DYNAMIC CHANGES IN SENSITIVITY TO LONG-WAVELENGTH INCREMENTAL FLASHES

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ABSTRACT

Probing with a small (0.4° in dia), long duration (197 msec), red ($\lambda = 674$ nm) test flash reveals that the time courses of adaptation and recovery differ for green ($\mu = 530$ nm) and red ($\mu = 674$ nm) conditioning fields (1.2° in dia) whose radiances are adjusted to raise the steady-state threshold by the same amount (0.5 log unit).

INTRODUCTION

Our understanding of colour vision has been much advanced by Stiles' two-colour increment-threshold technique (see, for example, the historical retrospect of Stiles, 1978; also Stiles, 1980). In experiments of this kind, measurements are made of the eye's sensitivity to a monochromatic test stimulus presented for a limited time on a uniform adapting or 'conditioning' field. Stiles' classical measurements were chiefly obtained under equilibrium conditions, that is, when the eye had fully adapted to a steady conditioning field and the incremental threshold had stabilised. But Stiles also made measurements under dynamic conditions, that is, when the sensitivity of the eye was changing as a result of changes in the conditioning field. Recent years have seen an increasing interest in these non-equilibrium conditions, in part because properties of post-receptoral chromatically-opponent channels seem to be especially prominent during transitional states of chromatic adaptation.

In the case of the short-wavelength mechanism, Stiles (1949a) himself showed that conditioning fields having equivalent effects under equilibrium conditions may differ in their effects under dynamic conditions. In particular, the time taken for the threshold of a violet flash ($\lambda = 430$ nm) to drop to twice the final equilibrium value (i.e. the light adaptation time) increases systematically from a low value of approximately 15 sec when $\mu < 500$ nm to a high value of approximately 60 sec when $\mu > 600$ nm. Such findings have been confirmed and extended by Augenstein and Pugh (1977).

Similarly, the course of dark adaptation of the short-wavelength mechanism is very different for long- and short-wavelength fields having equivalent

effects in the steady state; and indeed thresholds for short-wavelength targets may rise substantially after extinction of a long-wavelength conditioning field (Stiles 1949b). This is the phenomenon of transient tritanopia (Mollon and Polden 1975, 1977). These offset transient threshold elevations are well explored now. They are known to occur in the protanopic and deuteranopic eye and for small field decrements as well as for complete extinction of short wavelength fields (Mollon and Polden, 1977), and to be abolished if the adapting field is very bright (Mollon and Polden, 1976) or if a desaturating short-wavelength component is added to the long-wavelength field (Augenstein and Pugh, 1977).

Such transient phenomena of light and dark adaptation were, for a time, thought to be anomalies of the short-wavelength system, but there is an increasing suspicion that they reflect properties common to all chomatically opponent channels and that they are especially salient in the case of short-wavelength flashes only because the short-wavelength receptors contribute little to non-opponent channels (Polden and Mollon, 1980; Mollon this volume), and indeed poor relations of transient trianopia are seen in the phenomena of transient protanopia and transient deuteranopia (Mollon and Polden, 1977; Reeves, 1981; Maloney and Wandell, 1981). Thus small rises in threshold (0.1–0.4 log unit) occur for green ($\mu = 522$ nm) and red ($\mu = 641$ or 670 nm) test flashes following the extinction of dim backgrounds that are blue-green ($\mu = 496$ nm) or red ($\mu = 626$ or 655 nm), but not yellow ($\mu = 570$ or 578 nm).

These findings apply, of course, to early dark adaptation. When the target is chosen to favour the long-wavelength receptors, is it here also the case that fields that are equivalent in the steady state are not equivalent during early *light* adaptation? To answer this question we measured dynamic thresholds for a long-wavelength test flash ($\lambda = 674$ nm) on two background fields: one green ($\mu = 530$ nm), the other red ($\mu = 674$ nm). We found that when the fields were equated for their adaptive effect in the steady-state there were clear differences in the time course of adaptation, not only in dark adaptation but also in light adaptation.

METHODS

Stimuli were presented in a computer-interfaced two-channel Maxwellian-view system. The test stimulus was always a long wavelength ($\lambda = 674$ nm), small diameter (0.4°), long duration (197 msec) circular flash of light. The conditioning field stimulus was a concentric 1.2° diameter disc. Its wavelength ($\mu = 530$ or 674 nm) and radiance varied. Foveal fixation was aided by the presence of 4 dim orientation lights arranged in the shape of a cross (see inset, Fig. 1).

Two types of measurements were made: increment thresholds versus field radiance in the steady-state and dynamic increment thresholds versus time during early light and dark adaptation. In the steady-state type, the observer was first dark adapted for 10 minutes. Then his absolute sensitivity (i.e., increment threshold on a conditioning field of zero radiance) was measured
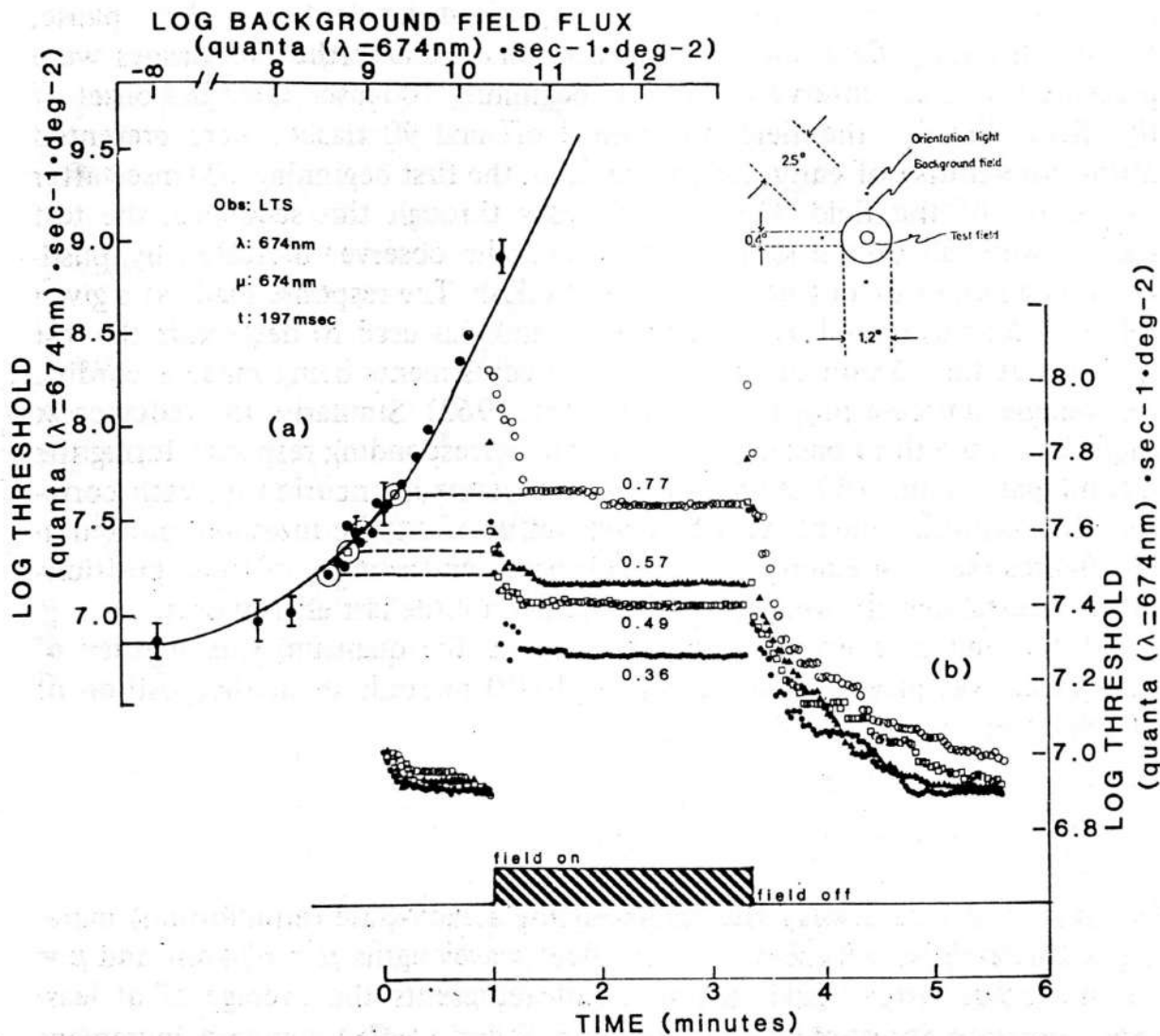
Fig. 1. (a) Steady-state increment threshold curve for observer LTS ($\lambda = \mu = 674\,\text{nm}$). Error bars represent one standard deviation of the mean. Inset depicts stimulus configuration for both steady-state and dynamic-state experiments. (b) Time course of light adaptation to and recovery from 2.33 min exposures to four conditioning fields which raise absolute test flash threshold by 0.36 (●), 0.49 (□), 0.57 (▲), and 0.77 (○) $\log_{10}$ units. A broken line connects the set of data obtained under dynamic (non-equilibrium) conditions with the steady-state threshold (identified by the same symbol and plotted to the left). The hatched region below curves indicates onset and offset of background field, occurring respectively at 1 min and 3.33 min after first threshold determination. Note that the scale of the right-hand ordinate is double that of the left-hand ordinate.

several times by a double random interleaved staircase procedure (Cornsweet, 1962). After further dark adaptation the conditioning field·radiance was raised and the observer's threshold was remeasured. This procedure was repeated until a series of increment thresholds were obtained for a range of increasing field radiances.

In the dynamic experiments, the time-varying threshold was tracked by means of the Method of a Thousand Staircases (Cornsweet and Teller, 1965; Mollon and Polden, 1980). Fifteen successive passes were made through the adaptation sequence and sensitivity was probed at a large number of instants $(\Delta t_1 \ldots \Delta t_n)$ during this sequence. At the beginning of each pass the observer dark adapted for 5 min. Thirty test flashes, occurring at 2-sec

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intervals, were then presented to the dark-adapted eye. After a 2-sec pause, the conditioning field was next turned on and a further 70 flashes were presented at 2-sec intervals, the first beginning 100 msec after the onset of the field. Finally, the field was turned off and 90 flashes were presented during the course of early dark adaptation, the first beginning 100 msec after extinction of the field. On the first pass through this sequence, the test flashes were all of the same radiance and the observer indicated by push-buttons whether or not he had seen each flash. The response made at a given value of Δt was stored by the computer and was used to determine the test radiance at that Δt on the next pass, the adjustments being made according to a single staircase procedure (Cornsweet, 1962). Similarly, the radiance at each Δt on the third pass depended on the corresponding response during the second pass. Thus 180 staircases were maintained concurrently, each corresponding to one value of Δt. For a given value of Δt, the threshold plotted in the figures (see, for example, Fig. 1b) is based on the mean of those positions of the neutral-density wedge that were visited on the last eight passes.

At the end of every experimental session, the quantum flux density of each beam was measured by placing a PIN-10 photodiode at the position of the observer's pupil.

RESULTS

Figures 1a and 2a display the results of the steady-state (equilibrium) increment threshold experiments for the field wavelengths $\mu = 674$ nm and $\mu = 530$ nm respectively. Each datum point represents the average of at least three separate threshold determinations. Stiles' (1978) standard increment threshold function $\zeta(x)$ is drawn through each data set. The conditioning field flux required to produce a tenfold loss in sensitivity for the 530 nm background was 8.5 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}; that required for the 674 nm background field was 9.5 log quanta $\cdot$ sec^{-1} $\cdot$ deg^{-2}.

Figure 1b shows a representative set of dynamic state increment threshold functions obtained for conditioning fields ($\mu = 674$ nm) that raise absolute increment threshold in the steady-state by 0.36, 0.49, 0.57, and 0.77 log units. All four curves indicate a sudden but short-lived loss of threshold sensitivity when the conditioning field is abruptly turned on. This onset transient appears to last less than 10 seconds.

A similar family of functions is shown for $\mu = 530$ nm. But here can be seen a more protracted adaptation to the conditioning field before the steady-state level is reached. The onset transients are of longer duration and greater magnitude. More than two mins may pass before the field adaptation is completed. The adaptation curves also appear to be biphasic.

To determine if these differences in threshold adaptation were reliable, dynamic thresholds for the two background field wavelengths were measured in a carefully counterbalanced design. The fluxes of the red and green conditioning fields were adjusted to raise the steady-state threshold for the test flash by approximately 0.5 log unit. For each field wavelength condition the dynamic adaptation and recovery functions were measured four times. The
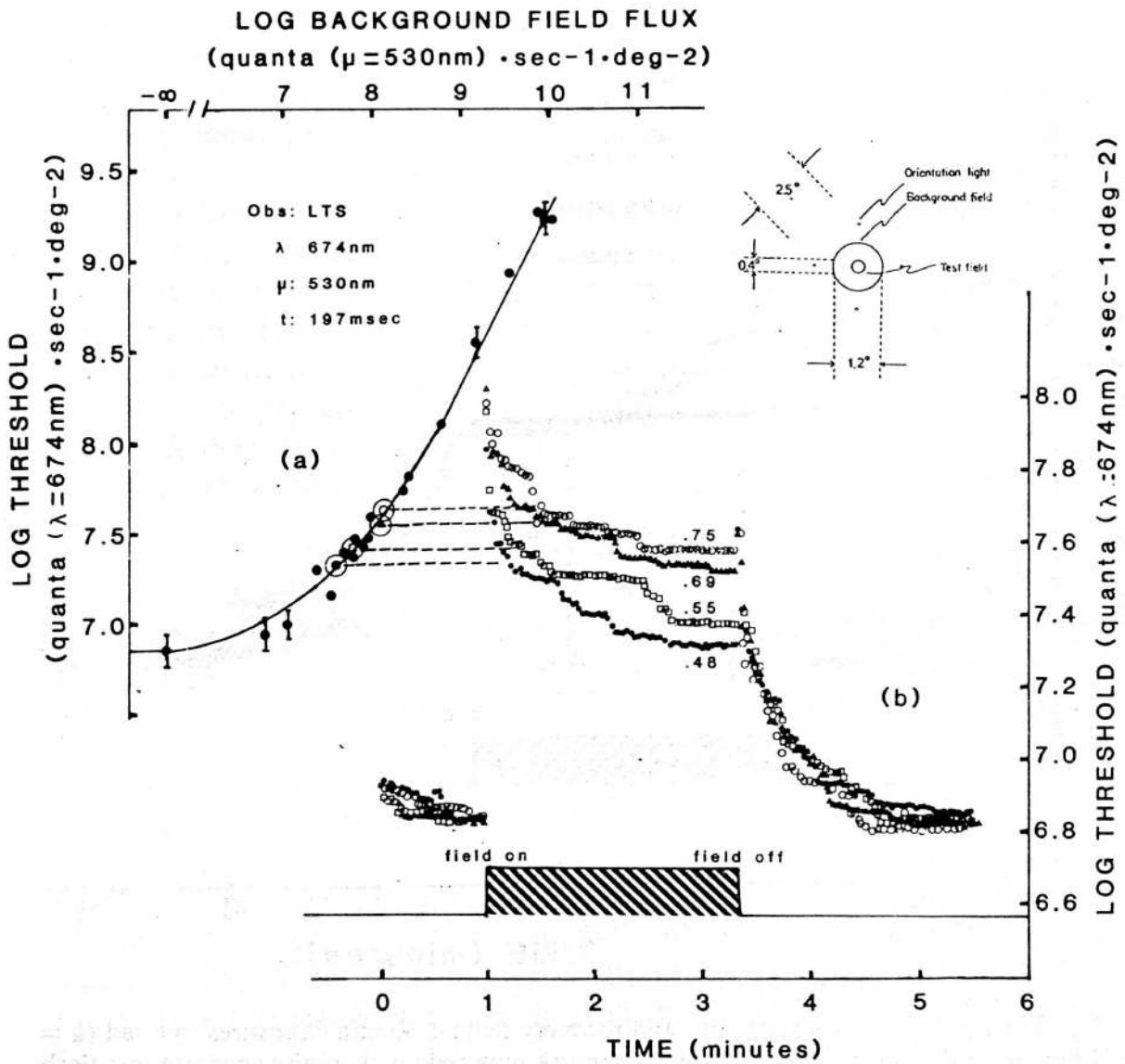
Fig. 2. (a) Steady-state increment threshold curve for observer LTS ($\lambda = 674$ nm, $\mu = 530$ nm). Error bars represent one standard deivation of the mean. (b) Time course of light adaptation to and recovery from 2.33 min exposures to four conditioning fields which raise absolute test flash threshold by 0.48 (•), 0.55 (□), 0.69 (▲), and 0.75 (○) $\log_{10}$ units. A broken line connects the set of data obtained under dynamic (non-equilibrium) conditions with the steady-state threshold (identified by the same symbol and plotted to the left). The hatched region below curves indicates onset and offset of background field, occurring respectively at 1 min and 3.33 min after first threshold determination. Note that the scale of the right-hand ordinate is double that of the left-hand ordinate.

averaged results are shown in Fig. 3. Immediately it can be seen that there are different time courses of adaptation and recovery for the two background fields. The onset transient for $\mu = 530$ nm is both greater in magnitude and longer in duration than that for $\mu = 674$ nm. In fact, the steady-state level is reached only after about 100 sec of adaptation to the green field as contrasted to about 18 sec of adaptation to the red field. Furthermore the adaptation curve appears to be biphasic.

On the other hand, the time course of threshold recovery (dark adaptation) appears to be slower for the red field and the data do not appear to be fitted by a single exponential curve. However, both the offset transients (about
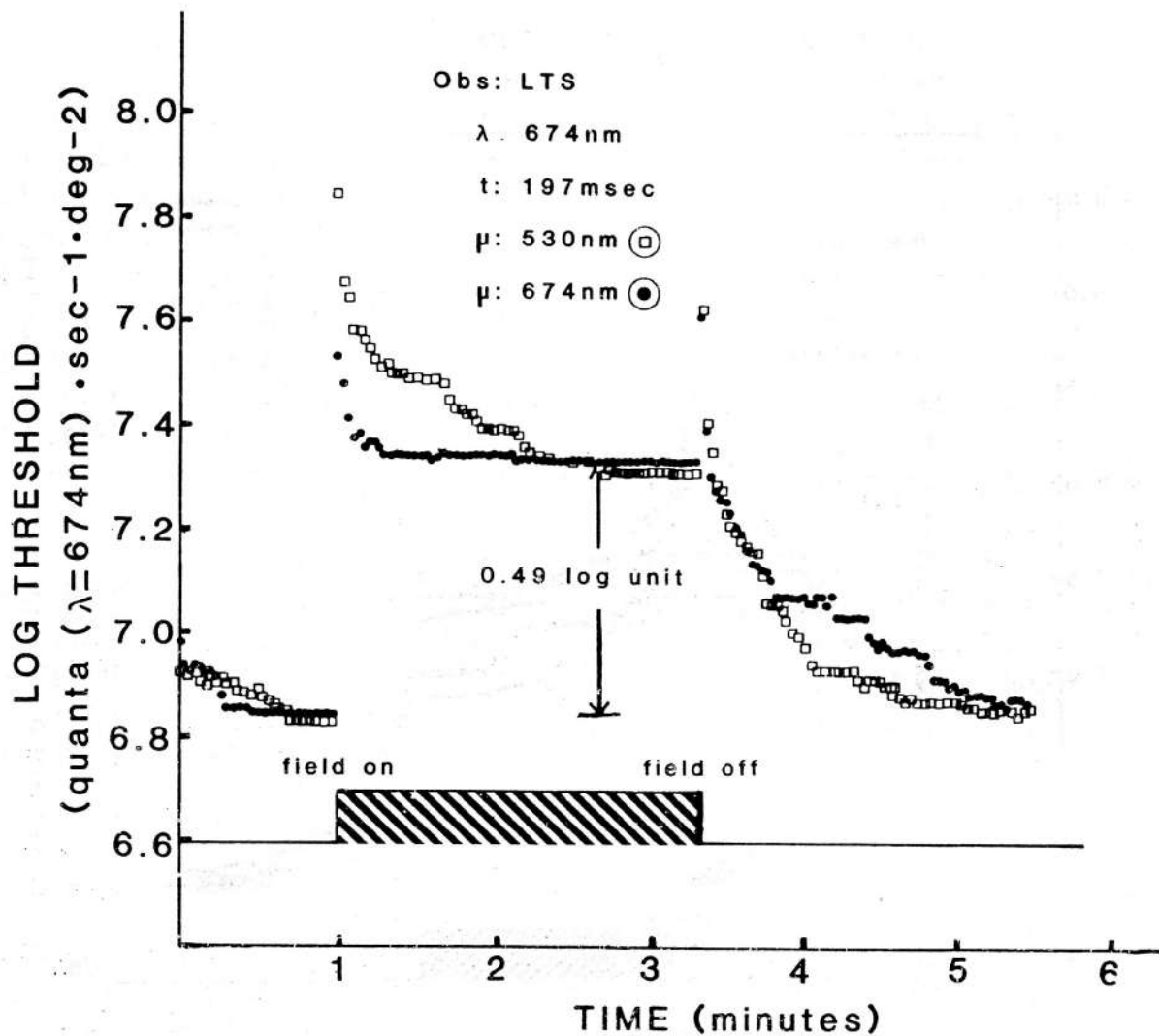
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Fig. 3. Time course of adaptation to and recovery from 2.33 min exposures to a red ($\mu = 674$ nm, •) and a green ($\mu = 530$ nm; □) conditioning field which raise absolute test flash threshold by approximately the same amount (0.5 log unit). The hatched region below the curves indicates the onset and offset of background field, occurring respectively at 1 min and 3.33 min after first threshold determinations.

0.3 log unit elevation above the steady-state level) and the time taken for the threshold to drop to twice the final equilibrium value (about 20 sec) are the same for the red and green fields.

DISCUSSION

Light adaptation. If (a) the detection of our 674-nm target depended on the same channel throughout the course of light adaptation to either 674-nm or 530-nm fields and if (b) this channel obeyed the Principle of Univariance (Rushton 1972), then the two light-adaptation functions of Fig. 3 should have identical shapes. Our results suggest that at least one of the conditions (a) and (b) does not hold. One possibility is that the steady-state thresholds are determined by different post-receptoral channels. In the homochromatic case ($\lambda = \mu = 674$ nm) it is unlikely that any part of the light-adaptation function depends on a chromatically opponent channel, whereas such a

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channel might well mediate the steady-state threshold for 674-nm targets on the 530-nm field. As in the case of the short-wavelength pathway (Pugh and Mollon, 1979), we might suppose that the recovery of sensitivity of a chromatically-opponent channel depends on a restoring force that builds up only slowly.

Why is there an inflexion in the light-adaptation function for $\mu = 530$ nm? Given the wavelengths of target and field, it seems unlikely that the inflexion represents a transition from detection by the middle-wavelength cones to detection by the long-wavelength cones. We tentatively suggest that (a) the early branch represents recovery at a non-opponent site, a site that is either in series or in parallel with a chromatically-opponent site and (b) the second branch represents the slower recovery of a chromatically-opponent site that mediates the steady-state threshold.

Dark adaptation. It also appears that a single univariant mechanism does not mediate thresholds during recovery from the two fields; but here it is for $\mu = 530$ nm that adaptation is slower. The transient loss of sensitivity 100 msec after termination of the field is similar for $\mu = 674$ nm and $\mu = 530$ nm and the two curves then run together for the first 30 sec of dark adaptation; but after that they diverge and there is a suggestion that the curve for $\mu = 674$ nm is biphasic. These findings are qualitatively similar to those described in an abstract by Brown (1981), who used 20-msec 650 nm targets subtending 20′ and who found that dark-adaptation curves were biphasic in the case of long-, but not short-, wavelength fields and that 'the half-life of recovery was faster for 500 and 480 nm fields than for longer wavelength fields, whether the intensities of the fields had been equated for π_5 or for test threshold immediately after the field was turned off'.

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