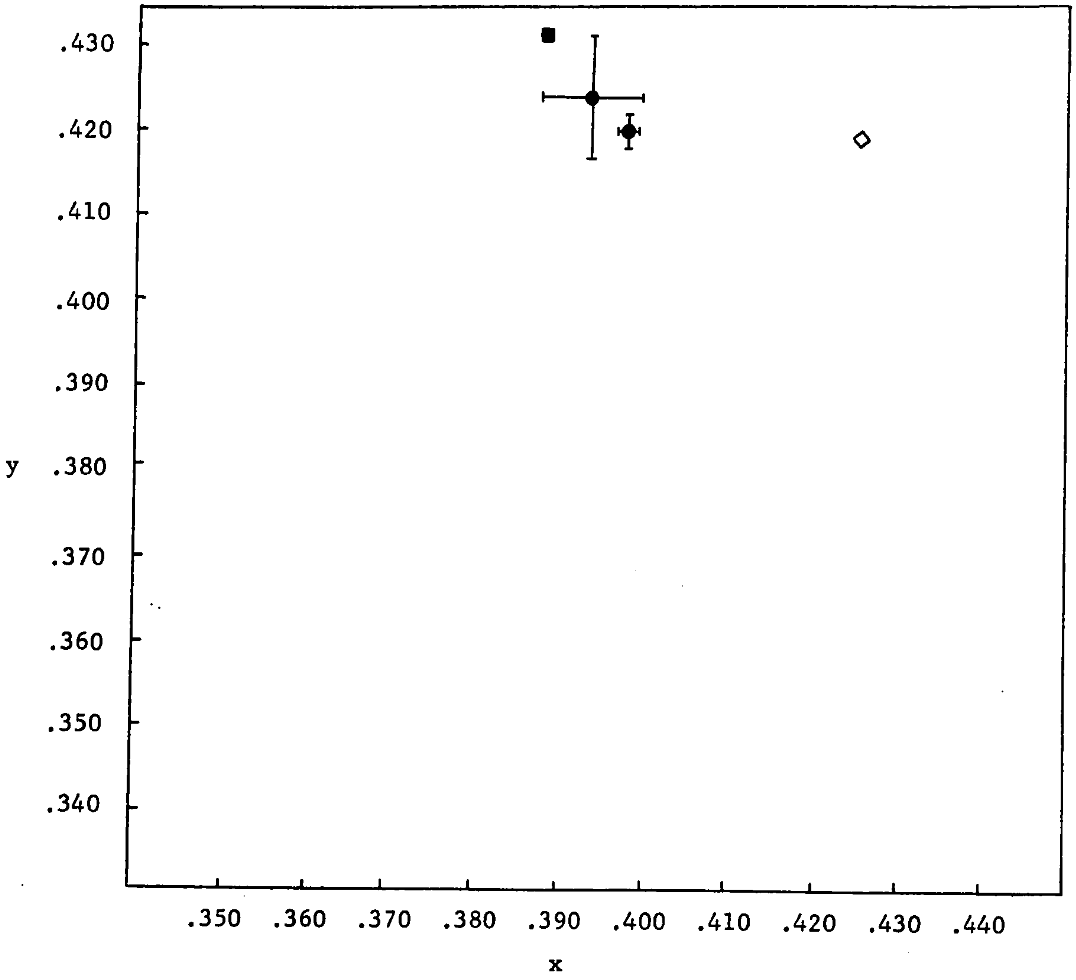

Figure 31. Experiment 5, observer J.W. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3886, y = .4314) and horizontal white stripes moving down (x = .3889, y = .4312) and the loci of his matches for stripes moving up ● (x = .3943, y = .4243) and stripes moving down ● (x = .3978, y = .4202) 24 hours after the final adapting session. Observer J.W. reports a clear impression of green on stripes moving up and red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

tion, shown in Figure 19. Observer T.C., whose original aftereffects (Figure 30) are small, makes highly reliable matches for even smaller aftereffects (Figure 32) visible 24 hours after his last adapting session. He reports a slight impression of green on stripes moving up and a clear impression of red on stripes moving down at this delayed test interval. These observers' matches demonstrate that direction-contingent color aftereffects, whether large or small-but-reliable, persist for many hours after the visual experience that creates them.

Two other observers exit the experiment after they have accumulated 6 hours of adaptation. Observer J.D., whose data are pictured in Figures 33 and 35, develops direction-contingent color aftereffects that are too small and unreliable to warrant further testing. Observer S.T. reports no aftereffects at all. His matches appear in Figures 34 and 36.

A survey of results from Experiment 5 shows that aftereffect colors roughly complementary to the adapting colors develop after observers accumulate a mean of 2.42 hours of experience viewing colored stripes that move in opposite directions. Direction-contingent color aftereffects take more time to develop than orientation-contingent ones. This fact fits a hierarchical model of connections among cortical neurons. Only one observer develops direction-contingent aftereffect colors that are as saturated as colors contingent upon the orientation of adapting stripes seen by observers in Experiment 4. Others develop weaker, but reliable, direction-contingent aftereffect colors. Weak aftereffect colors generalize to all velocities of motion for stripes moving in the appropriate direction. Saturated aftereffect colors are specific to the velocity, as well as the direction, of moving stripes. We assume that their specificity reflects the response re-

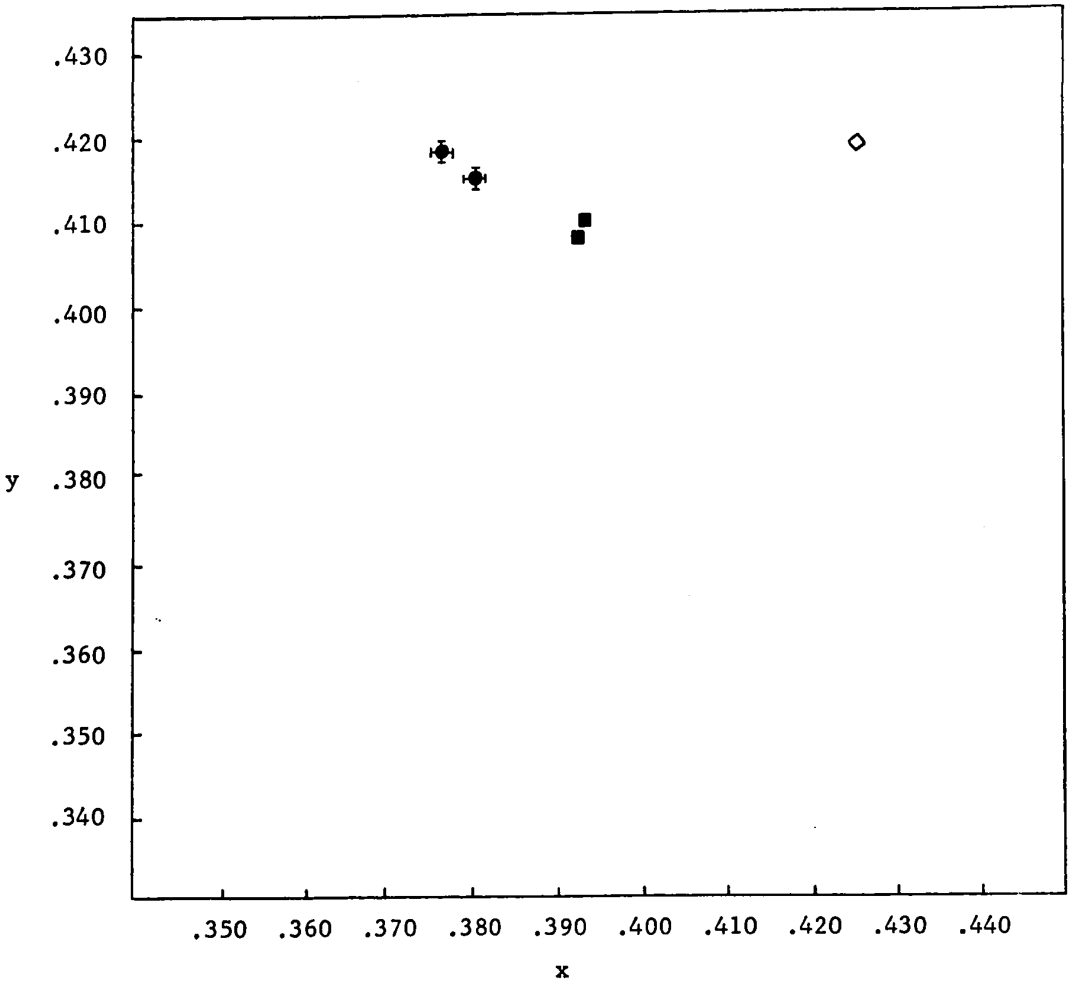

Figure 32. Experiment 5, observer T.C. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3919, y = .4076) and horizontal white stripes moving down (x = .3934, y = .4104) and the loci of his matches for stripes moving up ● (x = .3769, y = .4180) and stripes moving down ● (x = .3797, y = .4152) 24 hours after the final adapting session. Observer T.C. reports a slight impression of green on stripes moving up and a clear impression of red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

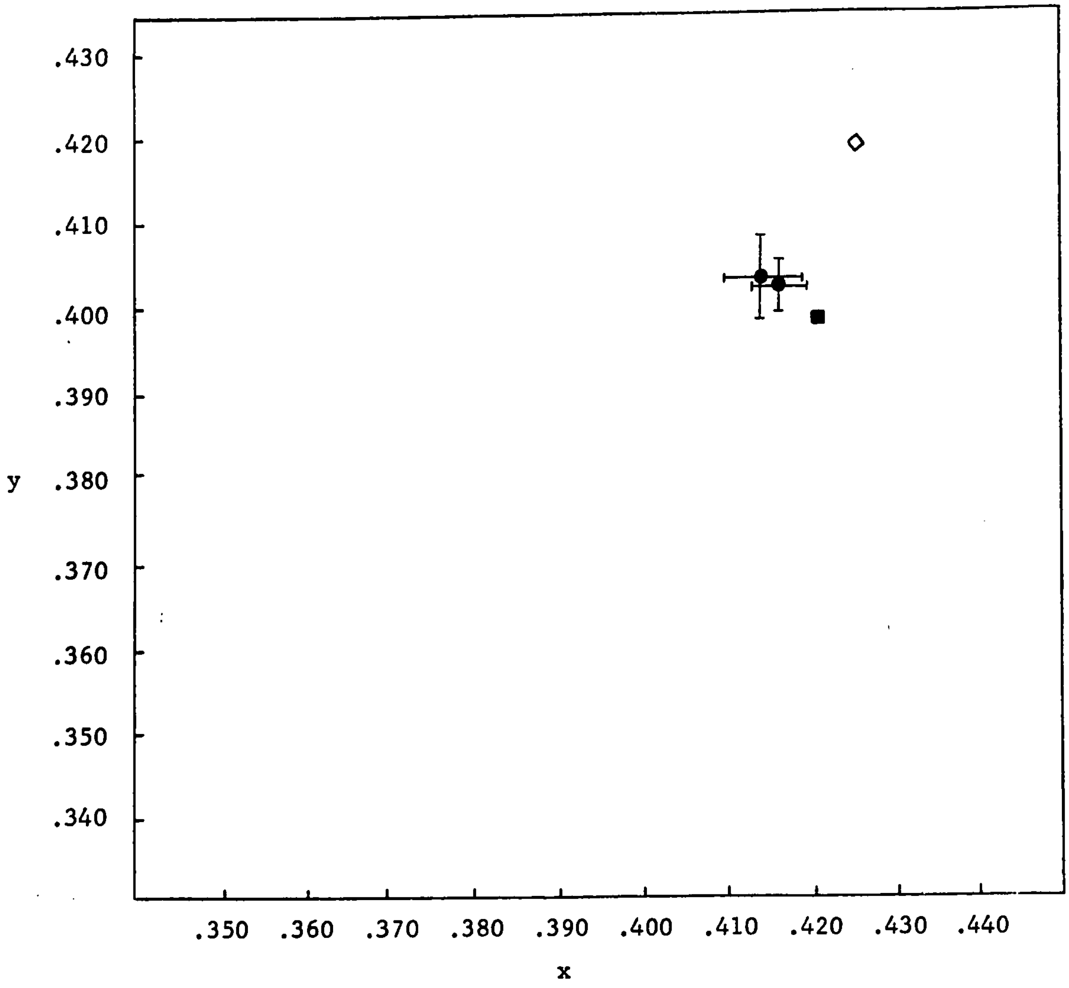

Figure 33. Experiment 5, observer J.D. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .4204, y = .3993) and horizontal white stripes moving down (x = .4214, y = .3990) and the loci of his matches for stripes moving up ● (x = .4144, y = .4036) and stripes moving down ● (x = .4164, y = .4034) after six cumulative hours of adaptation. Observer J.D. reports a slight impression of green on stripes moving up and a slight impression of red on stripes moving down. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

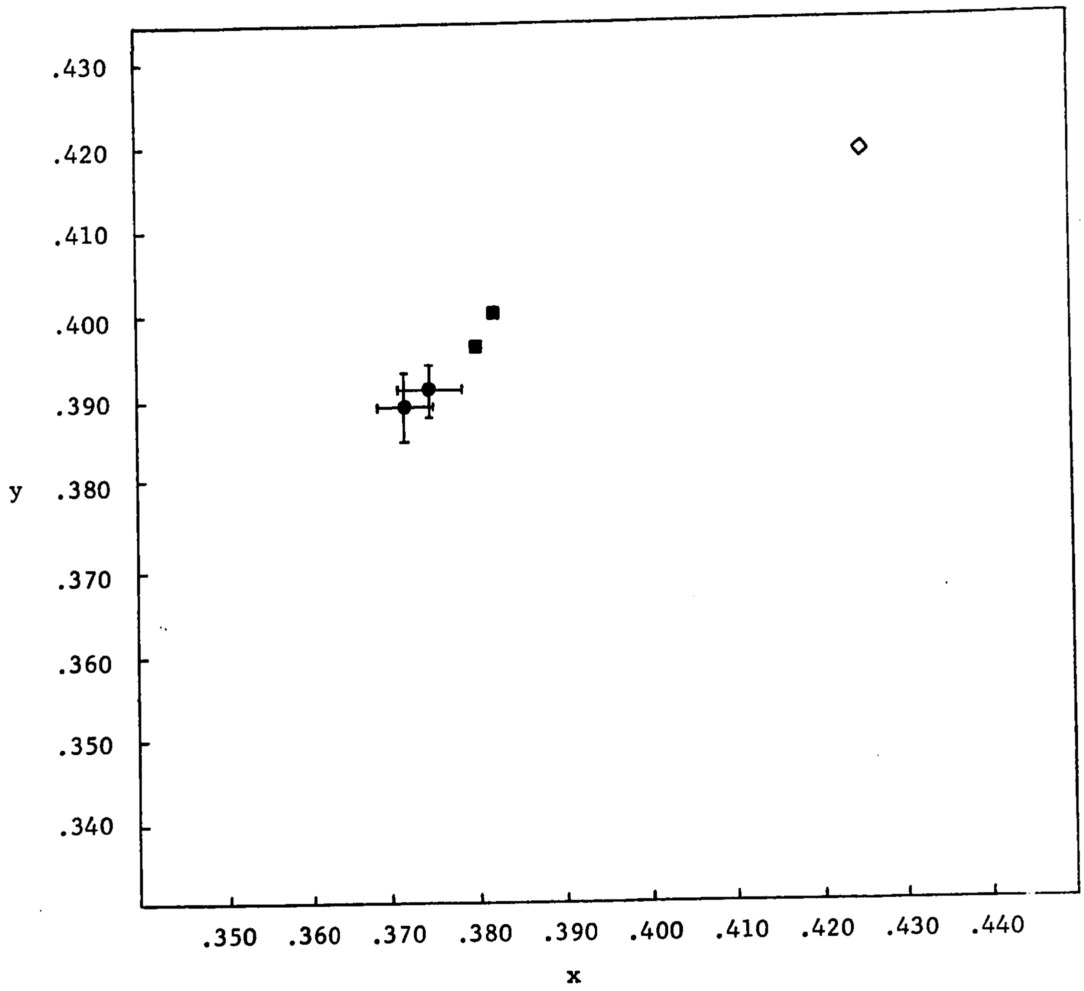

Figure 34. Experiment 5, observer S.T. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving up (x = .3825, y = .4000) and horizontal white stripes moving down (x = .3798, y = .3964) and the loci of his matches for stripes moving up ● (x = .3728, y = .3890) and stripes moving down ● (x = .3752, y = .3912) after six cumulative hours of adaptation. Observer S.T. reports a neutral color on stripes moving up and on stripes moving down. Each point represents a mean of five matches. Brackets indicate the standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

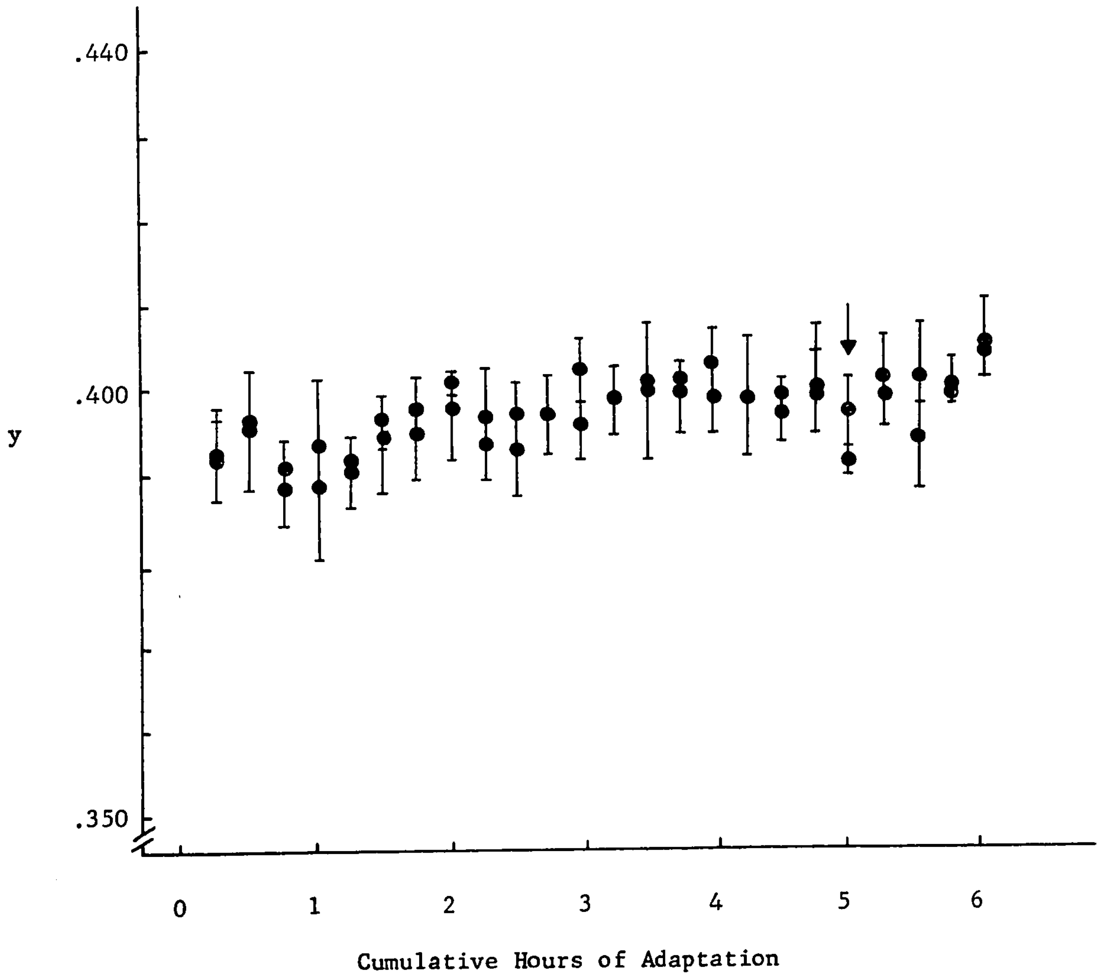

Figure 35. Experiment 5, observer J.D. The development of color aftereffects that are contingent upon the direction in which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving up ● and stripes moving down ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer J.D. reports a slight impression of green on stripes moving up and a slight impression of red on stripes moving down after 5 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

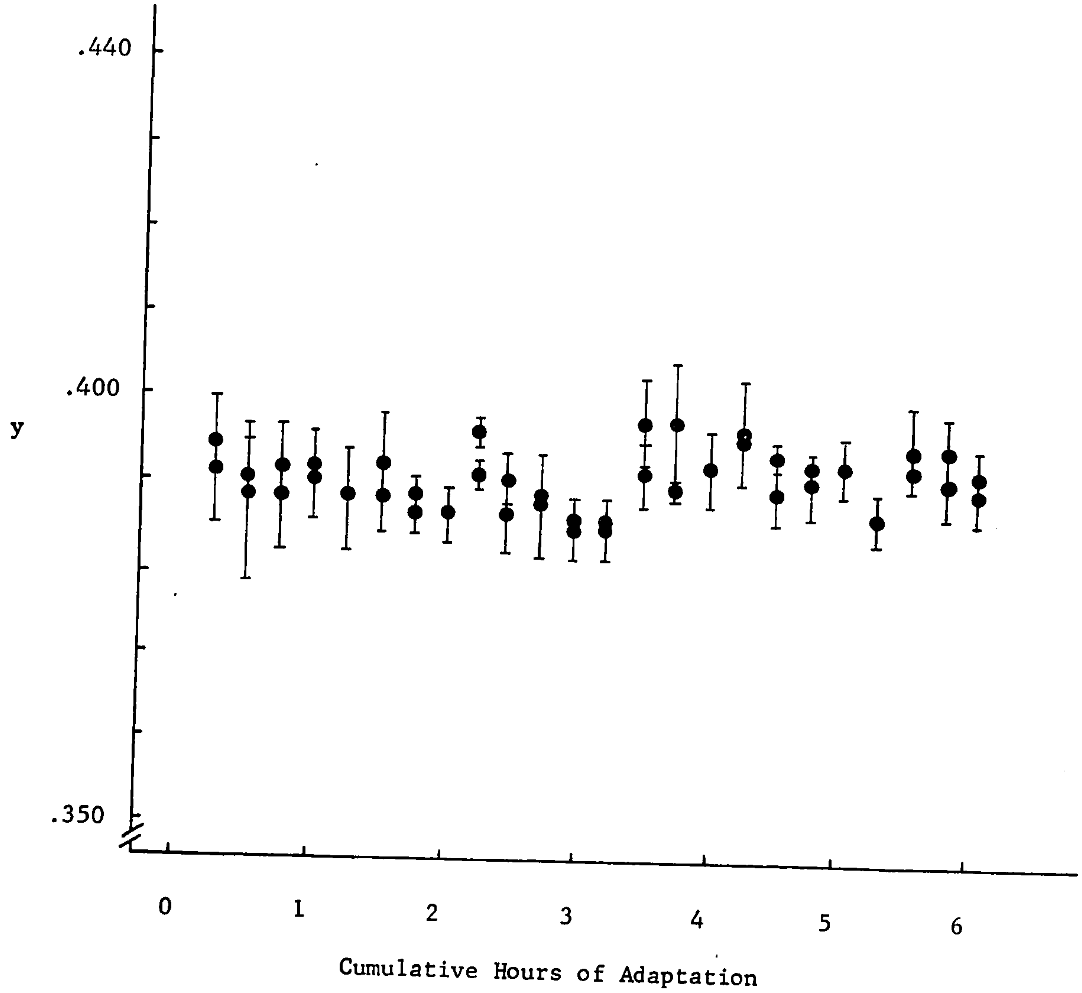

Figure 36. Experiment 5, observer S.T. The development of color aftereffects that are contingent upon the direction in which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving up ● and stripes moving down ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer S.T. reports a neutral color on stripes moving up and on stripes moving down. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

strictions of human cortical neurons. Direction-contingent aftereffect colors persist, at reduced saturation, for at least 24-96 hours after the observers' final visual sample of moving, colored stripes.

Experiment 6

Only one observer in Experiment 5 made color matches which clearly showed that his direction-contingent aftereffect colors were specific to the velocity of the moving stripe display. Other observers made matches which showed only slight velocity gradients. The critical experimenter remains unconvinced, given only these data, that motion-contingent color aftereffects involve cells with both direction and velocity response constraints. Experiment 6 uses a different strategy to examine the velocity preferences of adapting cells. Observers in Experiment 6 see two sets of adapting stripes. Both sets move in the same direction but each set has a different color and a different velocity. The experiment is designed to produce velocity-contingent color aftereffects. Again, observers in Experiment 6 make matches that show how velocity-contingent aftereffect colors develop over many adapting sessions. Their matches demonstrate (a) that the aftereffect colors they see are specific to the velocities to which they have adapted and (b) that these aftereffect colors persist well beyond a given adapting session.

Observers

Five students participated in Experiment 6

Stimulus Display and Procedure

In this experiment the 35-mm film loop carries opaque and transparent stripes whose contrast ratio is 0.89. Each stripe is 7.0 mm wide and subtends 48 min arc at 50 cm viewing distance. The spatial frequency of the stripe display is 0.62 cycles/degree visual angle.

During adaptation the observer sees horizontal magenta stripes moving at 1.80°/second alternate with horizontal yellow-green stripes moving at 3.10°/second. Both sets of stripes move down.

During matching trials the observer sees horizontal stripes moving at 1.80°/second and 3.10°/second which are objectively black-and-white. They are the same stripes that he sees during adaptation, without their color filters.

In this experiment observers make color matches in one generalization test. The generalization test varies the velocity of black-and-white stripes and asks the observer to match the color he sees on stripes moving at each velocity. Observers see stripes moving down at five different velocities (1.80°/second, 2.12°/second, 2.45°/second, 2.78°/second and 3.10°/second) in random order. They make three matches for each stripe velocity on a given day. Generalization testing continues for five days.

Observers return 24 hours (A.J. and J.K.) and 48 hours (A.P.) after their last adapting session to match horizontal stripes moving down at 1.80°/second and 3.10°/second.

Results

Figures 37, 38 and 39 display the loci of aftereffect colors that observers A.P., A.J. and J.K. see on black-and-white horizontal stripes moving down at 1.80°/second and similar stripes moving down at 3.10°/second after 6 cumulative hours of adaptation. All three observers report clear impressions of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Again, inspection of Figures 38 and 39 show that observers A.J. and

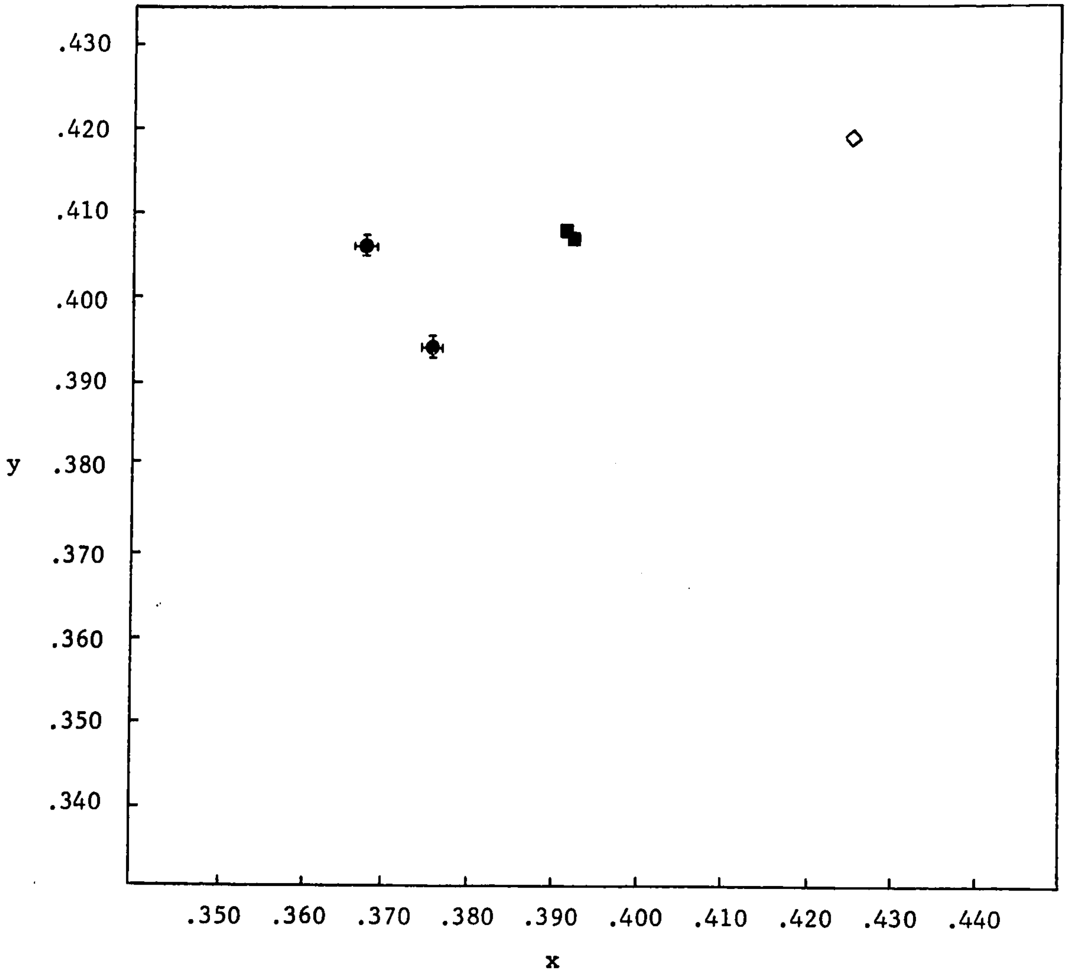

Figure 37. Experiment 6, observer A.P. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .3930, y = .4074) and horizontal white stripes moving down at 3.10°/second (x = .3926, y = .4078) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3684, y = .4060) and stripes moving down at 3.10°/second ● (x = .3768, y = .3943) after six cumulative hours of adaptation. Observer A.P. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

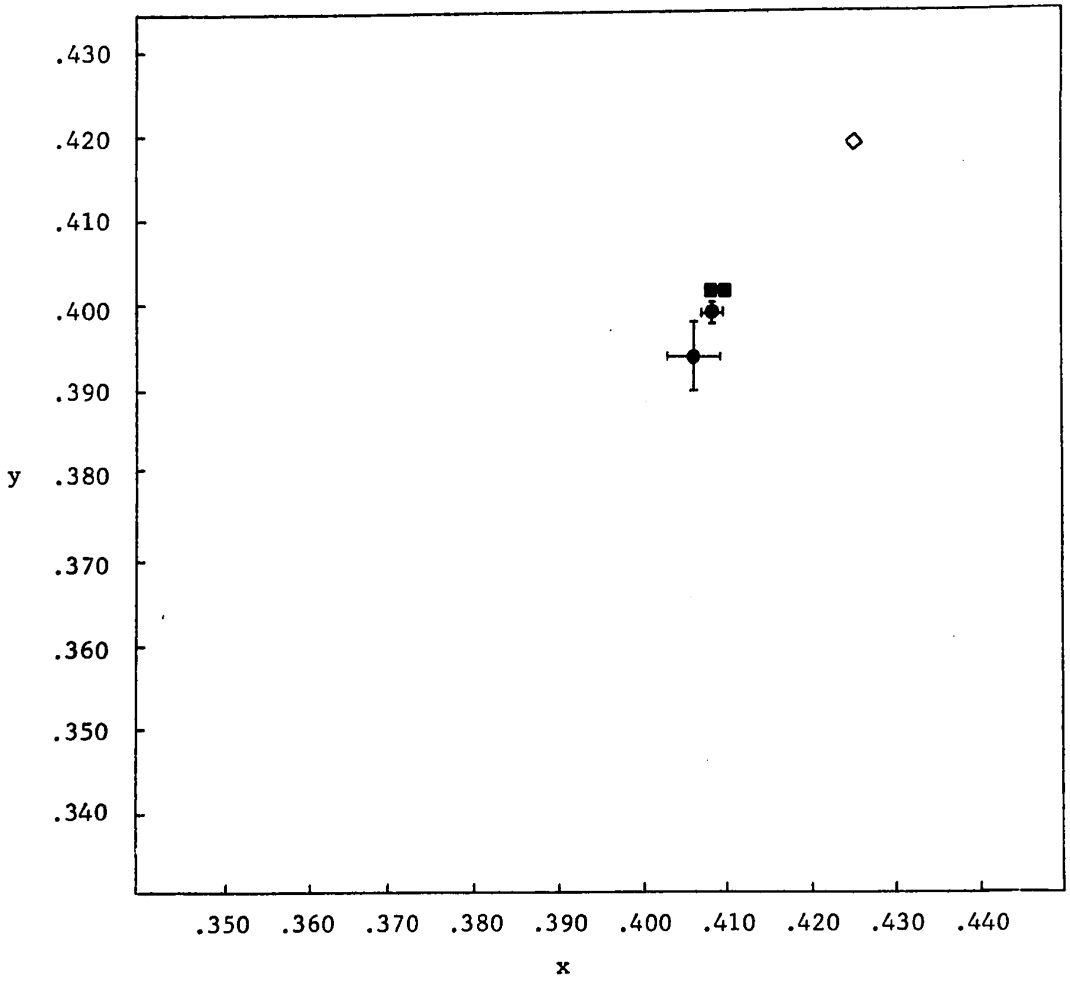

Figure 38. Experiment 6, observer A.J. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4080, y = .4022) and horizontal white stripes moving down at 3.10°/second (x = .4104, y = .4024) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .4084, y = .3991) and stripes moving down at 3.10°/second ● (x = .4064, y = .3945) after six cumulative hours of adaptation. Observer A.J. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

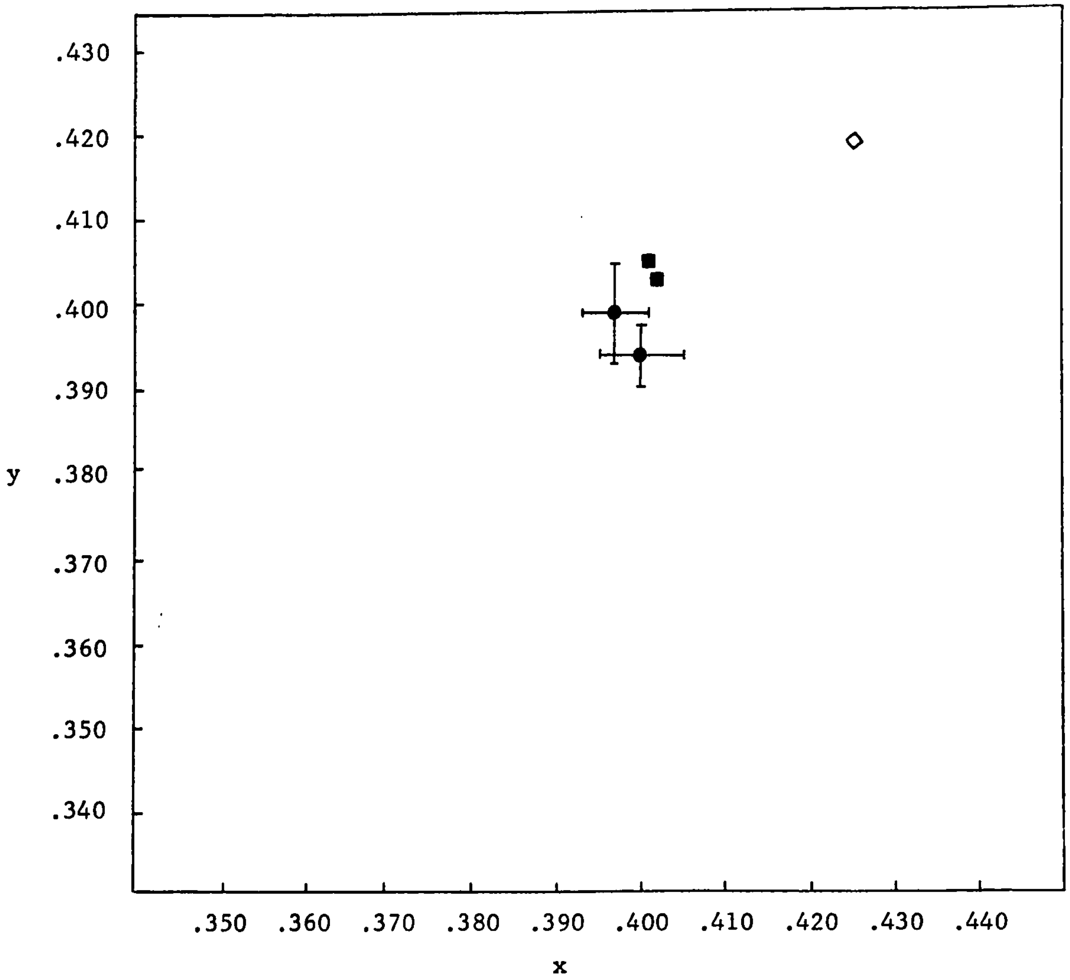

Figure 39. Experiment 6, observer J.K. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4010, y = .4052) and horizontal white stripes moving down at 3.10°/second (x = .4022, y = .4030) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3970, y = .3992) and stripes moving down at 3.10°/second ● (x = .3995, y = .3940) after six cumulative hours of adaptation. Observer J.K. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

J.K. are judging aftereffect colors in relation to one another, not in relation to their neutral reference points. Velocity-contingent color aftereffects in this experiment are about the size of direction-contingent color aftereffects for observers J.W. and T.C. in Experiment 5: they are small but quite reliable.

The development of velocity-contingent color aftereffects is illustrated, for each observer, in Figures 40, 41 and 42. Observer A.P. reports appropriate aftereffect colors after 3 cumulative hours of adaptation; observer A.J. after 2 1/4 hours and observer J.K. after 5 hours. Thus, observers require a mean of 3.42 cumulative hours of adaptation to develop velocity-contingent color aftereffects. This is an hour longer than the mean of 2.42 cumulative hours required by observers to develop direction-contingent color aftereffects in Experiment 5. The extra time probably reflects the extra constraint imposed upon adapting populations of neurons in the present experiment: each adapting population must include neurons which prefer one of the two adapting velocities as well as stripe motion down.

Figures 43, 44 and 45 present the loci of generalization matches that observers A.P., A.J. and J.K. make to black-and-white stripes moving down at several test velocities. Consider Figure 43. Observer A.P. reports a neutral color on stripes whose velocity is 2.45°/second. Stripes moving at 1.80°/second look green, as before, and stripes moving at 2.12°/second look slightly green. A red color appears on stripes moving at 3.10°/second, as in previous tests, while stripes moving at 2.78°/second look slightly red. Observer A.P.'s matches confirm his reports. Although the loci of aftereffect colors are close neighbors and their standard deviations overlap, it is clear that there is an orderly progression from green through red which

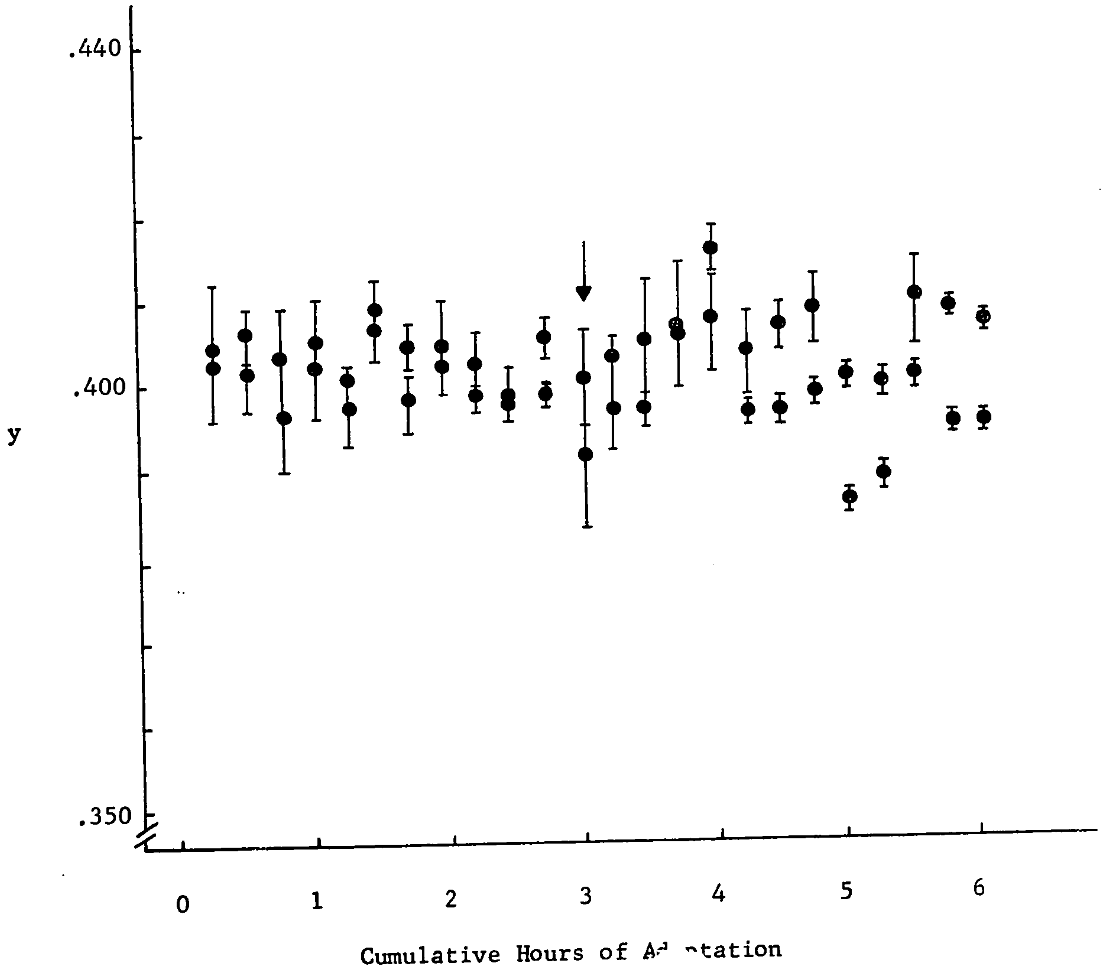

Figure 40. Experiment 6, observer A.P. The development of color aftereffects that are contingent upon the velocity at which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving down at 1.80°/second ● and stripes moving down at 3.10°/second ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer A.P. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second after 3 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

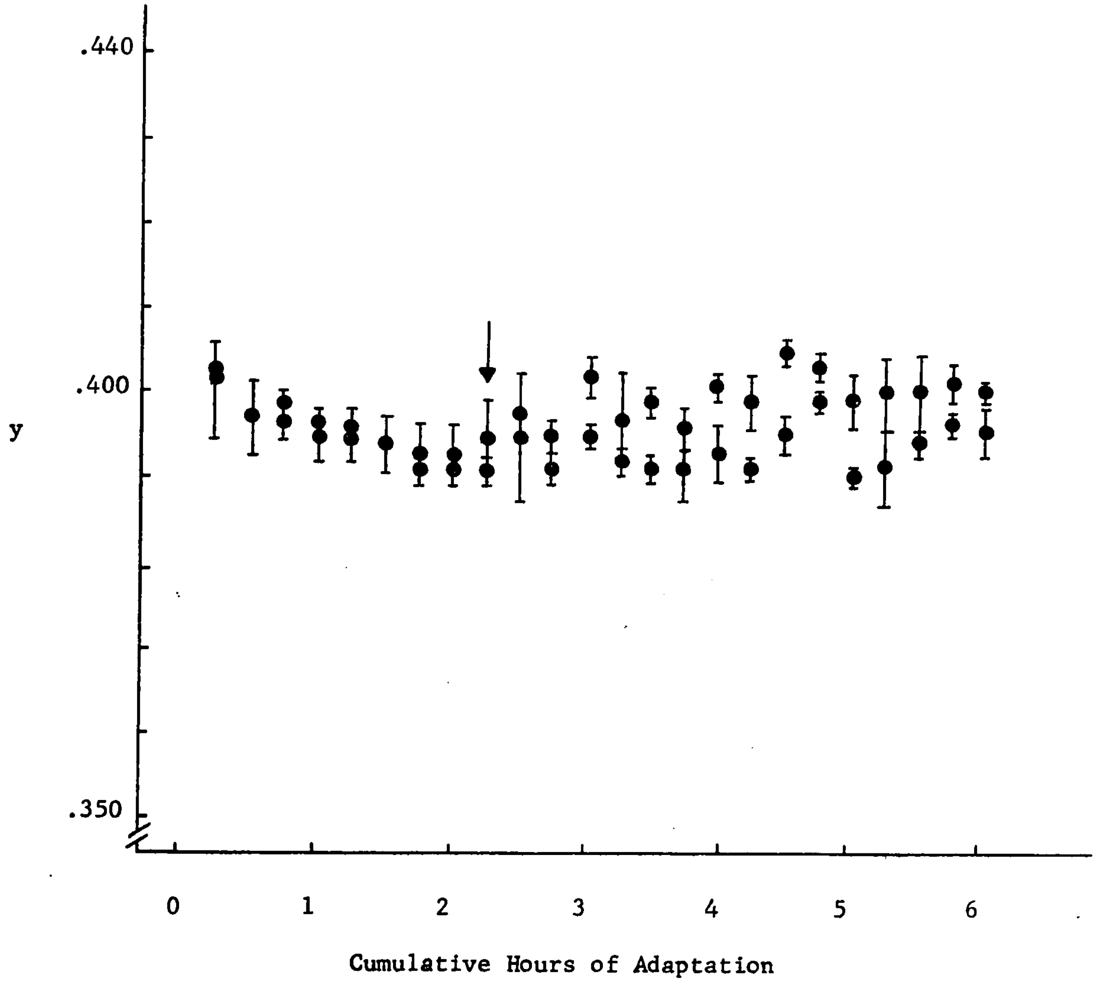

Figure 41. Experiment 6, observer A.J. The development of color aftereffects that are contingent upon the velocity at which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving down at 1.80°/second ● and stripes moving down at 3.10°/second ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer A.J. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second after 2 1/4 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

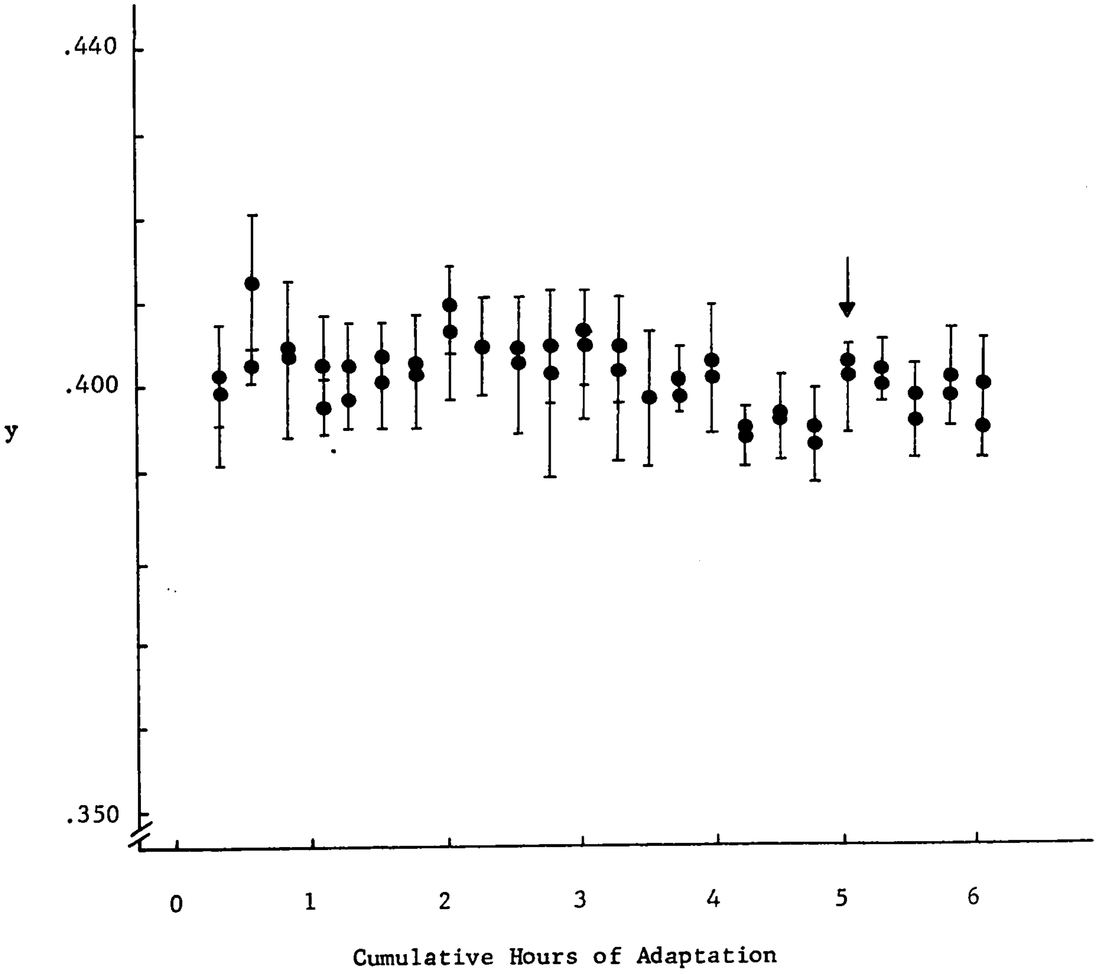

Figure 42. Experiment 6, observer J.K. The development of color aftereffects that are contingent upon the velocity at which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving down at 1.80°/second ● and stripes moving down at 3.10°/second ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer J.K. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second after 5 hours of adaptation, marked by the arrow. These colors remain visible throughout further adapting sessions. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

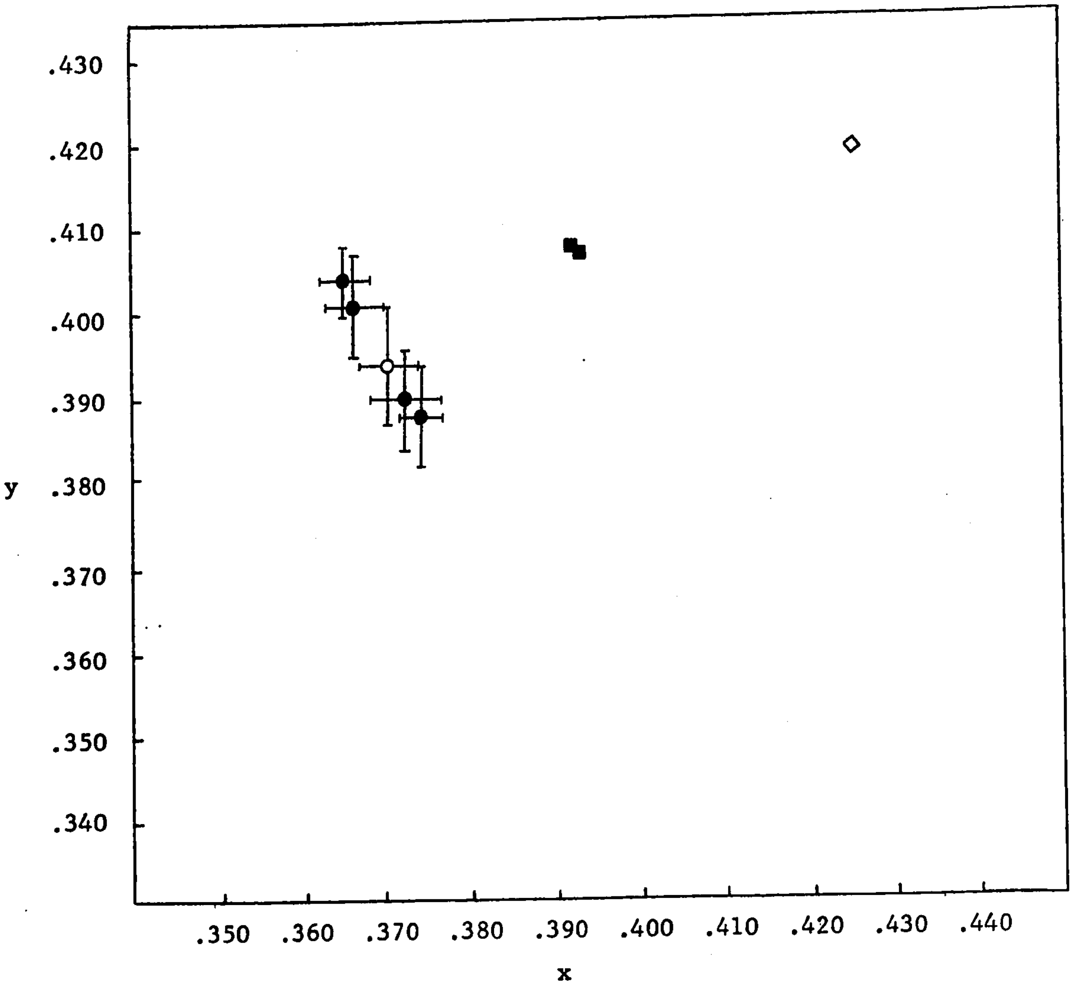

Figure 43. Experiment 6, observer A.P. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .3930, y = .4074) and horizontal white stripes moving down at 3.10°/second (x = .3926, y = .4078) and the loci of his matches for stripes whose velocities are 1.80°/second ● (x = .3654, y = .4042), 2.12°/second ● (x = .3661, y = .4013), 2.45°/second ○ (x = .3704, y = .3944), 2.78°/second ● (x = .3718, y = .4906) and 3.10°/second ● (x = .3747, y = .3883). Observer A.P. reports a neutral color on stripes whose velocity is 2.45°/second; stripes become greener as they approach 1.80°/second and redder as they approach 3.10°/second. Each point represents a mean of 15 matches. Brackets indicate standard deviations for each set of 15 matches along the x and y axes of the chromaticity diagram.

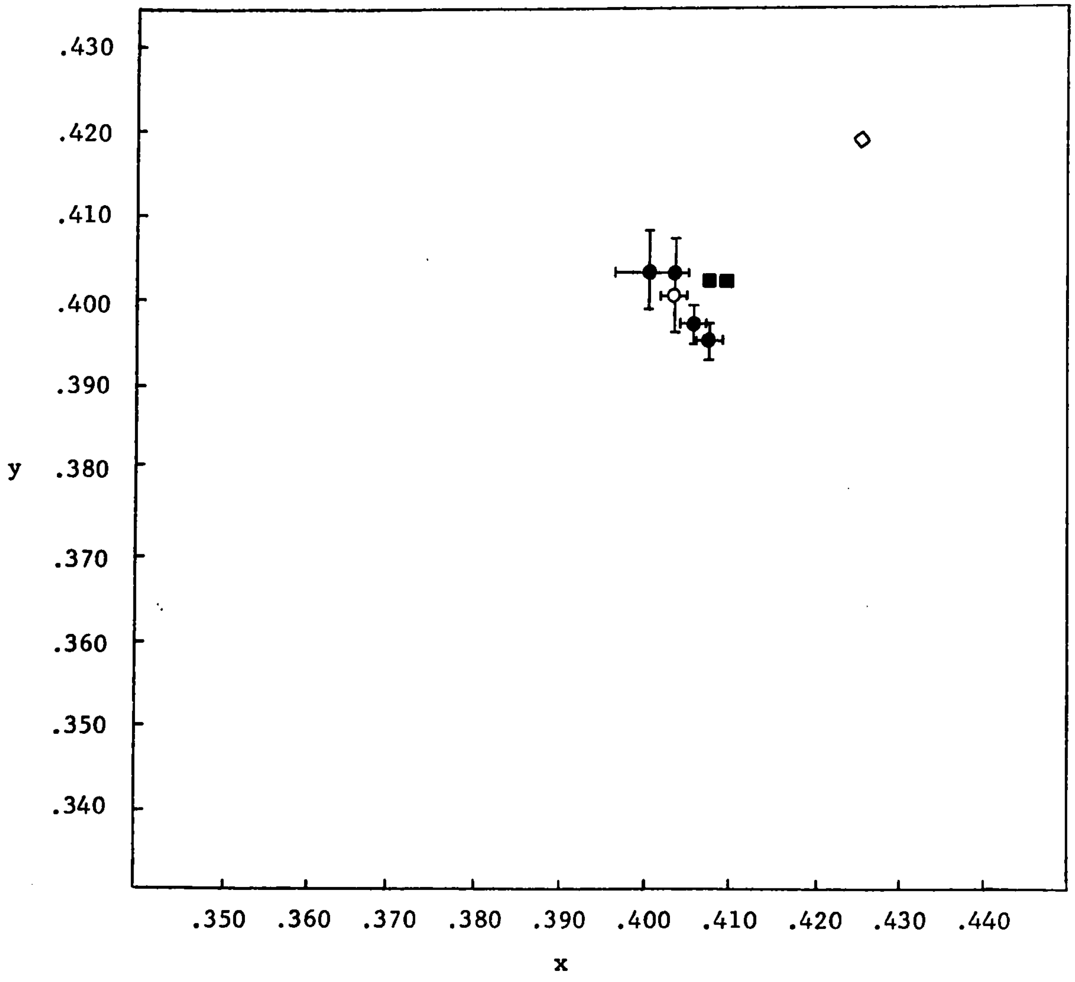

Figure 44. Experiment 6, observer A.J. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4080, y = .4022) and horizontal white stripes moving down at 3.10°/second (x = .4104, y = .4024) and the loci of his matches for stripes whose velocities are 1.80°/second ● (x = .4010, y = .4032), 2.12°/second ● (x = .4042, y = .4030), 2.45°/second ○ (x = .4044, y = .4009), 2.78°/second ● (x = .4060, y = .3973) and 3.10°/second ● (x = .4088, y = .3952). Observer A.J. reports a neutral color on stripes whose velocity is 2.45°/second; stripes become greener as they approach 1.80°/second and redder as they approach 3.10°/second. Each point represents a mean of 15 matches. Brackets indicate standard deviations for each set of 15 matches along the x and y axes of the chromaticity diagram.

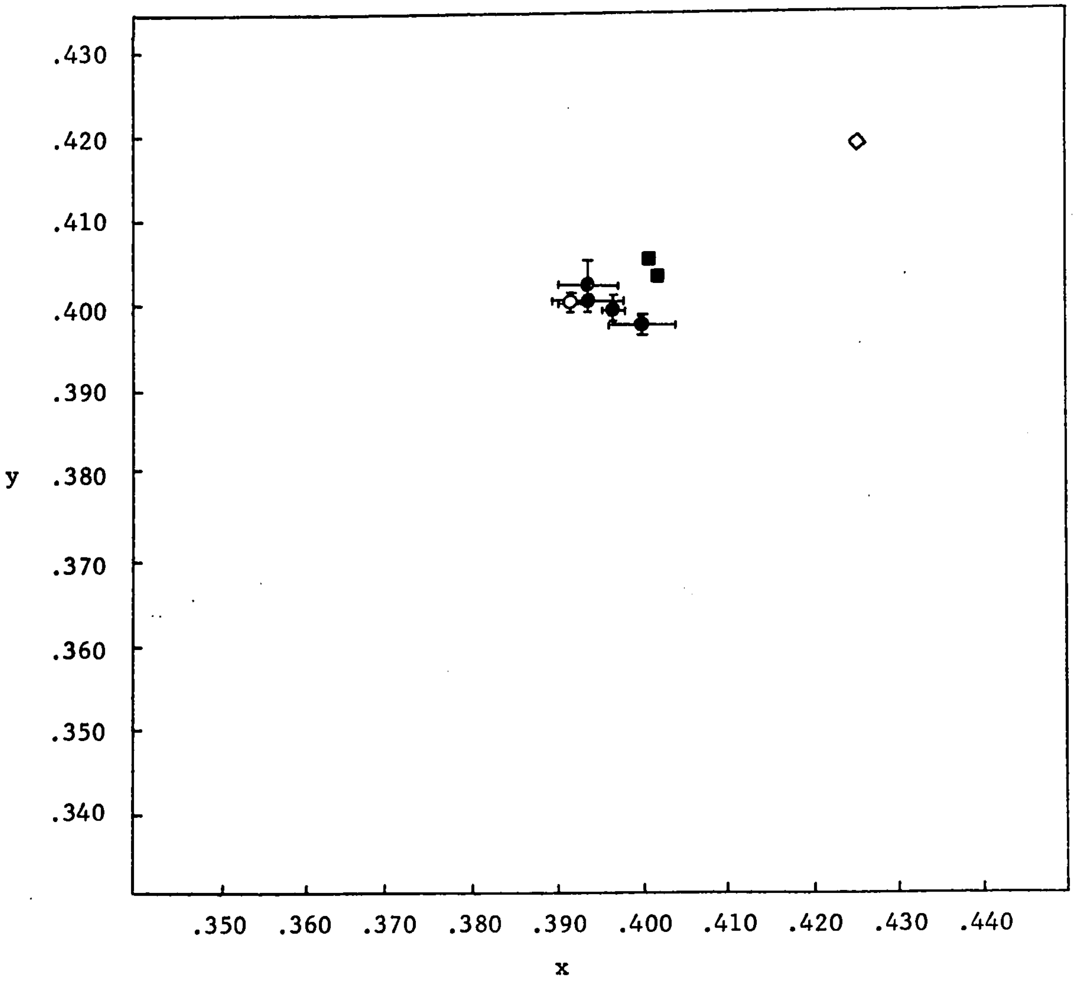

Figure 45. Experiment 6, observer J.K. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4010, y = .4052) and horizontal white stripes moving down at 3.10°/second (x = .4022, y = .4030) and the loci of his matches for stripes whose velocities are 1.80°/second ● (x = .3937, y = .4008), 2.12°/second ● (x = .3943, y = .4029), 2.45°/second ○ (x = .3925, y = .4004), 2.78°/second ● (x = .3970, y = .3993) and 3.10°/second ● (x = .3995, y = .3970). Observer J.K. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second; intermediate velocities look slightly green. Each point represents a mean of 15 matches. Brackets indicate standard deviations for each set of 15 matches along the x and y axes of the chromaticity diagram.

depends upon the velocity at which test stripes move. The loci of aftereffect colors on stripes moving at the adapting velocities (1.80°/second and 3.10°/second) clearly differ from one another and from the locus of the neutral color on stripes moving at 2.45°/second.

Because stripes moving at 2.45°/second look neutral to observer A.P., it is attractive to conclude that neurons adapting to red stripes moving at 1.80°/second and neurons adapting to green stripes moving at 3.10°/second do not tolerate velocity changes greater than about 0.65°/second. This conclusion is suspect for the following reason. We have no precise idea how many velocity-selective channels exist in human vision, or how selective any given channel may be. Suppose that the response range of neurons sensitive to stripes moving at 1.80°/second overlaps that of neurons sensitive to stripes moving at 3.10°/second. In the present experiment, one of those populations of neurons is adapting to red stripes and the second population is adapting to green stripes. In the region where their response ranges overlap, adaptation to red will cancel the effects of adaptation to green and no aftereffect colors will appear. The neutral color which observer A.P. reports on stripes moving at 2.45°/second may be the product of this cancellation, not an index of velocity-selectivity for each population of adapting cells. Although the existence of velocity-contingent color aftereffects assures us that there are neurons in the human visual system which prefer particular velocities, we cannot use color aftereffects in the present experimental design to assess their selectivity.

Generalization matches made by observer A.J., shown in Figure 44, confirm the picture presented by observer A.P.'s matches to stripes moving at various velocities. There is, on the whole, an orderly progression from green through red aftereffect colors which depends upon the velocity of moving test stripes. The loci of observer J.K.'s matches in generalization testing appear in Figure 45. While stripes moving at 1.80°/second clearly look green and those moving at 3.10°/second clearly look red, intermediate velocities all appear slightly green to observer J.K. and their loci cluster together.

Figures 46, 47 and 48 plot the loci of matches that observers A.P., A.J. and J.K. make to black-and-white stripes moving at 1.80°/second and 3.10°/second 24 to 48 hours after their final adapting sessions. Observer A.J., Figure 47, reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Comparing Figure 47 with Figure 38 shows that his aftereffect colors are as saturated after 24 hours' rest as they were immediately after an adapting session. After 48 hours' vacation from moving, colored stripes, observer A.P. reports a slight green color on stripes moving at 1.80°/second and a slight red color on stripes moving at 3.10°/second. His persisting aftereffects, Figure 46, are nearly as saturated as his immediate ones, Figure 37, but the locus of the green aftereffect color has shifted toward yellow on the CIE x,y-chromaticity diagram. The reason for this shift is obscure. Nor can we offer an adequate explanation for the reversal of aftereffect colors which observer J.K., Figure 48, experiences after a 24 hour break in the testing routine. Velocity-contingent color aftereffects persist, but with less reliability than their relatives, orientation- and direction-contingent color aftereffects.

Two observers who begin Experiment 6 leave after accumulating 6 hours of adaptation. Neither observer A.H. nor observer B.B. develops velocity-contingent color aftereffects. Figures 49-52 describe their matching pergreen through red aftereffect colors which depends upon the velocity of moving test stripes. The loci of observer J.K.'s matches in generalization testing appear in Figure 45. While stripes moving at 1.80°/second clearly look green and those moving at 3.10°/second clearly look red, intermediate velocities all appear slightly green to observer J.K. and their loci cluster together.

Figures 46, 47 and 48 plot the loci of matches that observers A.P., A.J. and J.K. make to black-and-white stripes moving at 1.80°/second and 3.10°/second 24 to 48 hours after their final adapting sessions. Observer A.J., Figure 47, reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Comparing Figure 47 with Figure 38 shows that his aftereffect colors are as saturated after 24 hours' rest as they were immediately after an adapting session. After 48 hours' vacation from moving, colored stripes, observer A.P. reports a slight green color on stripes moving at 1.80°/second and a slight red color on stripes moving at 3.10°/second. His persisting aftereffects, Figure 46, are nearly as saturated as his immediate ones, Figure 37, but the locus of the green aftereffect color has shifted toward yellow on the CIE x,y-chromaticity diagram. The reason for this shift is obscure. Nor can we offer an adequate explanation for the reversal of aftereffect colors which observer J.K., Figure 48, experiences after a 24 hour break in the testing routine. Velocity-contingent color aftereffects persist, but with less reliability than their relatives, orientation- and direction-contingent color aftereffects.

Two observers who begin Experiment 6 leave after accumulating 6 hours of adaptation. Neither observer A.H. nor observer B.B. develops velocity-contingent color aftereffects. Figures 49-52 describe their matching per-

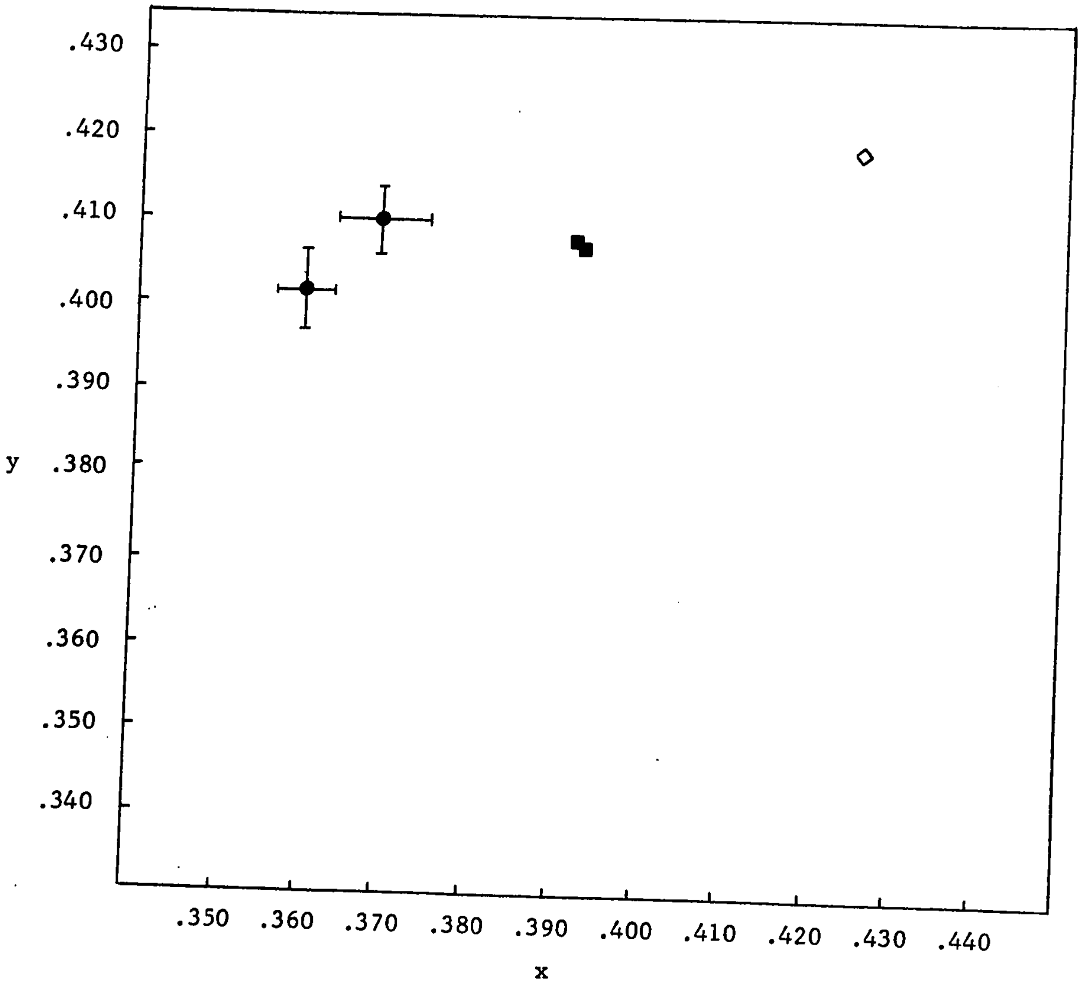

Figure 46. Experiment 6, observer A.P. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .3930, y = .4074) and horizontal white stripes moving down at 3.10°/second (x = .3926, y = .4078) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3693, y = .4108) and stripes moving down at 3.10°/second ● (x = .3609, y = .4024) 48 hours after the final adapting session. Observer A.P. reports a slight impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

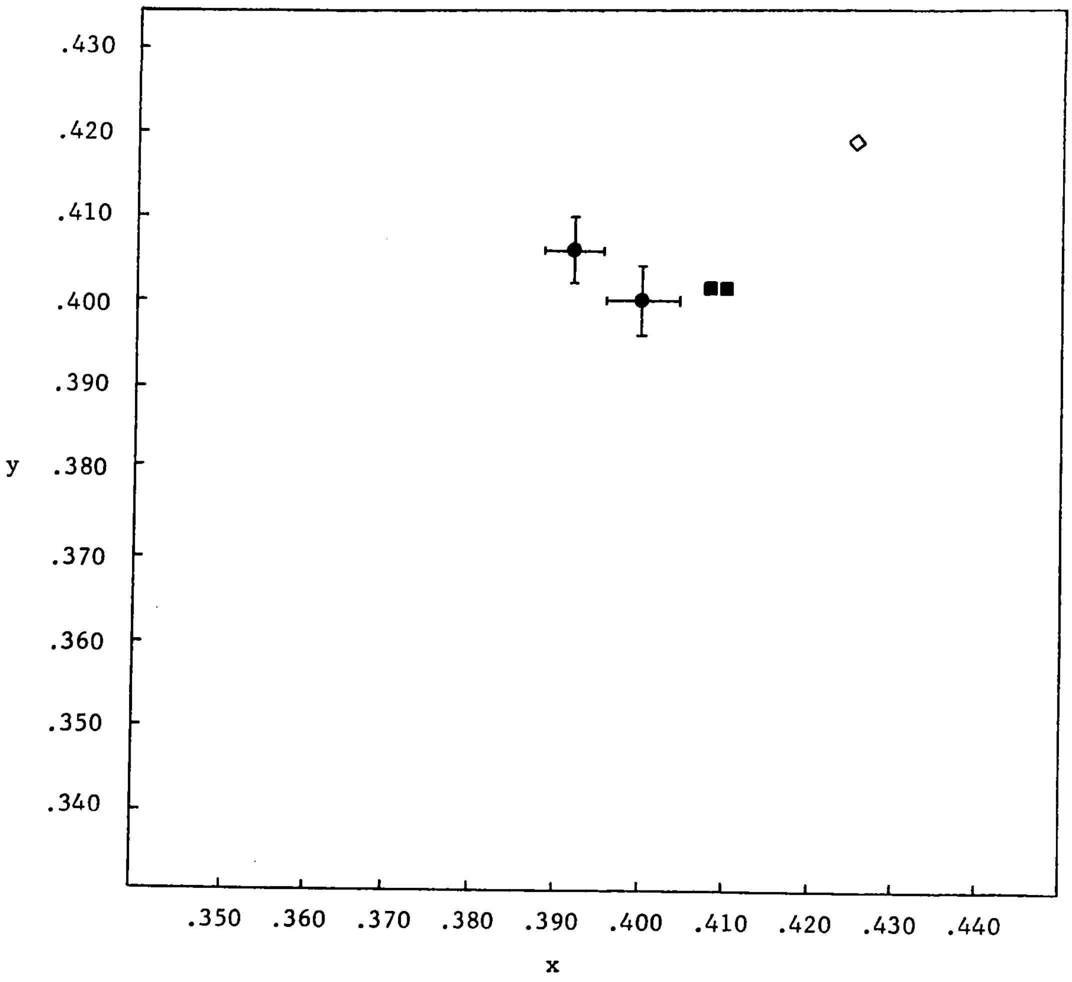

Figure 47. Experiment 6, observer A.J.. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4080, y = .4022) and horizontal white stripes moving down at 3.10°/second (x = .4102, y = .4024) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3927, y = .4058) and stripes moving down at 3.10°/second ● (x = .4008, y = .3996) 24 hours after the final adapting session. Observer A.J. reports a clear impression of green on stripes moving at 1.80°/second and red on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

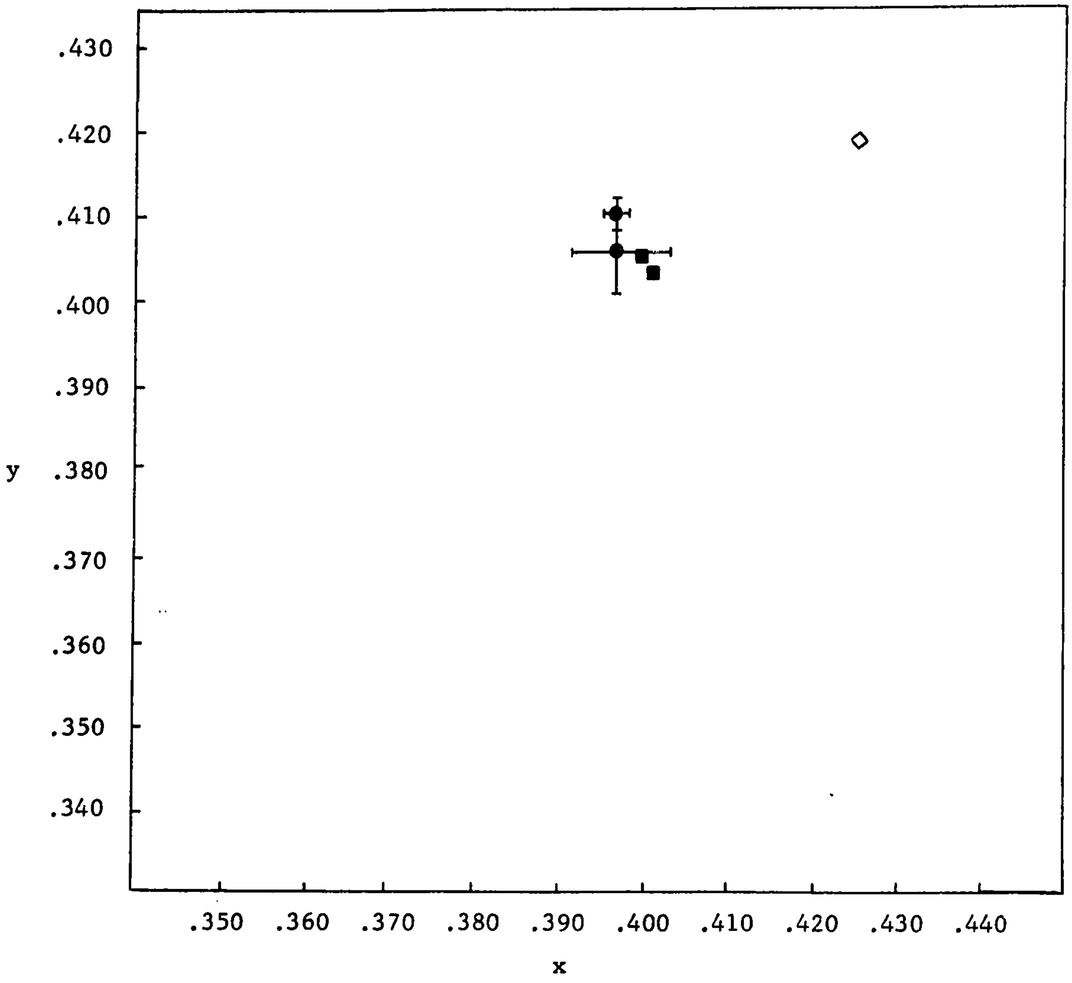

Figure 48. Experiment 6, observer J.K. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .4010, y = .4052) and horizontal white stripes moving down at 3.10°/second (x = .4022, y = .4030) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3977, y = .4064) and stripes moving down at 3.10°/second ● (x = .3980, y = .4098) 24 hours after the final adapting session. Observer J.K. reports a reversal of his previous aftereffect colors: stripes moving at 1.80°/second now appear slightly red and stripes moving at 3.10°/second now appear slightly green. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

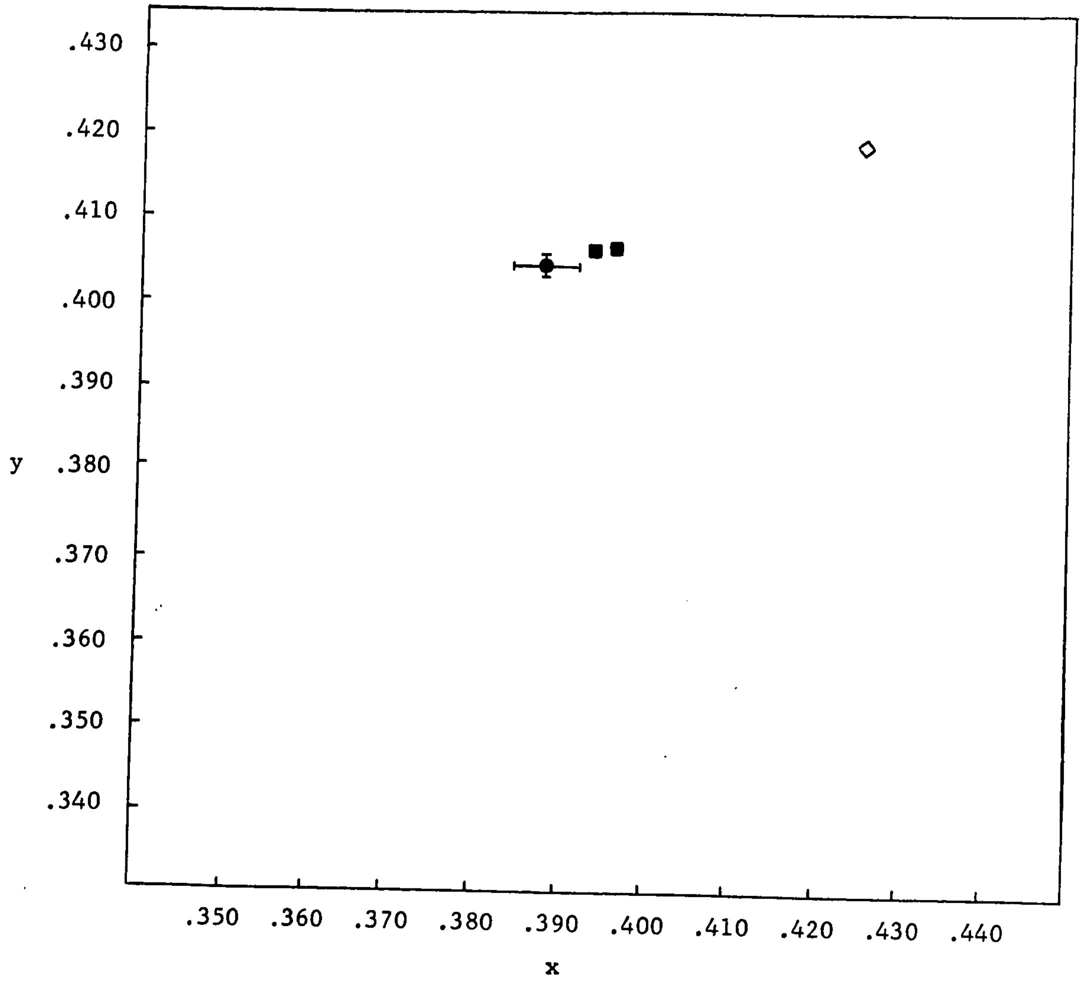

Figure 49. Experiment 6, observer A.H. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .3958, y = .4064) and horizontal white stripes moving down at 3.10°/second (x = .3938, y = .4063) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .3885, y = .4044) and stripes moving down at 3.10°/second ● (x = .3884, y = .4039) after six cumulative hours of adaptation. Observer A.H. reports a neutral color on stripes moving at 1.80°/second and on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

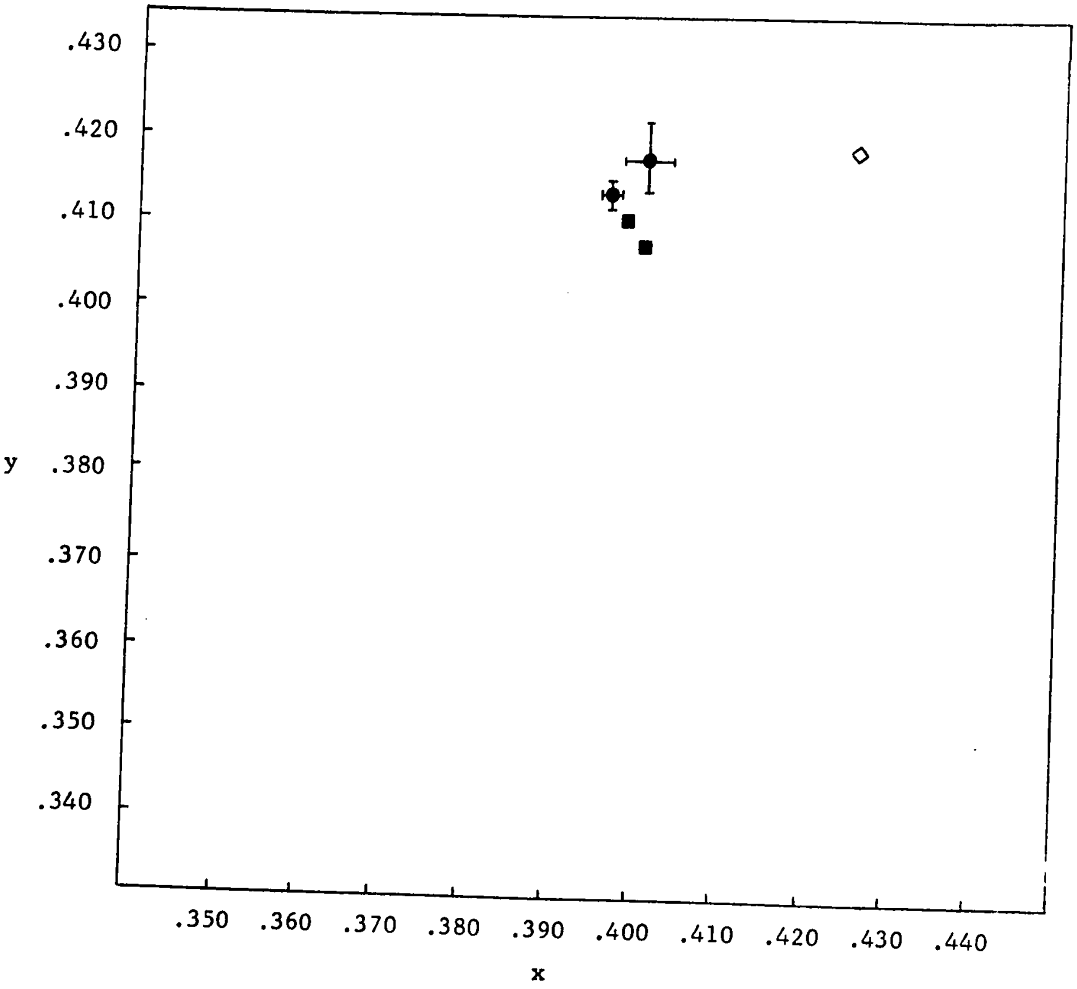

Figure 50. Experiment 6, observer B.B. The enlarged CIE x,y-chromaticity diagram shows the locus of "white" light ◇ produced by Standard Source A viewed through the glass filter (x = .4266, y = .4180), the loci of the observer's neutral points ■ for horizontal white stripes moving down at 1.80°/second (x = .3988, y = .4112) and horizontal white stripes moving down at 3.10°/second (x = .4002, y = .4086) and the loci of his matches for stripes moving down at 1.80°/second ● (x = .4007, y = .4182) and stripes moving down at 3.10°/second ● (x = .3970, y = .4147) after six cumulative hours of adaptation. Observer B.B. reports a neutral color on stripes moving at 1.80°/second and on stripes moving at 3.10°/second. Each point represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the x and y axes of the chromaticity diagram.

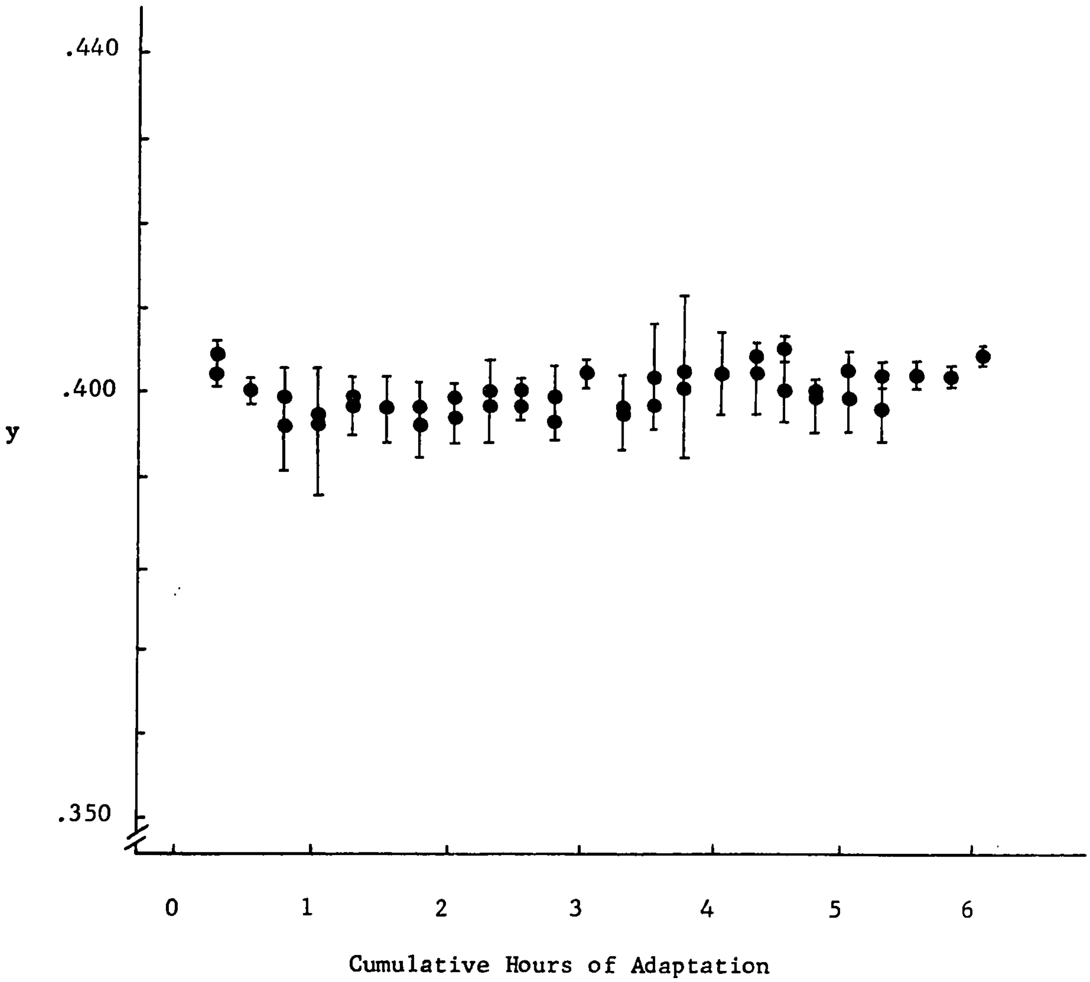

Figure 51. Experiment 6, observer A.H. The development of color aftereffects that are contingent upon the velocity at which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving down at 1.80°/second ● and stripes moving down at 3.10°/second ◐ after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer A.H. reports a neutral color on stripes moving at 1.80°/second and on stripes moving at 3.10°/second. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

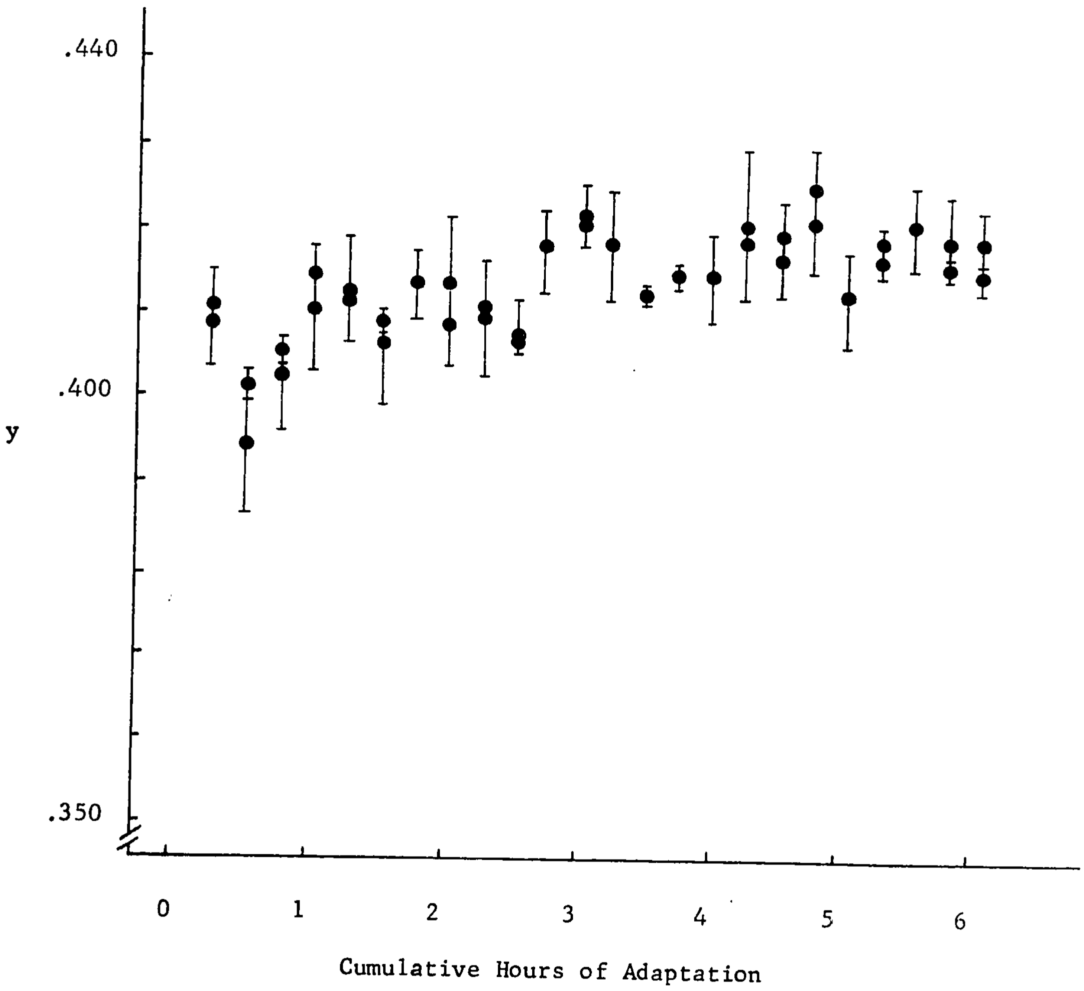

Figure 52. Experiment 6, observer B.B. The development of color aftereffects that are contingent upon the velocity at which adapting stripes move. The figure plots loci, along the y axis of the CIE x,y-chromaticity diagram, of matches that the observer makes for stripes moving down at 1.80°/second ● and stripes moving down at 3.10°/second ● after each 15 minute adapting session. The observer accumulates six hours (24 consecutive days) of adaptation. Observer B.B. reports a neutral color on stripes moving at 1.80°/second and on stripes moving at 3.10°/second. Each point on the figure represents a mean of five matches. Brackets indicate standard deviations for each set of five matches along the y axis of the chromaticity diagram.

formance throughout the adapting sessions in which they participate.

A brief summary will consolidate the results of Experiment 6. Color aftereffects that are contingent upon the velocity at which adapting stripes move develop after a mean of 3.42 cumulative hours of adaptation. Velocity-contingent aftereffect colors have the same hue and saturation as direction-contingent aftereffect colors. However, they take longer to develop--a fact which may reflect the additional constraint that velocity-contingency places upon the adapting cell populations. Velocity-contingent aftereffect colors are specific to the particular velocities presented during adaptation. Their specificity assures us that cortical neurons which undergo chromatic adaptation in the present experiment do have velocity preferences. Processes in those neurons must also store the change that occurs during chromatic adaptation since velocity-contingent color aftereffects persist for at least 24-48 hours after the observers' final adapting sessions.

Experiments in Section C have used techniques of visual colorimetry to measure the change that occurs when observers adapt to colored stripes. These measurements show that chromatic adaptation produces aftereffect colors that are roughly complementary to the colors of the adapting stripes. When observers report color aftereffects, their matches also indicate a color difference. Observers require different amounts of experience to develop different kinds of measurable color aftereffects. Orientation-contingent color aftereffects become visible after a mean of 0.50 cumulative hours of adaptation. Direction-contingent color aftereffects take a mean of 2.42 cumulative hours of adaptation to develop, while velocity-contingent color aftereffects are apparent to observers after a mean of 3.42 cumulative hours of adaptation. Colorimetric measurements show that aftereffect colors are specific to the orientation, direction and velocity of stripes in the adapting display. Aftereffect colors persist at reduced, though measurable, saturation for at least 24-96 hours after the final session in which observers view colored adapting stripes.

Discussion

The reader who reviews Experiments 1-6 finds that we must explain the following facts:

1) Aftereffect colors roughly complementary to the colors viewed by observers during adaptation appear on black-and-white test stripes.

2) An asymmetrical relation exists between color and motion. An observer who views moving, colored stripes develops motion-contingent color aftereffects. The same observer fails to see color-contingent motion aftereffects under controlled test conditions.

3) Motion-contingent color aftereffects develop with cumulative, spaced visual experience.

4) Aftereffect colors are specific to spatial features of the adapting display.

5) Aftereffect colors persist for hours after the end of the visual experience that creates them.

6) Motion-contingent color aftereffects, visible immediately after adaptation, are localized to those areas of the visual cortex that receive stimulation when the observer views moving, colored stripes.

7) Changes that create persisting motion-contingent color aftereffects, visible days later, must occur within the same cortical areas.

In the Introduction, we emphasized descriptions of phenomena, not statements of theory. This treatment is appropriate to an interdisciplinary area of research that has developed within the past 10 years. However, the descriptions of psychophysical phenomena offered in the Introduction are not atheoretical: they assume (a) that there are neurons in the human visual system which serve as feature detectors and (b) that these are the neurons which adapt to visual stimulation. It is time to consider alternative possibilities.

We have already seen that one theory, which avoids neurologizing and has proven useful in previous studies of sensory learning (Brogden, 1939, 1947), fails to explain the present data. To review the argument, suppose that color aftereffects are the product of simple association between two features of the adapting display--color and direction of stripe motion, for example. If this were true, observers viewing test stripes moving up should report the color that they originally saw on stripes moving in that direction. Instead, they report complementary aftereffect colors. A theory that relies on feature-feature associations predicts incorrect color aftereffects.

Adaptation-level theory (Helson, 1948, 1964) encounters a different problem. It predicts the correct aftereffect colors but fails to explain other facts. The theory, originally formulated to explain observer's reports of complementary afterimage colors, claims that the visual system adopts a new neutral point as a result of chromatic adaptation. Those elements that receive green stimulation shift their neutral point toward green so that colors from a wider region of the spectrum are rated red. Those elements that receive red stimulation do the obverse. But <u>which</u> elements? Why should aftereffect colors be specific to particular spatial features of the adapting display? The theory makes no specific predictions.

Another explanation for color aftereffects emphasizes retinal events and completely discounts the participation of specialized cortical neurons. This explanation says that color aftereffects are complementary color afterimages, the product of chromatic adaptation in peripheral receptors. Although peripheral chromatic adaptation must precede changes in higher visual centers, it cannot explain color aftereffects. Orientation-contingent color aftereffects do not obey Emmert's Law of afterimages (Murch, 1969) and remain visible under conditions that preclude the development of systematic afterimage patterns (Harris and Gibson, 1968a, 1968b). More importantly, it is difficult to see how complementary afterimages could explain the motion-contingent color aftereffects of Experiment 3, where two different colors appear on test stripes moving across exactly the same retinal area.

If one concedes that explanation of the present data requires neural elements with some kind of spatial organization, then one might seek that explanation in "dipole" theory. A "dipole" (Gibson and Harris, 1968; Harris and Gibson, 1968a, 1968b) links two retinal units in partnership. When light of the same intensity stimulates both units of the "dipole", the "dipole" simply maintains its spontaneous level of firing. When light of one intensity (e.g. a white stripe) stimulates one unit and light of a different intensity (e.g. a black stripe) stimulates the other unit, the balance of firing within the "dipole" is changed. This change signals the presence of a contour in the "dipole's" receptive field. If the "dipole's" feeder units are cones, then it could also respond to colored contours and undergo chromatic adaptation.

How well do "dipoles" account for available data on color aftereffects that are contingent upon the spatial features of visual displays? Let us consider orientation-contingent color aftereffects first. The partner units which feed a "dipole" may be connected by a straight line that falls along a particular axis of orientation on the retina. Suppose that axis of orientation is horizontal (90^o). Choose a red stripe, whose orientation is 45^o, flanked by a black stripe. The red stripe will illuminate one unit of the "dipole" and the black stripe will shade the other unit. It is easy to see that red-and-black stripes of many orientations--0°, 60°, 80°--will stimulate the "dipole" in exactly the same manner. In short, the "dipole" cannot make fine angular discriminations. Yet it must do so to explain the fact that one can obtain orientation-contingent color aftereffects when adapting stripes have orientations that differ by 45° (Fidell, 1970).

Simple cortical cells can make the fine angular discriminations required. We recall that a simple cortical neuron has a receptive field with an oblong center and elongated, opponent flanks. The center may be responsive to red contours and the opponent flanks responsive to green contours. Suppose that the cell's receptive field falls along a horizontal (90°) axis on the retina. Then a red stripe flanked by black stripes <u>or</u> a green stripe flanked by black stripes, falling at 90°, will stimulate the cell. As the stripe display tilts out of 90° orientation, it stimulates a smaller part of the receptive field area sensitive to the colored stripe, and the cell's firing rate declines. Cortical neurons with simple receptive fields, then, do make the fine angular discriminations required to explain Fidell's (1970) data.

One might make a "dipole" sensitive to contours moving in a particular direction by placing an inhibitory connection on one of its feeder units, in the manner of Barlow and Levick (1965). But it is difficult to see how a two-unit mechanism could detect velocity differences without extensive improvements. These improvements, in effect, convert "dipoles" into neurons with complex receptive field organization.

In Experiments 4-6 we have shown that orientation-contingent and motion-contingent color aftereffects are specific to spatial features of the displays that observers view during adaptation. It is apparent that we must rely upon the participation of cortical neurons whose receptive fields have opponent-spatial organization in order to explain this specificity. Furthermore, as we have argued in Experiment 3, these cortical neurons must also possess receptive fields that have opponent-chromatic organization. Only combined opponent-spatial and opponent-chromatic organization explains the asymmetrical relation between color and motion demonstrated in Experiment 3.

Having considered alternative explanations for their origin, we may turn to the most interesting fact about color aftereffects--their persistence beyond the adapting experience. We know from Experiment 3 that changes which sustain color aftereffects occur in the same cortical cells that receive stimulation during adaptation. Initially, cortical cells undergo chromatic adaptation which modifies their response for a short period of time. Additional experience, evidently, creates a further change which prolongs the effects of chromatic adaptation within the same cells for several days. We have suggested that habituation, or the conditioned inhibition of sensory responses, produces this lasting change. Are there data which support our suggestion?

Several studies demonstrate that lasting changes in cell response can occur as a result of repeated sensory stimulation. Starr and Livingston (1963), for example, describe a persisting reduction in the tonic response of subcortical auditory neurons after prolonged presentation of a loud sound to conscious cats. They found, in one animal, that stimulation periods of 10 minutes, 2 hours and 24 hours produced aftereffects that lasted 2 minutes, 1/2 hour and 6 hours respectively. Starr and Livingston attributed these lasting changes to long-term post-excitatory inhibition. Using a different paradigm, Morrell (1967) paired visual stimuli, which produced a stable post-simulus time histogram (PSTH) from a unit in the cat's visual cortex, with stimuli from other sensory modalities. Each of these stimuli also modified the PSTH in a clear and consistent manner. After paired stimulation, a specific change appeared in the PSTH. This change persisted for 20-60 minutes. Chow, Lindsley and Gollender (1968) employed the same paradigm while monitoring the responses of neurons in the cat's dorso-lateral geniculate nucleus. The cells which they studied showed dichoptic interaction. To understand what this means, suppose that the investigators record the response of a geniculate cell to stimulation which presents a light spot to the animal's contralateral eye. A well-formed PSTH appears. Then they record from the same cell while presenting a flash of light to the animal's ipsilateral eye. Ipsilateral stimulation evokes no response from the cell. However, when the investigators pair the contralateral light spot with the ipsilateral light flash, the form of the PSTH evoked by the light spot alone changes. Repeated pairing causes that change to last about 50 minutes.

These studies, as a group, show that it is possible to produce a lasting change in the response of single neurons sensitive to simple sensory stimulation. Given their data, our suggestion seems plausible. Persisting color aftereffects may well be the product of habituation which prolongs the adapted state of cortical cells sensitive to the display of moving, colored stripes. Our suggestion is particularly attractive because it is open to a direct test employing neurophysiological techniques. This test would monitor the activity of neurons, in the macaque monkey's visual cortex, that respond to displays of colored adapting stripes. Records that monitor cell activity during adaptation and continue to survey unit response for several additional hours should provide the information that we need. It is possible that changes in neural activity develop and then persist throughout the interval between adapting and testing sessions. Or (Masland, 1968) changes in neural activity may appear only when the original stimulus display is presented. In the interim, the cell may re-adopt its spontaneous firing rate.

Whatever its outcome, this experiment would be particularly valuable since it proposes a study of changes in cell response produced by a stimulus display identical to the stimulus display used in our psychophysical experiments. Under these circumstances, the relation between changes in cell response and alterations in visual perception should be especially clear.

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Appendix A

A Summary of the Theory of Visual Colorimetry

Visual colorimetry quantifies the color-matching properties of human eyes with normal trichromatic color vision. For the reader's convenience, this Appendix summarizes the theory of visual colorimetry. Murray (1952) and Wyszecki and Stiles (1967) offer comprehensive treatments of colorimetric theory and method.

The human eye is sensitive to wavelengths across the spectrum of radiant energy from 380 to 770 nm. Any light source which radiates energy at these wavelengths will, when viewed, produce a perception of color. This color is physically defined by its relative spectral energy distribution. The relative spectral energy distribution of a color specifies the amount of energy it radiates at each wavelength across the visible spectrum. Figure 1 shows the relative spectral energy distribution of CIE Standard Source A, a 500 watt tungsten filament lamp operating at a color temperature of 2854° K.

A broadband light source radiates energy across most of the visible spectrum. The tungsten filament lamp pictured in Figure 1 is a broadband source. A narrowband light source radiates energy across a small set of wavelengths while a monochromatic light source radiates energy at only one wavelength. The so-called spectral colors are realized by monochromatic light sources.

Placing a color filter between the light source and the eye produces a new color with its own relative spectral energy distribution. If the relative spectral energy distribution of the light source is given by $\Sigma_{\lambda}P_{\lambda}\Delta_{\lambda}$ then the relative spectral energy distribution of the filtered light is given by $\Sigma_{\lambda}P_{\lambda}T_{\lambda}\Delta_{\lambda}$ where P_{λ} is the amount of energy radiated by the source at each wavelength, T_{λ} is the percentage of that energy transmitted by the filter at each wavelength, and Δ_{λ} is the unit of increment across the spec-

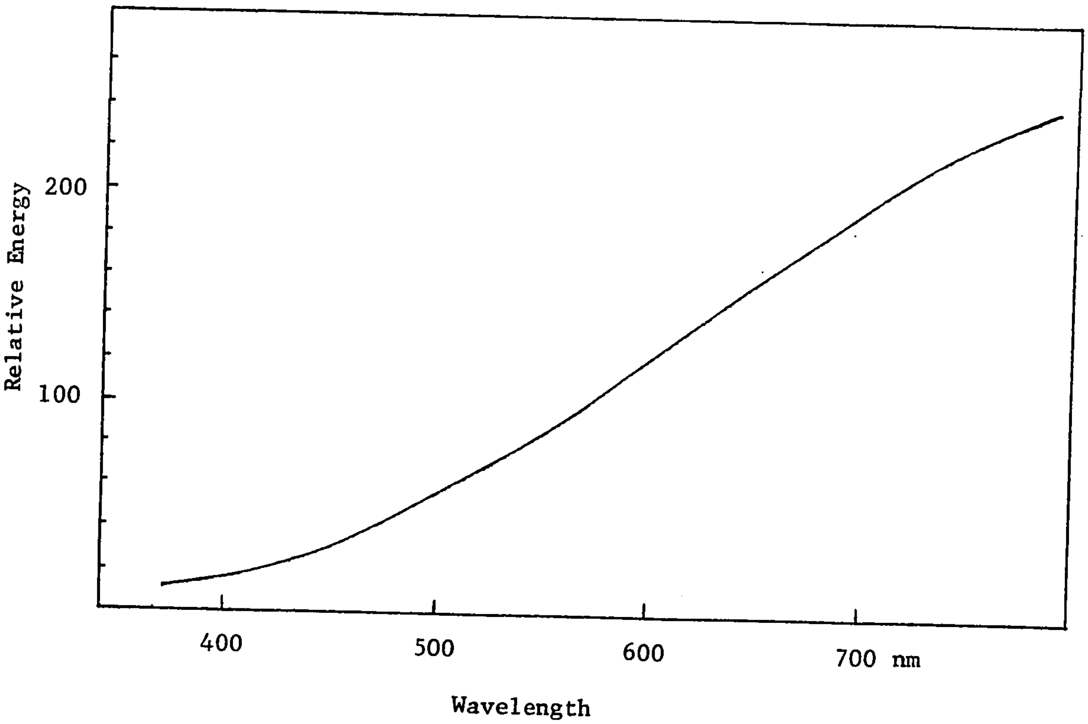

Figure 1. The relative spectral energy distribution of CIE Standard Source A. From Wyszecki and Stiles (1967, p. 33).

trum.

An observer can match any color by making an additive mixture of suitable amounts of three fixed primary colors. Grassmann formalized this trichromatic generalization as a description of color-matching in 1853. Grassmann's laws of additive color mixture state that: (1) An additive mixture of suitable amounts of three fixed primary colors will match any color. The primary colors remain independent--it is impossible to match one primary color by mixing the other two. (Sometimes the observer must add one of the primary colors to the target color in order to make a match. These cases, and the problems they create, are considered below.) (2) A match survives brightness changes that affect both colored fields equally. (3) If A matches B, and C matches D, then A + C matches B + D.

One may describe any color as an additive mixture of three primary colors. Consider the simple case where we wish to describe spectral color Q. The observer has monochromatic red, green and blue primary colors at his disposal and his task is to combine these primaries in amounts that will match the spectral color Q. The equation

$$Q = R \text{ red} + G \text{ green} + B \text{ blue} \qquad (a)$$

represents the match he makes. This equation states that a mixture using amount R of the red primary, plus amount G of the green primary, plus amount B of the blue primary matches the spectral color Q. The amount of each primary color used is that primary's <u>tristimulus value</u>.

Figure 2 shows a geometrical representation of additive color mixture. It is convenient to consider each primary color as a vector in 3-dimensional color space. A vector is a line with direction and length. Direction indicates the hue of each primary color. Length indicates the amount of each

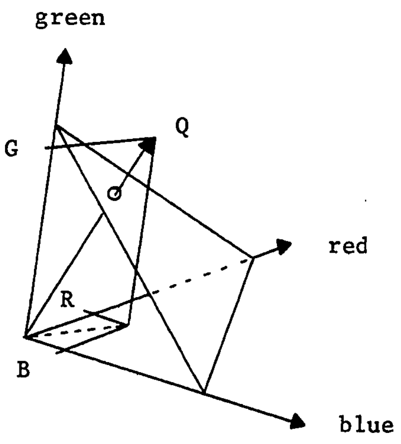

Figure 2. A geometrical representation of additive color mixture in 3-dimensional color space. Vectors green, red and blue represent monochromatic primary colors. G, R and B indicate the amount, or tristimulus value, of each primary color mixed to match the spectral color Q. Adapted from Wyszecki and Stiles (1967, p. 232).

primary color the observer uses to make his match. If three vectors represent the three primary colors, then their sum represents the mixed color that matches the spectral color Q.

We have just seen that an additive mixture of three monochromatic primary colors matches the spectral color Q. Guild (1931) and Wright (1928-29) asked observers to match each of the spectral colors using monochromatic red, green and blue primary colors of equal energy. They determined the amounts of each primary color the observers used to match each spectral color. These amounts, or tristimulus values, describe the color-matching properties of human eyes with normal trichromatic color vision. They are the color-matching functions, $\bar{r}_\lambda$, $\bar{g}_\lambda$ and $\bar{b}_\lambda$.

It is, of course, possible to describe the color of a broadband light source as an additive mixture of three primary colors. A broadband source radiates energy at many wavelengths. We already know that the human eye can match any one of those wavelengths (spectral colors) by mixing specified amounts of monochromatic red, green and blue primary colors. To obtain the tristimulus values R, G and B for a broadband source, we begin by listing the color-matching functions $\bar{r}$, $\bar{g}$ and $\bar{b}$ for each wavelength at which the source radiates energy. Then we weight these color-matching functions by the amount of energy P the light source radiates at each wavelength. Finally, we sum all the weighted color-matching functions $\bar{r}$, all the weighted color-matching functions $\bar{g}$, and all the weighted color-matching functions $\bar{b}$. The equations

$$R = \sum P_\lambda \bar{r}_\lambda \Delta_\lambda \qquad (b)$$

$$G = \sum P_\lambda \bar{g}_\lambda \Delta_\lambda \qquad (c)$$

$$B = \sum P_\lambda \bar{b}_\lambda \Delta_\lambda \qquad (d)$$

summarize these calculations which yield the tristimulus values R, G and B for a broadband light source.

Colors which share the same tristimulus values have the same vector in 3-dimensional color space: they match one another. Two broadband colors may have identical tristimulus values in the trivial case where their relative spectral energy distributions are also identical. Such colors are isomeric. On the other hand, two broadband colors may have identical tristimulus values but different relative spectral energy distributions. Such matching colors are metameric. Visual colorimetry makes quantitative descriptions of metameric color matches.

In 1931 the CIE (Commission Internationale de l'Eclairage) adopted the color-matching functions of Guild and Wright for international use. These functions, describing the average color-matching properties of observers with normal trichromatic vision, define the 1931 CIE Standard Observer.

The reader may inspect the color-matching functions in Figure 3. In the region of the spectrum from 435.8 to 546.1 nm, values of $\bar{r}_\lambda$ are negative. To match spectral colors in this region, the observer must "subtract" red from his three-primary mixture by adding red to the target color. This fact does not invalidate the trichromatic generalization but it does make computation inconvenient. To eliminate inconvenience, the CIE standardized a second set of color-matching functions in 1931. These new functions define the Standard Observer usually employed in colorimetric work.

To obtain color-matching functions which are always positive, the CIE constructed a set of three imaginary primary colors. The spectral primary colors which observers actually mix in experiments are produced by monochromatic light sources. They are, by definition, the most saturated colors that

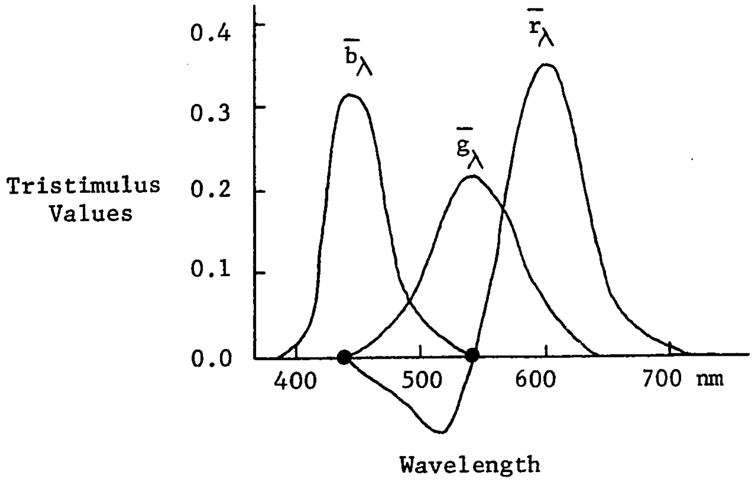

Figure 3. The color-matching functions of the 1931 CIE Standard Observer employing monochromatic red, green and blue primary colors. Note that the values of r_λ are negative in the region of the spectrum from 435.8 to 546.1 nm. From Wyszecki and Stiles (1967, p. 233).

we can make. The new CIE primary colors x, y and z are "supersaturated" colors which have no physical source. They are imaginary mathematical conveniences. In 3-dimensional color space, the vectors of these imaginary, supersaturated, primary colors extend beyond those of the spectral primaries. This means that one can make any color-match in the new system by mixing positive amounts of each primary color. One may calculate the amounts of each new primary color required to match every color across the visible spectrum. These amounts, or tristimulus values, are the new color-matching functions $\bar{x}_\lambda$, $\bar{y}_\lambda$ and $\bar{z}_\lambda$ shown in Figure 4.

The new color-matching functions $\bar{x}_\lambda$, $\bar{y}_\lambda$ and $\bar{z}_\lambda$ incorporate a second convenient feature. In 1924 the CIE adopted a standard photopic relative luminous efficiency function V_λ . This function gives the ratio of the radiant flux at $\lambda = 555$ nm to the radiant flux at comparison wavelength λ, when the two lights look equally bright under standard viewing conditions. The normalized function has a maximum value of unity. At Judd's suggestion, the CIE set the color-matching function $\bar{y}_\lambda$ equal to this standard photopic relative luminous efficiency function V_λ. This means that in 3-dimensional color space the vector Y representing primary color y carries all the brightness information and the primary colors x and z lie on a straight line of zero luminance. This straight line of zero luminance is the dotted line in Figure 5. The tristimulus value Y of a particular color is given by

$$Y = \Sigma_\lambda P_\lambda \bar{y}_\lambda \Delta_\lambda \tag{e}$$

Since

$$\Sigma_\lambda \bar{y}_\lambda \Delta_\lambda = 100.00 \tag{f}$$

the tristimulus value Y indicates the percent luminous emittance or transmittance of the color.

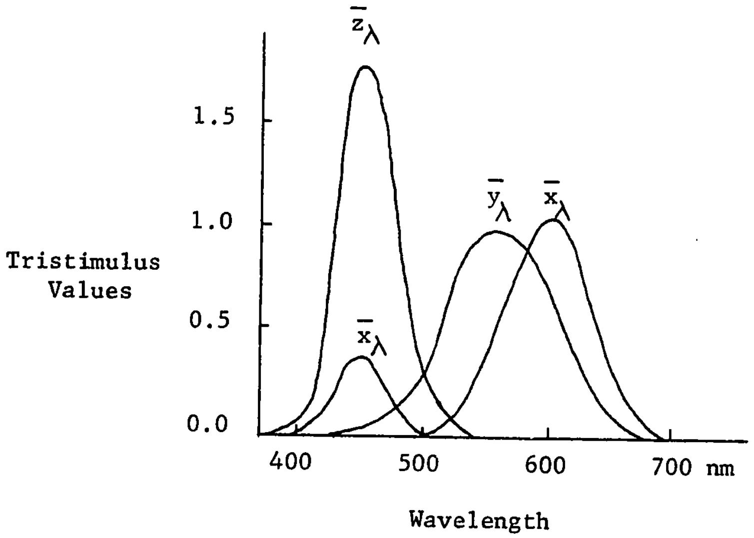

Figure 4. The color-matching functions of the 1931 CIE Standard Observer employing imaginary primary colors x, y and z. Note that all values of the color-matching functions are positive. From Wyszecki and Stiles (1967, p. 270).

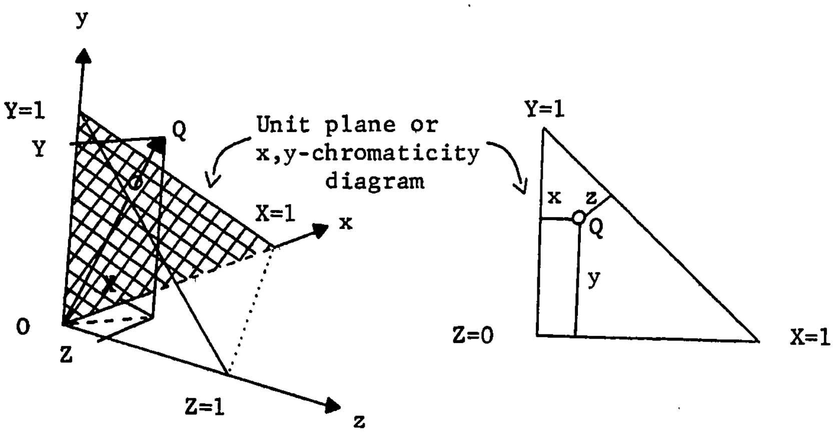

Figure 5. A geometrical representation of additive color mixture in 3-dimensional color space. Vectors y, x and z represent imaginary primary colors. Y, X and Z indicate the amount, or tristimulus value, of each primary color mixed to match the target color Q. The vectors x and y lie on a straight dotted line of zero luminance. Vector y specifies the luminance of the mixed color. For a given color, X + Y + Z = 1.0 in the unit plane or x,y-chromaticity diagram. The chromaticity coordinates x and y uniquely specify the locus of color Q on the x,y-chromaticity diagram. Adapted from Wyszecki and Stiles (1967, p. 232).

We have seen that a vector in 3-dimensional color space can represent a color. A convenient description of that color collapses the 3-dimensional color space into a 2-dimensional diagram, the CIE x,y-chromaticity diagram. Consider the cross-hatched plane in the 3-dimensional color space shown in Figure 5. In this plane

$$X + Y + Z = 1.00 \tag{g}$$

where X, Y and Z are the amounts, or tristimulus values, of each primary color x, y and z mixed to match the target color. This "unit" plane becomes the x,y-chromaticity diagram. To plot a mixed color as a point on the unit plane, one must compute its <u>chromaticity coordinates</u>. The ratio of each tristimulus value to the sum of all tristimulus values for the color gives its chromaticity coordinates

$$x = \frac{X}{X + Y + Z}\,, \quad y = \frac{Y}{X + Y + Z} \quad \text{and } z = \frac{Z}{X + Y + Z} \tag{h}$$

The coordinates x and y uniquely specify the locus of the color on the CIE x,y-chromaticity diagram in Figure 5.

The CIE x,y-chromaticity diagram is enlarged in Figure 6. Points specifying the locus of each spectral color form a U-shaped curve extending from monochromatic blue, through green, to red. Nonspectral purple colors form a line which joins the two ends of the curve. Note that the axes representing supersaturated primary colors x and y completely enclose the spectral colors.

The CIE has specified three Standard neutral light sources for use in colorimetric work. Source A is realized by a tungsten filament lamp operating at color temperature 2854° K. The reader will recall that Figure 1 pictures the relative spectral energy distribution of Source A. Sources B and C require special filters for their realization. Source B corresponds to direct sunlight, correlated color temperature 4870° K. Source C simulates

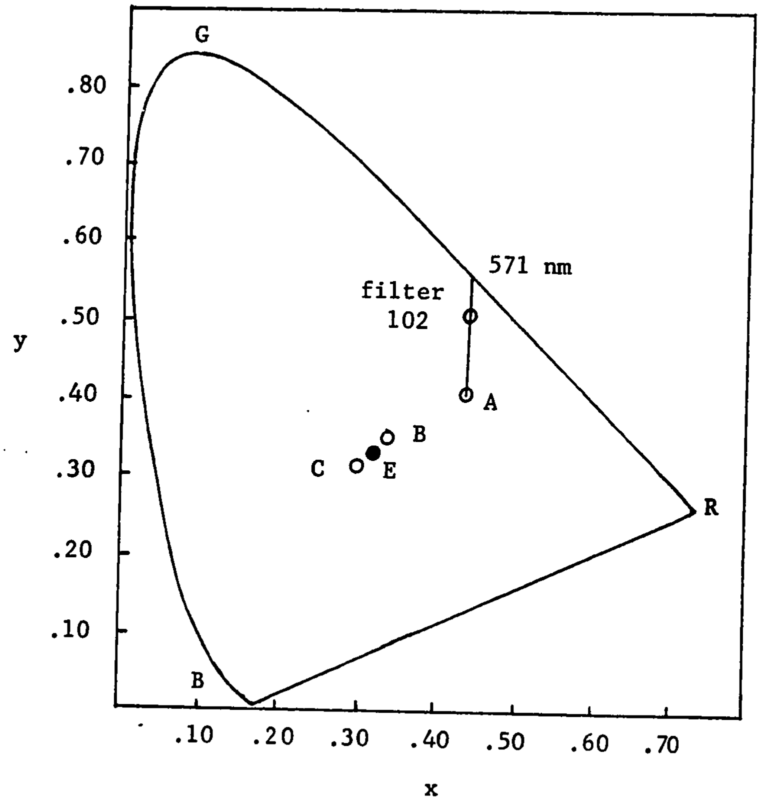

Figure 6. The 1931 CIE x,y-chromaticity diagram shows the spectrum locus, purple line, and loci of Standard Source A (x = .4476, y = .4074), Standard Source B (x = .3484, y = .3516), Standard Source C (x = .3101, y = .3162) and the equal energy Source E (x = 1/3, y = 1/3). The locus of Kodak Wratten filter 102 (yellow) viewed in Source A is x = .4534, y = .5132. Its dominant wavelength (hue) is 571 nm and its excitation purity (saturation) is 77.5. Adapted from Wyszecki and Stiles (1967, p. 270).

overcast sky, correlated color temperature 6770° K. These Standard Sources are plotted as points on the CIE x,y-chromaticity diagram in Figure 6. It is apparent that its lower color temperature displaces Source A toward yellow while the higher color temperatures of Sources B and C make them neighbors of the neutral equal-energy Source E.

Three attributes distinguish an observer's perception of color: brightness, hue and saturation. We have already seen that the color-matching function $\bar{y}_{\lambda}$ carries brightness information. The <u>dominant wavelength</u> of a color specifies its hue. Present a spectral color in a specific neutral light. If it matches the target color, its wavelength is the dominant wavelength of that target color. One can draw a straight line from the locus of the Standard Source used to view the color, through the locus of the color itself, to the point on the spectrum locus which corresponds to its dominant wavelength. Such a straight line appears on the CIE x,y-chromaticity diagram in Figure 6. It originates at the locus of Source A, passes through the locus of Kodak Wratten filter 102 (yellow), and intersects the spectrum locus at 571 nm, the dominant wavelength of the filtered color. An observer's subjective impressions of saturation correlate with the <u>excitation purity</u> of a color. Consider the distance between the loci of the Standard Source and the color. Let this be distance A. Then consider the distance between the locus of the Standard Source and the point on the spectrum locus which specifies the color's dominant wavelength. Let this be distance B. Then the ratio of distance A to distance B gives the excitation purity of the color. The excitation purity of the yellow color produced by Kodak Wratten filter 102 viewed in Source A is 77.5.

The 1931 CIE Standard Observer was developed under restricted experimental conditions. It is a valid description of the color-matching properties of normal human eyes only when observers view colors under conditions like those of the original matching experiments. These experiments employed fields of 2-4° angular subtense which restricted the matching task to foveal cones.

Appendix B

Relative Spectral Energy Distributions, Tristimulus Values and Chromaticity Coordinates for Filters Used in Experiments 4, 5 and 6

Table 1

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$		X	Y	Z
380	0.001		0.006	.842			.005
90	0.005		0.023	.827	.004		.019
400	0.019	0.001	0.093	.798	.015		.074
10	0.071	0.002	0.340	.770	.054	.002	.262
20	0.262	0.008	1.256	.765	.200	.006	.960
30	0.649	0.027	3.167	.762	.494	.020	2.413
40	0.926	0.061	4.647	.768	.711	.046	3.568
50	1.031	0.117	5.435	.760	.784	.088	4.130
60	1.019	0.210	5.851	.760	.774	.160	4.446
70	0.776	0.362	5.116	.762	.591	.276	3.898
80	0.428	0.622	3.636	.784	.336	.488	2.850
90	0.160	1.039	2.324	.794	.127	.824	1.845
500	0.027	1.792	1.509	.784	.021	1.404	1.183
10	0.057	3.080	0.969	.784	.044	2.414	.760
20	0.425	4.771	0.525	.784	.333	3.740	.412
30	1.214	6.322	0.309	.783	.950	4.950	.242
40	2.313	7.600	0.162	.785	1.816	5.966	.127
50	3.732	8.568	0.075	.794	2.963	6.802	.060
60	5.510	9.222	0.036	.782	4.308	7.212	.028
70	7.571	9.457	0.021	.780	5.905	7.376	.016
80	9.719	9.228	0.018	.777	7.552	7.170	.014
90	11.579	8.540	0.012	.752	8.707	6.422	.009
600	12.704	7.547	0.010	.710	9.020	5.358	.007
10	12.669	6.356	0.004	.678	8.590	4.309	.002
20	11.373	5.071	0.003	.643	7.312	3.260	.002
30	8.980	3.704		.598	5.370	2.214	
40	6.558	2.562		.555	3.640	1.422	
50	4.336	1.637		.499	2.164	.816	
60	2.628	0.972		.465	1.222	.452	
70	1.448	0.530		.412	.596	.218	
80	0.804	0.292		.367	.295	.107	
90	0.404	0.146		.311	.126	.045	
700	0.209	0.075		.263	.054	.020	
10	0.110	0.040		.223	.024	.008	
20	0.057	0.019		.187	.010	.004	
30	0.028	0.010		.153	.004	.002	
40	0.014	0.006		.122	.002		
50	0.006	0.002		.100			
60	0.004	0.002		.079			
70	0.002			.061			
	109.828	100.000	35.547		75.118	73.601	27.332

Chromaticity coordinates:

$$\frac{75.118}{176.051} = x \ .4266 \qquad \frac{73.601}{176.051} = y \ .4180$$

Table 2

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 92	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006					
90	0.005		0.023					
400	0.019	0.001	0.093					
10	0.071	0.002	0.340					
20	0.262	0.008	1.256					
30	0.649	0.027	3.167					
40	0.926	0.061	4.647					
50	1.031	0.117	5.435					
60	1.019	0.210	5.851					
70	0.776	0.362	5.116					
80	0.428	0.622	3.636					
90	0.160	1.039	2.324					
500	0.027	1.792	1.509					
10	0.057	3.080	0.969					
20	0.425	4.771	0.525					
30	1.214	6.322	0.309					
40	2.313	7.600	0.162					
50	3.732	8.568	0.075					
60	5.510	9.222	0.036					
70	7.571	9.457	0.021					
80	9.719	9.228	0.018					
90	11.579	8.540	0.012					
600	12.704	7.547	0.010					
10	12.669	6.356	0.004					
20	11.373	5.071	0.003	.643	.006	.068	.030	
30	8.980	3.704		.598	.126	1.131	.466	
40	6.558	2.562		.555	.319	2.092	.817	
50	4.336	1.637		.499	.388	1.682	.635	
60	2.628	0.972		.465	.392	1.030	.381	
70	1.448	0.530		.412	.360	.521	.190	
80	0.804	0.292		.367	.324	.260	.094	
90	0.404	0.146		.311	.274	.110	.040	
700	0.209	0.075		.263	.234	.048	.018	
10	0.110	0.040		.223	.201	.022	.008	
20	0.057	0.019		.187	.168	.010	.003	
30	0.028	0.010		.153	.138	.004	.001	
40	0.014	0.006		.122	.111	.002		
50	0.006	0.002		.100	.092			
60	0.004	0.002		.079	.072			
70	0.002			.061	.056			
	109.828	100.000	35.547			6.980	2.683	0.000

Chromaticity coordinates: $\frac{6.980}{9.663}$ = x .7223 $\frac{2.683}{9.663}$ = y .2776

Table 3

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 74	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006					
90	0.005		0.023					
400	0.019	0.001	0.093					
10	0.071	0.002	0.340					
20	0.262	0.008	1.256					
30	0.649	0.027	3.167					
40	0.926	0.061	4.647					
50	1.031	0.117	5.435					
60	1.019	0.210	5.851					
70	0.776	0.362	5.116					
80	0.428	0.622	3.636					
90	0.160	1.039	2.324					
500	0.027	1.792	1.509					
10	0.057	3.080	0.969	.784	.012		.036	.012
20	0.425	4.771	0.525	.784	.094	.040	.448	.049
30	1.214	6.322	0.309	.783	.134	.162	.847	.041
40	2.313	7.600	0.162	.785	.109	.252	.828	.018
50	3.732	8.568	0.075	.794	.066	.246	.565	.004
60	5.510	9.222	0.036	.782	.026	.143	.240	.001
70	7.571	9.457	0.021	.780	.008	.060	.076	
80	9.719	9.228	0.018					
90	11.579	8.540	0.012					
600	12.704	7.547	0.010					
10	12.669	6.356	0.004					
20	11.373	5.071	0.003					
30	8.980	3.704						
40	6.558	2.562						
50	4.336	1.637						
60	2.628	0.972						
70	1.448	0.530						
80	0.804	0.292						
90	0.404	0.146						
700	0.209	0.075						
10	0.110	0.040						
20	0.057	0.019						
30	0.028	0.010						
40	0.014	0.006						
50	0.006	0.002		.100	.003			
60	0.004	0.002		.079	.009			
70	0.002			.061	.014			
	109.828	100.000	35.547			0.903	3.040	0.125

Chromaticity coordinates: $\frac{0.903}{4.068}$ = x .2220 $\frac{3.040}{4.068}$ = y .7472

Table 4

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 75	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006					
90	0.005		0.023					
400	0.019	0.001	0.093					
10	0.071	0.002	0.340					
20	0.262	0.008	1.256					
30	0.649	0.027	3.167					
40	0.926	0.061	4.647					
50	1.031	0.117	5.435					
60	1.019	0.210	5.851	.782	.008	.008	.002	.046
70	0.776	0.362	5.116	.780	.072	.056	.026	.368
80	0.428	0.622	3.636	.777	.134	.057	.083	.487
90	0.160	1.039	2.324	.752	.136	.022	.141	.316
500	0.027	1.792	1.509	.710	.102	.002	.182	.154
10	0.057	3.080	0.969	.678	.062	.004	.190	.060
20	0.425	4.771	0.525	.643	.026	.011	.124	.014
30	1.214	6.322	0.309	.598	.008	.010	.050	.002
40	2.313	7.600	0.162					
50	3.732	8.568	0.075					
60	5.510	9.222	0.036					
70	7.571	9.457	0.021					
80	9.719	9.228	0.018					
90	11.579	8.540	0.012					
600	12.704	7.547	0.010					
10	12.669	6.356	0.004					
20	11.373	5.071	0.003					
30	8.980	3.704						
40	6.558	2.562						
50	4.336	1.637						
60	2.628	0.972						
70	1.448	0.530						
80	0.804	0.292						
90	0.404	0.146						
700	0.209	0.075						
10	0.110	0.040						
20	0.057	0.019		.187	.001			
30	0.028	0.010		.153	.002			
40	0.014	0.006		.122	.005			
50	0.006	0.002		.100	.014			
60	0.004	0.002		.079	.022			
70	0.002			.061	.027			
	109.828	100.000	35.547			0.170	0.798	1.447

Chromaticity coordinates: $\frac{0.170}{2.415}$ = x .0704 $\frac{0.798}{2.415}$ = y .3304

Table 5

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 47	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006	.842	.006			
90	0.005		0.023	.827	.017			
400	0.019	0.001	0.093	.798	.048	.001		.004
10	0.071	0.002	0.340	.770	.116	.008		.039
20	0.262	0.008	1.256	.765	.244	.064	.002	.306
30	0.649	0.027	3.167	.762	.326	.212	.008	1.032
40	0.926	0.061	4.647	.768	.349	.323	.021	1.622
50	1.031	0.117	5.435	.760	.335	.345	.039	1.820
60	1.019	0.210	5.851	.760	.300	.306	.063	1.755
70	0.776	0.362	5.116	.762	.242	.188	.088	1.238
80	0.428	0.622	3.636	.784	.185	.079	.115	.672
90	0.160	1.039	2.324	.794	.119	.019	.124	.276
500	0.027	1.792	1.509	.784	.064	.002	.114	.096
10	0.057	3.080	0.969	.784	.027	.002	.083	.026
20	0.425	4.771	0.525	.784	.008	.003	.038	.004
30	1.214	6.322	0.309					
40	2.313	7.600	0.162					
50	3.732	8.568	0.075					
60	5.510	9.222	0.036					
70	7.571	9.457	0.021					
80	9.719	9.228	0.018					
90	11.579	8.540	0.012					
600	12.704	7.547	0.010					
10	12.669	6.356	0.004					
20	11.373	5.071	0.003					
30	8.980	3.704						
40	6.558	2.562						
50	4.336	1.637						
60	2.628	0.972						
70	1.448	0.530						
80	0.804	0.292						
90	0.404	0.146						
700	0.209	0.075						
10	0.110	0.040		.223	.001			
20	0.057	0.019		.187	.002			
30	0.028	0.010		.153	.004			
40	0.014	0.006		.122	.008			
50	0.006	0.002		.100	.016			
60	0.004	0.002		.079	.024			
70	0.002			.061	.027			
	109.828	100.000	35.547			1.522	0.695	8.890

Chromaticity coordinates: $\frac{1.552}{11.137} = x\ .1394$ $\frac{0.695}{11.137} = y\ .0624$

Table 6

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 33	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006	.842	.028			
90	0.005		0.023	.827	.014			
400	0.019	0.001	0.093	.798	.006			
10	0.071	0.002	0.340					
20	0.262	0.008	1.256					
30	0.649	0.027	3.167	.762	.011	.007		.034
40	0.926	0.061	4.647	.768	.026	.024	.002	.120
50	1.031	0.117	5.435	.760	.060	.062	.007	.326
60	1.019	0.210	5.851	.760	.044	.044	.009	.257
70	0.776	0.362	5.116	.762	.012	.009	.004	.061
80	0.428	0.622	3.636					
90	0.160	1.039	2.324					
500	0.027	1.792	1.509					
10	0.057	3.080	0.969					
20	0.425	4.771	0.525					
30	1.214	6.322	0.309					
40	2.313	7.600	0.162					
50	3.732	8.568	0.075					
60	5.510	9.222	0.036					
70	7.571	9.457	0.021					
80	9.719	9.228	0.018					
90	11.579	8.540	0.012					
600	12.704	7.547	0.010					
10	12.669	6.356	0.004	.678	.014	.177	.088	
20	11.373	5.071	0.003	.643	.215	2.445	1.090	
30	8.980	3.704		.598	.383	3.439	1.418	
40	6.558	2.562		.555	.434	2.846	1.112	
50	4.336	1.637		.499	.419	1.816	.686	
60	2.628	0.972		.465	.400	1.051	.388	
70	1.448	0.530		.412	.358	.518	.180	
80	0.804	0.292		.367	.328	.264	.096	
90	0.404	0.146		.311	.281	.114	.041	
700	0.209	0.075		.263	.240	.050	.018	
10	0.110	0.040		.223	.206	.022	.008	
20	0.057	0.019		.187	.174	.010	.003	
30	0.028	0.010		.153	.142	.004	.001	
40	0.014	0.006		.122	.113	.002		
50	0.006	0.002		.100	.092			
60	0.004	0.002		.079	.072			
70	0.002			.061	.056			
	109.828	100.000	35.547			12.904	5.161	0.798

Chromaticity coordinates: $\frac{12.904}{18.863} = x \ .6840$ $\frac{5.161}{18.863} = y \ .2736$

Table 7

λ	1931 CIE color-matching functions weighted by the relative spectral energy distribution of Source A			Glass filter	Kodak Wratten filter 61	Tristimulus values		
	$\bar{x}$	$\bar{y}$	$\bar{z}$			X	Y	Z
380	0.001		0.006					
90	0.005		0.023					
400	0.019	0.001	0.093					
10	0.071	0.002	0.340					
20	0.262	0.008	1.256					
30	0.649	0.027	3.167					
40	0.926	0.061	4.647					
50	1.031	0.117	5.435					
60	1.019	0.210	5.851					
70	0.776	0.362	5.116					
80	0.428	0.622	3.636					
90	0.160	1.039	2.324	.794	.016	.002	.016	.037
500	0.027	1.792	1.509	.784	.118	.003	.211	.178
10	0.057	3.080	0.969	.784	.261	.014	.804	.252
20	0.425	4.771	0.525	.784	.336	.142	1.603	.176
30	1.214	6.322	0.309	.783	.331	.402	2.092	.102
40	2.313	7.600	0.162	.785	.284	.656	2.158	.046
50	3.732	8.568	0.075	.794	.220	.821	1.884	.016
60	5.510	9.222	0.036	.782	.148	.815	1.364	.005
70	7.571	9.457	0.021	.780	.086	.651	.813	.002
80	9.719	9.228	0.018	.777	.044	.428	.406	
90	11.579	8.540	0.012	.752	.016	.185	.136	
600	12.704	7.547	0.010	.710	.004	.050	.030	
10	12.669	6.356	0.004					
20	11.373	5.071	0.003					
30	8.980	3.704						
40	6.558	2.562						
50	4.336	1.637						
60	2.628	0.972						
70	1.448	0.530						
80	0.804	0.292						
90	0.404	0.146						
700	0.209	0.075						
10	0.110	0.040						
20	0.057	0.019						
30	0.028	0.010		.153	.002			
40	0.014	0.006		.122	.007			
50	0.006	0.002		.100	.018			
60	0.004	0.002		.079	.028			
70	0.002			.061	.031			
	109.828	100.000	35.547			4.169	11.517	0.814

Chromaticity coordinates: $\frac{4.169}{16.500} = x\ .2526$ $\frac{11.517}{16.500} = y\ .6980$

Appendix C

Formulae for Calculating Tristimulus Values and Chromaticity Coordinates for Mixed Colors Appearing on the Comparison Field of the 4-Primary Colorimeter Used in Experiments 4, 5 and 6

The tristimulus values X_m, Y_m and Z_m of a mixed color are given by

$$X_m = \text{Area R } X_R + \text{Area G } X_G + \text{Area C } X_C + \text{Area B } X_B \qquad \text{(a)}$$

$$Y_m = \text{Area R } Y_R + \text{Area G } Y_G + \text{Area C } Y_C + \text{Area B } Y_B \qquad \text{(b)}$$

$$Z_m = \text{Area R } Z_R + \text{Area G } Z_G + \text{Area C } Z_C + \text{Area B } Z_B \qquad \text{(c)}$$

where X_R, Y_R and Z_R are tristimulus values of Kodak Wratten filter 92 (red); X_G, Y_G and Z_G are tristimulus values of Kodak Wratten filter 74 (green); X_C, Y_C and Z_C are tristimulus values of Kodak Wratten filter 75 (cyan) and X_B, Y_B and Z_B are tristimulus values of Kodak Wratten filter 47 (blue). Tristimulus values calculated for the actual filters used appear in Tables 2-5, Appendix B. Area R of the red filter, Area G of the green filter, Area C of the cyan filter and Area B of the blue filter are the areas of each filter exposed to the face of the integrating bar at a particular filter holder setting. A computer program calculates tristimulus values X_m, Y_m and Z_m for each mixed color corresponding to each possible combination of horizontal and vertical filter holder settings. The unit of increment along either axis is 0.1 mm.

The chromaticity coordinates x, y and z of a mixed color are given by

$$x = \frac{X_m}{X_m + Y_m + Z_m}, \quad y = \frac{Y_m}{X_m + Y_m + Z_m} \quad \text{and } z = \frac{Z_m}{X_m + Y_m + Z_m} \qquad \text{(d)}$$

Appendix D

Colorimeter Photographs and Technical Specifications

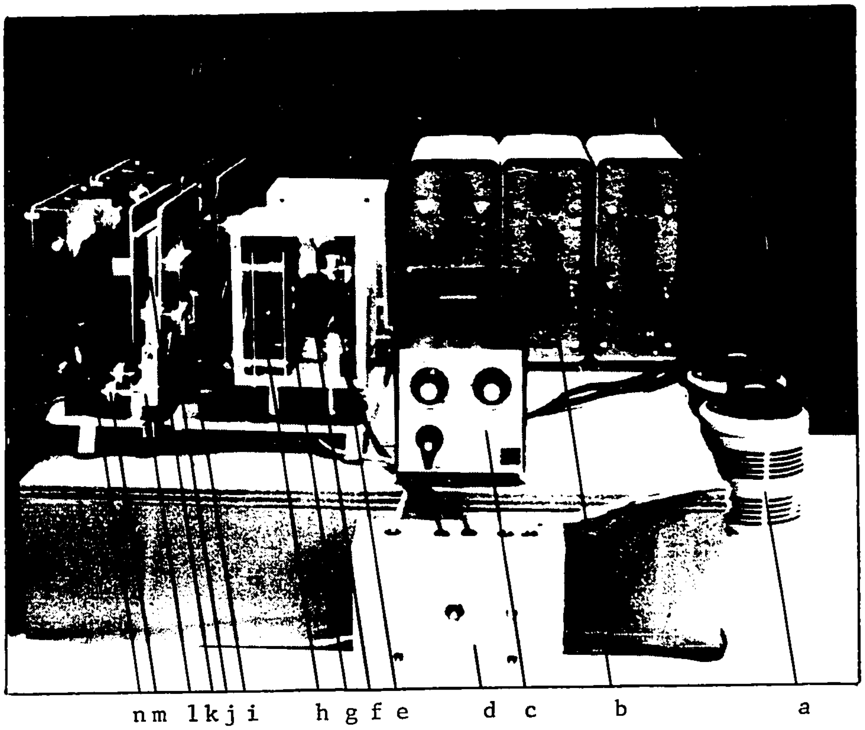

Figure 1. Components in the comparison channel of the 4-primary colorimeter used in Experiments 4, 5 and 6.

a) A Superior Electric Company Powerstat Type 116 regulates the voltage of current reaching the projection lamp.

b) Three Decade Interval Timers made by the Hunter Manufacturing Company Incorporated control the sequence of stimulus display presentation.

c) A Bodine Type ASH 201/DC Motor Control governs the speed of the motor which drives projector sprockets that advance a 35-mm film loop in the standard channel of the colorimeter.

d) A control box allows the experimenter to choose automatic or manual presentation of stimulus displays.

e) A General Electric DEB 1000 watt tungsten filament projection lamp illuminates the channel. The centigrade temperature of the lamp's filament, measured by a Leeds and Northrup Company Optical Pyrometer Number 8622-C, is equal to 2813° K. Since the filament temperature of tungsten lamps is usually 40° K lower than the actual color temperature of the lamp (Wyszecki and Stiles, 1967, p. 49), the lamp operates at a color temperature of 2853° K. Thus, its relative spectral energy distribution approximates that of CIE Standard Source A.

f) A Howard Company fan Model J075-3192 cools the projection lamp.

g) A plano-convex lens collimates light from the projection lamp and provides a uniform field, free of chromatic aberration, centered on the face of the plexiglass integrating bar.

h) A glass filter blocks energy at infrared wavelengths. Its relative spectral energy distribution, measured by a Beckman DU Spectrophotometer Model 2400, appears in Table 1, Appendix B.

i) A filter holder accommodates various luminance attenuators which control the brightness of the viewing field at the end of the channel.

j) A shutter occludes the channel.

k) A filter holder contains four primary color filters mounted in optically neutral cover glass. Their relative spectral energy distributions, measured by a Beckman DU Spectrophotometer Model 2400, appear in Tables 2-5, Appendix B. The filter holder restricts the available area of each filter to a square 34 x 34 mm.

l) A Rolyn Corporation microscope stage with vernier calibration on either arm carries the primary filter holder.

m) Two control knobs allow either the observer or the experimenter to vary the horizontal and vertical positions of the primary filter holder.

n) A 34 x 34 x 90 mm plexiglass integrating bar mixes light which passes through the four primary color filters. A jacket of black construction paper shields the integrating bar from extraneous light. Two 34 x 34 mm opal glass squares, placed flush against either end of the integrating bar, further diffuse the mixed light.

Figure 2. Components in the standard channel of the 4-primary colorimeter used in Experiments 4, 5 and 6.

a) A Bodine Speed Reducer Motor Type NSH-12R drives projector sprockets which advance a 35-mm film loop.

b) A filter holder contains two adapting color filters mounted in optically neutral cover glass. Their relative spectral energy distributions, measured by a Beckman DU Spectrophotometer Model 2400, appear in Tables 6 and 7, Appendix B.

c) A 35-mm film loop carries the stimulus displays.

d) A DC Timing Motor manufactured by the A. W. Haydon Company moves the adapting filter holder along a horizontal track, alternating the position of each filter in the center of the optical path each time its arm rotates 180°.

Other components in the standard channel are identical to those in the comparison channel. During experimentation, a black felt drape isolates each channel of the colorimeter from extraneous light.