

## TRANSIENT TRITANOPIA OF A SECOND KIND

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**Abstract**—Using a psychophysical method that allows the tracking of very rapid changes in sensitivity, we demonstrate an anomaly in the time-course of light adaptation for the short-wave mechanism: after the onset of a yellow (581 nm) field of  $\sim 10^{5.3}$  td the threshold for short-wave targets does not recover monotonically but continues to rise for several seconds before falling to its equilibrium value. The phenomenon is absent when the adapting field has a wavelength of 511 nm and has been adjusted to give a similar equilibrium value for the short-wave threshold.

Colour    Transient tritanopia    Light adaptation    Short-wave cones    Opponent processes

### INTRODUCTION

If the eye is adapted for some minutes to a bright long-wave field and the field is then extinguished, the threshold for short-wave targets does not recover according to the normal time-course of dark adaptation; the threshold actually rises when the field is extinguished and only after several seconds does it regain the level that obtained while the field was present (Stiles, 1949a). This anomaly of the dark adaptation of the short-wave cone mechanism has been called "transient tritanopia". We here report conditions under which the *light* adaptation of the short-wave mechanism also follows an unusual course. After the onset of an intense long-wave adapting field the threshold for short-wave targets continues to rise, so that 5 sec later the threshold may be more than 10 times higher than the value measured immediately after the onset of the field. The threshold passes through a sharp peak and then recovers towards its steady-state value. This remarkable phenomenon is illustrated in Fig. 2 of the present paper and should be contrasted with the classical course of light adaptation, where the maximal loss of sensitivity occurs at the onset of the field and the threshold immediately begins to recover towards its equilibrium value (Baker, 1949).

Although an unusual psychophysical method

must be used if precise measurements of the phenomenon are to be made, our stimulus conditions are not novel or complicated ones. Violet (436-nm) test flashes are presented on a bright yellow (581 nm) field. The diameter (1.54 deg of visual angle) and the duration (200 msec) of the test flash are chosen to take advantage of the greater spatial and temporal integration of the psychophysically-defined short-wave cone mechanism (Brindley, 1954; Krauskopf and Mollon, 1971; Uetsuki and Ikeda, 1971), and so maximize the sensitivity of that mechanism relative to the sensitivities of the middle- and long-wave cone mechanisms.

Under these conditions, sensitivity changes substantially and non-monotonically during the first 20 sec of adaptation to the bright yellow field. Since the rate of change of threshold may exceed 0.25 log unit per second (Fig. 2), it is not feasible to track the changing sensitivity by means of a conventional staircase procedure (Blough, 1955; Cornsweet, 1962a) or by a method of adjustment, such as used by Augenstein and Pugh (1977) to monitor light adaptation on moderately intense yellow fields. The step size of a conventional staircase would have to be very large if the staircase were not to lag behind the observer's changing sensitivity; and large steps would reduce the precision of the measurements. On the other hand, our purposes would not be well met by the recycling method that Crawford (1947) used to monitor the first second of light adaptation, a method in which

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only one test flash is presented during each cycle of adaptation and recovery; under our conditions, each cycle of adaptation and recovery would take many minutes.

We have therefore turned to a method used by Cornsweet and Teller (1965). We have earlier called this procedure the "Method of a Thousand Staircases" (Mollon and Polden, 1980). As in Crawford's method, the observer is repeatedly exposed to the same sequence of stimulation, but in each exposure to the sequence (each "pass"), sensitivity is probed at each of a pre-decided series of times ( $t_1 \dots t_n$ ) after the onset of stimulation; and for each time ( $t_i$ ) a separate staircase is maintained. Across successive passes ( $p_1 \dots p_m$ ), the target radiance at  $t_i$  on pass  $p_j$  is varied according to the response made at  $t_i$  on pass  $p_{j-1}$ , so as to converge on an accurate estimate of the observer's sensitivity at  $t_i$ . We describe below (Methods) the particular version of this "Method of a Thousand Staircases" that we used in the present experiments. Our general term for the method is intended to capture the idea that any number of staircases may be used; in the present case we used 60.

## METHODS

### *Apparatus*

The measurements were made with the Maxwellian-view system described by Mollon and Polden (1977). A new channel, derived from a 100W mercury arc source, was added to obtain intense short-wave test flashes. The timing and adjustment of stimuli and the recording of responses were managed by a PDP 11/03 computer. The intensity of the test flash could be rapidly altered by means of a circular neutral-density wedge mounted on a stepping motor. Since the range ( $3 \log_{10}$  units) of the wedge was sometimes insufficient, a sliver of neutral density filter, mounted on a vane, was programmed to switch into the beam when more density was required.

A 2-mm artificial pupil was mounted in front of the observer's pupil. Head position was maintained with a dental impression.

### *Stimuli*

The standard stimulus configuration is shown in the inset of Fig. 2. Except where stated, the test flash subtended 1.54 deg, was delivered to the centre of the fovea and had a duration of 200 msec. Its wavelength was 436 nm—the Hg

line isolated by means of a Barr and Stroud CS1 interference filter in series with a Wratten 48B gelatin filter. Fixation was guided by a diamond array of tiny white points.

The adapting field subtended 6.5 deg and was concentric with the test flash. The spectral bands for the 581-nm field, and for the 511-nm field used in Experiment 3, were selected by Barr and Stroud interference filters type CS2 in series with gelatin blocking filters. By means of a monochromator and PIN 10 photodiode mounted at the exit pupil, the spectral composition of each adapting field was measured directly, with blocking filters and other optical components in place. Bandwidths at half-height were approximately 15 nm for both adapting wavelengths.

The radiometric outputs of the test and adaptation channels were measured before and after each session. Our PIN 10 photodiode, in combination with its amplifier, had been calibrated absolutely and spectrally by the National Physical Laboratory six years before the present experiments; and was recalibrated by the same Laboratory one year after these experiments had been completed. The absolute sensitivity at 546.1 nm of the diode/amplifier combination was found to have remained stable to within 3%; and relative sensitivity was stable to within 1%.

### *Procedure*

In order to monitor the rapid changes of sensitivity that were of interest in the present experiments, we used a version of the Method of a Thousand Staircases (see Introduction). This version is illustrated in Fig. 1. On 15 separate passes ( $p_1 \dots p_{15}$ ) within one experimental day, the observer is dark-adapted for 2 min and is then exposed for 2 min to the adapting field, the interval between passes being at least 15 min. On each pass, 60 successive target flashes are presented at 2-sec intervals during exposure to the field, at times  $t_1 \dots t_{60}$ . Each flash is preceded by a brief warning tone. After each presentation the observer presses buttons to indicate whether or not he saw the flash. On the first pass,  $p_1$ , all targets are presented at the same radiance. At the end of each pass, the observer retires to a normally-lit environment and after 15 min the computer signals that the next 2-min pass can be made. On each pass the stimulus radiance at  $t_i$  is decreased if the observer detected the target at  $t_i$  on the previous pass and is increased if he did not detect it. The threshold for  $t_i$  is taken as the average of the

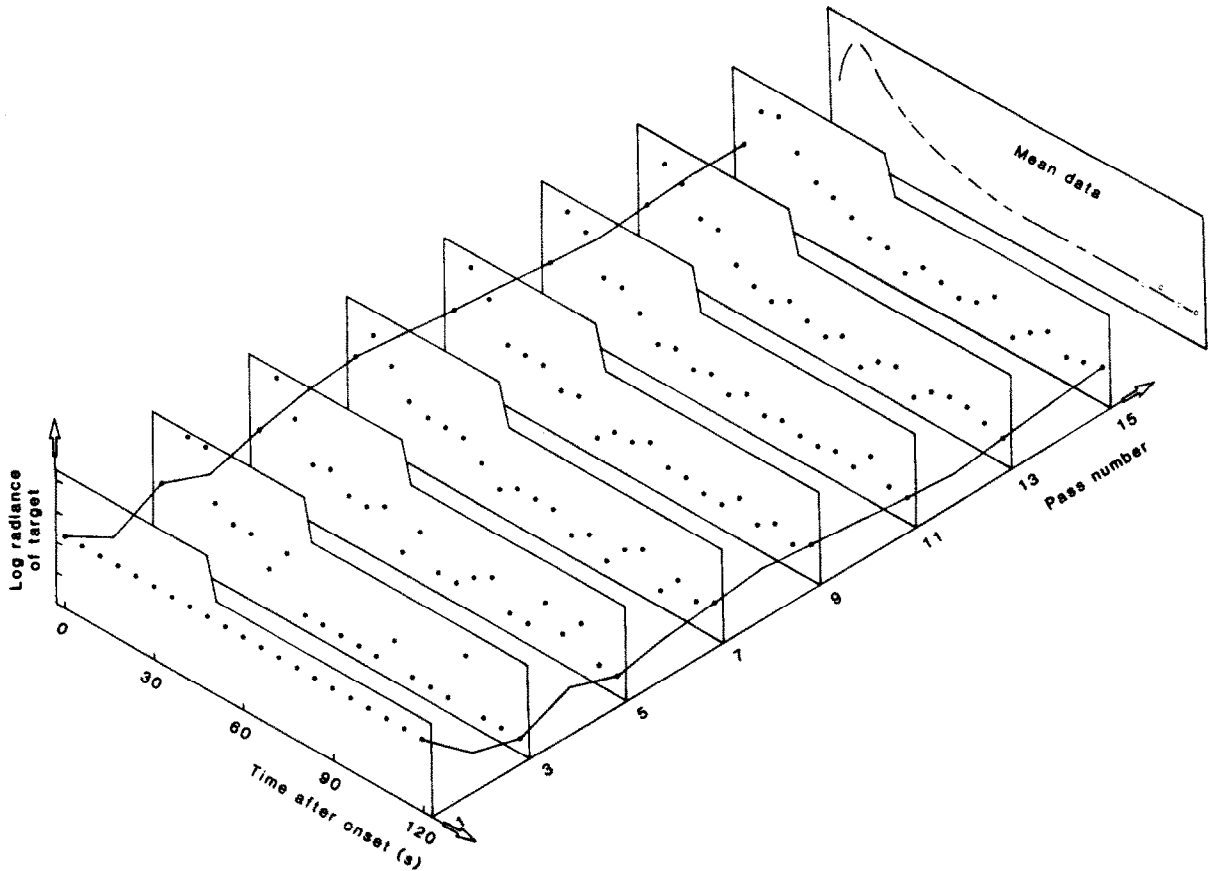


Fig. 1. An illustration of how the "Method of a Thousand Staircases" was used to obtain the data of subsequent figures. Individual passes of the experiment (see Methods) are represented in the present figure by vertical planes; and within each plane the solid points represent the test radiances presented at different times after the onset of the adapting field. For clarity, the diagram shows only alternate passes, and, within each pass, only every third presentation. On the first pass, all flashes are presented at the same radiance. On successive passes the radiance of a given test flash is adjusted according to the response given at the corresponding time in the preceding pass; these sequential adjustments for the first and the last of the staircases are represented by the two solid lines that run transversely through successive planes. The open circles in the rightmost vertical plane represent the average thresholds, which are derived from the responses made on passes 7-15 (see Methods).

radiances visited by the relevant staircase during the final 7 passes, plus the radiance that would next have been visited as a result of the response made on  $p_{15}$ .

The stepsize of the staircase (the factor by which radiance is altered between successive passes) is 0.90 log unit between  $p_1$  and  $p_2$ , and is thereafter reduced by 0.15 log unit between successive passes until it reaches a final value of 0.15 log unit after  $p_6$ .

In the present experiments the first target flash of each pass normally began 100 msec after the onset of the adapting field. An exception was the set of measurements made for observer D.D. (Fig. 2), where the first flash began 1000 msec after onset of the field.

#### Observers

The observers were male and performed normally on the Farnsworth-Munsell 100-hue test and the Nagel anomaloscope.

## RESULTS

### (1) Basic phenomenon

Figure 2 shows, for two observers the variation in the threshold for short-wave targets during the first 2 min of exposure to an intense yellow (581 nm) adapting field. In the case of observer A.S. the radiance of the field was  $10^{11.76}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  and in the case of D.D. this value was  $10^{11.48}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The ab-

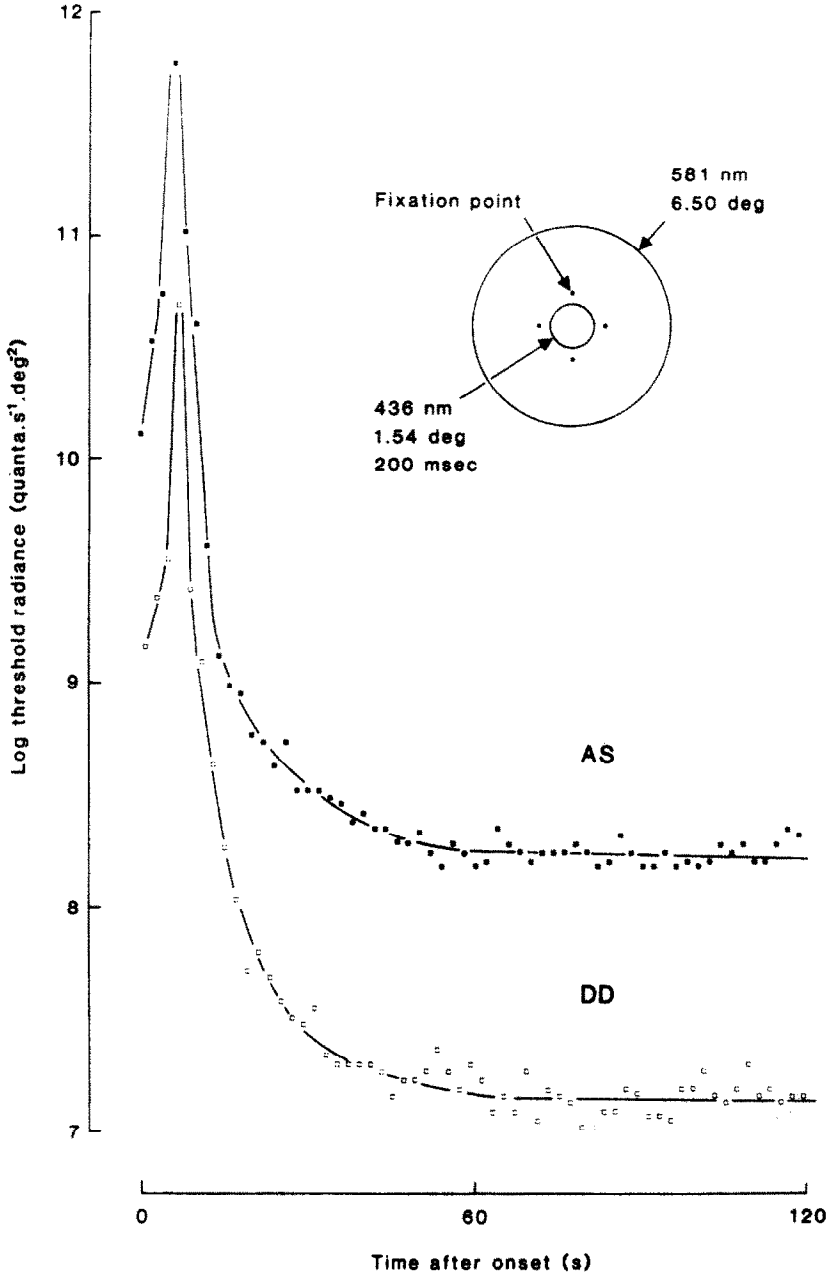


Fig. 2. The variation of the  $\log_{10}$  threshold radiance for detecting violet (436 nm) targets during the first two minutes of exposure to an intense yellow (581 nm) adapting field. In the case of observer A.S., the field had a radiance of  $10^{11.76}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ ; for observer D.D., this value was  $10^{11.48}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The inset (top right) shows the stimulus configuration: the observer fixated the center of the diamond-shaped array of fixation points. For A.S. the first flash began 100 msec after the onset of the field; for D.D. this interval was 1000 msec. The data points for D.D. are correctly placed; those for A.S. have been displaced 1.12 log units vertically upwards.

scissa of Fig. 2 represents the time from the onset of the yellow field and the ordinate represents the threshold radiance required for detection of the flash. For both observers, sensitivity to the violet target varies in the same way. Immediately after the onset of the field the threshold is found to have risen approximately

2.5  $\log_{10}$  units above the absolute threshold for the short-wave mechanism (the absolute threshold can be roughly estimated from threshold-vs-radiance curves such as those on the right-hand side of Figs 3 and 5). But remarkably the threshold then continues to rise for several seconds. After 6 or 8 sec it passes

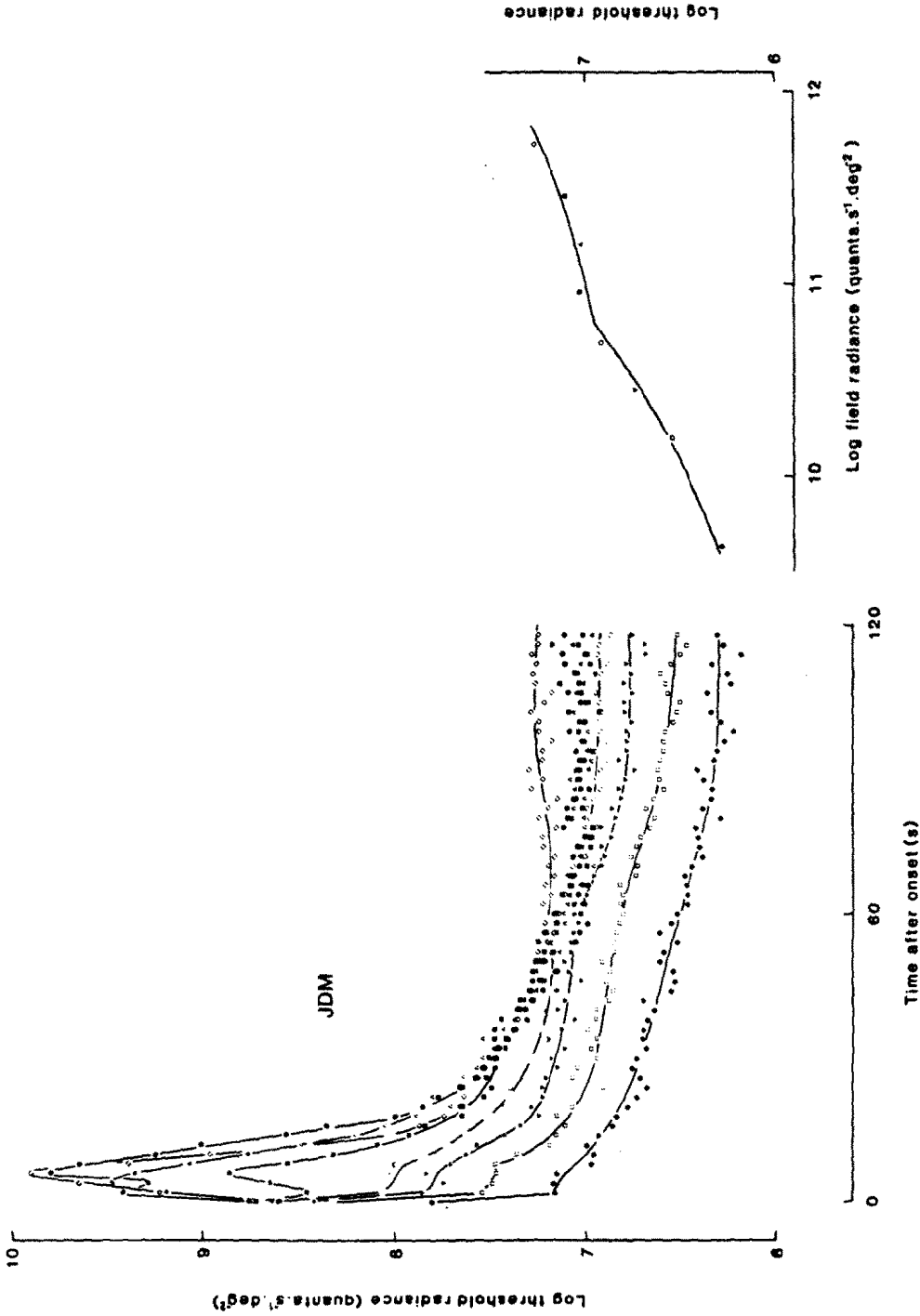


Fig. 3. Left-hand plot: the time-course of light adaptation for 436-nm targets presented on 581-nm fields. Different symbols represent different radiances of the field, as follows:  $\diamond$   $10^{11.72}$ ,  $\bullet$   $10^{11.45}$ ,  $\triangle$   $10^{11.20}$ ,  $\blacksquare$   $10^{10.95}$ ,  $\square$   $10^{10.70}$ ,  $\blacklozenge$   $10^{10.45}$ ,  $\blacklozenge$   $10^{10.20}$ ,  $\blacklozenge$   $10^{9.95}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . (To convert these values totrolands subtract 6.18 from the exponent.) The stimulus configuration was the same as that shown in the inset of Fig. 2. The first flash always began 100 msec after the onset of the adapting field. The solid lines are drawn to indicate the structure we believe may be present in the data; they have no theoretical significance. Each data point is based on two independent determinations of the threshold, i.e. two sets of 15 passes (see Methods). Right-hand plot: A v.v.r. (threshold-vs-radiance) function obtained by plotting the asymptotic values of the left-hand curves against the appropriate field radiance. Each of the plotted points represents the mean of the last six of the thresholds recorded in the corresponding light-adaptation curve. The solid lines represent Stiles' standard template, fitted by eye. Observer: J.D.M.

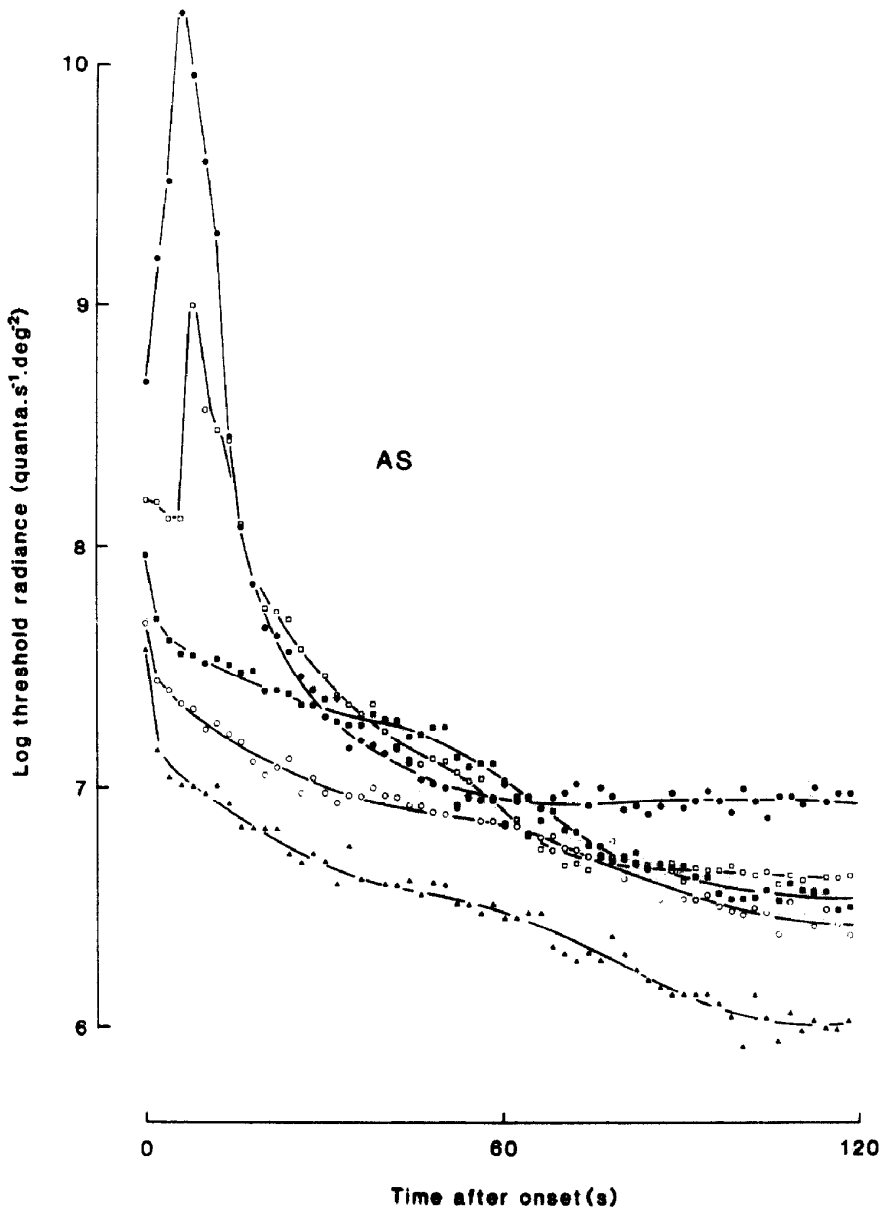


Fig. 4. The time-course of light adaptation for 436-nm targets presented on 581-nm fields. Different symbols represent different radiances of the field, as follows: ●  $10^{11.48}$ , □  $10^{10.93}$ , ■  $10^{10.70}$ , ○  $10^{10.50}$ , ▲  $10^{10.07}$  quanta·sec<sup>-1</sup>·deg<sup>-2</sup>. Details as for left-hand plot of Fig. 3. Observer A.S.

through a peak and only thereafter does it fall monotonically to its normal equilibrium value.

By their form, the functions of Fig. 2 recall Crawford's classical demonstration of the loss of sensitivity that occurs at the onset of an achromatic adapting field (Crawford, 1947; Boynton, 1961). But the present phenomenon is clearly distinct: the time-course of the Crawford effect is measured in hundredths of seconds and the maximum loss of sensitivity occurs for targets presented at the instant of onset of the field, whereas the present phenomenon has a time-

course measured in seconds and—what is most strange—the maximum loss of sensitivity occurs only after the field has been present for several seconds.

## (2) Variation of field radiance

The time-course of light adaptation for short-wave targets on long-wave fields was first examined by Stiles (1949b); and his results were confirmed and extended by Augenstein and Pugh (1977). Neither of these earlier studies revealed the rise and fall of sensitivity seen in

Fig. 2, but in both studies the long-wave field was of a lower radiance than that used to obtain the data of Fig. 2.

Figures 3 and 4 show how the time course of light adaptation for short-wave targets varies as a function of the radiance of a 581-nm adapting field. It is clear that the initial rise shown in Fig. 2 occurs only when the yellow field is of high radiance. For our least intense fields, which are comparable to the brightest of those used by Augenstein and Pugh, there is no delayed rise in threshold following the onset of the field. Thus our results do not contradict earlier measurements of the light adaptation of the short-wave cone mechanism. Our data (open squares in Fig. 3 and solid triangles in Fig. 4) confirm that at least 2 min of light adaptation are required before the threshold for short-wave targets reaches equilibrium on yellow fields of the order of  $10^4$  td (Stiles, 1949b; Augenstein and Pugh, 1977).

The asymptotic thresholds for each field condition have been projected to the right-hand side of Fig. 3 and are there plotted against field radiance to form a conventional threshold-vs-radiance (t.v.r) function. The latter serves to place our data in the context of the model of Stiles (1978). The t.v.r. function has two clear branches: the lower has the approximate test and field sensitivities of Stiles'  $\pi_1$  mechanism, and the upper branch has those of  $\pi_3$ . A modern view is that the two branches do not correspond to independent receptor systems. Rather, it is supposed, detection is mediated throughout by signals originating in the short-wave cones, but the two branches arise because there are two ways in which long-wave fields can modulate our sensitivity to these signals: weak fields act by polarising a post-receptoral chromatically-opponent site, whereas stronger fields may additionally act by producing a significant rate of absorptions in the short-wave receptors themselves (Pugh and Mollon, 1979).

The field radiances that produce a delayed loss of sensitivity are empirically ones that place the steady-state threshold on the  $\pi_3$  branch, that is to say, radiances of  $10^{10.7}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  ( $10^{4.52}$  td) or more. We note that these are fields that bleach significant fractions of the pigment in the middle- and long-wave cones: under equilibrium conditions, the most intense field used in the case of J.D.M. ( $10^{11.72}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ ) would bleach approximately 95% of the pigment in the middle- and long-wave cones, whereas the most intense

field used in the case of AS ( $10^{11.48}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ ) would bleach approximately 90% of the pigment (Rushton and Henry, 1968).

The data of Fig. 3 (left-hand panel) and Fig. 4 have a complex structure that is similar for the two observers. There are three features that deserve further comment.

(a) At some stages of recovery the more intense of two fields may yield the lower threshold (cf. open diamonds vs solid circles in Fig. 3, solid circles vs solid squares in Fig. 4). This finding may be explicable if the empirically measured threshold is in some way controlled by the rate of isomerisations in the long- and middle-wave cones. For there will be a period, a few seconds after the onset of exposure and before equilibrium is reached, when the more intense of two adapting fields is producing fewer isomerisations in those cones, since a greater proportion of the pigment molecules will have already been bleached (Cornsweet, 1962b). Operationally, the cross-over of the recovery curves contributes to one of the obvious features of the data—the clustering of the curves that occurs around the end of the first minute of light adaptation.

(b) At some of the intermediate field levels, the recovery curve exhibits a plateau near the end of the first minute and then turns downward again; in the case of both observers this inflexion is particularly clear for a field of approximately  $10^{10.5}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The plateaux occurring near the end of the first minute are reflected in the clustering of adaptation curves noted above (section a). In classical studies of *dark adaptation*, inflexions analogous to those seen here are associated with a transition between detection by one receptor system and detection by a second, but we judge that such an interpretation is implausible here. Under the present conditions the short-wave cones are likely to determine threshold throughout recovery. At a field level of  $10^{10.5}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  (581 nm) the *steady-state* threshold for the middle-wave cones lies at approximately  $10^{9.7}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  (Stiles, 1978), that is, more than 2 log units above the intermediate plateau in the recovery curve. Since the inflexion is unlikely to reflect a transition between receptor types, it may instead indicate that there are two post-receptoral channels, both with short-wave cone input but with different time constants of recovery (cf. Sharpe and Mollon, 1982).

(c) A feature of some of the recovery curves

for J.D.M. (Fig. 3) is the minor oscillation of the threshold between the second and sixth second of exposure. This secondary oscillation has most frequently been seen in data obtained from J.D.M. but in Fig. 3 does not occur for field radiances of  $10^{11.72}$  and  $10^{11.20}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . Since the curves of Fig. 3 are based on only two sets of passes per curve, we cannot be confident of the secondary oscillations that we have somewhat arbitrarily picked out with our solid lines. The results of Experiment 4, which was specifically directed to this issue, suggest that the oscillation is real.

### (3) Comparison of 511-nm and 581-nm fields

Under field conditions that isolate the  $\pi_1$  mechanism of Stiles and yield the same steady-state thresholds, the time course of light adaptation is already known to be dependent on field wavelength; and it is this observation that provided one of the first indications that the sensitivity of the "short-wave mechanism" can be modified by signals originating outside the short-wave cones. Thus, in the case of a short-wave adapting field (<500 nm) Stiles (1949b) found that it took only 15 sec for the  $\pi_1$  threshold to recover to twice its final equilibrium value, whereas it took 60 sec in the case of a long-wave adapting light, even though the two adapting fields were chosen to give the same threshold for short-wave targets in the steady state. This difference in recovery times was confirmed by Augenstein and Pugh (1977). Stiles wrote in 1949, "It appears in fact that the process responsible for the delay in the light adaptation of the 'blue mechanism' has associated with it a relative spectral sensitivity curve which is not that of the 'blue' mechanism itself and which may agree more closely with the curves of the 'red' or 'green' mechanisms." In 1949 Stiles believed that the "coupling" of cone mechanisms became apparent only when the retina was in a state of change. It later became clear that even in the steady state the sensitivity of the "blue" mechanism was partly controlled by other classes of receptor (Pugh, 1976; Pugh and Mollon, 1979; Polden and Mollon, 1980).

The present experiment is in the tradition of the experiments of Stiles (1949b) and Augenstein and Pugh (1977) in that we compare two fields of different wavelength ( $\mu$ ) that operationally yield the same steady-state threshold for targets detected by the short-wave cones; but our fields are of higher radiance. One field had a wavelength of 581 nm, as in Experiments

1 and 2, and its radiance was  $10^{11.48}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The second field had a wavelength of 511 nm and a radiance of  $10^{9.45}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The wavelength 511 nm was chosen because it appeared unique green to both subjects under the conditions of the experiment and thus would leave in equilibrium the putative "blue-yellow" process of Opponent Colours Theory (Hurvich and Jameson, 1957), a process that has been taken to correspond to the channel detecting short-wave signals (Pugh and Larimer, 1980).

Figure 5 contrasts results for the 581-nm and 511-nm fields in the case of J.D.M. Consider first the threshold-vs-radiance (t.v.r.) curves in the lower right-hand portion of the figure. These measurements were made in the steady state (i.e. after a minimum of 2 min of light adaptation). The data points represent steady-state thresholds for the 436-nm targets on varying radiances of the 511-nm (open circles) and 581-nm (solid circles) fields. As in the case of the t.v.r. function shown in Fig. 3, the function for the 581-nm field has two branches: the lower has the approximate test and field sensitivities of Stiles' short-wave mechanism  $\pi_1$ , and the upper has the sensitivities of  $\pi_3$  (Stiles, 1978, Table B). For the 511-nm field, as predicted by Stiles' scheme, there is only a single branch, which would correspond to  $\pi_1$ ; this branch is displaced leftwards by 1.49 log units relative to the  $\pi_1$  branch for the 581-nm field (this shift is consistent with Stiles' tabulated field sensitivities for  $\pi_1$ , which predict a displacement of 1.50 log unit.)

To obtain the time-courses of light adaptation shown in the left-hand part of Fig. 5, we made two complete sets of measurements for each field, in a counterbalanced *abba* design. The two fields produce closely similar equilibrium thresholds (arrowed points), but these final values are reached by strikingly different routes: when  $\mu = 581$  nm we observe the strange anomaly found earlier, but when  $\mu = 511$  nm the threshold recovers monotonically and adaptation is complete in 30 sec.

It is important to check that it is only signals originating in the short-wave receptors that determine the two sets of thresholds in the left-hand panel of Fig. 5. Stiles' tabulated sensitivities suggest that the *steady-state* thresholds for  $\pi_4$ , the middle-wave mechanism, would lie at  $10^{8.7}$  and  $10^{10.7}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  in the case of the 511 nm and 581-nm fields respectively. Although these values lie above all the empirically obtained thresholds of the left-hand panel, we



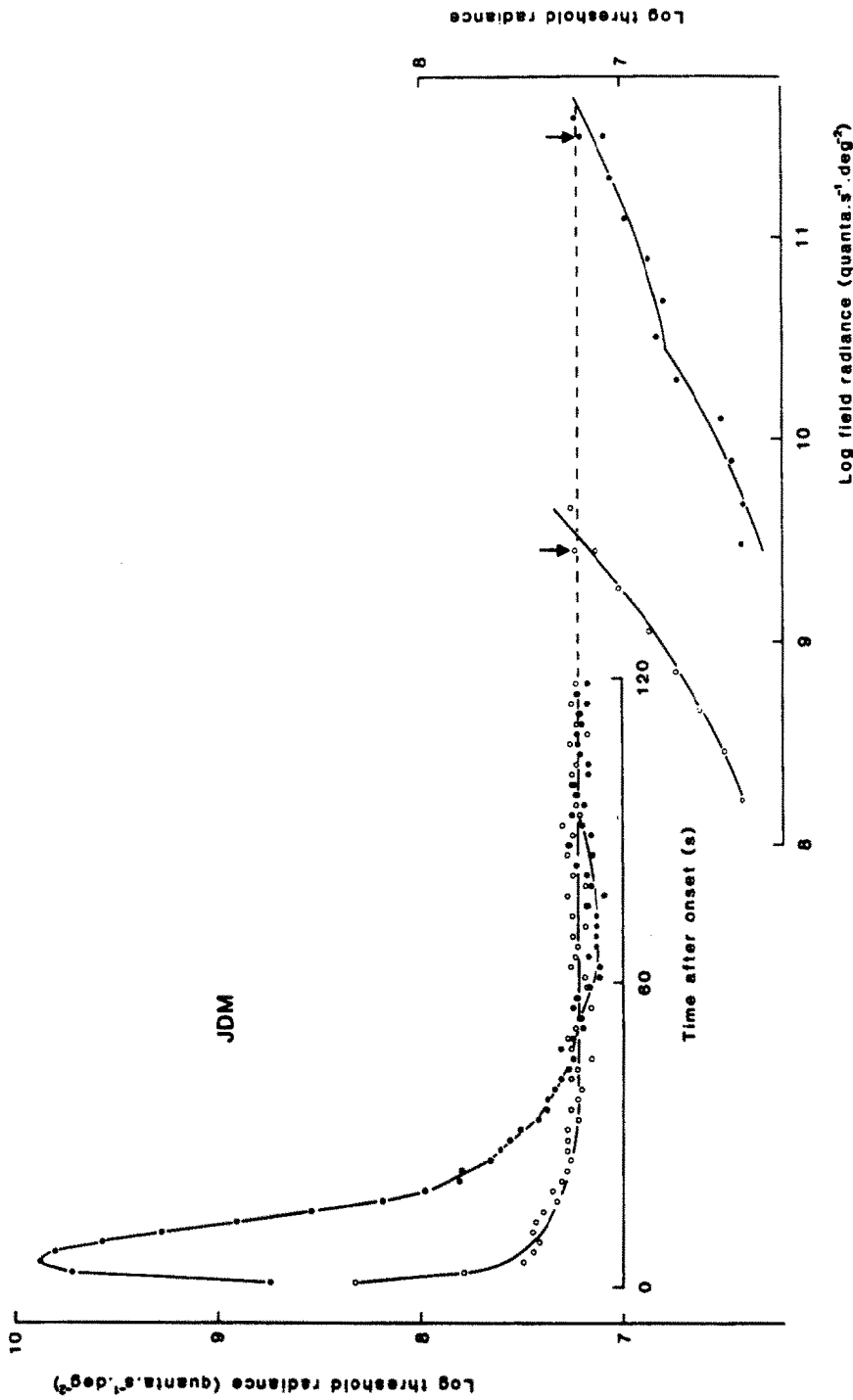


Fig. 5. *Upper-left*: a comparison of effects of 511-nm and 581-nm fields on the time-course of light adaptation when detection is mediated by the short-wave cones. The open circles represent thresholds following the onset of a 511-nm field, the solid circles the thresholds following the onset of a 581-nm field. The radiances of the fields were  $10^{9.45}$  and  $10^{11.48}$  quanta  $\text{sec}^{-1} \text{deg}^{-2}$  respectively (equivalent to  $10^{3.11}$  and  $10^{5.30}$  td). These radiances were chosen to ensure that the final equilibrium threshold was very nearly the same in the two cases. The stimulus configuration was as shown in Fig. 2, except that the field wavelength was either 511 or 581 nm. *Bottom-right*: conventional threshold-vs-radiance (t.v.r.) functions for 436-nm targets presented on steady fields of either 511 nm (open circles) or 581 nm (solid circles). Thresholds were measured by a randomised double-staircase procedure. Each data point represents the average of two separate determinations. The solid curves drawn through the t.v.r. data are Stiles' standard template fitted by eye. The open circle marked with an arrow is the average of the last twelve data points in the left-hand plot for the 511-nm field; the solid circle marked with an arrow is the corresponding average for the 581-nm field. These two points show the positions of the asymptotic thresholds of the recovery curves (left) when these thresholds are replotted in their rightful places on the t.v.r. curves (right). Observer: J.D.M.

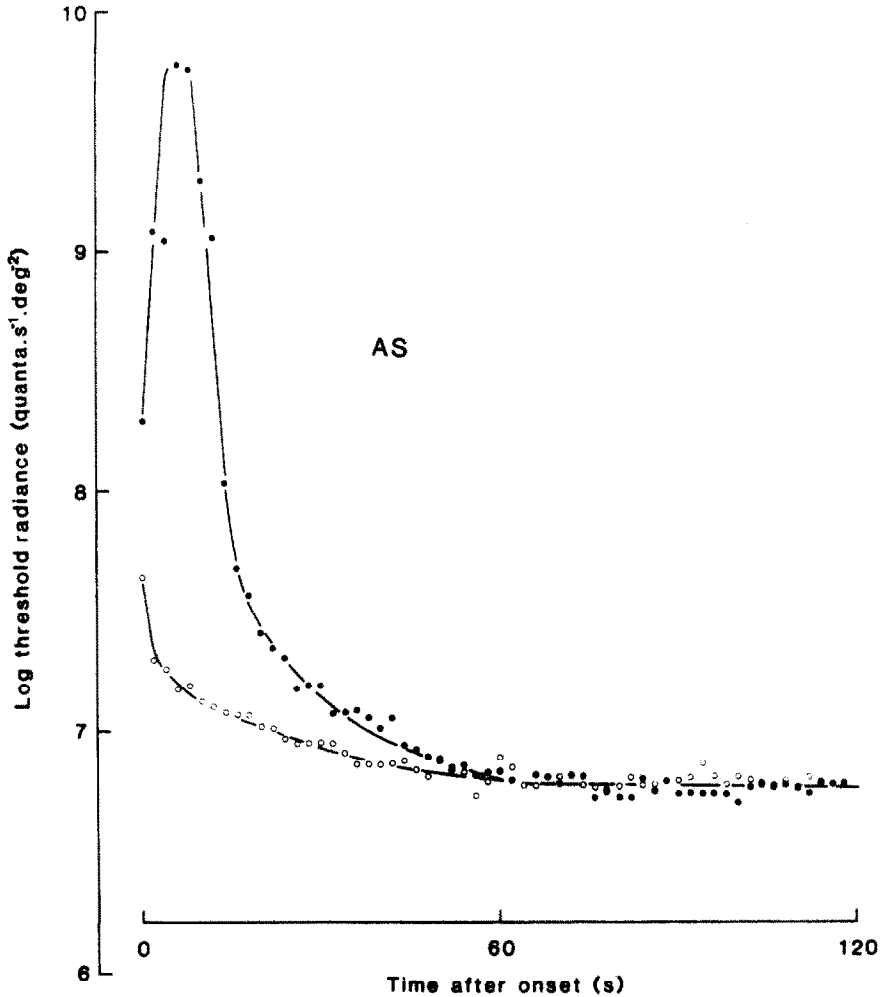


Fig. 6. The time-course of light adaptation to 511-nm (open circles) and 581-nm (solid circles) fields that produce the same threshold for 436-nm targets in steady state. Details as for left-hand panel of Fig. 5. Observer: A.S.

performed a control experiment in which the wavelength of the test flash was increased to 468 nm. For both field wavelengths, the light-adaptation curves for the 468 nm test flash were displaced vertically upwards by 0.15 log unit without change of form. The spectral sensitivity of Stiles' short-wave fundamentals would suggest an upward shift of between 0.25 and 0.26 log unit, whereas any data point determined by  $\pi_4$  ought to have moved *downwards* by 0.38 log unit. Thus throughout the course of the recovery curves of Fig. 5, detection is likely to be mediated by signals originating in the short-wave cones.

Figure 6 shows for observer AS a set of results similar to those shown in Fig. 5 for J.D.M. In this case, full t.v.r. curves were not obtained for the steady state; but on the basis of

preliminary measurements a radiance of  $10^{9.45}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  was chosen for the 511-nm field in order to give an asymptotic threshold comparable to that obtained for the 581-nm field. Conditions were tested in a counter-balanced *baab* sequence, the reverse of that used for J.D.M. The results closely resemble those for J.D.M. and show a similarly striking difference in the effects of two fields that have been equated for their steady-state effect on the threshold for 436-nm targets.

#### (4) *The secondary oscillation*

In discussing the data of Fig. 3 (observer J.D.M.) we noted that some of the curves exhibit a secondary oscillation during the first 10 sec of adaptation. In order to discover whether this fine structure can reliably be dem-

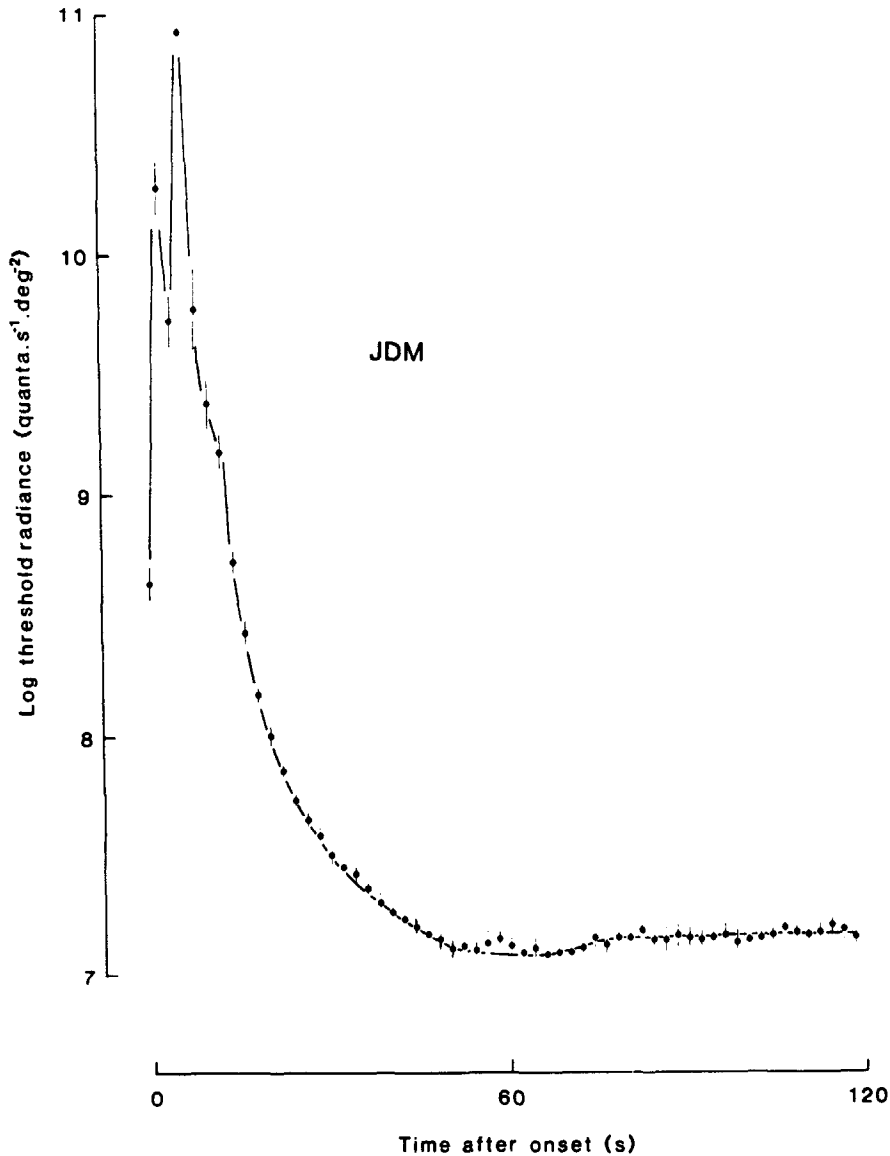


Fig. 7. The time-course of light adaptation for a 436-nm, 0.53-deg target presented on a 581-nm field of radiance  $10^{11.20}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ . The target was centered 1.25 deg to the left of a single fixation point. 8 complete sets of passes were made and the error bars represent  $\pm 1$  SEM. Note the oscillation of the threshold during the first 10 sec of adaptation. Observer: J.D.M.

onstrated, we ran observer J.D.M. through 8 sets of passes at a field radiance of  $10^{11.2}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ .

For this experiment, we changed the spatial parameters of the target. We reasoned that our large standard target (1.54 deg, centrally presented) extended over a morphologically heterogeneous retinal region (Polyak, 1941) and that any underlying oscillation might vary in its phase in the different local sub-regions that were stimulated. Thus the lack of correlation of the component oscillations might reduce the degree of modulation observed in the psychophysically

measured thresholds. We therefore reduced the diameter of the target to 0.53 deg and centered it 1.25 deg to the left of a single fixation point. It would thus stimulate a smaller retinal region, one that is morphologically more homogeneous and one where the short-wave cones are thought to be more evenly distributed (Brindley, 1954; Sperling, 1980).

The results of this experiment are shown in Fig. 7, where the solid points represent the mean thresholds derived from 8 sets of 15 passes, and the error bar represents  $\pm 1$  SE of the mean. The secondary oscillation is large relative to the size

of the error bars and thus appears to be a reliable feature of J.D.M.'s results. It may possibly be echoed in a discernible shoulder on the falling flank of the adaptation curve. Its relationship to the primary rise and fall of sensitivity remains unknown.

Another feature of Fig. 7 is worthy of note. Although the threshold after 100 msec of adaptation and that measured after 120 sec are similar to the corresponding values in Fig. 3, the peak threshold is 1.5 log units higher than the peak value recorded for the same field radiance in Fig. 3. If we are right in suspecting that the peak loss of sensitivity occurs at different times in different local areas of the fovea (see above), then we might indeed expect that the empirically measured psychophysical threshold will exhibit a greater rise in the case of small targets than in the case of large. In the case of large targets, owing to the underlying phase differences, there will be no instant when the loss of sensitivity is maximal in all the local regions of the fovea that are stimulated by the test flash. Alternatively, of course, our result may simply indicate that the magnitude of the transient loss of sensitivity is different in different local regions probed by our two targets.

#### DISCUSSION

Our main purpose in this paper has been to report the mysterious phenomenon of Fig. 2 and to outline the conditions under which it occurs. But some constraints can already be placed on possible explanations.

The difference between the effects of 511 and 581-nm fields (Experiment 3) adds to the accumulated evidence that the light-adaptation of the psychophysically-defined "blue mechanism" does not depend simply on a single class of cones (see e.g. Stiles, 1949b; Mollon and Polden, 1975; Pugh, 1976; Stromeyer *et al.*, 1978; Alpern and Zwas, 1979; Mollon and Polden, 1979; Polden and Mollon, 1980; Wisowaty and Boynton, 1980; Sperling *et al.*, 1983). Individual cones are thought to obey the Principle of Univariance (Rushton, 1972), that is to say, a single cone or single class of cone is unable to distinguish between lights of different wavelength that produce the same photon catch in those cones. If the light-adaptation curves for 511 and 581 nm fields (Figs 5 and 6) were determined only by the quantum catches in the short-wave receptors, then the two thresholds should be the same at all time points and not

only at the asymptotes. However, we have to be a little cautious in using this argument to claim the anomaly seen with the 581-nm field arises from a post-receptor interaction. Once we grant that the *steady-state* threshold for the short-wave mechanism can depend on signals originating in the long- and middle-wave cones (see above), we have acknowledged that fields equated to produce the same equilibrium threshold for short-wave targets may not be fields that produce the same quantum catch in the short-wave cones. In fact, our 511-nm field is likely to elevate threshold mainly by altering sensitivity at a distal site, a site at which sensitivity is determined only by the rate of quantum catch in the short-wave receptors; and the 581-nm field, on the other hand, is likely to produce a smaller quantum catch in the short-wave receptors, achieving much of its effect by polarizing a more proximal, chromatically opponent, site. Nevertheless, although the two fields are unlikely to be identical in their first-site effects, it is the 581-nm field that is likely to yield the smaller quantum catch in the short-wave cones; and yet it is this field that produces the anomaly. Thus we may have here an indication that the anomaly arises from an interaction between signals originating in different classes of cone.

Evidence pointing in the same direction can be found in an earlier study by Mollon and Polden (1980), in which the sensitivity to short-wave targets was monitored during light adaptation to a field that had both short-wave and long-wave components. Violet (440-nm) fields in the range  $10^{9.6}$ – $10^{10.88}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$  were combined with an intense yellow (575-nm) "auxiliary" field of fixed radiance ( $10^{11.7}$  quanta  $\cdot$  sec $^{-1}$   $\cdot$  deg $^{-2}$ ). In these more complicated conditions, the time-course of light adaptation is very different from that found here: the threshold first falls and then *rises* to a final level that is higher than its level at the onset of the field. We only belatedly came upon the anomaly of the present paper, an anomaly observed when the "auxiliary" field of Mollon and Polden (1980) is present alone. But since the addition of violet light to the field can completely reverse the direction of change of sensitivity during the first seconds of exposure, one might suspect that the new anomaly arises from an antagonistic interaction between signals originating in the short-wave receptors and signals deriving from other classes of receptor. The yellow field may polarize (and thereby desensitize) a chro-

matically opponent, postreceptor, site through which the short-wave signal must pass—as in the model of Pugh and Mollon (1979).

But some additional assumptions will be needed to explain why an intense yellow field has its maximal effect only after 6 sec. For example, one hypothesis might suppose that (a) the onset of the yellow field produces a significant signal from the short-wave cones themselves and thus the signals deriving from the middle- and long-wave cones are initially unable to polarize maximally the opponent site; (b) the opponent signal derived from the middle- and long-wave cones remains at a constant, saturated, value for the first six seconds of exposure; (c) the opponent short-wave signal wanes during this period. Thus the peak polarization, and the maximum loss of sensitivity, will occur when the short-wave signal has waned and the opposing long-/middle-wave signal has not yet begun to decline. An alternative hypothesis might place an integrator between the site of origin of the long-wave signal and the site at which it interacts with the short-wave pathway; if the long-wave signal were continuously declining (owing to bleaching), the output of the integrator would first rise and then fall. Further experiments will be needed to decide whether either of these explanations is plausible.

#### *Relationship to other phenomena*

The present anomaly of light adaptation recalls the anomalous loss of short-wave sensitivity after the extinction of long-wave adapting fields (Stiles, 1949a), the phenomenon termed "transient tritanopia" by Mollon and Polden (1975). Phenomena analogous to transient tritanopia have been found when red test flashes are used to monitor recovery from coloured fields (Mollon and Polden, 1977; Reeves, 1981a), or when the observer's task is to detect an explicitly chromatic target consisting of an alternation between red and yellow lights (Reeves, 1983) or when the threshold for green flashes is measured shortly after the transition between two fields of different colour that yield the same steady-state threshold (Reeves, 1982). The new effect (Fig. 2) can be added to this general family of "dynamic dyschromatopsias", the losses of chromatic sensitivity that occur at the onset and offset of coloured fields (Mollon, 1982).

The new effect is transient in nature; and, in that it is a loss of sensitivity of the short-wave mechanism, it is a tritanopia. How similar it is

to the transient tritanopia that occurs at the extinction of long-wave fields? There are two *prima facie* differences between the transient tritanopia that occurs at the extinction of fields and the tritanopia that follows the onset of fields. In the former case, the loss of sensitivity is thought to be maximal immediately after extinction of the field, whereas in the latter case the loss of sensitivity is maximal only when the field has been present for several seconds. Secondly, the new phenomenon occurs only for yellow fields of more than  $10^{4.7}$  td, whereas the extinction form of transient tritanopia is observed with much weaker fields and, in fact, declines as the field increases from  $10^5$  to  $10^6$  td (Mollon and Polden, 1976).

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