

Absence of transient tritanopia after adaptation to very intense yellow light

STILES reported¹ that after the eye had been adapted to light of high intensity and long wavelength, its sensitivity to violet test flashes did not recover according to the familiar dark-adaptation curve. Instead the threshold intensity for detecting short-wavelength flashes increased when the adapting field was turned off, and the peak sensitivity of the eye lay at long wavelengths. Yet it was by using very similar conditions that Auerbach and Wald² isolated a photoreceptor with peak sensitivity in the violet. This contradiction has not been resolved. Transient tritanopia (as we have provisionally termed the loss of sensitivity found by Stiles) has been reported by others³⁻⁶ and an electrophysiological counterpart has been described⁷; but equally there are findings that resemble the contrasting result of

Auerbach and Wald^{8,9}. Attempting to resolve this contradiction, we have discovered a second surprising property of transient tritanopia.

Although our previous measurements had shown that the phenomenon occurred over a large range of adaptation intensities, and became more marked as the intensity of the adaptation field increased¹⁰, we had not used fields quite as intense as the 6.0-7.0 log trolands used by those who had found that adaptation left the eye blue-sensitive, rather than blue-blind. Moreover, the suprathreshold hue-shift described previously³ does not occur if the adapting field is too bright. Stiles worked with a red field of 4.3 log trolands. We have therefore measured sensitivity to short wavelengths after adaptation to retinal illuminances that varied over the range 1.1-6.0 log trolands.

Blue (445 nm) test flashes were presented 400 ms after extinction of a yellow adapting field. Target flashes subtended 1° of visual angle, were presented to the fovea and lasted 15 ms. To secure very intense adapting fields, the interference filter previously used in the adapting beam⁵ was replaced by a gelatin spectral filter (Ilford No. 626) which has a peak transmission at 575 nm and a bandwidth at half height of 35 nm. The test flashes and the adapting field were concentric and were presented in Maxwellian view. Fixation was guided by four illuminated points that were arranged in a diamond with a vertical and horizontal separation of 3° and were adjusted in intensity so that they were just clearly visible against a particular adaptation field. For 3 s every 18 s the adapting field was interrupted by a dark interval and a single target flash was presented 400 ms after the field had been turned off. (We chose 400 ms because at this delay the brief increase in threshold found for white light¹¹ has ceased, but transient tritanopia is still marked⁵.) The experiment was under computer control and the threshold for detecting the flash on 50% of trials was measured by a double staircase procedure¹².

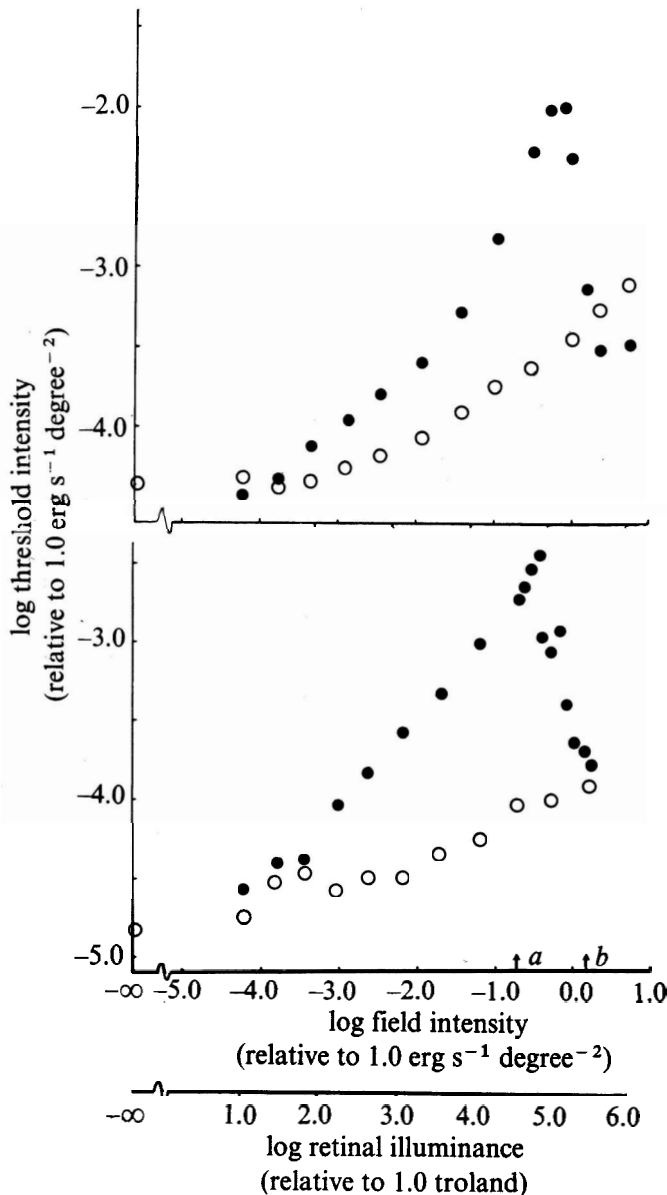


Fig. 1 Ordinate, threshold intensity at which blue target detected; abscissa, intensity of adapting field. ○, Log threshold intensity for detecting blue flash when a steady yellow field is present (conventional increment-threshold function); ●, threshold 400 ms after adapting field has been turned off (means of two runs). Field intensity marked *a* corresponds to adaptation level that gave results of Fig. 2; that marked *b* corresponds to level that gave results of Fig. 3. Observers: I.D.M. (upper panel), P.G.P. (lower panel).

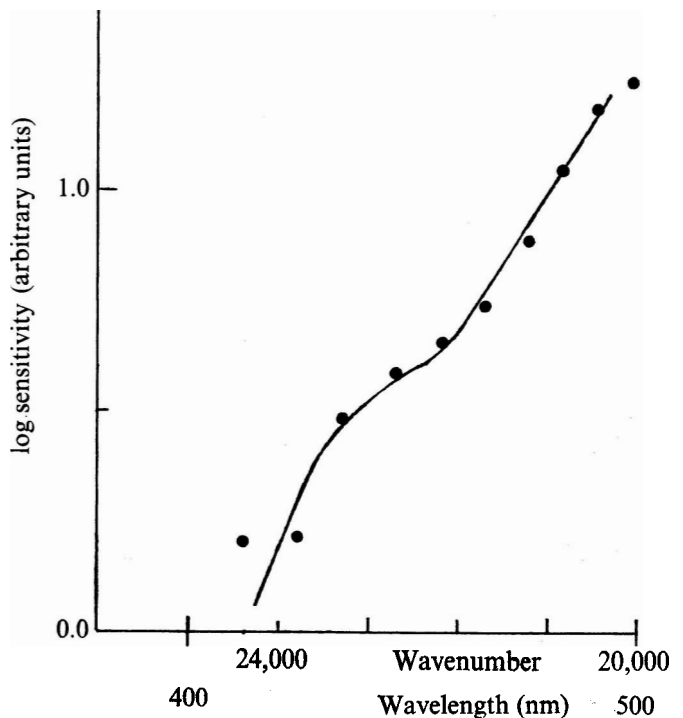


Fig. 2 Sensitivity of eye to short wavelengths 400 ms after a yellow adapting field of 4.58 log trolands has been turned off. Ordinate, reciprocal of intensity required to detect a test flash of varying wavelength. Conditions as for main experiment, except that several test wavelengths and only one adaptation intensity were used. Observer: P.G.P. Solid curve, Stiles' field sensitivity function for π₄ displaced vertically to give best fit to experimental points.

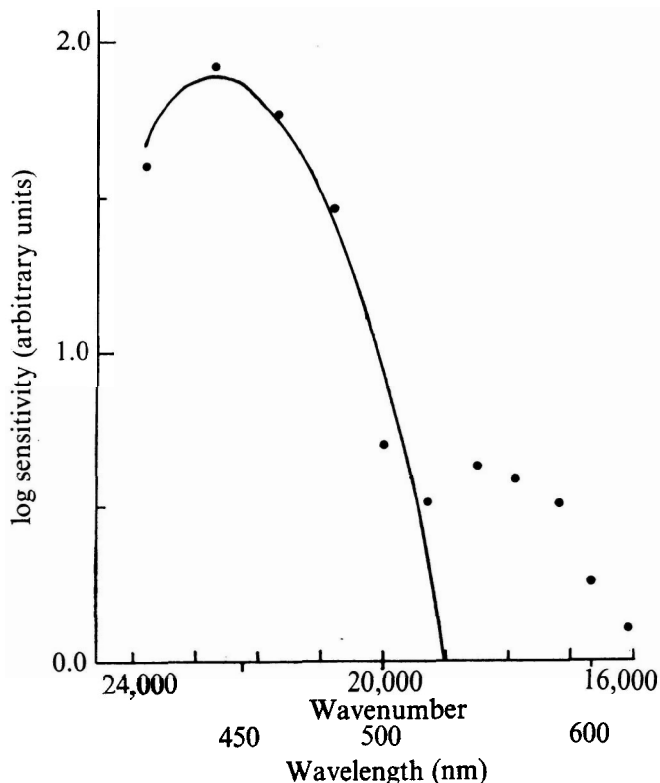


Fig. 3 Spectral sensitivity of eye 400 ms after extinction of a yellow field of 5.47 log trolands. Ordinate, reciprocal of intensity required to detect a test flash of varying wavelength. Observer: P.G.P. Solid function fitted to short wavelength points is Stiles' field sensitivity function for π_1 .

No data were gathered until the field had been cycling on and off for 4 min. Each estimate of the threshold was based on 50 trials.

Figure 1 shows results for two observers. When the field was present and was between 2.0 and 4.5 log trolands the mechanism responsible for detection was that termed π_1 by Stiles: note that transient tritanopia occurred even for fields that did not significantly adapt π_1 in the steady state. As the field increased to 5.0 log trolands there was an increasing difference between the threshold measured in the steady state and that measured 400 ms after the adapting field had been turned off. As Fig. 2 shows, however, the mechanism mediating detection of the flashes after extinction of a field of 4.58 log trolands had the spectral sensitivity of π_2 , Stiles' green-sensitive mechanism, and thus the true extent of the suppression of the blue cone mechanism is concealed: in this range of adaptation illuminance the theoretical threshold for π_1 must lie above the solid circles of Fig. 1.

The most unexpected results were found at an adaptation illuminance of about 5.0 log trolands. As the field that was turned off became brighter, the threshold fell precipitously. In other words, the eye became more sensitive to short wavelengths as the luminance of an adapting field was increased. Moreover, it was now a blue-sensitive mechanism that became responsible for detection of the 445-nm targets. Figure 3 shows the spectral sensitivity of the eye 400 ms after a field of 5.47 log trolands has been turned off; this can be compared with Auerbach and Wald's Fig. 4 (ref. 2) and contrasted with our Fig. 2.

It now seems clear why there are two apparently contradictory reports in the literature. Stiles' used an adapting field of 4.3 log trolands whereas those who did not report transient tritanopia^{2,8,9} used more intense fields. (The experiment of Norren and Padmos⁹ has a second relevant feature: an initial white bleaching field was

replaced by an intense long wavelength field designed to preserve the light adaptation of the red- and green-sensitive mechanism while the recovery of the blue-sensitive cones was followed. If transient tritanopia arises when a recovering long-wavelength mechanism inhibits or masks the signals from the blue-sensitive cones⁵, we should not expect the phenomenon in the conditions used by Norren and Padmos.) A difficulty for this resolution is posed by the results of Das³, who reported transient tritanopia after adaptation to a field of "1.86 $\times 10^6$ trolands"; but there is a discrepancy between this value and the abscissa of his Fig. 1.

The recovery of sensitivity at adaptation illuminances above 5.0 log trolands is sudden: in the case of both observers the function relating threshold to adaptation illuminance has a maximum slope steeper than -2 . Although little is known about this phenomenon, the recovery looks like a disinhibition and a working hypothesis might be that the point at which the threshold collapses represents the retinal illuminance at which some mechanism more sensitive to the long wavelength field has become too bleached, or otherwise too refractory, to inhibit or mask the blue-sensitive mechanism during early dark adaptation. Thus our results add to the suspicion⁵ that transient tritanopia represents not a direct effect of the extinction of the field on the blue cones but the inhibition or masking of the signals of the blue cones by a mechanism with different spectral sensitivity. The collapse of transient tritanopia in Fig. 1 occurs at approximately the field intensity at which the mechanism termed π_3 by Stiles replaces π_1 in the normal increment-threshold function: the inhibition seen in transient tritanopia is possibly related to an inhibition that marks the difference between π_1 and π_3 in the steady state. ' π_1 ' may represent those conditions in which the gain of the blue-sensitive mechanism is controlled by a long wavelength mechanism as well as by quanta absorbed directly by the blue-sensitive pigment.

Fields of $\sim 10^6$ trolands bleach a substantial fraction of the rhodopsin in the retina within 30 s (ref. 13) and prolonged observation of such fields (for example, in making the measurements of Fig. 3) left us with after-images that lasted for as long as 7 d. Stiles has told us that he noticed such after-images when working in similar conditions, and Brindley¹⁴ reported an after-image lasting 8 months, which was the cumulative result of repeated adaptation to high intensities. Although we can ourselves detect no permanent damage, we recommend caution in repeating our measurements: only one eye should be used and the possible dangers should be explained to all subjects.

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