AN ANOMALY IN THE RESPONSE OF THE EYE TO LIGHT OF SHORT WAVELENGTHS

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Adaptation of the human eye to long-wavelength light leaves it insensitive to short-wavelengths: a blue flash that is visible in the presence of a yellow adapting field may remain invisible for several seconds after the field has been turned off (see experiment 1 and Appendix). This 'transient tritanopia' occurs for a large range of adapting intensities, but is abolished if the adapting field is very bright (experiment 2). The loss of sensitivity is primarily confined to the blue-sensitive cone mechanism (experiments 2*a*, 3 and 4; and Appendix) and can be produced by small attenuations of the adapting field (experiment 5). It occurs in both foveal and parafoveal vision (experiment 6) but is absent when adapting and test stimuli are presented to opposite eyes (experiment 7). It was found in a protanope (experiment 9*a*) and, in a modified form, in a deuteranope (experiment 9*b*). No differences in sensitivity were found for blue flashes presented in the light and dark phases of a field flickering at a rate above the fusion frequency (Appendix).

The sensitivity of the blue-sensitive mechanism of the eye appears to be controlled not only by quanta absorbed by the blue receptors but also by a mechanism with a different spectral sensitivity.

Introduction

Sensory adaptation, if measured by loss of sensitivity, is usually found to be greatest at that value of a sensory dimension that corresponds to the adapting stimulus. Thus exposure to a frequency-modulated tone leads to a loss of sensitivity to modulation that is maximum at the modulation frequency of the adapting stimulus (Kay & Matthews 1972). An analogous result is found for adaptation to a spatially periodic visual stimulus. Occasional exceptions to this general rule can be found (e.g. Blakemore & Campbell 1969, Figure 10), but perhaps the most singular exception is that reported by Stiles (1949*a*): when the eye was adapted for some minutes to a red field of 20000 td† and the field was then extinguished, the most marked loss of sensitivity was at short wavelengths; and indeed the threshold for blue flashes actually rose above the value it had assumed when the field was present. We have suggested the name 'transient tritanopia' for this phenomenon (Mollon & Polden 1975) but by this term imply only an operational resemblance to the genetic colour deficiency; some justification for the term will be found in the results reported below.

Transient tritanopia is only one of a number of anomalous properties of the blue-sensitive mechanism of the eye. For example, the blue mechanism has larger space and time constants and a larger Weber fraction than the mechanisms sensitive to middle and long wavelengths; it contributes little or nothing to apparent brightness; and it is disproportionately vulnerable to diseases affecting the receptors. (For references see Stiles 1949*a*; Willmer 1961; Brindley 1970; Mollon & Krauskopf 1973; Whittle 1974; Mollon & Polden 1976*a*.) 'Transient tritanopia' should not be considered independently of the other anomalies of the blue mechanism and in particular should not be divorced from the analogous retardation of light adaptation found when the sensitivity of the blue-sensitive mechanism is measured after the onset of a long-wavelength field (Stiles 1949*b*). We may relate transient tritanopia to the recurrent suggestion that even in a steady state of adaptation the sensitivity of the blue mechanism is controlled not only by quanta absorbed directly by the blue cones themselves but also by signals from other classes of receptor (De Vries 1948; Stiles 1959; Brindley 1960, pp. 244–248). It is an open question which of the anomalous properties of the psychophysically defined blue mechanism are

† 1 td (troland) is the retinal illumination when a luminance of 1 cd/m^2 is seen through a pupil of area 1 mm^2. For light of wavelength 580 nm, taking transmission losses into account:

$$1 \text{ td} = 0.003 \text{ lm/m}^2 = 10^7 \text{ quanta s}^{-1} \text{ mm}^{-2} \text{ approximately.}$$

intrinsic properties of the blue receptors rather than consequences of (*a*) the neural connections within an association of blue receptors and (*b*) influences exerted on the blue mechanism by signals from other mechanisms.

The very existence of transient tritanopia has been the subject of controversy. Results similar to those of Stiles have been reported by Das (1964) and by Watkins (1969); an electrophysiological counterpart appears in recordings from retinal ganglion cells of the rhesus monkey (Gouras 1968, Figure 7); and the phenomenon of 'negative blue' discovered by Wright (1946) after adaptation to yellow fields in colour-matching experiments is surely the same phenomenon as the threshold effect found by Stiles. An early suggestion of transient tritanopia can be seen in Figures 2 and 4 of a paper by Roaf (1928). Yet Burch (1899), Brindley (1953), Auerbach & Wald (1954, 1955) and Du Croz & Rushton (1966) have each reported that the eye is blue-sensitive rather than blue-blind after adaptation to intense long-wavelength fields and indeed have used such conditions to isolate the short-wavelength receptors (cf. also Edridge-Green & Marshall Devereux 1909). The results of experiment 2 suggest a reconciliation for these apparently contradictory reports.

Methods

Apparatus

The apparatus consisted of a three-channel, Maxwellian-view optical stimulator linked to a laboratory computer. The arrangement is shown schematically in figure 1. Three beams are drawn from the same light source, a 12 V, 50 W, tungsten iodide projector lamp, which is underrun at 11.5 V from a stabilized d.c. power supply. Channel 1 normally provides the adapting beam and channel 2 the test beam; channel 3 is used when a second adapting field is required. In each beam, close to the first filament-image formed, are placed a variable neutral density filter (F1), with a range of 3 $\log_{10}$ units, and a variable interference filter (F2; Barr & Stroud, type CS 1). Both types of variable filter are circular in form and are mounted directly on the shafts of stepping motors, so that the intensity and wavelength of each beam can be placed under computer control. A single step of a motor corresponds to a change of approximately 0.01 $\log_{10}$ units of attenuation in the case of the neutral filters and of approximately 1 nm in the case of the interference filters. The bandwidth at half intensity of the interference filters was 20 nm, except in experiment 5*a*, when a variable filter giving a measured bandwidth (half-height) of 13 nm at 445 nm was substituted in order to improve measurements of test sensitivity at short wavelengths. Spectral blocking filters (Ilford 600 series and Kodak Wratten) and fixed neutral-density filters are placed in the collimated section of each beam (BF, ND). Infrared radiation is removed by cold mirrors (CM), which transmit infrared and ultraviolet radiation and reflect the visible, and by HA 3 heat-absorbing glass (HA). We placed cold mirrors rather than HA 3 glass in the non-collimated beams between the light source and the variable filters in order to keep chromatic aberration to a minimum.† The additional HA 3 glass, placed in the collimated section, serves primarily to prevent contamination of radiometric measurements by infrared leaks.

† We have found that some pieces of apparently clear HA 3 glass, from reputable manufacturers, are birefringent: random striations are seen when the glass is placed between crossed polarizers. It may be worth recording that, if such glass is placed in an optical path between two mirrors, Brewster polarization may cause unnoticed variations in stimulus intensity if the glass or a stimulus aperture is moved; and unwanted variations within the stimulus field may be present.

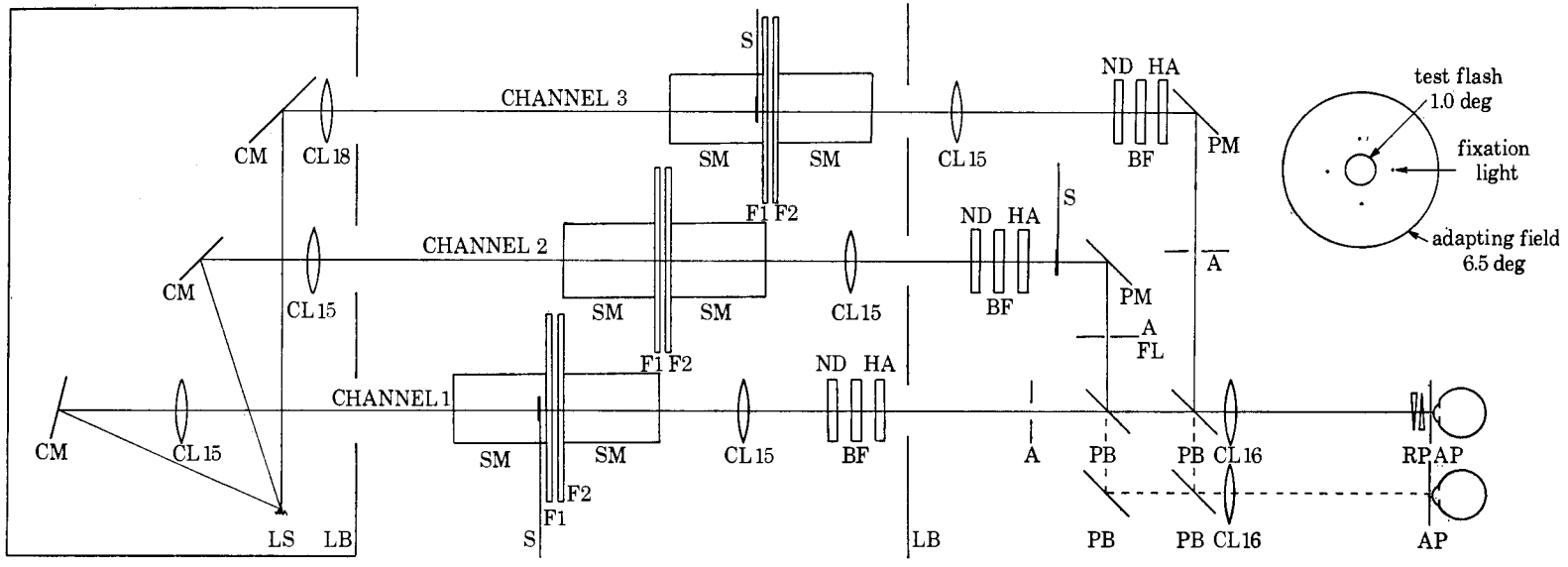


FIGURE 1. Optical system and (inset top right) arrangement of stimuli. A, stimulus aperture; AP, artificial pupil; BF, blocking filter; CL, convex lens (focal length in cm); CM, cold mirror; F1, continuously variable neutral density filter; F2, continuously variable interference filter; FL, fixation light; HA, heat-absorbing filter; LB, light baffle; LS, light source; ND, neutral density filter; PB, pellicle beam-splitter; PM, plane mirror; RP, Risley prism; S, shutter; SM, stepping motor.

Each adapting beam can be interrupted by a shutter (S) consisting of a balsa-wood vane mounted on a pen motor. The shutter in the test-beam consists of a similar vane mounted on an ex-military solenoid device. Rise and fall times are less than 2 ms.

The three beams are combined by pellicle beam splitters (PB), and filament image is formed at a 2 mm artificial pupil (AP) immediately in front of the cornea of the observer's right eye. The position of the observer's eye is maintained by a wax dental-impression that is mounted on adjustable cross-slides taken from a milling machine. In experiment 6 a pellicle and a lens were added to bring the test beam to focus at a second 2 mm pupil in front of the observer's left eye; and to facilitate fusion a Risley prism (RP) was placed in front of the right eye.

The duration and sequence of stimuli are controlled by off-line programming logic, but the titration of stimulus intensity and the recording of the observer's responses are under the control of a Modular One computer. In the experiments described here, we used the ONLI programming system for experimental control developed for the Modular One by S.E.G. Lea and C. K. Crook.

Stimuli

The areas of the target and the field are defined by circular apertures (A). Except where otherwise stated, the target was a disk subtending 1° of visual angle and the adapting field was a concentric disk subtending 6.5°. The observer fixated the centre of a diamond-shaped array of four bright points formed by the ends of single fibres from a fibre-optics light-guide introduced into channel 2 (FL). The horizontal and vertical separation of the fixation lights was 3°. They were adjusted in intensity so as to be just clearly visible against the particular field in use and remained illuminated throughout the stimulus sequence. The spatial arrangement of the stimuli is shown inset (top right) in figure 1.

Calibration

Stimulus intensities were measured with a PIN10 silicon photodiode (United Detector Technology) and operational amplifier, which, in combination, had been calibrated absolutely and spectrally by the National Physical Laboratory. The variable and fixed neutral density filters were calibrated *in situ* at each stimulus wavelength used. Fresh calibrations were made every few days, usually at the end of an experimental session. Especial care was taken to suppress infrared and ultraviolet leaks that would have distorted radiometric calibrations (when using only gelatin spectral filters we found that a total thickness of 6 mm of HA 3 glass, in addition to the cold mirrors, had to be present in the beam before infrared contamination was negligible).

Radiometric measurement of the adapting field was supplemented by photometric measurements: a screen coated with MgO was mounted 1 m beyond the artificial pupil and the diverging stimulus beam was allowed to project on to it. The luminance of this surface was estimated with a SEI photometer and retinal illuminance was calculated according to the procedure of Westheimer (1966). Radiometric and photometric measurements gave good agreement. Photometric measurements of the short-wavelength test-stimuli were not attempted, since estimates of the luminance of short-wavelength light are known to vary widely with the method of estimation.

In the figures, stimulus intensities are expressed in terms of ergs per second delivered to the cornea, divided by the area of the stimulus expressed in square degrees of visual angle; but, for

the convenience of the reader, abscissae are also given in trolands (td), units of retinal illuminance, and troland values are given in the text (see footnote, p. 208). Changes in stimulus intensities are expressed in '$\log_{10}$ units', equivalent to $\log_{10}$(first intensity/second intensity).

Stimulus wavelength was calibrated by mounting a monochromator (Hilger & Watts) immediately behind the artificial pupil and placing the silicon photodiode at the exit slit of the monochromator. The calibration of the monochromator was in turn checked every few months by reference to a mercury lamp and was found to be stable. Where interference filters were used the spectral calibration was made with the appropriate blocking filter in place. To establish wavelengths of peak transmission at the violet end of the spectrum and to measure bandwidths in all parts of the spectrum, a lock-in amplifier (Princeton Applied Research 128A) was used in conjunction with an episcotister that interrupted the beam at 400 Hz.

The time-interval generators were calibrated with an electronic stop-clock. The duration of the test-flash was measured directly by displaying the output of the photodiode on an oscilloscope.

Procedure

Thresholds were measured by a double staircase procedure (Cornsweet 1962). One staircase began well above threshold and the other well below threshold. The step size was initially 0.3 $\log_{10}$ units and was reduced to 0.1 $\log_{10}$ units after the staircases had crossed. The computer program switched randomly between the two staircases. There were 50 stimulus presentations within a block. The threshold was taken as the mean of those intensity levels visited after the staircases had first crossed and was thus typically estimated from the responses to between 30 and 40 presentations. The observer responded 'yes' or 'no' by means of push-buttons.

In most of the experiments to be described, the adapting field was interrupted every 18 s by a 3 s dark interval. A single test flash, lasting 18 ms, was introduced at a fixed delay (Δt) after each extinction of the field. A warning tone was presented 1 s before extinction of the field. Preliminary experiments showed that extending the adapting period beyond 15 s did not alter the results (cf. Baker *et al.* 1959); but the collection of data did not begin until the observer had completed a preliminary period of 4 min light adaptation to the recycling field; and at high field illuminances this initial adapting period had to be extended to 6 min before measurements were stable.

Measurements of the conventional increment threshold, on a steady field, were made in a similar way; but the interval between test flashes was reduced to 5 s after we had established that the measured threshold was not thereby altered.

Observers

The primary observers were the two authors. Systematic measurements have also been made on CS, a graduate student in another field, who became a trained observer in so far as he completed a long series of observations but who remained unaware of the purposes and results of the experiments. The basic phenomenon has been established for a number of other experienced observers; and measurements for the three original observers are given by Stiles in the Appendix.

PGP and CS are emmetropic. JDM is myopic and used a -5D correcting lens placed immediately before the artificial pupil. All three observers perform normally on the Farnsworth–Munsell 100-hue test and on the Nagel anomaloscope.

Results

Experiment 1: basic phenomenon

Figure 2 shows how the threshold for a 445 nm test-flash changes during the first seconds after extinction of a yellow (580 nm) adapting field that produced a retinal illuminance of $10^{3.9}$ trolands (equivalent to $10^{-1.4}$ erg s^{-1} deg $^{-2}$). Within a block of presentations the interval between offset of field and onset of target (Δt) was fixed; these delays were randomized between blocks. The results shown are the means of two runs. In each case the open circles and the broken lines mark the threshold when the steady adapting field was present.

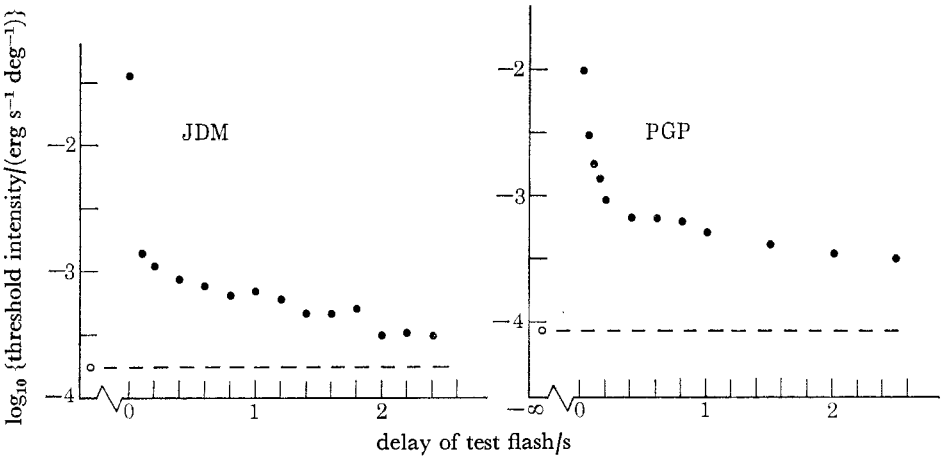


FIGURE 2. Log threshold intensity for a blue (445 nm) test flash at varying delays following the offset of a yellow (580 nm) field of intensity $10^{-1.4}$ erg s^{-1} deg^{-2}. o, – – –, incremental threshold when the field is present.

The threshold rises as soon as the field is extinguished† and after 2.5 s remains above the value recorded when the field is present. Thus a target that is clearly visible when the field is on becomes invisible when the field is turned off: in a very special sense, this result represents a failure of Weber's Law. We have found similar results using adaptation fields that gave retinal illuminances of $10^{2.0}$, $10^{3.5}$ and $10^{5.0}$ td. In the case of a $10^{5.0}$ td field the loss of sensitivity at $\Delta t = 0$ exceeded 3.0 log units and the threshold could not be measured; but it is in its duration that transient tritanopia most differs from the brief effects found for white light by Crawford (1947) and Baker *et al.* (1959). The measurements of Stiles (1949*a*) show a considerable loss of short-wavelength sensitivity at a delay of 2 s; and our informal observations suggest that transient tritanopia lasts for many seconds (see also the results given by Stiles in figure A 2 of the Appendix).

Figure 3 illustrates how the loss of sensitivity varies as a function of field intensity. Test (λ) and field (μ) wavelengths were 445 and 580 nm respectively. The open circles show the threshold on the steady field and thus constitute a conventional increment-threshold function. The solid points and the crosses correspond to the threshold 400 ms after the yellow field had been extinguished. Two sets of the latter measurements (made on separate days) are shown in order to illustrate variability. A delay of 400 ms was chosen because at this interval the effects

† There is probably in fact a loss of sensitivity immediately before the offset of the field (cf. figure 13): such effects are well known (Crawford 1947; Baker *et al.* 1959) and are not of primary interest here.

found for white light by Baker *et al.* (1959) are over (cf. also experiment 4 below), but transient tritanopia is still marked.

It is evident from figure 3 that the paradoxical rise in threshold occurs even at relatively low adapting illuminances (*ca.* $10^{1.3}$ td; $10^{-4.0}$ erg s^{-1} deg^{-1}) that in the steady state do not significantly alter the sensitivity of the blue-sensitive mechanism. (At a field intensity of approximately $10^{1.8}$ td ($10^{-3.5}$ erg s^{-1} deg^{-2}) the increment-threshold function shows a shallow inflexion, which corresponds to the transition between Stiles's π_2 and π_1. If Stiles's analysis is appropriate here,

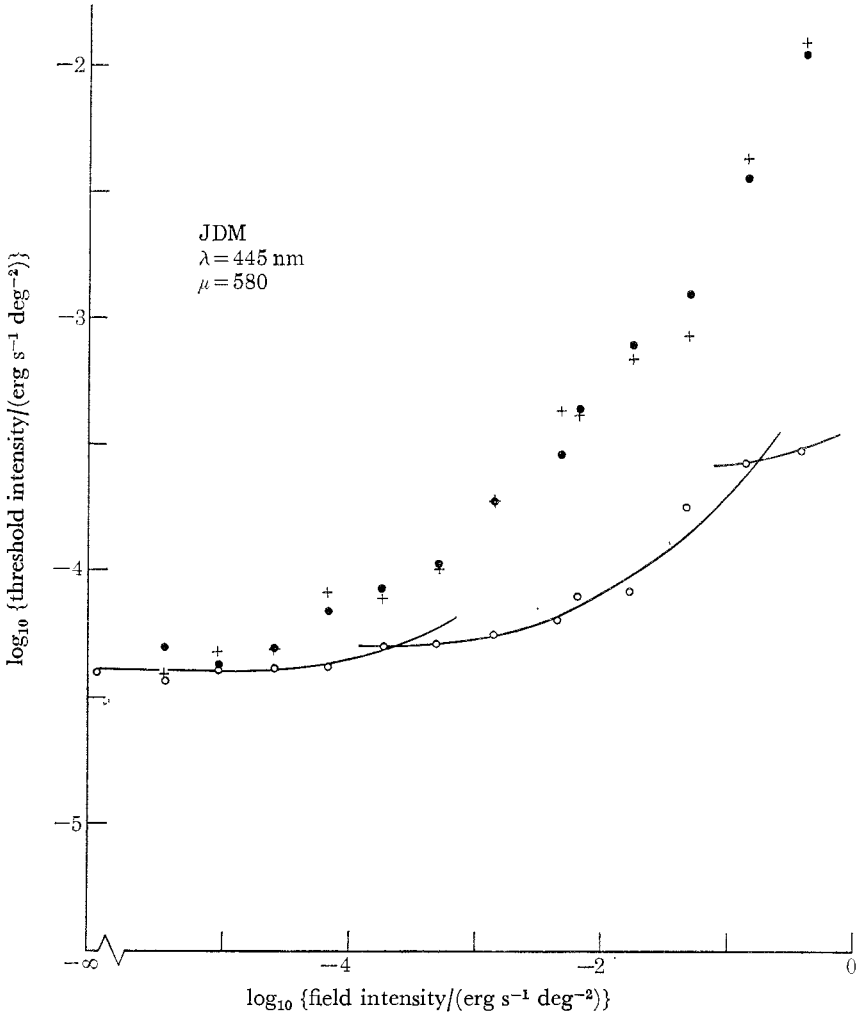


FIGURE 3. •, +, log threshold intensity 400 ms after the offset of adapting fields of varying intensity. o, incremental thresholds when a steady field is present. The solid lines fitted to the increment thresholds are Stiles's function $\zeta(x)$ (Wyszecki & Stiles 1967): this function is properly valid only for 200 ms flashes and no great weight should be placed on the curves fitted here. In Stiles's analysis, the three branches correspond to, from left to right, π_2, π_1 and π_3.

then the mechanism π_1, as well as π_2, is subject to transient suppression at field intensities that do not change its sensitivity in the steady state.) The loss of sensitivity increases as the field becomes more intense.

However, the solid points of figures 2 and 3 may not necessarily represent thresholds for the blue-sensitive cones and thus may not reveal the true magnitude of the suppression of the blue

mechanism: the 'thresholds' for the blue mechanism may lie above the measured thresholds, detection being mediated by another mechanism that is normally less sensitive to 445 nm radiation. (Evidence that this is so is provided by experiments 2*a* and 5*a*). Since the results seen in figure 2 may therefore reflect the changing sensitivities of two or more mechanisms, lines have not been drawn through the data points. Similarly the solid points of figure 3 can be taken only as a lower bound to the true function relating field intensity to the loss of sensitivity of the blue mechanisms.

There seems no doubt that transient tritanopia does occur. We have described elsewhere (Mollon & Polden 1976*a*) stimulus conditions that allow a convenient demonstration of the threshold elevation. What is probably a supra-threshold counterpart of the threshold elevation can be readily seen by gazing at a yellow field of moderate brightness ($\sim$ 700 cd/m^2) and then examining a blue patch: the latter will appear a rich peacock or bottle green colour (Mollon & Polden 1975).

The following experiments were designed to investigate a number of properties of transient tritanopia. (Preliminary accounts of experiments 2 and 8 have been published (Mollon & Polden 1976*b*, 1975).) As a working hypothesis it is supposed that during changes in light or dark adaptation the signals from the blue receptors are attenuated or masked by signals from a mechanism with a different spectral sensitivity. The latter might be one or both of the long-wavelength mechanisms; it might just conceivably be the rods or a mechanism with an unknown spectral sensitivity.

Experiment 2: extension to fields of high intensity

The supra-threshold hue shift mentioned in the last section does not occur if the adapting field is too bright. All those authors mentioned in the Introduction who did not observe transient tritanopia used adapting illuminances significantly greater than the $10^{4.3}$ td used by Stiles. Measurements have therefore been extended to include adapting illuminances up to approximately $10^{6.0}$ td. In order to secure more intense fields, the interference filter used in experiment 1 was removed from the adapting beam, but a yellow gelatin filter (Ilford no. 626) was retained. (Prolonged observation of fields of between $10^{5.0}$ and $10^{6.0}$ td (for example, in making the measurements of figure 5*b*) left us with after-images that lasted as long as 7 days. Stiles (personal communication) tells us that he noticed these slowly cumulative after-images when working with similar conditions. The after-image reported by Brindley (1953) 8 months after repeated exposure to high intensities in fact persisted for 10 years (personal communication), although it did not impair acuity and did not prove to be permanent. We can ourselves detect no permanent damage, but caution is probably required in measurements of this kind: only one eye, perhaps the non-preferred eye, should be used and the possible dangers should be explained to all subjects.)

Measurements are shown in figure 4 for four observers. Observer JK is Dr J. Krauskopf, who kindly served as a guest observer for this experiment: extensive data on the right eye of this observer are available in the literature. As before, the open circles represent the conventional increment-threshold (t.v.i.) function. The inter-subject variability in these functions is comparable to that found by Stiles (1946). All four observers show an inflexion in the t.v.i. curve between $10^{4.0}$ and $10^{5.0}$ td; the upper branch corresponds to Stiles's π_3. The solid points represent the threshold 400 ms after the field has been extinguished. For adapting fields of less than $10^{5.0}$ td the results resemble those of figure 3 but as the field becomes still brighter the function for Δt = 400 ms in each case shows a sharp cusp and the threshold falls precipitously.

The slope of this part of the function is steeper than -2. When the adapting field approaches $10^{6.0}$ td (results for JDM and JK) the threshold 400 ms after extinction of the field lies below its value when the field is present: transient tritanopia is absent. Measurement for JDM using a Wratten 23A (orange) filter in the adapting beam gave similar results, although the negative slope to the right of the cusp was not so steep.

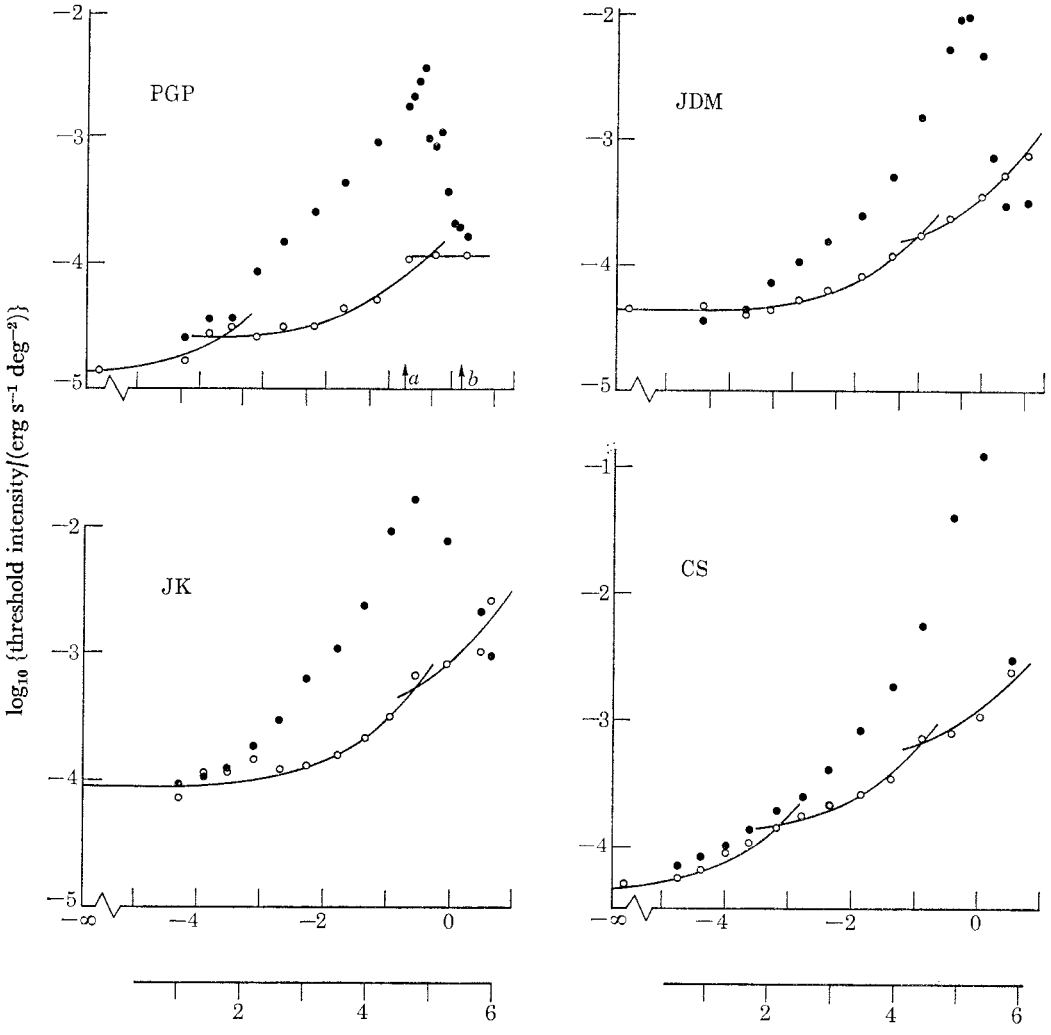


FIGURE 4. ○, log threshold intensity for detecting a blue (445 nm) flash when a steady yellow field (575 nm) is present. ●, threshold 400 ms after the adapting field has been turned off. For PGP, JDM and CS each point represents the mean of two runs; the data for JK are for single runs. The solid lines fitted to the open circles are Stiles's function $\zeta(x)$ (Wyszecki & Stiles 1967). The field intensities marked (*a*) and (*b*) on the plot for PGP correspond to the adaptation levels that gave the results of figures 5*a* and 5*b* respectively.

Although the sudden collapse of transient tritanopia is as mysterious as the phenomenon itself, there now seems to be no necessary contradiction between the results of Stiles and those of authors who used adapting fields of $10^{6.0}$ and $10^{7.0}$ td. Another critical variable may be the length of the adaptation period: as the latter is increased we have noticed that the threshold at $\Delta t = 400$ ms first rises and then falls, before becoming stable after 6 min (the adaptation period used for the present measurements).

Phenomenological observations

Observers noticed striking changes in the appearance of the test flash as the adapting level was increased. Detailed records were kept for JDM, who reported as follows. In the adapting range $10^{1.1}$–$10^{5.0}$ td, test flashes at $\Delta t = 400$ ms usually appeared achromatic at threshold and had a temporally sharp quality; but above $10^{5.0}$ td they appeared blue and were spatially and temporally diffuse in the way characteristic of flashes seen only with the blue mechanism – a 'blue gloom without definite shape', in the happy phrase of De Vries (1946*a*). Above threshold, after adaptation to fields of between $10^{1.1}$ and $10^{2.5}$ td the test flashes appeared blue, between $10^{3.0}$ and $10^{5.0}$ log td they appeared peacock or green above threshold, and between $10^{5.0}$ and $10^{6.0}$ td they again appeared blue. The after-image of the yellow field at $\Delta t = 400$ ms was black at the lowest adapting illuminances, a rose or ruby colour at intermediate levels, and a desaturated, luminous blue or turquoise at the highest levels.

Experiment 2a: spectral sensitivities

The variation of the phenomenal appearance of the test flash suggests that the same mechanism might not be responsible for detection to the left and right of the cusp in figure 4. We have therefore made formal measurements of spectral sensitivity at adapting illuminances of $10^{4.58}$ td and $10^{5.47}$ td, the levels marked *a* and *b* on PGP's results in figure 4. Measurements were made 400 ms after offset of the field and the procedure was as before except that the field illuminance was held constant and test wavelength (λ) was varied in successive blocks.

Results are shown in figures 5*a* and 5*b*. The mechanism mediating detection of the flashes 400 ms after extinction of a field of $10^{4.58}$ td (figure 5*a*) appears to have the spectral sensitivity not of the blue mechanism but rather of π_4, Stiles's green-sensitive mechanism (see also Appendix). Thus the theoretical thresholds for the blue mechanism probably lie above the empirical points in this range of adapting illuminances. However, when the adapting field is increased to give a retinal illuminance of $10^{5.47}$ td (figure 5*b*), the eye has become blue-sensitive rather than blue-blind and for $\lambda < 500$ nm the mechanism active at threshold resembles one of Stiles's blue mechanisms, π_1 or π_3.

We add to our working hypothesis the supposition that transient tritanopia is abolished at the intensity of the adapting field at which the as yet unidentified inhibitor becomes too bleached, or otherwise too refractory, to exercise its inhibitory effect on the blue mechanism.

Experiment 3: $\lambda = 475$ nm

An instructive condition is that where the test flashes are of a rather longer wavelength than 445 nm. Figure 6 shows results for the case where $\lambda = 475$ nm and the field is yellow (Ilford gelatin filter no. 626). Each point represents the mean from two runs. The conventional increment-threshold function (open circles) shows at least two branches, as was classically found for similar conditions by Stiles (1953, Figure 7): the lower branch is probably Stiles's green mechanism, π_4, and the second branch, π_1. The solid points, which represent the threshold 400 ms after extinction of the field, initially lie below the increment threshold function, as would be expected if (*a*) the test flashes were detected by π_4, and (*b*) the latter mechanism recovered normally when the adapting field was removed. With increasing brightness of the field the increment-threshold function shows one, possibly two, inflexions, but the solid points form a smooth curve passing upwards through the increment threshold points. We may suppose

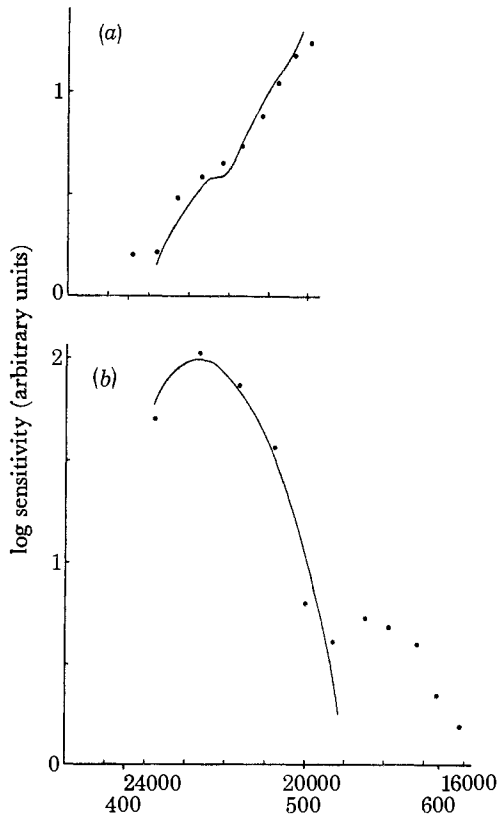


FIGURE 5. The spectral sensitivity of the eye 400 ms after the offset of a yellow field of either $10^{4.58}$ (*a*) or $10^{5.47}$ (*b*) td. The solid function fitted to (*a*) is Stiles's function for $\pi_{4\mu}$ displaced vertically to give the best fit to the experimental points; the solid function fitted to the short-wavelength points of (*b*) is Stiles's $\pi_{1\mu}$. Observer: PGP.

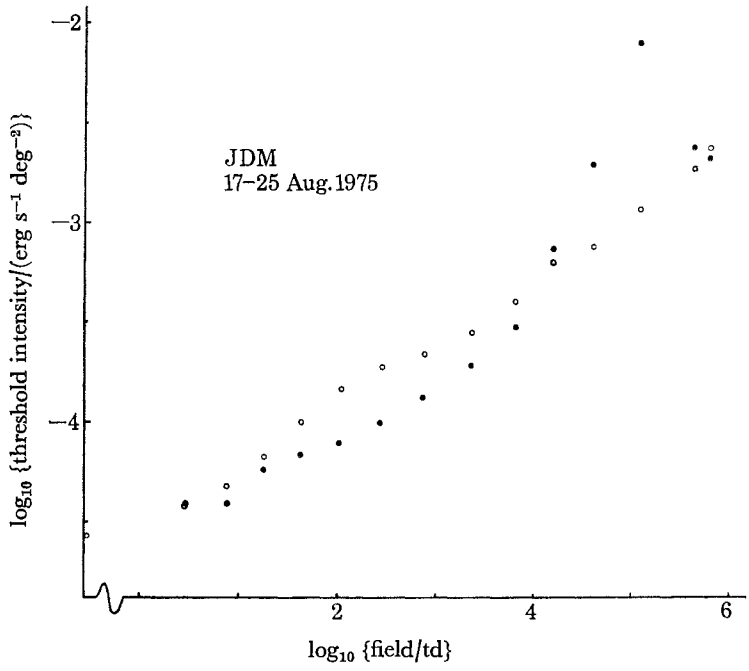


FIGURE 6. ○, log increment thresholds for blue-green (475 nm) test flashes presented on a steady yellow field (Ilford spectral filter no. 626). ●, log threshold 400 ms after offset of the field.

that although the blue cones have taken over detection in the steady state, it is π_4 that continues to mediate detection of the flashes at $\Delta t = 400$ ms. At about $10^{5.0}$ td there is a cusp as before and the threshold falls. As before, the observer reported that the cusp was associated with a change in the phenomenal appearance of the test flash from an achromatic or green 'blip' to a spatially and temporally diffuse blue blur.

The results of experiment 3 suggest why transient tritanopia does not appear in the results of Rinalducci (1967, 1968). Rinalducci's adapting fields were between $10^{1.0}$ and $10^{2.41}$ td, but his blue targets were produced by a broad-band Wratten 47B gelatin filter and would probably have been more nearly equivalent in their visual effects to the 475 nm target used in our experiment 3 than to the 445 nm target used in experiments 1 and 2. This is all the more likely to be true of the smaller of his two test stimuli, owing to the relative insensitivity of π_1 to small fields (Brindley 1954). Moreover, since his results for blue targets after adaptation to red fields probably reflect two mechanisms, π_1 and π_4 (according to the field size and to Δt), there are no grounds for Rinalducci's conclusion that the equivalent-background principle (Stiles & Crawford 1932) fails for these conditions: the principle could be expected to hold only within a particular π mechanism.

Experiment 4: transient protanopia? transient deuteranopia?

Experiments 2*a* and 3 suggest that it is only, or is disproportionately, the blue receptors that are suppressed in early dark adaptation. However, before seeking to explain transient tritanopia in terms of a property peculiar to the blue mechanism, we should more systematically check that it is not merely an instance of a more general phenomenon that might, for example, always occur when adapting field and test stimulus are approximately complementary in colour. Four other heterochromatic conditions have therefore been sampled: (*a*) yellow targets after adaptation to a blue field (the mirror-image condition to that of experiment 1); (*b*) red targets after adaptation to yellow; (*c*) green targets after adaptation to a complementary red; and (*d*) red targets after adaptation to green.

For condition (*a*) the Ilford 626 yellow filter previously used in the adapting beam was placed in the test beam; and the variable interference filter of the adaptation beam, in combination with a Wratten 47B blocking filter, was set to give a wavelength of 445 nm. In condition (*b*) the wavelength of the test flash was 670 nm and the adapting field was provided as in experiments 2 and 3 by the Ilford 626 yellow filter. The red and green stimuli of conditions (*c*) and (*d*) were 670 nm and 492 nm respectively and were produced by appropriate combinations of interference and blocking filters; these wavelengths are complementaries with respect to CIE source C (Wyszecki & Stiles 1967, Table 3.30). Other experimental arrangements were as for experiment 1.

Results (means of two runs in each case) are shown in figure 7. In no case except (*d*) do the solid points, representing thresholds at $\Delta t = 400$ ms, lie above the open circles, which represent conventional increment thresholds: there is no clear evidence of effects comparable to transient tritanopia.

However, a small threshold elevation is found in condition (*d*) when red targets are presented after adaptation to green fields of low intensity. This effect, though small, was also found for PGP (results not shown) and to confirm its existence an ancillary experiment was performed at an adapting illuminance of $10^{-0.51}$ td ($10^{-5.21}$ erg s^{-1} deg^{-2}). The observer was JDM. The threshold on the field and the threshold at $\Delta t = 400$ ms were each measured five times in

an alternating sequence. The mean threshold at Δt = 400 ms was 0.09 $\log_{10}$ units higher than the mean increment threshold and this difference was significant (Mann–Whitney $U = 0$, $p = 0.004$). It may be noteworthy that under the conditions of this experiment the liminal increment was seen as a change of hue and the interruption of the field left a dark red after-image of a very similar colour to the target. 'Transient protanopia' is a minor effect in com-

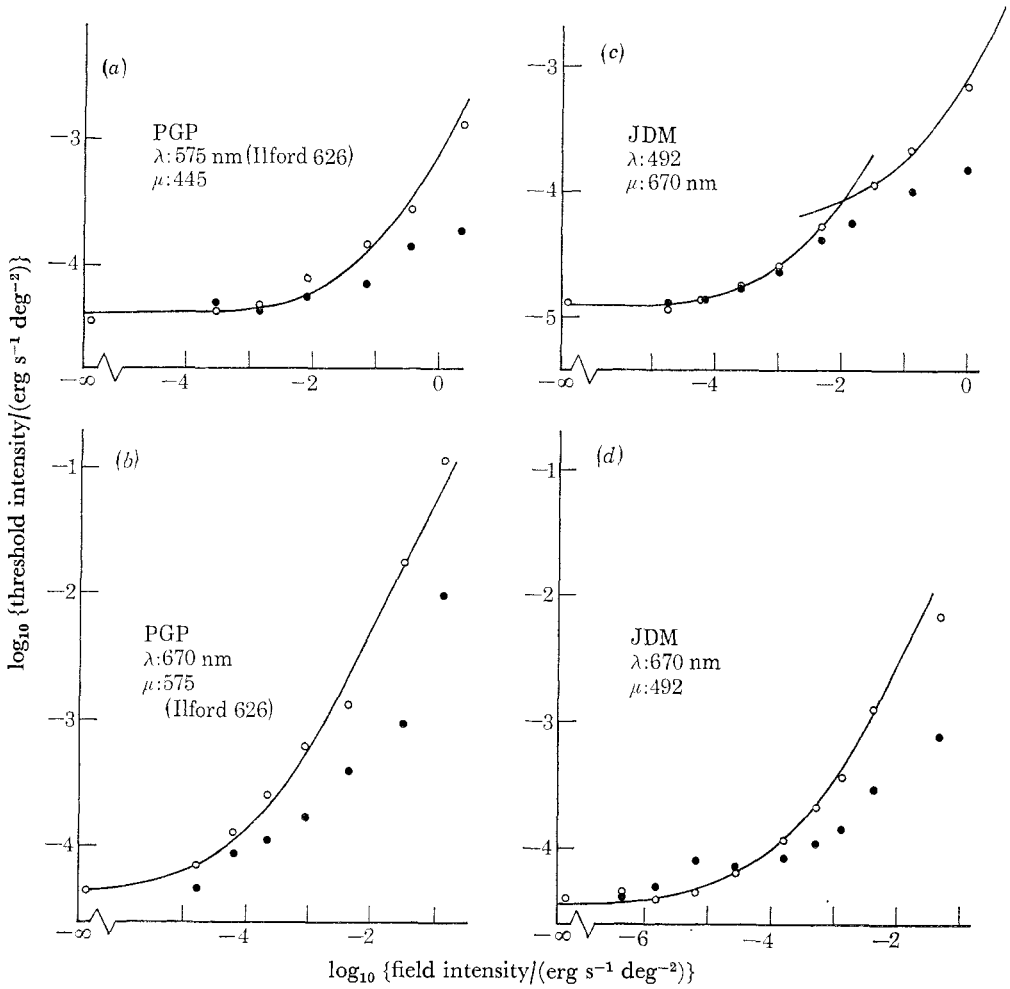


FIGURE 7. Increment thresholds (○) and thresholds at Δt = 400 ms (●) for different combinations of λ and μ. The solid lines fitted to the increment thresholds are in each case Stiles's $\zeta(x)$ function (Wyszecki & Stiles 1967): no theoretical weight is placed on these curves since they are properly valid only for a 200 ms flash.

parison with transient tritanopia and we do not pursue it here experimentally, but it may be significant and we shall return to it in the Discussion.

There is another aspect of figure 7 that we do not fully understand. In panel (*c*) the function for Δt = 400 ms shows a clear (and reliable) inflexion that resembles the inflexion in the increment threshold function. Following Stiles (1939), we might take the upper branch of the increment threshold function (open circles) to correspond to a blue-sensitive mechanism; but at Δt = 400 ms we might expect the blue mechanism to be inoperative, so that the solid points would correspond to π_4 at all field intensities. Thus we might expect the function for

Δt = 400 ms to be uninflected and to resemble that of figure 6, possibly passing above the open circles at high intensities. This condition would probably repay further investigation.

Experiment 5: partial decrements

In a sense, the transient tritanopia seen after a yellow field is extinguished is too large an effect: the suppression of the blue mechanism is so considerable that its true extent is concealed from us by the intervention of the normally less sensitive green mechanism (experiment 2*a*). In order to reduce the phenomenon to tamer proportions, but also because it is of both theoretical and practical importance to know how small a change in a long-wavelength field will disturb the sensitivity of the blue mechanism, we have studied the effect of introducing a 3 s attenuation of the field where previously the field had been extinguished. Where the attenuation is small the remaining field may be thought of as an auxiliary field (Stiles 1953), which serves to maintain the light adaptation of the long-wavelength mechanisms.

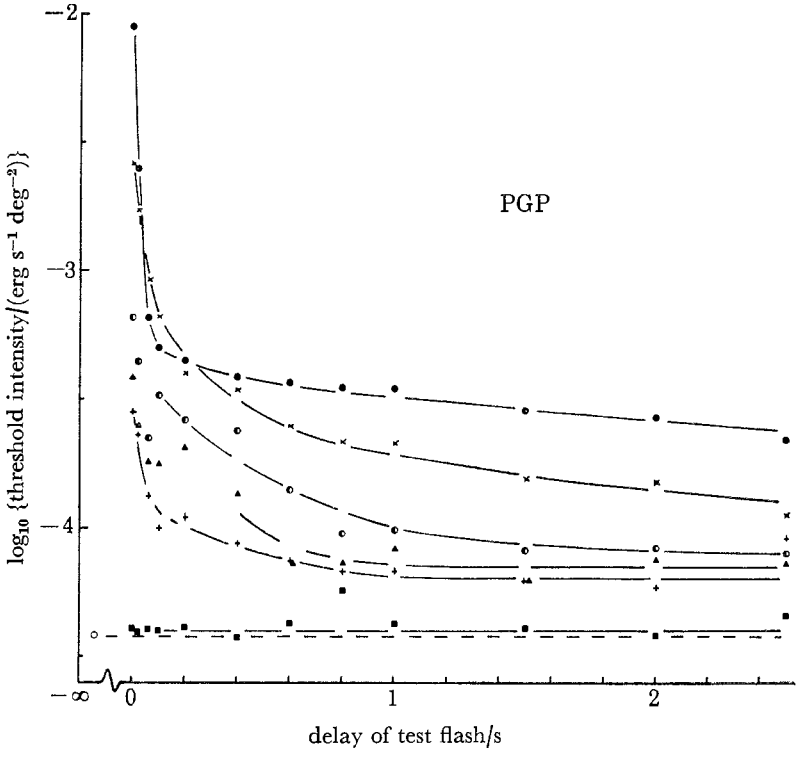


FIGURE 8. Variation of the threshold for a 445 nm test flash in the 2.5 s following partial attenuations of a yellow field that produces a retinal illuminance of $10^{3.5}$ td. ●, complete offset; ×, 1.12 log units attenuation; ◐, 0.80 log units attenuation; ▲, 0.61 log units attenuation; +, 0.49 log units attenuation; ■, 0.12 log units attenuation. The increment threshold when the steady field is present is shown by the single open circle to the bottom left.

Slivers of gelatin neutral-density filter were mounted on the vane of the pen motor in the adapting beam and the vane was adjusted so that now it attenuated the beam rather than interrupting it as previously. The densities used, measured *in situ*, were as follows: 0.12, 0.49, 0.61, 0.80, 1.12, in addition to complete extinction. A single experimental session, lasting several hours, was devoted to a single decrement. The entire experiment occupied a period of six

weeks, two experimental sessions being devoted to each decrement. The order of conditions was randomized.

Figure 8 shows the variation of the threshold for a 445-nm target in the 2.5 s following partial attenuations of a yellow field. The retinal illuminance before attenuation was always $10^{3.5}$ td (observer: PGP). Figures 9 and 10 show how the threshold at $\Delta t = 400$ ms varies as a function of the brightness of the adapting field (observers: JDM, CS). (The solid lines in figures 8–10 have no theoretical significance and are intended only to guide the reader's eye. The results for

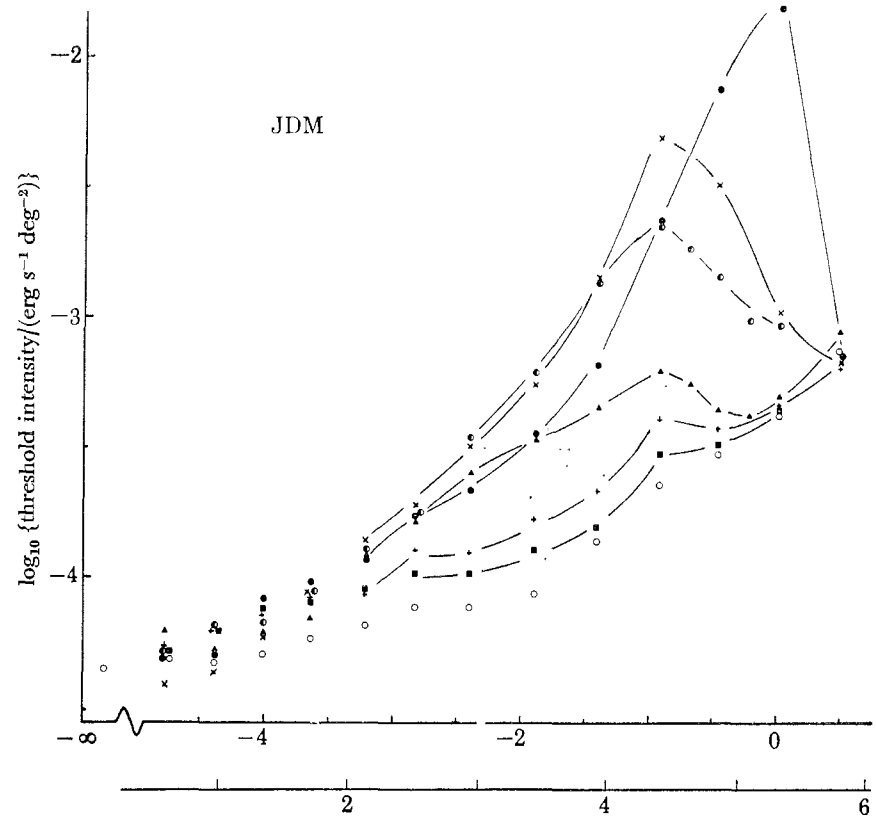


FIGURE 9. Threshold for a 445 nm test flash 400 ms after attenuation of a yellow field as a function of the intensity of the field. ●, complete offset; ×, 1.12 log units attenuation; ◦, 0.80 log units attenuation; ▲, 0.61 log units attenuation; +, 0.49 log units attenuation. ■, 0.12 log units attenuation. ○, the threshold on the steady field. The solid lines are added to guide the reader's eye and are not intended to have theoretical significance. Observer: JDM.

attenuations of 0.61 and 0.80 were very variable and it is not possible to say whether the oscillations visible in the results between $\Delta t = 0$ and $\Delta t = 600$ ms (figure 8) are reliable.) As before, the conventional increment thresholds are shown as open circles. It is clear that for all three observers a considerable loss of sensitivity is produced by an attenuation of only 0.49 log units. The loss of sensitivity increases rapidly as the attenuation is increased from 0.49 to 0.80; and for JDM and CS, at intermediate adapting illuminances, attenuations of 0.80 and 1.12 produce a greater loss of sensitivity than does complete extinction of the field. For these observers, the greatest loss of sensitivity of all, at intermediate adaptation levels, is produced by the 0.80 decrement.

The functions of figures 9 and 10 are complex and yet have a systematic structure that is

qualitatively similar for the two observers. To explain why (for JDM and CS) the functions for 0.80 and 1.12 decrements lie above the function for complete offset at intermediate adapting illuminances, we may suppose that the attenuated yellow field maintains the light adaptation of π_4 and that the measured thresholds are either those of π_4 or those of a now disclosed blue

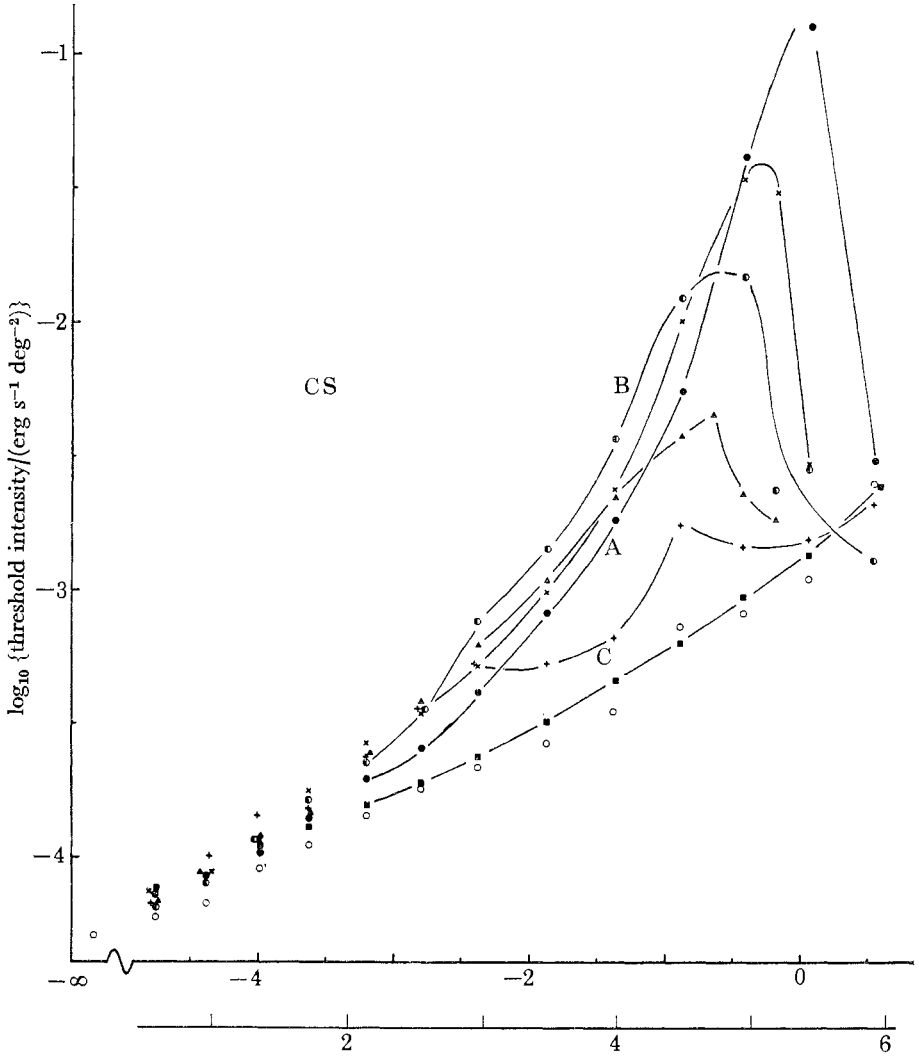


FIGURE 10. As for figure 9, but for observer CS. The letters A, B and C correspond to the conditions under which test sensitivities were measured in experiment 5*a* (see figure 11).

mechanism. Where, after smaller decrements of the field, the empirical thresholds lie below those for complete offset, we suppose that detection is mediated by the blue receptors. (These interpretations are tested in experiment 5*a*.)

All the functions show a peak at an adapting level between $10^{4.0}$ and $10^{5.0}$ td. The peak shifts to the left as the attenuation is reduced. This latter result seems to weaken the supposition that transient tritanopia is abolished at a fixed level of bleaching of a long-wavelength mechanism. However, it is probably necessary to reserve judgement on this question, for the position of the empirical peak depends on the relative sensitivities of the green and blue mechanisms. For

the smaller decrements the peaks all coincide roughly with an inflexion in the increment threshold function, an inflexion that corresponds to the transition from 'π_1' to 'π_3'.

Phenomenological observations

JDM recorded the following. At field illuminances of about $10^{1.0}$ td, attenuations of only 0.49 or 0.61 produced a dark after-image, even though a yellow field remained present. Around $10^{2.5}$ td the after-image was purple and at slightly higher intensities it assumed first a pale rose and then a salmon pink colour. At the highest intensity used, a central blue blotch was present at Δt = 400 ms. For this observer, the test flash always appeared blue at threshold, except after complete offset.

Experiment 5a: test sensitivities

To check our interpretation of the effects of partial attenuations of a moderately bright, yellow field, we have sampled spectral sensitivity to the test flash at the points marked A, B and C in figure 10. The procedure was as for experiment 2*a* and the observer was CS. A corresponds to complete extinction of the field, B to 0.80 log units of attenuation and C to 0.49 log units of attenuation. The unattenuated field produced a retinal illuminance of $10^{3.92}$ td.

Results are shown in figure 11. After 0.49 log units attenuation (C) the spectral sensitivity

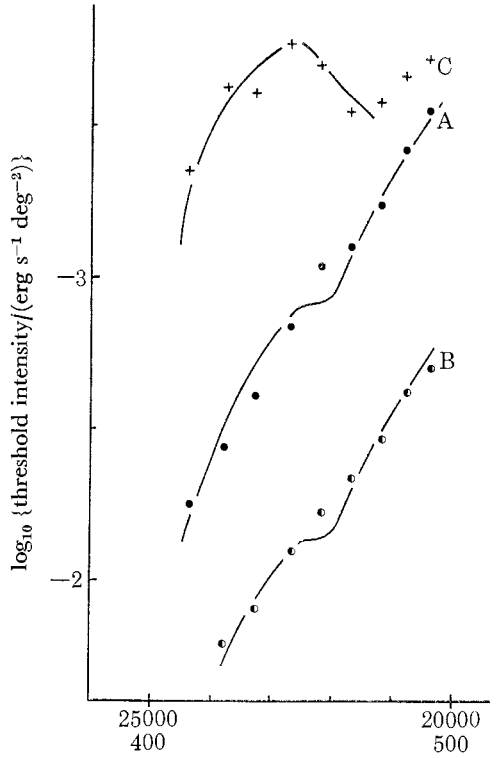


FIGURE 11. Spectral sensitivities for the test flash after attenuation of a yellow field that produces a retinal illuminance of $10^{3.92}$ td. A, after complete extinction of the field. B, after 0.80 log units attenuation. C, after 0.49 log units of attenuation. Curve A is correctly placed in its absolute position. Curve C has been moved arbitrarily upwards by 0.5 log units and curve B has been moved downwards by 0.5 log units. The solid line fitted to C is Stiles's $\pi_{1\mu}$ function; that fitted to A and B is his $\pi_{4\mu}$ function.

below 470 nm is approximately that of π_1, Stiles's blue mechanism. Spectral sensitivity after complete offset (A) or after 0.80 log units of attenuation (B) is very different and resembles that of π_4, Stiles's green mechanism, which is represented by the solid line.† We conclude that for CS the mechanism most sensitive to blue flashes after offset, or after 0.80 log units attenuation, of a moderately bright yellow field is the green-sensitive mechanism.

The fact that small changes in the brightness of a long-wavelength field can produce transient tritanopia reveals a danger in the method of measuring field sensitivity that was introduced by De Vries (1946*b*)but was consistently eschewed by Stiles. In De Vries's method, which recommends itself by its speed, the test flash is set at a fixed intensity relative to its absolute threshold and the intensity of the background is adjusted to bring the test flash to threshold. The method has been recently adopted by Bender & Ruddock (1974) and by Estévez *et al.* (1975). It is clear that this procedure should be used only with the greatest caution in measuring the field sensitivity of the blue mechanism, since transient tritanopia will be introduced by small changes in the field as the observer makes his adjustments or, in particular, as an automated titration is pursued. The distortion will not merely be of absolute sensitivity, for the relative loss of sensitivity will vary with field wavelength.

Experiment 6: parafoveal measurements

Does transient tritanopia depend on retinal position, in the way that Rushton (1968) found that interaction between cones and rods could be revealed in only one well-chosen region? Figure 12 shows measurements of transient tritanopia made in the nasal parafovea. The central foveal measurement was made as before with the diamond array of fixation lights. For eccentric measurements a single fixation light was mounted on a lateral slide in the collimated section of channel 3. As the eccentricity of the target was increased, the observer's mouth-bite was advanced laterally to ensure that the beam continued to pass through the centre of his pupil. The size of the test spot was reduced to 45 min. The yellow adapting field (Ilford 626) produced a

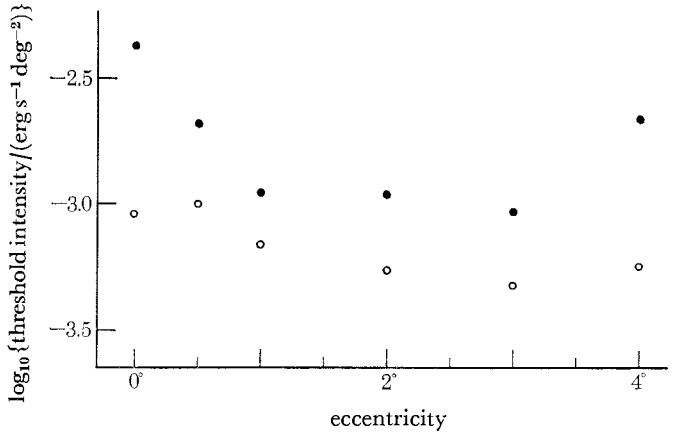


FIGURE 12. Transient tritanopia as a function of retinal eccentricity. ○, incremental threshold for 445 nm target on steady yellow field. ●, threshold 400 ms after 0.485 log units attenuation of field. Observer: JDM.

† The bandwidths of our interference filter at short wavelengths are not negligible (see Methods). The data points of figure 11 are plotted against wavelength of peak transmission. This procedure becomes misleading where the sensitivity of a mechanism is falling very rapidly or where the pass band of the filter is skewed. If we assume that the mechanism active at threshold has the sensitivity of π_4 and if we convolute the falling sensitivity of π_4 with the pass band of our filter, effective wavelengths are increased at short wavelengths (by 9 nm at 400 nm; 4 nm at 410 nm; 2 nm at $\lambda > 420$ nm). These corrections do not affect the main conclusion.

retinal illuminance of $10^{4.41}$ td. In view of the results of experiment 5, a decrement of only 0.485 log units was used, in order to maintain the light adaptation of π_4, π_5 and π_0 and so allow the true variation of transient tritanopia to appear.

Transient tritanopia is clearly present in the parafovea, although it appears to be less marked at small eccentricities than it is at the foveal centre. As is usually found, the incremental thresholds for the blue mechanism are higher in the fovea than in the immediate parafovea.

The Maxwellian-view system was not designed for studying peripheral vision and its geometry prevented systematic measurements at eccentricities greater than 4°. However, limited measurements were made at an eccentricity of 22.5° in the temporal retina by viewing a small fixation light through an ancillary lens placed to the observer's right. These measurements were difficult, owing to the Troxler effect, and the variability was higher than for central vision; but clear evidence was found that 400 ms after a 0.485 log unit decrement of a yellow field the threshold had risen by more than 1.0 log units. JDM reported that the flashes appeared blue when the field was steady but were seen as white 'blips' at $\Delta t = 400$ ms.

Both PGP and JDM reported a spatial illusion when making these measurements: although the test flash was always centred in a 6.5° field, it often appeared close to the more peripheral edge of this field. The illusion persisted when the target was of the same spectral composition as was the field, an observation that suggests that the phenomenon is not a consequence of chromatic aberration.

Experiment 7: haploscopic presentation

We have made a limited number of measurements under conditions where the test flash and adapting field were presented to opposite eyes. By the addition of a third pellicle and pairs of polarizers, the apparatus was modified so that the test flash was delivered to the left eye and the primary adapting field to the right. The primary adapting field was interrupted for 3 s every 18 s as in earlier experiments. In some conditions a steady auxiliary field, drawn from channel 3, was present in the left eye. It was congruent with the primary adapting field and was of the same spectral composition (Ilford 626). The diamond-shaped array of fixation lights was visible to both eyes. A Risley prism, placed before the right artificial pupil, was used to assist fusion. The observer was JDM.

TABLE 1. CONDITIONS AND RESULTS FOR EXPERIMENT 7
(HAPLOSCOPIC PRESENTATION)

($\log_{10}$ {adapting field (right eye)/td}	($\log_{10}$ auxiliary field (left eye)/td}	Δt/ms	change in sensitivity ($\log_{10}$ units)
4.5	2.7	400	−0.08
4.5	1.7	400	−0.04
3.5	1.7	400	−0.11
3.5	1.7	2000	−0.08
2.5	0.7	400	−0.03
2.0	1.6	400	+0.04
4.4	—	2000	0.00
3.5	—	2000	+0.15

Clearly a great number of combinations of adapting and auxiliary fields might be examined. The conditions we have sampled are summarized in table 1. Other of our measurements suggest that the $10^{2.7}$ and $10^{1.7}$ td auxiliary fields would ensure that detection of the 445 nm test flash

was by the blue mechanism and that the difference in the sensitivities of blue and green cones was great enough for a transient tritanopia to reveal itself (cf. figure 6 above). Measurements were, however, made for the conditions where the left eye was dark-adapted and the auxiliary field was absent. The reason for including these conditions was that the auxiliary field might just conceivably prevent transient tritanopia by, say, rivalrously masking a contralateral after-image (cf. Makous, Teller & Boothe 1976). Unfortunately, when no auxiliary field is present, the test sensitivities of the foveal blue and green mechanisms are very close at short wavelengths and therefore, for these conditions, λ was reduced to 420 nm and the duration of the test flash was increased to 100 ms, in order to favour the blue mechanisms and increase slightly the margin within which transient tritanopia might reveal itself.

The last column of the table shows the difference between log sensitivity (reciprocal threshold) measured in the steady state and that measured at Δt. A negative value indicates a loss of sensitivity at Δt. Most values are the means of two estimates. It can be seen that the changes are very small and probably within experimental error, even though the adapting illuminances would produce a large loss of sensitivity under monocular conditions. In the case where the auxiliary field was absent and $\Delta t = 2$ s no loss of sensitivity was measured. Thus the conditions examined here provide little evidence for a dichoptic version of transient tritanopia.

We have not observed supra-threshold blue targets to look green after contralateral adaptation to a yellow field, even though we have examined a wide range of test and adapting intensities that yield the monocular after-effect.

Experiment 8: *silent substitution*

To determine whether the sensitivity of the blue cone mechanism is controlled only by light absorbed by the blue pigment, an experiment was performed in which the yellow field was turned off as before but was immediately replaced by a dimmer green field that had the same adaptive effect on π_1 in the steady state. The threshold for 445 nm targets was measured at varying delays after the transition between 580 nm and 525 nm fields.

Underlying this experiment is the principle that Rushton (1972) has called the principle of univariance. A single retinal cone, or single class of cones, is colour blind. The input to a particular cone can vary in both wavelength and intensity, but once a quantum has been absorbed all information about its wavelength is lost. Thus, in theory, it is possible to adjust the intensities of two lights of different wavelengths until they are indistinguishable to the blue receptors, although they will remain distinguishable to other classes of receptor and thus will appear of different colours to the observer. If the adaptive state of π_1 is independent of that of the other π mechanisms, then two adapting fields that equally reduce the sensitivity of π_1 must be producing equal quantum catches in the blue cones. And if the sensitivity of π_1 remains independent when that of other mechanisms is changing, then there should be no disturbance of the 445 nm threshold when the transition is made between the two adapting fields.

The threshold for 445 nm flashes was measured on a steady yellow field of $10^{3.94}$ td ($10^{-1.36}$ erg s^{-1} deg^{-2}) and a steady green field was then adjusted (between blocks of trials) until it raised the threshold for the 445 nm flash to the same level. The two mean thresholds were within 0.01 log units for JDM and within 0.05 log units for PGP. These incremental thresholds were approximately 0.5 log units above the absolute threshold for the targets and ancillary experiments show that in each case detection was by π_1. Figure 13 shows that transient tritanopia still occurs when the transition is made between two fields that have the same adaptive effect

in the steady state. (Indeed, for both observers, the loss of sensitivity is greater than that found after simple offset of a yellow field of the intensity used here, probably because the green field sustains the light adaptation of π_4.)

We are led to conclude that the sensitivity of π_1 is controlled not only by quanta absorbed by the blue pigment itself but also by signals from a mechanism with a different spectral sensitivity.

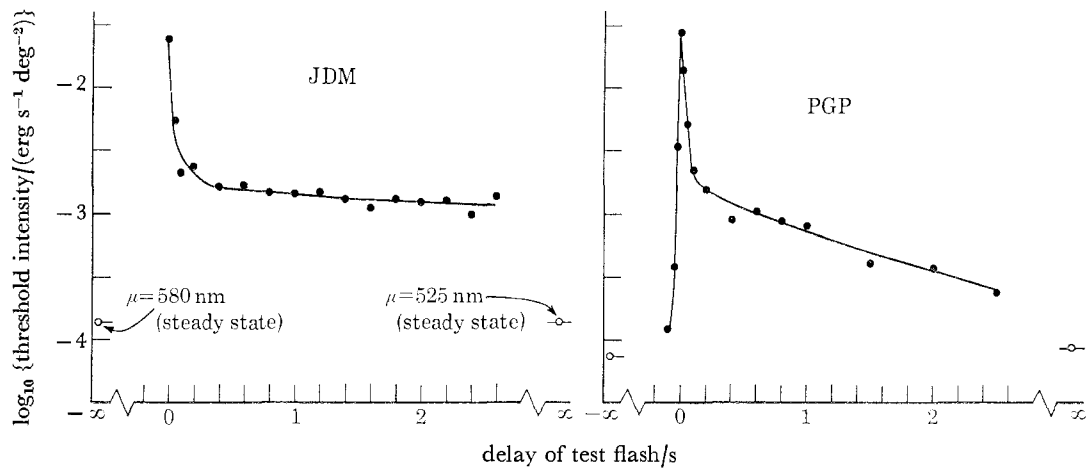


FIGURE 13. •, threshold for 445 nm target following transition between 580 and 525 nm fields that produce the same threshold elevation in the steady state. ○, the two steady-state thresholds. For PGP thresholds are shown for negative delays, i.e. for times just before the transition between fields.

One way of considering the present experiment is as a temporal analogue of the demonstration by Pugh (1976) that long- and short-wavelength fields are super-additive in their adaptive effects on π_1. The present experiment does not determine whether the interaction is confined to the steady state. A variation of the method used here could be employed to identify the spectral sensitivity of the inhibitor:† the principle would be to find pairs of fields that yielded no transient tritanopia when the transition was made between them. The difficulty would be to keep to a minimum the concomitant changes in absorption by the blue pigment; and, of course, there may be two or more inhibitors with different spectral sensitivities.

We do not wish to rule out entirely the possibility that the inhibitor acts from within the blue receptors. Although the principle of univariance may describe the output of receptors, we can identify a second assumption that deserves to be independently spelt out. This is the assumption that inputs that produce the same output from a receptor have indistinguishable effects at all preceding stages of visual excitation. A particular suggestion by King-Smith (1974) may be taken to illustrate just one way in which this assumption might fail. To explain MacLeod's paradox, King-Smith supposes that light passing through the centre of the pupil will produce a distribution of adaptation within the outer segment of a cone that is different from the distribution produced by light that passes through the periphery of the pupil and falls obliquely on the receptors. If we grant King-Smith's hypothesis, we might well expect the output of the individual receptor to show a transient as an axial beam is substituted for an oblique beam, even though the two beams produce identical outputs in the steady state. Now, it is not inconceivable that long and short wavelengths might produce different distributions of adaptation

† By using the term 'inhibitor' it is not intended to make any assumption about the nature of the interaction. See Discussion.

within the receptor or might in some other way (for example, by acting through different pigments or different states of a single pigment) contradict our second assumption. Silent substitution between long- and short-wavelength fields might then become impossible. The results of Pugh (1976) are also open to an account of this kind.

Experiment 9: dichromatic observers

If either the red cones alone or the green cones alone were the source of inhibition, we might possibly, though not necessarily, expect transient tritanopia to be absent in either protanopia or deuteranopia. A protanope and a deuteranope have been examined in order to determine whether the dichromat does offer a short cut to identifying the source of transient tritanopia.

Experiment 9a: protanope

The protanopic observer, PB, is emmetropic and aged 27. He was shown to be protan by the Farnsworth–Munsell 100-hue test and by the low intensity of the yellow (580 nm) that he matched to the red (652 nm) of a Nagel anomaloscope. He was accepted as a dichromat on the basis of the following criteria: (*a*) he accepted the normal match on the Nagel anomaloscope; (*b*) he accepted matches at all R–G ratios; and (*c*) he generated matches at all R–G ratios.

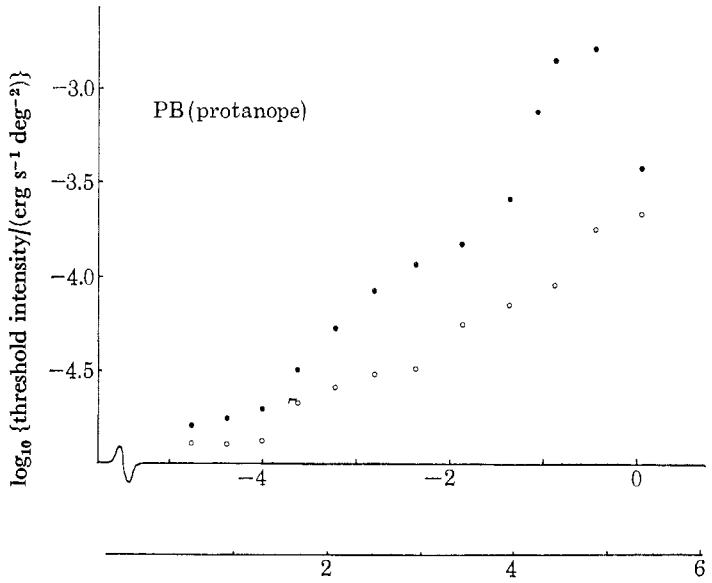
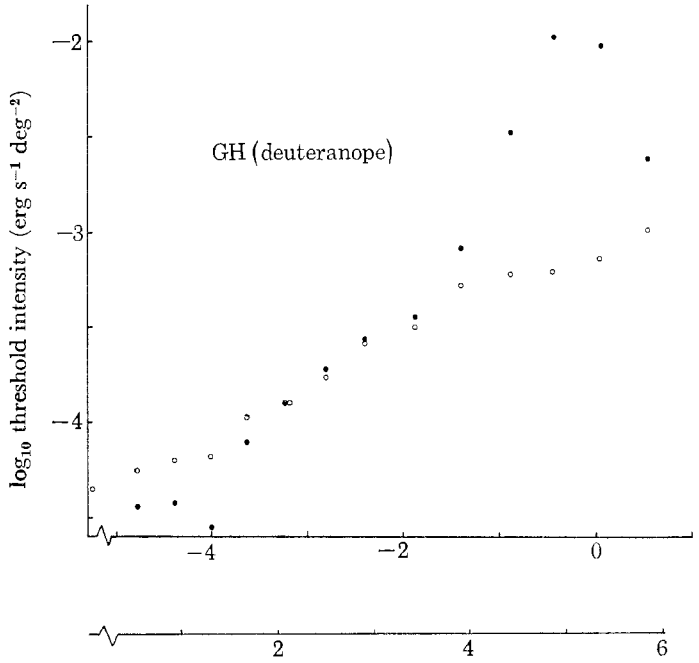


FIGURE 14. Results for protanope, PB. ○, threshold for 445 nm target when a steady yellow field is present. ●, threshold 400 ms after offset of field. (Cf. figure 4, which shows comparable results for normal observers.)

PB made a set of incremental threshold observations and a set of observations at $\Delta t = 400$ ms under the conditions used for normal observers in experiment 2. His results, shown in figure 14, have the two main features of those for normals (shown in figure 4): there is clear evidence of transient tritanopia at adapting illuminances below $10^{5.0}$ td and there is a paradoxical recovery of sensitivity at the highest levels. The mechanism that determines his incremental thresholds appears to have a field sensitivity similar to that of JDM and PGP.

Experiment 9b: deuteranope

The deuteranopic observer, GH, is emmetropic and aged 22. He showed himself to be deutan by his performance on the Farnsworth–Munsell 100-hue test and by his normal brightness matches on the Nagel anomaloscope. He was shown to be a dichromat by the same criteria as for PB. In addition, GH reported that a wavelength of 507 nm appeared colourless to him when he was adapted to CIE illuminant C. The exact position of this point was established by driving the interference wedge in channel 1 with the double-staircase program normally used to measure increment thresholds (see Methods). 1° monochromatic stimuli were presented for 2 s against a dark field and GH responded 'warm' or 'cold' by pressing the keys normally corresponding to 'yes' or 'no'. For several seconds before each flash he was asked to deflect his gaze to a white screen illuminated with illuminant C.



lower scale, $\log_{10}$ {retinal illuminance/td}; upper scale, $\log_{10}$ {field intensity/(erg s^{-1} deg^{-2})}

FIGURE 15. Results for deuteranope, GH. Symbols as for figure 14.

GH was tested under the conditions of experiment 2 and his results, the means in each case of two runs, are shown in figure 15. At adapting illuminances of less than $10^{4.0}$ td this subject shows no transient tritanopia, but more intense fields produce a loss of sensitivity that reaches a maximum of 1.25 $\log_{10}$ units. The onset of transient tritanopia coincides with a very clear inflexion in the increment-threshold function. Above 5.0 log td the transient tritanopia declines, as it does for all other observers tested.

Thus transient tritanopia has been found to be present in a protanope and a deuteranope, although in the latter it was present only within a limited range of adapting intensities.

Discussion

The existence of transient tritanopia should now be beyond question; previous doubts seem to be removed by the results of experiment 2. The loss of sensitivity appears to be primarily confined to the blue mechanism (experiments 2*a*, 3 and 4). An attenuation of an adapting field by as little as 0.5 $\log_{10}$ units is enough to induce transient tritanopia (experiment 5). The phenomenon is present in parafoveal and peripheral vision (experiment 6), but does not occur when target and adapting field are presented dichoptically (experiment 7). It is found in a protanope and, in a modified form, in a deuteranope (experiment 9).

The existence of transient tritanopia probably clears up the mystery left by the experiments of Mandelbaum & Mintz (1941) on the recovery of sensitivity for differently coloured test flashes after various chromatic adaptations. Mandelbaum & Mintz found little difference in recovery curves for red, green and violet test flashes following adaptation to moderately bright yellow fields and did not find the double-branched functions that, by analogy with the classical rod–cone recovery curves, might be expected if the spectral sensitivity curves of the cones were well separated (see Appendix). They took their results to support Hecht's theory that the maxima of the three cone sensitivities are clustered close together near the peak of the photopic visibility function. An alternative interpretation is that their recovery curves for violet test flashes in part reflect the recovery of the green cones, not the blue cones, and that the recovery of the blue receptors was delayed by the phenomenon of transient tritanopia. Similarly, transient tritanopia may explain why Banks & Munsinger (1974, p. 815) were unable to reveal a blue receptor after adaptation to a yellow field (Wratten no. 16) of moderate brightness.

Our main purpose in the experiments reported here has been only to establish some basic properties of transient tritanopia. However, we adopt as working hypotheses the suppositions that during early dark adaptation the signals of the blue cone mechanism are subject to inhibition from a mechanism with a different spectral sensitivity; and that when the latter is almost fully bleached by intense long-wavelength fields the blue mechanism is disinhibited. We do not know whether the operational inhibition is achieved by masking or by an attenuation of the signals from the blue cones; and equally unknown is the site of interaction, although experiment 7 suggests that it does not lie in channels in which binocular signals have been combined, while the observation of Gouras (1968) suggests that the interaction occurs at or before the level of the retinal ganglion cell. The interaction may be *chemical*: different classes of receptor may, for example, compete for a limited supply of a particular substance, as Rushton (1968) supposed rods and cones competed for 11-*cis*-retinaldehyde; or diffusion of a transmitter released in the dark by long-wavelength mechanisms may prevent response in the blue channel. *Neural* interaction between cone mechanisms is well established at the level of ganglion cells in the primate retina (Gouras 1968) and at the level of the S-potential in the fish retina (see, for example, Naka & Rushton 1966). Antagonistic interaction between red and green receptors has been recorded in the turtle and has been attributed to feedback from horizontal cells (Fuortes, Schwartz & Simon 1973). In fish, at least two anatomical bases for direct interaction between receptors have been described: (*a*) the gap junctions between neighbouring pedicles and spherules, and (*b*) the basal processes of cone pedicles that invaginate the synaptic cavities of neighbouring cones. In the rudd, the latter link only cones of different type (Scholes, 1975). (The identification of cone types was by photographic densitometry.) Of particular interest is Scholes's observation that connections between green ('accessory') and blue ('single') cones in the rudd are

unidirectional: basal processes from the blue cones invaginate the pedicles of the green cones, but the contrary does not occur. This observation may seem prima facie to be the opposite of what we are looking for, but the basal processes may well be post-synaptic to the cones they invaginate. Of course, colour vision has evolved independently in fish and in higher mammals, but the biological reasons for an asymmetric interaction between cone types may be similar. Finally, we do not wish to exclude the possibility that the inhibition occurs within the blue receptors.

We have noted (experiment 5) that there is a rough correspondence between the adaptation level at which transient tritanopia begins to decline and that at which 'π_3' replaces 'π_1' in the increment-threshold function (although compare the results for the deuteranope, figure 15). There are several observations that support the hypothesis that *in the steady state* the sensitivity of the blue mechanism can be secondarily controlled by a mechanism sensitive to long wavelengths. (*a*) The field sensitivity function for π_1 has a secondary mode at long wavelengths and does not resemble the absorption spectrum for a single pigment. (*b*) The sensitivity of π_1 to orange fields ($\log B_{or}$) is much more variable, across subjects, than is either (i) the sensitivity of π_1 to blue test stimuli ($\log b_{bl}$) or (ii) the sensitivity of the green mechanism, π_4, to orange fields ($\log G_{or}$) (Stiles 1946). (*c*) There is no correlation between $\log b_{bl}$ and $\log B_{or}$ whereas there is some correlation between $\log G_{or}$ and the sensitivity of π_4 to blue test flashes (Stiles 1946). (*d*) The quantity $\frac{B_{or}}{b_{bl}} \Big/ \frac{G_{or}}{g_{bl}}$ increases proportionately with $\log B_{or}$, a result that suggests that the variability in B_{or} is not due merely to a passive filter lying in front of all receptors (Stiles 1946). To these findings may be added the important demonstration by Pugh (1976) that long- and short-wavelength fields are super-additive in their effects on π_1. We might suppose that 'π_1' and 'π_3' represent the same blue cones in different states of inhibition and that Stiles's earlier term 'limited conditioning effect' (Stiles 1939) is the more appropriate way to denote the inflexion in the t.v.i. function. The hypothesis could be generalized to include π_2, which would represent a distinct state of inhibition.

We may end by considering one specific version of the hypothesis that transient tritanopia arises from an interaction between long- and short-wavelength mechanisms. This hypothesis places the interaction in the blue–yellow opponent-colour channel of Hurvich & Jameson (1957) and supposes that the removal of a long-wavelength adapting field causes, in this channel, activity that corresponds to the presence of a short-wavelength background. This activity constitutes noise and raises the threshold for detecting a blue target. Its phenomenal counterpart is a bluish after-image. However, if we wish to entertain this hypothesis we must explain why it is disproportionately the blue mechanism that is subject to masking in this way. To account for the latter finding we could make the additional assumption that signals from the blue cones do not have access to the luminosity channels of the visual system. Several authors have made this assumption in order to account for the disproportionate contribution of the blue cones to hue (Guth *et al.* 1968; Mollon & Krauskopf 1973; Smith & Pokorny 1975; cf. also Hunt 1967). Whittle (1974) has provided some direct evidence that flashes detected with the blue cones are seen only as changes in saturation and not as changes in brightness (but cf. Marks 1974). In his sample of on-centre ganglion cells in the retina of the rhesus monkey, Gouras (1968) found that non-opponent 'phasic' units received input from cones sensitive to long and middle wavelengths but not from the blue-sensitive cones; a short-wavelength cone input, from a mechanism resembling π_1, was found only in 'tonic' units, which were organized in a spectrally and

spatially antagonistic manner. Mollon & Krauskopf (1973) have suggested that several of the anomalous properties of the blue mechanism may not necessarily be intrinsic properties of the blue receptors but may arise because signals from the blue cones are transmitted only via chromatic channels. Now, if adaptation to a green field leaves the equivalent of a red field, the contribution of the red mechanism to the chromatic channels may be masked, but its signal can also travel over the luminosity channel and under many conditions its threshold may not significantly rise. The signals of the blue cones do not enjoy this choice of pathways and thus are subject to transient tritanopia.

An opponent-colour account of transient tritanopia is supported by the small 'transient protanopia' found in experiment 4 and associated with a red after-image, but equally we may note that transient tritanopia was abolished under the one condition where there was a blue after-image (experiment 5). Certainly an opponent-colour hypothesis needs additional assumptions to accommodate the absence of transient tritanopia at high intensities (experiment 2). The question must remain an open one. Clearly required are measurements of the spectral sensitivity of the inhibitory mechanism: an extension of experiment 8 may offer one way of securing such measurements.

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Appendix:
Early threshold observations of transient tritanopia

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This appendix gives a brief account of the original threshold observations of transient tritanopia, which at the time were reported only summarily in a paper to the Cambridge 1947 Conference on colour vision. (Stiles 1949*a*). The object was to see whether the theory of increment thresholds for coloured test stimuli exposed on coloured background fields to which the eye was fully adapted could be extended to the threshold recovery curves following extinction of the adapting field. The results of Mandelbaum & Mintz (1941) referred to above made this doubtful. As the adaptation condition most likely to provide a critical test, a monochromatic field in the red of wavelength $\mu = 640$ nm was chosen, of diameter 10° and of an intensity of about 2×10^4 td, which was just below the level at which the response of the 'blue-sensitive' cone mechanism would be subject to the so-called 'limited conditioning effect'. According to the steady state theory, for the monochromatic test stimulus used (a square of 1° side exposed in flashes of duration 0.2 s and viewed foveally) the curve relating the increment threshold $U(\lambda)$ for any test wavelength λ to the intensity $W(\mu)$ of the red adapting field to which the eye was fully adapted, would be the resultant of three component curves associated respectively with 'blue-', 'green-', and 'red-sensitive' cone mechanisms (later named π_1, π_4, π_5) as shown for the particular case $\lambda = 475$ nm in the scheme on the left-hand side of figure A 1. It was expected by analogy with foveal recovery curves obtained with test and field stimuli both white, that on extinction of the field the threshold

for each mechanism would drop rapidly at first and would then asymptote to the steady value appropriate to zero field. This ignores the period usually of less than 1 s in the white light case when there occurs a brief rise in threshold usually associated with 'neural' competition between the signals of the extinguished field and the test flash. Thus for $\lambda = 475$ nm recovery from a 2×10^4 td red adapting field would yield a threshold recovery showing a transition from a 'blue' to a 'green' branch, as suggested in the right-hand side of figure A 1. For short wavelengths, $\lambda <$ about 450 nm, or moderate wavelengths, λ between about 510 and 590 nm, the

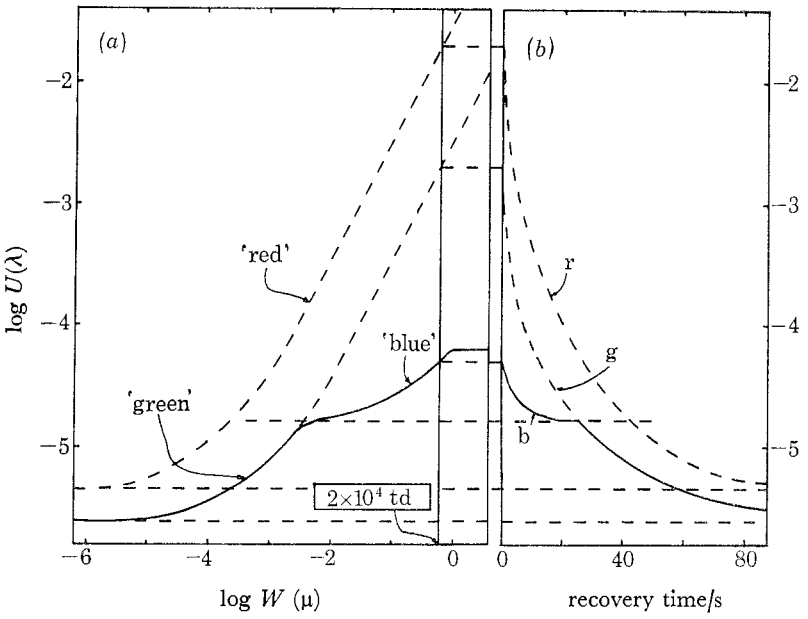

FIGURE A1. (*a*) Curve of log (threshold) against log (field intensity) for steady adaptation to the field, and its derivation from the corresponding curves for the assumed 'red', 'green' and 'blue' cone mechanisms. Wavelengths: test stimulus 475 nm, field 640 nm. (*b*) Threshold recovery curves following the extinction of a field of wavelength 640 nm, as depicted in (*a*), and of intensity 2×10^4 td, according to the anticipated extension of the steady state theory to the non-equilibrium case. (Schematic.)

theory would indicate a single-branch recovery curve, and for long wavelengths, $\lambda > 590$ nm, a transition point from a 'green' to a 'red' branch. These transition points might be difficult to establish if the component recovery curves at intersection differed only slightly in gradient. But the first observations showed a failure of the theory of a quite different kind; for test stimuli of short wavelength removal of the adapting field was followed not by recovery but by an actual, and considerable, increase in the increment threshold.

To confirm this observation, the early stages of recovery were investigated by a cyclic method in which it was arranged to adapt the eye for at least four minutes to the field and then to expose and occult the latter repeatedly in cycles, usually of 30 s on, 15 s off. During the off periods, the test stimulus of a particular wavelength and of fixed intensity was flashed at 2, 5, 8, 11 and 14 s after the preceding moment of extinction, and the subject responded 'seen' or 'not seen' after each flash. By repeating the sequence of cycles for a suitable range of intensities of the test stimulus, frequency of seeing curves and 50 % increment thresholds could be determined for each of the five recovery times. Figure A 2 gives a selection of the early recovery curves obtained in this way. Those show the change in log threshold at various times after the extinc-

tion of the field. The figure shows (*a*) that for all three subjects, at the 2 s observation times there is an increase in threshold for the short wavelength test stimulus, as against a recovery drop in threshold for the moderate and long wavelength stimuli, (*b*) that the differences in magnitude of these changes for the three subjects are considerable, and (*c*) that for all test wavelengths, the threshold after 2 s falls off with time in a regular fashion.

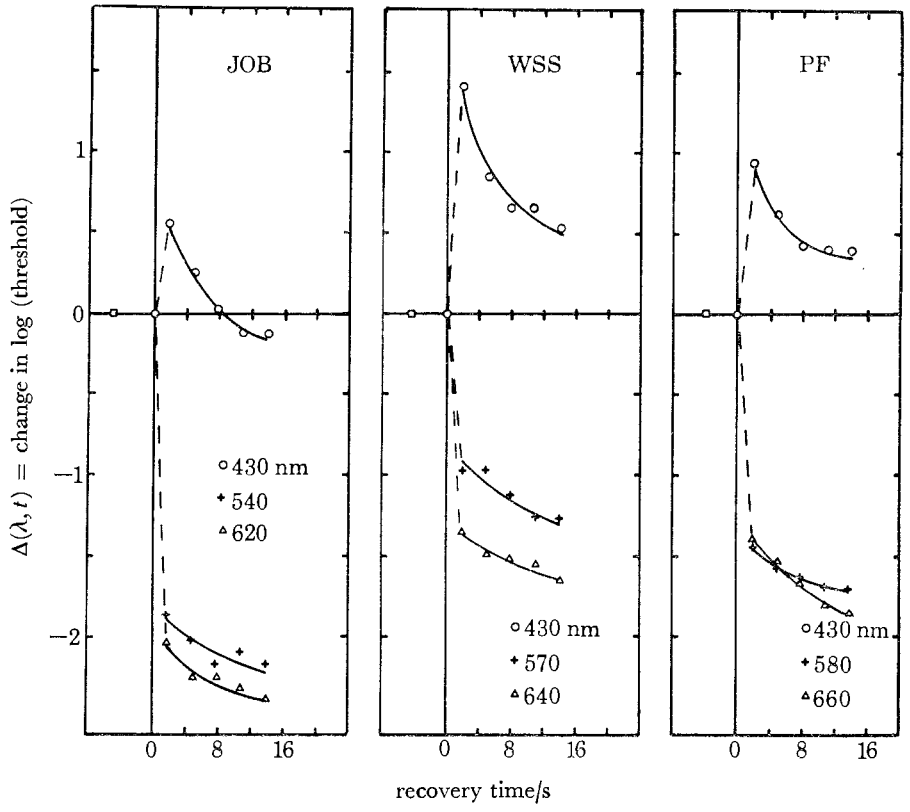

FIGURE A 2. Early threshold recovery curves for test stimuli of different wavelengths and for three subjects: JOB (aged 20), WSS (aged 46), PF (aged 20). The quantity plotted is: $\Delta(\lambda, t)$ = log (threshold at t s after extinction of field) − log (threshold on zero field), where λ is test wavelength, and the field used had wavelength 640 nm and intensity 2×10^4 td.

Most observations were made for the subject (WSS) who gave the largest threshold increase at short wavelengths, and his results are summed up in the four sets of data, A to D, of figure A 3 which in each case represent log (threshold sensitivity), log $(1/U(\lambda))$, plotted against wavenumber. On the steady state theory, the spectral variation of threshold sensitivity on a field of zero intensity (data set A) is derived in the way indicated schematically in the figure as the greatest of the sensitivities of the 'blue', 'green', and 'red' mechanisms. After adaptation to any adapting field the component sensitivity curves are all reduced by factors that depend on the intensity and colour of the field. Thus for the red field used, the results (data set B) correspond to a small decrease (about 0.6 log units) in the 'blue' sensitivity, a large (about 2.3 log units) decrease in the 'green' sensitivity, and a considerably larger (at least 2.9 log units) decrease in the 'red' sensitivity, so that it is doubtful whether the latter is having any part in determining the threshold even at the long wavelengths. The remarkable feature of the 2 s recovery data (C) is that the peak in the spectral sensitivity corresponding to the 'blue' component has disappeared,

suggesting that on extinction of the field the 'blue' mechanism becomes abruptly so much less sensitive that its increment threshold exceeds that of the 'green' mechanism and the latter takes over the detection of the test stimulus even in the short wavelength range. At the 14 s recovery time (plot D) there appears some sign of a relative rise in the sensitivity at short wavelengths and this is borne out by the comparison of 2 and 14 s thresholds shown as graph (*b*) in figure A 4. Ultimately such a rise must develop to become the elevation in the zero field curve that is attributed to the 'blue' mechanism. At long wavelengths, for this subject the data suggest that

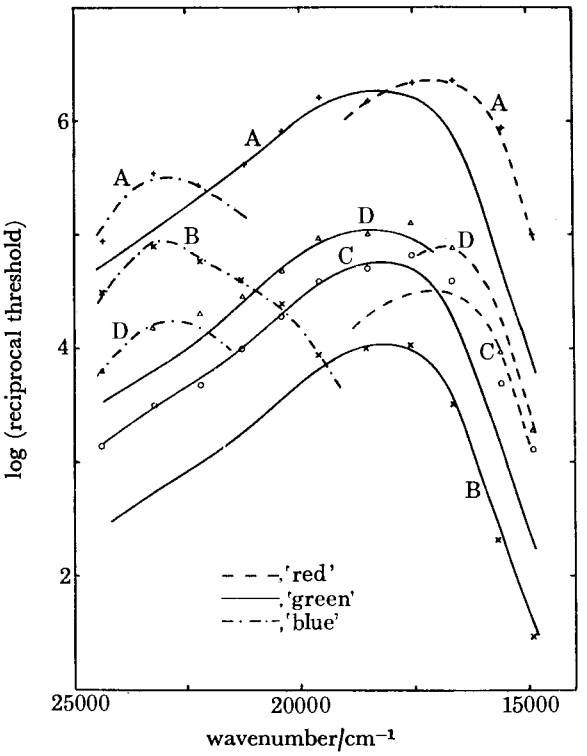

FIGURE A 3. Observed threshold sensitivities (reciprocal thresholds) for subject WSS for four adaptation conditions: A, zero field (+); B, steady adaptation to field of wavelength 640 nm and intensity 2×10^4 td (×); C, 2 s after extinction of the field (o); D, 14 s after extinction of the field (△). The curves shown suggest how each set of data can be represented, very approximately, as the upper envelope of three spectral sensitivity curves associated respectively with three colour mechanisms, the effect of different adaptation conditions being to shift, independently, the heights of the three curves.

at the 2 s recovery time the 'red' system has recovered sufficiently rapidly compared with the 'green', to take over from the latter the detection of the test stimulus but this take-over seems not to have progressed as might have been expected in the 2 to 14 s period (see figure A 4*b*).

For the other subjects, PF and JOB, the variations with wavenumber of the threshold sensitivities on the steady red field and at the 2 s recovery time, when compared with the corresponding data for WSS, agree in showing that the pronounced peak in the blue in the steady field condition is absent from the data for 2 s recovery. It was concluded that for these three subjects the spectral sensitivity in early recovery was identifiable with that of the 'green' mechanism, except at long wavelengths where for WSS, but possibly not for the others, it appears that the 'red' mechanism has already recovered enough to take over. Apart from this, the three subjects show a noteworthy difference which is brought out by plotting the threshold change, steady

field to 2 s recovery value, against wavenumber (figure A 4*a*). While the variations with wavenumber are similar, except for some difference at long wavelengths, the subjects differ considerably in the magnitude of the changes. Take subject JOB; he gave the smallest anomaly – the smallest positive value of $\Delta(\lambda, 2)$ at $\lambda = 430$ nm – but also a correspondingly large negative value at longer wavelengths. In net effect this means that the 'green' mechanism for this subject recovered its sensitivity more rapidly than for the others. Apart from these – certainly considerable – differences in speed of recovery the three subjects gave a consistent picture.

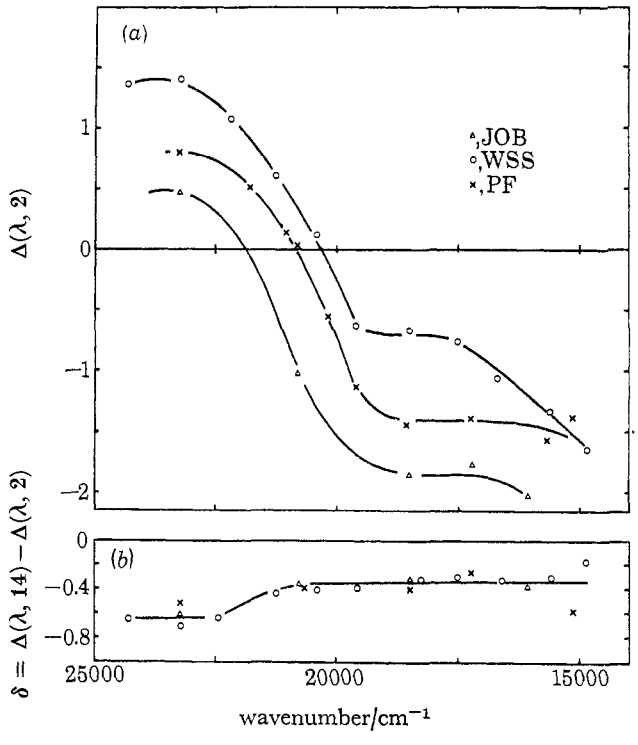

FIGURE A 4. Comparison of data for three subjects. See legend to figure A 2.

Although no theoretical explanation of the anomaly was advanced, an experiment was made to test one extreme possibility, namely that in steady adaptation to the long wavelength field, the 'blue' response mechanism is brought into a condition in which the long-wave light itself acts to facilitate the mechanism's sensitivity, by some photochemical or even purely physical excitation process. If this process had a very short time constant so that it would cease to be effective in a fraction of a second after the removal of the long-wave light, the disappearance of the dominating peak sensitivity in the blue in the recovery curves might result. In the experiment made, the adapting field and the test stimulus were both 'flickered' but in accurate synchrony. Each field cycle of duration T s was made up of $0.89T$ s on, 0.11 T s off, while the test stimulus was exposed once for 0.056 T s in each cycle of the train of cycles contained in the 0.2 s test flash duration. The phase of the test stimulus in the cycle could be varied so that it was exposed either in the centre of the dark period of the field cycle or at various instants in its light period. The stimuli were obtained from a tungsten lamp of approx. 3000 K colour temperature with Ilford spectrum filters, violet (601) and green (604) for the test, and red (608) for the field. With a suitably chosen field intensity, the observation conditions approached closely those of the

monochromatic study for test stimuli at wavelengths respectively near the maximum in the blue of data B in figure A 3 and in the flat central region of the same curve. The measurements were made after reducing the time period T so that the subject saw flicker neither in the field nor in the 0.2 s test flashes (T around 30 ms). The results for the two subjects used (PF and JOB) showed no certain difference between the increment thresholds for test flashes exposed respectively on the light and on the dark periods of the cycle, and this held for both the violet and the green test stimuli:

test stimulus	log (threshold on exposed field) − log (threshold on occulted field)
violet	+0.031 (mean value)
green	−0.029 (mean value)

It was concluded that whatever the cause of the short wave anomaly it did not come into action to any significant extent in the first 30 ms of recovery.

The threshold recovery measurements of Das (1964) by methods similar to the above but using an orange adapting field (effective wavelength, 600 nm, intensity, 3×10^4 td) confirmed the transient tritanopia anomaly. Das also followed the complete recovery process from a much more intense orange field of about 1.8×10^6 td and obtained some evidence of multibranch recovery curves. However, the principal work on recovery from very intense fields was that of Du Croz & Rushton (1966) leading, quite unambiguously, to recovery curves with two branches, in rather good accord with what would be predicted from the steady state theory, but providing at the same time no positive evidence of transient tritanopia. This work necessarily raised doubts about the earlier observations of the anomaly, doubts that have now been resolved as a by-product of the present investigations by Mollon & Polden. These have brought to light several most unexpected and significant features of transient tritanopia that demand a new coordinating hypothesis – not yet apparent – about the behaviour of the blue-sensitive cone response mechanisms in non-equilibrium conditions.

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