

# Impulse-response functions for chromatic and achromatic stimuli

David C. Burr

*Istituto di Neurofisiologia del Consiglio Nazionale delle Ricerche, S. Zeno 51, Pisa, and Dipartimento di Psicologia, Università di Roma, Italy*

M. Concetta Morrone

*Scuola Normale Superiore and Istituto Policattedra di Discipline Biologiche, Università di Pisa, Italy*

Received June 1, 1992; revised manuscript received December 7, 1992; accepted February 25, 1993

Thresholds were measured for detecting pairs of briefly flashed stimuli displayed successively at variable onset asynchronies. The stimuli were 1 cycle/deg vertical sinusoidal gratings, modulated either in luminance (yellow-black) or in color (red-green). The successive presentations were either of the same contrast (positive) or of opposite contrast (negative), yielding four separate summation curves: positive and negative summation for color and for luminance. Both the positive and the negative curves followed a shorter time course for luminance than for color, implying a faster response at threshold. To calculate impulse response functions from the summation data, we assumed that the neural impulse response from two successive stimuli sum linearly at threshold, that thresholds are determined by probability summation of the combined impulse response over time, and that the impulse response can be described by an exponentially damped frequency-modulated sinusoidal function with four free parameters. The predicted impulse responses for luminance and for color are quite different, being biphasic for luminance and monophasic for color. Fourier transform of these functions yielded estimates of the amplitude and the phase functions of hypothetical visual detectors: the amplitude functions predicted well the contrast sensitivity of counterphased gratings (as a function of temporal frequency) both for luminance and for chromatic stimuli.

## 1. INTRODUCTION

Evidence from a wide range of studies has shown that the temporal properties of chromatic visual mechanisms are different from those of luminance visual mechanisms. Sensitivity for luminance flicker is band pass, whereas that for chromatic flicker is low pass (for both uniform and patterned stimuli), and the temporal resolution is much lower for chromatic modulation.<sup>1,2</sup> Simple reaction times for chromatic transients (hue substitution) are considerably slower than for luminance transients under similar conditions,<sup>3</sup> by 40–80 ms (depending on wavelength), and simultaneity judgments suggest that both the apparent onset and the apparent offset of a briefly displayed chromatic stimulus lag behind those of a similar luminance stimulus.<sup>4</sup> Latency estimates from visual evoked potentials<sup>5</sup> are also consistent with longer processing times for chromatic stimuli, about 40 ms for the particular stimuli used (red-green of a standard color monitor).

Summation studies provide perhaps the clearest indication of the temporal characteristics of a system, and these studies also point to longer processing times for chromatic stimuli. Thresholds for detecting chromatic change (purity thresholds) decrease with time for longer periods than do thresholds for luminance change<sup>6,7</sup> suggesting longer integration times.

The impulse response (the theoretical response to an infinitely short stimulus) is a fundamental characteristic of any system, as it predicts how the system will respond to any arbitrary stimulus (over a given linearity range), and it is conveniently related to the frequency response by

means of the Fourier transform. The impulse response of the luminance system has been studied extensively<sup>6–12</sup> with a variety of techniques. One technique is to estimate the impulse response from flicker-sensitivity curves, from the Fourier transform. Since the flicker-sensitivity data contain information only about amplitude, the phase spectrum must be assumed, and most studies assume minimum phase (discussed in Subsection 4.B). With this approach, Swanson *et al.*<sup>7</sup> derived impulse-response functions from flicker thresholds and suggested basic differences between luminance and chromatic vision: impulse responses for luminance stimuli were diphasic, and those for chromatic stimuli were monophasic. They then went on to show that these hypothetical impulse responses predicted the different forms of summation threshold, nicely combining the periodic with the aperiodic approaches to studying temporal characteristics.

One powerful and direct technique for estimating impulse responses is to measure sensitivity for two consecutive pulses as a function of pulse separation.<sup>8</sup> Uchikawa and Ikeda<sup>13</sup> applied this technique in a limited form to chromatic stimuli by measuring the probability of detecting two consecutive chromatic transients or luminance transients at various pulse-onset asynchronies. The response functions that they derived for chromatic stimuli were monophasic, of a form similar to those of Swanson *et al.*<sup>7</sup> However, it should be pointed out that like Swanson *et al.*, Uchikawa and Ikeda used a minimum-phase filter to model the data, and this assumption can influence the form of the predicted impulse response (discussed further in Section 4).

The current study extends the two-pulse summation technique to provide a further estimate of luminance and chromatic impulse-response functions for patterned stimuli. It differs from previous studies in several key respects: (1) the stimuli were spatially modulated gratings rather than uniform light patches; (2) detection thresholds (rather than probability of seeing for fixed contrasts) were measured for all conditions; (3) measurements were made both for positive summation (identical stimuli) and negative summation (equal-but-opposite stimuli); (4) minimum phase was not assumed; and (5) the impulse response obtained by this technique was compared with flicker measurements made under similar conditions. The results agree well with previous studies in suggesting that the impulse response for luminance vision is diphasic and, further, suggest that the impulse response for color vision is monophasic. Implications of the monophasic response to motion detection and other phenomena are discussed. These results have been published in abstract form.<sup>14</sup>

## 2. METHODS

### A. Stimuli

The stimuli were generated by framstore (Cambridge Research Systems) and displayed on the face of a Barco color monitor (CDC T 6551), with suitable luminance linearization, at 120 frames/s and 500 lines/frame. The waveforms were vertical sinusoidal gratings of 0.25 cycle/cm, corresponding to 1 cycle/deg when viewed from 2.28 m. The stimulus was vignetted (by software) to a circle of diameter 23 cm, with the rest of the monitor set to mean luminance (16 cd/m<sup>2</sup>) and color.

The stimuli were modulated either in luminance or in chromaticity. Both types of stimuli were made by combining red and green sinusoidal gratings (produced by modulation of the red and the green guns of the monitor) of identical contrast and luminance. The luminance stimuli were made by summing the red and the green gratings, and the chromatic stimuli were made by subtracting them (adding in counterphase). To minimize stimulation of short-wavelength cones, the stimuli were viewed through Kodak Wratten filters (No. 16), which heavily attenuated wavelengths below 520 nm. The CIE coordinates were red:  $x = 0.651, y = 0.348$ ; green:  $x = 0.403, y = 0.59$ . Equiluminance was established by flicker photometry, with the amplitude ratio of red-to-green waveforms adjusted to produce minimal flicker of the stimulus when modulated at 16 Hz.

The gratings were generated on the framstore, with standard techniques. As the digital-to-analog converters of the framstore were 8 bits for each color, only 256 luminance levels per color could be controlled directly. To increase contrast resolution, particularly for conditions in which observers were more sensitive, the waveform was sampled in space or in time (or in both). For spatial sampling, 3 pixels in 4 were set to mean luminance, reducing contrast by a factor of 4 (2 bits); for temporal sampling every alternate frame was set to mean luminance, providing another factor of 2 (1 bit). This increased the effective resolution to 11 bits. The decrease in spatial or temporal resolution did not affect the experiment, as the spatial sampling was not resolvable at the observed distance and the temporal sampling was used only at low-

stimulus temporal frequencies (below 8 Hz). Measurements made in the same condition, with and without the sampling, confirmed that the spatial and temporal samplings had the desired effect on contrast.

Two types of stimulus presentation were employed: either a double presentation of two brief (8-ms) successive displays or a continuous presentation of a contrast-reversed grating, vignetted within a temporal Gaussian window (time constant 230 ms). For the double presentation the successive stimuli were of either identical or equal-but-opposite contrast (see Fig. 2 below).

### B. Procedure

Thresholds were measured by a two-alternative-forced-choice procedure. The stimulus was presented in one of two successive intervals (each marked by a tone), which observers had to identify by pressing the appropriate response button. The contrast of both stimuli varied according to the QUEST procedure,<sup>15</sup> which estimated thresholds after each trial and placed the contrast of the following trial near that estimate. The final estimate of threshold was made by fitting the frequency-of-seeing functions (percent correct versus contrast) for all trials of a given condition (minimum 200 trials per condition) with a Weibull<sup>16</sup> function:

$$p = 1 - 0.5 \exp[-(C/C_t)^\beta], \quad (1)$$

where  $p$  is proportion correct,  $C$  is contrast,  $C_t$  is contrast at threshold, and  $\beta$  is a constant determining the slope of the function.

The two free parameters,  $C_t$  and  $\beta$ , were determined by minimizing the residual mean-square error between data and prediction, with the simplex<sup>17</sup> algorithm.

## 3. RESULTS

### A. Two-Pulse Summation

Thresholds were measured for detecting pairs of briefly pulsed gratings presented successively at variable stimulus-onset asynchronies (SOAs). The two successive stimuli were of either identical contrast or equal-but-opposite contrast. The task of the observers was simply to identify the temporal interval in which the double pulse occurred: they were not required to give further judgments about the nature of the stimulus. Contrast sensitivity for the task was defined as the inverse of the contrast of the pulses at threshold.

As outlined in Section 2, the stimuli (both gratings in the pair) were modulated either in luminance (yellow-black) or in chromaticity (equiluminance: red-green). Figure 1 shows the results for all four conditions. The curves in Figs. 1A and 1B refer to luminance stimuli and in Figs. 1C and 1D to chromatic stimuli. Open symbols show data for the positive (same-contrast) summation condition and closed symbols for the negative (opposite-contrast) condition. The continuous curves passing through the data are predictions from the model, to be discussed in Subsection 3.B.

Consider first the data for luminance-modulated pairs of identical contrast (Figs. 1A and 1B). At very brief SOAs, Block's law applies: the two stimuli summate completely, which increases sensitivity by a factor of 2 compared with

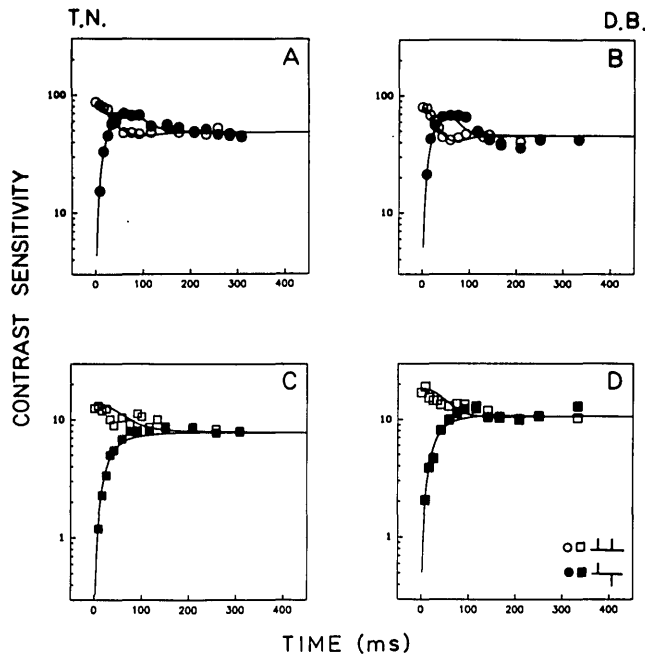


Fig. 1. Contrast sensitivity for the double-pulse presentations as a function of SOA. A, B, curves refer to measurements with luminance-modulated (yellow-black) stimuli; C, D, curves refer to measurements with chromatic-modulated (red-green) stimuli. Open symbols, positive summation condition (both stimuli of the same contrast sign); filled symbols, negative condition (stimuli reversed in contrast). The data points at zero SOA (positive condition) were obtained by doubling the sensitivity to the single pulse (dividing it into two pulses, each of half-contrast), so the sensitivity to a single pulse is a factor of 2 lower than the first open symbol. Zero SOA in the negative condition is impossible. The smooth curves passing through the data were obtained by the fitting procedure described in the text. The square root of the average squared residual for the combined fit of the positive and negative conditions were 0.51 (luminance) and 0.99 (color) dB for TN and 0.87 and 0.99 dB for DB.

that in the single presentation. Summation decreased steadily with increasing stimulus asynchrony, dropping to zero near 60 ms, before asymptoting at 1 or 2 dB (12–25%) above the sensitivity for the single pulse. For the stimuli of opposite contrast, sensitivity was poor at short SOAs, improving rapidly to peak near 60 ms (where the positive curve is minimum) before asymptoting to values similar to those of the positive condition. Note that at the optimal offset (~60 ms), the stimuli of opposite contrast summate positively, improving sensitivity by over 4 dB. These results are similar to many obtained previously with luminance stimuli.<sup>7–9</sup>

The results for the equiluminant stimuli were quite different (Figs. 1C and 1D). For the positive condition, summation decreased more gradually with SOA, reaching an asymptote around 100 ms (without the slight dip observed in the curves for the luminance condition). Similarly, sensitivity for the negative condition increased more gradually with SOA and did not show the sharp peak evident in the curves for luminance stimuli. The results for both conditions suggest that the response to equiluminant stimuli is more sustained than that to luminance stimuli.

## B. Impulse-Response Functions

The data plotted in Fig. 1 suggest basic differences in temporal response to luminance and to chromatic stimuli. To

quantify these differences better, we attempted to derive impulse-response functions for luminance and chromatic pathways from the data plotted in Fig. 1. To do this, we made three assumptions:

1. At threshold, the neural responses produced by two successive stimuli sum linearly over time (small-signal linearity).
2. Detection thresholds are predicted by probability summation of the response over time, with the index of probability summation given by  $\beta$  of Eq. (1) (see Ref. 18 for details and experimental justification of this assumption).
3. The impulse response  $I(t)$  can be well approximated by an exponentially damped, frequency-modulated sinusoid, governed by four free parameters:

$$I(t) = a_0 H(t) t \sin\{2\pi[a_1 t(t+1)^{-a_2}]\} \exp(-a_3 t), \quad (2)$$

where  $t$  is time (in seconds). All parameters  $a_i$  were positive:  $a_0$  governs the overall gain of the function,  $a_1$  governs the fundamental frequency of oscillation,  $a_2$  governs the modulation of frequency over time, and  $a_3$  governs the steepness of the exponential decay.  $H(t)$  is the Heaviside function:

$$H(t) = 0, \quad t < 0;$$

$$H(t) = 1, \quad t \geq 0.$$

Put simply, Eq. (2) describes a function that commences at zero and oscillates over time with decreasing (or constant) frequency, while being progressively damped to zero. The function is multiplied by  $t$  so that continuity of the function and its first derivative at  $t = 0$  is ensured. With four free parameters, the function can take on a variety of forms, which correspond to many reasonably stable filter responses.<sup>19</sup>

From assumption 1 (small-signal linearity), the visual response  $R(t, \tau)$  to two stimuli of equal contrast presented briefly with temporal offset  $\tau$  will be given by the sum of the two impulse responses  $I$ :

$$R(t, \tau) = K[I(t) + sI(t + \tau)], \quad (3)$$

where  $s = \pm 1$ , depending on whether summation was positive or negative.

From the probability-summation assumption, sensitivity  $S(\tau)$  at SOA  $\tau$  is determined by raising the absolute value of the function  $R(t, \tau)$  to the power  $\beta$  [from Eq. (1)], integrating over time, and raising the result to the power  $1/\beta$ :

$$S(\tau) = \left[ \int |R(t, \tau)|^\beta dt \right]^{1/\beta}. \quad (4)$$

Because the integral of Eq. (4) is not easily solved analytically, we calculated the parameters for the impulse-response functions with a reiterative procedure, simplex<sup>17</sup> that minimized the least-squares error between data and predictions.

Figure 2 illustrates the procedure for two experimental conditions: stimuli of either identical (Fig. 2A) or opposite (Fig. 2B) contrast, presented at 60 ms SOA. Each presentation was assumed to produce a neural impulse response that, for a given set of parameters of Eq. (2), will resemble the responses shown in Figs. 2C and 2D (dashed

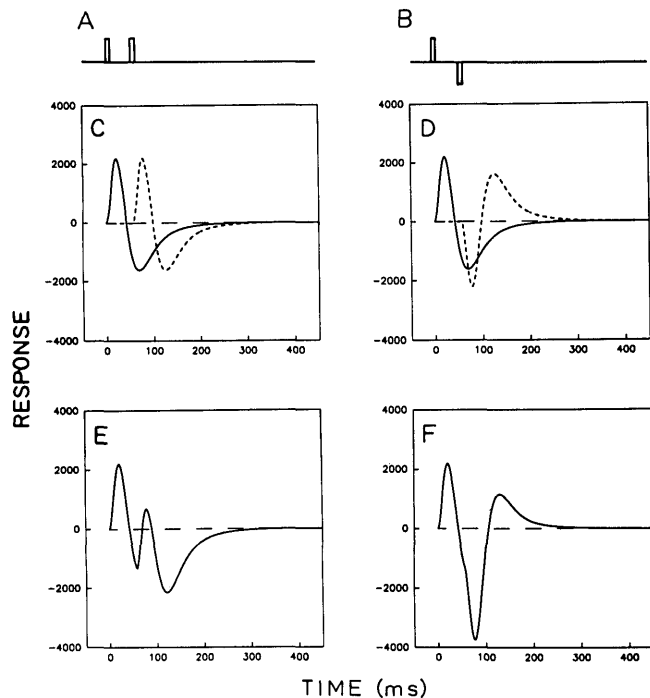


Fig. 2. Illustration of the technique for predicting summation curves from impulse-response functions. A and B illustrate the stimuli: two brief pulses with stimulus-onset-asynchrony of 60 ms, of either the same (positive condition) or opposite (negative condition) contrast. C and D illustrate an example of impulse-response functions elicited by each pulse. Assuming that the responses sum linearly, the resultant response is shown in E and F. To obtain sensitivity, the absolute values of these curves are raised to the power  $\beta$  of Eq. (1) (evaluated as 4.0) and integrated over time, and the result is raised to the power  $1/\beta$ . It is obvious that at this SOA, the hypothetical impulse response to the two stimuli of opposite contrast will be stronger than the response to one stimulus alone or to the pair of the same contrast.

curves indicate responses to the second stimulus). Assuming that the responses sum linearly, the combined responses will be as shown in Figs. 2E and 2F. These responses were then summed probabilistically over time [following Eq. (4)] to give an estimate of sensitivity for each condition. The logarithm of this estimate was subtracted from the logarithm of the measured sensitivity at that condition and squared to give an estimate of residual error. This procedure was repeated for each data point and the squared residuals summed to give an estimate of total residual error. The simplex<sup>17</sup> procedure minimized this error by repeatedly adjusting the parameters of Eq. (2), and it reestimated the sum of residuals. After 4000–5000 iterations, the improvement of each iteration was marginal (<0.0001%), and the procedure was terminated.

The continuous curves of Fig. 3 show the hypothetical impulse-response functions that produced the best fit of the data plotted in Fig. 1 (the dashed curves are minimum-phase functions, discussed in Subsection 3.C). For both observers, the luminance impulse response was quite different from the chromatic response. The luminance functions are diphasic, with a clear negative lobe following the initial positive response, while the chromatic functions are virtually monophasic, with a single positive lobe (except for a slight secondary ripple with observer DB). The time to peak is much faster for the luminance functions, about 26 ms, compared with 53 ms for color. Note,

however, that this delay is relative to the onset of the impulse response, not an estimate of absolute delay in the visual system.

The continuous curves of Fig. 1 show the thresholds predicted from the impulse response. In all cases the curves followed the data reasonably well. The average deviation from the data (given by the square root of the average squared residual) was less than 1 dB (<0.05 log unit).

It is fairly easy to understand intuitively how the different forms of impulse response lead to the different summation curves of Fig. 1. For example, the strong positive summation of luminance stimuli of opposite contrast results from the fact that at SOA's of  $\sim 60$  ms, the second (negative) lobe elicited by the first stimulus will coincide with the first (negative) lobe elicited by the second stimulus, giving positive summation. When the stimuli have the same phase, the positive and negative lobes will tend to oppose each other, thus decreasing sensitivity. The example of Fig. 2, which uses the hypothetical luminance impulse response for DB, illustrates this point. However, because the chromatic impulse response is monophasic, both the positive and the negative summation curves tend to decrease or increase monotonically with SOA.

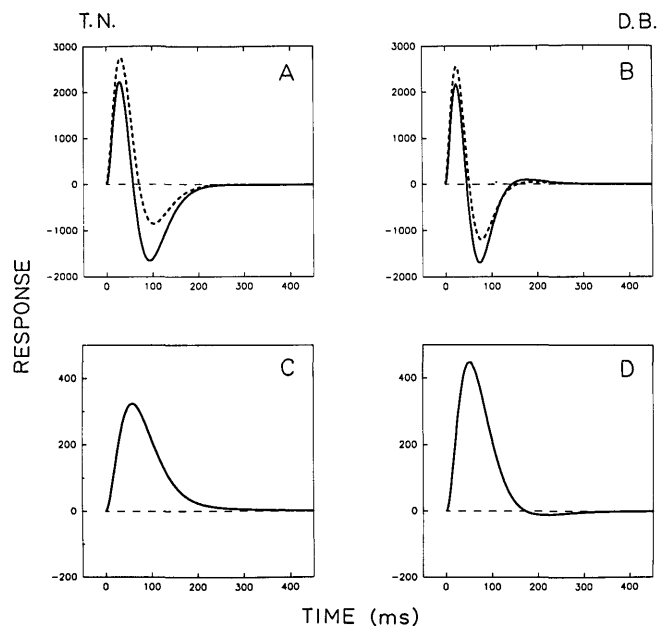


Fig. 3. Continuous curves show hypothetical impulse-response functions for luminance (A, B) and color (C, D), derived from the data plotted in Fig. 1 (see text for details). The dashed curves show impulse responses for minimum-phase filters with identical amplitude spectra (for the chromatic condition, they superimpose exactly for both observers). All continuous curves are described by Eq. (2), with the parameters given in Table 1.

Table 1. Parameters of Eq. (2), Describing Impulse-Response Functions Shown in Fig. 3

	Luminance		Color	
	D.B.	T.N.	D.B.	T.N.
$a_0$	$1.80 \times 10^5$	$1.50 \times 10^5$	$3.08 \times 10^4$	$1.57 \times 10^4$
$a_1$	13.6	11.3	5.1	5.67
$a_2$	5.0	4.74	3.54	4.99
$a_3$	27.3	22.2	24.2	17.9

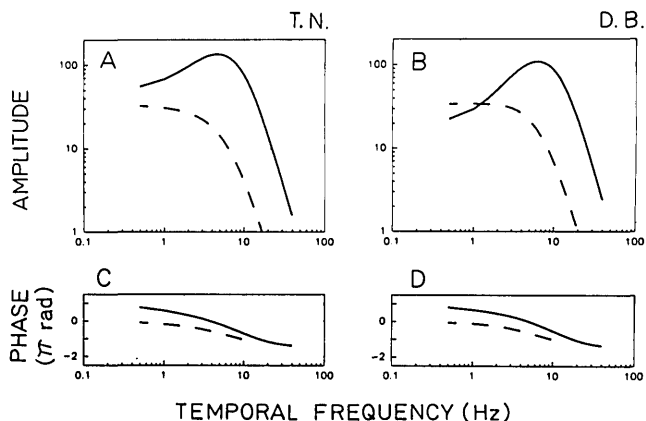


Fig. 4. Gain and phase of hypothetical filters for luminance (solid curves) and color (dashed curves), obtained by discrete Fourier transform of the impulse-response functions plotted in Fig. 3.

### C. Temporal-Frequency Tuning

For a linear system, the temporal-frequency tuning function is related directly to the impulse response by means of the Fourier transform. Since we have assumed an approximation of linearity near threshold (assumption 1), hypothetical tuning functions for the luminance and the color visual systems can be obtained by taking the Fourier transform of the impulse response plotted in Fig. 3. The results are shown in Fig. 4. As is to be expected, the amplitude curves for the luminance condition are band-pass functions, peaking around 8 Hz and attenuating for higher and lower frequencies. The gain curves for the color condition, however, are low pass, beginning to attenuate around 5 Hz and cutting off more quickly than gain curves in the luminance condition.

The phases associated with the amplitude spectra are interesting. Inspection would suggest that at least for the luminance condition, the filters are not minimum phase. To evaluate the deviation from minimum phase, impulse responses were calculated from the amplitude spectra plotted in Fig. 4, with phase spectra calculated from the Hilbert transform of the logarithm of the amplitude spectra.<sup>20</sup> For the chromatic condition, the minimum-phase impulse responses exactly superimpose those obtained directly, showing that these responses are in fact minimum phase. However, for the luminance condition, the two minimum-phase impulse responses differ from those obtained directly, showing that Eq. (2) does not necessarily correspond to a minimum-phase filter.<sup>19</sup>

### D. Predicting Steady-State Thresholds

The frequency tuning curves of Fig. 4 have a form similar to that of the temporal contrast-sensitivity curves obtained with drifting or counterphased gratings.<sup>1</sup> However, to test whether the impulse responses quantitatively predict contrast-sensitivity measures, we measured contrast sensitivity of contrast-reversed gratings under the same conditions as those used for the double-pulse thresholds. These measurements were made with counterphased gratings, vignetted by a Gaussian window of 230-ms time constant, using the forced-choice procedure described in Section 2. The results of the measurements, for both luminance and chromatic stimuli, are shown by the symbols in Fig. 5.

The response of a linear system to any stimulus is given by convolving the stimulus with the impulse response. As before, we assume that detection threshold is determined by probability summation of the response over time. For each temporal frequency  $\omega$ , sensitivity  $S(\omega)$  is given by

$$S(\omega) = \left[ \int |R(\omega, t)|^{\beta} dt \right]^{1/\beta}, \quad (5)$$

where  $R(\omega, t)$  is the response over time, given by convolution of the impulse response with the stimulus, and  $\beta$  [from Eq. (1)] is the probability-summation index, taken as 4.0, the average experimental value.

The continuous curves of Fig. 5 show the temporal sensitivity curves for luminance and for color predicted from the impulse response. The agreement between predicted and measured sensitivity is good. The average deviation from the data (square root of average squared residual) is about 3 dB, a reasonable approximation given that there were no free parameters in the fitting procedure.

## 4. DISCUSSION

This study was designed to estimate the impulse response of color and luminance vision to patterned stimuli. At the level of light adaptation (147 Td) and spatial frequency (1 cycle/deg) used in this study, the estimated impulse-response function for luminance stimuli was diphasic, while that for color was monophasic.

### A. Assumptions

The data analysis rested on three major assumptions: (1) small-signal linearity, (2) probability summation at threshold, and (3) that the impulse-response functions for both luminance and color could be approximated by the exponentially damped frequency-modulated sine wave of Eq. (2).

Small-signal linearity is a standard assumption for most studies of this type and finds some justification in the literature.<sup>9,10</sup> Further support is given by the fact that the

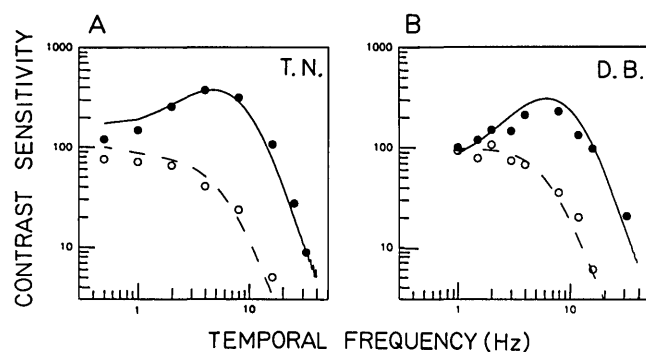


Fig. 5. The data points show contrast sensitivity for detecting luminance (filled circles) and chromatic (open circles) gratings, counterphased at variable temporal frequency. The stimuli were presented within a Gaussian temporal window (time constant, 230 ms). The curves represent predicted contrast sensitivity, obtained by convolving the hypothetical impulse-response functions plotted in Fig. 3 with the stimulus and applying probability summation over time (see text). The square roots of the average squared residual between prediction and data were 2.0 (luminance) and 2.29 (color) dB for TN and 2.15 and 2.0 dB for DB. This fit is reasonable, given that there are no degrees of freedom in the prediction.

thresholds for both chromatic and achromatic contrast-reversed gratings were predicted well by convolution of the impulse response with the stimulus and applying the same model of probability summation. Any major nonlinearity should be revealed by a systematic mismatch between predicted and measured thresholds, at least at some temporal frequencies.

Probability summation results simply from the fact that multiple observations over time increase the probability of a response from a noisy detection process.<sup>21</sup> This phenomenon does not rest on any specific model of detection,<sup>22</sup> and many empirical studies have shown that it can account for much of the dependency of sensitivity on spatial or temporal extent.<sup>18</sup> For many applications, taking account of the probabilistic effects of independent detectors may have little effect, but, as Watson<sup>23</sup> has demonstrated, it can be important in predicting impulse-response functions. A further advantage of this approach is that the identical model could be applied to predicting two-pulse and flicker thresholds, which may explain in part why the predictions were better than many previous attempts.

The third assumption was that the functions could be modeled by an exponentially damped frequency-modulated sinusoid with four free parameters, governing overall gain, fundamental frequency, frequency modulation, and damping. We favored this function over the more conventional  $n$ -pole filter, because we found that with fewer degrees of freedom it converged more readily on the data,<sup>19</sup> irrespective of initial conditions (which often can be a problem<sup>10</sup>). To test whether the function was overly restrictive, we allowed the phase of the sinusoidal modulation to vary at will and found that it always tended to settle at 0 (or 180 deg). However, with this extra parameter, the fitting procedure was less robust and did not always converge.

### B. Comparison with Other Estimates of Impulse Response

Since the choice of analytic function that describes the impulse response will to some extent influence its shape, it is interesting to compare the results with previous results. Many estimates of impulse response assume that the response derives from a minimum-phase filter, a causal filter that produces the minimal number of oscillations and the smallest first moment for any given amplitude spectra.<sup>24</sup> Given these properties, it is therefore not surprising that impulse responses derived with this prediction tend to be monophasic for color and diphasic for luminance.

Because the analytic expression describing our impulses does not assume minimum phase,<sup>19</sup> it is interesting to compare our results with those from a minimum-phase filter of the same amplitude spectrum. The simulations<sup>25</sup> show that the measured impulse responses for the chromatic condition, but not those of the luminance condition, were minimum phase. However, the luminance impulse responses did not diverge drastically from minimum phase and were clearly diphasic.

Most previous estimates of impulse response for luminance stimuli predicted a diphasic response of the type shown in Fig. 3. However, Rouffs and Blommaert<sup>10</sup> (in one of the few studies that does not assume minimum phase) predicted triphasic impulse-response functions for the luminance system, with the second lobe the highest in amplitude (but see also Watson<sup>23</sup>). This result was

reinforced by Tyler,<sup>12</sup> with a clever technique requiring subjects to adjust the phase spectrum of the temporal waveform directly.

To discriminate unambiguously between the two possibilities would require far more subtle techniques than those used here and elsewhere. We merely point out that the diphasic response of the type suggested here is more consistent with evidence suggesting faster reaction times,<sup>3</sup> apparent onset and offset,<sup>4</sup> and VEP latency<sup>5</sup> than a triphasic function in which the major response develops late, about the time of the single peak in the chromatic response. The difference in time to peak of the luminance and chromatic impulse responses of Fig. 3 are  $\sim 30$  ms, which is similar to the estimate obtained by visual evoked potentials<sup>5</sup> under conditions similar to those described here.

The chromatic impulse responses are similar in general shape to those estimated previously by the two-pulse technique<sup>13</sup> but are somewhat faster, about 60 ms compared with 120 ms. This difference may reflect differences in the experimental conditions (100 compared with 147 Td, 45' spot compared with 1 cycle/deg grating), or it may result from the fact that the previous data were collected only for positive summation (providing less constraint) or from the different fitting procedures. However, the estimates of both luminance and chromatic impulse responses follow more closely those of Swanson *et al.*<sup>7</sup> both in general shape and in time to peak. For the conditions most similar to those used here (90-Td, 2-deg patch; see Fig. 3 of Ref. 7), the chromatic impulse response is  $\sim 70$  ms and the luminance impulse response is  $\sim 40$  ms.

Note also that although the precise form of the impulse response for luminance may depend to some extent on the constraints imposed by the fitting procedure, the data reported here show that the functions for chromatic stimuli are clearly different and are monophasic. This conclusion is easily appreciated by inspection of the summation data. A second negative lobe in the impulse response must lead to positive summation of stimuli of reversed polarity at some SOA's together with negative summation (inhibition) of stimuli of identical polarity at these asynchronies. Yet both positive and negative summation curves were clearly monotonic for both observers, asymptoting at the same level with no crossovers.

The impulse response of retinal ganglion cells (derived from the amplitude and the phase spectra for small signals)<sup>26</sup> show interesting similarities to those suggested here. Cells that project to geniculate magnocells respond to luminance stimuli in a way consistent with a diphasic impulse response (similar to the luminance responses of Fig. 3), while cells projecting to parvo cells have almost monophasic impulse responses, again not unlike those reported here.

### C. Motion

One of the most striking qualitative differences between luminance and chromatic vision is that the sensation of motion is greatly reduced at equiluminance: the motion of purely chromatic stimuli appears slower, jerkier, and less compelling than that induced by luminance stimuli.<sup>27</sup> Most recent models of motion perception rely on front-end units with spatiotemporal impulse-response functions that show inhibition in both space and time.<sup>28</sup> It is tempting

to suggest that the weakened sensation of motion at equiluminance may result directly from the lack of the temporal inhibition that is necessary for constructing the velocity-tuned filters for first-order motion sensation.

While most visual illusions are preserved to a greater or lesser extent at equiluminance, metacontrast masking disappears completely.<sup>29</sup> Metacontrast has been linked closely with motion and may be explained readily as a result of fusion or summation of the stimuli by spatio-temporally tuned motion mechanisms.<sup>30</sup> Again, the lack of temporal inhibition in chromatic mechanisms is consistent with the failure of the spatiotemporally separated stimuli to summate with one another, which would explain the lack of metacontrast at equiluminance.

## ACKNOWLEDGMENTS

This research was supported by targeted grant *Robotica* 92.01084.PF67 from the Italian Consiglio Nazionale delle Ricerche and by the National Research Programme for Bioelectronics, contract Ministry for Universities and Research, and SGS Thompson Microelectronics.

## REFERENCES AND NOTES

- H. DeLange, "Research into the dynamic nature of the human fovea—cortex systems with intermittent and modulated light. I. Attenuation characteristics with white and colored light," *J. Opt. Soc. Am.* **48**, 777–784 (1958); D. H. Kelly, "Spatio-temporal frequency characteristics of color-vision mechanisms," *J. Opt. Soc. Am.* **64**, 983–990 (1974); M. D. Regan and C. W. Tyler, "Wavelength-modulated light generator," *Vision Res.* **11**, 43–56 (1971).
- J. J. Wisowaty, "Estimates for the temporal response characteristics of chromatic pathways," *J. Opt. Soc. Am.* **71**, 970–977 (1981).
- M. J. Nissen and J. Pokorny, "Wavelength effects on simple reaction times," *Percept. Psychophys.* **22**, 457–462 (1977); M. J. Nissen, J. Pokorny, and V. Smith, "Chromatic information processing, *J. Exp. Psychol. Percept. Perform.* **5**, 406–419 (1979).
- R. W. Bowen, "Latencies for chromatic and achromatic visual mechanisms," *Vision Res.* **21**, 1457–1466 (1981).
- A. Fiorentini, D. C. Burr, and M. C. Morrone, "Spatial and temporal characteristics of colour vision: VEP and psychophysical measurements," in *From Pigment to Perception: Advances in Understanding Visual Processing*, A. Valberg and B. B. Lee, eds. (Plenum, New York, 1991), pp. 139–150.
- V. C. Smith, R. W. Bowen, and J. Pokorny, "Threshold temporal integration of chromatic stimuli," *Vision Res.* **24**, 653–659 (1984).
- W. H. Swanson, T. Uneno, V. C. Smith, and J. Pokorny, "Temporal modulation sensitivity and pulse-duration thresholds for chromatic and luminance perturbations," *J. Opt. Soc. Am. A* **4**, 1992–2005 (1987).
- M. Ikeda, "Temporal summation of positive and negative flashes in the visual system," *J. Opt. Soc. Am.* **55**, 1527–1534 (1965); "Temporal impulse response," *Vision Res.* **26**, 1431–1440 (1986).
- J. A. J. Roufs, "Dynamic properties of vision—II. Theoretical relationships between flicker and flash thresholds," *Vision Res.* **12**, 279–292 (1972).
- J. A. J. Roufs and F. J. J. Blommaert, "Temporal impulse and step responses of the human eye obtained psychophysically by means of a drift-correcting perturbation technique," *Vision Res.* **21**, 1203–1221 (1981).
- A. B. Watson and J. Nachmias, "Patterns of temporal interaction in the detection of gratings," *Vision Res.* **17**, 893–902 (1977).
- C. W. Tyler, "Psychophysical derivation of the impulse response through generation of ultrabrief responses: complex inverse estimation without minimum-phase assumptions," *J. Opt. Soc. Am. A* **9**, 1025–1040 (1992); C. W. Tyler and L. L. Kontsevich, "Waveform optimization for phase reconstruction of the impulse response," *J. Opt. Soc. Am. A* **10**, 1005–1013 (1993).
- K. Uchikawa and I. Ikeda, "Temporal integration of chromatic double pulses for detection of equal-luminance wavelength changes," *J. Opt. Soc. Am. A* **3**, 2109–2115 (1986).
- D. C. Burr and M. C. Morrone, "Temporal impulse response functions for luminance and colour," *Invest. Ophthalm. Vis. Sci.* **33**, 1314 (1992).
- A. B. Watson and D. G. Pelli, "QUEST: a Bayesian adaptive psychometric method," *Percept. Psychophys.* **33**, 113–120 (1983).
- W. Weibull, "A statistical distribution function of wide applicability," *J. Appl. Mech.* **18**, 292–297 (1951).
- J. A. Nelder and R. Mead, "A simplex method for function minimization," *Comput. J.* **7**, 308–313 (1964).
- A. B. Watson, "Probability summation over time," *Vision Res.* **19**, 515–522 (1979); N. Graham, "Visual detection of aperiodic stimuli by probability summation among narrow band channels," *Vision Res.* **17**, 637–652 (1977); J. Robson and N. Graham, "Probability summation and regional variation in contrast sensitivity across the visual field," *Vision Res.* **21**, 409–418 (1981); M. J. Mayer and C. W. Tyler, "Invariance of the slope of the psychometric function with spatial summation," *J. Opt. Soc. Am. A* **3**, 1166–1172 (1986).
- When parameter  $a_2$  of Eq. (2) equals zero, the Laplace transform  $F(p)$  associated with this impulse response is
 
$$F(p) = \frac{4\pi(p + a_3)a_1a_0}{[(p + a_3)^2 + (2\pi\tilde{a}_1)^2]}$$
 This filter is minimum phase, as all zeros and poles fall on the left-hand side of the complex plane. However, when  $a_2 \neq 0$  analytically deriving the filter equation is difficult but the filter is not necessarily minimum phase.
 The reason for choosing Eq. (2) rather than the more conventional  $n$ -pole approach for modeling impulse response was that unless many constricting assumptions are made about the order of poles and zeros, the functions have too many degrees of freedom for the robustness of the minimization procedure.
- The minimum-phase filters were calculated from the amplitude spectra  $A(i)$  of the impulse-response functions (see Fig. 4), with standard techniques. For minimum-phase filters, the phase spectra  $\Phi(i)$  are related to the logarithm of the amplitude spectra by means of the Hilbert transform, which is readily evaluated by the fast-Fourier transform:
 
$$\Phi(i) = -j \text{FFT}\{\text{sgn}(i)\text{FFT}^{-1}[\log|A(i)|]\},$$
 where  $j = \sqrt{-1}$ ;  $i$  is the frequency index; FFT is the fast-Fourier transform and  $\text{FFT}^{-1}$  its inverse; and  $\text{sgn}$  is the sign function. For more details the reader is referred to R. R. Read and S. Treitel, "The stabilization of two-dimensional recursive filters via the discrete Hilbert transform," *IEEE Trans. Geosci. Electron.* **GE-11**, 205–207 (1973).
- D. M. Green and J. A. Swets, *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966).
- D. G. Pelli, "Uncertainty explains many aspects of visual contrast detection and discrimination," *J. Opt. Soc. Am. A* **2**, 1508–1532 (1985); "On the relation between summation and facilitation," *Vision Res.* **27**, 119–123 (1985).
- A. B. Watson, "Derivation of the impulse response: comments on the method of Roufs and Blommaert," *Vision Res.* **82**, 1335–1337 (1982).
- J. D. Victor, "Temporal impulse response from flicker sensitivities: causality, linearity, and amplitude do not determine phase," *J. Opt. Soc. Am. A* **6**, 1302–1303 (1989); G. Dagnelie, "Temporal impulse response from flicker sensitivities: practical considerations," *J. Opt. Soc. Am. A* **9**, 659–672 (1992).
- Note that this procedure does not require arbitrary extrapolation rules for predicting unmeasurable responses at low temporal frequencies, which can alter the minimum-phase impulse-response functions markedly (see Ref. 24).

26. J. Kremers, B. B. Lee, J. Pokorny, and V. C. Smith, "Responses of macaque ganglion cells and human observers to compound periodic waveforms," *Vision Res.* (to be published).
27. V. S. Ramachandran and R. L. Gregory, "Does colour provide an input to human motion perception?" *Nature* **275**, 55-56 (1978); P. Cavanagh, C. W. Tyler, and O. E. Favreau, "Perceived velocity of moving chromatic gratings," *J. Opt. Soc. Am. A* **1**, 893-899 (1984); D. Lindsey and D. Y. Teller, "Motion at isoluminance: discrimination/detection ratios for moving isoluminant stimuli," *Vision Res.* **30**, 1751-1761 (1990); P. Cavanagh and S. Anstis, "The contribution of color to motion in normal and color-deficient observers," *Vision Res.* **31**, 2109-2148 (1991); K. T. Mullen and J. C. Boulton, "Absence of smooth motion perception in colour vision," *Vision Res.* **32**, 483-488 (1992).
28. J. P. H. Van Santen and G. Sperling, "Elaborated Reichardt detectors," *J. Opt. Soc. Am. A* **2**, 300-321 (1985); E. H. Adelson and J. R. Bergen, "Spatio-temporal energy models for the perception of motion," *J. Opt. Soc. Am. A* **2**, 284-299 (1985); D. C. Burr, J. Ross, and M. C. Morrone, "Seeing objects in motion," *Proc. R. Soc. (London) Ser. B* **227**, 249-265 (1986).
29. R. W. Bowen, J. Pokorny, and D. Cacciato, "Metacontrast masking depends on luminance transients," *Vision Res.* **17**, 971-975 (1977).
30. D. C. Burr, "Summation of target and mask metacontrast stimuli," *Perception* **13**, 183-192 (1984).