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## Dark Adaptation in the Presence of Waning Background Luminances\*

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The course of dark adaptation following low-level pre-exposure was determined against background luminances whose logarithms decreased linearly with time. Luminance was reduced by 7 log units over periods of 3.5, 7, 14, and 21 min. Transient adapting fields of this kind yield curves that remain increasingly behind the time course of normal dark thresholds; the delay varies with the rate of background change. Increment thresholds derived from such dark-adaptation curves exceed corresponding thresholds for stationary adapting fields by as much as 1.25 log unit, particularly during the scotopic portion of steep luminance descents. The deficit in contrast sensitivity may be attributed to the additive action of the real background plus the equivalent background resulting from the pre-exposure bleach. Dark thresholds measured during temporary removal of a gradually decreasing field luminance are persistently elevated. This suggests that prolonged exposure to waning illumination may slow dark adaptation below its maximum rate.

INDEX HEADING: Vision.

Dark adaptation of the human eye is usually measured in complete darkness after pre-exposure to light. There are few studies<sup>1-8</sup> in which the increase of sensitivity was determined in the presence of one or a series of adapting fields. Introduction of such fields not only restricts dark adaptation to the increment threshold for the lowest prevailing luminance, but also delays scotopic adaptation. At higher levels, backgrounds eventually shift the time of the cone break and even affect photopic thresholds. Consecutive exposure to a sequence of descending luminance steps, therefore, is not equivalent to continuous adaptation in the dark. If, instead of stationary backgrounds, flashes variable in luminance, duration, and number are interspersed at different times after pre-exposure, recovery from momentary threshold elevation is fast, with little if any permanent effects on subsequent adaptation.<sup>9-14</sup>

Large abrupt changes from light to darkness, commonly used in laboratory studies, hardly ever occur in nature. They may be considered as abnormal stimulus conditions if they exceed the instantaneous sensitivity gain afforded by the dilation of the pupil and by early cone adaptation.<sup>6</sup> In this experiment, dark adaptation was measured against graded backgrounds whose range and rates of change were more compatible with the decline of natural illumination as, for example, at sunset.

The global luminance of the sky decreases over almost 7 log units (with a constant rate of change of log luminance from  $10^2$  to  $10^{-3}$  mL) as the sun travels from approximately  $5^\circ$  above to  $15^\circ$  below the horizon.<sup>15,16</sup> During this period, the eye has to increase its sensitivity by a factor of more than a million, to maintain its optimum performance in spite of greatly varying luminance levels. In nature the corresponding change of threshold takes place over a period of 1.5-2 h as compared with 15-45 min under the usual laboratory conditions. Thus, by experimental standards, adaptation to the dark can proceed faster than is required by the rate of darkening in a natural environment. The question

arises whether a gradually decreasing background delays dark adaptation and in what manner.

Hardly any data pertinent to this problem can be found in the literature. In a study of night flying, Beebe-Center, Carmichael, and Mead<sup>15</sup> suggested that during twilight the eye adapts fast enough to keep up with the fall of environmental illumination. However, Allen and Carter,<sup>17</sup> investigating traffic visibility in the mesopic and scotopic range, proposed that the state of adaptation of the eye lags behind the change of illumination that occurs after sunset. Neither opinion is supported by observational evidence.

In approaching this problem, three types of delayed dark adaptation ought to be distinguished. The first one is related to the difference in time or value between regular dark thresholds and increment thresholds determined upon a graded background. The second delay refers to the difference between increment thresholds measured against fixed and waning backgrounds of equal luminances. The third delay is defined by the difference between dark thresholds recorded after pre-exposure only or during short periods of intermittent extinction of a transient adapting field. All three delays are discussed with the rate of background change as the parameter. Tungsten light was used throughout the experiment eliminating possible favorable effects on rod threshold kinetics that might result from the reddening of the sky during evening hours.

### METHOD

#### Subject

One of the authors, ATN, served as observer.

#### Apparatus

A three-channel visual discriminometer<sup>18</sup> was employed for threshold measurements. One channel provided the stimulus, a  $1^\circ$  white square presented for 0.04 s at  $10^\circ$  from the center on the horizontal meridian in the nasal field. The second channel furnished a circular back-

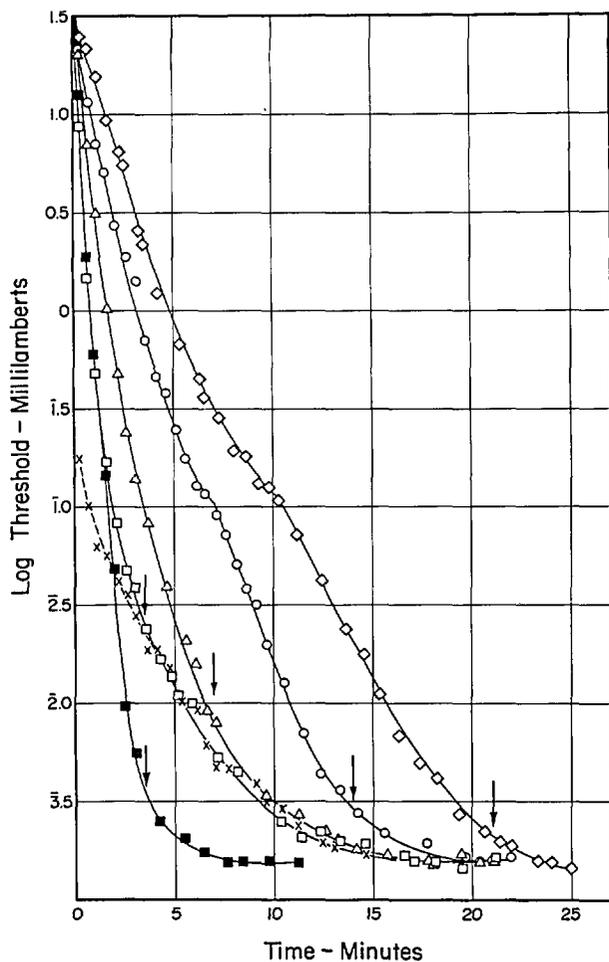


FIG. 1. Increment thresholds measured against log background luminance decreasing linearly with time. Backgrounds changed over 7 log units within 3.5 min ( $\square$ ), 7 min ( $\triangle$ ), 14 min ( $\circ$ ), 21 min ( $\diamond$ ), and 3.5 min with no pre-exposure ( $\blacksquare$ ). Arrows indicate times of background extinction. Normal dark thresholds recorded in the absence of any background luminance ( $\times$ ) largely coincide with the curve for the steepest background slope and are omitted after becoming invariant.

ground of  $30^\circ$  angular subtense and was also used for pre-exposure. Through the third channel, a small red fixation mark was superimposed onto the field. The whole stimulus arrangement was seen in maxwellian view with an effective pupil of 1.5-mm diameter. All observations were made from inside a light-proof booth built around the head of the discriminometer. A chin-forehead rest was used to assure proper positioning.

### Procedure

Thresholds were determined by use of the method of limits combined with preset stimulus luminances. Measurements were preceded by 45 min of dark adaptation followed (except where noted) by 5-min pre-exposure to 325 mL. Five procedures were used. (1) Adaptation in complete darkness. Thresholds were taken for a period of 21 min. Four curves were recorded.

(2) Dark adaptation to a waning background. From the level of pre-exposure log background luminance was gradually reduced, at a constant rate, to a value of  $3.25 \times 10^{-5}$  mL by a second experimenter. The total change was completed within 3.5, 7, 14, and 21 min; at the end of these periods background luminance was set at zero. After the initial bleach, thresholds were measured for a duration of 21 min or longer until a level had been reached. Three runs for each rate of background change were made in a random order. (3) Dark adaptation to a waning background without previous pre-exposure. Beginning with a background of 325 mL, the log of the adapting luminance was linearly and continuously reduced over 7 log units within 3.5 min. Results from four runs were obtained. (4) Log  $\Delta I$  vs log  $I$  function. Increment thresholds were determined for the same range of backgrounds as above, presented in successive steps of 0.2 to 0.5 log unit. To reach a steady state, the observer adapted for 90 s to each luminance level. Thresholds were established four times in ascending and descending order. (5) Instantaneous adaptation to complete darkness after intermittent extinction of a waning background. Dark thresholds were obtained while the adapting luminance, changing over periods of 14 and 21 min, was temporally blocked by a cardboard inserted

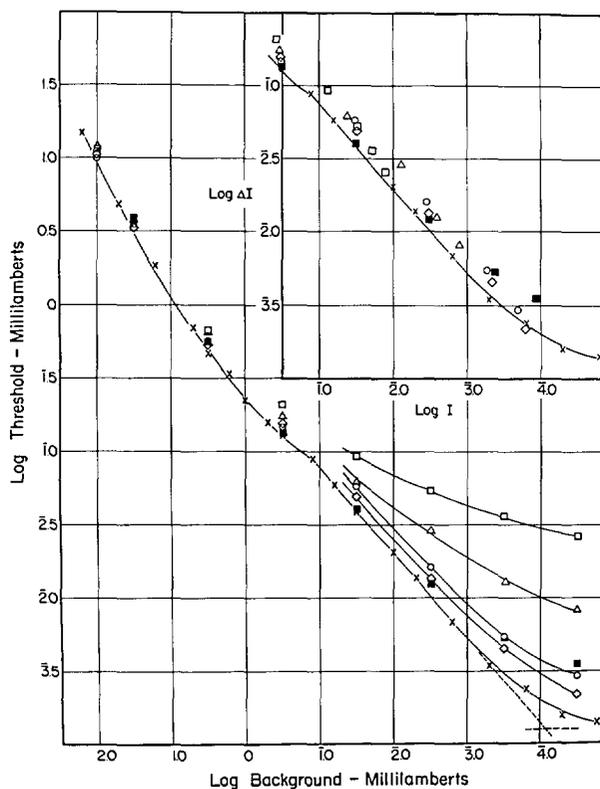


FIG. 2. Increment thresholds vs background luminance obtained under stationary ( $\times$ ) and dynamic conditions (other symbols, same as in Fig. 1) for various rates of background change. The intersection of the broken lines denotes the value of *Eigenlicht*. Inset: Increment thresholds are replotted against the log of the sum of real and equivalent backgrounds.

into the light path. These dark intervals lasted from 15 to 90 s, and one to three threshold measurements were made while the invisible background continued to decrease at a constant rate. Before and after each extinction, increment thresholds were measured as described under (2). Three runs were completed for both rates of luminance change.

## RESULTS

Average thresholds were obtained by pooling individual measurements from the various runs within half-minute or, after 10 min, full-minute intervals. Mean dark-adaptation curves for the experimental conditions (1)–(3) are presented in Fig. 1. After termination of pre-exposure, the threshold in complete darkness fell from 1.50 log mL (steady state) almost instantaneously by as much as 2.25 log units before entering the measured portion of the dark-adaptation curve ( $\times$ ). The curve does not appear to have a cone break but decreases smoothly for 2 log units and reaches a plateau after 15 min. For purposes of clarity, threshold values for the last 6 min are omitted from the graph.

In comparison, curves obtained in the presence of a waning background decrease gradually from the starting value through 4.0 log units until they approach the final scotopic level. Their slopes vary according to the rate of background change. Only the curve representing the shortest background duration of 3.5 min coincides in its lower portion with the course of normal dark adaptation. Thresholds measured against more slowly changing field luminances are increasingly displaced to the right and reach their end levels progressively later. For backgrounds descending over 14 and 21 min, curves show a discontinuity at a threshold value of 0.1 mL, which may be indicative of the cone break.

Adaptation to the fastest-changing field luminance recorded without pre-exposure proceeds almost linearly from the beginning to the end and overtakes ordinary dark thresholds after 2 min.

Figure 2 depicts the  $\Delta I$  vs  $I$  curve for stationary adapting fields, compared to increment thresholds measured against decreasing backgrounds. Thresholds for transient field luminances were derived from Fig. 1 after converting time on the abscissa into the background luminances presented at given moments. Resulting values were plotted, decreasing toward the right, to indicate the sequence in which they were obtained in the experiment. Through most of the photopic range, increment thresholds for steady and transient backgrounds run close together, the second group being slightly elevated. Beginning at a luminance of about 0.3 mL, however, the waning backgrounds yield considerably higher readings than measurements for steady state. This difference of threshold rapidly becomes greater with decreasing background luminance and increasing rate of change. A maximum threshold elevation of 1.25 log unit is found when the adapting

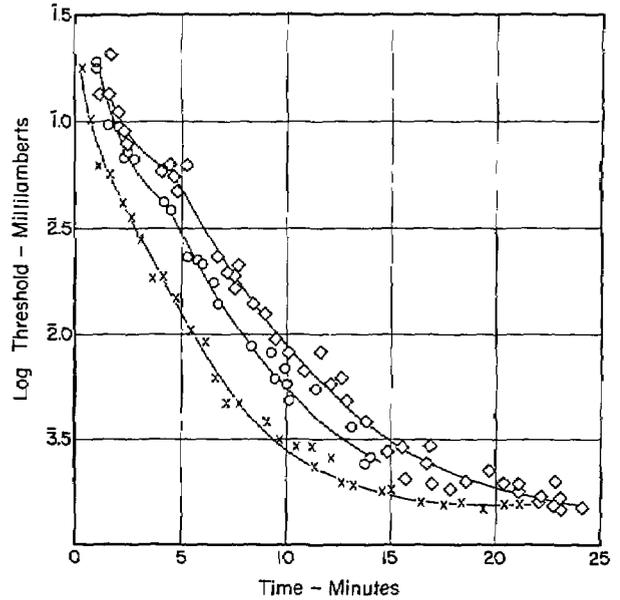


FIG. 3. Dark thresholds determined after pre-exposure only ( $\times$ ) and during temporary extinction of background luminances decreasing over periods of 14 min ( $\circ$ ) and 21 min ( $\diamond$ ). Values for transient backgrounds were pooled from 3 runs each.

field assumes its minimum value 3.5 min after pre-exposure. In contrast, a deviation as small as 0.2 log unit is measured when the same low background is presented after 21 min. Threshold differences for the other curves referring to intermediate rates of change are between these two extremes. With a waning background lasting 3.5 min, but no pre-exposure, thresholds deviate little from the  $\Delta I$  vs  $I$  curve for equilibrium. The greatest increment amounts to only 0.4 log unit, as compared to 1.25 log unit in the pre-exposed eye.

When the background luminance prevailing at any moment during the course of dark adaptation is temporarily turned off, thresholds measured shortly thereafter are considerably lowered, but they are still an average of 2 times (for 14-min change) to 3 times (for 21-min change) higher than those found during normal dark adaptation (Fig. 3). Several consecutive dark thresholds taken within such intervals of temporary background removal are uniformly elevated and do not seem to approach the standard curve recorded during undisturbed adaptation in darkness.

## DISCUSSION

Time courses for increment thresholds, determined against a waning background, lag behind the regular dark-adaptation curve obtained without background illumination. The difference between both types of thresholds is predominately influenced by two factors, level and duration of pre-exposure and rate of background change. Only the latter variable was investigated in this study. When steeply decreasing field luminances are used, delays are restricted to the first few minutes of dark adaptation after extinction of the pre-exposure

light. For backgrounds with gentler slopes, thresholds are elevated in value or delayed in time throughout the entire curve.

Results suggest that a linear rate of decrease of log background luminance does not necessarily produce a linear log-threshold-vs-time curve. Even though the rapid phase of instantaneous adaptation is straightened out, a discontinuity at about the same luminance level as the cone-rod transition in the  $\Delta I$  vs  $I$  curve is not always eliminated. A kink associated with the normal dark-adaptation curve would also be expected to remain if it were sufficiently marked. Our data do not indicate whether the levels of the increment-threshold and dark-adaptation breaks that usually coincide are affected when recovery from bleaching occurs in the presence of a changing adapting field.

Increment thresholds upon transient backgrounds are higher than those determined against fixed levels of equal luminance. This holds notably for high rates of background change and at low luminances, i.e., for conditions under which the time course of increment thresholds in Fig. 1 deviates least from that of normal dark thresholds. In turn, curves with great temporal delays during dark adaptation yield only small increases of increment threshold. The difference between thresholds for dynamic and stationary backgrounds should disappear entirely when the adapting luminance changes sufficiently slowly for recovery to reach equilibrium.

A comparison of threshold elevations found with and without pre-exposure (3.5-min background) suggests that most of the increment has to be attributed to pigment bleaching, although less than 6% rhodopsin was affected by the initial illumination. To account for the inverse relationship between the threshold elevation and the interval separating pre-exposure and measurement, increment thresholds in the lower-right half of Fig. 2 were replotted. First, the aftereffect of the pre-exposure was calculated by finding for each dark threshold (Fig. 1,  $\times$ ) the corresponding equivalent background luminance in the  $\Delta I$  vs  $I$  curve for steady state.<sup>1,2</sup> In two instances, dark thresholds measured while the background was temporarily turned off (Fig. 3, circles and diamonds) were substituted in the calculation to include the aftereffect of the waning background. A last and final correction was made for the *Eigenlicht*. This dark light of the retina is given by the intersection of the two broken lines that are tangential to the increment-threshold curve for steady state in Fig. 2. To incorporate the *Eigenlicht*, its value has to be added in each case. This may be done by simply using the extrapolated continuation, instead of the curve itself, for translating dark thresholds into equivalent background luminances. Increment thresholds obtained without pre-exposure (filled squares) were corrected only for *Eigenlicht*.

The sum of the equivalent background obtained in this manner and the real background at any time during

dark adaptation represents the total effective background. Because actual luminance decreased faster than equivalent luminance, real backgrounds that reached their minima soon after pre-exposure should be affected most by the correction. This expectation is confirmed by adapting fields from 0.3 mL downward. If plotted against the logarithm of their revised adapting luminances, increment thresholds are shifted to the left and data points are brought within close proximity of the  $\Delta I$  vs  $I$  function for steady state (inset). A remaining difference of about 0.15 log unit throughout the entire curve may indicate a constant experimental error. This near coincidence lends support to the Blakemore and Rushton<sup>8</sup> concept of linear additivity of real and equivalent backgrounds and extends it to ratios ranging from 1000:1 to 1:1000.

External backgrounds, by adding to equivalent or internal backgrounds, are believed to raise the increment threshold through a reduction of the signal-to-noise ratio<sup>19</sup> in the receptor pool.<sup>8,20,21</sup> However, to some extent they also seem to affect the sensitivity of the receptors directly. The increase of dark thresholds measured after removal of a transient luminance over those recorded during regular dark adaptation (Fig. 3) can be explained only by the prolonged exposure to the waning background. The extent of the threshold increase may depend on the combined effects of duration and luminance of the preceding illumination. Uncertain is whether the observed increments are caused passively by a delayed recovery from the pre-exposure light or actively by rebleaching.

Because the waning adapting fields in our experiment were fairly weak, a neural rather than a photochemical explanation of these data appears to be indicated. Yet, dark thresholds measured consecutively during the same period of intermittent background extinction or after the background luminance had been set at zero (Fig. 1, arrows) do not exhibit the rapid gain characteristic for neural recovery.<sup>4</sup> Instead, they resemble longer-lasting threshold elevations found in the dark-adapted eye after temporary exposure to low photopic luminance levels.<sup>22</sup> Unless a slow process of neuronal reorganization<sup>23</sup> accounts for our results, they may be tentatively interpreted as genuine retardations of dark adaptation. Future study of pigment regeneration in the presence of waning adapting fields is necessary to investigate the nature and origin of these delays.

Is adaptation in the presence of a waning background delayed behind its potential rate? Our data indicate that the eye approaches optimum performance for light discrimination when the adapting luminance decreases at a rate not exceeding 1 log unit in 3 min. Under such conditions, the time course of increment thresholds is significantly prolonged and accompanied by an elevation of dark thresholds. These relationships ought to be valid also for slower transitions from light to dark, such as those occurring during twilight and dusk.

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## REFERENCES

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<sup>1</sup> B. H. Crawford, Proc. Roy. Soc. (London) B123, 69 (1937).

<sup>2</sup> B. H. Crawford, Proc. Roy. Soc. (London) B134, 283 (1947).

<sup>3</sup> L. L. Sloan, Am. J. Ophthalmol. 33, 1077 (1950).

<sup>4</sup> M. J. Zigler, E. Wolf, and E. S. King, J. Opt. Soc. Am. 41, 354 (1951).

<sup>5</sup> R. G. Hattwick, J. Opt. Soc. Am. 44, 223 (1954).

<sup>6</sup> H. D. Baker, M. D. Doran, and K. E. Miller, J. Opt. Soc. Am. 49, 1065 (1959).

<sup>7</sup> W. A. H. Rushton, J. Physiol. (London) 156, 193 (1961).

<sup>8</sup> C. B. Blakemore and W. A. H. Rushton, J. Physiol. (London) 181, 629 (1965).

<sup>9</sup> L. K. Allen and K. M. Dallenbach, Am. J. Psychol. 51, 540 (1938).

<sup>10</sup> E. A. Suchman and H. P. Weld, Am. J. Psychol. 51, 717 (1938).

<sup>11</sup> D. A. Grant and F. A. Mote, J. Exptl. Psychol. 39, 610 (1949).

<sup>12</sup> R. D. Gunkel and H. Bornschein, Arch. Ophthalmol. 57, 681 (1957).

<sup>13</sup> E. J. Sweeney, J. Opt. Soc. Am. 49, 667 (1959).

<sup>14</sup> E. Wolf, in *Flash Blindness Symposium, Proceedings*, edited by J. M. Davies and D. T. Randolph (U. S. Army Natick Laboratories, Armed Forces, National Research Council, Committee on Vision, Washington, D. C., 1967), p. 6.

<sup>15</sup> J. G. Beebe-Center, L. Carmichael, and L. C. Mead, Aeronaut. Eng. Rev. 3, 9 (1944).

<sup>16</sup> K. Bullrich, Ber. Deutsch. Wetterdienst. (US-Zone) 4, 2 (1948).

<sup>17</sup> M. J. Allen and J. H. Carter, J. Am. Optom. Assoc. 35, 25 (1964).

<sup>18</sup> W. J. Crozier and A. H. Holway, J. Gen. Physiol. 22, 341 (1939).

<sup>19</sup> H. B. Barlow, Vision Res. 4, 47 (1964).

<sup>20</sup> W. A. H. Rushton, J. Physiol. (London) 178, 141 (1965).

<sup>21</sup> J. J. DuCroz and W. A. H. Rushton, J. Physiol. (London) 183, 481 (1966).

<sup>22</sup> S. M. Luria and J. A. S. Kinney, U. S. Naval Med. Res. Lab., Groton, Conn., Rep. No. 347, 20, 1 (1961).

<sup>23</sup> H. B. Barlow, R. FitzHugh, and S. W. Kuffler, J. Physiol. (London) 137, 338 (1957).

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