

DARK ADAPTATION OF THE LONG-WAVELENGTH SENSITIVE CONES

ANGELA M. BROWN*

Vision Research Laboratory, University of Michigan, Ann Arbor, MI 48109, U.S.A.

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Abstract—Long-wavelength sensitive (L) cone dark adaptation curves were measured with a 10-msec, 20' v.a., 650 nm test flash and a moderate intensity adapting field. When the 650 nm and 500 nm fields were equated for the L cones, the dark adaptation curve fell faster for the 500 nm field than for the 650 nm field. Over the range of adapting lights used, no adjustment of the intensities of the two fields made their dark adaptation curves similar. When 500 nm light was added to the 650 nm field, dark adaptation was faster. Visual sensitivity is not regulated by any single photoreceptor type in this experiment.

INTRODUCTION

According to the principle of univariance, the wavelength composition of an adapting field has no effect by itself on the sensitivity of the eye in any experiment where the adapting signal arises in only one type of photoreceptor. For any pair of adapting lights differing only in wavelength composition, there must exist an intensity ratio at which the photoreceptors absorb photons at the same rate from the two fields. At that intensity ratio, all visual effects of the adapting fields must be identical; in a dark adaptation experiment, the two fields must produce identical dark adaptation curves. In the present experiments, 650 and 500 nm adapting fields were adjusted in intensity to produce equal test thresholds during light adaptation, which should equate them for the action spectrum of the long-wavelength sensitive (L) cones (Wandell and Pugh, 1980a). These adapting backgrounds produced dramatically different dark adaptation curves. This finding could have two explanations: either the adapting signal originated in a photoreceptor type with an action spectrum different from the L cones, or else the principle of univariance does not apply here because the adapting signals originate in more than one type of receptor. No adjustment of the relative intensities of the adapting fields made the dark adaptation curves identical. Furthermore, even a small amount of 500 nm light added to the 650 nm adapting field made recovery faster than with the 650 nm adapting field alone; increasing the intensity of the 650 nm field always produced slower recovery. Therefore, the effects of the adapting fields used in these experiments depend on signals originating in more than one receptor type.

It would come as no surprise that sensitivity is regulated by more than one type of photoreceptor if

the test were detected by means of signals originating in some receptor in addition to the L cones. The 650 nm test flash used in the present experiments is unlikely to stimulate any photoreceptors other than the L and possibly the middle-wavelength sensitive (M) cones. To rule out M cone detection, M cone absolute threshold was estimated in three ways. First, the difference between Stiles' π_4 and π_5 field sensitivity action spectra is 0.68 log units at 650 nm. Assuming that the L and M cones are the only receptors that affect π_5 and π_4 sensitivity respectively, and that the two cone systems do not differ appreciably in their Weber fractions or their spatial and temporal integration properties, this is an estimate of the difference in absolute threshold between the L and M cones at 650 nm. Second, a similar calculation was based on measurements of the π -mechanisms of subject A.M.B. The absolute threshold of π_4 at 650 nm was estimated from the absolute threshold for a 480 nm, 200 msec test flash and the π_5 field sensitivity action spectrum. The difference between the estimated π_4 absolute threshold at 650 nm and the π_5 absolute threshold measured with a 650 nm, 200 msec test flash was 1.02 log units. Third, M cone absolute threshold was estimated using two protanopes as subjects. Their absolute thresholds for the 650 nm test flash were both about 0.98 log unit higher than the absolute threshold for the normal subjects. The dark adaptation data for A.M.B. were never more than 0.9 log units above absolute threshold. All the data for A.M.B. fell to within 0.65 log units above absolute threshold within 12 sec after the adapting field was turned off. Test threshold for J.W.D. was always less than 0.65 log units above absolute threshold during dark adaptation. It is therefore unlikely that the test flash was detected by the M cones during the dark adaptation part of the present experiments.

The test flash used in these experiments was a 10 msec, 20' visual angle, 650 nm test flash. This test was chosen because it seemed likely to be detected via

*Present address: Department of Psychology, University of Washington, Seattle, WA 98195, U.S.A.

channels whose sensitivity is regulated by L cone signals only. The sensitivity of the eye to long duration, long-wavelength test flashes is clearly regulated by several types of cone during steady light adaptation (Wandell and Pugh, 1980b, Sharpe and Mollon, 1982) and during dark adaptation (Wandell, 1977; Sharpe and Mollon, 1982), and interaction between receptors occurs in detection as well (Boynton, Ideka and Stiles, 1965). When a brief test flash is used, these interactions appear to be minimized (Wandell and Pugh, 1980b, Reeves, 1981, Ikeda, 1964).

While the use of the small, brief, long-wavelength test flash seemed especially likely to produce dark adaptation curves that reflect the recovery of a single class of cone, the present experiments show evidence that several types of visual receptor control visual sensitivity under these conditions.

METHODS

All the experiments to be reported here were run on a three-channel Maxwellian view system. One channel provided the foveal, 650 nm test flash which subtended 20' of visual angle. The light for the test flash was produced by a deep red GaAsP light emitting diode (LED), and it was made monochromatic by passing it through an interference filter. The test was flashed on for 10 msec every 500 msec, a tone was simultaneously sounded each time it was presented. The intensity of the test flash was controlled by means of a neutral density wedge whose position was continuously recorded with an $x-y$ plotter.

The other two channels provided the 10 deg adapting fields. The bandwidth of the adapting lights was about 10 nm. The intensities of the adapting fields used in these experiments ranged between 8.35 and 10.64 log photons $\text{deg}^{-2} \text{sec}^{-1}$ at 650 nm and between 8.41 and 10.20 log photons $\text{deg}^{-2} \text{sec}^{-1}$ at 500 nm. This corresponds to between 1.21 and 3.66 log phot. td. The very brightest adapting light bleached less than 0.2% of the visual pigment in the L cones.

The subjects in the main experiments were two women with normal color vision. One of the subjects (A.M.B.) wore a spectacle lens during most experiments (o.d. = -1.75 sph, -2.25 cyl, axis 96 deg), but the data collected using an untinted soft contact lens were comparable in every way. The other subject had 20/20 vision and needed no correction. The two protanopic men mentioned in the introduction tested as protanopes on the Ishihara pseudoisochromatic plates, the Farnsworth-Munsell 100-hue test, and the Nagel anomaloscope. Each could establish a colorimetric match between a 450 nm plus 650 nm bichromatic light and a 500 nm standard.

The subject's head was held in position by a bite bar. During the experiment, two small fixation points 1 deg apart, located above and below the test field stop, were illuminated by broadband green LED's.

Their intensity was manually adjusted during the experiments to keep them just bright enough to gain fixation, but dim enough not to alter test threshold.

Procedure

After 5 min of initial dark adaptation, the adapting field was presented for 2 or 3 min. Increment threshold was measured by the method of adjustment, and the 3-min duration was used whenever the adapting field elevated test threshold by more than 1.5 log units above absolute threshold.

At the end of the light adaptation period, the subject turned the field off, simultaneously started the time base of the $x-y$ plotter, and immediately began to manipulate the wedge to keep the test at threshold. First the wedge was adjusted until the test just disappeared, then it was turned until the test became just visible, then decreased, then increased, and so forth. For each condition, this procedure was followed until four to six runs were completed, at which time the background conditions were changed and the experimental procedure was repeated.

The data in this experiment were the intensities of the test flash at which the wedge changed direction. The increment threshold value was calculated by averaging the data measured during the last 30 sec of light adaptation, during which time test threshold was approximately constant. The threshold during dark adaptation was computed as a function of time by averaging the data within 5-sec time bins.

RESULTS

Experiment 1

In the first experiment, dark adaptation curves following exposure to 650 and 500 nm adapting fields were compared. The recovery showed two phases. Immediately after the adapting field was removed, test threshold fell abruptly. The first threshold that could be measured on the dark adaptation curve (the average of all data occurring in the first 5 sec in the dark) was never more than 0.9 log units above absolute threshold, whereas test threshold during the presentation of the adapting field was as much as 2.5 log units above absolute threshold. The second phase consisted of a gradual recovery from the first phase threshold to the absolute threshold.

If visual sensitivity is regulated only by signals originating in the L cones, then fields equated for the L cones ought to produce identical dark adaptation curves. It may be seen in Fig. 1 that recovery from the 500 nm field was faster than recovery from the 650 nm field.

While Fig. 1 shows that the L cones do not regulate threshold alone, it does not rule out the possibility that a single photoreceptor type with a different action spectrum could provide the adapting signal in these experiments. The latter hypothesis can be ruled out by showing that, no matter how we adjust the intensities of the adapting fields, the dark adaptation

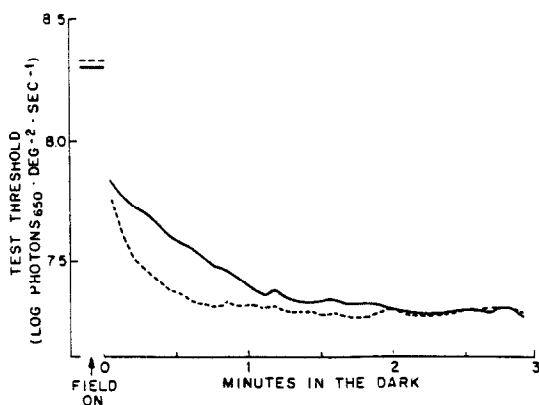


Fig. 1. Dark adaptation curves measured after exposure to 500 nm. 9.05 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ (dashed curve) and 650 nm. 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ (solid curve) adapting fields. The fields were approximately equated to provide equal steady-state increment thresholds (horizontal dashed and solid lines at the left).

curves cannot be made identical. In the first six graphs in Fig. 2, the continuous curves are copies of a single dark adaptation curve. These data were measured after adaptation to a 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ 650 nm adapting field. The data presented for comparison (triangles) were measured with six different 500 nm adapting fields at intensities that ranged over 1.8 log units. None of the 500 nm dark adaptation curves coincides with the 650 nm curve, even though the 650 nm curve has been slid vertically by less than 0.15 log units to agree with the 500 nm curve at absolute threshold. Similarly, the four graphs in the lower part of Fig. 2 show a single dark adaptation curve measured with a 500 nm adapting field at 10.20 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ (broken lines). The circles are dark adaptation curves measured with 650 nm adapting fields ranging over 1.5 log units in intensity. Here, too, no 650 nm field produced a dark adaptation curve similar to the one produced by the 500 nm field. Late in recovery, the two curves measured after adaptation to the very brightest 500 nm field and to the 650 nm field at 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ nearly coincide. In that experiment, the quantum flux from the 500 nm field was greater than that from the 650 nm field by a factor of ten. If the latter parts of those curves reflected activity in a single cone pigment, that pigment would have its peak spectral sensitivity even further in the long wavelength part of the spectrum than the L cones. There is no known human visual pigment with such an action spectrum. In any case, the discrepancy in the early part of the curve remains and cannot be explained by any single class of cone.

These dark adaptation curves cannot be made identical by adjusting the intensity of the adapting field. We may conclude from this result that the signal controlling sensitivity to this test flash during dark adaptation does not originate in any single type of visual photoreceptor.

Experiment II

The principle of univariance requires that if the single-receptor adaptation hypothesis holds in this experiment, then suitably adjusted adapting fields of all wavelengths must also produce identical dark adaptation curves when each is presented superimposed on a common adapting field. This common adapting field may be of any spectral composition whatever; it may even have the same wavelength as one member of the equated pair, in which case the intensity of the common field is simply increased.

The 650 nm data from Fig. 2 appear again in Fig. 3 on a single set of axes. The speed of recovery decreases as the intensity of the 650 nm adapting field increases, and higher intensity backgrounds produce higher thresholds both while the adapting field is present and after the light goes off. If 650 nm light is added to a 650 nm adapting field, test threshold is always higher during dark adaptation.

In Experiment II, 500 nm light was added to a 650 nm adapting field. The intensity of the 650 nm field remained constant at 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ throughout the experiment. The intensity of the 500 nm added field ranged from 8.35 to 10.20 log quanta $\text{deg}^{-2} \text{sec}^{-1}$. The color appearance of the bichromatic field ranged from orange at the lowest intensity, through a slightly yellowish white at 8.67 log quanta $\text{deg}^{-2} \text{sec}^{-1}$, to green at the highest intensity of the 500 nm added field. The continuous lines in Fig. 4 are the 650 nm data and the broken lines are the 500 nm data taken from Fig. 2. The circles are dark adaptation data obtained after exposure to the bichromatic adapting fields. While increasing the intensity of the 650 nm adapting field always resulted in higher thresholds during dark adaptation, adding even a small amount of 500 nm light to the 650 nm field resulted in lower thresholds during dark adaptation.

Similar results were obtained on observer J.W.D. In Fig. 5, the solid and broken lines are data obtained with 650 and 500 nm fields, respectively. The horizontal lines before $t = 0$ are the increment threshold values. When they are equated as in the upper graph, the dark adaptation curves differ. The data in the lower graph were measured with adapting fields 0.8 log units more intense, presumably still equated for the L cones. They do not coincide, either. The circles are the dark adaptation curves that result when the 650 and 500 nm fields are presented together. For subject J.W.D. as for A.M.B., the addition of 500 nm light to the 650 nm adapting field causes a decrease in threshold during dark adaptation.

DISCUSSION

These experiments show that cone dark adaptation measured with a brief, long-wavelength test flash is complicated. This is in striking contrast to comparable steady light adaptation experiments, where test

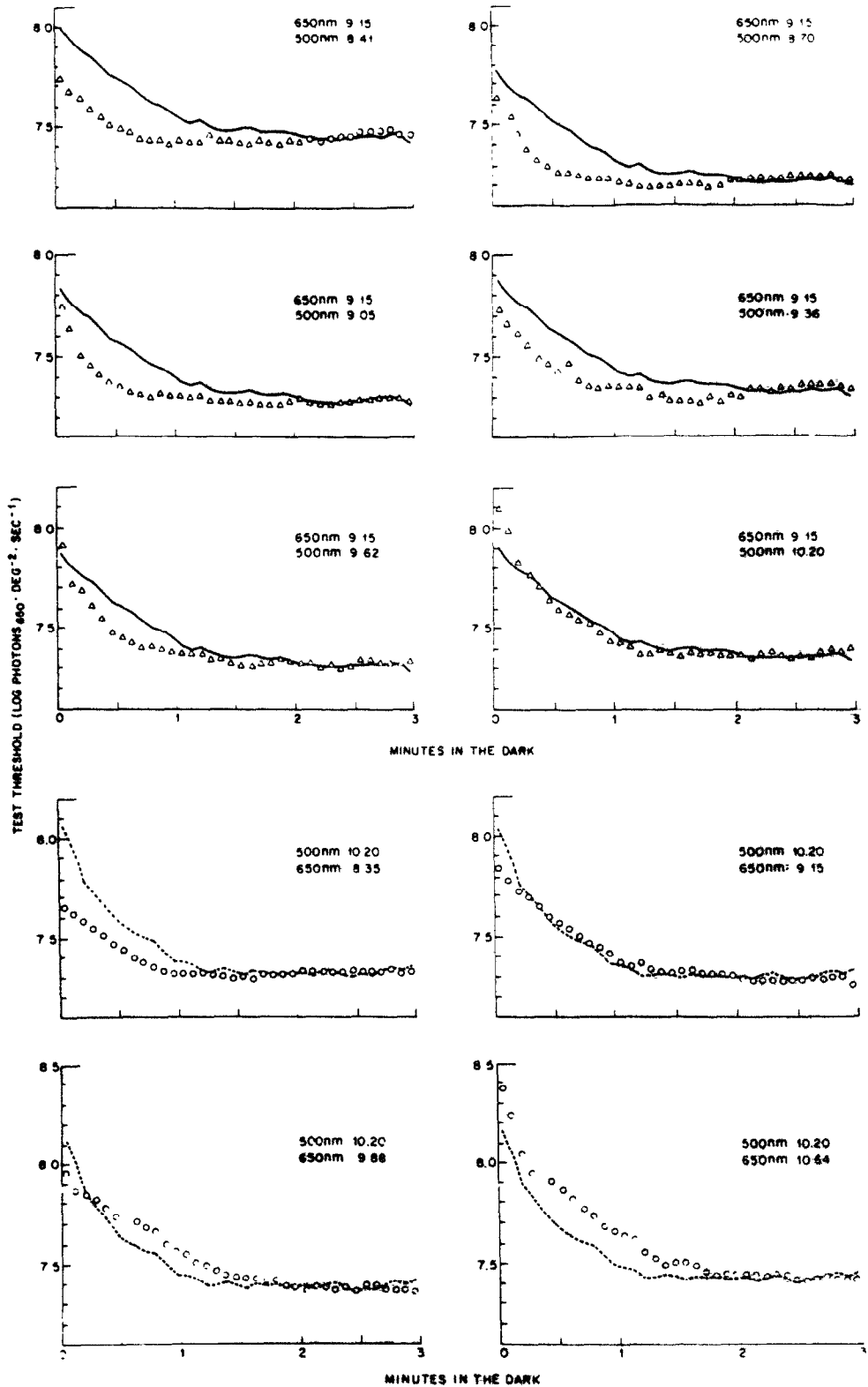


Fig. 2. Top six panels: a dark adaptation curve measured with a 650 nm, 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ adapting field (solid lines) is compared to curves measured with 500 nm adapting fields at 8.41, 8.70, 9.05, 9.36, 9.62 and 10.20 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ (triangles). Lower four panels: a dark adaptation curve measured with a 500 nm, 10.20 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ adapting field (dashed lines) is compared to curves measured with 650 nm adapting fields at 8.35, 9.15, 9.88 and 10.64 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ (circles).

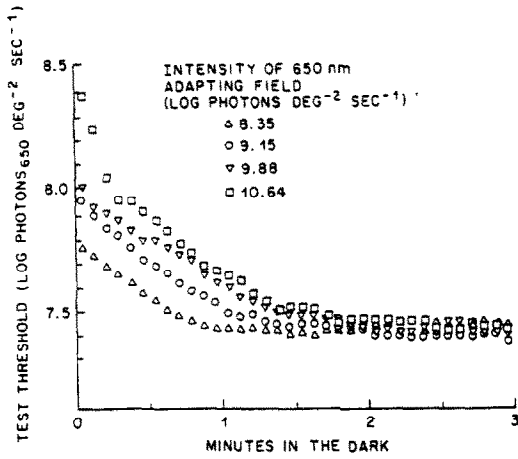


Fig. 3. Dark adaptation curves measured with 650 nm adapting fields at 8.35, 9.15, 9.88 and 10.64 log quanta $\text{deg}^{-2} \text{sec}^{-1}$.

threshold appears to depend entirely on signals arising in the L cones (Wandell and Pugh, 1980a).

During dark adaptation, only the L cones detect

the test flash used in these experiments. On the other hand, at least two types of visual photoreceptor with different spectral sensitivities produce adapting signals that control test threshold. This has been demonstrated in two ways. First, when dark adaptation is measured with adapting fields of different spectral composition, different dark adaptation curves result. These differences do not disappear no matter how the intensities of the adapting fields are adjusted. Second, when even a small amount of 500 nm light is added to a 650 nm preadapting field, dark adaptation proceeds more rapidly than when the 650 nm field is used alone. In contrast, the addition of 650 nm light to the 500 nm adapting field delays recovery during dark adaptation. This cannot be explained by any model in which adaptation is controlled by a single univariant type of photoreceptor.

The cone phase of dark adaptation cannot easily be separated into three independent branches, each controlled by a single type of cone. The short-wavelength sensitive (S) cones show complex behavior known as "transient tritanopia" during dark adaptation. Detection threshold for short wavelength test flashes,

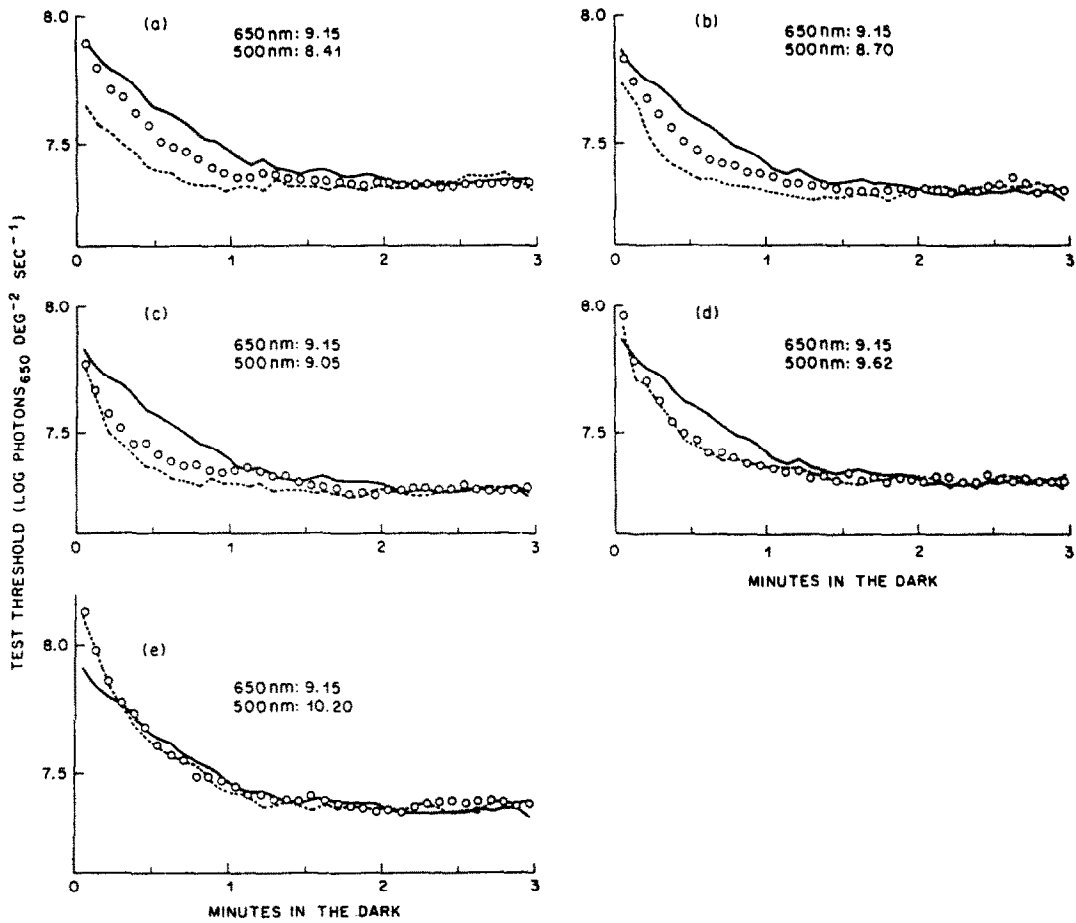


Fig. 4. Dark adaptation curves measured after exposure to monochromatic fields (lines) and bichromatic (circles) adapting fields. The 650 nm adapting fields (solid lines) are all at 9.15 log quanta $\text{deg}^{-2} \text{sec}^{-1}$; the 500 nm adapting fields (dashed lines) are a 8.41, 8.70, 9.05, 9.62 and 10.20 log quanta $\text{deg}^{-2} \text{sec}^{-1}$. The circles are the dark adaptation curves that result when the two monochromatic adapting fields are used together.

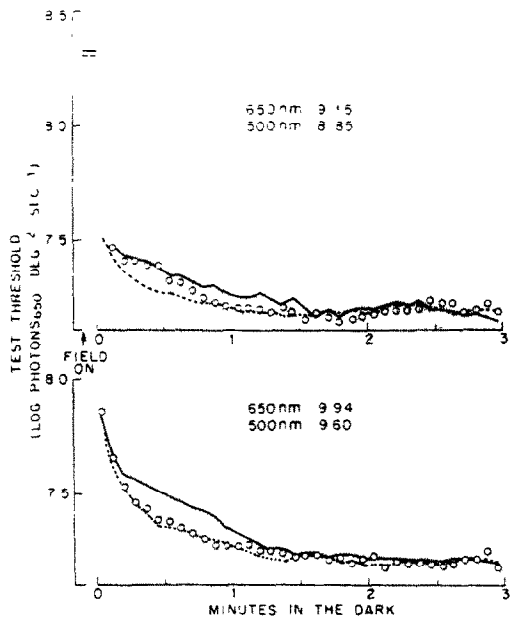


Fig. 5. Dark adaptation curves for a second subject. The horizontal lines on the left of the top graph are the steady-state threshold values for the 500 nm (dashed line) and the 650 nm (solid line) adapting fields, which have been adjusted in intensity so these values are nearly equal. The dark adaptation curves shown with solid and dashed lines starting at 2.5 sec are dark adaptation curves measured after adaptation to these same monochromatic fields. The circles are the dark adapting curves that result when the two monochromatic adapting fields are used together.

which are presumably detected by means of S cone signals during steady adaptation, may increase or decrease in the first few seconds of dark adaptation, depending on the wavelength composition of the adapting field. This phenomenon was originally reported by Stiles (1949), and has recently been studied extensively (Augenstein and Pugh, 1977; Mollon and Polden, 1977; Pugh and Mollon, 1979). Threshold elevation occurs when the adapting field is long-wavelength; it can be abolished by the addition of a suitable quantity of short-wavelength adapting light (Augenstein and Pugh, 1977). These findings are experimental proof that the principle of univariance does not hold for these conditions.

Two studies have reported data suggesting that the L cones are unaffected by signals from other types of photoreceptor as they recover their sensitivity after exposure to bleaching fields (du Croz and Rushton, 1966; Hollins and Alpern, 1973). While neither study investigates the question of univariance very thoroughly, it would not be surprising that adaptation effects dependent on processes occurring within the photoreceptors should predominate when significant visual pigment is bleached. At more moderate adapting field intensities, behavior is clearly complex (Hollins and Alpern, 1973; Auerbach and Wald, 1955; Auerbach, 1960; Mollon and Polden, 1977; Reeves, 1981). A clear relationship exists between the wave-

length composition of the adapting field and the time-course of dark adaptation for L cone-equated adapting fields (Wandell, 1977; Sharpe and Mollon, 1982). Some authors report two-branched L cone dark adaptation curves (Auerbach, 1960; Sharpe and Mollon, 1982; Wandell, 1977). The 650 nm dark adaptation curves shown here are not exponential in shape (Fig. 3), and they show a hint of the two-branched form reported by Auerbach (1960) and Sharpe and Mollon (1982). All the experiments summarized above involve the use of long-duration test flashes. Reeves (1981) investigated "transient protanopia", a smaller effect similar to transient tritanopia only occurring with long-wavelength test flashes. He reports that the transient threshold elevation disappears when the long-wavelength test flash is small in diameter and brief. However, even these data, if examined carefully, show small but systematic differences in the effects of adapting fields depending on their wavelength; those results are therefore not inconsistent with the results reported here.

How is the complexity of the dark adaptation experiments reported here to be reconciled with the univariance of the results of the comparable increment threshold experiments? One possibility is that adaptation occurs at two sites within a single pathway. The adapting signal at one site could arise in only the L cones and affect sensitivity under steady adaptation and perhaps under dynamic conditions as well. At the other site, the adapting signal could arise in more than one type of cone, but affect sensitivity under dynamic conditions only. Under steady adaptation, the gain of the latter stage would be held constant by a "restoring force" (Pugh and Mollon, 1979). Such a system would produce univariant increment threshold data, but would also produce dark adaptation data that reflect signals arising in several types of cone.

Another possibility is that many channels mediate detection under different experimental conditions. Suppose, for example, that the test flash can be detected by either one of two pathways, one of which fulfills the single-receptor adaptation hypothesis and one of which does not. If this is the case, then the relative sensitivities of the two channels need not be the same under steady and dynamic conditions. If different channels determine threshold in each case, then the discrepancy between the well-behaved increment threshold curves and the unexpected behavior of the dark adaptation curves is more understandable.

This scheme implies that the π -mechanisms studied in an increment threshold experiment may be only a subset of the pathways used by the eye to perceive visual stimuli. There may be many visual mechanisms that never determine detection threshold during any increment threshold experiment, and therefore cannot fulfill the definition of a π -mechanism. Some of these mechanisms may mediate detection at threshold

under dynamic conditions, but some of them may never do so.

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