
The spectral sensitivities of the middle- and long-wavelength cones: an extension of the two-colour threshold technique of W S Stiles

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Abstract. When a tiny centred test flash is presented on a small concentric background, the threshold rises with background radiance more quickly than Weber's law would predict. It is argued that under such conditions it is possible, by means of a test sensitivity method, to isolate either the M-cone or the L-cone types *throughout the visible spectrum*. As predicted, double-branched M- and L-cone tvr functions are found when the test flash and the field are of the same wavelength. From the independent vertical displacements of the two branches as test wavelength is varied, it is possible to derive spectral sensitivities that agree well with dichromatic sensitivities and König fundamentals. The test sensitivities deviate from π_4 at longer wavelengths and from π_5 at shorter wavelengths.

1 Introduction

The trichromacy of colour perception arises, it is thought, because there are only three types of cone, each containing a different photosensitive pigment. If we are to understand colour vision, we must know the spectral sensitivity of each type of cone and must understand how detection and discrimination are related to the signals that the cones produce and to the transformations that those signals undergo in the postreceptoral pathways.

Many psychophysical stratagems have been put forward for estimating the 'cone fundamentals', the spectral sensitivities of the individual classes of cone. One group of procedures rests on the assumption that the dichromatic visual system is a reduced form of the normal trichromatic system. Other methods use trichromatic observers, but seek, by some experimental manoeuvre to cause the observer's response to depend upon signals deriving from only a single class of photoreceptor. Twenty-five years ago a wide variety of candidate fundamentals remained in play, but recent years have seen a quiet convergence of psychophysical estimates, and most theorists would now concur that the (corneal) peak sensitivities of the three cone types lie in the violet (430-440 nm), in the green (530-540 nm), and in the yellow-green (560-570 nm). By analysis of dichromatic data (Wysecki and Stiles 1967, pages 412-418) and by increment-threshold measurements on trichromats (Stiles 1953, 1978), W S Stiles contributed centrally to this convergence of opinion.

However, despite the first-order agreement that now obtains, there remain unresolved differences among current estimates of the sensitivities of the middle-wavelength (M) and long-wavelength (L) cones. As an example, consider the differences between the M and L König fundamentals derived by Smith and Pokorny (1975), and the π_4 and π_5 field sensitivities of Stiles (1953, 1978): π_4 is significantly shallower than the Smith-Pokorny M fundamental at longer wavelengths, and π_5 is shallower than the Smith-Pokorny L fundamental at shorter wavelengths.

Estimates of the cone sensitivities from dichromats can never be more secure than the assumptions that are made about the relationship of dichromatic to trichromatic vision, and specifically the assumption that dichromats simply lack one of the three cone types of normal vision (eg Vos and Walraven 1971; Smith and Pokorny 1975).

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This is a plausible assumption, but may actually be incorrect, particularly in light of recent evidence that observers who are dichromats when tested with small fields often become anomalous trichromats when tested with large fields (Nagy 1980; Breton and Cowan 1981), and that hybrid genes may be present on the X-chromosome of some dichromats (Nathans et al 1986).

In this paper we describe a modification of Stiles's two-colour increment-threshold procedure. The modified method, applied to normal trichromats, yields M and L fundamentals that resemble dichromatic spectral sensitivity functions derived from dichromatic confusion loci.

1.1 *The two-colour threshold technique and model of W S Stiles*

The two-colour threshold technique has been summarised in a number of publications, including Enoch (1972) and Marriot (1976). Most of the papers by Stiles to which reference is made in this paper have been reprinted in a single volume (Stiles 1978). Stiles (eg 1953, 1959) typically used a 1-deg diameter foveal test flash of 200-ms duration presented in the centre of a 10-deg diameter adapting background. In the two-colour experiment, the threshold radiance (N_λ) of a test field of wavelength λ is determined for an adapting field of radiance M_μ and wavelength μ . Thresholds are determined under 'steady-state' conditions: that is, the subject is fully light-adapted to the background field before the measurement of a threshold begins.

For many combinations of λ and μ Stiles obtained threshold-versus-radiance (tvr) curves, plots showing how $\log N_\lambda$ varies as a function of $\log M_\mu$ (see, for example, figure 2). His model was based on the orderly way these tvr curves were altered as λ and μ were altered. Changes in λ lead to vertical displacements either of the whole curve, or of component branches of the curve: the curve, or branch, moves as a unit along the ordinate without change in shape. Changes in μ lead to similar displacements along the abscissa. In the former case the curve, or individual branch, is said to obey the 'test displacement rule', and in the latter case it is said to obey the 'field displacement rule'.

Obedience to the displacement rules suggests the existence of a visual mechanism that has an invariant spectral sensitivity, and in his earlier work Stiles hoped that the orderly movements of tvr branches might allow him to derive the spectral sensitivities of the three types of cone thought to be present in the trichromatic foveola. He supposed that a particular class of cone has a characteristic spectral sensitivity, and that the effect on those cones of a quantal flux N_1 at wavelength λ_1 is the same as that of a quantal flux N_2 at any other wavelength λ_2 , provided that N_1 and N_2 are in the inverse ratio of the spectral sensitivity values at those wavelengths (see eg Stiles 1948, page 98; 1949, page 139; 1959, page 102). The concept of substitutability of one wavelength for another was later epitomised by Rushton in the 'principle of univariance': "For each class of receptor, the result of light depends upon the effective quantum catch, not upon what quanta are caught" (Mitchell and Rushton 1971).

If, for a given branch of a tvr curve, the psychophysical threshold is entirely controlled by signals deriving from a single, univariant, class of cones, then the branch must obey the displacement rules. For all that varies with λ and μ is the probability that a given photon will be absorbed to yield an isomerisation. To reproduce the tvr curve at a new test wavelength or at a new field wavelength we need only multiply all values of N_λ by a constant factor, or all values of M_μ by a constant factor, so the tvr branch should move bodily along the ordinate in the one case, or along the abscissa in the other. These displacements directly reflect the changing probability of photon absorption and give a measure of spectral sensitivity that is called a 'tv λ ' curve when the test wavelength is varied, and an 'fv μ ' curve when field wavelength is varied. Since the tvr curve is of fixed shape, the tv λ curve can *in principle* be derived by measuring

thresholds at a single value of M_μ , and an $fv\mu$ curve can be derived by estimating the value of M_μ that gives a constant threshold value of N_λ ; but in adopting these abbreviated procedures the experimenter forgoes the security of knowing that the displacement rules hold (or misses the revelation that they fail).

The existence of just three foveal detection mechanisms, corresponding to the three classes of cone, was not supported by Stiles's later measurements of two-colour increment thresholds. As early as 1939 he described the 'limited conditioning effect', an inflexion observed in the tvr curve for the short-wavelength cones when the field was of long wavelength (Stiles 1939). This and other 'failures' of the displacement rules led him to recast his analysis in terms of seven ' π mechanisms' rather than three classes of cone. A π mechanism is to be thought of as an association of end-organs, "the association being effected somewhere in the neural system through which the nervous activity initiated by light absorption in the end-organs is transmitted to the brain" (Wyszecki and Stiles 1967, page 572). A π mechanism is identified when a tvr curve, or some branch of it, obeys the displacement rules over a range of values of λ and μ . Thus Stiles requires a π mechanism to behave in critical respects *as if* its sensitivity were controlled by one cone type, even though the majority of π mechanisms are unlikely to correspond to single classes of cone. It should be mentioned, however, that Stiles identified some mechanisms (eg the high intensity middle- and long-wavelength mechanisms, π'_4 and π'_5) without establishing that they obeyed the displacement rules; and the tests for the mechanisms later called π_4 and π_5 were performed with the 63-ms test flash that he used in his early work on his own eye, and not with the 200-ms flash used to obtain the published field sensitivities.

1.2 Reconstruction of increment sensitivities

Stiles did not measure tvr functions for every possible combination of λ and μ ; but from his tabulated field sensitivities of the π mechanisms it is possible to work backwards and to predict the foveolar increment threshold for a large range of combinations of λ , μ , and M_μ . The reconstruction requires the assumption that the displacement rules hold for all λ and μ , and the assumption that the test sensitivity is related to the field sensitivity by a fixed ratio.

For each mechanism, Stiles assumed that $\log N_\lambda$ is related to $\log M_\mu$ by a function of fixed form. The template for this standard tvr curve is tabulated in table 7.5 of Wyszecki and Stiles (1967) and in table A of Stiles (1978). For each value of μ the horizontal position of the template can be predicted from the horizontal position of one particular point on the curve. This point, which is conveniently called the 'criterion point', lies 1 log unit above the absolute threshold of the mechanism (ie the threshold when the field is zero). These field sensitivities are tabulated in table 7.6 of Wyszecki and Stiles (1967) and in table B of Stiles (1978).

To fix the *vertical* position of the criterion point we must know the test sensitivity of the mechanism. This is estimated by multiplying the field sensitivity by a constant, known as the Weber fraction. The latter is defined as the ratio of the threshold radiance, N_λ , to M_μ when $\lambda = \mu$ and N_λ has been raised 1 log unit above its value on a zero field. Although Stiles estimated this fraction at only one value of λ , the same ratio can be used at all other test wavelengths, since the model assumes that the relative spectral sensitivities are identical for test and field. The estimated Weber fractions are given in table 7.4 of Wyszecki and Stiles (1967).

Once the template has been horizontally and vertically positioned, the value of N_λ for any value of M_μ can be estimated from the template. The prediction can be repeated for each of the π mechanisms in turn, and the expected psychophysical threshold is then that of the most sensitive mechanism.

1.3 Sensitivity to the adapting field

The much quoted sensitivities of π_4 and π_5 were derived by the abbreviated $fv\mu$ method. Details of the experimental conditions were published much later (Stiles 1978, page 19). Test wavelengths of 500 and 667 nm were used for π_4 and π_5 measurements, respectively, in an attempt to isolate those mechanisms for all μ . The duration of the test flash was 200 ms. For each λ , the value of M_μ that raised N_λ 1 log unit above its value on a zero field was determined as a function of μ . The results, tabulated as $1/M_\mu$, were averaged across four subjects: three females aged 20–30 years and one male aged 51 years.

For a field sensitivity to correspond to the spectral sensitivity of a single class of cone, the signal that determines psychophysical sensitivity must be attenuated only as a function of the rate at which photons are absorbed from the field by that class of cone, and must be independent of the rates at which photons are absorbed by other classes of receptor. The assumption that such independence holds has been called the 'field quantum-catch hypothesis' by Wandell and Pugh (1980a); in applying the idea to π mechanisms, Mollon (1982) used the term 'principle of adaptive independence'.

Much effort has been expended in trying to show that the principle of adaptive independence holds true. Three methods have been used to check for this critical property. A direct method is to compare the test and field sensitivities of the same mechanism. Using low-intensity adapting fields of 667 and of 500 nm, Stiles (1959, figures 6 and 8) himself made this check and found good agreement between the test spectral sensitivity and the envelope of the test sensitivities predicted from the field sensitivities of π_4 and π_5 ; but in each condition the low-intensity field isolated one mechanism over only a limited range of test wavelengths. Failures of this test with high-intensity fields (Stiles 1959, figures 7 and 9) led Stiles to postulate the modified high-intensity forms of π_4 and π_5 : π'_4 and π'_5 .

The two remaining methods have been prominent in more recent research into the nature of π_4 and π_5 ; the first, obedience to the field displacement rule, was introduced above; the second has been called field additivity. Field additivity holds if the effect of any mixture of lights on a particular mechanism is equivalent to the effect of a linear sum of their components, spectrally weighted according to the sensitivity function of that mechanism (De Vries 1949; for a formal account see, for example, Sigel and Pugh, 1980)⁽¹⁾.

Under Stiles's π_5 isolation conditions, Sigel and Pugh (1980) and Wandell and Pugh (1980b) have shown that tv_r curves obey the field displacement rule, although only if M_μ is such that N_λ is not more than 1.2 log units above its value on a zero background⁽²⁾. At field radiances that raise N_λ more than about 1.5 log units, the field displacement rule is not obeyed (Stiles 1953, 1959; Sigel and Pugh 1980; Wandell and Pugh 1980b). Field additivity holds if the combined background field does not raise N_λ more than 1.2 log units above its value on a zero background (Sigel and Pugh 1980), although at higher radiances marked subadditivity is observed (Wandell and Pugh 1980b)—the effect of the combined field is less than predicted.

Recent tests of the predictions of the field displacement rule under π_4 conditions are less clear. The experimental results of Sigel and Brousseau (1982) suggested to them

⁽¹⁾ As Wandell and Pugh (1980a) allow, a failure of either the displacement rules or field additivity could logically be taken to imply that the cones themselves fail to obey the principle of univariance, rather than that the sensitivity of a π mechanism is not mediated by a single cone class. A failure of univariance is not inconceivable, particularly in light of evidence that different regions of the outer segment of photoreceptors can adapt independently (eg Lamb et al 1981).

⁽²⁾ A factor of $10^{1.2}$. All expressions in which 'log' appears refer to the common logarithm with the base 10.

that the field displacement rule was not obeyed even at low background radiances. This interpretation, however, has been questioned by Reeves (1982). He noted that rod intrusions would be difficult to avoid when a 500-nm flash was presented on dim or zero fields, and he pointed out that this intrusion would vary with the field wavelength, extending over a greater range of field radiances when the field was of long wavelength. Reeves fitted an empirically derived template to the same data, but gave less weight to thresholds at low background radiances; deviations from the fitted template were then reduced. In order to eliminate rod intrusions, Kirk (1985) made measurements on the cone plateau. He found that shape invariance held for π_4 in the case of one observer and failed in the case of a second. Failures of field additivity were found for both observers.

Since Stiles expediently derived the field sensitivity of π_5 by estimating the background radiances that raised N_λ only 1 log unit or less above its value on a zero field, π_5 cannot be rejected as a cone candidate on the basis of tests of the field displacement rule or the prediction of field additivity. At such threshold elevations there is no conclusive evidence that the mechanism violates either of the tests.

It is remarkable that field sensitivity measurements under π_5 conditions can satisfy such tests and yet yield spectral sensitivities that depart from König fundamentals (eg Smith–Pokorny's L function) even more than does Stiles's original π_5 ; examples are the π_5 sensitivity of observer 'CS' of Sigel and Pugh (1980), and the long-wavelength field sensitivity obtained with 10-ms flashes for observer 'Brian' of Wandell and Pugh (1980a).

1.4 *Field sensitivity versus test sensitivity; and the running together of tvr curves*

A field sensitivity curve can correspond to the action spectrum of a class of cones only if adaptive independence obtains. The interpretation of test sensitivity measurements, on the other hand, does not require us to assume adaptive independence, since the adaptive states of the cones are held approximately constant as λ is altered. Why then did Stiles adopt the field sensitivity method for his principal measurements of the long- and middle-wave mechanisms?

The answer is that the field sensitivity method, under Stiles's conditions, is the more likely to separate the two mechanisms over the full spectral range. Under other conditions, however, the test sensitivity method may be the more likely to separate the two mechanisms. To explain this we will consider two classes of cone, called A and B for purposes of generality. In deriving the sensitivity of class A by the field sensitivity method the experimenter should, in principle, choose a test wavelength that maximises S_A/S_B where S_A and S_B are the sensitivities of the two classes of receptor; and in the test sensitivity method he should choose a field wavelength at which class B is maximally suppressed relative to class A, the wavelength at which S_B/S_A is maximal. When the field sensitivity of A is measured, the worst isolation will occur when $\lambda = \mu$, since μ will necessarily be the field wavelength that maximally suppresses the sensitivity of A relative to B; and when the test sensitivity of A is measured, the worst isolation similarly occurs when $\lambda = \mu$, although now because λ will necessarily be the test wavelength that minimises the relative sensitivity of A to the test.

We argue that the relative success of the test and field sensitivity methods, other problems apart, depends upon the slopes of the tvr branches of A and B. Consider the general case at some $\lambda = \mu$ where $\log(S_A/S_B)$ is k , and the asymptotic slope of the function relating $\log N_\lambda$ and $\log M_\mu$ is m . In the region of asymptotic slope we assume the formula of the tvr function is:

$$\log N_\lambda = m(\log M_\mu) + c, \quad (1)$$

where c is some constant.

Consider a point $(x, mx + c)$ on the tvr curve for the cone type more sensitive to λ and μ , A. Assuming that A and B have similar Weber fractions, at $\lambda = \mu$ the corresponding point on the tvr curve for B lies at $(x + k, mx + c + k)$, since if k is the difference in the test and field sensitivities, the branch B relative to A will be displaced k along the ordinate, and k along the abscissa (see above). How far above or below the tvr curve for A will this point lie? From equation (1) it follows that for branch A when $\log M_\mu = x + k$, the following relationship holds: $\log N_\lambda = m(x + k) + c$. Thus the point $(x + k, mx + c + k)$ on the tvr function for B lies $(mx + c + k) - [m(x + k) + c]$ above the tvr function for A, which is equal to $k - mk$. Thus when $m = 1$, the two functions coincide, but when $m < 1$, B lies above A, and when $m > 1$, A lies above B.

We will illustrate this with the three examples shown in figure 1. For the sake of argument we assume that $\log(S_A/S_B)$ is maximal. Initially, we will consider only threshold elevations at which both branches have attained nonzero asymptotic slope; such regions are shown by the solid portions of the tvr branches drawn in the figure. In the three panels (a), (b), and (c) the asymptotic slopes of the tvr branches, m , are 0.5, 1.0, and 2.0 respectively. Since $\lambda = \mu$ and $\log(S_A/S_B) = k$, branch B relative to branch A has in each case been displaced along the ordinate by the distance k , and along the abscissa by the same amount. When $m = 0.5$, as shown in the uppermost panel, branch B lies $0.5k$ above branch A. Since A is exposed, we can obtain the sensitivity of A, but can never obtain the sensitivity of B. Furthermore, since μ is chosen so that

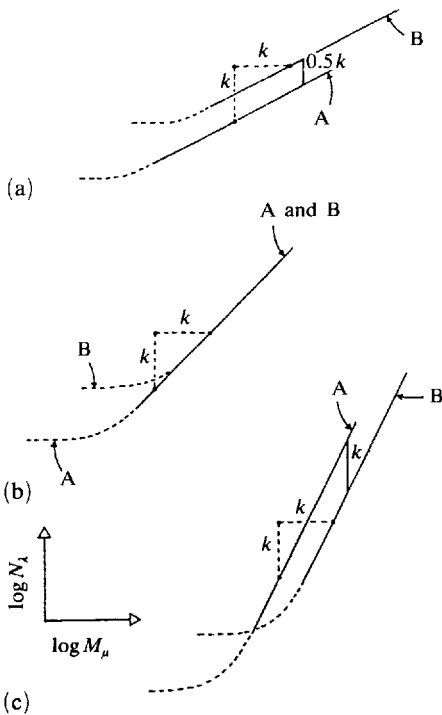


Figure 1. Predictions of the relative positions of two tvr branches A and B with nonzero asymptotic slopes of (a) 0.5, (b) 1.0, (c) 2.0. The regions of asymptotic slope are represented by the solid portions of the tvr branches. In each case, branch B relative to branch A has been displaced along the ordinate by the distance k , and along the abscissa by the same amount. When the asymptotic slopes are 0.5 (a), branch B lies $0.5k$ above branch A, but when they are 2.0 (c), branch B lies k below A, and when the final slopes are 1.0 (b), the two branches coincide. The regions of the tvr branches below the regions of asymptotic slope are represented by dashed lines. For further details see text.

$\log(S_A/S_B)$ is maximised, varying μ will reduce this ratio, increasing the horizontal (and hence the vertical) separation between the two branches. Thus the field sensitivity of A can be obtained at $\lambda = \mu$ and throughout the spectrum. When $m = 2.0$, as shown in the lowermost panel, B lies k below A. For $m = 2.0$ we can obtain the sensitivity of B in the region of asymptotic slope, but not the sensitivity of A. Since λ maximises $\log(S_A/S_B)$, varying λ will increase the vertical separation between branch B and branch A. Under these conditions the test sensitivity of B can be obtained at $\lambda = \mu$ and throughout the spectrum. When $m = 1.0$, as shown in the middle panel, the two branches A and B coincide in the region of asymptotic slope. Clearly, in this region it is never possible to be sure of the sensitivity of A or of the sensitivity of B. Neither of the two methods has the advantage under these conditions.

The arguments above apply equally to the case where $\log(S_B/S_A)$ is maximised, so that either the field sensitivity of B ($m = 0.5$) or the test sensitivity of A ($m = 2.0$) can be determined. For simplicity, we have considered only regions where the two branches have attained asymptotic slope. Below this region the slopes of tvr branches typically decrease until reaching a final region of zero slope corresponding to absolute threshold. This behaviour is shown as the dashed portions of the tvr branches of figure 1. This reduction in slope has the effect of exposing branch A at lower threshold elevations—as can be seen in figures 1b and 1c. Since A is exposed in each condition, it is possible, at least in principle, to estimate the field sensitivity of A at $\lambda = \mu$ and throughout the spectrum, as long as measurements are confined to sufficiently low threshold elevations. Under Stiles's conditions, which correspond to figure 1b, the field sensitivity method has the clear advantage, since it is never possible to estimate the test sensitivity of the less sensitive mechanism for $\lambda = \mu$.

The separation of the branches in our example also depends upon the sensitivity ratio $\log(S_A/S_B)$. If this ratio is too small, the separation between the two branches may also be too small to ensure adequate isolation of one of the mechanisms throughout the spectrum, either for a test sensitivity or a field sensitivity determination. Within the terms of Stiles's own model, the isolation of π_5 in Stiles's field sensitivity measurements is adequate: in the homochromatic conditions of the far red, when $\lambda = \mu = 667$ nm, the sensitivity difference between π_4 and π_5 is 0.73 log unit, so the two branches do not run together until well after the threshold has been raised by more than 1 log unit. But the isolation of π_4 is inadequate when $\lambda = \mu = 500$ nm. For here the tabulated sensitivity of π_4 is only 0.143 log unit more than that of π_5 ; and the calculated separation of the two mechanisms at the 'field point' (the point 1 log unit above absolute threshold at which Stiles estimated the sensitivity of π_4) is only 0.03. Thus, within the terms of Stiles's own model, the tabulated sensitivity of π_4 must be suspect at 500 nm, and also at shorter wavelengths, since π_4 and π_5 run nearly parallel below 500 nm. Other evidence (such as tritanopic colour-matching functions) implies that the sensitivity of the long-wavelength cones continues to decrease, relative to that of the middle-wavelength cones, between 500 and 460 nm; and thus the tabulated sensitivity of π_4 must be seriously questioned throughout the short-wavelength region.

The superposition of π_4 and π_5 seen in figure 1b is a property of tvr branches that has gone largely unremarked in the Stilesian literature. It is curious that despite this coincidence, Stiles estimated his Weber fractions at $\lambda = \mu$. There is a distinct possibility, therefore, that the estimates of the Weber fractions of π_4 and π_5 are not independent.

1.5 Sensitivity to the test field

From the preceding it follows that, whatever the choice of backgrounds, a tv λ method cannot isolate both the M- and L-cones throughout the spectrum unless a procedure is

adopted that will cause adaptation to exceed Weber's law⁽³⁾. Despite this problem, a number of attempts have been made to isolate cone sensitivities by means of a simple $tv\lambda$ method—notably attempts by Wald (1964).

Stiles himself made extensive two-colour $tv\lambda$ measurements beginning as early as 1939. Many of his $tv\lambda$ functions are published in his reply to Wald (Stiles 1964). Relevant to our introduction to M- and L-cone test sensitivities are the field sensitivities of π'_4 and π'_5 . It may seem surprising that we now return to a consideration of the 'field sensitivities' of the longer-wavelength 'prime' mechanisms. It is important, however, to recognise that despite this designation as field sensitivities, π'_4 and π'_5 sensitivity functions were actually derived by a modified $tv\lambda$ method. Stiles measured $tv\lambda$ functions on low- and high-intensity adapting fields. For the middle-wavelength $tv\lambda$ functions, 667 nm fields of either 29.2 or 2506 td were used (Stiles 1964, figure 1, curves L and M), and for the long-wavelength $tv\lambda$ functions, 500 nm fields of either 42.8 or 1552 td were used (see curves D and F). To obtain the π'_4 and π'_5 sensitivities Stiles modified the π_4 and π_5 field sensitivities by wavelength-dependent factors derived from the difference between the high-intensity and low-intensity $tv\lambda$ functions. The account of this method (Stiles 1978, page 20) is slightly misleading because it omits to point out an additional assumption that was made to determine π'_4 at longer wavelengths. The low-intensity middle-wavelength $tv\lambda$ function is determined by π_5 , not by π_4 , at long wavelengths (see Stiles 1959, figure 6). From a consideration of the available data we believe that at longer wavelengths π'_4 was determined from the difference between the middle-wavelength high-intensity $tv\lambda$ function and the *predicted* π_4 test sensitivity (predicted from the π_4 field sensitivity function). This prediction is shown in Stiles (1959, figure 6).

Wald (1964) made extensive $tv\lambda$ measurements on intense chromatic backgrounds. He produced 'green' and 'red' functions that differ from Stiles's π_4 and π_5 mainly at longer and shorter wavelengths, respectively. The direction of these differences is consistent with dichromatic estimates, but—this correspondence apart—there is little evidence to support Wald's contention that his sensitivity functions are those of isolated cone types. For reasons discussed above, if adaptation proceeds according to Weber's law, and if the Weber fractions of the M- and L-cone mechanisms are similar, isolation is impossible under homochromatic conditions. More recently, using a flicker photometric method, Eisner and MacLeod (1981) found, like Wald, an approach to dichromatic test sensitivities under chromatic adaptation, with a suggestion of an asymptotic convergence on these sensitivities with increasing intensity. Yet in this case, as in Wald's, there is no truly independent evidence that Weber's law was exceeded. Thus the claims of cone isolation under steady-state adaptation must be treated with caution. This argument, of course, applies equally to Stiles's 'prime' functions.

We will return to the early $tv\lambda$ estimates below.

1.6 *Adaptation on small fields exceeds Weber's law: test field isolation?*

From the preceding arguments it follows that a full $tv\lambda$ function could be obtained for a single cone type if a way could be found of raising adaptation more rapidly with M_μ than is predicted by Weber's law. The results of Crawford (1940), Westheimer (1965, 1967), and others show that incremental sensitivity depends not only upon the amount of light falling on the retinal region on which the test flash is presented, but also upon the distribution of light falling around that region. Typically, as the diameter of the background increases beyond that of the test field, the increment threshold first rises

⁽³⁾ This argument applies equally to adapting fields of complex spectral character, such as the purple field used by Wald (1964). In such cases the test sensitivities of π_4 and π_5 will be coincident at higher background radiances when λ is tritanopically metameric with the adapting field.

until it reaches a maximum value at some 'critical' background diameter; and then falls, reaching an asymptotic value beyond which further increases in diameter have no effect. These findings suggest that background fields close to the 'critical' size may result in sensitivity losses exceeding those implied by Weber's law. And, indeed, such fields have been found to give rise to tvr functions that exceed Weber's law at higher background radiances (McKee 1970; Hayhoe and Tinker 1979; Buss et al 1982).

If, under small-field conditions, the slope of the component branches of tvr functions exceeds that of Stiles's template at higher threshold elevations, then, for some combinations of λ and μ , tvr functions would be expected to be clearly double-branched. At those wavelengths test (and field) sensitivities can then be estimated from the positions of the two branches. Figure 2 shows the tvr functions that would be expected for the specific case of $\lambda = \mu = 650$ nm, first under Stiles's standard conditions (figure 2a), and second when the field diameter is reduced (figure 2b). In the latter case, detection at higher background radiances will be mediated by a middle-wavelength cone mechanism.

We propose that the detection sensitivities of the two mechanisms that underlie the two branches of the double-branched tvr functions depend only on the rate at which photons are absorbed by a single cone class, and are independent of the rates of absorption in other cone classes. Thus, from the principle of univariance it follows that each branch should obey the test displacement rule as λ is varied. When the two mechanisms are of similar sensitivity, small deviations away from the predicted threshold behaviour would be expected because of probability summation between independent mechanisms.

Intrusions by the short-wavelength cones are unlikely under our conditions, since the test field is small, brief, and falls upon the tritanopic central foveola.

We note that a related technique has previously been used by King-Smith and Webb (1974), who obtained dichromat-like sensitivities by transiently overloading the cone mechanisms with background fields of sudden onset. Sensitivities were obtained by means of an abbreviated tv λ method. Only a limited test of the predictions of the test displacement rule was performed.

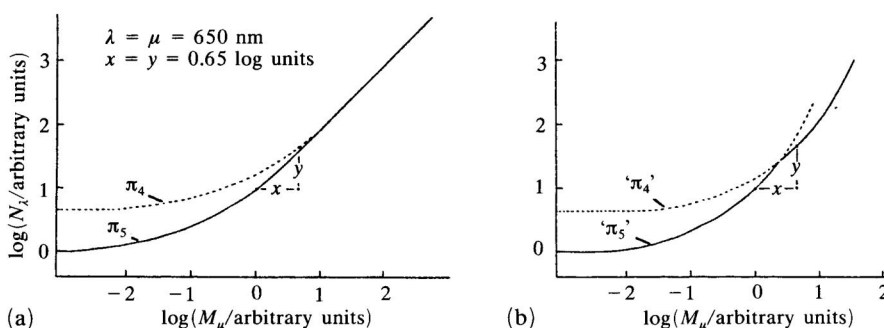


Figure 2. Predictions of the relative positions of the π_4 and π_5 tvr branches for $\lambda = \mu = 650$ nm, using the tabulated field sensitivities of Stiles's π_4 and π_5 , and using either (a) Stiles's standard template shape to describe the shape of each branch, or (b) a steeper template shape, similar to that found under our small-field adaptation conditions. Since π_4 is approximately 0.65 log unit less sensitive than π_5 at 650 nm, and since the Weber fractions of the two mechanisms are nearly identical, in each case the π_4 branch has been shifted horizontally right, and vertically up by 0.65 log unit relative to the π_5 branch.

2 Method

2.1 Apparatus

The apparatus was a conventional Maxwellian-view optical stimulator linked to a Digital PDP 11/23 laboratory computer. The Maxwellian-view system has been

described before (Mollon and Polden 1977). Channel 1 provided the test field, and channel 3 provided the adapting field (see their figure 1). Since 1977 a 100-W mercury arc lamp has been added to provide the light for the test field channel (the light source of the adapting field channel remains a 12-V, 50-W tungsten iodide lamp). In the following experiments an achromatising lens (Bedford and Wyszecki 1957) was placed immediately before the artificial pupil.

Wavelengths were selected by interference filters. A variable interference filter (Barr and Stroud, CGS1) in combination with a Wratten 24 gelatin blocking filter was used to select the 647 nm test light; the bandwidth at half-maximum of this combination was 18 nm⁽⁴⁾. 555-nm and 574-nm test lights were selected by combinations of fixed interference filters (Barr and Stroud), and gelatin blocking filters (for 555 nm an Ilford 625, and for 574 nm an Ilford 626); the bandwidth at half-maximum of these combinations was 6 nm. The other test and the two field wavelengths were selected by use of three-cavity, blocked interference filters with bandwidths of between 8 and 10 nm (Melles Griot or Oriel Scientific). Infrared and ultraviolet radiation was removed by HA-3 glass and by Wratten gelatin filters, respectively. Two variable neutral density filters (Barr and Stroud), mounted on computer-controlled stepping motors, varied the attenuation of the beams. Fixed neutral density filters were added when additional attenuation was required.

The shutter, a balsa-wood vane mounted on an army-surplus solenoid, had rise and fall times of less than 2 ms. Blank trials in the forced-choice procedure were achieved by reversing the polarity of the voltage applied to the solenoid. This operation, which had the effect of moving the balsa-wood vane in the opposite direction, gave rise to an audible click that was indistinguishable from the sound of the shutter opening normally. The shutter was positioned so that movement in the reverse direction did not expose the test beam.

The position of the observer's eye was maintained by a dental wax impression rigidly mounted on an adjustable $x-y$ positioner taken from a milling machine.

2.2 Stimuli

The sizes of the test and field stimuli were defined by small circular field-stops. In all experiments a test flash, 3-min visual angle in diameter and 17-ms duration, was presented in the centre of a background field. The diameter of the background field was 7 min and 8 min for subjects MD and AS, respectively. These choices of background size were not arbitrary. Following the method used by Crawford (1940) and Westheimer (1965, 1967), we measured incremental thresholds as a function of the diameter of the background field (keeping the radiance of the background field constant). For the small 3-min test field the background diameter that gave rise to the highest increment threshold was found to be close to 7 min for subject MD and close to 8 min for subject AS.

The observer fixated the centre of the background field with the aid of two fixation points that were positioned 36-min horizontally either side of the centre of the background field.

2.3 Calibration

Stimulus radiances were measured with a PIN-10 silicon photodiode (United Detector Technology) and operational amplifier. This combination was cross-calibrated against a similar combination that had previously been calibrated absolutely and spectrally by the National Physical Laboratory, England. Without the addition of a lock-in amplifier and an episotister, radiometric measurements made with the small field-stops in place were unreliable. For convenience, daily calibrations were performed with larger field-stops in

⁽⁴⁾ This combination, which has a relatively large bandwidth, was used to allow direct comparisons with the results of earlier experiments not described here.

place. Appropriate corrections were then applied to compensate for the different field areas. Neutral density filters, fixed and variable, were calibrated in situ for all test and field wavelengths used. Particular care was taken in calibrating the interference filters: a combination of the PIN-10 and amplifier, a monochromator (Hilger and Watts), a lock-in amplifier (Princeton Applied Research 128A), and an episicotister (Rofin) allowed a check for any side-band leaks; the same combination of instruments was used to measure the centre wavelength and the bandwidth at half-height of each interference filter in situ. The monochromator was calibrated with the use of a reference mercury lamp. Timing was by means of a programmable clock accurate to 0.01%. The durations of the test flash were checked with the PIN-10 and an oscilloscope with a calibrated time base.

2.4 Procedure

The observer light-adapted to the background field for 3 min prior to an experimental run. The 'ball-park' threshold estimation was by a double staircase procedure (Cornsweet 1962). One staircase began well above threshold and the other well below threshold. The observer's task was to respond "yes" or "no" according to whether the flash could or could not be seen. The staircases alternated until they crossed, after which six trials were presented on a single staircase. The average position of the variable neutral density filter, on these six trials, provided the starting point for the forced-choice procedure that followed. The ball-park procedure lasted a minimum of 1.5 min; therefore the total light-adaptation time before actual data collection was more than 4.5 min.

The final threshold was estimated by a temporal two-alternative forced-choice procedure. Two tones separated by 800 ms preceded two intervals in which the flash might occur. By means of push buttons the observer indicated in which interval the flash occurred. A single staircase procedure was used. If the observer made two consecutive correct responses, the flash radiance was reduced by 0.1 log unit. If the observer was incorrect on any trial, the flash radiance was increased by 0.1 log unit. Such a procedure tracks a probability of being correct of 0.71 (Wetherill 1963). An experimental session ended after twelve reversals, the threshold being estimated from the average of those twelve reversal positions. There was a break of at least 10 min between each threshold estimation.

2.5 Observers

Two experienced psychophysical observers were employed in this work: AS is emmetropic; MD is myopic and astigmatic (3-D concave and 1-D spherocylindrical correcting lenses were positioned immediately before the artificial pupil). Both observers performed normally on the Farnsworth-Munsell 100-hue test and the Nagel anomaloscope.

2.6 Template shapes

If a particular mechanism obeys the test displacement rule, then there exists a single template shape that will describe the threshold behaviour of that mechanism at all test wavelengths. From our tvr data we needed to determine both the shape of the appropriate template, and its position at each test wavelength (ie the spectral sensitivity function of the mechanism). To do this we used an iterative technique similar to that described by Sigel and Pugh (1980). Data were shifted to produce a least-squares fit to a first estimate of the template shape (this first estimate was derived by eye). The shifted data points were then averaged within 0.1 log unit 'bins' and these averages were used to produce a second estimate of the underlying template shape; the procedure could then be repeated to produce a third estimate, and so on. When two successive estimates of the template shape were similar, the last estimate was used as our estimate of the

threshold behaviour of that mechanism. The spectral sensitivities of the cone mechanisms were then derived by shifting the data to provide a best least-squares fit to the final template estimate. In practice, the first estimate of the template shape by eye proved to be similar to the second estimate derived by this computer technique. Template shapes were estimated independently for each subject.

Shifting the template vertically for a least-squares fit to the data required that the template first be fixed horizontally. Horizontal positions for the upper branch of the double-branched curves were determined from the shapes of single-branched tvr functions. For each μ , the single-branched tvr data were averaged in the y -direction; the best horizontal fit of the template to these averaged data was then taken to be the horizontal position for the subsequent fitting procedure. In this way we estimated the horizontal position for the M-cone mechanism for $\mu = 673$ nm, and that for the L-cone mechanism for $\mu = 481$ nm. The horizontal position for fitting to the lower branches was estimated by eye from a consideration of all the tvr curves exhibiting this branch.

For double-branched tvr functions the template shape had to be fitted twice: once to the lower branch and once to the upper branch. Before this could be carried out by the computer shifting technique, a decision had to be made as to which of the two branches each data point was on. This decision was made subjectively after first fitting the template shapes to the data points by eye. Our analysis did not take into account the effects of probability summation. Such effects would be apparent as small deviations below the fitted templates at their intersections.

3 Results

For subject AS, test sensitivities were derived by fitting templates to tvr functions measured at twenty-four combinations of λ and μ . From these results we were able to choose combinations of μ and M_μ to limit detection to either the M-cone or the L-cone mechanism for all λ . Using these combinations of μ and M_μ we experimentally derived a second estimate of the cone sensitivities for subject AS by the abbreviated tv λ method (see above).

For subject MD, full tvr curves were measured at only seven combinations of λ and μ . This subset was measured to confirm the results for subject AS, and to determine independently two combinations of μ and M_μ for which detection should be mediated by either the M-cone or the L-cone mechanism for all λ . The primary estimate of the cone sensitivities for MD was then derived by the abbreviated tv λ method.

The data points shown below as tvr plots represent the average of two threshold measurements. The data points composing the test sensitivity functions estimated by the tv λ method represent the average of eight increment threshold measurements; the error bars shown in the figures represent $\pm 2SE$ (standard error between sessions).

3.1 Template shapes and positions

For subject AS, template shapes were estimated from tvr functions measured at a total of forty-four combinations of λ and μ . The twenty additional combinations, which were measured to estimate M- and L-cone *field* sensitivities, are reported elsewhere (Stockman 1983). A separate determination was carried out for the M- and the L-cone mechanisms. We found no important differences between the template shapes for the two mechanisms.

A similar determination was carried out for subject MD on the basis of nine tvr functions. Data for the M- and L-cone mechanisms were pooled to provide a common estimate of the template shape for the two mechanisms. (The template shape for subject MD is fitted to the data shown in the lower half of figure 7.)

The final estimate of the template shape for subject AS is fitted to the tvr functions in figures 3 and 5. In the text that follows, the position of the template will be given as the coordinates ($x = \log M_\mu$, $y = \log N_\lambda$) of the point on the template corresponding to a 1 log unit elevation of threshold above the base of the template. This point on the template will be referred to as the 'criterion point'. Test sensitivities derived from tvr curves will be given as $\log(1/N_\lambda)$ at the criterion point.

3.2 The M-cone test sensitivity function

Figure 3 shows the twelve tvr functions for subject AS measured on a 673-nm field. The tvr functions have been positioned correctly with respect to the scale on the abscissa. The logarithmic scale on the ordinate is given in arbitrary units, and for clarity the functions have been shifted so that the branches attributed to the M-cone mechanism are vertically separated by 1.4 log units. The absolute scale on the ordinate can be reconstructed for each test wavelength from the y -coordinate (increment threshold) of the criterion point on the template, which is given for each wavelength in column 2 of table 1.

By the method described above, the template for subject AS was fitted to the branch thought to represent the M-cone mechanism. The criterion point on the template was fixed at a field radiance of $10^{10.60}$ quanta $s^{-1} \text{ deg}^{-2}$, and the template was then shifted vertically to produce a least-squares fit to the data points on that branch. If a second, lower, branch (thought to represent the L-cone mechanism) was evident, then the procedure was repeated for that branch, with the criterion point on the template fixed at a field radiance of $10^{9.50}$ quanta $s^{-1} \text{ deg}^{-2}$. For each λ , table 1, column 2 gives the increment threshold corresponding to the y -coordinate of the criterion point on the template after fitting.

The results for subject AS appear to be consistent with the predictions of the test displacement rule, but only if it is applied to two mechanisms at some test wavelengths. At test wavelengths ≤ 588 nm the data points on each tvr function can be described by the template shape, vertically displaced, with the criterion point fixed horizontally at $10^{10.60}$ quanta $s^{-1} \text{ deg}^{-2}$. At test wavelengths > 588 nm the tvr function at higher background radiances can be described by the template shape, vertically displaced, with

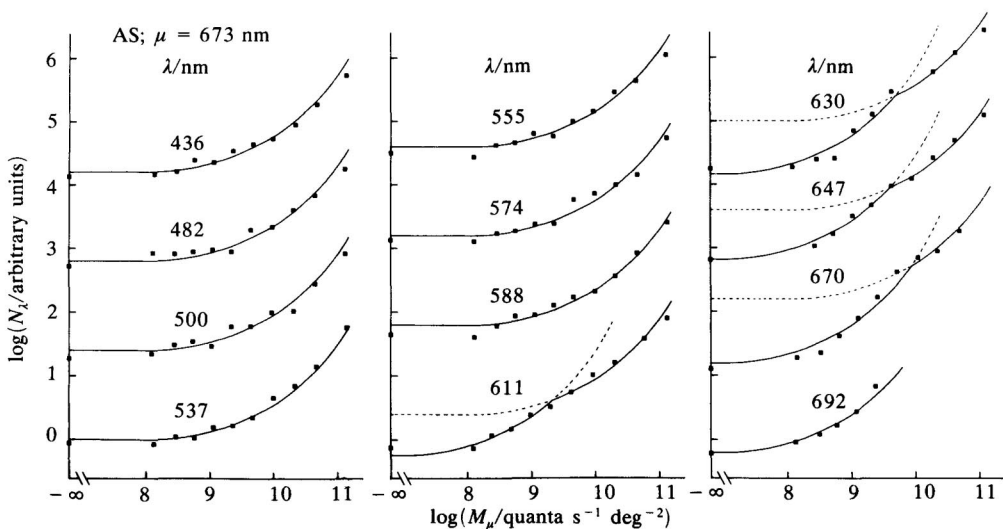


Figure 3. Twelve tvr functions for subject AS measured on a 673-nm field. For clarity the functions have been shifted vertically so that the M-cone branches in each panel are separated by 1.4 log units. Each data point is the average of two measurements made during different sessions. For details see the text.

the criterion point also fixed at $10^{10.60}$ quanta s^{-1} deg^{-2} ; the template, however, clearly cannot describe the tvr function at lower background radiances. These apparent failures of the test displacement rule are consistent with the hypothesis that under those conditions detection is mediated by a second cone mechanism. At test wavelengths >588 nm the tvr function at lower background radiances can be described by a simple vertical displacement of the template shape, but with the criterion point fixed horizontally at $10^{9.50}$ quanta s^{-1} deg^{-2} . One exception on nearly all the tvr functions is the increment threshold measured on the field of highest radiance: the increment threshold falls consistently about 0.1 log units below the fitted template. Since the effect appears to be largely independent of test wavelength, it will have little effect on the shape of the sensitivity function.

Figure 4 (filled circles) shows the test sensitivity functions derived from the results shown in figure 3. The ordinate is the y -coordinate of the criterion point, with a sign change so that it represents the logarithm of test sensitivity rather than the logarithm of threshold radiance at the criterion point 1 log unit above absolute threshold. The filled circles correspond to the test sensitivity of the upper branch of the tvr function at longer test wavelengths and the single branch of the tvr function at shorter test wavelengths. We note that the test sensitivities derived from the lower, L-cone, branches of the tvr functions at longer test wavelengths compare well with the same sensitivities estimated on a 481-nm field (see below). This similarity provides support for the hypothesis that the lower branch of the double-branched curve represents detection mediated by the L-cone mechanism.

Since a branch thought to represent the M-cone mechanism can be identified at all the test wavelengths shown in figure 3, it is possible to choose a radiance of the 673-nm background for which detection is by that mechanism at all those test wavelengths. Since that branch appears to obey the predictions of the test displacement rule, the reciprocal of the increment threshold on that background field measured against test wavelength should be related by the addition of a logarithmic constant to the test sensitivity function derived by template fitting.

Columns 3 and 4 of table 1 give the average and standard errors of the eight increment thresholds measured at various test wavelengths on a 673-nm field of $10^{10.73}$ quanta s^{-1} deg^{-2} radiance. The open circles of figure 4 represent the reciprocal

Table 1. M-cone test thresholds. The second column gives the value of the test threshold 1 log unit above absolute threshold derived for subject AS by fitting templates to tvr curves; the third and fifth columns give the mean values of the test threshold obtained at a fixed field radiance by the abbreviated method. The values given for test thresholds represent $\log(N_\lambda/\text{quanta } s^{-1} \text{ deg}^{-2})$. The values given in the fourth and sixth columns represent twice the standard error of the mean.

λ/nm	Subject AS			Subject MD	
	$\log N_\lambda$ (tvr)	$\log N_\lambda$ (tv λ)	2SE	$\log N_\lambda$ (tv λ)	2SE
436	9.50	9.54	0.06	10.08	0.07
482	8.90	9.04	0.05	9.47	0.05
500	8.65	8.70	0.05	9.16	0.09
537	8.30	8.32	0.05	8.88	0.07
555	8.22	8.35	0.08	8.80	0.08
574	8.27	8.41	0.05	8.90	0.07
588	8.47	8.59	0.07	9.05	0.04
611	8.94	8.97	0.06	9.50	0.09
630	9.40	9.46	0.06	9.96	0.06
647	9.83	10.17	0.04	10.42	0.05
670	10.62	10.80	0.06	-	-

of the average increment thresholds plotted against wavenumber. The function has been displaced vertically to align with the function derived by template fitting. In its shape and spectral position, the function derived by the abbreviated $tv\lambda$ method agrees well with that obtained by fitting templates to tvr data (solid circles).

For subject MD, four tvr functions were measured on a 649-nm field (for $\lambda = 482, 555, 611,$ and 647 nm). At shorter test wavelengths a single branch was found with an M-cone spectral sensitivity, whereas at longer wavelengths two branches were found: the lower with an L-cone sensitivity and the upper with an M-cone sensitivity. These results, like those for subject AS, are consistent with the predictions of the test displacement rule applied to one mechanism at shorter test wavelengths, but applied to two mechanisms at longer test wavelengths.

The tvr results for subject MD enabled us to choose for him a radiance of the 649-nm background at which detection should be mediated by the M-cone mechanism at all test wavelengths. We were therefore able to determine the test sensitivity of the M-cone mechanism for subject MD by the abbreviated $tv\lambda$ method. Columns 5 and 6 of table 1 give the average and standard errors of the eight increment thresholds measured at various test wavelengths on a 649-nm field of $10^{9.89}$ quanta $s^{-1} \text{ deg}^{-2}$ radiance. The filled squares in figure 4 represent the logarithm of the reciprocal of the

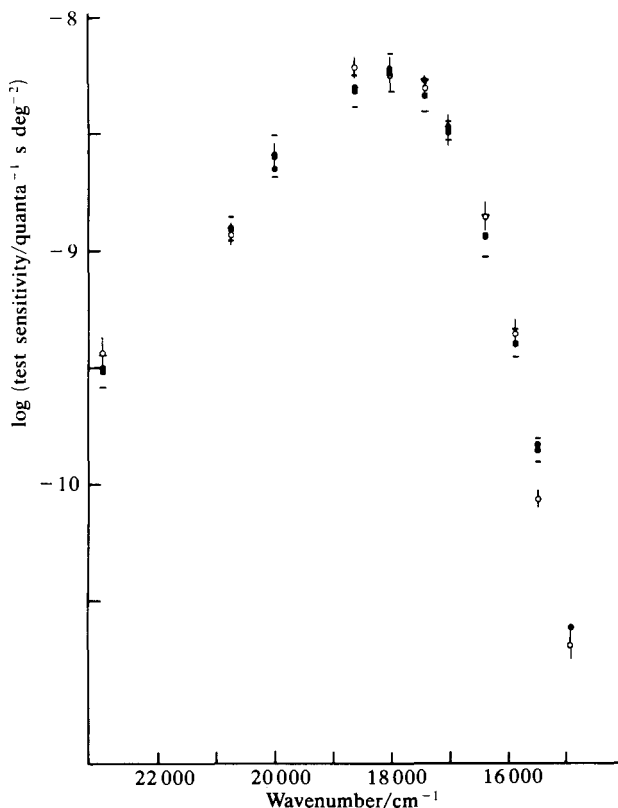


Figure 4. M-cone test sensitivity functions for subjects AS (circles) and MD (filled squares). The function for subject AS denoted by the filled circles was derived from the vertical positions of the template shown in figure 3. The functions denoted by the open circles (AS) and filled squares (MD) were derived by the abbreviated $tv\lambda$ method; each data point is the average of eight estimates. The error bars are $\pm 2SE$; the vertical bars are the standard errors for subject AS, and the horizontal bars those for subject MD. The scale is correct for the function derived by template fitting (filled circles); each point on this function corresponds to $\log(1/N_\lambda)$ at the criterion point on the fitted template. The two functions derived by the abbreviated $tv\lambda$ method have been shifted vertically to align with this function.

average increment thresholds plotted against wavenumber. The function has been displaced vertically to align with the function for subject AS derived by template fitting.

The agreement between the shapes and spectral positions of the three functions shown in figure 4 is very good. The agreement across subjects suggests that the techniques measured the sensitivity of a visual process that is common to the two subjects.

3.3 The L-cone test sensitivity function

Figure 5 shows the twelve tvr functions for subject AS measured on a 481-nm background field. As in figure 3, the tvr functions have been positioned correctly with respect to the scale on the abscissa; the logarithmic scale on the ordinate is given in arbitrary units; and for clarity the functions have been shifted so that the branches

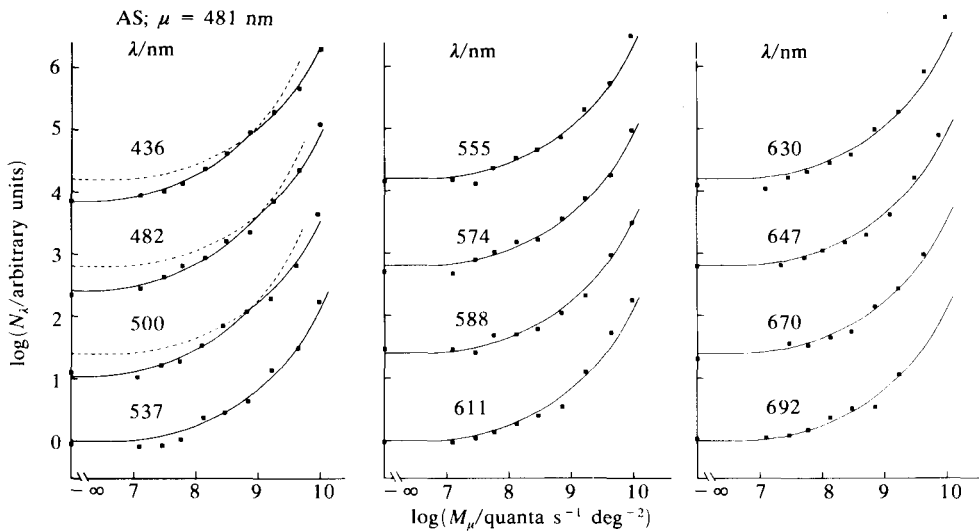


Figure 5. Twelve tvr functions for subject AS measured on a 481-nm field. As in figure 3, the functions have been shifted vertically so that the M-cone branches in each panel are separated by 1.4 log units. Each data point is the average of two measurements made during different sessions.

Table 2. L-cone test thresholds. The second column gives the value of the test threshold derived for subject AS by fitting templates to tvr curves; the third and fifth columns give the mean values of the test threshold obtained at a fixed field radiance by the abbreviated method. The values given for test thresholds represent $\log(N_\lambda/\text{quanta s}^{-1} \text{deg}^{-2})$. The values given in the fourth and sixth columns represent twice the standard error of the mean.

λ/nm	Subject AS			Subject MD	
	$\log N_\lambda$ (tvr)	$\log N_\lambda$ (tv λ)	2SE	$\log N_\lambda$ (tv λ)	2SE
436	9.69	10.26	0.08	10.39	0.06
482	9.33	9.67	0.10	9.73	0.15
500	8.91	9.25	0.07	9.32	0.10
537	8.30	8.74	0.06	8.97	0.05
555	8.14	8.62	0.06	8.85	0.08
574	8.17	8.65	0.03	8.85	0.06
588	8.24	8.69	0.05	8.99	0.07
611	8.41	8.80	0.03	9.00	0.13
630	8.66	9.14	0.04	9.24	0.08
647	9.11	9.55	0.06	9.71	0.10
670	9.56	10.21	0.04	10.14	0.09
692	10.35	-	-	-	-

attributed to the L-cone mechanism are vertically separated by 1.4 log units. (The absolute scale on the ordinate can be reconstructed for each test wavelength from column 2 of table 2.)

By the method described earlier, the template for subject AS was fitted to the branch thought to represent the L-cone mechanism. The criterion point on the template was fixed at a field radiance of $10^{9.20}$ quanta $s^{-1} \text{ deg}^{-2}$, and the template was then shifted vertically to produce a least-squares fit to the data points on that branch. For $\lambda < 537$ nm, a second, lower, branch (thought to represent the M-cone mechanism) was evident; for these wavelengths the procedure was repeated for that subset of data points with the criterion point on the template fixed at a field radiance of $10^{8.80}$ quanta $s^{-1} \text{ deg}^{-2}$. For each λ , column 2 of table 2 gives the test intensity corresponding to the y-coordinate of the criterion point on the template after fitting.

Deviations from the fitted template shapes are relatively small. At a test wavelength of 537 nm the increment thresholds fall below the template shape at low background radiances. This may be the result of probability summation, since at that wavelength the M- and L-cone mechanisms would be expected to have similar test sensitivities at low background radiances. A further deviation is apparent at a test wavelength of 630 nm, where the tvr function is steeper than the template shape.

In general, the results are consistent with the predictions of the test displacement rule applied to the L-cone mechanism at longer test wavelengths, but applied to the L- and M-cone mechanisms at shorter test wavelengths.

Figure 6 (closed circles) shows the L-cone test sensitivity function derived from the data shown in figure 5. The test sensitivity of the lower, M-cone, branch is consistent

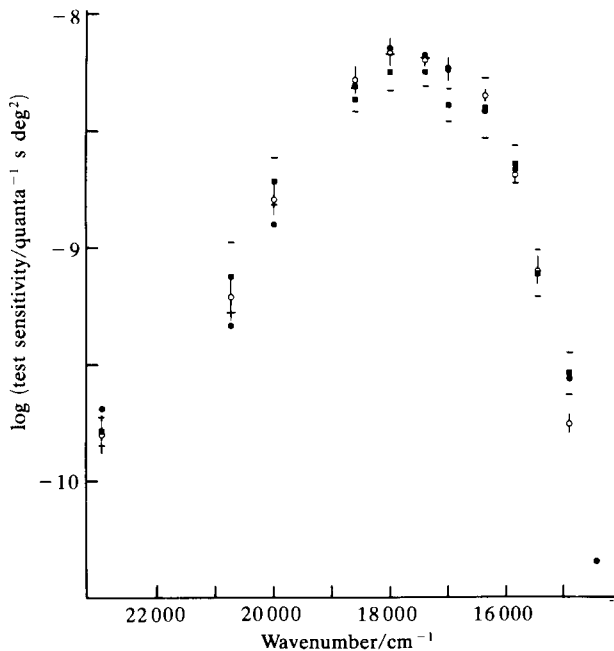


Figure 6. L-cone test sensitivity functions for subjects AS (circles) and MD (filled squares). The function for subject AS denoted by the filled circles was derived from the vertical positions of the template shown in figure 5. The functions denoted by the open circles (AS) and filled squares (MD) were derived by the abbreviated tv λ method; each data point is the average of eight estimates. The error bars are $\pm 2\text{SE}$; the vertical bars are standard errors for subject AS, and the horizontal bars those for subject MD. The scale is correct for the function derived by template fitting; the two functions derived by the abbreviated tv λ method have been shifted vertically to align with this function.

with the shapes of the M-cone test sensitivities reported in the previous section (see Stockman 1983).

From our tvr data we were able to choose a radiance of the 481-nm background for which detection should be by the L-cone mechanism at all test wavelengths. Columns 3 and 4 of table 2 give the average and standard errors of the eight increment thresholds measured at various test wavelengths on a 481-nm field of $10^{9.63}$ quanta $s^{-1} \text{deg}^{-2}$ radiance. The open circles in figure 6 show the test sensitivities for subject AS derived by the $tv\lambda$ method, shifted vertically to align with the function derived by template fitting. As in the case of the M-cone mechanism, the agreement between the shapes and the spectral positions of the functions estimated by the two methods for subject AS is good.

Three tvr functions were measured for subject MD on a 481-nm field (for $\lambda = 482, 555, \text{ and } 647 \text{ nm}$). The results we found were consistent with those for subject AS. For subject MD a double-branched function was evident at $\lambda = 482 \text{ nm}$, $\mu = 481 \text{ nm}$, but we note that the separation of the two branches was less than that found for subject AS (see Stockman 1983). This difference is consistent with the differences between the L-cone sensitivity for subjects AS and MD at $\lambda = 482 \text{ nm}$ (see below). From the tvr data for subject MD we were able to choose a radiance of the 481-nm background for which detection should be by the L-cone mechanism at all test wavelengths. Columns 5 and 6 of table 2 give the mean and standard error for the eight increment thresholds measured at various test wavelengths on a 482-nm field of $10^{9.31}$ quanta $s^{-1} \text{deg}^{-2}$ radiance. Figure 6 (filled squares) shows the L-cone test sensitivities for subject MD derived by the $tv\lambda$ method, shifted vertically to align with the function for subject AS derived by template fitting. The agreement between the shapes of the functions for subjects AS and MD is not as good as that found between the shapes of the M-cone test sensitivity functions (see figure 4). The test sensitivities suggest that subject MD is relatively more sensitive than subject AS at 482 nm and at 500 nm. A difference in ocular pigmentation between subjects AS and MD is unlikely to account for these differences, because similar differences were not found when the test sensitivities of the M-cone mechanism were compared. Since the differences are at most about 0.2 log units they may be attributable to experimental error (we note that the standard errors for subject MD are unusually large at 482 and 500 nm). Alternatively, the differences may reflect a contamination by the M-cone mechanism at those two wavelengths, or they may reflect a real difference between the L-cone photopigments for these two observers.

4 Discussion

4.1 Double-branched tvr functions

It was argued in the introduction that under small-field adaptation conditions double-branched tvr functions should be found for certain combinations of λ and μ . Such functions are found for subject AS at $\lambda = 611, 630, 647, \text{ and } 670 \text{ nm}$, $\mu = 673 \text{ nm}$; and at $\lambda = 436, 482, \text{ and } 500 \text{ nm}$, $\mu = 481 \text{ nm}$ (see figures 3 and 5). For subject MD double-branched functions are found at $\lambda = 611 \text{ and } 647 \text{ nm}$, $\mu = 649 \text{ nm}$; and at $\lambda = 482 \text{ nm}$, $\mu = 481 \text{ nm}$ (only a limited number of combinations were used for subject MD). At the other wavelength combinations used, the tvr functions are single-branched. To allow comparisons with the predictions illustrated in figure 2, figure 7 shows tvr functions for subjects AS and MD measured at $\lambda = 647 \text{ nm}$; $\mu = 649 \text{ nm}$. The positions and shapes of the templates shown in this figure are based, in part, upon tvr data obtained at other wavelengths (see Stockman 1983).

The double-branched character of the curves for $\lambda = 482 \text{ nm}$, $\mu = 481 \text{ nm}$ is more marked than would be predicted from Stiles's model; this is because the sensitivity

difference between the M- and L-cone mechanisms, particularly for subject AS, is greater than that predicted by Stiles's π_4 and π_5 field sensitivities.

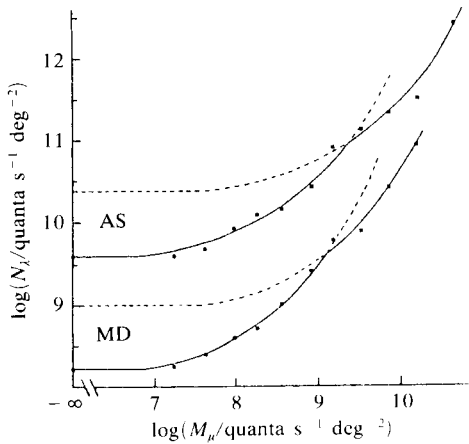


Figure 7. Tvr functions for subjects AS and MD measured at $\lambda = 647$ nm, $\mu = 649$ nm. These functions are included for comparison with the predictions shown in figure 2. The scale on the ordinate is correct for the tvr function for subject MD. For clarity, the function for subject AS has been shifted vertically upwards by 1.5 log units.

4.2 The test displacement rule

The experimental results showed a first-order agreement with the predictions of the test displacement rule. Specifically, if the wavelength of λ was varied, and the wavelength of μ remained constant, then each branch can be described by the template shape, displaced only vertically. This supports the hypothesis that each branch represents detection mediated by the output of one cone class. However, minor deviations from the template shape (of the order of 0.2 log units) are apparent for some combinations of λ and μ . Although these may be the result of experimental variability, they may represent real failures of shape invariance.

From the shapes of our tvr functions we are able to define the spectral sensitivities of the M- and L-cone mechanisms. To our knowledge, this is the first time that the test sensitivities of both the M- and the L-cone mechanisms have been derived from the displacements of tvr curves throughout the visible spectrum.

4.3 S-cone intrusion

There is no evidence in our experimental work of any systematic deviations that might be attributed to a short-wavelength cone mechanism. This is consistent with earlier reports that the central area of the foveola is tritanopic (eg König and Köttgen 1894; Willmer and Wright 1945; Wald 1967). Williams et al (1981) have recently provided strong evidence that this tritanopia results from a complete absence of functioning S-cones within a central area of the foveola roughly 20 min in diameter.

4.4 Comparisons with other estimates

Figures 8, 9, and 10 are included to allow comparisons between the M- and L-cone sensitivity functions presented here and other estimates of those functions. In figures 8, 9, and 10 the filled circles represent the test sensitivity functions for subject AS derived by template shifting; and the open circles and filled squares represent test sensitivity functions for subjects AS and MD, respectively, derived by the abbreviated $tv\lambda$ method.

Figure 8 shows comparisons between estimates of the M-cone spectral sensitivity. The upper continuous line, A, represents Stiles's π_4 field sensitivity function. There is poor agreement between the shape of the experimental functions and the shape of π_4 .

Smith–Pokorny M fundamental. Minor, but consistent, differences are apparent at some wavelengths. For example, between 481 and 535 nm the sensitivities lie below the continuous curve, whereas at 437 and 673 nm the sensitivities lie above the curve. These differences, however, are small.

The continuous line C represents an M fundamental calculated by the first author (Stockman 1983; see also the Appendix) from confusion points given by Estévez in Wyszecki and Stiles (1982, page 616). At middle and long wavelengths the M fundamental agrees well in shape and spectral position with the M-cone test sensitivities. Minor, but consistent, deviations are apparent: for example, at 481 and 502 nm the sensitivities fall below the fundamental. This comparison suggests that the confusion points given in Wyszecki and Stiles are appropriate. Owing to an error, the tabulated sensitivities shown in Wyszecki and Stiles (1982, table 3 [8.2.5]) were calculated not from the stated protanopic confusion loci, but from $r_{pc} = 1.0381$ and $g_{pc} = -0.0388$ (see the note added in proof, Nunn et al 1984). The M fundamental calculated from the confusion loci given in Wyszecki and Stiles (curve C) more closely agrees in the long-wavelength range with other estimates of the M fundamental, including the present data, than does the fundamental actually tabulated in Wyszecki and Stiles.

The lowest continuous line, D, represents the average spectral sensitivity function of five protanopes measured by Hsia and Graham (1957) and transformed to an equal-quantum spectrum. The agreement between the shapes and spectral positions of the sensitivity functions and the Hsia and Graham protanopic sensitivity function is remarkably good. The diamonds in the bottom comparison represent the average foveolar spectral sensitivities of two protanopes taken from figure 3 of Willmer (1949) and transformed to an equal-quantum spectrum. There is reasonable agreement between the shape of our sensitivity functions and the protanopic sensitivities, although at 481 and 502 nm the experimental data lie above the luminosity curve.

Figure 9 shows comparisons between estimates of the L-cone spectral sensitivity. The uppermost continuous line, A, represents Stiles's π_5 field sensitivity function. There is poor agreement between the experimental functions and π_5 . In the figure they are aligned with the π_5 function at middle and long wavelengths. The π_5 field sensitivity function is then too shallow at shorter wavelengths to describe our experimental data. These differences cannot easily be attributed to individual variation in lens and macular pigmentation, since similar differences were not found in the corresponding M-cone comparison.

The continuous line B represents the Smith–Pokorny L fundamental transformed to an equal-quantum spectrum. In shape and spectral position, our sensitivity functions resemble well the Smith–Pokorny L fundamental. Minor differences are apparent in some spectral regions: for example, at wavelengths shorter than 502 nm the sensitivities tend to lie slightly below the continuous curve, whereas at 612 nm they tend to lie above it.

The lowermost continuous line, C, represents the average spectral sensitivity function of six deuteranopes measured by Hsia and Graham (1957) and transformed to an equal-quantum spectrum. The agreement between the shapes and spectral positions of the sensitivity functions and the Hsia and Graham deuteranopic sensitivity functions is impressive. Also in the bottom comparison, the diamonds represent the average foveolar spectral sensitivities of two deuteranopes taken from figure 5 of Willmer (1949) and transformed to an equal-quantum spectrum. There is good agreement between the shapes of our sensitivity functions and the deuteranopic sensitivities.

Perfect agreement between different estimates of the cone sensitivities is unlikely, particularly at shorter wavelengths, because of individual differences in lens and macular pigmentation, and in photopigment density. Given that the different estimates

were obtained with different test stimuli, ranging in diameter from 3 min to 2 deg, the M- and L-cone test sensitivities agree remarkably well with dichromatic estimates.

4.5 Earlier $tv\lambda$ functions

Figure 10 shows comparisons between our estimates of the M- and L-cone spectral sensitivity functions, and earlier $tv\lambda$ estimates. The upper portion of the figure shows a comparison of our L-cone test sensitivities with Wald's 'red' function [redrawn from figure 12, Wald (1964), subject RH] and with Stiles's π'_5 ; and the lower portion shows a comparison of our M-cone test sensitivities with Wald's 'green' function [redrawn from figure 10, Wald (1964), subject RH] and with Stiles's π'_4 .

With the exception of π'_5 the agreement between the test sensitivity estimates is very good. In comparison, the agreement between π'_5 and our L-cone test sensitivities is poorer: the shape of π'_5 is too depressed at middle wavelengths to describe our data.

We argued in the introduction that cone isolation should not be possible with a conventional $tv\lambda$ method. Why, then, do the M- and L-cone test sensitivities measured by Wald, and Stiles's π'_4 come so close to the sensitivities that we believe to be those of the cones? Given that adaptation proceeds according to Weber's law, and that there is probability summation between independent mechanisms of similar sensitivity, deviations from cone sensitivities (in the direction of sensitivity improvements) of the order of 0.2 log unit would be expected for homochromatic test and field conditions. The absence of such deviations could suggest that at high background radiances the more suppressed cone type suffers a loss of sensitivity greater than that implied by Weber's law. Eisner and MacLeod (1981) argued that their flicker photometric sensitivity estimates approached those of isolated cones for this reason.

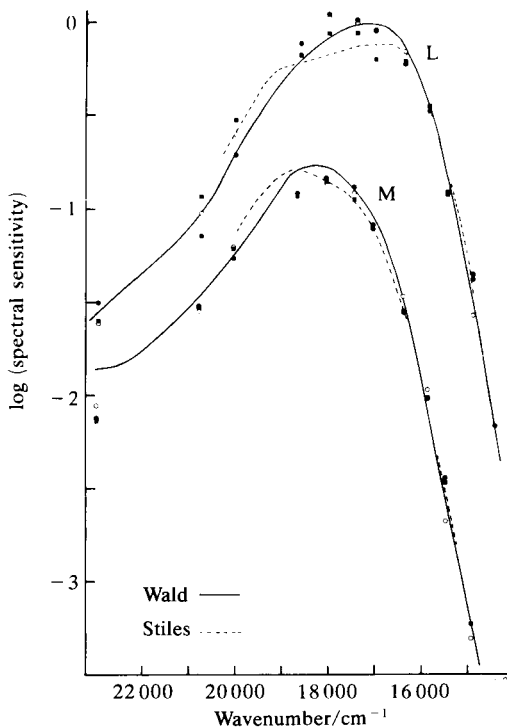


Figure 10. Comparisons between the M- and L-cone test sensitivities and earlier test sensitivity estimates. Upper comparison: L-cone test sensitivities. Lower comparison: M-cone test sensitivities. Symbols as for figures 8 and 9. The continuous lines are Wald's 'red' (upper comparison) and 'green' (lower comparison) sensitivity functions. The dashed lines are Stiles's π'_5 (upper comparison) and π'_4 (lower comparison) sensitivity functions.

The experimental data can be aligned with the π_4 function at short and middle wavelengths; this alignment is shown in the figure. The π_4 field sensitivity function is then too shallow at longer wavelengths to describe the experimental data.

The continuous line B represents the Smith-Pokorny M fundamental transformed to an equal-quantum spectrum [the Smith-Pokorny M- and L-cone fundamentals are taken from Boynton (1979, appendix part III, page 404)]. Overall, there is good agreement between the shapes and spectral positions of the sensitivity functions and the

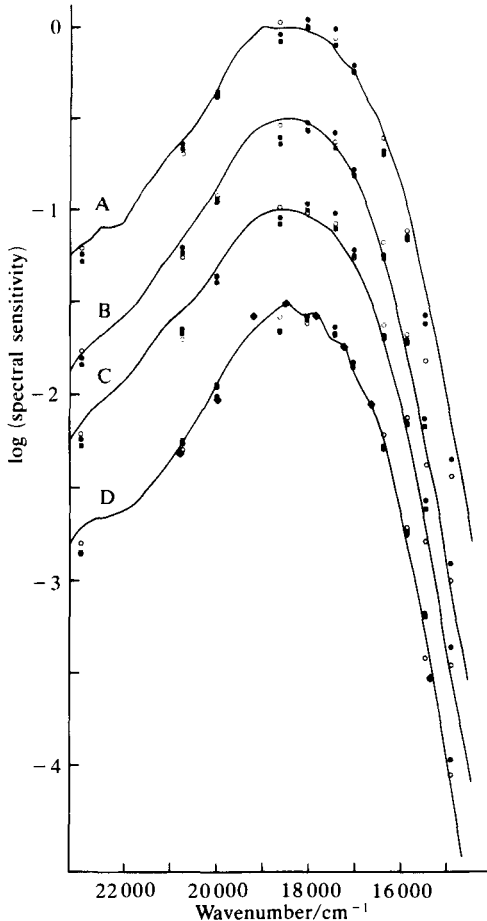


Figure 8. Comparisons between the M-cone test sensitivities and other estimates. Line A represents Stiles's π_4 field sensitivity function; line B the Smith-Pokorny M fundamental; line C the M fundamental calculated by the first author from confusion points given by Estévez in Wyszecki and Stiles (1982); and line D the average spectral sensitivity function of five protanopes measured by Hsia and Graham (1957). The diamonds in the bottom comparison represent the average foveolar spectral sensitivity curve of two protanopes measured by Willmer (1949).

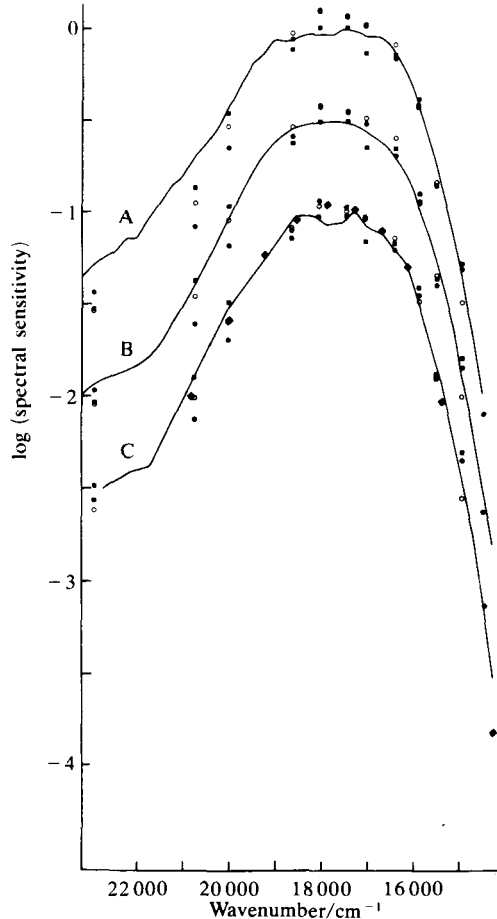


Figure 9. Comparisons between the L-cone test sensitivities and other estimates. Line A represents Stiles's π_5 field sensitivity function; line B the Smith-Pokorny L fundamental; and line C the average spectral sensitivity function of six deuteranopes measured by Hsia and Graham (1957). The diamonds in the bottom comparison represent the average foveolar spectral sensitivity curve of two deuteranopes measured by Willmer (1949).

In figures 8, 9, and 10 the open circles and filled squares represent test sensitivity functions for subjects AS and MD, respectively, derived by the abbreviated $tv\lambda$ method; and the filled circles represent the test sensitivity functions for subject AS derived by template shifting.

4.6 Conclusions

The comparisons above show a clear trend: the middle- and long-wavelength test sensitivity functions presented in this paper agree well with the shapes of the corresponding König fundamentals and dichromatic sensitivity functions, but do not agree well with the field sensitivity functions of Stiles (π_4 and π_5).

The derivation of the König fundamentals depends upon the assumption that dichromacy is a reduced form of normal colour vision, ie that dichromats lack one of the three cone types. Given this assumption, and also that the experimental conditions used in the work of Hsia and Graham (1957) and Willmer (1949) minimise the possibility of intrusions by the S-cone mechanism, their deuteranopic and protanopic sensitivity functions might be expected to reflect the sensitivity of the L- and M-cone types, respectively⁽⁵⁾. The excellent overall agreement between the sensitivity functions of the M- and L-cone mechanisms and the protanopic and deuteranopic sensitivity functions of Willmer, and Hsia and Graham suggests that the sensitivity measurements presented in this paper may reflect the sensitivities of two of the three cone types that determine normal colour matches.

We have presented evidence, obtained with variants of Stiles's own methods, that an approach to M- and L-cone test isolation is possible under small-field adaptation conditions. Stiles (1959) concluded that, of all his longer-wavelength cone mechanisms, the spectral sensitivity of π_4 was likely to be closest to that of single cone type. We agree.

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⁽⁵⁾ The deuteranopic and protanopic spectral sensitivity functions estimated by Hsia and Graham (1957) and Willmer (1949) were measured under conditions that would be expected to disadvantage detection by the short-wavelength cone mechanism. Detection by the S-cone mechanism can be disadvantaged by making the test flash small and brief, and, additionally, by presenting the test flash (which must of necessity be small) to only the very central foveola. The deuteranopic and protanopic spectral sensitivity functions estimated by Hsia and Graham (1957) were measured with a 4-ms duration, 42-min diameter test flash. Given the relatively large test field, however, some contamination from the short-wavelength cone mechanism might be expected at the shortest wavelengths measured. Willmer (1949) estimated deuteranopic and protanopic sensitivities by measuring the absolute threshold of a foveally presented, 8-min diameter, 12-ms test flash for various test wavelengths. Under these conditions, little or no intrusion from the S-cone mechanism might be expected.

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Appendix

Values listed in table A1 were obtained from the Stiles and Burch (1955) 2-deg colour-matching functions, $\bar{r}(n)$, $\bar{g}(n)$, and $\bar{b}(n)$ [tabulated in Wyszecki and Stiles (1982, table 3 |8.2.5|)] by means of:

$$M(n) = kn[0.0352\bar{r}(n) + 1.4412\bar{g}(n) + 0.1199\bar{b}(n)],$$

where n is the wavenumber, and k is a scaling constant chosen to make $\log M(18750) = 0$.

Table A1. Logarithms of the relative spectral sensitivity of the M fundamental (from Stockman 1983). For details see above.

n/cm^{-1}	$\log M(n)$	n/cm^{-1}	$\log M(n)$
25500	-2.9367	19500	-0.1274
25250	-2.6132	19250	-0.0586
25000	-2.4018	19000	-0.0181
24750	-2.1362	18750	0.0000
24500	-1.8888	18500	-0.0037
24250	-1.7490	18250	-0.0099
24000	-1.6019	18000	-0.0342
23750	-1.4496	17750	-0.0790
23500	-1.3554	17500	-0.1230
23250	-1.2621	17250	-0.2094
23000	-1.1759	17000	-0.3095
22750	-1.0898	16750	-0.4514
22500	-1.0311	16500	-0.6267
22250	-0.9819	16250	-0.8468
22000	-0.9217	16000	-1.1016
21750	-0.8396	15750	-1.3981
21500	-0.7538	15500	-1.7186
21250	-0.6665	15250	-2.0585
21000	-0.5928	15000	-2.4421
20750	-0.5395	14750	-2.7898
20500	-0.4824	14500	-3.1664
20250	-0.3957	14250	-3.5715
20000	-0.3033	14000	-3.9677
19750	-0.2062	13750	-4.2649