

## THE MECHANISM OF DARK-ADAPTATION

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**Abstract**—An analysis is given of the various possible components of the dark-adaptation process. A distinction is made between: *Photochemical* component ( $f_1$ ), *neural receptor* component ( $f_2$ ), *spatial summation* component ( $D$ ), *temporal summation* component ( $T$ ) and a *quantum coincidence* component ( $k$ ). These various components partly reveal themselves in different ways in dark-adaptation curves obtained by sensitivity measurements as a function of time for different target-sizes, different target-colours and different retinal locations.

Experiments were carried out in order to study the relative contribution of each component for foveal as well as for peripheral vision.

Foveal adaptation appears to be governed by the component  $f_1$  and perhaps also  $f_2$ . In phase I of peripheral adaptation a small  $D$ -component is added and in phase II of peripheral adaptation only the  $k$ -component is active.

The behaviour of the resting potential of the human eye during dark-adaptation does not bear a simple relation to any of the neural components mentioned in the present paper.

**Résumé**—On analyse les diverses composantes possibles du processus d'adaptation à l'obscurité. On distingue: une composante *photochimique* ( $f_1$ ), une composante du *récepteur nerveux* ( $f_2$ ), une composante de *sommation spatiale* ( $D$ ), une composante de *sommation temporelle* ( $T$ ) et une composante de *coïncidence quantique* ( $k$ ). Ces diverses composantes sont partiellement mises en évidence de plusieurs façons dans les courbes d'adaptation à l'obscurité obtenues par la mesure de la sensibilité en fonction du temps pour différentes dimensions de tests, différentes couleurs de tests et différentes positions sur la rétine.

On a réalisé des expériences dans le but d'étudier la contribution relative de chaque composante pour la vision fovéale ainsi que périphérique.

L'adaptation fovéale semble gouvernée par la composante  $f_1$  et peut-être aussi par  $f_2$ . Dans la phase I de l'adaptation périphérique, il s'ajoute une petite composante  $D$  et dans la phase II de l'adaptation périphérique la composante  $k$  est seule active.

Le comportement du potentiel de repos de l'oeil humain durant l'adaptation à l'obscurité ne présente de relation simple avec aucune des composantes nerveuses mentionnées dans le présent travail.

**Zusammenfassung**—Es wird eine Analyse der verschiedenen möglichen Bestandteile des Prozesses der Dunkeladaptation gegeben. Eine Unterscheidung wird gemacht zwischen: einer photochemischen Komponente ( $f_1$ ), einer Nerven-Receptor-Komponente ( $f_2$ ), einer räumlichen Summations-Komponente ( $D$ ), einer zeitlichen Summations-Komponente ( $T$ ), und einer Quantenkoinzidenz-Komponente ( $k$ ). Diese verschiedenen Komponenten zeigen sich zum Teil auf verschiedene Weise in Dunkeladaptationskurven, welche durch Messungen der Empfindlichkeit als Funktion der Zeit für verschiedene Scheibengrößen, Scheibfarben, und Netzhautlagen erhalten wurden.

Es wurden Experimente durchgeführt, um den relativen Beitrag jeder Komponente sowohl für das zentrale als auch für das periphere Sehen zu studieren.

Die foveale Adaption scheint durch die Komponente  $f_1$  und vielleicht auch durch  $f_2$  bestimmt zu werden. In der Phase I der peripheren Adaption kommt ein kleiner  $D$ -Anteil hinzu, während in der Phase II nur die  $k$ -Komponente wirksam ist.

Das Verhalten des Ruhopotentials des menschlichen Auges während der Dunkeladaptation ergibt keine einfache Beziehung zu irgendeiner der in dieser Abhandlung aufgeführten Nerven-Komponenten.

## 1. INTRODUCTION

SINCE the publication of the classical experiments of AUBERT (1865) on dark-adaptation an impressive amount of psychophysical measurements has been carried out on the human eye and it would appear that the experimental material would suffice to allow us to draw some theoretical conclusions on the mechanisms underlying this interesting and important phenomenon.

From the beginning it was accepted that peripheral, presumably retinal, mechanisms were largely or completely responsible for the decrease of the absolute threshold in the course of dark-adaptation, a decrease which amounts to a factor  $10^5$  under the most favourable experimental conditions (pre-adaptation to white light at a high intensity level; a large test field, presented to the peripheral parts of the retina). The mere fact that the state of dark-adaptation of one eye is independent of the state of dark-adaptation of the other eye has always been one of the strongest arguments in favour of peripheral mechanisms of dark-adaptation. Another strong argument for purely retinal mechanisms of dark-adaptation has arisen from electrophysiological work on the human eye. It has been shown by several investigators that the change of the *b*-wave of the human ERG in the course of dark-adaptation closely follows the change of the absolute threshold as determined by means of psychophysical methods.

Thus if we try to give a theoretical interpretation of the phenomena of dark-adaptation we must focus our attention on the retina. Our knowledge of the objective properties of the retina can be classified under the following headings:

- (A) Anatomy,
- (B) Photochemistry,
- (C) Neurophysiology (including electrophysiology).

*(A) Anatomy*

The most important contribution of anatomy towards understanding the phenomena of dark-adaptation is without any doubt the "duplicity theory" formulated in its final form by VON KRIES (1896).

The wealth of arguments in favour of the concept that the human retina contains two receptor mechanisms, which act to a large degree independently of each other, is so overwhelming that we may accept its validity as an established fact.

A number of other anatomical observations, mainly pertaining to retinomotoric phenomena like pigment migration and contraction of the outer lids of the cones, although very interesting from a physiological point of view, have hardly influenced our theoretical concepts of human dark-adaptation owing to the fact that they are mainly observed in lower vertebrates and are not demonstrable in the human eye.

*(B) Photochemistry*

The discovery of the photochemical bleaching of rhodopsin by BOLL (1877) and the stream of subsequent work in this field largely influences the theories of dark-adaptation up to the present day.

The fact that the rods contain a visual pigment with a spectral absorption which is nearly similar to the spectral sensitivity of the dark-adapted eye, combined with the fact that the concentration of rhodopsin increases during dark-adaptation, makes it attractive to consider whether the increase of the concentration of rhodopsin in itself is sufficient to

explain the decrease of the absolute threshold (the increase of sensitivity) during the course of rod-adaptation. The discovery of another pigment, iodopsin, by WALD (1937) with a spectral absorption which is supposed to represent the photopic sensitivity curve of the human eye and with a *time* course of regeneration *in vitro* which is nearly identical to the *time* course of human cone-adaptation opens a similar perspective for a photochemical theory of cone-adaptation.

Such a photochemical theory of dark-adaptation would be easily acceptable if it could be shown that the increase of sensitivity during cone- and rod-adaptation is directly proportional to the increase of the concentration of iodopsin and rhodopsin, respectively (if we assume that these photopigments are present in a diluted solution), or more briefly formulated that for any particular moment of dark-adaptation

$$\text{for cone-adaptation } C_i = K_i S \quad (1)$$

$$\text{for rod-adaptation } C_r = K_r S \quad (2)$$

in which formulae  $S$  denotes the sensitivity of the eye (the reciprocal of the absolute threshold) at a certain moment,  $K_i$  and  $K_r$  are constants which are characteristic for the iodopsin and the rhodopsin systems,  $C_i$  and  $C_r$  are the concentrations of iodopsin and rhodopsin.

This simple theory, which suggests that the visual pigment is present in the receptor cell in the form of a dilute solution and that the sensitivity is the subjective correlate of the probability of the absorption of a light quantum by the receptor cell, is in direct conflict with an abundance of experimental evidence which shows that the increase of the concentration of rhodopsin during dark-adaptation is much smaller than the corresponding increase of the sensitivity of the eye.

HECHT (1929) made the assumption, based on experiments on the clam, *Mya*, that at any moment of dark-adaptation the logarithm of the sensitivity is directly proportional to the logarithm of the concentration of the visual pigment or in formulae

$$\text{for cone-adaptation } C_i = K_i \log S \quad (3)$$

$$\text{for rod-adaptation } C_r = K_r \log S \quad (4)$$

in which formulae  $K_i$  and  $K_r$  are constants characteristic for the cone and rod systems.

Hecht has shown that the acceptance of the conditions (3) and (4) makes it possible to describe the course of human dark-adaptation by means of the "dynamics of a bimolecular reaction isotherm". He thus concluded that "during dark-adaptation the photopigment is being replenished in the rods and in the cones independently as if in each case it were being formed by the chemical interaction of at least two other substances".

WALD (1955) is still convinced of the validity of the relations (3) and (4). He believes that "light- and dark-adaptation have their primary source in the bleaching and resynthesis of the visual pigments of the rods and cones". However, he believes that "more central phenomena-changes in the sensitivities of neurones and synapses along the optic pathway may also play a role. . . . They probably are responsible also for only a minor portion of the range of visual adaptation. To a first approximation light- and dark-adaptation seem to reflect the fall and rise of visual pigment; and specifically in the form that the log sensitivity runs parallel with pigment concentration."

From this quotation we learn that Wald is forced to admit that the full range of dark-adaptation cannot be explained by photochemistry alone. Recently some strong arguments against a purely photochemical explanation of dark-adaptation have arisen. BAUMGARDT (1949) and others have calculated that the number of quanta absorbed in the rods at

moderate illumination levels is too small to cause an appreciable change in the concentration of rhodopsin.

RUSHTON and CAMPBELL (1954) developed a method which made it possible to measure the change in the density of rhodopsin in the living human eye. They established that "unless fairly bright photopic illumination is used, there is no appreciable change in the density of retinal rhodopsin. Thus changes in visual sensitivity cannot be due to an alteration in the chance of a quantum being absorbed; it must be entirely due to a change in the efficacy of the quantum when it is absorbed."

From this quotation we may conclude that RUSHTON and CAMPBELL (1954) go so far as to deny a photochemical mechanism of dark-adaptation. Recently it has been made clear by WALRAVEN and BOUMAN (1960) that the change in apparent hue when the light enters the pupil through more eccentric parts is due to a shortening of the pathway of the incident light through a fairly concentrated solution of the photopigment in the receptor. According to their explanation of this aspect of the Stiles-Crawford effect such a dependence of apparent hue on the site of entrance of the light in the pupil would disappear when the concentration of the photopigment became small. However, only for very high brightness levels did BRINDLEY (1953) find such an effect.

In any case it seems clear that a purely photochemical theory of dark-adaptation does not meet the experimental facts and we will have to consider the possible existence of neural mechanisms if we wish to explain the experimental data.

### (C) Neurophysiology

The existence of neural mechanisms of dark-adaptation does not only follow in an indirect way from the failure of the photochemical theories to explain all phenomena of dark-adaptation but also in a direct way from psychophysical experiments on the human eye.

Many investigators have shown that the *range* of adaptation increases with an increase of the test-field area. We mention here BEST (1950), BOUMAN and TEN DOESSCHATE (1953) and ARDEN and WEALE (1954). This effect can be partly explained by an increase of the diameter of the area of complete integration during dark-adaptation (ARDEN and WEALE (1954)) which clearly represents a neural mechanism of dark-adaptation. BOUMAN and TEN DOESSCHATE (1953) have shown that the effect can also be ascribed to a change of the critical number of coincident quanta (a concept which will be discussed in the next sections), thus indicating another neural mechanism. In the older literature several authors have considered neural mechanisms of adaptation, e.g. LYTHGOE (1940), CRAIK and VERNON (1941) and THOMSON (1949).

The most direct argument in favour of neural components of adaptation stems from electrophysiological work on the eye of *Limulus*. HARTLINE (1957) reported about his adaptation experiments on the *Limulus*-eye. He determined "frequency of spike curves" for different adaptational conditions.

The microelectrode was situated in the visual apparatus in such a position that at least one synaptic connection had to be passed by the response on its way to the higher centres. He measured the probability of occurrence of at least one spike response as a function of the intensity of flashes presented to the *Limulus*-eye. He found that the "frequency of spike curves" can exactly be described by the formula

$$W(\bar{N}, k) = 1 - e^{-f\bar{N}} \sum_{p=0}^{k-1} \frac{f\bar{N}^p}{p!}$$

in which  $W(\bar{N}, k)$  is the probability that for an average number of quanta  $\bar{N}$  in an actual flash,  $k$  effective quantum absorptions occur as predicted by Poisson's distribution of statistical events and  $f$  is the fraction of the incident light that is absorbed in the photopigment. HARTLINE (1957) found that for different conditions of adaptation different  $k$ -values are valid. The  $f$ -value, however, was the same for all curves. His  $k$ -values varied between two and about 100. This important change of the value of  $k$  with the state of adaptation points to the importance of a nervous component in dark-adaptation. It is indeed the same effect which was found for the human eye by BOUMAN and TEN DOESSCHATE (1953). It also seems important that Hartline's shallowest curve corresponds to  $k=2$ , the same number which was found by BOUMAN and VAN DER VELDEN (1947) for the dark-adapted human eye.

Hartline's very objective studies by means of electrophysiological methods show that this property of the human eye should be considered as a general property of visual receptor systems.

## 2. THEORETICAL ANALYSIS OF THE POSSIBLE COMPONENTS OF DARK-ADAPTATION

In order to facilitate the analysis of the different components of the process of dark-adaptation we want to introduce a system of terms and symbols:

Mechanism	Term	Symbol
(A) Increase of the concentration of the photopigment	photochemical component	$f_1$
(B) Neural-adaptation of the single receptor	neural receptor component	$f_2$
(C) Increase of the retinal summation area	area component	$D$
(D) Increase of retinal summation time	time component	$T$
(E) Decrease of the minimum number of coincident quanta	coincidence component	$k$

### *Ad A and B—Photochemical component and neural receptor component ( $f_1$ and $f_2$ )*

The sensitivity of the fully dark-adapted eye is so high that it is easy to prove that at the absolute threshold for short light flashes the chance that one receptor is hit by more than one quantum is negligible. The consequence of this statement is that the absorption of one quantum by an active molecule of photopigment is not only sufficient for the decomposition of one molecule of photopigment but that this decomposition is sufficient to produce a response of the receptor in the dark-adapted retina. An increase of the threshold in the light-adapted state could be explained by one of the following hypotheses:

- (1) In the light-adapted eye *more than one* quantum is necessary for the decomposition of one molecule of photopigment. This hypothesis seems to be most improbable on physical and chemical grounds.
- (2) In the light-adapted eye the concentration of photopigment is less than in the dark-adapted eye. This is the mechanism which we have called the *photochemical component* ( $f_1$ ). We have seen in the preceding section that the importance of this component has been overestimated in the past. However, assuming that this mechanism is present, it will be clear that an increase of the concentration of active

photopigment during dark-adaptation will result in an increase of the probability that an active molecule is hit by a quantum of incident light radiation.

- (3) The fact that the absorption of one quantum by one active molecule is *sufficient* to cause a response of the receptor does not mean that *every* absorption results in an effective spike response.

If we call the probability that an absorption will result in an effective spike response  $p$  per cent, we may consider the possibility that the value of  $p$  is less for the light-adapted eye than for the dark-adapted eye even under the condition that the concentration of the photopigment remains unaltered. This possible mechanism we have denoted by the term *neural receptor component* ( $f_2$ ).

Both components  $f_1$  and  $f_2$  have a very simple effect on the threshold of the eye. They act in the same way as if a filter is removed from before the eye. The influence of this factor is independent of the area of the test field ( $d^2$ ) or from the duration of the stimulus ( $t$ ).

#### *Ad C and D—Area component (D) and time component (T)*

It is a well-known fact that two subliminal point stimuli will be able to produce a supraliminal response if they are applied within a critical distance ( $D$ ) and within a critical duration ( $T$ ). The critical distance is generally considered to coincide with the area of validity of Ricco's law of complete spatial summation. The critical duration  $T$  covers the time within which Bloch's law of complete temporal summation is valid. It will be clear that an increase of  $D$  or  $T$  respectively during the course of dark-adaptation will result in an increase of the probability of a supraliminal response. These effects are denoted here as *area component* ( $D$ ) and *time component* ( $T$ ) respectively. Their real existence has been shown by means of experiment (VAN DER BRINK and BOUMAN, 1954; ARDEN and WEALE, 1954).

#### *Ad E—Coincidence component (k)*

It has been shown by several investigators that the phenomena at the visual threshold level are governed by relatively simple quantum-statistical considerations. We assume that the retina is stimulated by a circular test field with diameter ( $d$ ) during a time ( $t$ ). A visual response will be elicited if a critical number of quanta ( $k$ ) is effectively absorbed within a critical area with diameter ( $D$ ) and within a critical time ( $T$ ). This simple hypothesis allows us to apply Poisson's formula to the theoretical treatment of the problem. Experimental data on the behaviour of the probability of a visual response as a function of the stimulus intensity, the diameter of the test field ( $d$ ) and the duration of the stimulus ( $t$ ) can be explained by assuming that for the dark-adapted eye  $k=2$ . The authors of the present paper (BOUMAN and TEN DOESSCHATE (1953)) have shown that for the light-adapted eye  $k=>2$ . The variation of  $k$  with the state of adaptation represents a neural mechanism of dark-adaptation which we have denoted by the term *coincidence component* ( $k$ ).

From the considerations given above we may conclude that of the different components of dark-adaptation the first one ( $f_1$ ) is purely photochemical in origin. All others should be classified as neural components. The  $f_2$  component is a relatively simple neural component belonging to the single receptor. The other neural components ( $D$ ,  $T$  and  $k$ ) have a more complicated character. The common characteristic of this group of mechanisms is a change of the switching arrangement within *groups* of receptors during the course of dark-adaptation.

In the discussion of the experiments which will be described in the next section much attention is given to the behaviour of the threshold energy of a test flash as a function of its diameter ( $d$ ). It will clarify the discussion if we describe, in advance in a very schematic way, the theoretical influence of the different components of dark-adaptation on this function.

In order to simplify our arguments still further we will assume that under all circumstances  $t < T$ . By accepting this condition we eliminate the  $T$ -component of dark-adaptation from our arguments.

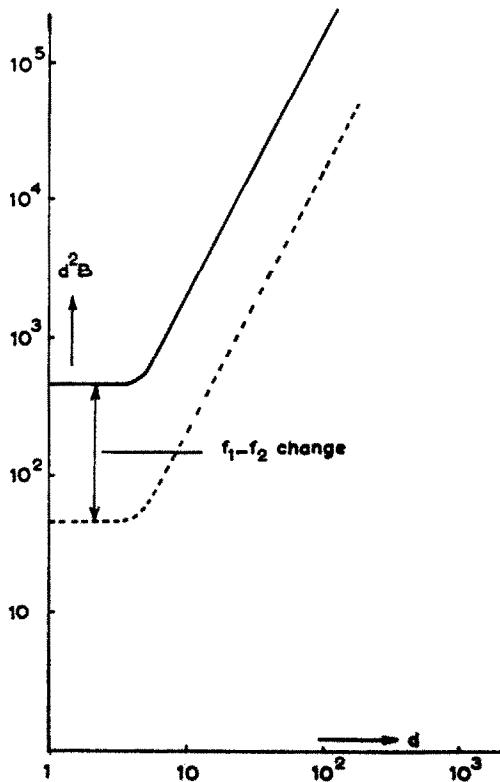


FIG. 1. Effect of  $f_1$  or  $f_2$ -component on the function  $d^2 B_{\text{threshold}} = f(d)$ .

In Fig. 1 the upper (drawn) line gives the threshold energy  $d^2 B$  of a test flash with diameter ( $d$ ) as a function of ( $d$ ) or in a shorter notation

$$d^2 B_{\text{threshold}} = f(d).$$

(In this function  $B$  is the threshold luminance of the test flash.)

We observe that the function consists of two distinct parts, on the left a horizontal part and on the right a part with a positive slope. The left horizontal part covers the range of  $d$  values within which complete spatial summation occurs or in other words the range for which  $d < D$ . The second part of the function (the part with a positive slope) corresponds to the condition  $d > D$ . (We will see below that the slope of this part is determined by the critical number of coincident quanta  $k$ . In Fig. 1 the slope is quite arbitrarily drawn for  $k = 20$ .) The lower function (dotted line) shows the effect of an increase of the concentration

of active photopigment ( $f_1$ -component) by a factor 10 (the value 10 is quite arbitrarily accepted) but the same effect is obtained if the spike-efficiency of the individual receptor ( $f_2$ -component) increases by a factor 10.

In Fig. 2 the effect of an increase of the area of complete spatial summation ( $D^2$ ) by a factor 10 (or an increase of  $D$  by a factor  $\sqrt{10}$ ) is shown. The effect of the  $D$ -component becomes apparent as soon as  $d$  exceeds the original value of  $D$  (dotted line). The curve assumes a positive slope for large  $d$ -values with  $k$  again 20.

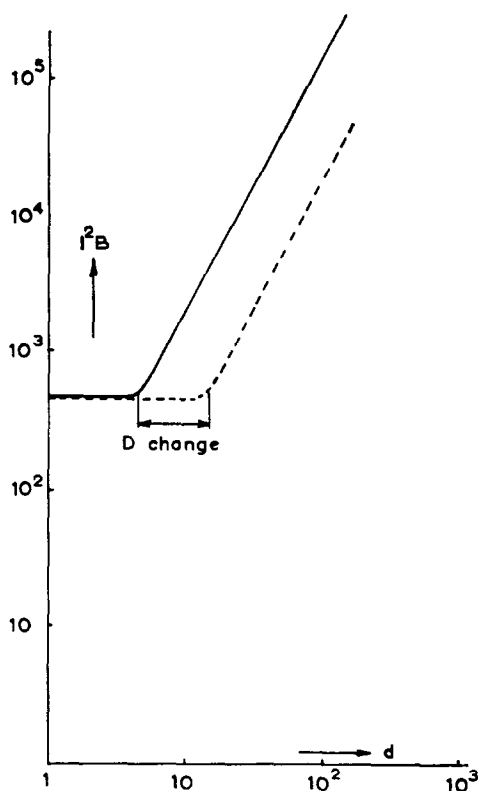


FIG. 2. Effect of  $D$ -component on the function  $d^2 B_{\text{threshold}} = f(d)$ .

The effect of the  $T$ -component need not be considered here for we assumed that  $t < T$  under all circumstances.

In Fig. 3 we show the effect of a decrease of  $k$  by a factor 10 on the function  $d^2 B_{\text{threshold}} = f(d)$ .

Earlier it has been shown by BOUMAN and VAN DER VELDEN (1947) that the positive slope of the function is proportional to

$$d^{2(k-1)/k}$$

The upper (drawn) function is drawn for  $k=20$  (slope =  $+38/20$ ). The lower (dotted) line represents  $k=2$  (slope =  $+1$ ).



The results obtained from Figs. 1-3 may be summarised in the following way:

(1) Effect of  $f_1$  and  $f_2$ -component: A lowering of the threshold by a "filter"-factor which is independent of  $d$ .

(2) Effect of  $D$ -component: No effect as long as  $d < D$ . An increasing effect over the range within which  $d$  exceeds the original value of  $D$  but has not reached the final value of  $D$ . After  $d$  exceeds the final value of  $D$ , the effect remains constant.

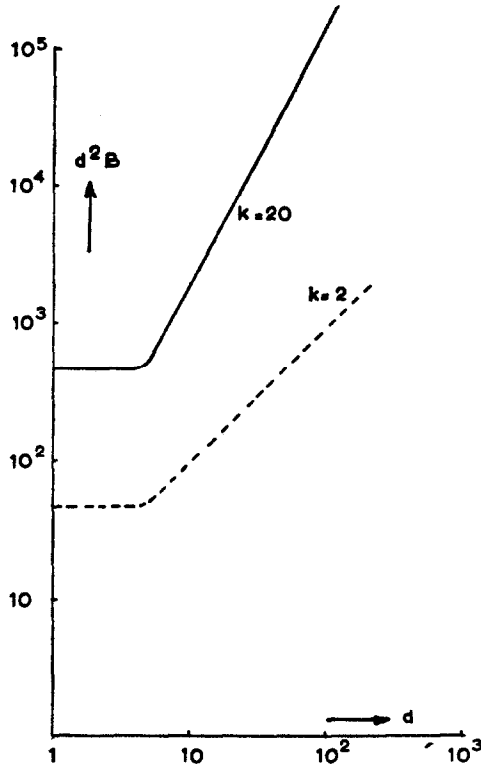


FIG. 3. Effect of  $k$ -component on the function  $d^2 B_{\text{threshold}} = f(d)$ .

(3) Effect of  $k$ -component: A constant effect for  $d < D$ . This effect is proportional to  $k$ . An increasing effect for  $d > D$ .

Figure 4 combines the results from Figs. 1-3 and thus represents the combined effects of the different components of dark-adaptation on the function  $d^2 B = f(d)$ .

### 3. EXPERIMENTAL

#### (1) Introduction

In the preceding section we have shown that an experimental study of the threshold energy of test flashes as a function of the state of dark-adaptation and the diameter ( $d$ ) of the test field and for small duration of the test flash ( $t < T$ ) offers interesting possibilities for an analysis of the different components which may play a part in the complicated process of dark-adaptation.

It was our aim to study the mechanism of dark-adaptation for rod- and cone-adaptation separately as far as possible. Therefore, we were obliged to carry out threshold determinations for red and green test fields which were presented to the fovea as well as to the periphery during the complete course of dark-adaptation. In order to obtain maximum adaptation effects an extremely high level of pre-adaptation to white light was adopted. By means of this device we hoped to give all components their fullest chance to present themselves.

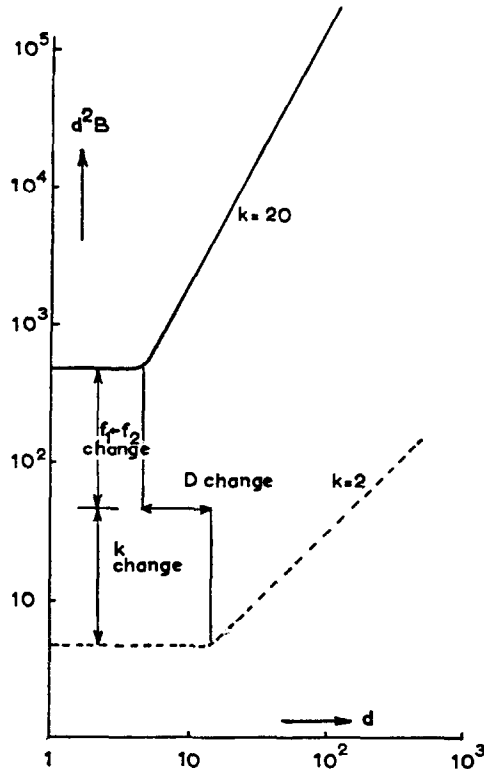


FIG. 4. Combined effect of the different components on the function  $d^2B = f(d)$ .

## (2) Experimental Procedure and Apparatus

All experiments were carried out on the right eye of a well-trained forty-year-old male observer. (The right eye of the subject is myopic (2 D) and shows a mild degree of deuteranomaly.)

In all experiments the subject was pre-adapted during 3 min to a field with diameter  $18^\circ$  which was observed in Maxwellian view through an artificial pupil with diameter 2 mm. The pre-adaptation light was obtained in the following way: the artificial pupil coincided with the image of a tungsten ribbon filament lamp which was run at 14 A. At this current strength the lamp has a colour temperature of  $2848^\circ\text{K}$ . The luminous flux passing through the artificial pupil was experimentally determined and amounted to 0.125 lumen. The luminance of the adapting field was equivalent to about  $5.5 \times 10^5 \text{ cd/m}^2$ , corresponding to a retinal illumination of  $2.2 \times 10^6$  trolands. The pre-adaptation period was followed by a 30-min period of

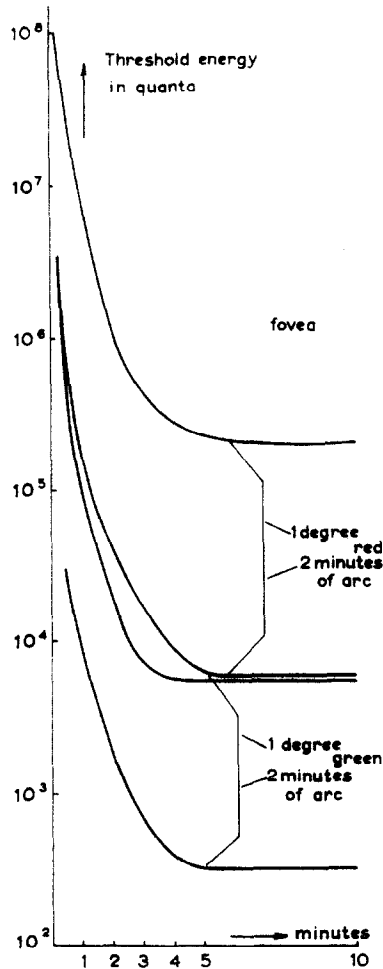


FIG. 5. Results for red and green, fovea. Curves averaged from five independent measurements.

dark-adaptation. During this latter period the threshold energy of a test flash was determined at small intervals. A 50 per cent chance of observation was considered to be the threshold level.

The curves presented in Figs. 5-7 were obtained from the experimental data in the following way:

The current running through the tungsten ribbon filament lamp was recorded by means of a recording ammeter. Every light flash which was observed by the subject was recorded on the same paper by means of an electrical signal. As soon as the probability of seeing reached more than 50 per cent the current was reduced by a certain amount and remained at its new level until the probability of seeing at this new level was again more than 50 per cent. This procedure was repeated during the complete course of dark-adaptation.

Afterwards the 50 per cent probability-of-seeing curves were marked in the finished records and smooth lines were drawn through the experimental 50 per cent points. For

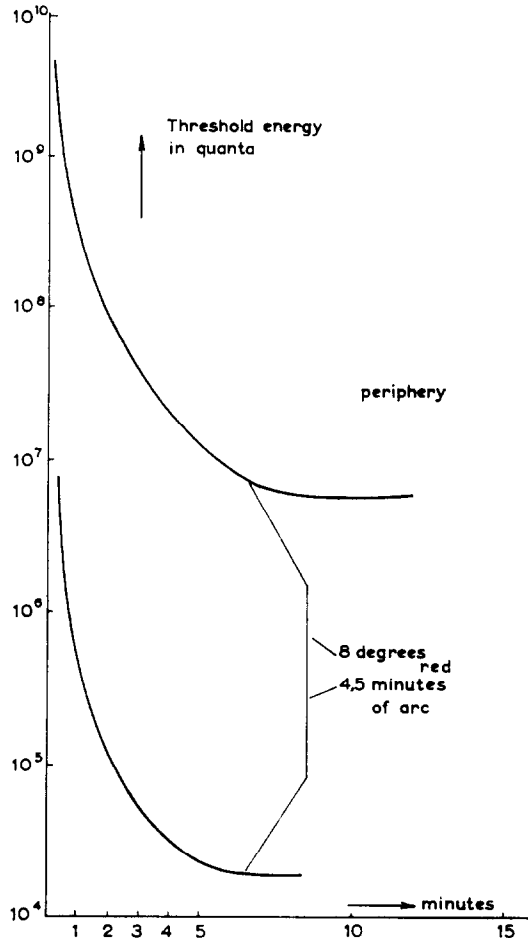


FIG. 6. Results for red light, periphery. Curves averaged from five independent measurements.

every experimental condition we carried out at least five completely independent experiments. The records obtained in these five experiments were averaged by means of graphical interpolation. The interpolation curve still represented lamp current against time of adaptation. By means of the calibration data of the lamp, the filters and the monochromator, the average current data were converted into radiant energy (expressed in quanta). The curves in Figs. 5-7 are the result of this graphical interpolation.

From the foregoing description of the experimental procedure it will be clear that in Figs. 5-7 no experimental points are given. The curves should be considered as smooth curves drawn through a very large number of experimentally determined points. The spread of the values did not exceed a standard deviation of about 70 per cent.

The curves are comparable to classical curves of dark-adaptation which are also used for clinical reasons. In these clinical procedures, however, the curves represent the *log threshold luminance* as a function of the time of dark-adaptation. In the curves presented in this section the *log threshold energy* (luminance multiplied by area of the test field) is plotted as a

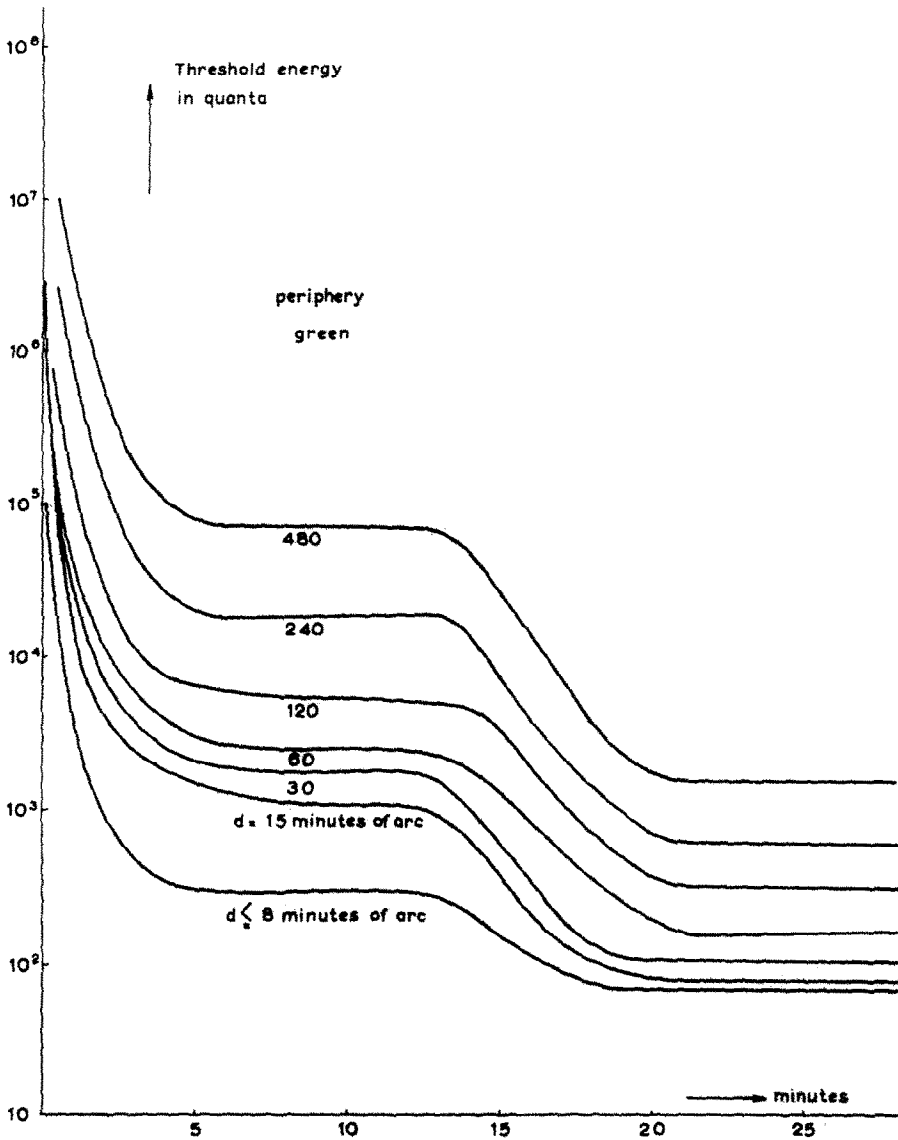


FIG. 7. Results for green light, periphery. Curves averaged from five independent measurements.

function of the time of dark-adaptation. Experiments were carried out for red ( $650 m\mu$ ) and green ( $525 m\mu$ ) test flashes with duration 0.1 sec presented to the fovea or to the periphery ( $7^\circ$  temporal of the fovea). The diameter of the test field ranged from  $1.9'-1^\circ$  for the foveal and from  $1.9'-8^\circ$  for the peripheral measurements. The test field was also observed in Maxwellian view through the artificial pupil (2 mm). The colour of the test field was varied by means of a double monochromator adjusted at a maximum band width of about  $25 m\mu$ . The luminance of the test field was continually varied by adjusting the current

strength of the light source of the monochromator and discontinuously by means of a set of neutral filters. All threshold energies in this section are expressed in quanta.

### (3) *Experimental Results and Discussion*

In Fig. 5 we give the experimental data for the fovea for red and green test flashes plotted as log threshold energy as a function of the time of dark-adaptation and for different diameters ( $d$ ) of the test flash.

In order to be able to interpret these figures one should consider the theory presented in section 2.

Similarity of the *shape* of the curve for small and large test fields excludes the possibility that  $D$  or  $k$ -component are active. Such a similarity can only be explained by the activity of the  $f_1$  and/or the  $f_2$ -component. The foveal measurements presented in Fig. 5 clearly fulfil this condition for red as well as for green test flashes, showing that foveal-adaptation is completely governed by photochemical and/or neural receptor adaptation. The total amplitude of foveal-adaptation amounts to a factor which is about equal to 100. From the curves presented here no conclusions can be drawn with respect to the relative contribution of the  $f_1$  and the  $f_2$ -component. From other sources of information mentioned in section 1 we know that foveal dark-adaptation cannot be explained by means of the  $f_2$ -component alone. It has been shown by Brindley that the difference in optical density of the photopigment in the light- and the dark-adapted fovea is sufficient to cause a difference in the shape of the spectral absorption curve. If we assume that in the dark-adapted fovea the maximum absorption by the photopigment is about 50 per cent, a decrease to maximum 10 per cent is needed to account for the required change in the shape of the spectral absorption curve in the light-adapted eye (see also WALRAVEN and BOUMAN (1960)). We may thus conclude that foveal dark-adaptation is at least partly due to the  $f_1$ -component.

We may now proceed to the analysis of the peripheral measurements.

From Figs. 6 and 7 we learn that for small test fields ( $d < 4.5'$ ) and within the first 12 min of dark-adaptation for red as well as for green test flashes the situation can be simply described by stating that the shape of the curves is within the margin of experimental error similar to the shape of the foveal curves. This result strongly suggests that for small test fields in the periphery during the first 12 min of dark-adaptation the cones alone are responsible for the increase of the sensitivity. Furthermore, we may conclude that in this respect the peripheral cones are identical to the foveal cones. Summarizing, we may conclude that the curves describing foveal-adaptation and the first phase of peripheral-adaptation for small test fields for red as well as for green are all identical. Under these conditions adaptation is governed by the cones only and the mechanisms concerned are only the  $f_1$  and perhaps the  $f_2$ -component.

For large test fields the situation is much more complicated. For a red  $8^\circ$  test field the curve is monophasic and at the first glance its form seems to be identical with that of the foveal curves and the peripheral curves for small test fields. A closer examination reveals that the range of adaptation for the red  $8^\circ$  field exceeds the range for the  $4.5'$  red field by a factor 2. In order to explain this discrepancy the activity of one of the neural components ( $D$  or  $k$ ) has to be taken into consideration. (We will see below that the effect is probably due to the  $D$ -component.)

The curves for green test fields in the periphery (Fig. 7) all clearly show a diphasic form, thus presenting the well-known "break" of the curve for dark-adaptation which is classically

ascribed to the transition of cone- to rod-adaptation. Perhaps some reader will be surprised by the fact that the "break" is so pronounced and that it shows itself not earlier than the twelfth minute of dark-adaptation. This fact is easily explained by considering the unusually high level of pre-adaptation ( $2.2 \times 10^6$  trolands).

In discussing the results (Fig. 7) we will refer to the two phases of the curve as phase I and phase II. Phase I for the curve for  $8^\circ$  green (Fig. 7) is identical in form to the peripheral curve for  $8^\circ$  red (Fig. 6). Here also we find that the amplitude of phase I of the  $8^\circ$  curve

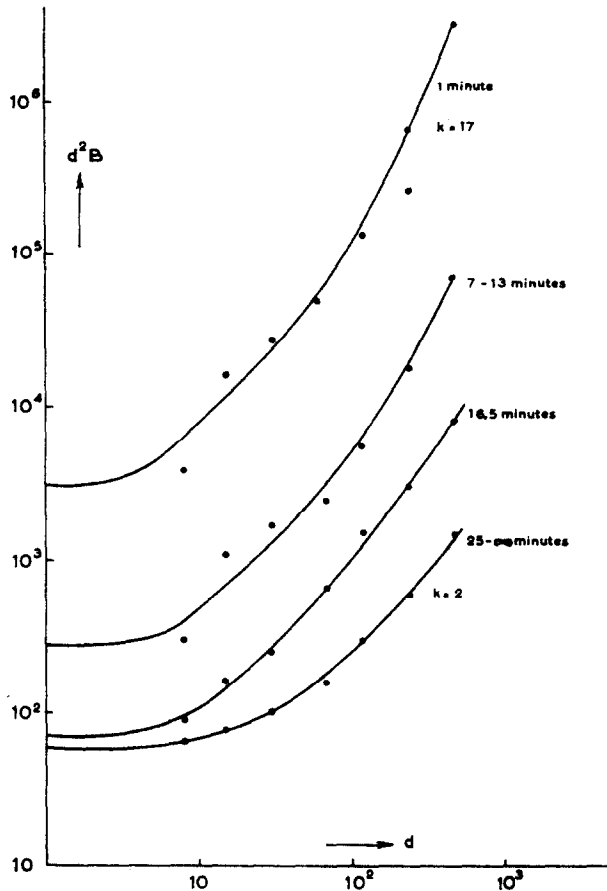


FIG. 8.  $d^2B=f(d)$ ; peripheral measurements for green light at different levels of dark-adaptation.

between the first and eighth minute of dark-adaptation exceeds that of the small field curve by a factor 2. Here also the effect must be explained by the activity of the  $D$  or  $k$ -component (and again it will be shown below that it is probably due to the  $D$ -component).

From Fig. 7 we learn that for phase II of the green curves the amplitude of adaptation increases appreciably if the diameter ( $d$ ) is increased from  $7.5'$  to  $8^\circ$  (i.e.  $480'$ ). This clearly indicates that part II of the curves for peripherally presented green test fields is governed to a large extent by neural components ( $D$  and/or  $k$ ). We have seen in section 2 that it is

possible to separate the effect of these components by studying the behaviour of the threshold energy as a function of  $d$ . Therefore we give in Fig. 8 vertical sections of the set of curves presented in Fig. 7.

The curves given in Fig. 8 show log threshold energy ( $d^2B$ ) as a function of  $d$ . Each curve pertains to a certain moment of dark-adaptation. The slope of the curve between 1 and 12 min of dark-adaptation appears to correspond to  $k \approx$  about 17. At the end of dark-adaptation the slope corresponds to  $k=2$ . We may state therefore that in phase II of dark-adaptation the  $k$ -effect should amount to a factor  $17/2 \approx 8$ . This change in  $k$  value ought at least to appear in phase II of the curves for small fields in Fig. 7. From this figure we learn that for small

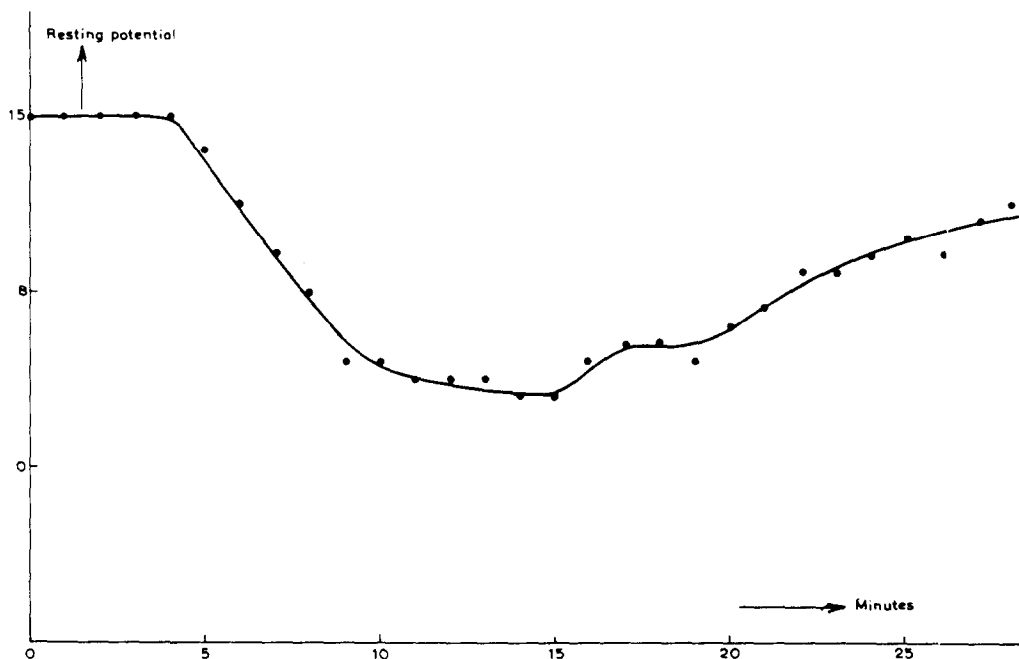


FIG. 9. Resting potential as a function of the time of dark-adaptation for the same subject on whom all experiments in the present paper were carried out and with the same conditions of pre-adaptation.

fields ( $d < 8'$ ) the amplitude of adaptation in phase II of the curve amounts to a factor 6. Thus the range of adaptation during phase II is nearly completely explained by the decrease of  $k$ . We may conclude that phase II of the peripheral dark-adaptation curve is governed by the  $k$ -component only and that in this phase  $f_1$ ,  $f_2$  and  $D$ -component are absent. Furthermore, from the fact that the  $k$ -component is "spent" completely on phase II of dark-adaptation we may conclude that the neural component in phase I must be the  $D$ -component.

It means that in phase I,  $D$  changes approximately by a factor  $\sqrt{2} = 1.4$ . We mentioned already the relatively small variations in  $D$  as found by VAN DER BRINK and BOUMAN (1954) by more direct experiments. They were indeed of the same order of magnitude as deduced from the present experiments.



We may summarise our conclusions about the mechanisms of dark-adaptation in the following scheme:

Foveal-adaptation  $f_1$  at least a factor 5  
perhaps  $f_2$  but if so not more than a factor 20

Peripheral-adaptation

in phase I  $f_1$  at least a factor 5  
perhaps  $f_2$  but if so not more than a factor 20  
 $D$  approximately a factor 1.5

in phase II  $k$ -component by a factor 6 to 8

#### 4. THE RELATION BETWEEN NEURAL COMPONENTS OF ADAPTATION AND THE RESTING POTENTIAL OF THE HUMAN EYE

TEN DOESSCHATE and TEN DOESSCHATE (1956, 1957) have shown that the resting potential of the human eye as determined from the amplitude of the electrooculogram behaves in a complicated way in the course of dark-adaptation. They suggested the possibility that this behaviour of the resting potential is the objective correlate of the activity of neural-adaptation. In order to test this hypothesis we determined the behaviour of the resting potential of the observer on whom the experiments described in the present paper were carried out. The pre-adaptation level was also identical to that which was used in the threshold experiments.

In Fig. 9 we give the resting potential as a function of the time of dark-adaptation.

From a comparison between Fig. 9 and Fig. 7 we learn that the resting potential is constant during the steep decrease of the threshold in phase I. The resting potential drops during that part of phase I in which the threshold is more or less constant. The resting potential reaches a minimum at the point of transition from phase I to phase II. It increases slowly during phase II. Apparently there is no simple relation between the behaviour of the resting potential during dark-adaptation and the different neural components of dark-adaptation.

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