Phase-dependent sensitivity to heterochromatic flicker

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Received December 23, 1985; accepted March 19, 1986

We measured modulation sensitivity to a pair of equally luminous sinusoidally modulated lights (568 and 630 nm) as a function of their relative phase. Measurements were made for 2, 3, 6, and 12 Hz at a retinal illuminance of 100 Td. The data indicated that two processes were active and their outputs combined by a vector summation rule. There was a phase shift of $-18^\circ$ to $-20^\circ$ (630 nm leads 568 nm) at 6 Hz, no phase shift at 12 Hz, and an indeterminate shift at 3 Hz. At frequencies where a phase shift was observed, our analysis indicated that the phase shift affected sensitivities measured at all relative phase settings. These results are inconsistent with models postulating equal contributions of long-wavelength- and middle-wavelength-receptors to centers and surrounds of processes responsible for the detection of luminance flicker.

Among deLange’s\textsuperscript{1,2} pioneering achievements in assessment of temporal modulation sensitivity was the experimental method of modulating an equally luminous pair of chromatic lights either in phase (producing luminance modulation) or counterphase (producing chromatic modulation). Such luminance and chromatic modulation yield clearly distinct attenuation characteristics occupying different frequency bands.\textsuperscript{3,4} In the frequency range of 1 to 50 Hz, the attenuation characteristics for in-phase (luminance) stimulation are bandpass in shape; sensitivity peaks in the range of 8 to 10 Hz and declines with increasing or decreasing frequency. Attenuation characteristics of counterphase (chromatic) stimulation are low pass at low luminances but may be bandpass at higher luminances\textsuperscript{3}; sensitivity is greatest at 1 Hz and declines rapidly with increasing frequency.

DeLange\textsuperscript{2} also demonstrated perceptual phase shifts for counterphase stimulation at low photopic levels of adaptation. He found that the residual flicker following flicker photometric matching was further reduced if the sinusoidal components of the stimuli were modulated with a compensatory physical phase shift away from counterphase. The required compensation varied with the chromaticities of the heterochromatic pairs and was dependent on frequency.\textsuperscript{5,6} Perceptual phase shifts have been demonstrated reliably at low photopic adaptation levels.\textsuperscript{4-6} It is not clear which visual mechanisms contribute to perceptual phase shifts. Warraven and Leebeck\textsuperscript{4} hypothesized that the phase shifts were due to temporal differences between cone types and affected only visual mechanisms that processed luminance modulation.

A weakness of the paradigm introduced by deLange is that adjustment of phase in the flicker minimization technique physically alters both the luminance and the chromaticity components of the stimulus. Since flicker was minimized rather than eliminated for many experimental conditions, at least two visual mechanisms must be implicated. Thus visual channels sensitive to chromatic modulation may also play a role in achieving the percept of minimum flicker. The deLange paradigm does not permit analysis of the contributions of a chromatic component to this percept. Further, the flicker minimization technique is subject to criteria on changes with frequency.

The purpose of the present study was to assess modulation sensitivity as a function of the relative phase of sinusoidally modulated, flicker-photometrically matched chromatic lights. Physiological phase shifts are resolved by this technique when minimum or maximum modulation thresholds occur at physical phase settings other than 0 and 180°. Unlike deLange’s flicker minimization paradigm, measurement of modulation threshold provides a psychophysical task that remains unambiguous and invariant with changes in frequency. Since modulation threshold at settings other than 0 and 180° relative phase involve both luminance and chromatic modulation, additional analysis allows us to estimate the degree of summation of chromatic and luminance signals in flicker detection.

METHODS

Observers
Two observers were used, both with normal (corrected) visual acuity and normal color vision (Nagel anomaloscope and Farnsworth–Munsell 100-hue test).

Apparatus
A two-channel, computer-controlled Maxwellian-view optical system, shown schematically in Fig. 1, was used. Sources $L_{560}$ and $L_{568}$ were (Monsanto MV5752 and MV5252) light-emitting diodes here called red and green LED’s, respectively. Light from these two sources was combined by a dichroic mirror (DM) and focused by a lens (L) through an artificial pupil (AP) onto the observer’s cornea. The field of view, defined by a circular field stop (FS), subtended $2^\circ$ visual angle. Radiance was varied by adjusting the currents through the LED’s. Additionally, neutral-density filters could be placed in filter boxes $F_1$ and $F_2$ to adjust separately the radiances of the two LED’s within a range adequate for electronic adjustment. Neutral-density filters could also be placed in filter box $F_3$ to adjust the radiances of the combined beams.
Stimuli of the desired frequency and phase setting were generated digitally on a PDP-15 (Digital Equipment Corporation) computer and consisted of two lists of 360 values stored in computer core. Each list represented one cycle of a sinusoidal waveform. Temporal modulation of $L_{560}$ and $L_{630}$ was produced by sequentially writing values from each of the lists to separate 12-bit, digital-to-analog converters. A laboratory-constructed interface between the computer and the LED's rendered the radiance of each LED linear for the digitally generated voltages. Two ganged potentiometers on the interface simultaneously controlled the modulation amplitude of each LED. A third potentiometer and neutral-density filters placed in $F_2$ served to equate the luminances of the two LED's during flicker photometry.

The LED light outputs were calibrated with a UV-100B photodiode (EG&G) placed at the exit pupil of the apparatus. The LED's were modulated in counterphase and equated for photodiode response, and the residual peak-to-peak amplitude ripple was measured. Expressing ripple as a percentage of the modulation of either LED, deviation from linearity by this method increased monotonically with modulation and was 0.8% at 80% modulation.

Modulation thresholds were measured as a function of the phase difference in modulation of the equiluminant LED's. Test frequencies were 2, 3, 6, and 12 Hz. A time-average retinal illuminance of 100 Td was maintained throughout the experiment.

Procedure

Observers viewed the stimulus field in a darkened room with their heads restrained by bite plates made of dental impression wax. Each experimental session began with a luminance match of the red and green primaries by flicker photometry. The median of five matches was the setting used during the session. All data were obtained by the method of adjustment. Throughout an experimental session, observers had access to a knob for adjusting modulation and a two-position switch with which to initiate a trial and then signal the computer to record a modulation setting. Since the modulations of the red and green LED's were held equal throughout the study, modulation thresholds were calculated from the following relation for either LED:

$$M = \frac{I_{\text{max}} - I_{\text{min}}}{I_{\text{max}} + I_{\text{min}}}$$

where $I_{\text{max}}$ and $I_{\text{min}}$ correspond, respectively, to the maximum and minimum excursions in intensity of the LED during one cycle of sinusoidal modulation.

Modulation thresholds were measured as a function of the phase difference in modulation of the equiluminant LED's. Test frequencies were 2, 3, 6, and 12 Hz. A time-average retinal illuminance of 100 Td was maintained throughout the experiment. At each frequency, data were gathered for 18 phase settings at 20° phase intervals from $-160°$ ($L_{560}$ leading $L_{630}$) to $180°$ (counterphase). Stimuli at a given phase setting were presented randomly during a session, with five trials being presented per phase condition per session. All plotted data represent averages of ten trials per condition obtained in two experimental sessions.

Derivation of Visual Channel Responses at Threshold

Let $M$ represent the modulation, $\theta$ represent the physical phase difference (in degrees) between the sinusoidally modulated red and green primaries, $f$ represent the frequency (in hertz), $L$ represent the time-averaged luminance, and $C$ the time-averaged chromaticity of the primaries. Then the following equation describes the time-dependent change in luminance, $L(t)$, and chromaticity, $C(t)$, as a function of $M$, $\theta$, and $f$:

$$L(t) = L + \frac{M}{2}[\sin(\frac{ft}{360}) - \theta] + \sin(\frac{ft}{360})$$

$$C(t) = C + \frac{M}{2}[\sin(\frac{ft}{360}) - \theta] - \sin(\frac{ft}{360})$$

By trigonometric identities for the sum and difference of sinusoids, Eqs. (2) and (3) can be rewritten as follows:

$$L(t) = L + [M \cos(\theta/2)][\sin(\frac{ft}{360}) - \theta]$$

$$C(t) = C + [M \sin(\theta/2)][\cos(\frac{ft}{360}) - \theta]$$

The physical modulation depths are $M \cos(\theta/2)$ for luminance, $M_L$, and $M \sin(\theta/2)$ for chromaticity, $M_C$. A change in $\theta$ alters only the relative values of $M_L$ and $M_C$. The phase difference between the luminance and chromaticity components of the stimulus remains fixed at $90°$, i.e., luminance and chromaticity remain modulated in quadrature regardless of the setting of $\theta$.

Derivation of Visual Channel Responses at Threshold

It is customary in a linear treatment of visual channels to express channel response in terms of the physical modulation, $M$, to that channel and the channel's sensitivity, $S$; i.e., $R = SM$. $R$ is treated as the normalized channel response; when detection is assumed to be mediated by a single visual channel, $R$ for that channel is given a value of unity for input sufficient to achieve threshold detection. Channel sensitivity, therefore, may be expressed as $S = 1/M_T$, where $M_T$.
represents threshold modulation. The response of a visual channel to modulation, M, therefore, is

\[ R = M(1/M_T). \]  

(6)

If there were no physiological phase shifts the sensitivities of the chromatic and luminance channels could be calculated directly as the reciprocals of threshold modulations measured at 180° and 0°, respectively. To account for a physiological phase shift, \( \phi \), in the quantitative model, it would seem appropriate to assume that physiological inputs to the chromatic and luminance channels would each differ from the corresponding physical inputs in that the effective differences in phase between the red and green primaries are \( \theta - \phi_C \) and \( \theta - \phi_L \), respectively, rather than \( \theta \) alone. Let \( M_{LT} \) and \( M_{CT} \) represent threshold modulation at phase settings that isolate luminance and chromatic channels, respectively. The modulation sensitivity of visual channels sensitive to physical modulation of luminance and chromaticity, respectively, is given by functions of \( \theta \) and \( \phi \):

\[ M_L = (M_{LT})/\cos[(\theta - \phi_L)/2], \]  

(7)

\[ M_C = (M_{CT})/\sin[(\theta - \phi_C)/2]. \]  

(8)

Figure 2 shows the expected modulation sensitivity of two independent channels with different values for \( M_{LT} \) and \( M_{CT} \), \( M_{CT} \) being shown as the more sensitive in the left panel and \( M_{LT} \) in right panel. The dashed lines on Fig. 2 show the predicted channel responses for a phase shift of 20° for both \( \phi_C \) and \( \phi_L \).

It is apparent that only the phase shift of the process contributing most to detection is likely to be resolved at a given phase setting. A difference in phase between channels will be demonstrated by a failure of symmetry in the data around the phase axis of the more sensitive channel. At frequencies where the sensitivities of the two channels differ greatly, such asymmetry will be difficult to test since modulation threshold will be determined by the more sensitive channel at most phase settings. Additionally, asymmetry may be obscured by variability in observer performance. At frequencies where both channels have nearly equal sensitivity, two difficulties arise. First, detection will be determined by both channels at most phase settings and the source of the resultant phase shift will become indeterminate. Second, the dependence of observer sensitivity on phase setting is reduced. The analysis may thus be simplified by assuming equivalent shifts in both channels.

RESULTS AND ANALYSIS

Modulation thresholds are plotted as a function of phase angle for observers DTL (Fig. 3, left panel) and DHL (Fig. 3, right panel) for the four test frequencies at 100 Td. Tabulated results may be found in Ref. 8. Positive values of phase correspond to \( L_5 \) modulation leading \( L_3 \). Error bars indicate \( \pm 1 \) standard error of the mean (SEM). The smooth curves drawn through the data are fits to the data obtained using a quantitative model described in a later section.

At 2 Hz, both observers required less modulation to detect primarily chromatic flicker (phase angles around 180°) than luminance flicker. Modulation thresholds at 3 Hz were nearly invariant with phase setting for both observers. At 6 and 12 Hz, both observers required less modulation to detect primarily luminance flicker than chromatic flicker.

While threshold modulations were symmetric about a vertical line drawn through the 0° setting at 12 Hz, they clearly
were not symmetric about such a line at 6 Hz. Comparisons of the 12- and 6-Hz data for both observers indicate that the 6-Hz data appeared displaced both vertically and horizontally relative to the observer's 12-Hz data. At 12 Hz, minimum and maximum modulation thresholds occurred at phase settings of 0° and 180°, respectively, for both observers. However, at 6 Hz, these thresholds occur at −20° and 160°. There is no evidence of residual asymmetry around the −20° axis. We interpreted these results as evidence for physiological phase shifts at 6 Hz. By similar analysis, there was also, to a lesser degree, evidence of physiological phase shift in DTL's 2-Hz data.

Model

A convenient tool for analyzing summation is a formulation derived from Quick's\(^9\) equation for probability summation expressed in terms of visual response:

\[
R = (|R_L|^P + |R_C|^P)^{1/P},
\]

where \(R\) is the overall response to stimulation [see Eq. (6)] given the response \(R_L\) and \(R_C\) of the two independent channels and the threshold is unity. A virtue of the Quick formulation is that, by varying only parameter \(P\), the data can be compared with predictions based on linear summation (\(P = 1\)), peak detection (\(P = \infty\)), and probability summation (1 ≤ \(P\) ≤ \(\infty\)). Solving for \(M\) at threshold and substituting Eqs. (7) and (8) yields

\[
M = 1/(|\cos((\theta - \phi)/2)/M_{LT}|^P + |\sin((\theta - \phi)/2)/M_{CT}|^P)^{1/P}.
\]

The largest differential predictions for \(P\) between 1 and \(\infty\) occur when the independent channels have similar thresholds. This condition occurred at 3 Hz for observer DTL, who showed threshold invariance at this frequency. Figure 4 shows calculations of Eq. (10) for \(P\) equal to 1, 2, and \(\infty\) with \(\phi\) at zero. Both peak detection and linear summation predict systematic deviations from average threshold. For stimuli modulated in quadrature, invariance of modulation threshold with phase is predicted only when probability summation with \(P\) around 2 is assumed. This result can be inferred from inspection of Eq. (10). When channel sensitivities (\(M_{LT} = M_{CT}\)) and physiological phase differences are set equal, the sine and cosine terms on the right-hand side of

![Fig. 3. Average modulation thresholds as a function of phase setting. Data are plotted for the four test frequencies: 2, 3, 6, and 12 Hz. Error bars above and below each data point indicate ±1 SEM. The curves drawn through the data for each frequency were derived from a model of flicker detection described in the text. Left panel shows data for observer DTL; right panel shows data for observer DHL.](image1)

![Fig. 4. Comparison of the 3-Hz data of observer DTL with summation model predictions based on three values of summation index (\(P\)). Dotted line, \(P = 1\); solid line, \(P = 2\); dashed line, \(P = \infty\). Error bars above and below each data point indicate ±1 SEM.](image2)
the equation can be replaced by a constant ($\sin^2 X + \cos^2 X = 1$).

We evaluated the generality of this finding across frequency and observer with the aid of a least-squares optimization program. Without simplification of the analysis, the program would have had to optimize 13 parameters for each observer: a single value of $P$ and values of $\phi$, $M_{LT}$, and $M_{CT}$ at each frequency. We chose a two-step procedure. In one optimization procedure, we fixed eight parameters by using graphical estimates for $M_{LT}$ and $M_{CT}$ and solving for $\phi$ and $P$. This procedure gave values of $P$ near 2. In a second optimization procedure, we set $P$ at 2 and solved for $\phi$, $M_{LT}$, and $M_{CT}$. The two optimization procedures gave converging results, and the robustness of the results was checked for a wide range of choices of $P$ and $M_{CT}$. The results of the analysis and the sum of squared residuals (SS) resulting from each fit are tabulated in Table 1. The SS (calculated from residuals from 20 data points) varied from 0.12 to 0.38 for observer DTL and from 0.41 to 0.97 for observer DHL.

The solid curves in Fig. 3 represent these fits, except at 3 Hz, where the luminance and chromaticity components remain modulated in quadrature regardless of the relative phase in the modulation of the red and green lights. Since the luminance and chromaticity components can be expressed as sums and differences of the sensitivities of different cone types, our analysis is formally equivalent to an analysis using cone types rather than channels as the orthogonal components. An exception is that of Kranda and King-Smith, who modeled detection thresholds for bichromatic pulses of light with probability summation across four channels and $P$ set to about 4.

**DISCUSSION**

Walraven and Leebeeck postulate that perceptual phase shifts measured at low photopic luminance levels occur largely because of temporal differences in the receptor types that form channels mediating flicker detection. In their analysis, the middle-wavelength-sensitive (MWS) receptor response lags behind the long-wavelength-sensitive (LWS) response and produces a net signal in their luminance channel when the flickering stimulus is modulated physically in counterphase. Several investigators have attributed these phase shifts to rod intrusion at low photopic adaptation levels. Our data, gathered at 100 Td, show phase shifts opposite in direction to those of Walraven and Leebeeck and cannot similarly be attributed to rod intrusion.

It seems unlikely that our results can be explained in terms of temporal differences between cone receptors of differing spectral sensitivity. Since the time Walraven and Leebeeck reported their results, several studies have failed to find qualitative temporal differences between LWS and MWS mechanisms. The latency required by our results at 6 Hz (18.5 msec) would have been easily resolved by the techniques employed in these studies. While it is known that adaptation level can increase the temporal response of photoreceptor mechanisms, the stimuli used in our study adapt the LWS receptor type relatively more than the MWS. Thus predictions based on differential adaptation are in conflict with the results of our study.

One might ask how estimates of physiological phase shift obtained from our paradigm are related to the physiological phase components of the temporal modulation transfer functions for chromatic and luminance modulation. Equations (4) and (5) indicate that luminance and chromaticity components remain modulated in quadrature regardless of the relative phase in the modulation of the red and green lights. Since the luminance and chromaticity components can be expressed as sums and differences of the sensitivities of different cone types, our analysis is formally equivalent to an analysis using cone types rather than channels as the orthogonal components. At any given frequency, our physical phase plots are affected only by a relative physiological phase difference of such components.

The observed phase shifts occur as a result of interactions between two processes exhibiting different spectral sensitivities. Our 6-Hz data can be explained by assuming that the mechanism mediating luminance flicker detection possesses an imbalance in the weighting of receptor types in the excitatory and inhibitory portions of receptive fields. In this scheme, the phase shift arises from differential delays before

### Table 1. Best Fits and Sum of Squared Residuals Obtained Assuming $P = 2$ and Optimizing $MO$, $M_{180}$, and $\phi$ at Each Frequency by Least-Squares Criterion

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Frequency (Hz)</th>
<th>2</th>
<th>3</th>
<th>6</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>DTL</td>
<td>$MO$ ($\pm$SD)</td>
<td>3.65(0.126)</td>
<td>1.94(0.039)</td>
<td>1.50(0.026)</td>
<td>1.99(0.048)</td>
</tr>
<tr>
<td></td>
<td>$M_{180}$ ($\pm$SD)</td>
<td>1.67(0.049)</td>
<td>2.21(0.047)</td>
<td>6.44(0.178)</td>
<td>10.77(0.423)</td>
</tr>
<tr>
<td></td>
<td>$\phi$ ($\pm$SD)</td>
<td>-15.36(3.470)</td>
<td>-18.12(1.115)</td>
<td>-1.49(1.280)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>SS</td>
<td>0.38</td>
<td>-</td>
<td>0.12</td>
<td>0.37</td>
</tr>
<tr>
<td>DHL</td>
<td>$MO$ ($\pm$SD)</td>
<td>2.07(0.143)</td>
<td>0.75(0.006)</td>
<td>0.76(0.037)</td>
<td>0.91(0.046)</td>
</tr>
<tr>
<td></td>
<td>$M_{180}$ ($\pm$SD)</td>
<td>0.85(0.040)</td>
<td>1.22(0.012)</td>
<td>5.41(0.438)</td>
<td>9.68(0.819)</td>
</tr>
<tr>
<td></td>
<td>$\phi$ ($\pm$SD)</td>
<td>-6.75(5.700)</td>
<td>-19.89(2.240)</td>
<td>1.27(1.790)</td>
<td>1.99(0.046)</td>
</tr>
<tr>
<td></td>
<td>SS</td>
<td>0.41</td>
<td>-</td>
<td>0.63</td>
<td>0.97</td>
</tr>
</tbody>
</table>
combination of outputs of the spectrally dissimilar components. This may occur in the outer retina. In the macaque monkey, stimulation of spectrally and spatially opponent cells with flickering light introduces a delay in the inhibitory response of the surround relative to the excitatory response of the center (see, e.g., Gouras and Zrenner23). Our results can be accounted for by postulating that flicker detection is mediated by mechanisms of center-surround organization, of which the majority consist of MWS centers and LWS surrounds. With this organization, MWS responses will be processed, on average, more rapidly than LWS responses. Support for the hypothesis that MWS preferentially populates the center of spectrally opponent flicker mechanisms can be drawn from other studies. Within the central 2° of the macaque visual field, a majority of spectrally opponent cells have receptive fields with MWS centers and antagonistic LWS surrounds.4 Ingling and Martinez25 require a similar asymmetry to account for weightings of LWS and MWS contributions to opponent and nonopponent channels. They also propose that their analysis, coupled with the assumption of the center-surround processing delays suggested by Gouras and Zrenner,20 offers an explanation for the shift in color appearance of spectral lights flickered at moderate frequencies.

If inhibitory interactions between receptors of differing spectral sensitivity underlie the observed phase shifts, one is necessarily led to the conclusion that, in the frequency range where phase shifts are observed, the detection of both luminance and chromatic flicker is mediated by retinal mechanisms that possess differing spectral sensitivities of center and surround. One of the first to link spectral opponency to both luminance and chromatic flicker detection was Kelly,26 who investigated the contributions of inhibitory mechanisms to the detectability of purely luminance or chromatic flicker. The frequency characteristics of these mechanisms are similar for the two types of flicker, leading Kelly26 to conclude that inhibition occurs primarily between receptors of differing type.

Recent theories of flicker detection hold that detection of both luminance and chromatic flicker may be mediated by a single spectrally and spatially opponent channel.27,28 Such a channel conveys information that is, mathematically, the composite of both luminance and chromatic information. While the phase shift data can be incorporated into such models in the same manner as described above, an additional assumption is required to account for the rule of combination that we derived from our data. For example, a summation index of 2 is consistent with the visual events following demultiplexing occurring as independent processes. An alternative assumption, that each component is passed after spatial filtering through a squaring element before the detector, seems unlikely. Krauskopf29 has shown that a squaring element cannot play a role in the detection of transient light stimulation.

ACKNOWLEDGMENTS

This work was supported in part by National Institutes of Health National Eye Institute research grant EY00901 to J. Pokorny. This paper is based in part on the doctoral dissertation of Delwin T. Lindsey, University of Chicago, 1985. A preliminary report was presented at the 1979 Annual Meet-

ing of the Optical Society of America. Bill Swanson provided detailed comments on a draft of this manuscript.

REFERENCES

24. F. M. De Monasterio and P. Gouras, “Functional properties of

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