# A TAXONOMY OF TRITANOPIAS

J.D. MOLLON
*(Cambridge, U.K.)*

*'How different is blue from every kind of colour. For blue is like the sea, the sea is like the firmament and the firmament is the Throne of Glory.'*

Babylonian Talmud, Menahot 43.

## ABSTRACT

Our vision has a number of anomalous features when detection or discrimination is mediated only by signals originating in the short-wavelength receptors. A summary list of these 'anomalies of the blue mechanism' is given and two groups are provisionally distinguished, firstly a group that directly or indirectly reflect the basic insensitivity of the short-wavelength mechanism and secondly a group of interrelated phenomena that are observed during light and dark adaptation to coloured fields. Some of the former group probably arise from properties of the short-wavelength receptors themselves; the second group almost certainly arise from interactions between long- and short-wavelength signals.

Under conditions of tritanopic viewing, short-wavelength stimuli often look bluish. To explain this paradox, it is argued that the brain always seeks to reduce discrepancies between sensory inputs and that in this case it chooses to eliminate the discrepancy at that wavelength at which the residual opponent signal from the dichromatic retina is strongest and least easily suppressed. This wavelength, close to 470 nm, looks blue, not green, under conditions of trichromatic observation.

## INTRODUCTION

The short-wavelength receptors of man and of macaque species have a peak sensitivity close to 420 nm and a bandwidth that is greater, in wavenumber units, than that of the Dartnall nomogram (Bowmaker et al., 1979, 1980; Bowmaker and Dartnall, 1980). There is nothing unusual about the gross appearance of these receptors when, in the course of microspectrophotometry, they are inspected by means of an infra-red converter. But there is certainly plenty that is curious about our vision when detection or discrimination is mediated only by signals originating in the short-wave receptors. I set out here to rehearse these psychophysical anomalies, ordering them in what seems cur-

*Docum. Ophthal. Proc. Series, Vol. 33, ed. by G. Verriest*

 *ISBN 90 6193 729 9*

rently the most appropriate way and subdividing them into two groups. Such lists of the 'anomalies of the blue mechanism' have a long history (e.g. Willmer, 1961; Trezona, 1970) and the present one is intended merely as a working handlist, useful for discussion; it should not be allowed to conceal the interconnections between the anomalies and at the end I try to trace the several anomalies to a smaller number of basic principles. Space allows only summary discussion and illustrative citations. A general background is provided by Boynton's review of current colour theory in this volume.

## THE ANOMALIES OF THE SHORT-WAVE MECHANISM: GROUP A

### *1. Absolute sensitivity*

From Stiles' measurements of $\pi_1$, Barlow (1958) calculated that the quantum efficiency of the short-wave system was nearly one hundredfold poorer than that of the long- and middle-wave mechanisms, $\pi_4$ and $\pi_5$. This is the difference in terms of sensitivity at the cornea. At the receptor level this discrepancy will be less, since the lens has an optical density of the order of 0.5 at 420 nm (Wyszecki and Stiles, 1967); and indeed it is the rapidly changing density of the lens in this spectral region that presumably accounts for the displacement of the peak psychophysical sensitivity to a longer wavelength.

### *2. Incremental sensitivity*

The Weber fraction ($\Delta I/I$ for detection of an increment on a steady background of intensity $I$) is about 4.6 times greater than that for $\pi_4$ and $\pi_5$ (Wyszecki and Stiles, 1967, Table 7.4). However, any single Weber fraction must always be arbitrary, being dependent on the spatial and temporal parameters of the target and the integrative properties of the mechanism. The values traditionally given for the $\pi$ mechanisms are for Stiles' standard conditions of a 200-msec, 1-deg flash (Stiles, 1978) and correspond to only one point on a temporal contrast-sensitivity function and one point on a spatial contrast-sensitivity function. If we change the spatial and temporal frequency spectra of the short-wave target by making it very small or very brief, the Weber fraction and the absolute threshold of the short-wave mechanism rise much more than those of $\pi_4$ and $\pi_5$ and we obtain the near-tritan states, 'small-field tritanopia' and its temporal analogue, which I shall call 'tachistoscopic tritanopia'.

### *3. Small-field tritanopia*

In the classical experiment of Brindley (1954) a violet or green target of varying diameter was centred 55′ below the fixation point and had a duration of 95 msec. The value log (sensitivity to green targets/sensitivity to violet targets) increased by 0.64 $\log_{10}$ units as target size was reduced from 30′ to 2.5′, i.e. the Weber fraction for the short-wave mechanism increased relative

to that of the middle-wave mechanism by 4.4 times (this may be an underestimate since Brindley does not demonstrate formally that the short-wave mechanism remains isolated for the smallest targets).

### *4. Tachistoscopic tritanopia*

The results of Krauskopf and Mollon (1971, Fig. 4) imply an analogously disproportionate increase in the Weber fraction of the short-wave mechanism when 10 msec rather than long flashes are used. In a study of colour naming, Weitzman and Kinney (1967) explicitly compared the consequences of reducing stimulus area and stimulus duration: in both cases a tritan-like neutral band was found in the yellow-green (570–580 nm). The range of wavelengths studied by Weitzman and Kinney was limited and a more extensive study of 'tachistoscopic tritanopia' would be valuable.

### *5. Space constants*

(*a*) *Ricco's Area.* In the tradition of Farnsworth (1955), I should like to emphasise that small-field tritanopia and tachistoscopic tritanopia are not to be treated as special phenomena but are best explained in terms of the basic insensitivity of the short-wavelength mechanism and are simply the other side of the coin to the greater space and time constants of this mechanism. The reason that the Weber fraction is only 4.6 times poorer for the short-wavelength mechanism, $\pi_1$, under Stiles' conditions is that greater integration in time and space tends to compensate for the essential insensitivity of the mechanism. Brindley (1954) found that Ricco's area (the area within which complete reciprocity of intensity and area exists at threshold) was about 13′ for short-wavelength flashes centred 55′ below the foveola centre, whereas the critical area for the long-wavelength mechanisms was less than 4′. However Brindley made no attempt to equate the adaptive states of the short- and long-wavelength mechanisms. Since Ricco's area for each mechanism may well vary independently according to its own adaptive state and since the short-wavelength mechanism may be little adapted by long-wave lights, one really requires a design analogous to that of Krauskopf and Mollon (1971) in which the adaptive states of the mechanisms are systematically varied. A similar problem arises for many of the comparisons in this list, although there is not space to mention it on every occasion.

(*b*) *Spatial resolution.* Sensitivity is often gained only at the expense of resolution. The poorness of spatial resolution of the isolated short-wavelength mechanism was shown by Stiles (1949a) for a checkerboard pattern and by Brindley (1953, 1954) for a square-wave grating (see Table 1). Blackwell and Blackwell (1961) showed Snellen acuity to be reduced in blue cone monochromats. Later workers have measured the full contrast-sensitivity-function (Table 1): as would be expected from the variety of conditions, there is some variation in the values obtained for maximum acuity, but resolution is never better than 10 cycles. deg$^{-1}$ and the peak of the CSF is very consistently

*Table 1.*

| Reference | Subjects | Conditions | Maximum Acuity (cycles/ deg) | Peak sensitivity (cycles/ deg) |
|---|---|---|---|---|
| Brindley (1953) | Normal | Artificial monochromacy 1°18′ target field | 2.5 | |
| Brindley (1954) | Normal | Long-wavelength adapting fields 4° target field | 4 | |
| Green (1968; (1972) | Normals | Yellow adapting field 4° × 1.5° target field. 1 sec flashes | 6–10 | 1–2 |
| Green (1972) | Blue cone monochromats | No background 445 nm, $10^{2.1}$ td. | 10 | 1–2 |
| Daw and Enoch (1973) | Blue cone monochromats | 530 nm adapting field 5° 'flashed' target, '4° away from fovea' | 4 | 1 |
| Daw and Enoch (1973) | Normals | 530 nm adapting field 450 nm target, 'fovea' | 6–8 | |
| Kelly (1974) | Normal | Yellow adapting field 8° steady grating | 5 | 1 |
| | Normal | Yellow adapting field 8° grating flickering at 1.5 Hz | 6 | < 0.5 |
| Cavonius and Estévez (1975) | Normals | Approximate silent substitution for $\pi_4$ and $\pi_5$. Yellow adapting field. Test field normally 2 deg, but never < 1.5 periods | 10 | 1 |
| Klingaman and Mostowitz-Cook (1979) | Normals | VECP to flashed 6-deg checkerboard on bright yellow field | < 10 | 1 |

placed close to 1 cycle. $deg^{-1}$, a value lower than the peak frequency typically reported for $\pi_4$ or $\pi_5$ or for achromatic stimuli.

Owing to its depressed and displaced CSF, the short-wave mechanism cannot contribute to the detection of sharp edges. Thus Tansley and Boynton (1978), having adjusted the relative intensity of two juxtaposed, differently coloured fields until the boundary between them was minimally distinct, found that the rated distinctiveness of the residual border could be represented by placing all colours on a continuous line rather than in the plane normally needed to represent differences between equiluminant colours; and when the two colours constituted a tritan pair (and thus provided no spatial transient for the long-and middle-wavelength cones) the border dissolved completely. Similarly, Valberg and Tansley (1977) showed that when monochromatic targets were juxtaposed to a standard white light, the rated distinctiveness of the border, when plotted against the wavelength of the monochromatic lights, resembled a tritanope's saturation function. Boynton *et al.*

(1977) found (for some conditions and observers) that introducing a gap between two small fields actually improved the chromaticity discrimination of tritan pairs.

### 6. *Time constants*

(*a*) *Critical durations.* Although Stiles (1949a) briefly mentions that he had not found differences between $\pi$ mechanisms in their integration times, Krauskopf and Mollon (1971) show that the critical duration for Bloch's law (the limit of time-intensity reciprocity at threshold) is greater for the short-wavelength mechanism than for the long- and middle-wavelength mechanisms both at dark-adapted and at asymptotic levels. In the case of a 500-nm adapting field, as the threshold rose by two $\log_{10}$ units from its dark-adapted value, the critical duration for short-wavelength targets fell from ca 300 msec to ca 100 msec, whereas critical durations for long-wavelength targets fell from 150 msec to 50 msec over an equivalent range of sensitivity. It is an open question whether all or part of this difference reflects a difference between receptors or whether it reflects the fact that signals from the long-wavelength receptors have access to post-receptoral channels that are not available to short-wavelength receptors (see below).

(*b*) *Temporal resolution.* Brindley *et al.* (1966) reported that the short-wavelength mechanism, when isolated with long-wavelength fields, has a maximum CFF of only 18 Hz, a value about 3 times less than that typically obtained for $\pi_4$ and $\pi_5$. Green (1969) measured the full temporal CSF for the short-wavelength mechanism and reported that the peak sensitivity did not lie at a frequency lower than that for the long- and middle-wavelength mechanisms; he suggested that the depressed CFF of the short-wavelength mechanism was a consequence only of its reduced contrast sensitivity and not of a true difference in time constants. However, Kelly (1974) reports that the corner frequency for the short-wavelength mechanism does occur at lower frequencies and Mollon and Polden (1978a) suggest that a difference in time constants may have been masked in Green's study by the use of a fluorescent tube coated with a long-wavelength phosphor of long time constant. Wisowaty and Boynton (1980), instead of relying on the traditional long-wavelength adapting field, isolated the short-wavelength mechanism by means of silent substitution, that is, by alternating lights of 439 and 492 nm, which are confusable by a tritanope; they suggest that the peak of the temporal CSF does lie at low frequencies, in fact at 2 Hz under the conditions they examined.

(*c*) *Latency.* Mollon and Krauskopf (1973) measured reaction times to liminal, monochromatic increments on monochromatic fields and found latencies to be substantially longer for the short-wavelength mechanism at both dark-adapted and asymptotic levels (there was a good correlation, for different adaptive states, between the critical duration and the reaction time). A direct phenomenological demonstration of the longer latency of the blue mechanism is described by Mollon and Polden (1976).

### *7. Tritanopia of the central foveola*

Is there a tritanopia of the central region of the foveola that is additional to the small-field tritanopia found elsewhere? This celebrated question has been persuasively answered in the affirmative by Williams *et al.* (1981a). Measuring increment thresholds for the same wavelength but under conditions that isolate either short- or middle-wavelength receptors, they found an apparently complete absence of the short-wavelength mechanism in a central area of 20′. This result cannot be attributed to macular pigment, since a comparable loss is not found when the same test stimulus is used but the adaptational conditions favour the middle-wave mechanism. Williams *et al.* also show that colour matches made with the centre of the foveola are truly tritanopic. They used a successive colour-matching technique and thus circumvented two of the classical problems of studying foveolar tritanopia – the possibilities that the short-wave signal, though present, either fades during fixation or does not allow spatial resolution of the two parts of a small bipartite field.

### *8. Neonatal tritanopia*

Preliminary measurements of increment thresholds on long-wavelength fields suggest that some 2-month-old infants behave as if tritanopic (Pulos *et al.* 1980). I have discussed elsewhere a possible interpretation of this neonatal tritanopia (Mollon, 1982; see also below).

## GROUP B: ADAPTATIONAL ANOMALIES

A second group of anomalies concern the adaptive effects on the blue mechanism of coloured fields. It has become somewhat artificial to list these separately, since they are nowadays thought to be intimately connected (Pugh and Mollon, 1979). Moreover, they are probably not true anomalies of the short-wave system, for several of them have analogues when the targets are of long- and middle-wavelengths (although these latter effects are usually less dramatic).

### *9. Limited conditioning effect*

Stiles found that the t.v.i. ('threshold versus-intensity') curve for violet flashes on a long-wave field shows a plateau when the background produces a retinal illuminance in the range 4–5 log Td, before rising again at higher illuminances (Stiles, 1953). He attributed the two branches to distinct mechanisms, $\pi_1$ and $\pi_3$, but his original term for the plateau – the 'limited conditioning effect' (Stiles, 1939) – now seems more appropriate for reasons that will emerge below.

### *10. Response saturation*

Unlike the other cone mechanisms the short-wavelength system shows saturation in the steady state. That is to say, when violet targets are presented on

violet or blue fields of increasing intensity – in the presence of a fixed long-wavelength 'auxiliary' field – the incremental threshold rises more quickly than is described by Weber's Law (Mollon and Polden 1977a). This 'saturation' has another curious feature: the state of insensitivity to violet increments is reached only after many seconds of adaptation and after the threshold has passed through a much lower value (Mollon and Polden, 1978, 1980; Stromeyer *et al.* 1979).

### *11. Superadditivity of adapting field*

If we assume that $\pi$ mechanisms obey the Principle of Univariance (Rushton 1972) and are adaptively independent, and if we obtain, for a given mechanism, t.v.i. curves for two different field wavelengths, $\mu_1$ and $\mu_2$, then we can calculate what should be the effect on threshold of a given mixture of $\mu_1$ and $\mu_2$. In a study of field additivity for Stiles' blue mechanism $\pi_1$, Pugh (1976) showed that thresholds for $\pi_1$ could be predicted in this way if both $\mu_1$ and $\mu_2$ were of short wavelength ($< 500$ nm) but the fields were 'superadditive' (more potent than predicted) if a short-wavelength field was combined with one of wavelength $> 550$ nm.

### *12. Light adaptation*

The adaptation of the short-wavelength mechanism to long-wavelength fields is known to be very slow (Stiles, 1949a; Augenstein and Pugh, 1977). Recent measurements by P.G. Polden, A. Stockman and myself show that the time course of adaptation has a very strange structure to it when the adapting field is of an intensity that places the observer on the '$\pi_3$ plateau' (say, $\sim 10^{11}$ quanta. $sec^{-1}$. $deg^{-2}$ at 600 nm). During the first few seconds of exposure to the field the threshold for violet targets *rises*, instead of falling as is normally the case during early light adaptation. In Figure 1, which shows the first 90 s of adaptation to a 600 nm field of 5.22 Td, the first 200 msec flash begins 200 msec after the onset of the field; 2 s later the threshold has risen by more than 1 $\log_{10}$ unit. The data were obtained by means of the 'Method of a Thousand Staircases' (Mollon and Polden, 1980), which allows sensitivity to be sampled accurately at a set of precisely known moments in the course of adaptation.

### *13. Transient tritanopia*

In the experiment of Fig. 1 the observer remained on his mouthbite for another 90 s after the field had gone off and the results show the remarkable loss of short-wavelength sensitivity that occurs when a long-wave adapting stimulus is suddenly removed. This phenomenon was described by Stiles (1949b) and was termed 'transient tritanopia' by Mollon and Polden (1975, 1977b). Under the conditions of Fig. 1, the threshold of a flash beginning 200 msec after removal of the field is more than 2 log units higher than that obtaining when the field was present and more than 15 s must pass before the latter value is regained. It is significant that transient tritanopia is reduced or

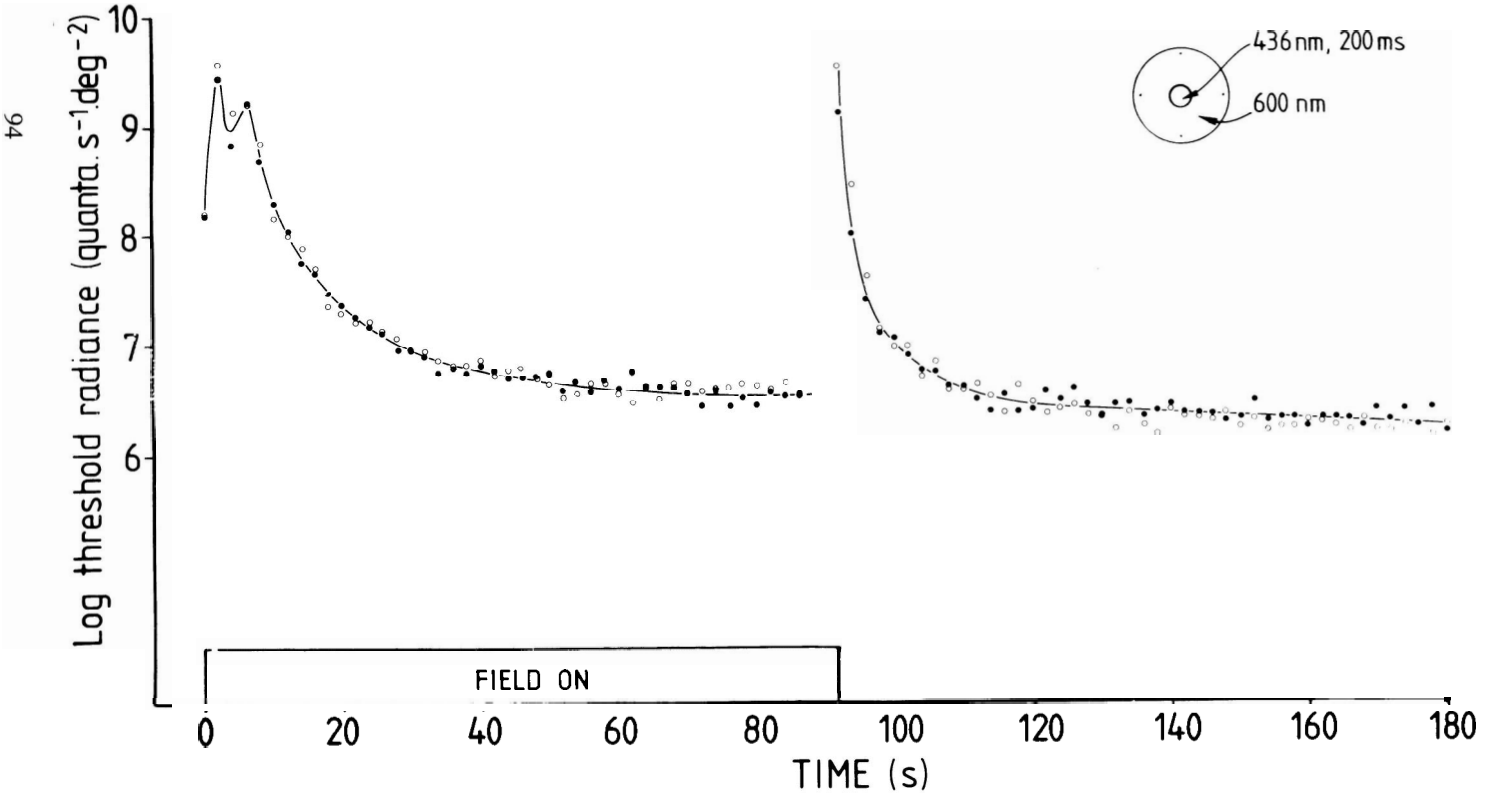


*Fig. 1.* Illustration of the transient losses of short-wavelength sensitivity that occur at the onsets and offsets of bright, long-wavelength fields. The observer (JDM) first dark adapted for 2 minutes. Then an orange (600 nm; 5.8 deg) field of 5.22 Td was turned on and sensitivity was probed every 2 seconds with a violet (436 nm; 1.5 deg; 200 msec) target centred on the foveola. After 90 seconds of light adaptation the field was turned off and sensitivity was tracked for a further 90 seconds. The first flash occurred 200 msec after onset of the field; and the first flash during dark adaptation occurred 200 msec after offset of the field. Repeated passes were made through the adaptation sequence according to the Method of a Thousand Staircases (Mollon and Polden, 1980), with a minimum interval of 10 minutes between exposures to the field. Two complete sequences of passes were made on different days; the two sets of resulting thresholds are represented by different symbols. Details of the apparatus are given by Mollon and Polden (1977). The present results were obtained specially to illustrate this paper but resemble those obtained in other similar experiments on this and other subjects. The small oscillation in sensitivity at about the fourth second of light adaptation has been often obtained for this observer. The large rise in threshold during the first two seconds of light adapation has been found for all six subjects so far tested.

abolished if (a) the long-wavelength field is extremely intense and is maintained for several minutes (Mollon and Polden, 1976), if (b) the adapting field also includes a short-wavelength component (Augenstein and Pugh, 1977) if (c) the adapting field is flickered (Loomis, 1980; Reeves, 1981a) or if (d) the subject is a blue-cone monochromat (Hansen *et al.*, 1978). Transient tritanopia proves to have analogues for long- and middle-wavelength targets (Mollon and Polden, 1977b; Reeves, 1981b) and should now be seen as only one of a class of 'dynamic dyschromatopsias' that occur at the onsets and offsets of coloured fields (Mollon, 1982).

## EXPLANATORY PRINCIPLES

A small number of principles may account for many of the anomalies in the above list.

### *I. The short-wavelength receptors are rare*

This has long been advanced as an explanation of the basic insensitivity of the short-wavelength system (e.g. De Vries, 1949) and of its poor spatial resolution; increased spatial and temporal integration may have arisen as compensations. Evidence that the short-wavelength receptors are rare is provided by microspectrophotometry: in man, and in the primates *Macaca fascicularis* and *Saimiri sciureus*, the short-wavelength receptors represent less than 10% of the sampled cones (Bowmaker and Dartnall, 1980; Bowmaker *et al.*, 1980; Jacobs *et al.*, 1981). Particularly persuasive is evidence from a histological staining technique (Marc and Sperling, 1977) and from the histological damage produced by intense blue light (Sperling, 1980); for here the numerosity of the putative short-wavelength cones prettily parallels Brindley's (1954) psychophysical results for the variation of $\pi_1$ sensitivity with retinal eccentricity. The frequency of the putative short-wavelength cones is as low as 2–3% in the centre of the foveola, rises to a peak of 16% in a zone equivalent to an eccentricity of 1 deg and falls to 8–10% in the parafovea. There is also evidence that the short-wavelength receptors occur in a regular mosaic and Williams *et al.* (1981b) offer convincing psychophysical evidence for a punctate distribution of short-wavelength receptors in the foveola.

### *II. Signals originating in the short-wavelength receptors have access only to a chromatically opponent subset of postreceptoral channels. Such channels are most sensitive to input perturbations when they are in the middle of their response range*

The origins of these hypotheses, and the evidence for them, are reviewed by Pugh and Mollon (1979) and Polden and Mollon (1980). It is supposed that an opponent channel becomes insensitive to small changes in its input when it is *polarized*, that is, driven to one or other extreme of its response range.

To explain the form of the t.v.i. curve for violet increments on a long-

wavelength field, Pugh and Mollon suppose that the $\pi_1$ branch is due to increasing polarization of a long-wavelength site by a signal originating in the long-wavelength receptors; in this range of field intensity, the field produces only a negligible rate of isomerisations in the short-wavelength receptors. However, owing to bleaching and to other forms of response compression, the long-wavelength signal cannot grow indefinitely; hence the limited conditioning effect. Eventually, however, the long-wavelength field becomes intense enough to produce direct absorptions in the short-wave receptors and the '$\pi_3$' branch results. The 'superadditivity' found by Pugh (1976) arises under conditions where the short- and long-wavelength components of the field act at largely different sites. Response saturation occurs when increasing the intensity of a short-wavelength field leads to concomitant increases in attenuation at two successive sites in the short-wavelength pathway – the receptors themselves and the opponent site that follows. Transient tritanopia arises (Pugh and Mollon suggest) because a restoring force serves to reduce the polarization of the opponent site during maintained adaptation to a long-wavelength field. The restoring force depends on the input to an integrator with a long time constant and it continues to act when the adapting field is suddenly removed. The unopposed restoring force now polarizes the opponent site in the contrary sense and a transient loss of sensitivity results. The loss of sensitivity at the onset of intense long-wave fields (Fig. 1) is also almost certainly due to polarization of an opponent site, but the initial delay is mysterious.

Whereas signals from the short-wavelength receptors appear to reach us only via opponent channels, signals originating in the long- and middle-wavelength receptors have access to a variety of postreceptoral channels, opponent and non-opponent, and so in their case the full extent of the dynamic dyschromatopsias is concealed from us as other channels come into play.

### *III. Signals originating in the short-wavelength cones have little or no access to the superior colliculus*

That this is so is reported by de Monasterio (1978, a, b) on the basis of electrophysiological recordings. I mention it here because it might explain neonatal tritanopia, if we supposed that the looking behaviour of the infant was controlled entirely by the superior colliculus (see Mollon 1982 pp 76–78).

### *IV. Chromatic aberration*

The preceding three principles may in their turn perhaps all be traced to the chromatic aberration of the eye. When longer wavelengths are present the short-wavelength component of the retinal image will normally be out of focus and thus of no use for spatial discrimination. Nature intends us to use our short-wavelength receptors only for hue discrimination and so restricts their numbers and the postreceptoral channels to which they have access.

## RELATION BETWEEN GROUPS A AND B

The adaptational anomalies (Group B), and the theory to which they have led, imply that the long-wavelength adapting field classically used to isolate the short-wavelength system is not the innocent instrument that it has usually been taken to be. By polarizing a postreceptoral opponent site, it may place the short-wavelength mechanism in a suboptimal part of its response range. Many of the studies cited in Group A are open to this difficulty. Of particular interest is the report of King-Smith, Zisman and Bhargava (cited by Mollon, 1977; see also the paper by Alvarez, King-Smith and Bhargava in the present volume) that in several disorders of the retina and optic nerve the loss of blue sensitivity for incremental targets is greater for flashes presented on a yellow field than for flashes on a white field. This intriguing result suggests that measurements of the Stiles type may often reveal a tritan-like defect, not because the short-wavelength receptors are damaged but because the dynamic range of colour-opponent channels has been reduced. It might be very instructive to study the Group B anomalies in visual disorders.

## THE TRITANOPIC PARADOX

Tritanopia should never be equated with the absence of a blue sensation. On the contrary, a puzzling rule emerges from the literature: if an observer concurrently has, or recently has had, access to normal trichromatic vision but, as a result of unilateral disease or of the stimulus parameters, is viewing under tritanopic conditions, then his visual sensations will be dominated by two hues, one of which will typically be blue. Operationally, it is bluish stimuli that he will choose when asked to make trichromatic matches to short-wavelength stimuli seen under tritanopic conditions. Alpern, Kitahara and Krantz (1981) give results for an observer who was tritanopic in one eye (as a result of central serous retinopathy) but trichromatic in the other: when this observer was asked to name, or to match dichoptically, stimuli seen with his tritan eye, it seemed that all wavelengths shorter than his mid-spectral tritan neutral point appeared bluish when presented to his dichromatic eye. But one does not have to be a unilateral tritanope to experience this paradox. Under conditions of foveolar tritanopia, short-wavelength targets appear blue to many normal observers, provided that the wavelength is not so short as to approximate to the second tritan neutral point that lies near 400 nm. The tritanopia of the centre of the foveola can be conveniently experienced by inspecting, from a distance of more than 2 metres, Plate 6 of the City University test (1st Ed.); and the green and blue targets that are then confused may both look blue. Systematic measurements were made by Middleton and Holmes (1949) who asked their observers to fixate isolated Munsell chips subtending $1'$ or $2'$ and then to match them using an array of larger, identically-illuminated samples. Although there were individual differences, it was found that the matches typically collapsed on to a line in chromaticity space that ran in the direction greenish-blue (487–490 nm) to orange (595–625 nm), rather than from unique green to red. The subset of chromaticities

used in matching the tritan stimuli resembled approximately those used by the patient of Alpern *et al.* Similarly, there occurs an increase in the proportion of 'blue' to 'green' responses as one passes from trichromatic to tritan-like[1] vision when illumination is reduced (Middleton and Mayo, 1952) or when the targets are displaced to the periphery (Gordon and Abramov, 1977) or when targets are reduced in duration (Weitzman and Kinsey, 1967).

How should we explain this paradox? Well, we know that the brain abhors contradictions between inputs and exercises itself to eliminate them. This is classically demonstrated by the adjustments that occur when the input to one or both eyes is optically distorted (Welch, 1979). Now, if one retina, or part of a retina is dichromatic but if trichromatic vision is otherwise available to the observer (recently or concurrently), then it is never possible completely to eliminate discrepancies between signals from 'bad' and 'good' retinae. For in this case, any given signal from the dichromatic retina can be mapped on to a large set of discriminable signals from the trichromatic retina. However, it is plausible to suppose that the system chooses to minimise the discrepancy at that wavelength at which the residual opponent signal from the dichromatic retina is strongest and is least easily ignored. This is the crucial assumption of the present argument. In the case of tritanopia the residual opponent signal from the dichromatic retina must pass through its short-wavelength maximum near 470 nm, since it is in this region, and not in spectral regions that look green, that the ratio of M-cone sensitivity to L-cone sensitivity has its highest value. That the latter is so is implied by the colour matches of tritanopes (Wright, 1952) and by microspectrophotometric measurements. Now, examined with the normal retina, wavelengths near 470 nm look blue and we assume that it is wavelengths in this region that will yield consistent (and bluish) sensations whether they are examined with trichromatic or dichromatic retina. (Why 470 nm does not look green to the normal eye is, of course, another question.)

In the context of the hypothesis above it is instructive to consider the results of Ingling, Scheibner and Boynton (1970), who asked their observers to give colour names to 3′, 75 msec monochromatic targets. When the targets were delivered to the centre of the foveola, 'blue' responses were common (in the case of observer RMB they were much more frequent than green responses), but what is especially interesting is that the distribution of these responses roughly reflects the proportion of the short-wavelength primary required in a *tritanope's* colour match and thus presumably the spectral variation in the ratio of M- to L-cone sensitivity. The 'blue' responses pass through a maximum near 460 nm and fall to a minimum at the two tritan neutral points near 400 nm and 570 nm. In particular, the proportion of 'blue' responses actually decrease in the spectral region (420–440 nm) where the sensitivity of the short-wavelength cones is increasing relative to that of the L- and M-cones.

In summary, to explain the paradox that short-wavelength stimuli often look bluish under tritanopic conditions of viewing, we have reasoned as

[1] By 'tritan-like' I mean primarily that a neutral zone occurs in the spectral region 570–580 nm.

follows. Faced with a discrepancy between (concurrent or successive) sensory inputs from trichromatic and dichromatic retinae and being built to reduce such discrepancies as far as possible, the brain chooses to eliminate the discrepancy at that wavelength at which the opponent signal is strongest and least easily suppressed.

## REFERENCES


Alpern, M., Kitahara K. and Krantz. D.H. What colours does a tritanope see? Investig. Ophthalmol. Vis. Sci: 20, Suppl., p. 206 (Abstr.) (1981).

Augenstein, E.J. and Pugh, E.N. The dynamics of the $\pi_1$ colour mechanism: further evidence for two sites of adaptation. J. Physiol. 272: 247–281 (1977).

Barlow, H.B. Intrinsic noise of cones. In Visual Problems of Colour. National Physical Laboratory Symposium: 615–639. London: H.M. Stationery Office. (1958).

Blackwell, H.R. and Blackwell, O.M. Rod and cone receptor mechanisms in typical and atypical congenital achromatopsia. Vision Res., 1: 62–107 (1961).

Bowmaker, J.K., Dartnall, H.A.J. and Mollon, J.D. The violet-sensitive receptors of primate retinae. J. Physiol. 292: 31P (1979).

Bowmaker, J.K., Dartnall, H.J.A. and Mollon, J.D. Microspectrophotometric demonstration of four classes of photoreceptor in an Old World primate, *Macaca fascicularis.* J. Physiol. 298: 131–143 (1980).

Bowmaker, J.K. and Dartnall, H.J.A. Visual pigments of rods and cones in a human retina. J. Physiol. 298: 501–512 (1980).

Boynton, R.M., Hayhoe, M.M. and MacLeod, D.I.A. The gap effect: chromatic and achromatic visual discrimination as affected by field separation. Optica Acta 24: 159–177 (1977).

Brindley, G.S. The effects on colour vision of adaptation to very bright lights. J. Physiol. 122: 332–350 (1953).

Brindley, G.S. (1954) The summation areas of human colour-receptive mechanisms at increment threshold. J. Physiol. 124: 400–408 (1954).

Brindley, G.S., Du Croz, J.J. and Rushton, W.A.H. The flicker fusion frequency of the blue sensitive mechanism of colour vision. J. Physiol. 183: 497–500 (1966).

Cavonius, C.R. and Estévez. Contrast sensitivity of individual colour mechanisms of human vision. J. Physiol. 248: 649–662 (1975).

Daw, N.W. and Enoch, J.M. Contrast sensitivity, Westheimer function and Stiles-Crawford effect in a blue cone monochromat. Vision Res. 13: 1669–1680 (1973).

De Vries, Hl. An extension of Helmholtz's theory of colourvision. Rev. Opt. (Paris) 28: 91–100 (1949).

de Monasterio, F.M. Properties of concentrically organised X and Y ganglion cells of macaque retina. J. Neurophysiol. 41: 1394–1417 (1978a).

de Monasterio, F.M. Properties of ganglion cells with atypical receptive field organisation in retina of macaques. J. Neurophysiol. 41: 1435–1449 (1978b).

Farnsworth, D. Tritanomalous vision as a threshold function. Die Farbe, 4: 185–197 (1955).

Gordon, J. and Abramov, I. Color vision in the peripheral retina. II. Hue and saturation. J. opt. Soc. Amer. 67: 202–207 (1977).

Green, D.G. The contrast sensitivity of the colour mechanisms of the human eye. J. Physiol. 196: 415–429 (1968).

Green, D.G. Sinusoidal flicker characteristics of the color-sensitive mechanisms of the eye. Vision Res. 9: 591–601 (1969).

Green, D.G. Visual acuity in the blue cone monochromat. J. Physiol. 222: 419–426 (1972).

Hansen, E., Seim, T. and Olsen, B.T. Transient tritanopia experiment in blue cone monochromacy. Nature, 276: 390–391 (1978).

Ingling, C.R., Scheibner, H.M.O. and Boynton, R.M. Colour naming of small foveal fields. Vision Research 10: 501–511 (1970).
Jacobs, G.H., Bowmaker, J.K. and Mollon, J.D. Protan and deutan colour vision in squirrel monkeys. Nature, 292: 541–543 (1981).
Kelly, D.H. Spatio-temporal frequency characteristics of color vision mechanisms. J. opt. Soc. Amer. 64: 983–990 (1974).
Klingaman, R.L. and Moskowitz-Cook, A. Assessment of the visual acuity of human color mechanisms with the visually evoked cortical potential. Invest. Ophthal. Vis. Sci. 18: 1273–1277 (1979).
Krauskopf, J. and Mollon, J.D. The independence of the temporal integration properties of individual chromatic mechanisms in the human eve. J. Phvsiol. 219: 611–623 (1971).
Marc, R.E. and Sperling, H.G. Chromatic organisation of primate cones. Sci. 196: 454–456 (1977).
Middleton, W.E.K. and Holmes, M.C. The apparent colours of surfaces of small subtense – a preliminary report. J. opt. Soc. Amer. 39: 582–592 (1949).
Middleton, W.E.K. and Mayo, E.G. The appearance of colours in twilight. J. opt. Soc. Amer. 42: 116–121 (1952).
Mollon, J.D. The oddity of blue. Nature 268: 587–588 (1977).
Mollon, J.D. Color Vision. Ann. Rev. Psychol. 33: 41–85 (1982).
Mollon, J.D. and Krauskopf, J. Reaction time as a measure of the temporal response properties of individual colour mechanisms. Vision Res. 13: 27–40 (1973).
Mollon, J.D. and Polden, P.G. Absence of transient tritanopia after adaptation to very intense yellow light. Nature, 259: 570–572 (1976b).
Mollon, J.D. and Polden, P.G. Saturation of a retinal cone mechanism. Nature, 265: 243–246 (1977a).
Mollon, J.D. and Polden, P.G. An anomaly in the response of the eye to light of short wavelengths. Phil. Trans. roy. Soc. B. 278: No. 960 (1977b).
Mollon, J.D. and Polden, P.G. On the time constants of tachistoscopes. Quart. J. exp. Psychol. 30: 555–568 (1978a).
Mollon, J.D. and Polden, P.G. An anomaly of light adaptation. Investig. Ophthalmol. and Visual Sci. 17, Supplement p 177 (Abstr.) (1978b).
Mollon, J.D. and Polden, P.G. A curiosity of light adaptation. Nature, 286: 59–62 (1980).
Polden, P.G. and Mollon, J.D. Reversed effect of adapting stimuli on visual sensitivity. Proc. roy. Soc. B. 210: 235–272 (1980).
Pugh, E.N. The nature of the $\pi_1$ mechanism of W.S. Stiles. J. Phvsiol. 257: 713–747 (1976).
Pugh, E.N. and Mollon, J.D. A theory of the $\pi_1$ and $\pi_3$ colour mechanisms of Stiles. Vision Res. 19: 293–312 (1979).
Pulos, E., Teller, D.Y. and Buck, S.L. Infant colour vision: a search for short-wavelength-sensitive mechanisms by means of chromatic adaptation. Vision Res. 20: 485–493 (1980).
Reeves, A. Transient tritanopia after flicker adaptation. Vision Research 21: 657–664 (1981a).
Reeves, A. Transient de-sensitisation of a red-green opponent site. Vision Research 21: 1267–1277 (1981b).
Rushton, W.A.H. Pigments and signals in colour vision. J. Physiol. 220: 1–31 P. (1972).
Sperling, H.G. Blue receptor distribution in primates from intense light and histochemic studies. In Verriest (1980) Colour Vision Deficiencies V, pp 30–44, Bristol: Hilger.
Stiles, W.S. The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. Proc. roy. Soc. B. 127: 64–105, (Reprinted in Stiles (1978)). (1939).
Stiles, W.S. Investigations of the scotopic and trichromatic mechanisms of vision by the two-colour threshold technique. Rev. Opt. (Paris) 28: 215–237. (Reprinted in Stiles (1978)). (1949a).
Stiles, W.S. Increment thresholds and the mechanisms of colour vision. Docu. Ophthalmol. 3: 138–163. (Reprinted in Stiles 1978). (1949b).
Stiles, W.S. Further studies of visual mechanisms by the two-colour threshold technique.

Coloquio sobre problemas opticos de la vision, I, pp 65–103. Gen. Assembly int. Un. pure Phys. Madrid. (Reprinted in Stiles (1978)). (1953).
Stiles, W.S. Mechanisms of Colour Vision, Academic Press, London and New York, (1978).
Stromeyer, C.F., Kronauer, R.E. and Madsen, J.C. Response saturation of short-wavelength cone pathways controlled by colour-opponent mechanisms. Vision Res. 19: 1025–1040 (1979).
Tansley, B.W. and Boynton, R.M. Chromatic border perception: the role of red- and green-sensitive cones. Vision Res. 18: 683–697 (1978).
Trezona, P.W. Rod participation in the 'blue' mechanism and its effect on colour matching. Vision Res. 10: 317–332 (1970).
Valberg, A. and Tansley, B.W. Tritanopic purity-difference function to describe the properties of minimally distinct borders. J. opt. Soc. Amer. 67: 1330–1335 (1977).
Weitzman, D.O. and Kinney, J.A. Appearance of colour for small, brief, spectral stimuli, in the central fovea. J. opt. Soc. Amer. 57: 665 (1967).
Welch, R.B. Perceptual modification. New York: Academic Press (1979).
Williams, D.R., Macleod, D.I.A. and Hayhoe, M. Foveal tritanopia. Vision Res. 21: 1341–56 (1981a).
Williams, D.R., MacLeod, D.I.A. and Hayhoe, M. Punctate sensitivity of the blue-sensitive mechanism. Vision Res. 21: 1357–1375 (1981).
Willmer, E.N. Human colour vision and the perception of blue. J. theoret. Biol. 2: 141–179 (1961).
Wisowaty, J.J. and Boynton, R.M. Temporal modulation sensitivity of the blue mechanism: measurements made without chromatic adaptation. Vision Res. 20: 895–909 (1980).
Wright, W.D. The characteristics of tritanopia. J. opt. Soc. Amer. 42: 509–521 (1952).
Wyszecki, G.W. and Stiles, W.S. Colour Science, Concepts and Methods, Quantitative data and formulas. New York: Wiley. (1967).

Author's address:
Department of Experimental Psychology
Downing Street
Cambridge CB2 3EB
U.K.