
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 tvr 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

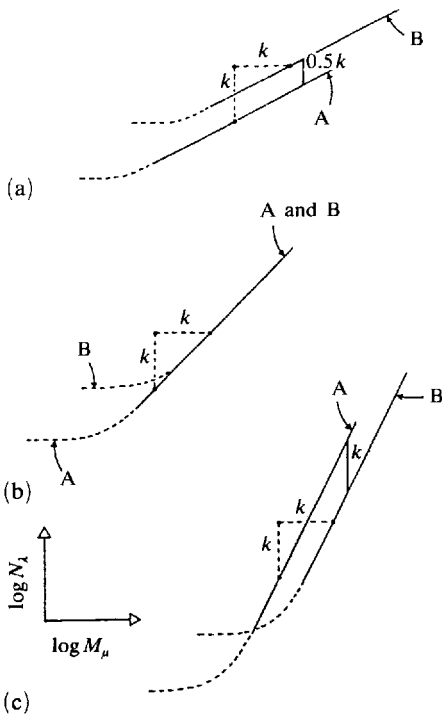


Figure 1. Predictions of the relative positions of two tvr branches A and B with nonzero asymptotic slopes of (a) 0.5, (b) 1.0, (c) 2.0. The regions of asymptotic slope are represented by the solid portions of the tvr branches. In each case, branch B relative to branch A has been displaced along the 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.

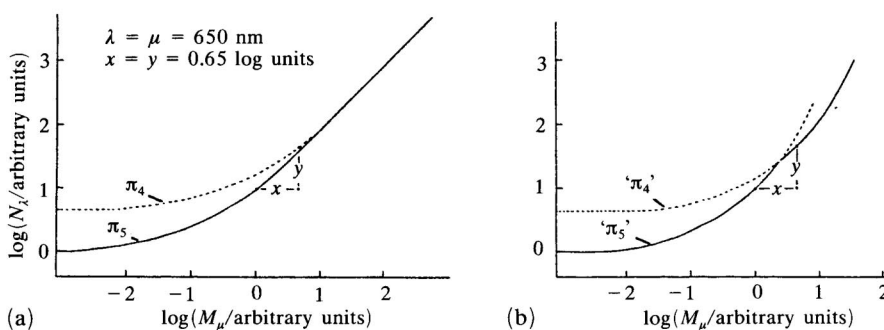


Figure 2. Predictions of the relative positions of the π_4 and π_5 tvr branches for $\lambda = \mu = 650$ nm, using the tabulated field sensitivities of Stiles's π_4 and π_5 , and using either (a) Stiles's standard template shape to describe the shape of each branch, or (b) a steeper template shape, 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 episotister (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.)

