Toxoplasma, but similar to *Hammondia* and *Sarcocystis* (*7*), the oocysts of the new *Besnoitia* sp. are not infectious to the final host. Although a host change appears obligatory between mouse and cat as in *Sarcocystis* and *Hammondia* (*1, 2*), a facultative transmission among efficient intermediary hosts may be possible as observed with *B. jellisoni*, *B. besnoiti*, and *B. darlingi*, all of which can be subinoculated from one to another intermediate host (*4, 7, 8*). It should be pointed out that an oocyst stage of *B. jellisoni* has not been recovered in eleven cats, six bobcats, and one cougar, or in other carnivores examined so far [three foxes, three dogs, one coyote, eight procyonids, four skunks, one owl, one hawk, and one boid, one colubrid, and three viperid snakes (J.K.F.)] *Besnoitia jellisoni* persists in mice for over a year, but mice are relatively poor hosts for the *Besnoitia* under study. In laboratory rats, cysts are more stable. The native intermediary host in Hawaii has not been identified; however, another cat shedding oocysts, 13 by 16 μm, was observed in Hawaii 7 days after it arrived in the laboratory. Since oocysts were found before the known prepatent period, it seemed likely that the cat had been infected outside the laboratory. Mice to which some of these oocysts were fed developed high ($>1:1000$) IFA titers to *Besnoitia bradyzoites*.

The identification of a carnivore as a final host of *Besnoitia* brings this organism into a closer relation with *Toxoplasma*, *Hammondia*, and *Sarcocystis*, the cycles of which were recently described (*2, 9, 10*). These findings appear to confirm the recently reported life cycle of *B. besnoiti* from cattle (*11*) and may help to uncover life cycles of *B. tarandi* from reindeer, *B. bennetti* from horses, and others which are of economic and veterinary importance. It may also be possible to devise control measures, once the host supporting the sexual cycle has been identified.

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Luminous and Chromatic Flickering Patterns Have Opposite Effects

Abstract. *When stimulated in phase by a sinusoidally flickering, uniform field, the red and green cone systems tend to inhibit each other. This inhibition is minimized by (i) counterphase (luminance) patterns or (ii) red/green (chromaticity) flicker. However, when (i) and (ii) are combined, the usual flickering-pattern effect is reversed: instead of enhancing chromatic flicker, counterphase patterns tend to suppress it.*

At frequencies below 10 hertz, the visual sensitivity to sinusoidally flickering stimuli depends on the spatial pattern of the stimulus. This low-frequency sensitivity is least when the flickering stimulus is a patternless, uniform field with no surround, but is greatly increased by so-called counterphase patterns, in which different parts of the visual field flicker in opposite phases (*1*). The effectiveness of such stimuli increases with the number of edges (that is, phase reversals) in the pattern; the optimum stimulus is a rectilinear, counterphase grating with stripes subtending about 10 minutes of visual angle. However, even a single edge (for example, a split field with right and left halves flickering in opposite phases) is sufficient to greatly increase the flicker sensitivity, as shown by the open symbols in Fig. 1.

Sensitivity to luminous flicker characteristically reaches a maximum at about 10 hertz, decreasing at higher and lower frequencies. The low-frequency flank of this passband can be explained in terms of lateral inhibition in the retina (*2*). When the entire field is flickering uniformly, inhibiting pathways provide a form of automatic gain control, which tends to counteract the variation of the stimulus if it is varying slowly enough. Therefore, the uniform-field sensitivity decreases at low frequencies.

The presence of a counterphase edge interferes with this gain control, because the increasing stimulus on one side of the edge and the decreasing stimulus on the other side have opposite effects on the local gain, so that it tends to remain constant in the vicinity of the edge. Therefore, the stimulus amplitude is not attenuated as much near a counterphase edge as it is in a uniform field; this increases the flicker sensitivity as shown by the open squares in Fig. 1. The split-field sensitivity still shows a maximum at 8 hertz, decreasing for lower frequencies, probably because lateral inhibition is still effective at some distance from the counterphase edge (*3*).

However, quite different results are obtained when the hue of the stimulus is varied while its luminosity is held constant. Chromatic flicker sensitivity is typically a low-pass (rather than a bandpass) function of frequency; it decreases monotonically over the same frequency range where the luminous flicker sensitivity is increasing, as shown by the filled symbols in Fig. 1. In these experiments, the chromaticity was varied sinusoidally about the yellow point indicated by the CIE diagram inset in Fig. 1 (*4*). At full modulation, the extreme chromaticities were a saturated red and green (also shown in the inset), very similar to van der Horst's chromatic flicker primaries (*5*); their luminance ratio was adjusted to minimize low-frequency luminous flicker. However, none of these choices is critical,

because chromatic flicker sensitivity curves have the same low-pass shape for a wide variety of chromaticity paths and luminance ratios (*6*).

Most previous studies of flickering patterns have dealt only with luminous flicker, but we have repeated our split-field counterphase experiment with the chromatic stimulus just described. In this experiment, the right half of the field changed from red to green as the left half changed from green to red, and vice versa; but the chromaticities, luminance, and size of the field remained the same as in the patternless chromaticity experiment (*7*).

The result of this experiment was exactly the reverse of the counterphase effect obtained with luminous flicker. Instead of increasing the low-frequency sensitivity, the chromatic split-field pattern greatly decreases it, as shown by the filled squares in Fig. 1. This reversal seems highly significant in terms of the information processing operations of the visual system.

Our data can be explained in terms of mutual inhibition or antagonism between red-sensitive and green-sensitive cone systems; inhibition within a given cone system seems to play no significant role in this experiment (*8*). Let us assume that the red and green cone systems antagonize each other only when they are stimulated in the same phase. This preserves the explanation given above for the luminous flicker data, but with the spatially inhibitory pathways also playing specific color roles. With patternless red/green flicker, however, the red and green cone systems are stimulated in opposite phases and can no longer inhibit each other; this accounts for the monotonic shape of the chromatic flicker curves.

Finally, the split-field stimulus decreases the chromatic flicker sensitivity by reversing the process that increased the luminous flicker sensitivity. Instead of interfering with lateral inhibition, the spatial phase reversal now permits some lateral inhibition to take place across the counterphase edge, because the red cones on the left side of the field are now stimulated in the same phase as the green ones on the right, and vice versa. Thus the same inhibitory pathways may be involved in both the increase of luminous flicker sensitivity and the decrease of chromatic flicker sensitivity caused by counterphase patterns.

If so, the frequency response of these pathways as inferred from either the luminous or the chromatic flicker experiments should be the same. For luminous flicker, this inhibitory filter characteristic has previously been calculated (*1*) by the formula $(m_U - m_S)/(m_U + m_S)$, where m_U is the threshold modulation for the uniform field at a given frequency and m_S is the corresponding split-field threshold. A similar calculation can be made from the chromatic flicker data by changing the sign of this formula (in effect, interchanging the roles of m_U and m_S). This has been done, and the results of both calculations are plotted for comparison in Fig. 2. Both smooth curves through the data points were drawn from the same template. Apart from a constant factor (of about 1.6), both luminous and chromatic experiments yield the same inhibitory frequency response, although the shapes of the luminous and chromatic sensitivity curves are quite different.

This tends to confirm that the 10-hertz maximum of flicker sensitivity is simply a by-product of two independent mechanisms: a high-frequency filtering process followed by a low-frequency one (*2*). Similar experiments with more elaborate spatial patterns (for example, checkerboard and striped gratings) suggest other properties of the retinal pathways; these will be reported elsewhere (*9*).

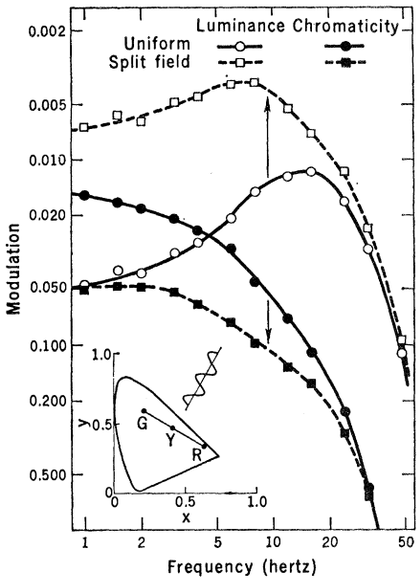

Fig. 1. Sensitivity to luminous (open symbols) and chromatic (filled symbols) flicker in a 10-degree field; artificial pupil, 2.3 mm; retinal illuminance, 10^3 trolands. [Chromatic flicker varied about the point Y in the inset CIE diagram (*4*), reaching the chromaticities G and R at maximum modulation.] Circles show the sensitivity when the entire field is flickering uniformly. When the field is split into two halves, flickering in opposite phases (squares), the luminous sensitivity increases, while the chromatic sensitivity decreases.

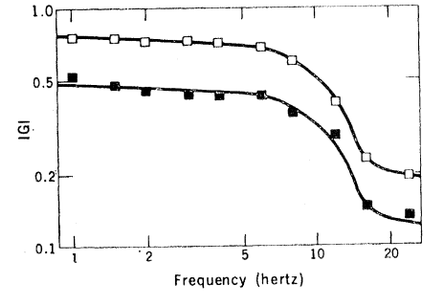

Fig. 2. Frequency response of lateral pathways extending across the counterphase edge, calculated from the luminous (open symbols) and chromatic (filled symbols) flicker data of Fig. 1, according to the formula $|G| = \pm (m_S - m_U)/(m_S + m_U)$. The two curves were drawn from the same template (see text).

This tends to confirm that the 10-hertz maximum of flicker sensitivity is simply a by-product of two independent mechanisms: a high-frequency filtering process followed by a low-frequency one (*2*). Similar experiments with more elaborate spatial patterns (for example, checkerboard and striped gratings) suggest other properties of the retinal pathways; these will be reported elsewhere (*9*).

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3. This effect is eliminated by introducing more counterphase edges, suitably spaced apart (*1*).
4. The coordinates of the inset in Fig. 1 are the standard trichromatic coefficients used in the international colorimetric system of the Commission Internationale de l'Eclairage (CIE).
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6. For examp → D. Regan and C. W. Tyler [*Vision Res.* **11**, 1307 (1971)] obtained low-pass curve shapes with sinusoidal modulation along the spectrum locus, centered at wavelengths from 500 to 622 nm. The limiting case for out-of-phase stimulation of the red and green cones should occur when one of these cone types is "silent," that is, equally sensitive to both extremes of the chromatic stimulu → O. Estevez and H. Spekreijse [*Vision Res.* **14**, 823 (1974)] tested this case, obtaining the same low-pass curve shape under both silent-red and silent-green conditions.
7. By the method of adjustment, the subject discriminated temporal variation from a steady, uniform field; such variation anywhere in the field was considered above threshold. With a split field, the subject made judgments only when fixating the dividing line, but no particular localization of sensation was reported near the threshold of either luminous or chromatic flicker. Standard deviations less than the width of a plotting symbol (about 10 percent of the modulation value) were generally obtained, by averaging 5 luminous-flicker settings or 12 chromatic flicker settings. (Uniform, chromatic flicker judgments are the most difficult of all four types; luminous flicker, split-field judgments are the easiest.)
8. Opponent interactions between (rather than within) classes of cone cells may be the chief source of lateral inhibition. This is suggested by the shape of both the chromatic flicker curves (*5*, *6*) and the luminance flicker curves obtained under intense chromatic adaptation; see D. H. Kelly, *J. Opt. Soc. Am.* **64**, 983 (1974).
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