cone b-wave responses of the normal observers or the ERG's of four patients with congenital stationary night blindness. With less than 20 minutes of dark adaptation or in the presence of background lights of less than 580 nm (Fig. 2), no response was obtained from the rod monochromats and no rod response from these normal observers. Testing of dichromatic observers with this stimulus indicated that 70 percent of the cone response was generated by long wavelength ("red") cones and about 30 percent by middle wavelength ("green") cones.

13. A 2-minute exposure to a 65°, 491-nm (40-nm half bandwidth) field of 2000 photopic trolands was used. This light was calculated to bleach approximately 27 percent of rod photopigment [W. A. H. Rushton, *J. Physiol. (London)* **156**, 166 (1961); E. Pugh, Jr., *ibid.* **248**, 393 (1975)] and 9 percent of cone photopigment [T. N. Cornsweet, *Visual Perception* (Academic Press, New York, 1970), p. 153].
14. In a pilot experiment with the 640-nm stimulus and the 491-nm bleach, dark-adaptation curves obtained psychophysically from three normal observers showed that the cone plateau (dark-adapted cone threshold) was reached at approximately 2 minutes in the dark and the rod plateau by 28 minutes in the dark.
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16. Backgrounds were photometrically equated at 25 photopic trolands. In addition to the photometric calibration, we observed that psychophysical increment thresholds for a 0.5°, 640-nm flash falling on the rod-free area of the fovea varied within 0.3 log unit over these backgrounds, confirming that they were matched with respect to cone light adaptation.
17. Conversion from photopic to scotopic trolands was calculated according to G. Wyszecki and W. S. Stiles [*Color Science, Concepts and Methods, Quantitative Data and Formulas* (Wiley, New York, 1967), p. 226].
18. An adaptational effect on the cone b wave not mediated by rods but presumably by cone function alone was shown also in the following way: the 600 nm background was increased stepwise from 25 to 500 photopic trolands and cone b-wave implicit time systematically decreased by 9 msec. But 500 photopic trolands is equivalent to 63 scotopic trolands, which is below the background level for a rod effect on the cone ERG under the present test conditions (Fig. 2B).
19. Patients with retinitis pigmentosa and night blindness have cone b-wave implicit times that are normal in the dark [M. A. Sandberg. E. L. Berson, M. H. Effron, *Invest. Ophthalmol. Visual Sci.* **19** (Suppl.), 259 (1980); E. L. Berson, *Vision Res.* **20**, 1179 (1980)], but delayed about 10 msec in the light [E. L. Berson, P. Gouras, M. Hoff, *Arch. Ophthalmol.* **81**, 207 (1969); E. L. Berson, *Trans. Am. Acad. Ophthalmol. Otolaryngol.* **81**, 659 (1976)]. These delays in the light could reflect a primary cone defect or, in view of this study, be secondary to diminished rod function, at least in part.
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Color and Luminance: Independent Frequency Shifts

Abstract. *Simultaneous opposite spatial frequency shifts can be obtained in chrominance and luminance channels. The chrominance shift cannot be transferred interocularly. Chrominance and luminance channels seem to perform similar but independent spatial frequency analyses.*

One task in vision research is that of determining to what extent visual dimensions such as spatial frequency, luminance, and color are processed in the same or in separate channels. We report that a spatial frequency shift (*1*) can be induced with chromatically defined gratings and that this shift can occur independently of a luminance-induced shift; this result implies that spatial frequency is analyzed separately in chrominance and luminance channels.

Investigations of color channels have shown that some effects can be obtained with chromatically defined stimuli, whereas others cannot (*2*, *3*). While it is known that color information can be used in spatial frequency analysis, chrominance and luminance channels have never been clearly dissociated. Virsu and Haapsalo (*4*) induced color-based spatial frequency shifts, but their gratings contained both luminance and chrominance differences, and so the effect may have been mediated by a channel in which the two are linked. Such a linkage appears possible as some form-color effects require both luminance and chrominance contrast (*5*). Stromeyer *et al.* (*6*) showed that exposure to sinusoidal violet gratings elevates the threshold for violet but not red gratings, again showing that color can be used in spatial frequency analysis, but not conclusively showing independence of color from luminance.

Much previous work has shown that color-related effects do not transfer interocularly, thus implying that chrominance channels are driven monocularly (*7*). However, there is some indication that the relation between chrominance channels and ocular dominance is complex (*8*). We examine this problem with respect to the chromatic spatial frequency shift.

In the two experiments, observers were exposed to red-green or black-white square-wave gratings like those used by Blakemore and Sutton (*1*) to induce a spatial frequency shift. The stimuli were generated by computer on a color television monitor (*9*).

We used red-green gratings in order to eliminate the operation of luminance channels and thereby isolate chrominance channels. This aim can be achieved only indirectly, however, and there is no general agreement as to the appropriate psychophysical technique (*10*). Some researchers opt for luminance matching by heterochromatic flicker photometry or the minimal distinct border technique; others use brightness matching. We used a combination of these techniques to approximately equate red and green (*11*). Because we could not be certain that we were not activating luminance channels, we used an opposing aftereffects paradigm to ensure that no residual luminance differences in the color stimuli could mediate a frequency shift in a luminance channel.

Accordingly, observers were adapted to alternate presentations of red-green and black-white gratings in which the former were arranged so that the upper grating was of higher spatial frequency than the lower, and the reverse was true for the latter (Fig. 1). Thus, if there is a residual luminance difference in the chromatic gratings, any resulting luminance-based frequency shift with the chromatic test would be overwhelmed by the shift in the opposite direction generated by the achromatic gratings. A color-based frequency shift is therefore direct evidence of an independent chrominance channel.

Observers sat 2.5 m from the display,

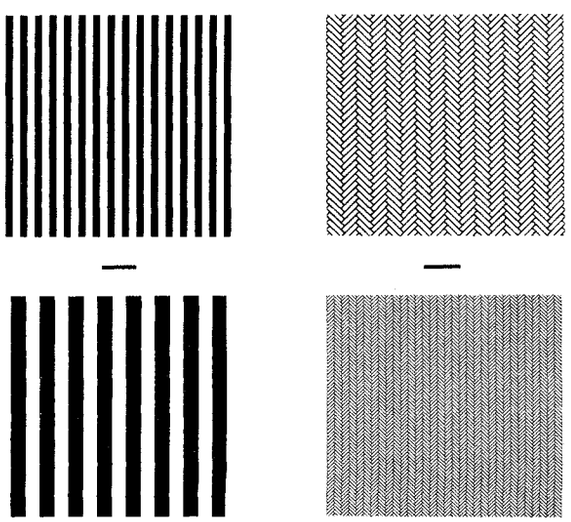

Fig. 1. Schematic representation of the adapting stimuli used in experiments 1 and 2. The black-white gratings are represented on the left, and the red-green gratings on the right. The relative locations of high and low spatial frequencies are reversed. The test gratings were of intermediate equal frequencies, similarly arranged above and below a central fixation point.

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which was 7.5° high and 6.0° wide. Each grating was 3.5° high, and they were separated by a 0.5° space containing a 1.0° horizontal fixation bar. The adaptation frequencies were 5 and 2.5 cycles per degree; the test gratings were 3.75 cycles per degree.

In experiment 1, we tested four sophisticated observers to determine (i) whether opposite independent chromatic and achromatic spatial frequency shifts can be obtained and (ii) whether they transfer interocularly. During an initial adaptation period, the chromatic and achromatic gratings alternated every 15 seconds. Viewing was monocular. After a 30-second blank period, there were two chromatic and two achromatic tests, one each for the adapted and unadapted eyes. Test duration was 5 seconds, separated by 5-second intervals. Observers gave magnitude estimates on a scale from 0 to 10 (10 corresponding to a 2:1 frequency ratio) of the apparent difference between the upper and lower test gratings. There followed 2.5 minutes of readaptation and then another test period. This sequence was repeated to give four test periods.

For the adapted eye, the chromatic and achromatic tests gave appropriate aftereffects in opposite directions, as predicted (Fig. 2a). For color, the mean magnitude estimate was 1.63 [t (3) = 7.12, $P < .01$]; for black and white, it was 1.78 [t (3) = 4.28, $P < .025$]. They did not differ significantly from each other [t (3) = 0.19]. The chromatic test for interocular transfer showed no significant shift [$\bar{X} = .08$, t (3) = 2.92].

The achromatic test for interocular transfer showed a significant shift in the predicted direction [$\bar{X} = .72$, t (3) = 3.48, $P < .05$]. This was not significantly smaller than the shift in the adapted eye [t (3) = 2.92].

The purpose of experiment 2 was to compare the chromatic and achromatic frequency shifts when induced simultaneously as in experiment 1, with each of those shifts induced alone. This comparison can provide an estimate of the degree of independence of the channels.

Three groups of eight naïve observers each were tested. All exposure was binocular. For group 1, the procedure was the same as in experiment 1. Group 2 observers were adapted to chromatic gratings only, and group 3 to achromatic gratings. For both of these groups the size of the stimuli were the same as in

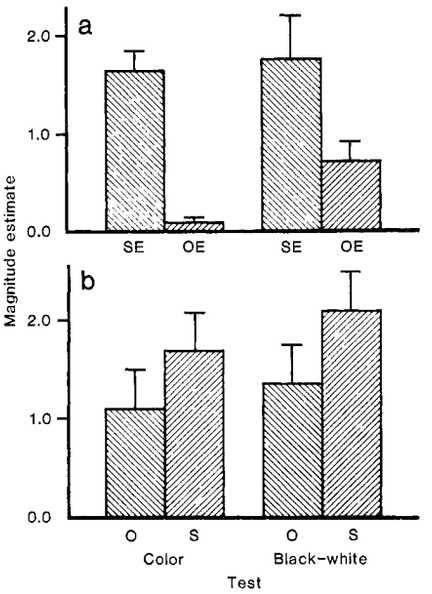

Fig. 2. (a) Mean magnitude estimate as a function of test and eye. Abbreviations: *SE*, the same eye was adapted and tested; *OE*, the other, unadapted, eye was tested. Vertical bars represent one standard error of the mean. (b) Mean magnitude estimates made by the groups in the opposing and in the simple shift conditions. Abbreviations: *O*, scores for observers adapted to both chromatic and achromatic gratings; *S*, observers in each of the two simple conditions (groups 2 and 3).

experiment 1, but the procedure was modified slightly because there was only one kind of grating: the adaptation periods were 6 minutes and the refresh periods were 1½ minutes.

Observers in group 1 had simultaneous and opposite shifts for color [mean magnitude estimate = 1.11, t (7) = 2.87, $P < .025$] and for achromatic gratings [$\bar{X} = 1.38$, t (7) = 3.55, $P < .001$] (Fig. 2b). Observers in groups 2 and 3 also reported appropriate shifts [color $\bar{X} = 1.69$, t (7) = 4.42, $P < .005$; achromatic $\bar{X} = 2.09$, t (7) = 5.22, $P < .002$]. The shifts obtained in the opposing condition did not differ significantly from the corresponding shifts obtained in the simple condition.

Simultaneous opposite chrominance and luminance spatial frequency shifts can therefore coexist. This result points to the existence of pure chrominance channels tuned to spatial frequency and implies that chrominance and luminance channels in the visual system perform similar but separate spatial frequency analyses. Recent research (*12*) shows that this is also true for threshold elevation. Why the chrominance shift does not transfer interocularly is puzzling, as the mechanism for the transfer seems to be available, at least in monkeys (*13*). Possibly the chrominance shift is mediated at a level peripheral to the locus of binocular combination, or interocular transfer may involve a complex series of interactions (*7, 14*).

Note added in proof: In a recent experiment we changed a number of variables and obtained interocular transfer of a chromatic frequency shift.

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