

## Review Article

# Into the twilight zone: the complexities of mesopic vision and luminous efficiency

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### Abstract

Of all the functions that define visual performance, the mesopic luminous efficiency function is probably the most complex and hardest to standardise or model. Complexities arise because of the substantial and often rapid visual changes that accompany the transition from scotopic to photopic vision. These are caused not only by the switch from rod to cone photoreceptors, but also by switches between different post-receptoral pathways through which the rod and cone signals are transmitted. In this review, we list several of the complexities of mesopic vision, such as rod–cone interactions, rod saturation, mixed photoreceptor spectral sensitivities, different rod and cone retinal distributions, and the changes in the spatial properties of the visual system as it changes from rod- to cone-mediated. Our main focus, however, is the enormous and often neglected temporal changes that occur in the mesopic range and their effect on luminous efficiency. Even before the transition from rod to cone vision is complete, a transition occurs within the rod system itself from a sluggish, sensitive post-receptoral pathway to a faster, less sensitive pathway. As a consequence of these complexities, any measure of mesopic performance will depend not only on the illumination level, but also on the spectral content of the stimuli used to probe performance, their retinal location, their spatial frequency content, and their temporal frequency content. All these should be considered when attempting to derive (or to apply) a luminous efficiency function for mesopic vision.

**Keywords:** destructive interference, flicker sensitivity, luminance, luminous efficiency functions, mesopic, phase delays, photopic, scotopic

### Introduction

The visual system is able to operate effectively from starlight to bright sunlight; over a change in illumination by more than a factor of  $10^{11}$ , despite the limited (approximately  $10^2$ ) response range of its constituent neurones. One of the ways in which it achieves this is by switching between two different types of photoreceptor with partially overlapping operating ranges: the sensitive rods, functioning at lower levels of illumination, and the less sensitive cones, functioning at higher levels.

*Figure 1* illustrates the range of illumination levels to which the human eye is exposed, from absolute rod

threshold and the detection of a few photons to levels that bleach almost all of the photopigment. The range is divided into three regions according to which types of photoreceptor are functioning. The scotopic region, within which only rods operate, starts at absolute rod threshold and ends at cone threshold. The photopic region, within which only cones operate, begins at rod saturation and extends to the highest illumination levels. Finally, between cone threshold and rod saturation lies the mesopic region, within which both rods and cones operate. This intermediary region is the one that concerns us in this review. We discuss several of its complexities, but focus, in particular, upon the complexities that arise because of the large *temporal* differences between rod- and cone-generated signals. These differences are caused in part by differences between the responses of the rod and cone photoreceptors themselves (e.g. Baylor, 1987), but they are additionally caused by the differences between the responses of the rod and cone post-receptoral pathways (see Sharpe and Stockman, 1999). Because mesopic vision is inherently

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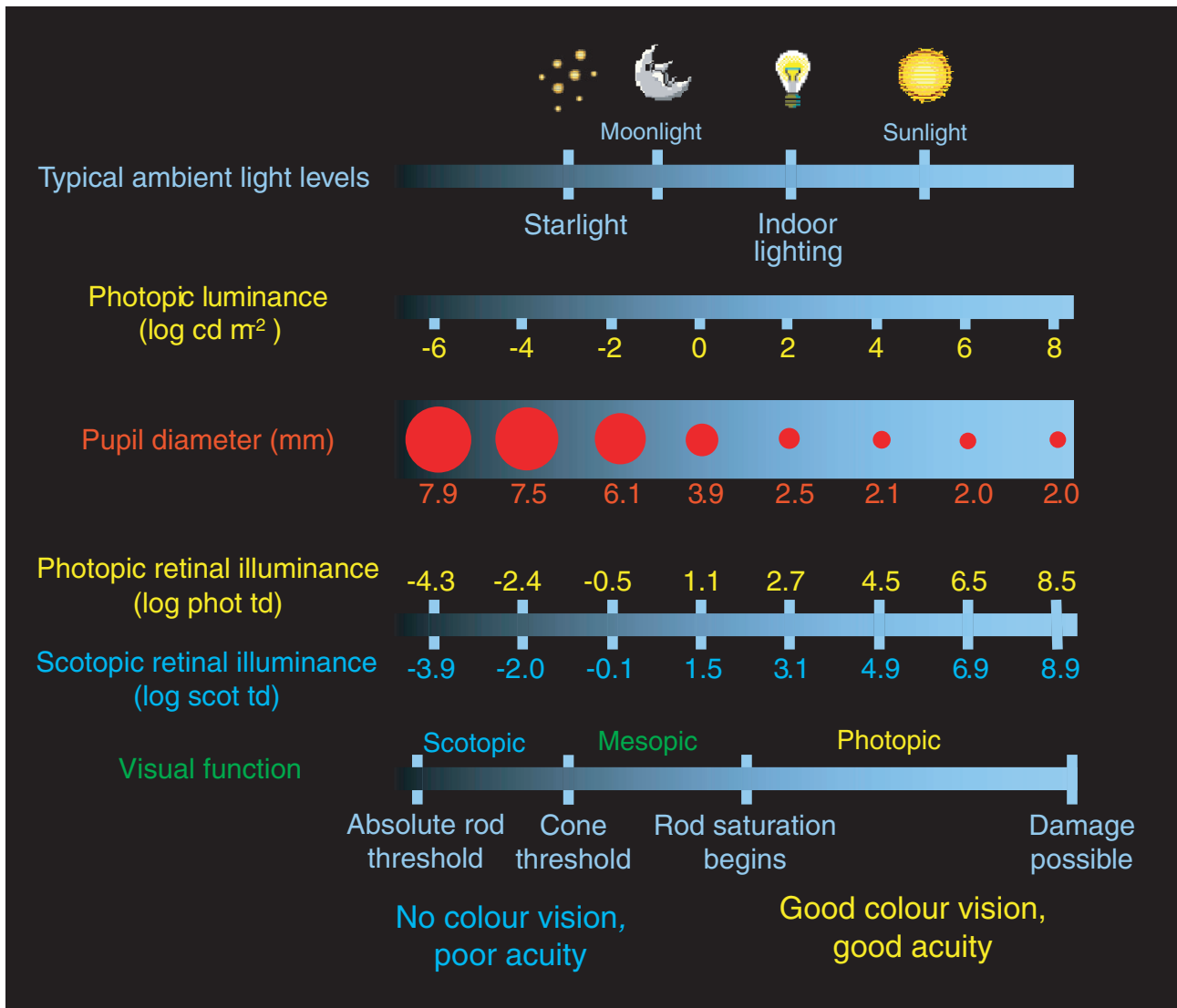
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**Figure 1.** Illumination levels. Typical ambient light levels are compared with photopic luminance (log cd m<sup>-2</sup>), pupil diameter (mm), photopic and scotopic retinal illuminance (log photopic and scotopic trolands respectively) and visual function. The scotopic, mesopic and photopic regions are defined according to whether rods alone, rods and cones, or cones alone operate. The conversion from photopic to scotopic values assumed a white standard CIE D65 illumination (based on the design of Hood and Finkelstein, 1986).

much more complex than either scotopic or photopic vision, by way of introduction, we will begin by discussing each of these first.

### Scotopic and photopic vision

Scotopic luminous efficiency and scotopic vision are comparatively straightforward because they depend on the behaviour of a single *univariant* photoreceptor type, the rods. Univariance means that the photoreceptor response varies only according to the number of photons that are absorbed. All that varies with photon wavelength is the *probability* that a photon will be absorbed, not the photoreceptor response *after* it has

been absorbed. As a result, individual photoreceptors are colour blind: changes in wavelength are indistinguishable from changes in intensity. A consequence of univariance is that *when the rods are isolated* the rod spectral sensitivity or scotopic luminous efficiency function [ $V'(\lambda)$ ] is additive below rod saturation (i.e. below high mesopic luminance levels where the rod response range is exceeded and the rods are no longer capable of delivering a differential signal). Thus, scotopic luminous efficiency fulfils the basic requirement of any system of photometry, which is that the luminous efficiency of any mixture of lights is the sum of the efficiencies of the components of the mixture; otherwise known as Abney's Law (Abney and Festing, 1886; Abney, 1913).

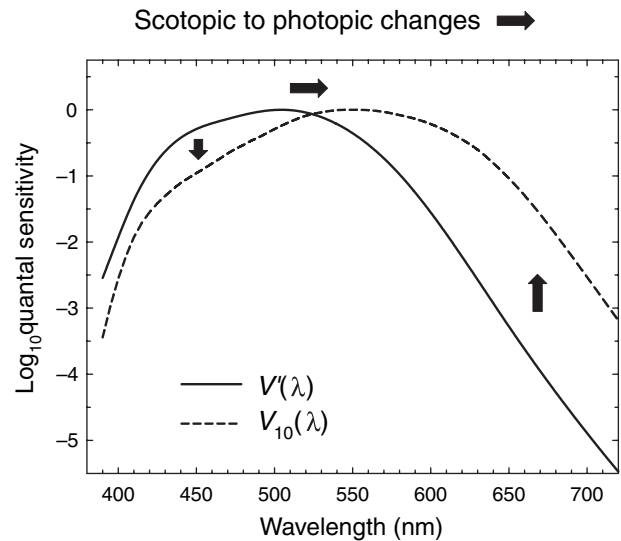
Additivity is less likely to hold if vision depends upon more than one photoreceptor, which is the case for photopic vision, where two or three different types of cone photoreceptor are contributing their responses. In fact, additivity then only holds under fairly restricted measurement conditions. For photopic vision, such restricted conditions include minimum flicker (heterochromatic flicker photometry or HFP), in which continuously alternating lights of different wavelength are matched in luminance to minimise the perception of flicker, and minimally distinct border (or MDB), in which the relative intensities of the two half fields are set so that the border between them appears 'minimally distinct'. Both of these techniques appear to satisfy additivity under some conditions; however, additivity does not hold for techniques, such as side-by-side heterochromatic brightness matching, typically used to estimate mesopic luminous efficiency (e.g., Sperling, 1958; Wagner and Boynton, 1972).

But, even for the very restricted conditions of HFP and MDB, it should be recognised that the photopic luminous efficiency function,  $V(\lambda)$ , falls into a quite different category from the scotopic function,  $V'(\lambda)$ , because it depends on the outputs of at least two cone photoreceptor types. Yet,  $V(\lambda)$  is often treated as if it were [like  $V'(\lambda)$ ] the spectral sensitivity of a univariant photoreceptor. Unlike photoreceptor spectral sensitivities, however, the shape of  $V(\lambda)$  changes with chromatic adaptation (e.g. De Vries, 1948; Eisner and MacLeod, 1981; Stockman *et al.*, 1993). Thus, the photopic (and by extension the mesopic) luminous efficiency function can only be of limited applicability, because it defines luminance strictly only under the conditions for which it was measured. Different functions must be derived for different conditions, and any given function is not straightforwardly generalisable to other conditions of adaptation – particularly to other conditions of chromatic adaptation. In contrast, in the scotopic range the luminous efficiency function does not change with adaptation.

In short, the problem is that although the scotopic luminous efficiency function is determined primarily by receptor events, the photopic and mesopic functions are determined by post-receptor as well as receptor events.

### The challenge of mesopic photometry

Figure 2 shows the CIE scotopic  $V'(\lambda)$  (continuous line) and the Commission Internationale de l'Éclairage (CIE) 1964 10-deg photopic  $V_{10}(\lambda)$  (dashed line, also known as the  $\bar{y}_{10}(\lambda)$  colour matching function) luminous efficiency functions. The retinal region over which the photopic  $V_{10}(\lambda)$  function was measured is more similar to that over which  $V'(\lambda)$  was originally measured than the 2-deg



**Figure 2.** CIE scotopic  $V'(\lambda)$  (continuous line) and the CIE 1964 10-deg photopic  $V_{10}(\lambda)$  (dashed line, also known as the  $\bar{y}_{10}(\lambda)$  colour matching function) luminous efficiency functions. The arrows highlight the scotopic to photopic changes (see text).

photopic  $V(\lambda)$  function, so it is the more appropriate function for comparison. Sometimes known as the Purkinje shift (Purkinje, 1823), the transition from scotopic to photopic conditions causes a shift in the wavelength of peak sensitivity ( $\lambda_{\max}$ ) from 504 to 550 nm in quantal units (or from 507 to 555 nm in energy units), a relative increase in sensitivity to longer wavelengths, and a relative decrease in sensitivity to shorter wavelengths (see arrows, Figure 2).

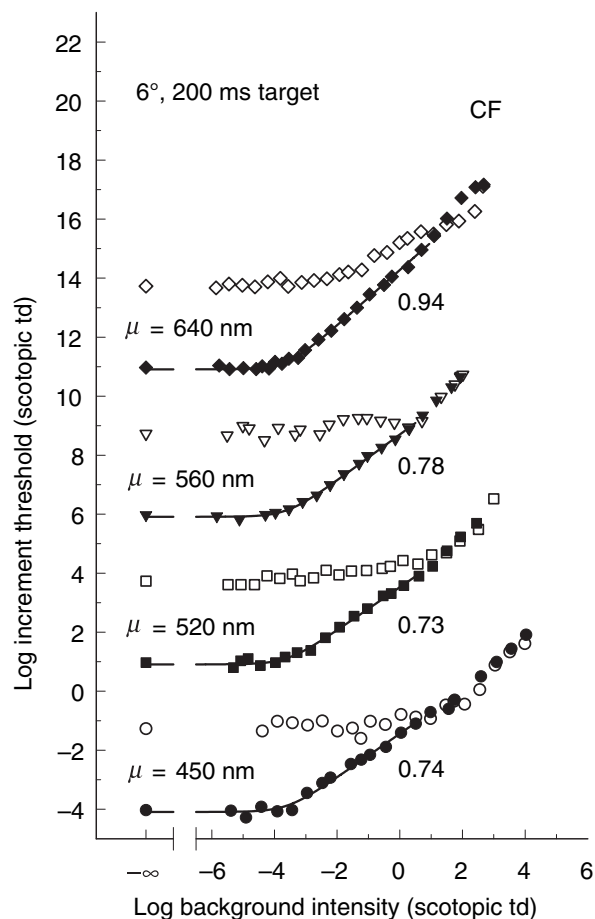
The challenge of mesopic photometry is to characterise how luminous efficiency changes between the scotopic and photopic levels. Previously, the main approach has been to measure mesopic luminous efficiency functions as a function of mesopic intensity level and then to try to model them as combinations of the scotopic and photopic functions. The modelling has proved to be difficult.

Mesopic luminous efficiency functions have been measured several times before (e.g. Walters and Wright, 1943; Kinney, 1958; Palmer, 1968; Kokoschka, 1972; Yaguchi and Ikeda, 1984; Nakano and Ikeda, 1986; Sagawa and Takeichi, 1986; Viénot and Chiron, 1992; He *et al.*, 1998). Were the relationships between the mesopic luminous efficiency function and the scotopic and photopic functions simple – for example a weighted linear combination, the weights of which changed with luminance – mesopic photometry would be relatively straightforward. The relationship, however, is complex. Several attempts have been made to model empirically the scotopic to photopic transition. Implicit in most of these models is the assumption that rod and cone signals interact. For instance, Palmer (1968) derived a non-linear empirical formula relating  $V'(\lambda)$  and  $V_{10}(\lambda)$ , while Kokoschka and Bodmann (1975) derived a model in

which the contributions of the three different cone types as well as the rods were considered (see also Trezona, 1991). More recently, Ikeda and Shimozono (1981) and Sagawa and Takeichi (1986) modelled the logarithm of the mesopic luminous efficiency as the weighted sum of the logarithms of the scotopic and photopic functions (i.e. their geometric mean), but they both used the CIE brightness rather than the CIE luminance function (see also Yaguchi and Ikeda, 1984; Nakano and Ikeda, 1986). In fact, as these authors argue, as mesopic luminous efficiency is typically measured by direct brightness matching, a photopic brightness matching function is likely to be more appropriate than a luminance function. Brightness matching, however, does not obey Abney's law (see above).

In an attempt to overcome the additivity failures that are inherent in the use of the direct brightness matching method, He and co-workers used a binocular synchronicity method (which they refer to as a reaction time difference method) to measure mesopic visual performance (Bierman *et al.*, 1998; He *et al.*, 1998). Their technique effectively uses a version of the 'field' sensitivity method of Stiles (1978). The subject adjusts the illumination level in the test eye so that the onset of a white flash in that eye appears synchronous with the onset of a second white flash presented simultaneously to the reference eye. In their experiment, the background illumination in the reference eye was fixed at 589 nm and at one of three mesopic luminance levels, while the background illumination in the test eye was set at one of several wavelengths, but could be adjusted in luminance by the subject in order for the two flashes to appear synchronous. The authors claim that for each fixed level in the reference eye the mesopic luminous efficiency function obtained – by finding the illumination at each background wavelength that made the flashes appear synchronous – can be modelled by a simple linear combination of  $V'(\lambda)$  and  $V_{10}(\lambda)$  (He *et al.*, 1998). For further information about the synchronicity method, see also CIE (1989, 2001). Although promising, binocular synchronicity measures must be influenced by the complex changes in rod-cone delay that accompany changes in adaptation level (see below), as well as by the changes in delay caused by changes in the relative rod and cone contributions to the detection of the two flashes, neither of which are likely to be simple. An obvious complication, given that the adapting field wavelength in one eye is varied from long to short wavelengths, is that the luminous efficiency will be distorted by the additional suppression of the rods by the cones, which are excited more by long-wavelength background fields (see Figure 3).

The difficulties of mesopic photometry are to some extent unavoidable. They derive from a number of inherent complexities of mesopic vision, some of which



**Figure 3.** The effect of background wavelength ( $\mu$ ) on the form of the rod incremental threshold-versus-intensity curve for a normal observer, CF. The target conditions were chosen to favour the rods relative to the cones (see text, for details). Four background wavelengths are shown: 450 (circles), 520 (squares), 560 (triangles) and 640 (diamonds) nm. The open symbols represent the thresholds measured against steady backgrounds; the filled symbols, those measured for the same stimulus conditions during the plateau that terminates the cone phase of recovery, before rods recover enough to respond, following exposure to a white (3100 K) bleaching light of  $7.7 \log_{10}$  photopic trolands. All the curves are correctly placed with respect to the axis of the abscissa, but the axis of the ordinates is correct only for the lowest curve in each of the three panels; the other curves are displaced upward in  $5 \log_{10}$  unit intervals. The solid lines drawn through each set of incremental threshold data are fitted, theoretical curves; their slope is indicated to the right. See Sharpe *et al.* (1992) for full details. (Reprinted from the *Journal of Physiology*, Vol. 463, Sharpe L.T., Stockman A., Fach C.C., Markstahler U. Temporal and spatial summation in the human rod visual system, pp 325–348, copyright 1993, used with permission from Blackwell Publishing Ltd).

have been acknowledged and others of which have been ignored. We discuss some of these complexities next.

### Complexities of mesopic photometry

Mesopic vision and mesopic photometry are complex because they depend on the outputs of both the rods

and the cones. Not only are there differences in the rod and cone photoreceptor responses themselves, but also in the properties of the post-receptoral pathways subserving the rod and cone signals before they merge. The scotopic system must be sensitive enough to respond to just a few photons at low levels, so that it must integrate signals over space and time. Such integration is less important for the photopic system, which can therefore provide better spatial and temporal acuity. However, both systems reduce their spatial and temporal integration to some extent as their adaptation levels increase. By trading off integration for acuity, their sensitivities are reduced and their dynamic ranges extended. In general, though, photopic (cone) integration is less for any given condition than scotopic (rod) integration.

#### *Complexity 1: more than one photoreceptor operates*

Mesopic vision depends upon more than one photoreceptor. Mesopic luminous efficiency is therefore unlikely to be additive, since it will reflect the effects of any selective adaptation at the rod and cone photoreceptors or within their pathways before their signals merge. As discussed above, mesopic luminous efficiency curves cannot be predicted from simple linear combinations of the photopic and scotopic efficiency curves, nor does the combination change in a simple way with luminance.

#### *Complexity 2: rods and cones interact*

Figure 3 shows incremental thresholds or threshold-versus-intensity (TVI) curves (open symbols) from Sharpe *et al.* (1992) measured in a normal trichromat, CF, using a 520-nm target against different backgrounds. Cone thresholds, which were measured for the same target and background conditions but during the plateau terminating the cone phase of recovery (before the rods have fully recovered) after a bleach of  $7.7 \log_{10}$  photopic td, are shown as filled symbols. Below the cone thresholds, rods mediate target detection.

The slope of the TVI function is steeper on the 640 nm background wavelength than on the shorter wavelength backgrounds, even over those intensity ranges below cone threshold within which only rods determine threshold. As the main difference between the 640 nm field and the other fields is that it more strongly excites cones, this indicates that the sensitivity of the rods to an incremental target is not determined by quantal absorptions in the rods alone but by quantal absorptions in both the rods and the cones. Thus, mesopic luminous efficiency must depend on the mean chromaticity of the illumination and its relative stimulation of the rods and cones.

There is substantial literature on rod–cone interactions and how they affect visual sensitivity (e.g. Frumkes *et al.*, 1972, 1973, 1986; Makous and Boothe, 1974; Frumkes and Temme, 1977; Latch and Lennie, 1977; Bauer *et al.*, 1983a,b; Goldberg *et al.*, 1983; Alexander and Fishman, 1984; Coletta and Adams, 1984; Buck *et al.*, 1985; Shapiro, 2002). Such interactions must be incorporated into any complete model of mesopic luminous efficiency.

#### *Complexity 3: rods saturate*

Mesopic luminous efficiency changes abruptly and non-linearly in the region of rod saturation (e.g. Aguilar and Stiles, 1954; Adelson, 1982), which begins at about  $2.0 \log_{10}$  scotopic trolands (sc td) and extends to about  $3.0 \log_{10}$  sc td. In this region, the rod contribution to mesopic luminous efficiency is no longer linear or straightforward. As a result, mesopic luminous efficiency function in the rod saturation region is both extremely difficult to predict, and extremely difficult to measure.

#### *Complexity 4: rods and cones have different spatial distributions on the retina*

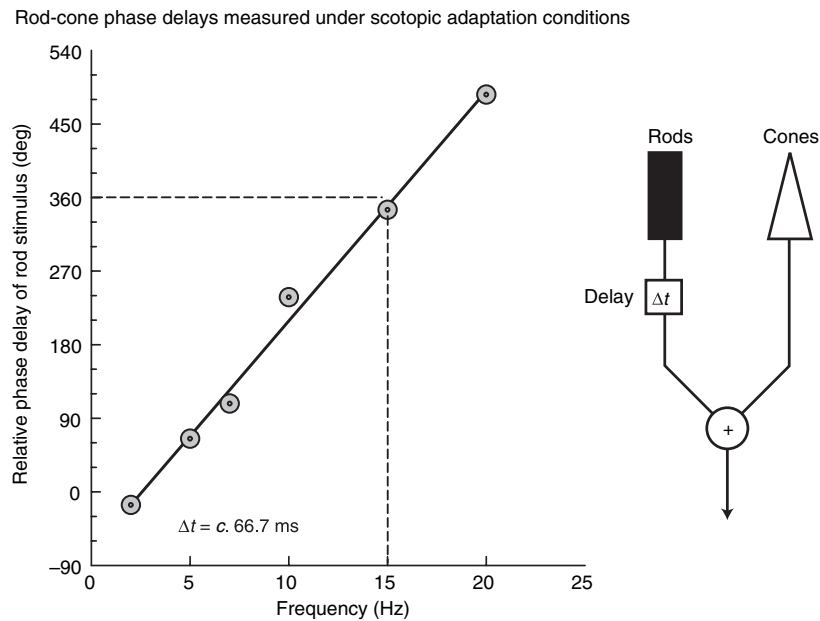
Cone density peaks in the centre of the fovea, where rods are absent, while rods peak at an eccentricity of about  $20^\circ$  of visual angle (e.g. Østerberg, 1935; Curcio *et al.*, 1990). Thus, the mesopic luminous efficiency function will depend critically on the spatial location and size of the visual stimulus.

#### *Complexity 5: rod and cone vision have very different spatial contrast sensitivities*

Scotopic and photopic vision exhibit different spatial acuities (e.g. König, 1897; Hecht and Mintz, 1939). Further their spatial contrast sensitivity functions have markedly different shapes at moderate to high spatial frequencies (e.g. D'Zmura and Lennie, 1986; Hess *et al.*, 1987). For example, the rod spatial contrast sensitivity function peaks at approximately 0.9 cycles per degree, whereas the cone function peaks at about 2.8 (D'Zmura and Lennie, 1986). As a result of these differences, mesopic luminous efficiency will depend upon the spatial frequency content of the visual stimulus (i.e. size, sharpness of border, etc.).

#### *Complexity 6: temporal differences between rod and cone signals*

Because of the substantial differences in temporal properties between rod- and cone-mediated vision, measures of mesopic luminous efficiency *and* measures



**Figure 4.** Rod-cone phase delays (degrees) measured as a function of frequency (dotted grey circles) at a scotopic adaptation level of  $-0.43 \log$  scotopic trolands (just below the null or region of invisible flicker in *Figure 13*). A flickering 500 nm rod-detected target and a 680-nm cone-detected target were superimposed in the centre of a larger, dim deep-red background. The observer adjusted the two flickering lights away from opposite phase to perfect the null. Based on Sharpe *et al.* (1989). The slope of the line fitted to the data is consistent with a time delay between the rod and cone signals of *c.* 66.7 ms. Inset shows the convergence of the rod and cone pathways with an additional delay of  $\Delta t$  interposed in the rod pathway.

of visual performance under mesopic conditions will be strongly dependent not only on the relative sensitivities of the rods and cones, but also on the temporal characteristics of the stimuli used to make those measurements. Thus, targets of different duration may produce mesopic luminosity functions with different rod-to-cone weightings.

The luminous perception of steadily-viewed targets will, of course, be less influenced by temporal differences between the rod and cone signals than that of flickering or transient targets. In a real-world environment, however, perfectly steady targets are seldom encountered (and would in any case perceptually fade). Mesopic vision, like scotopic and photopic vision, depends upon temporal transients. Rod and cone temporal differences will thus profoundly affect most measures of mesopic visual performance in real-world situations as well as many measures made in laboratory situations, such as synchronicity settings, reaction times, flicker photometry and flicker detection.

#### Rod-cone delays

It is well known that rod vision is much more sluggish than cone vision (e.g. Hecht and Schlaer, 1936; Arden and Weale, 1954; Veringa and Roelofs, 1966; MacLeod, 1972). Although an oversimplification, it is helpful to think of this sluggishness as an extra delay ( $\Delta t$ ) in the rod pathway, as modelled in the inset of *Figure 4*. A

more exact, objective approach is to measure the delay as a function of temporal frequency (i.e. to measure the phase delay,  $\Delta\theta$ , as a function of temporal frequency). Such measurements can be made by perceptually nulling (i.e. cancelling the flicker percept between) two sinusoidally flickering lights, chosen so that one light is detected by the rods and the other by the cones.

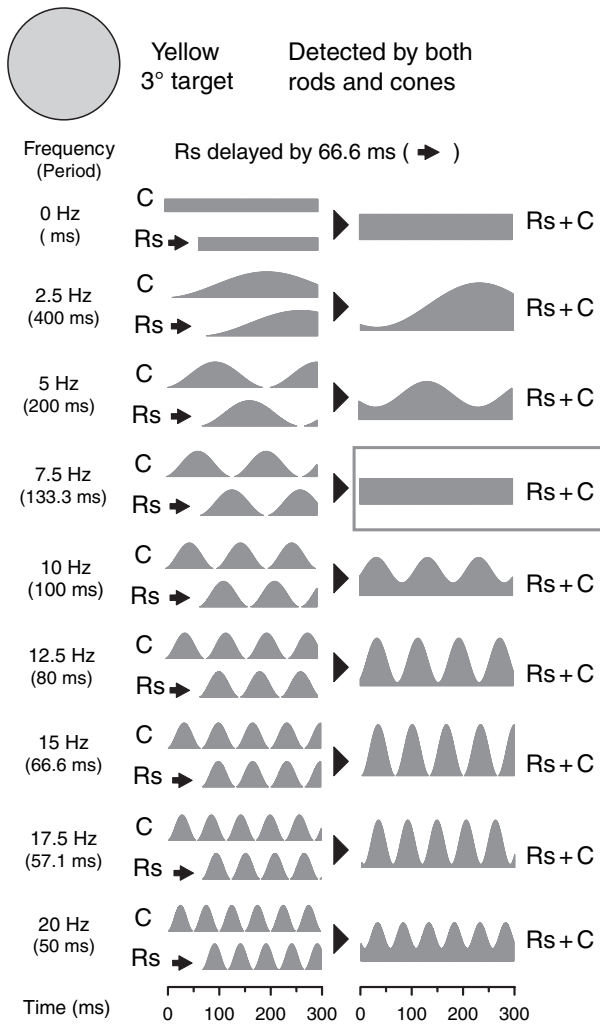
If the two lights were in opposite phase (i.e.  $180^\circ$  apart in phase), equal in effective intensity, and seen by a single photoreceptor type, then the two would destructively interfere to produce a steady (or nulled) output at all frequencies. If, however, the two opposite-phase lights were seen separately by rods and cones, then, because of the rod-cone delay, they would not null each other at most frequencies (unless the delay was a multiple of the flicker cycle). To produce a null, the rod light would have to be physically advanced away from opposite phase by the same amount that the signals it produces are delayed *within* the visual system relative to the cone signals. These adjustments, made as a function of frequency, yield the rod-cone phase lag data shown in the left panel of *Figure 4*. We refer to these data as pertaining to *scotopic* levels, even though the cones are stimulated by one of the flickering lights, because the adaptive state of the rods is within the scotopic range, and the cones are used only as a reference.

If the delay is a true time delay, rather than, for example, persistence (which can delay some frequencies by more than others), the required relative phase

adjustment should be a linear function of frequency. The line fitted to the data shows that this is at least approximately correct for the rod-cone delay. The line is consistent with a one cycle (360 deg) delay being reached by about 15 Hz. Given that the period of one cycle at 15 Hz is 66.7 ms, it follows that this value approximates the rod-cone time delay,  $\Delta t$  (but see Figure 9).

*Rod-cone self-cancellation*

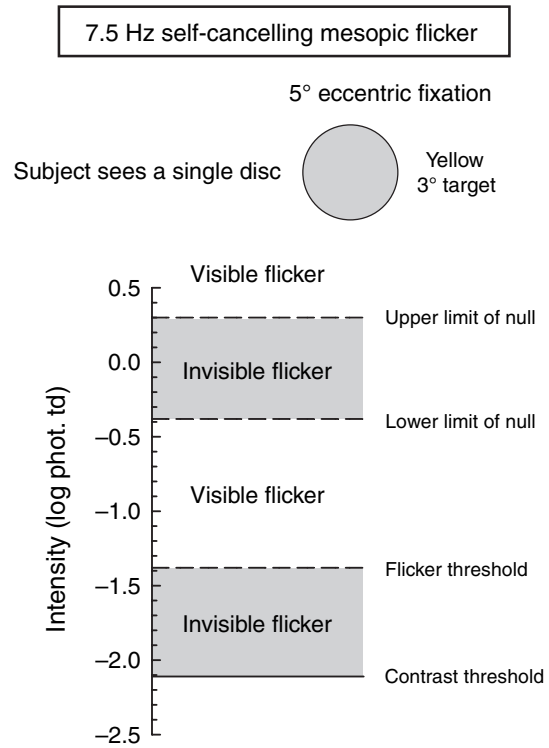
Instead of ensuring that two flickering stimuli are seen separately by rods and cones, we could instead choose a single, flickering light that is seen by *both* rods and



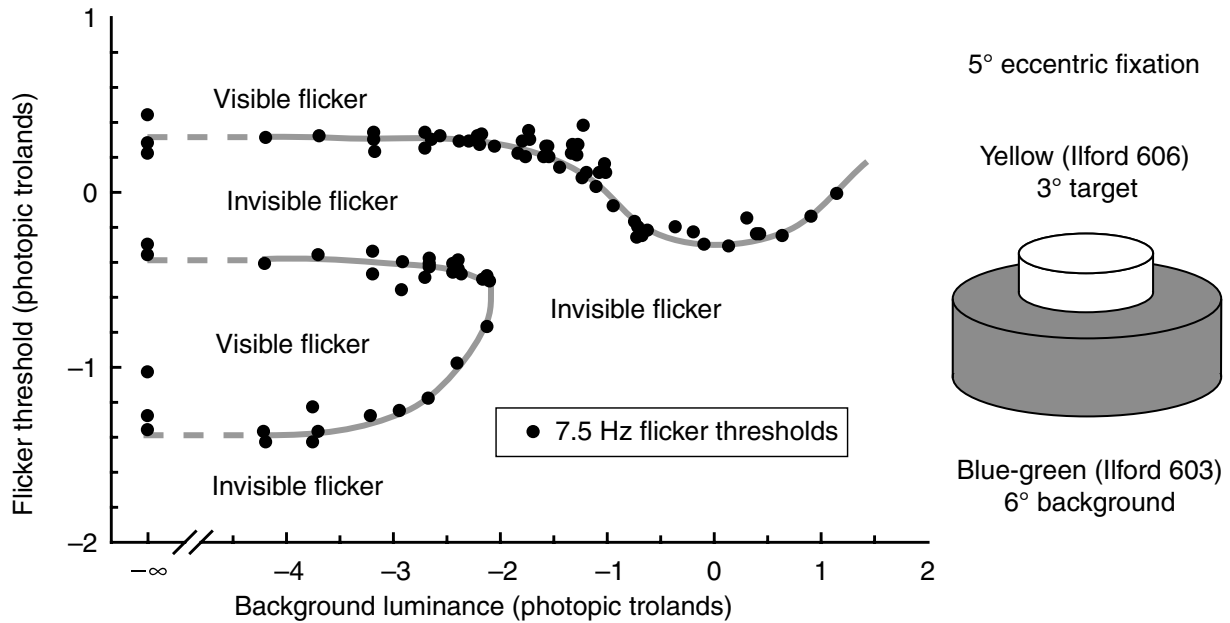
**Figure 5.** A sinusoidally-flickering, broadband, yellow target of 3 deg of visual angle is detected by both rods and cones at mesopic levels, though the former signal is delayed relative to the latter (MacLeod, 1972). Here, we show for different temporal frequencies, the effect of adding together two sinusoids (Rs + C), one of which is detected by the slow rod pathway (Rs) and is delayed by 66.7 ms relative to the second, which is detected by the cones (C). The box highlights that at 7.5 Hz the two sinusoids destructively interfere and cancel each other.

cones – as would be fairly common in real-life mesopic situations. The effect of a rod-cone delay of 66.7 ms on the detectability of flicker is illustrated in Figure 5. At low frequencies and at frequencies near 15 Hz, the rod and cone flicker signals constructively interfere to produce a larger signal than either signal alone. At 7.5 Hz, however, the delay is such that the rod and cone signals destructively interfere and cancel each other. We refer to this as self-cancellation.

The phenomena of rod-cone self-cancellation, which is summarised in Figure 6, was first reported by MacLeod (1972). In his original experiments, the subject was presented with a single disc of light, which flickered at 7.5 Hz. At very low luminance levels, neither the disc nor the flicker can be detected. As the intensity is increased, the disc becomes visible as the contrast threshold is crossed, but it remains steady and non-flickering until the flicker threshold is crossed. At 7.5 Hz, the flicker (but not the disc) disappears at an intensity above the flicker threshold (the lower limit of null) and then reappears again at a still higher intensity (the upper limit of null).



**Figure 6.** 7.5 Hz self-cancelling mesopic flicker. The perceptual effects of increasing the intensity of a yellow disc, 3 deg visual angle in diameter, presented at 5 deg eccentricity, and flickering at 7.5 Hz. At very low intensity levels, neither the disc nor flicker can be detected. As the intensity is increased, the disc becomes visible at the contrast threshold, but the flicker remains invisible until the flicker threshold is crossed. At the lower limit of null, the 7.5 Hz flicker disappears, only to reappear at the upper limit of null. Based on data from Figure 1 of MacLeod (1972).



**Figure 7.** Flicker detectability contours for 7.5 Hz flicker plotted as a function of background retinal illuminance ( $\log_{10}$  photopic trolands). The filled circles through which the continuous line has been drawn represent points at which the 7.5 Hz flicker is just visible. The detectability function is interrupted by a substantial region within which the flicker is invisible. Areas of visible and invisible flicker are noted. Inset shows the experimental conditions: a 3 deg diameter yellow target was presented in the centre of a 6 deg diameter blue-green background at an eccentricity of 5 deg. The wavelengths were selected by the use of broadband Ilford filters as noted. Based on *Figure 1* of MacLeod (1972).

The effect of rod adaptation on the null can be gauged by superimposing the yellow disc on a blue-green background, which selectively adapts the rods. By increasing the intensity of the background, the rods become increasingly less sensitive relative to the cones. *Figure 7* shows that as the rods are adapted by increasing the background level, the rod flicker threshold rises, as expected, and meets the lower limit of the null. Above the null, the flicker reappears at the upper limit of the null. With further increases in background level, the upper limit of the null falls. This fall occurs because the cone flicker signal is no longer cancelled by the rod signal. The final rise in flicker threshold above 0.5 log photopic td is due to the blue-green background adapting the cones. Rod-cone flicker cancellation has also been described by van den Berg and Spekreijse (1977).

*Phase interactions and spectral sensitivity*

Constructive and destructive interference between rod and cone signals will alter the mesopic luminous efficiency function. If we assume that the mesopic luminous efficiency [ $V_{mes}(\lambda)$ ], is a linear combination of the CIE scotopic luminous efficiency [ $V'(\lambda)$ ] and the CIE 1964 10-deg photopic luminous efficiency [ $V_{10}(\lambda)$ ], then:

$$\log_{10} V_{mes}(\lambda) = b + \log_{10} \sqrt{[a \cos \Delta\theta V_{10}(\lambda) + V'(\lambda)]^2 + [a \sin \Delta\theta V_{10}(\lambda)]^2}, \tag{1}$$

where  $a$  is the relative photopic weight,  $b$  is a scaling factor, and  $\Delta\theta$  is the phase delay between the rod and cone signals. We can predict  $V_{mes}(\lambda)$  for various values of  $a$  and  $\Delta\theta$ .

*Figure 8* shows the theoretical predictions for two values of  $a$ . In the left panels,  $a = 0.20$ , which makes the scotopic and photopic luminous efficiencies equal at 570 nm ( $a$  is given relative to unity peaks of the  $V'(\lambda)$  and  $V_{10}(\lambda)$  luminous efficiency functions). In the right panels,  $a = 1.94$ , which makes them equal at 500 nm. The predictions are shown for  $\Delta\theta = 0, 45, 90, 135$  and  $180^\circ$ .

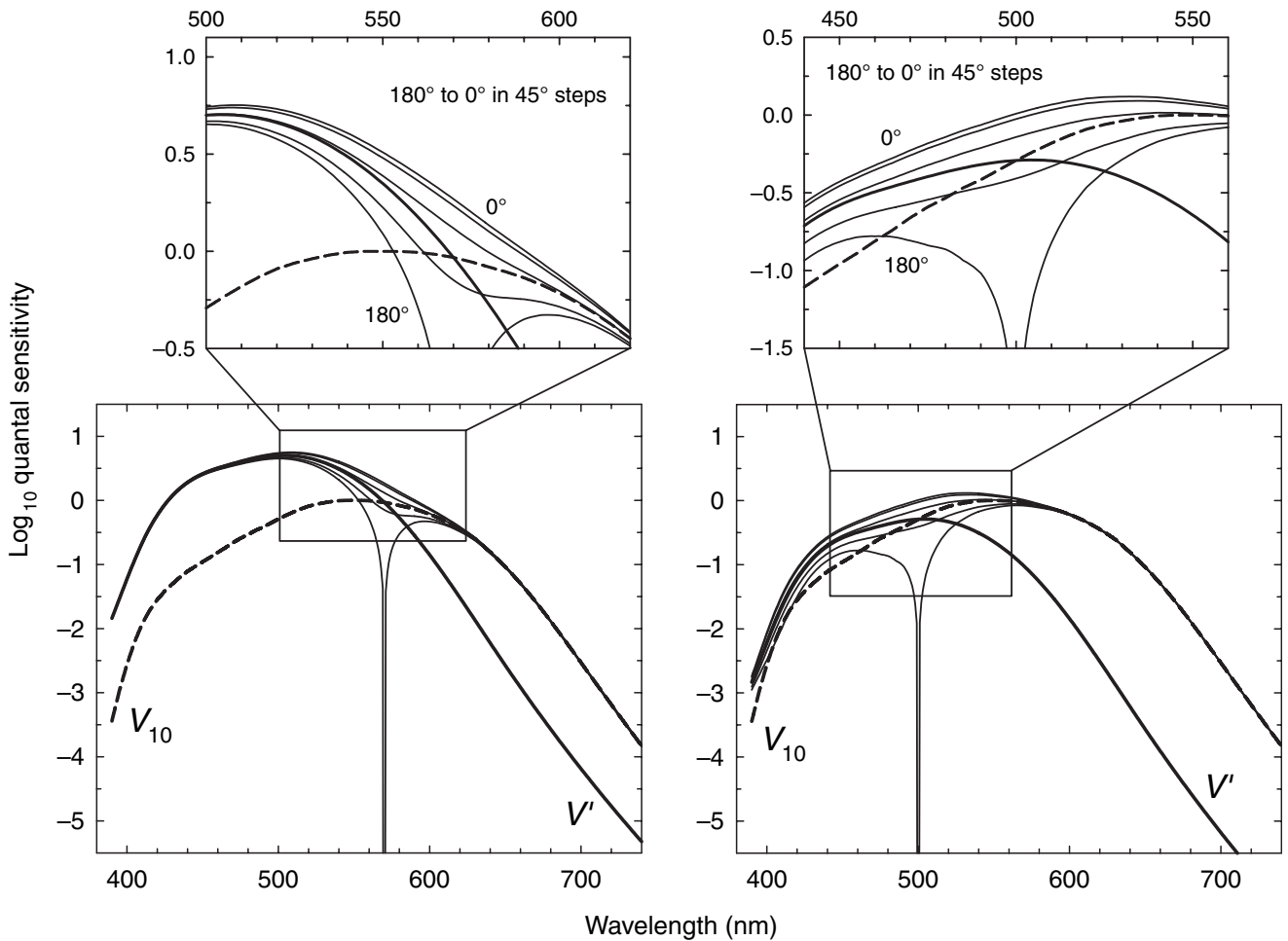
As expected, the largest losses of sensitivity occur when  $\Delta\theta = 180^\circ$  and the rod and cone sensitivities are equal. In practice, the sensitivity will never go to zero, because of non-linear distortion, retinal scatter and other factors. The loss of sensitivity gets smaller as either the rod and cone sensitivities become unequal or as  $\Delta\theta$  becomes smaller than  $180^\circ$ . Changes in the relative rod-cone sensitivity ( $a$ ) will result from changes in wavelength (but see below), while changes in  $\Delta\theta$  will result from changes in frequency.

Additionally, the value of  $a$  will depend upon the relative adaptation of the rods and cones and thus on the spectral content of the environment in which the mesopic luminous efficiency is measured or to which it is to be applied.

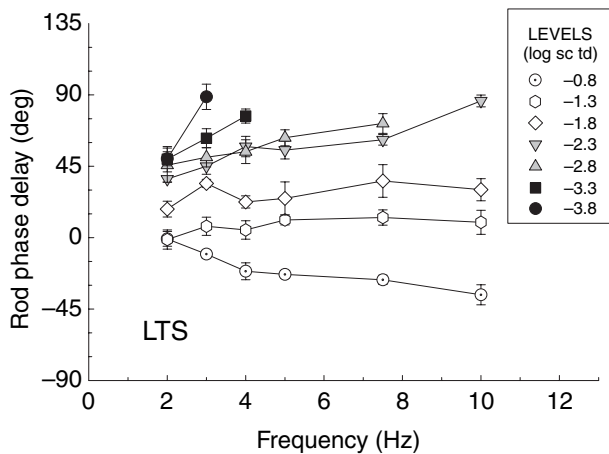
*Rod signals speed up with adaptation*

So far, we have assumed a rod-cone time delay of 66.6 ms, which is consistent with the rod-cone phase





**Figure 8.** Theoretical predictions of mesopic luminous efficiency (thinner continuous lines) based on Equation (1) for two values of  $a$  (the relative photopic weight). In the left panels,  $a = 0.20$ , which makes the scotopic ( $V'$ ) and photopic ( $V_{10}$ ) luminous efficiencies equal at 570 nm. In the right panels,  $a = 1.94$ , which makes them equal at 500 nm. The insets highlight the areas of interest. Also shown are the CIE scotopic  $V'(\lambda)$  (continuous line) and the CIE 1964 10 deg photopic  $V_{10}(\lambda)$  (dashed line).



**Figure 9.** Rod phase delays as a function of temporal frequency between signals generated in the left eye and those generated in the right eye for normal observer LTS. The adaptation level in the right eye was fixed at  $-1.30 \log$  scotopic trolands. The adaptation level in the left eye was varied according to the key. For further details see text.

delays and the rod-cone self-cancellation described above. When rod phase delays are measured employing a binocular cancellation technique using only rod stimuli, so that the measurements are truly scotopic (in the sense that cones are unstimulated), there is clear evidence that the rod system speeds up substantially from absolute rod threshold (low scotopic) to rod saturating (high scotopic) levels. *Figure 9* shows unpublished data from our laboratory. They are rod phase delays measured binocularly using 500 nm targets with the level in the right eye fixed at  $-1.3 \log_{10}$  sc td level, and the level in the left eye varied from  $-3.8$  to  $-0.8 \log_{10}$  sc td. The phase delays at  $-1.3 \log_{10}$  sc td level are, therefore, roughly  $0^\circ$  (as the two eyes are in the same state of adaptation), while those at lower levels are phase delayed and those at higher levels are phase advanced. As can be seen in *Figure 9*, the changes in phase delay between levels are substantial. These changes are also reflected in changes in rod temporal summation (e.g. Sharpe *et al.*, 1993a).

The changes in phase delay should have comparatively little influence on the scotopic luminous efficiency over the low to middle scotopic range, because only one receptor system is involved. At mesopic levels, however, the changes are likely to become significant, because they will alter the rod-cone phase delay and therefore the interaction between the rod and cone signals. Though significant, these changes are still likely to be relatively small, compared with those originating from one additional complexity that is found at mesopic levels.

*Multiple rod signals at mesopic levels*

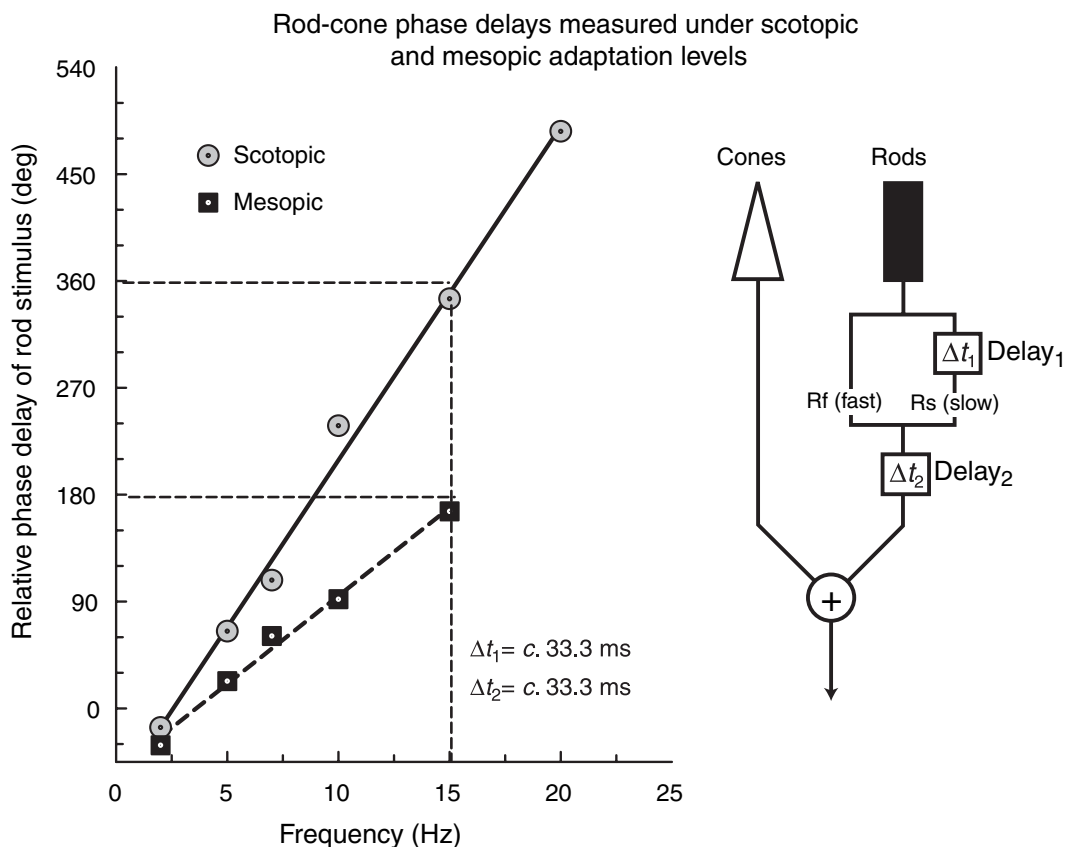
Mesopic photometry is further complicated by the emergence of a second, faster rod pathway at mesopic levels. Evidence for this pathway comes from several sources, including rod-cone phase and electroretinogram (ERG) data (Conner, 1982; Sharpe *et al.*, 1989; Stockman *et al.*, 1991, 1995).

Figure 10 shows the scotopic rod-cone phase delays previously seen in Figure 4. At higher scotopic or

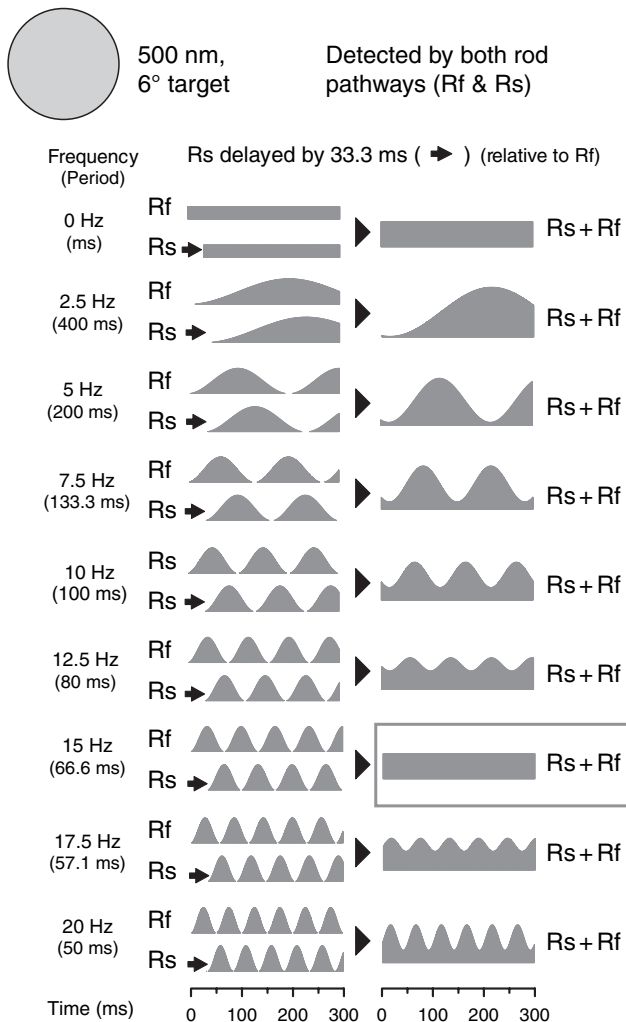
mesopic levels, there is an abrupt reduction in the rod-cone phase delay (as shown by the black dotted squares). Once again, it is helpful to think of these changes in terms of shortening time delays. As depicted in the inset, the change in rod-cone delay from scotopic to mesopic levels can be modelled as a reduction in the time delay by  $\Delta t_1$ . We assume that a transition occurs because a faster rod pathway with a time delay of  $\Delta t_2$  takes over the transmission of the rod signal from a slower pathway with a time delay of  $\Delta t_1 + \Delta t_2$ . The slopes of rod-cone phase delays are consistent with time delays of  $\Delta t_1 = \Delta t_2 \approx 33.3$  ms.

*Rod self-cancellation*

We can produce rod self-cancellation, similar to rod-cone cancellation, by using a 500 nm target that is below cone threshold, but is detected by both the slow and the fast rod pathways. The effect of a slow to fast rod pathway delay of 33.3 ms on the detectability of rod flicker is illustrated in Figure 11. This figure is similar to



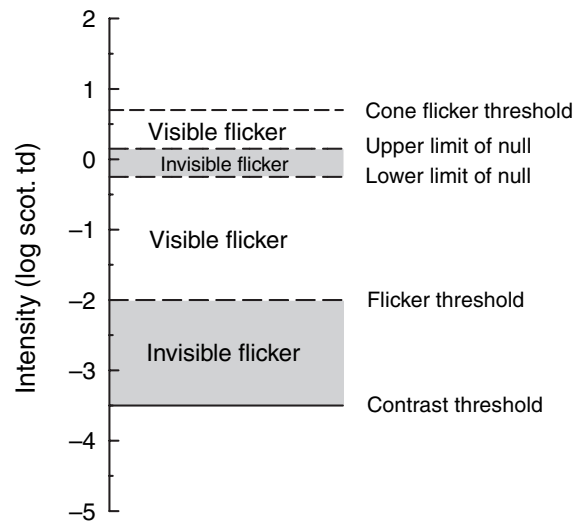
**Figure 10.** Rod-cone phase lags measured as a function of temporal frequency shown previously in Figure 4 (dotted grey circles) obtained at a scotopic adaptation level of  $-0.43$  log scotopic trolands just below the 15 Hz null region (see Figure 13) compared with phase lags measured at 1.16 log scotopic trolands, which lies above the null region (black dotted squares). A flickering 500 nm rod-detected target and a 680-nm cone-detected target were superimposed in the centre of a larger, deep-red background. The deep-red background was present to suppress the cones and to make them less likely to detect the 500 nm target. The slopes of lines fitted to the scotopic (continuous line) and mesopic (dashed line) data are consistent with time delays of  $\Delta t_1 = \Delta t_2 \approx 33.3$  ms. Inset shows the convergence of the slow and fast rod and cone pathways. The delay in the fast rod pathway is  $\Delta t_2$ , while that in the slower pathway is  $\Delta t_1 + \Delta t_2$ . Based on Sharpe *et al.* (1989).



**Figure 11.** A flickering 500 nm target of the appropriate intensity is detected by both rod pathways though the slower signal is delayed relative to the faster (Sharpe *et al.*, 1989). Here, we show for different temporal frequencies, the effect of adding together two sinusoids (Rs + Rf), one of which is seen by the slow rod pathway (Rs) and is delayed by 33.3 ms relative to the second, which is seen by the fast rod pathway (Rf). The box highlights the phenomenon that the two sinusoids destructively interfere and cancel each other at 15 Hz.

Figure 5, except that with a delay of 33.3 ms, rather than 66.6 ms, between the two signals, the frequency at which they destructively interfere and cancel each other is 15 Hz rather than 7.5 Hz.

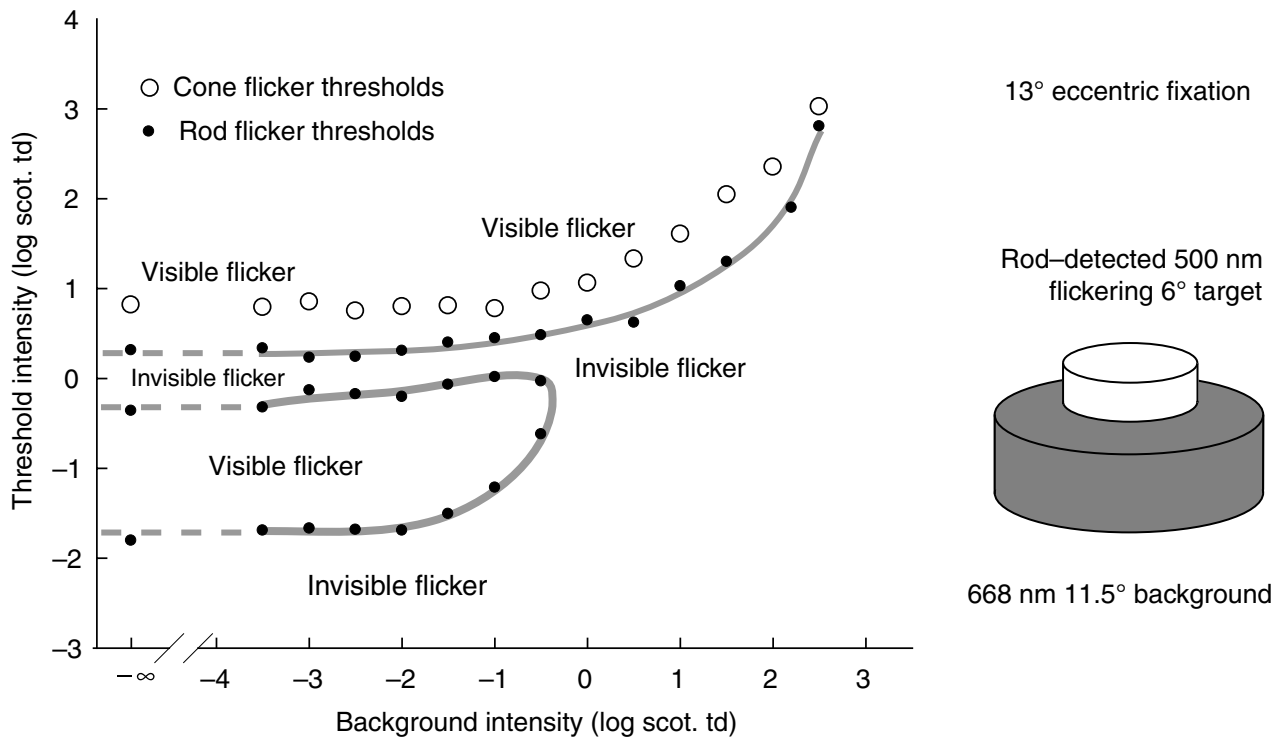
The perceptual consequences of rod-rod self-cancellation are shown in Figure 12. These effects were first evident in the work of Conner (1982), and were quantified and further elucidated by Sharpe *et al.* (1989). The subject is presented with a 500-nm target flickering at 15 Hz. The progression of perceptual phenomena is similar to that for rod-cone self-cancellation shown in Figure 6. As the intensity is increased, the flicker first appears as the flicker threshold is



**Figure 12.** 15 Hz self-cancelling scotopic flicker. The perceptual effects of increasing the intensity of a 500-nm disc, 6 deg diameter in visual angle, presented at 13 deg eccentricity, and flickering at 15 Hz. At 15 Hz the flicker (but not the disc) disappears at an intensity above the flicker threshold (the lower limit of null) and then reappears again at a still higher intensity (the upper limit of null). As the flicker null region between these limits (shaded area) occurs below the cone flicker threshold, it must be a property of rod vision; a conclusion which is confirmed by the finding that the null is found in a rod monochromat who lacks functioning cone vision (Stockman *et al.*, 1991). Based on data from Sharpe *et al.* (1989). See also Figure 6.

crossed, but then disappears at the lower limit of null, only to reappear again at the upper limit of null. Importantly, these transitions all occur below cone flicker threshold, which suggests they are scotopic phenomena.

If the 500 nm target is superimposed on a deep red background of variable intensity, which is specifically chosen to desensitise or adapt the cones relative to the rods, the null and its consequences for flicker and luminous detection can be followed to higher luminances. Figure 13 shows 15 Hz rod detectability data (filled circles). Conspicuously, the detectability data are complex, with a discontinuity occurring near a background intensity of 0 log<sub>10</sub> sc td, where the flicker percept is lost, even though the thresholds are well below the cone flicker threshold (open circles). Additionally, alongside the break in the curve is a suprathreshold region within which 15 Hz flicker is invisible or nulled (Sharpe *et al.*,



**Figure 13.** 15 Hz rod flicker detectability data for a normal observer plotted as a function of background retinal illuminance ( $\log_{10}$  scotopic trolands). The filled circles through which the continuous line has been drawn represent points at which the 15 Hz flicker is just visible. The detectability function appears double-branched, but it is discontinuous, being interrupted by a region within which the flicker is invisible. Areas of visible and invisible flicker are noted. The nulled region is well below the cone flicker thresholds measured before the rods have recovered from an intense bleach (open circles). Inset shows the experimental conditions: a 6 deg diameter, 500 nm target was presented in the centre of an 11.5 deg diameter, 668 nm background at an eccentricity of 13 deg. Based on data from Sharpe *et al.* (1993b).

1989). The discontinuity and flicker null are consistent with destructive interference between a fast rod signal and a slow one that is delayed by approximately 33.3 ms.

Rod-rod self-cancellation can also be demonstrated in the ERG. *Figure 14* shows the ERG responses to 15 Hz Ganzfeld flicker in a normal observer, LTS. The responses have been arranged vertically so that the intensity level, which is given in  $\log_{10}$  scotopic trolands to the right of each record, increases upwards. With increasing flicker intensity, the ERG amplitude at 15 Hz grows slightly, but then falls to a minimum at an intensity corresponding to the perceptual null, before growing once more. Moreover, in accordance with destructive interference, the ERG responses rapidly reverse in phase by a half cycle as the null intensity is crossed. The coincidence of the minimum in the ERG with the perceptual null is important because it suggests that the electrical cancellation measured electrophysiologically and the neural cancellation measured perceptually are manifestations of the same phenomenon.

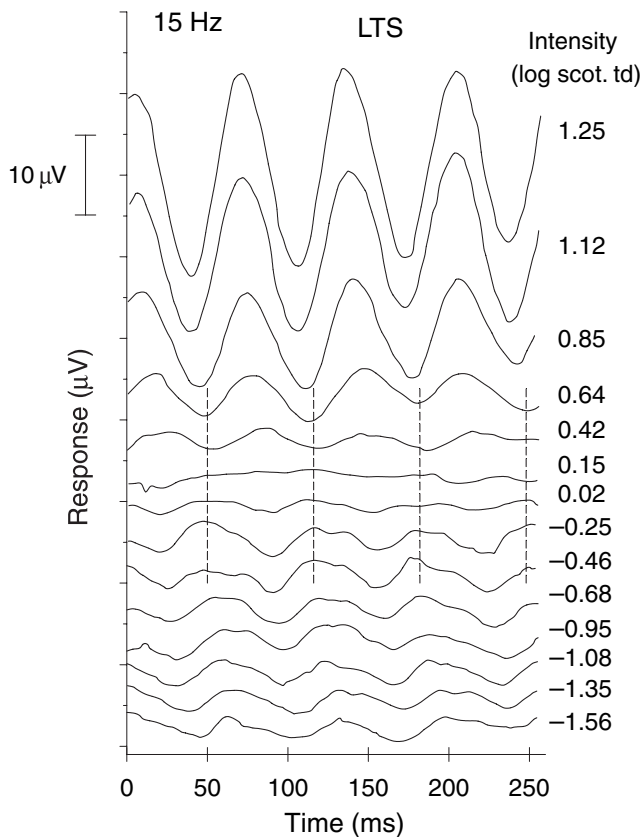
#### *Rod-rod phase interactions and spectral sensitivity*

Signals in the slow and fast rod pathways combine to produce a resultant rod signal, which in turn interacts

with the cone signal. The two rod signals can alter the mesopic luminous efficiency function in two ways. First, depending on the phase delay between them and their relative amplitudes, the slow and fast rod signals will interfere either constructively or destructively, so changing  $a$ , the relative photopic-scotopic weight in Equation (1). If the slow and fast signals destructively interfere, then  $a$  will increase (i.e. the scotopic contribution to luminous efficiency will decrease), whereas if they constructively interfere,  $a$  will relatively decrease (i.e. the scotopic contribution will relatively increase). Secondly, the phase delay between the two rod signals and their relative amplitudes determine the phase delay of the resultant rod signal, and thus the rod-cone phase delay,  $\Delta\theta$  in Equation (1). The effects of  $\Delta\theta$  and  $a$  on the mesopic luminous efficiency function were discussed and illustrated above (see *Figure 8*).

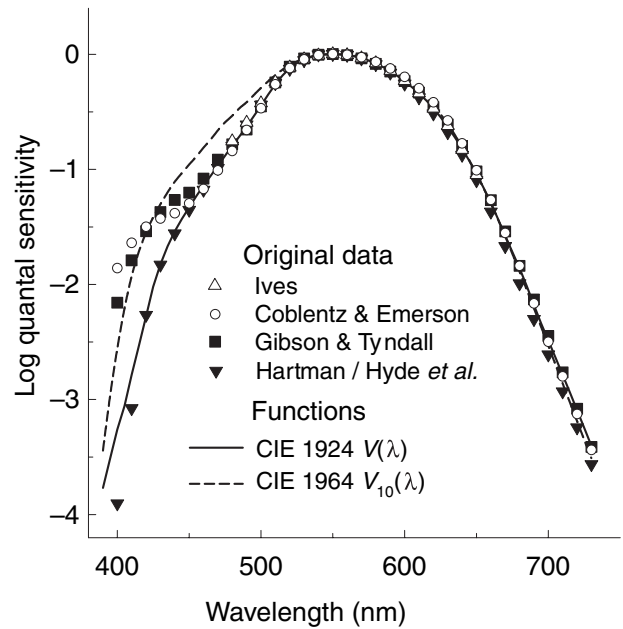
#### **Choice of photopic function for predicting mesopic luminous efficiency**

The mistakes that were made in deriving the photopic  $V(\lambda)$  function, which was adopted by the CIE in 1924 (CIE, 1926), are a warning to those who are in the process of defining a mesopic standard.  $V(\lambda)$  is a hybrid



**Figure 14.** Ganzfeld electroretinogram recordings at 15 Hz for a normal observer LTS. The time-averaged flicker intensity increases upwards in steps of approximately 0.2  $\log_{10}$  unit steps from  $-1.56$  to  $1.25 \log_{10}$  scotopic trolands. The vertical dashed lines demonstrate how the phase abruptly changes by  $180^\circ$  between the flicker luminances immediately above and below the flicker null (in the region  $c. 0.02$ – $0.15 \log_{10}$  scotopic trolands). The recordings have been shifted vertically for clarity. (Reprinted from *Visual Neuroscience*, Vol. 12, Stockman A, Sharpe L.T., R  ther K., Nordby K. Two signals in the human rod visual system: a model based on electrophysiological data, pp 951–970, copyright 1995, used with permission from Cambridge University Press).

function, artificially smoothed and symmetrised from very divergent data measured using very different procedures at several laboratories. The 1924  $V(\lambda)$  function was originally proposed by Gibson and Tyndall (1923). It is shown in *Figure 15* as the continuous line. Even though they were unrepresentative of the other data, and patently wrong, the Hartmann data became the CIE standard for photopic luminance efficiency at short wavelengths. As a result, the 1924  $V(\lambda)$  function deviates from typical luminance efficiency data (e.g. filled squares, open circles) by a factor of nearly 100 in the violet, a problem which continues to plague both colorimetry and photometry today. Potentially, these errors will be propagated if the same flawed photopic  $V(\lambda)$  function is used as a component of a new mesopic standard.



**Figure 15.** The luminosity measurements by Ives (1912) (open triangles), Coblentz and Emerson (1918) (open circles), Gibson and Tyndall (1923) (filled squares) and Hyde *et al.* (1918) including data from Hartmann for 400–490 nm (filled inverted triangles), which were used to derive the CIE 1924  $V(\lambda)$  function (continuous line). Also shown is the CIE 1964  $V_{10}(\lambda)$  function (dashed line).

Obviously, some of the problems inherent in  $V(\lambda)$  can be avoided by choosing a different photopic luminosity standard, especially if one considers that a luminosity standard for the central 2 deg of vision is not necessarily appropriate for mesopic vision anyway. Although not ideal because it is based mainly on limited photometric measurements made at only four wavelengths in only a subset of the Stiles and Burch (1959) observers, an alternative is the  $V_{10}(\lambda)$  luminous efficiency function. This function was adopted by the CIE in 1964 for the central 10 deg of vision (see *Figure 2*). It is shown by the dashed line in *Figure 15*, for comparison with the  $V(\lambda)$  function and the luminosity data used in the derivation of  $V(\lambda)$ . The difference between  $V_{10}(\lambda)$  and  $V(\lambda)$  is more than a log unit at short wavelengths and remains significant up to even 525 nm: wavelengths at which the rods are very sensitive.

The  $V_{10}(\lambda)$  function was used in the mesopic models devised by, for example, Palmer (1968) and Kokoschka and Bodmann (1975). However, Ikeda and Shimozono (1981) and Sagawa and Takeichi (1986) both used the CIE brightness rather than the CIE luminance function to model mesopic luminous efficiency. Given that mesopic luminous efficiency is typically measured by direct brightness matching, a photopic brightness matching function may well be more appropriate than a minimum flicker function. Unfortunately, as we have already emphasised, this also means that mesopic

luminous efficiency is determined by a technique that yields non-additive data. While an additive system of mesopic photometry is certainly more practicable, we may in the end have to accept that mesopic photometry is inherently non-additive and must be modelled as such.

### Conclusions

Mesopic vision and mesopic luminous efficiency are complex. As argued above, any measure of mesopic performance is likely to be dependent upon adaptation, spectral composition, spatial frequency, temporal frequency, retinal location and retinal area. Moreover, it is likely to be non-additive. Clearly, this is not an area for the fainthearted.

Despite these difficulties, some practical standard for mesopic photometry is required. If accuracy is paramount, however, then the only consistently reliable way of estimating mesopic luminous efficiency is to measure it for each new application. Indeed, a single practical standard that can be usefully generalised to predict mesopic performance for all conditions may not be achievable.

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