Frequency-specific color adaptation in the human visual system*

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Following prolonged exposure to two vertical grating patterns differing in spatial frequency—one pattern illuminated in green light alternated with the other pattern illuminated in red light—human observers will sometimes report seeing desaturated complementary colors when presented with a neutrally illuminated test field consisting of adjacent halves of the two adapting gratings. The number of such color reports increases as the difference between the spatial frequencies of the adapting gratings increases. This frequency-specific chromatic aftereffect is similar to that obtained with orientation-specific color adaptation and may be mediated by neural “channels,” sensitive to both color and frequency input, which are similar to units known to exist in the visual systems of lower organisms.

In recent years the properties of aftereffects of pattern-specific chromatic adaptation in the human visual system have met with vigorous investigation. Orientation specificity of such aftereffects has been demonstrated repeatedly, starting with McCollough (1965). That is, if horizontal and vertical gratings with, say, red and green illumination, respectively, are viewed alternately for several minutes, then subsequent observations of corresponding neutrally illuminated test gratings will yield reports of desaturated green and red. Such chromatic aftereffects are maximal when the adapting gratings have an angular divergence of 90 deg and aftereffect strength decreases as the adapting gratings become closer in orientation (Fidell, 1970).

Hubel and Wiesel (1968) have demonstrated the existence of neurons in monkey striate cortex which respond optimally to lines of a particular orientation and color. Insofar as the visual system of man resembles that of monkey, one might expect that a similar sort of neural element mediates the aftereffects of orientation-specific color adaptation described above. Indeed, neurophysiological studies of cortical neurons in higher mammalia (Campbell et al, 1968; Hubel & Wiesel, 1968) not only point to the existence of orientation selectivity but also specify the angular tuning—which is relatively broad—of such elements.

In addition to orientation specificity, single cells maximally sensitive to a particular spatial frequency of a specifically oriented grating pattern have been found in cat visual cortex (Campbell et al, 1969).

Psychophysical evidence, i.e., selective threshold elevation following prolonged exposure to achromatic gratings of a particular spatial frequency (Blakemore & Campbell, 1969a, b), suggests that spatial frequency-specific neural elements exist in the human visual system as well as in that of the cat. Presumably, these elements are maximally tuned to a given spatial frequency and are less sensitive to higher and lower spatial frequencies. In humans, for relatively low spatial frequencies, the bandwidth of these hypothetical channels is about four octaves of frequency (cf. text Figs. 8 and 13, Blakemore & Campbell, 1969b). This implies that neural elements maximally responsive to a grating of a particular spatial frequency will respond minimally, if at all, to a grating with four times that frequency. However, as the frequency difference between the gratings approaches zero, the neural elements maximally responsive to the one grating frequency should respond more vigorously to the other grating frequency.

If color information is also processed by these channels, then one should be able to demonstrate frequency-specific color adaptation. Indeed, chromatic aftereffects which vary in strength as a function of the similarity between the line densities of adapting and test gratings have been shown indirectly by Teft and Clark (1968), and similar line-spacing effects have been noticed by Fidell (1968) and Harris and Gibson (1968). More recently, Stromeyer (1971) has shown that such chromatic aftereffects are strongest when the spatial frequencies of the adapting and test gratings are identical and that aftereffect strength decreases as the difference between the frequencies of the adapting and test gratings is increased.

In addition to demonstrating spatial frequency-specific color adaptation

(with methodological innovations), the study presented here investigated the magnitude of the difference between the spatial frequencies of two adapting gratings necessary for producing simultaneously two, clear, frequency-specific chromatic aftereffects. Employing the hypothetical neural model discussed above as an explanation for pattern-specific color adaptation, the following prediction was made.

If two adapting gratings of the same orientation—one illuminated with red light, the other with green light—are close in spatial frequency, then on alternate presentations of these gratings, neural elements maximally responsive to either grating frequency should also respond strongly to the frequency and color information of the other grating. Since in this case competing color information is being transmitted alternately on both frequency-tuned neural channels, no color aftereffects should develop. However, if the two adapting gratings are sufficiently different in spatial frequency, neural elements maximally responsive to either frequency will not respond to the other frequency. Hence, different color information will be transmitted along two widely separated frequency-specific channels, and chromatic aftereffects should develop. Specifically, no chromatic aftereffects should be observed when the two adapting gratings are very close in spatial frequency, and separate aftereffects should be clearly established when the two adapting gratings differ by about two octaves of frequency, the half-bandwidth of these hypothetical neural channels (Blakemore & Campbell, 1969b).

METHOD

Subjects

Five males and five females, students and staff at Stanford University, were used as Ss. All Ss had normal color vision.

Apparatus and Procedure

A modified two-channel tachistoscope was used to present the adapting and test grating patterns. Eleven vertical grating patterns were employed. Each pattern could be mounted into a square aperture at the rear of the apparatus, which had a 7.5-deg width at a viewing distance of 40 in. One of the patterns, termed the reference pattern, had a spatial frequency of 3.33 cycles/deg. Starting with the reference pattern, 10 other patterns, termed varied-frequency patterns, were constructed with successively higher spatial frequencies such that the frequency of any one of these patterns was 14.9% higher than that of the pattern just lower in spatial

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Fig. 1. Number of appropriate color reports as a function of the spatial frequency of the varied-frequency gratings. Arrow indicates the spatial frequency of the reference grating.

frequency. Thus, the 11 patterns covered a two-octave frequency range and had values of 3.33, 3.83, 4.40, 5.06, 5.81, 6.67, 7.67, 8.81, 10.13, 11.63, and 13.37 cycles/deg.

Each of the 10 Ss was run in one experimental session per day for a total of 10 days. During a given experimental session, the reference pattern and 1 of the 10 varied-frequency patterns were used during both the adapting and test phases of the session. Thus, each S was adapted and tested with the reference pattern coupled with each varied-frequency pattern. Order of presentation of these pairs was randomized for each S. In order to minimize the possibility of response bias, each S was asked to judge the color of the two patterns, presented side by side and neutrally illuminated, prior to each adaptation session. If S indicated that he saw, say, green in one of the patterns, then during adaptation this pattern was illuminated in green light. Thus, if any color aftereffect specific to that pattern developed, it would be pinkish—the reverse of S's preadaptation response.

During the adapting phase, the reference and varied-frequency patterns were alternately presented at 10-sec intervals for a total viewing time of 15 min. The two adapting patterns were back-illuminated (General Electric 100-W CDD tungsten bulb), one in red light (Kodak filter No. 29, dominant wavelength 632.7 nm, transmission 11%), the other in green light (Kodak filter No. 58, dominant wavelength 538.2 nm, transmission 19.8%). While

adapting, S, with head on a chinrest, continuously scanned the patterns as they were presented in order to minimize the effects of local retinal adaptation.

After adaptation S was given a 30-sec rest interval, after which the same two grating patterns, now neutrally illuminated, were presented side by side so that S could make simultaneous comparisons of the two patterns. (Luminance of the test patterns was 538 mL.) Initially S was asked if he saw color in either of the two test patterns. If "no color" was reported, the response was recorded and the session ended. If S reported that he did see color in one or both of the test fields, he was asked whether the color(s) was pink or green. Thus, one of the three possible categories of verbal response—"no color," "pink," or "green"—was recorded by E for each of the two test patterns. A response was considered appropriate if S reported either one or both of the predicted aftereffect colors, i.e., the complementary of the color associated with a particular grating pattern during adaptation.

RESULTS AND DISCUSSION

The results are displayed in Fig. 1. Inspection of the figure indicates that the hypothesis of the experiment was confirmed. As predicted, when the spatial frequency difference between the reference and varied-frequency patterns was only 14.9%, none of the Ss reported appropriate color aftereffects. However, all Ss reported appropriate color aftereffects when the differences between spatial frequencies of the reference and the varied-frequency patterns were close to two octaves of frequency. Moreover, it is evident that as the frequency difference between the patterns increased from near zero to near two octaves of frequency, the number of appropriate color reports also increased. As a measure of monotonicity, Spearman's rank correlation coefficient, correlating ranked frequency difference with ranked number of appropriate color aftereffect reports, was calculated. The value obtained was 0.98 ($t = 13.93$, $df = 8$, $p < .001$).

The results of the present study are clearly consistent with those of previous investigations (Fidell, 1968; Harris & Gibson, 1968; Teft & Clark, 1968); in particular, the observations of Stromeyer (1971) are confirmed and extended. Our findings dovetail nicely with psychophysical and neurophysiological evidence discussed above (Blakemore & Campbell, 1969a, b; Campbell et al, 1969) and

clearly support the notion that broadly tuned spatial-frequency analyzers, which are also color sensitive, characterize the visual system of man as well as that of lower organisms.

Similar "feature analytic" interpretations of orientation-specific chromatic aftereffects have been proposed (e.g., McCollough, 1965; Fidell, 1970), but at present consensus on the nature of the neural units mediating such effects is lacking (cf. Harris & Gibson, 1968). While inferences from psychophysical evidence to neurophysiological mechanisms must be advanced with caution, the degree of correspondence between both sorts of findings, with respect to both orientation and spatial frequency specificity, is encouraging and suggestive. Regardless of interpretation, spatial frequency-specific chromatic adaptation in the human visual system must now be regarded as a well-documented phenomenon.

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