

# Luminance

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Luminance was introduced by the CIE as a photometric analog of radiance. This implies that an additive spectral-luminosity function characterizes the human observer. In practice, many different spectral-sensitivity functions characterize human vision, although few produce the additive spectral-luminosity function  $V(\lambda)$ , which is suitable for use in practical photometry. Methods that give rise to additive spectral-sensitivity functions that most resemble  $V(\lambda)$  tend to have in common the use of spatial or temporal frequencies that will discriminate against signals from the short-wavelength-sensitive cone pathways or against signals in other chromatic pathways. Some of the difference among results obtained with different techniques seems to reflect the extent to which the methods can bring about changes in the state of chromatic adaptation, but it also seems likely that not all tasks tap the same postreceptoral mechanisms. Psychophysical evidence is equivocal regarding the nature of the postreceptoral mechanisms: some evidence suggests just three mechanisms, one of which has a spectral sensitivity that is like  $V(\lambda)$ ; other evidence suggests the existence of multiple mechanisms with different spectral sensitivities. Physiological recordings from neurons in the macaque's visual pathway suggest that the properties of the magnocellular system may be sufficient to account for spectral-sensitivity functions measured with the techniques of heterochromatic flicker photometry, minimally distinct border, and critical flicker fusion. These are the psychophysical methods that yield spectral sensitivities that are most like  $V(\lambda)$ . Other methods of measuring spectral sensitivity seem more likely to depend on signals that travel through the parvocellular system.

## PSYCHOPHYSICS

Visual photometry has its roots in the scientific and industrial need for measurement and specification of the visual effectiveness (loosely, brightness) of light. Visual comparison photometers were first described in the early part of the eighteenth century.<sup>1</sup> The need for a standard luminous-efficiency function arose when physical photometry became an alternative to visual photometry. Given a standard luminous-efficiency function, it is possible to calculate visual effectiveness directly from the spectral distribution of energy in a light source. It is also possible to construct photoelectric photometers by placing filters in front of detectors so that the spectral sensitivity of the filtered detector mimics the standard luminous-efficiency function.

Luminance is the photometric analog of radiance. Radiance is measured by the amount of heat generated by a surface and is by nature additive. Luminance is thus formally defined by the CIE as the integrated radiance of a source,  $L_{e,\lambda}$ , weighted by the spectral luminosity  $V(\lambda)$  of the CIE<sup>2</sup> Standard Observer:

$$L_V = k_m \int_{\lambda} L_{e,\lambda} V(\lambda) d\lambda, \quad (1)$$

where  $k_m$  is a constant that relates lumens to watts.  $V(\lambda)$  is the standard instrument for establishing the relative visual effectiveness of lights of different wavelengths. Equation (1) implies, by definition, that  $V(\lambda)$  must be additive, regardless of the spectral composition of the components. Additivity is imperative for a workable system of

photometry, yet several plausible techniques for characterizing human luminous efficiency not only fail to yield measurements that meet this requirement but provide inconsistent measurements. Moreover, substantial individual differences in luminous efficiency mean that the standard observer was derived from an average of many individuals and represents no individual observer.

We should perhaps be surprised that a linear photopic luminous-efficiency function can be obtained under any circumstances. The initial absorption of light by photoreceptors is linear, and the photoreceptor signal is proportional to quantal absorption over a substantial range above the absolute threshold for vision.<sup>3</sup> However, photopic luminous efficiency depends potentially on three classes of cone photoreceptor, each of which has (or is connected to) a subsequent neural mechanism that has the capacity for relatively independent light adaptation.<sup>4</sup> Mechanisms of light adaptation are highly nonlinear; moreover, the dependence of photopic spectral sensitivity on three classes of potentially independently adaptable photoreceptors guarantees that there will be no unique spectral-sensitivity function. In this context, additive and stable spectral luminous-efficiency functions are improbable. Nonetheless, methods do exist that yield them.

The CIE  $V(\lambda)$  function, adopted in 1924,<sup>2</sup> is based primarily on measurements obtained with the use of one such method—heterochromatic flicker photometry (HFP), although it is to some degree based on measurements obtained from step-by-step brightness matching.  $V(\lambda)$  represents the weighted spectral sensitivities of a large number of human observers from seven separate studies

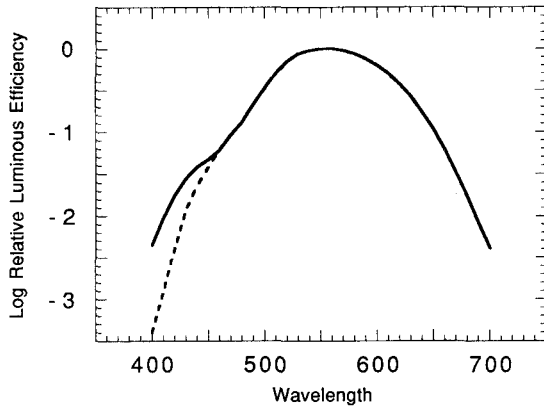


Fig. 1. Spectral luminous-efficiency function of the 1924 CIE Standard Observer  $V(\lambda)$  (dashed curve) and the Judd<sup>6</sup> revision for the short-wavelength end of the spectrum (solid curve). The two curves coincide for wavelengths greater than 460 nm.

(Fig. 1, dashed curve). The methods used to choose and combine the data sets are described by Kaiser.<sup>5</sup> The combination of measurements from different laboratories that used different techniques led to a curve that was later widely considered to represent normal luminous efficiency at longer wavelengths but to underestimate luminous efficiency at short wavelengths. Judd<sup>6</sup> proposed a revision of  $V(\lambda)$  to remedy this defect (Fig. 1, solid curve). Although the revised function is widely used in basic work on color vision and has been acknowledged by the CIE,<sup>7</sup> the 1924  $V(\lambda)$  function remains the standard for photometry.<sup>8</sup>  $V(\lambda)$  and Judd's revision of it are intended to characterize a field of 2 deg but are satisfactory for fields as wide as 4 deg. Since spectral sensitivity varies substantially among individuals,<sup>9-13</sup> it is common in visual experiments to use the individual observer's photometric match. Kaiser<sup>14</sup> suggested the term sensation luminance to describe this quantity.

Modern analyses of  $V(\lambda)$  suggest that the curve results almost entirely from a sum of signals from the long-wavelength-sensitive (LWS) and middle-wavelength-sensitive (MWS) cones in proportions close to 2:1.<sup>15-18</sup> The short-wavelength-sensitive (SWS) cones seem to contribute little, if anything, except under unusual circumstances.<sup>19</sup>

$V(\lambda)$  is a useful and well-established standard for photometry, but beyond that its significance for visual function is unclear. Some uses of the concept of luminance were discussed by Smith and Pokorny.<sup>20</sup> Among visual scientists, modern interest in  $V(\lambda)$  stems most directly from the widespread belief that, at some stage beyond the receptors, signals from the three classes of cone are combined to yield three transformed signals. One strong interpretation of  $V(\lambda)$  is that it represents the spectral sensitivity of one of these postreceptoral mechanisms. The most radical alternative interpretation is that  $V(\lambda)$  is merely a contrivance, measured under peculiar circumstances that have little to do with the normal operation of the visual system, to satisfy the need for a linear system of photometry. We consider these and other interpretations in later sections, but first we review briefly various ways to measure luminous efficiency, and then we summarize their results. Differing degrees of additivity, and systematic differences between different measurements of

what are considered a basic characteristic of photopic vision, are major elements in the puzzle of luminance, and we need to appreciate these if we are to develop a clear understanding of  $V(\lambda)$ .

## PHOTOPIC SPECTRAL-EFFICIENCY FUNCTIONS

Using HFP, Abney and Festing<sup>21</sup> and Abney<sup>22</sup> first established the additivity of luminances; linear additivity has since become known as Abney's law. Additivity is not only of practical importance in establishing a system of photometry; it also says much about mechanisms underlying spectral-sensitivity functions (discussed below).

Spectral sensitivities measured by HFP have generally shown good agreement with Abney's law and for this reason provide the principal foundation of  $V(\lambda)$ . In contrast, spectral sensitivities that are derived from matching the brightnesses of juxtaposed (and usually steady) fields of different spectral composition show substantial deviations from additivity. Because brightnesses do not add, even at a nominally fixed adaptation level, there is no standard brightness function analogous to the  $V(\lambda)$  of the standard observer. CIE Committee TC 1.4 (Ref. 23) summarized the evidence and provided a function (Fig. 2, dashed curve) that can be used to gauge the brightness of spectral lights. This function cannot be used for nonspectral lights, for which the failures of additivity are complex.<sup>24</sup> Luminous-efficiency functions that are derived from brightness matching are broader than those obtained with HFP, particularly at short wavelengths. A major practical consequence of these differences between HFP and brightness matches is that equiluminant lights of different colors usually do not appear equally bright. Several investigators have explained the peculiarities of brightness perception by suggesting that more than one underlying neural process determines brightness.<sup>24-28</sup>

There are many other methods for measuring spectral sensitivity, but they can be placed in just two general categories: (1) methods that yield sensitivity functions resembling the function obtained with the use of HFP and show additivity or relatively small failures and (2) methods that yield functions unlike the function obtained with

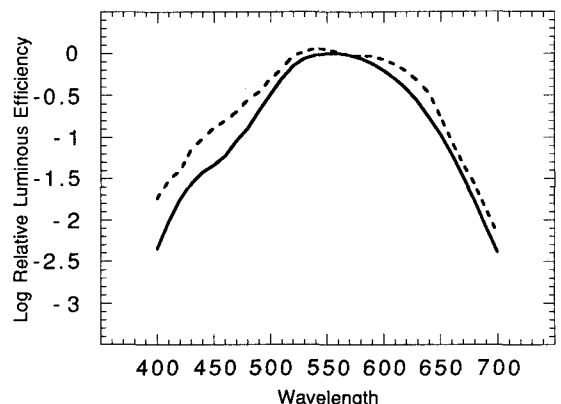


Fig. 2. Comparison of the Judd<sup>6</sup>  $V(\lambda)$  spectral luminous-efficiency function (solid curve) with the CIE<sup>7</sup> brightness-matching function (dashed curve).

**Table 1. Some Methods of Measuring Spectral-Sensitivity Functions**

	Evaluated Function	Reference Number
Methods Using Temporal or Spatial Alternation		
HFP	Spectral sensitivity: $V(\lambda)$ -like <sup>a</sup>	9, 29–32
	Additivity: Yes at low photopic luminances	32–36
	No at high photopic luminances	37
Grating Visual Acuity	Spectral Sensitivity: $V(\lambda)$ -like	38–40
	Additivity: Yes	41
Motion Minimization	Spectral sensitivity: $V(\lambda)$ -like	18, 42, 43
	Additivity: Yes	44
Direct Heterochromatic Photometry		
Brightness Matching	Spectral sensitivity, small: $V(\lambda)$ -like	45, 46
	Additivity: Yes	46
	Spectral sensitivity, large: Broader than $V(\lambda)$	23, 32, 47–52
	Additivity: No	24, 49, 53–58
Step by Step	Spectral sensitivity: $V(\lambda)$ -like	59–61
MDB	Spectral sensitivity: $V(\lambda)$ -like	49, 56
	Additivity: Yes	49, 62, 63
Checkerboard Patterns	Spectral sensitivity, $V(\lambda)$ -like: 3' juxtaposed elements	64
	Additivity: Yes	64
	Spectral sensitivity: 3' separated elements	64
	Additivity: No	64
Threshold Methods		
Absolute Threshold	Spectral sensitivity, small, brief: $V(\lambda)$ -like	46, 65–67
	Additivity: Yes	46
	Spectral sensitivity, large, long: Commonly a notch near 570 nm	23, 68, 69
	Additivity: No	57, 70, 71
Increment Threshold on White Background	Spectral sensitivity, small, brief: $V(\lambda)$ -like	72
	Additivity: Minor failures	73, 74
	Spectral sensitivity, large, long: Three broad peaks	72, 75
	Additivity: No	76
Radiance for Flicker Fusion	Spectral sensitivity: $V(\lambda)$ -like, low photopic luminance	77–79
Landolt C Visual Acuity	Spectral sensitivity: $V(\lambda)$ -like	80, 81
	Additivity: Yes	82
Increment Grating Detection	Spectral sensitivity, 1 Td: $V(\lambda)$ -like	83
	Additivity: Yes	83
	Spectral sensitivity, 1000 Td: Broad	83
	Additivity: Spatial-frequency dependent at 1000 Td	83
Speeded Response		
Criterion Reaction Time	Spectral sensitivity: $V(\lambda)$ -like	84, 85

<sup>a</sup> $V(\lambda)$ -like refers to a spectral-sensitivity function having approximately the same bandwidth as  $V(\lambda)$  and no major irregularities.

the use of HFP and usually show large additivity failures. We summarize a number of these studies briefly in Table 1.

### Spatiotemporal Variables

It is clear from a survey of Table 1 that additivity tends to depend on methods that exploit moderate to high temporal or spatial frequencies. Even psychophysical methods that do not usually give rise to  $V(\lambda)$  tend to do so when stimuli are small and brief. For example, heterochromatic brightness matching and absolute threshold give rise to relative spectral sensitivities like those measured by flicker photometry, when stimuli subtend visual angles of 10' or less.<sup>46</sup> Differences among spectral-sensitivity functions

become most conspicuous when stimuli are large and (for stimuli that do not flicker) continuously visible. Through their use of relatively high temporal or spatial frequencies, most methods that give rise to additive spectral-sensitivity functions tend to discriminate against signals in SWS-cone pathways and those in other chromatic pathways.

### Effects of Adaptation

Most discussions of additivity deal with a visual system in a steady state of adaptation. An obviously important question is how the luminous-efficiency function is affected by changes in the overall level or chromaticity of illumination. As Ingling *et al.*<sup>62</sup> point out, receptor satu-

ration ought to preclude linearity at high light levels. However, recent measurements of cone-receptor responses in primates<sup>3,86</sup> give rather high values for receptor saturation and then only for flashed stimuli, leaving the gain-controlling mechanisms of light adaptation<sup>67</sup> to be much more relevant and pervasive nonlinear influences on spectral sensitivity.

All techniques for measuring spectral sensitivity require the comparison of lights of different spectral composition presented either jointly in nulling procedures such as HFP, minimally distinct border (MDB), and brightness matching or sequentially in threshold procedures such as critical flicker fusion (CFF) and increment threshold procedures. Hence all photometric procedures that involve presentation of suprathreshold lights have the potential to adapt the three classes of cones differentially. The mechanisms of light adaptation bring about large changes in sensitivity that follow changes in ambient illumination, but at the same time they appear to provide a linear operating range for small departures from the prevailing level. The effect of this on the spectral-sensitivity function will depend substantially on the method of measurement. For example, in the method normally used for HFP, a variable-radiance test wavelength is alternated with a standard white, causing the state of chromatic adaptation to vary with test wavelength. The effect is limited because the relatively rapid alternation of fields, one of which is a constant white, ensures that each point on the retina is adapted to some average chromaticity that is anchored by the white field. Spectral sensitivities measured by a CFF technique<sup>79</sup> at moderate and high luminances are narrower than those obtained with the use of conventional HFP at comparable light levels, presumably representing more extreme wavelength-dependent adaptations.<sup>87</sup>

Although we would expect the wavelength-dependent variations in the state of chromatic adaptation resulting from HFP to have only minor effects on the shape of  $V(\lambda)$  at low luminance levels, changing the overall level of illumination could rather easily bring about changes in the shape of the HFP-determined function. Further, if increasing the overall level of illumination caused the gain of the MWS cones to decline less rapidly than that of the LWS cones (or differentially altered the temporal characteristics of the two classes of cone), we would expect the shape of the spectral-sensitivity function to change. An increase in radiance does result in narrowing of spectral-sensitivity curves obtained by HFP,<sup>10,29,62,88</sup> but the effect is probably due primarily to wavelength-dependent chromatic adaptation.<sup>87</sup>

The foregoing discussion suggests that only under rather narrow circumstances does the visual system behave linearly in the way that is required for a satisfactory system of photometry to be obtained. We should perhaps not be surprised, in view of the profoundly nonlinear effects of light adaptation. Moreover, we should not be surprised that techniques that provide different opportunities for light adaptation in the three classes of cone yield different spectral-sensitivity curves. However, we also need to consider additional factors that might explain why different methods give rise to different spectral-sensitivity functions. An obvious possibility is that the different techniques tap different underlying mechanisms that have different spectral sensitivities. Next we examine the modern concept of the postreceptoral channels for color

vision and provide a framework within which to explore underlying mechanisms.

## POSTRECEPTORAL MECHANISMS OF COLOR VISION

$V(\lambda)$  evidently must arise from some sort of combined activity in two or more classes of cone (probably just the LWS and MWS cones). A widely held view of the organization of color vision, traceable to Hering,<sup>89</sup> postulates a postreceptoral stage of representation at which one combines signals from the LWS-, MWS-, and SWS-cone types by taking their sums or differences. What is the nature of these postreceptoral mechanisms, and how do they contribute to the generation of  $V(\lambda)$ ?

The trichromacy of normal color matches demonstrates that we need three independent mechanisms (i.e., spectrally selective filters), but it does not limit to three the number of possible postreceptoral mechanisms. Various psychophysical methods (reviewed by Graham<sup>90</sup>) can be used to discover their properties. Early analyses of postreceptoral mechanisms (e.g., Refs. 89 and 90) were based on observations regarding color appearance and led to the modern conception of three channels,<sup>91</sup> two of which are presumed to give rise to the red-green and blue-yellow dimensions of appearance, and a third to the light-dark (achromatic) dimension. Recent work has used other methods, notably those that examine the discriminability or detectability of lights of different chromaticity or the detectability of particular lights after adaptation (habituation) to others, to explore the number of mechanisms and their properties.

### Number of Mechanisms and Spectral Sensitivities

Discriminations among lights that differ in chromaticity but not in luminance<sup>92,93</sup> can be succinctly well-described by supposing that they depend on signals from just two independent postreceptoral mechanisms, one of which is sensitive to SWS-cone excitation and one to the ratio of  $L/(L + M)$ -cone excitation.<sup>94</sup> When chromatic discriminations are extended to three dimensions, thresholds can be well described by assuming probability summation of signals from two independent chromatic mechanisms and an achromatic one,<sup>50,95-101</sup> with the achromatic mechanism having the spectral sensitivity of  $V(\lambda)$ .

Three separable mechanisms, one carrying an achromatic signal and two carrying chromatic signals of the kind identified above, also appear to be fundamental in quite different kinds of experiments that examined the effects on discrimination or color appearance of habituation to lights modulated in different directions in a three-dimensional color space.<sup>102,103</sup> Spectral sensitivities derived by Poirson and Wandell<sup>104</sup> are like those obtained in discrimination experiments. Three mechanisms have also been identified by hue-cancellation methods (see, e.g., Ref. 91), although it is clear that the spectral sensitivity of the putative red-green mechanism is not the same as that of the red-green mechanism identified in discrimination or habituation experiments.

Other evidence from a variety of studies points to a more complex organization of postreceptoral chromatic mechanisms, suggesting that there are more than three mechanisms<sup>105,106</sup> or that there are interactions among three mechanisms.<sup>107-109</sup>

### Spatiotemporal Characteristics

To the extent that we can isolate a single postreceptoral mechanism by making a suitable choice of stimulus chromaticities, we can explore its spatial and temporal properties. By confining stimulus modulation to lights that are isoluminant and hence providing no varying signal to any mechanism with the  $V(\lambda)$  spectral sensitivity, many studies have shown impaired resolution of high spatial and temporal frequencies. Thus, by inference, mechanism(s) with the  $V(\lambda)$  spectral sensitivity support these functions under normal viewing conditions. Although it has been common practice in recent years to establish the relative radiances of lights that lead to maximally degraded performance on a task and by implication silence an achromatic mechanism, there have been few direct measurements of spectral sensitivity. In the spatial domain, Shioiri and Cavanagh<sup>110</sup> have shown that form perception is more impaired when object elements are equally luminous than when they are equally bright. In the temporal domain  $V(\lambda)$  appears to provide a good description of a mechanism that has high temporal resolution and short latency. Pokorny *et al.*,<sup>111</sup> using HFP-equated stimuli, measured the duration necessary for detection of a chromatic test substituted within a larger white field and found a wavelength dependence that closely resembled a saturation-discrimination function. When the chromatic stimuli were presented as increments or decrements of  $\pm 0.07$  log unit, the wavelength dependence was weakened, indicating that isoluminance defined by HFP silences another detection mechanism. Similarly, two-pulse resolution,<sup>112</sup> temporal brightness enhancement,<sup>113</sup> and reaction-time measures<sup>114</sup> all show greatest chromatic isolation at the HFP match. The wavelength dependence observed for reaction time to substituted stimuli has been confirmed with two independent methods of isolating chromatic activity.<sup>115,116</sup> The spectrally opponent mechanisms on which isoluminant discriminations depend have relatively poor spatial and temporal resolving power.<sup>117-121</sup> Potent demonstrations of impaired discrimination of isoluminant figures<sup>122</sup> and impaired perception of figural movement<sup>123</sup> suggest that form vision depends relatively little on the mechanisms that function under isoluminant conditions. The obvious inference is that these chromatic mechanisms lack the sensitivity and/or the spatiotemporal bandwidth of the putative achromatic mechanism. This is probably true of the pathway that receives signals from SWS cones, where, even though a stimulus modulated along a tritanopic confusion line can produce substantial modulation of the signal to SWS cones, performance is poor, perhaps as a result of the low sampling density. What accounts for the apparently poor performance with red-green isoluminant stimuli is less clear. The greatest modulation of signals to LWS and MWS cones that one can produce with isoluminant stimuli is  $<20\%$  (versus  $100\%$  for achromatic stimuli), so from the outset the visual system is presented with inherently weaker signals. Few studies of visual performance under isoluminant conditions take account of this wavelength dependence.

Of course, isoluminant patterns occur rarely in nature, and we know little about how spectrally opponent mechanisms operate when both chromaticity and luminance vary. Nevertheless, it is widely believed that form vision depends principally on an achromatic mechanism with a spectral sensitivity much like  $V(\lambda)$ . This is why questions

regarding the substrate of  $V(\lambda)$  are of such broad interest in vision research.

### Summary of Psychophysical Results and Conclusions

Some types of psychophysical experiments seem to isolate just three independent postreceptoral mechanisms of color vision, one of which appears to have the spectral sensitivity of  $V(\lambda)$ ; other kinds of observations (e.g., studies of masking or habituation, chromatic induction) suggest less independence or the existence of multiple spectrally selective mechanisms. It is of course possible that three early postreceptoral mechanisms later give rise to more than three higher-level ones and that different kinds of psychophysical tasks engage mechanisms at different levels. By the same token, several distinct visual mechanisms may have the  $V(\lambda)$  spectral sensitivity. It is relatively easy to imagine how this might arise: if  $V(\lambda)$  is a linear combination of the signals from L and M cones in the proportions that they occur in the retina, then any mechanism that draws input indiscriminately from L and M cones (or even one that pools indiscriminately the inputs from earlier mechanisms with a variety of biased inputs) will have  $V(\lambda)$  spectral sensitivity. One way to pursue this issue is to ask what physiological observations have revealed regarding the substrate of  $V(\lambda)$ .

### PHYSIOLOGICAL SUBSTRATE OF THE LUMINOSITY FUNCTION

Physiologists have characterized the cone inputs to two major classes of retinal ganglion cells and their counterparts in the lateral geniculate nucleus<sup>124-126</sup> (LGN). One class, known as M cells or broadband cells, projects to the magnocellular layers of the LGN. MWS and LWS cones contribute to both centers and surrounds,<sup>127-130</sup> which in most neurons have similar spectral sensitivities. In some neurons the LWS cones contribute more substantially to the surround than to the center.<sup>128</sup> It is not clear whether SWS cones make any contribution to the receptive fields; if they do, it must be small.<sup>125,131</sup> The other class of neuron, known as P cells, projects to the parvocellular layers of the LGN. P cells are much more numerous than M cells, have chromatically opponent receptive fields, and fall into two principal groups according to whether they receive inputs from SWS cones. In the present context we are concerned only with neurons that receive their principal inputs from MWS and LWS cones; SWS cones provide negligible, if any, input to these cells.<sup>125,132</sup> By and large these red-green opponent P cells have receptive fields with center-surround organization. There is general agreement that, for neurons with receptive fields in and near the fovea, one type of cone (LWS or MWS) feeds the center, although at present there is controversy over whether only one type of cone (MWS or LWS) or both types provide input to the surround.<sup>132-134</sup> In any event, the differential contributions of the two cone classes to center and surround ensure that P cells respond well to chromatic modulation of stimuli that cover the whole receptive field.

The parvocellular pathway might be thought of as an improbable origin of the luminosity function, but it is worth drawing attention to some circumstances under which P cells could give rise to it. Gouras and Zrenner<sup>129</sup> observed that a  $V(\lambda)$ -like spectral-sensitivity function could be obtained from P cells that were stimulated by

spatially uniform fields flickering at high rates. Such a transformation from an opponent spectral sensitivity can be explained by the notion that surround signals reach the site of center-surround interaction later than do those from the center, so that at high temporal frequencies the signal from the surround is delayed enough to arrive at the site of combination in the same phase as the signal from the center. Recent estimates<sup>134</sup> suggest that the surround signal follows the center signal by  $\sim 5$  ms, so a P cell could have  $V(\lambda)$  spectral sensitivity only at much higher temporal frequencies than are used in psychophysical measurements with HFP.<sup>130</sup> Since P cells behave quite linearly when in a stable state of adaptation, addition of signals from two or more P cells with overlapping receptive fields could give rise to mechanisms with spectral sensitivities matching  $V(\lambda)$ .<sup>135</sup> In fact, as we discuss below, this appears not to occur, but the fact that simple transformations of the signals from P cells can give rise to  $V(\lambda)$  cautions us against attaching too much significance to a simple correspondence between  $V(\lambda)$  and some physiologically measured spectral sensitivity.

With these caveats in mind, it seems likely that the magnocellular (broadband) pathway gives rise to the flicker-photometrically determined luminosity function and perhaps also to the luminosity functions determined by MDB and minimum-motion methods. The M pathway has been widely regarded as the substrate of  $V(\lambda)$ ,<sup>127,130</sup> and recent, detailed measurements of the spectral sensitivities of M cells, obtained with the use of both HFP<sup>136</sup> and MDB,<sup>131</sup> show gratifyingly close agreement with  $V(\lambda)$  at all but the shortest wavelengths, where uncertainties regarding absorption by lens and macular pigment render comparisons difficult. A good deal of physiological and anatomical evidence implicates the M pathway in the analysis of movement, and it is therefore a plausible substrate of luminosity functions measured with the minimum-motion technique.<sup>18</sup> To the extent that the minimum-motion method does tap only the M system, it provides strong evidence that SWS cones make no contribution to the receptive fields of M cells. It would be valuable to have this directly examined in physiological experiments.

Other perceptual tasks that give rise to  $V(\lambda)$ -like spectral-sensitivity functions—CFF and reaction time—are plausibly connected with activity of the M system, although no direct measurements have been made on single cells. M cells have substantially better temporal resolution than do P cells.<sup>137,138</sup> We would expect perceptual reaction times to be dominated by the fastest-responding pathways.<sup>114,116,139,140</sup> Although the conduction velocity of the M pathway slightly exceeds that of the P pathway, the M system's much greater contrast sensitivity<sup>137,141,142</sup> could confer substantial advantages in the kinds of simple reaction-time tasks that are used to measure spectral sensitivity.

The argument that the M pathway determines spectral sensitivity would be strongest if we could show that the P pathway was silent to the test and comparison lights during the measurements that give rise to  $V(\lambda)$ . However, under most of the above conditions the P pathway is quite active. Although it is unlikely that the P cells respond to flicker at the CFF for M cells, the chromatic modulations

that give rise to flicker-photometric nulls in M cells excite P cells vigorously, the MDB stimuli that result in the least M cell activity to a drifting border excite P cells well, and suprathreshold stimuli used in reaction-time tasks will excite P cells as well as M cells. We therefore must suppose that the large signals in the P pathway are ignored or suppressed by mechanisms in cortex and interpret cautiously the argument connecting  $V(\lambda)$  and the M pathway.

The M system is an improbable substrate of luminosity functions obtained by some other methods. Spectral sensitivities that are measured by acuity criteria, with the use of resolution (gratings) or recognition (Landolt C) targets, are like  $V(\lambda)$  and additive (see Table 1), yet the mosaic of M cells, which beyond the center of the fovea has been characterized fully,<sup>143,144</sup> can unambiguously resolve spatial frequencies that are only one third as high as those that can be unambiguously resolved by the human observer or the macaque monkey. Individual M cells have such high contrast sensitivity that they can resolve spatial frequencies higher than those that can be resolved by their mosaic,<sup>137,145,146</sup> but it is not clear whether they contribute to psychophysically measured acuity for high spatial frequencies. Psychophysical observations on monkeys in which M or P pathways have been selectively damaged<sup>147-150</sup> confirm that acuity for high spatial frequencies is much impaired by damage to the P pathway, but only at the lowest spatial frequencies and at low contrasts does one see any effects of damage to the M pathway.

The spectral sensitivity that is derived from the absolute threshold for small, brief stimuli is like  $V(\lambda)$  and additive,<sup>46</sup> yet most threshold stimuli appear colored.<sup>151-153</sup> Similarly, the spectral-sensitivity function that is obtained with small stimuli briefly presented on a white background (which also appear colored at threshold) is like  $V(\lambda)$ <sup>153</sup> and shows modest additivity failures.<sup>73,74</sup> Physiological measurements of increment thresholds for small stimuli presented against white backgrounds<sup>154</sup> show that P cells are probably mainly responsible for this, although we cannot exclude the possibility that the M system also contributes to the threshold.

We are thus left with a paradox: the behavior of M cells can explain  $V(\lambda)$  obtained with the favored methods of HFP, MDB, and minimum motion, but the mosaic of M cells has insufficient resolving power to explain the  $V(\lambda)$  spectral-sensitivity functions obtained with an acuity criterion, and it cannot support the high spatial resolution that is taken to be the hallmark of the putative achromatic mechanism that supports form vision. P cells exist in numbers large enough to provide the spatial resolving power expected of this mechanism, and they evidently play an important role in spatial resolution but do not have the appropriate spectral sensitivities. To resolve this difficulty we must explore more deeply an issue that was raised above, namely, the possibility that multiple, physiologically distinct mechanisms have the  $V(\lambda)$  spectral sensitivity or spectral sensitivities very much like it.

## MULTIPLE MECHANISMS WITH $V(\lambda)$ -LIKE SPECTRAL SENSITIVITY?

A number of investigators<sup>124,155,156</sup> have noted that the arrangement of opponent mechanisms in the receptive field

of a typical P cell, i.e., the chromatically opponent mechanisms being segregated in center and surround, results in the cell's being sensitive to chromatic modulation at low spatial frequencies at which the stimulus can drive both center and surround and sensitive to achromatic modulation at higher spatial frequencies at which the stimulus can drive only the center. The upshot is that, given suitable decoding machinery, the P system is fully capable of carrying a signal that can give rise to an achromatic mechanism with the properties that psychophysical considerations lead us to expect. Lennie and D'Zmura<sup>135</sup> suggested that the multiplexed signals conveyed by P cells might be decomposed in visual cortex, and they proposed a simple scheme whereby this might be accomplished.

It has been known since Hubel and Wiesel's<sup>157</sup> first recordings from macaque striate cortex that the chromatic properties of cortical neurons differ sharply from those of neurons in LGN. Later analyses of the spatiochromatic characteristics of receptive fields<sup>158,159</sup> showed that in cortex there is indeed a major transformation of chromatic characteristics that results in most neurons responding well to achromatic stimuli. Inputs from M and P cells are well segregated in the recipient layers of striate cortex,<sup>160</sup> but we know little regarding how signals from the two pathways are dealt with in upper and lower layers. Although the average spectral sensitivity of neurons in the upper layers is close to  $V(\lambda)$ , few individual neurons have the spectral sensitivity of  $V(\lambda)$ ; indeed, the spectral sensitivities of many that respond well to achromatic stimuli clearly differ from  $V(\lambda)$ , generally having narrower spectral-sensitivity functions that result from their receiving opposed (albeit weakly opposed) inputs from MWS and LWS cones.<sup>159</sup> Cells with this weakly opponent organization are chromatically heterogeneous and form no sharply identified group, yet they are so numerous and generally have such finely tuned spatial and orientational selectivities that there can be little doubt that they play some important role in form vision. Could this heterogeneous population of cells give rise to  $V(\lambda)$ -like spectral-sensitivity functions in acuity tasks and those involving detection of punctate lights? To answer that question fully we need an explicit model of detection that incorporates assumptions regarding the numbers of cells involved and how they contribute to the perceptual decision. However, if we suppose that the visual stimulus activates several cells, linear combination of signals from these might reasonably be expected to give rise to a spectral-sensitivity curve that reflects the average of the spectral sensitivities of the individual cells.

It thus seems to us highly likely that multiple underlying mechanisms can give rise to psychophysical spectral-sensitivity functions that are like  $V(\lambda)$ . What the mechanisms have in common is the capacity to draw signals from L and M cones in the proportions that these cones exist in the retina. This is not to say that all the mechanisms avoid inputs from S cones; the physiology is not decisive on this. However, with the exception of minimum-motion measurements, the principal techniques for measuring spectral sensitivity psychophysically (e.g., HFP, MDB, CFF, or a spatial-acuity measurement) use temporal or spatial frequencies to which we know the SWS-cone system is relatively insensitive.

## SUMMARY

We have examined the concept of luminance, its expression in the CIE  $V(\lambda)$  function, and the possibility that it reflects the spectral sensitivity of an identifiable underlying mechanism. Psychophysical observations show that several quite different ways to measure luminous efficiency yield spectral-sensitivity curves that resemble, but are not always the same as,  $V(\lambda)$ . What all methods have in common is that they appear to draw on the activity of LWS and MWS cones in approximately the proportions that these exist in the retina. Methods that give rise to additive spectral-sensitivity functions that most resemble  $V(\lambda)$  tend to have in common the use of spatial or temporal frequencies that will discriminate against signals from SWS cones. Some of the difference among results obtained with the use of different techniques seems to reflect the extent to which the methods can bring about changes in the state of chromatic adaptation, but it also seems likely that not all tasks tap the same postreceptor mechanisms. Psychophysical evidence is equivocal regarding the nature of the postreceptor mechanisms: some evidence suggests the existence of just three, one of which has a spectral sensitivity that is like  $V(\lambda)$ ; other evidence suggests the existence of multiple mechanisms with different spectral sensitivities. Physiological recordings from neurons in the macaque's visual pathway suggest that the properties of the magnocellular system may be sufficient to account for spectral-sensitivity functions that are measured with the techniques of heterochromatic flicker photometry, minimally distinct border, critical flicker fusion, and reaction time. These are the psychophysical methods that yield spectral sensitivities that are most like  $V(\lambda)$ . It is more likely that other methods of measuring spectral sensitivity depend on signals that travel through the parvocellular system.

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