THE EFFECT OF SLOW INTERMITTENT LIGHT STIMULATION ON THE HUMAN ERG*

by

EDGAR AUERBACH

(Jerusalem, Israel)

With 9 figures

INTRODUCTION

An effect which a photic stimulus exerts on the responses to consecutive stimuli was studied. It was noticed in the framework of a larger study on the human ERG (to be published elsewhere). Those results of the larger study which are relevant for the understanding of this presentation will be shortly discussed.

Repetitive stimulations were used at rates which are slow compared to the time course of the individual electrical response. It is therefore doubtful whether the term 'flicker' is appropriate. The definition at what flash rate a stimulation begins to represent a true flicker may be of more than of semantic interest. The minimal rate per unit of time necessary for a train of photic stimuli to represent flicker may be defined from the electrophysiological point of view as the flash rate which just coincides with the time course of the bioelectrical response of the retina. It may, on the other hand, be also defined as the largest interval between stimuli at which a response just displays a change in the wave pattern as compared with the response to the first stimulus (20–25 seconds between flashes). The author is at present inclined to favor the first definition.

APPARATUS AND PROCEDURE

Experiments were performed on 12 normal subjects aged 25 to 45 years placed in an electrically shielded cage. In each case a mydriatic (Cyclogyl) was applied. The recordings were binocular. The corneal electrodes (low-vacuum contact lens electrodes of HENKES) were fixed to each eye, and the indifferent electrode (silver clips of 9 mm diameter) were fastened to the

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mid-supraorbital rim of each side. A ground electrode was attached to the ear lobe.

The voltage of the line power supply was stabilized. A condenser-coupled Dual Beam Cathode Ray Oscilloscope (DuMont 333 or Tektronix 502) was used. The one beam was split by an electronic switch, and the two corneal electrodes were connected to the split beam oscilloscope inputs through AC Grass preamplifiers. The upper sweep of the split beam was used for recordings from the right eye and the lower sweep for recordings from the left eye. The second beam was generally used as a time-marker to indicate the beginning of each recording.

A Grass photostimulator (PS-1) was used. The light source was a Xenon filled flash tube (U6LC). The five relative intensity steps provided were checked and found to be of satisfactory accuracy. The flash duration was about 10 μsec. The peak luminance was about 6×10^7 mL (BORNSCHEIN & GOODMAN (1957)). The stimulating light was at a distance of 15 cm from the subject's forehead.

The cut-off frequencies of all preamplifier filters were set at 500 c/s. after comparing the electrical responses with those obtained with the filters kept fully open. The time constants of the recording channels were 0.1 sec. In all recordings the downward deflections indicate negative polarity.

The oscilloscope traces were photographed with a Grass Kymograph Camera (C4E). The oscilloscope sweep and camera were synchronized and coincided with the onset of stimulation.

The eyes were exposed for 10 minutes to an adapting light of about 17,000 mL. Solitary stimuli were delivered in the light and in the dark beginning 50 msec. after the light was turned off.

At a steady state in the scotopic phase of dark adaptation trains of stimuli were applied at rates ranging from one per second up to one every 30 seconds. The train of repetitive stimuli was then interrupted by a period of at least 30 seconds after which one additional stimulus was applied. The response to each stimulus was individually photographed.

The evaluation procedure*:

Latencies were measured from the onset of stimulation to the maxima of the downward and the upward deflections respectively. Negative wave amplitudes were determined by measuring the vertical distance from the base line down to the peak, and positive wave amplitudes by measuring the vertical distance between the lowest negative peak and the positive peak.

* See remarks at the end of Discussion.

RESULTS

THE ERG IN RESPONSE TO SOLITARY STIMULI

(introductory remarks)

The ERG related to stimulus strength and dark adaptation

Under the experimental conditions used the ERG produced by solitary stimuli was comprised of up to five positive potentials and up to four negative potentials. The appearance of these potentials in the ERG was a function of the stimulus strength. The 5th positive potential could be suppressed either by a steady dim background illumination or by the use of an intermittent stimulation of one per second applied at regular intervals during the process of dark adaptation. This suppression can be noted in all figures except Fig. 1 which is schematic and Fig. 2 and Fig. 9 where dark adaptation was completely undisturbed.

The first two negative potentials appeared in the ERG taken under all conditions during light adaptation and dark adaptation no matter how high the stimulus strength used, while the 3rd and 4th negative potentials could be produced only by stimuli within a range of low intensities. When a certain low-intensity stimulus was used the 1st positive potential could not be elicited as part of the positive wave group, i.e. did not increase in amplitude, but appeared as a small positive deflection within the negative wave group, giving rise to the appearance of the 3rd negative potential. When a still lower stimulus intensity was used, the 2nd positive potential likewise was not elicited as part of the positive wave group but appeared as a small positive deflection within the negative wave group together with the 1st positive potential, giving rise to the 4th negative potential. In addition, a stimulus of this low strength elicited the slow positive potentials maximally or nearly so with the result that they dominated the pattern of the ERG. On the other hand, the energy necessary to produce maximally or nearly so all the positive potentials of shorter peak latency (the 1st, 2nd and 3rd) as part of the positive wave group suppressed the positive potentials of long peak latency. There is thus a relation between the stimulus strength and the latency of the different positive potentials in terms of threshold; the shorter the peak latency of a positive potential, the more energy is necessary to elicit it as part of the positive wave group.

There is a characteristic difference in the recovery of the five positive potentials from light adaptation. The schematic graph in Fig. 1 illustrates the recovery of the 1st, 2nd and 3rd positive potentials on the one hand, and that of the 4th and 5th positive potentials of the ERG on the other hand. Due to the behavior of the positive potentials during dark adapta-

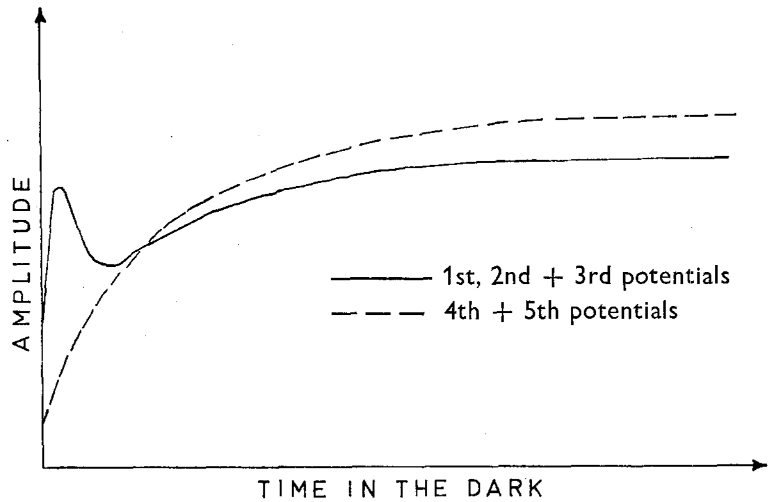

Fig. 1

The mode of recovery from light adaptation of the positive potentials of the ERG. (Schematic).

tion and to their differences in threshold, the first three positive potentials are ascribed mainly to photopic activity while the 4th and 5th positive potentials are ascribed mainly to scotopic activity. Likewise, the first two negative potentials appear to be connected to photopic activity, and the 3rd and 4th negative potentials to scotopic activity.

Use of low-intensity stimuli to demonstrate mainly the scotopic potentials

Since the mainly scotopic components of the ERG (the 4th and 5th positive potentials) are more sensitive toward photic stimuli than the mainly photopic components (the 1st, 2nd and 3rd positive potentials), low-intensity stimuli had to be used in order to demonstrate them clearly in the electrical response. Their maximal elicitation excludes thus the clear demonstration of the photopic potentials. This is demonstrated in the recordings of Fig. 2 which shows the last ERG in the light followed by recordings taken during dark adaptation. A certain stimulus intensity has been used which was low enough to elicit the scotopic 4th and 5th positive potentials largely, and just strong enough to elicit partly the photopic 1st and 2nd positive potentials. These two potentials then appeared as small humps on the ascending limb of the positive wave group. There are thus three positive elevations in the ERGs obtained both during light adaptation and during the first part of dark adaptation (in Fig. 2 up to 2.00 in the dark). The first elevation comprises the photopic potentials, and the 2nd

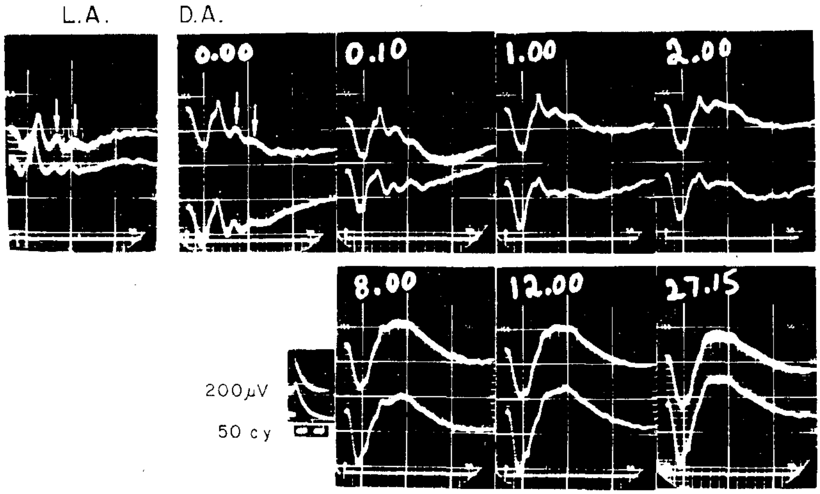

Fig. 2

The ERG during dark adaptation. Low-intensity stimuli used here did not suppress the long-latency positive potentials (arrows), and produced the 1st and 2nd positive potentials only partly; they appear indistinctly on the ascending limb of the positive wave group whose first peak is formed by the 3rd positive potential. The arrows indicate the 4th and 5th positive potentials, i.e. the 2nd and 3rd elevations. The fast potentials which build up the 1st elevation are shown in Fig. 3 and in the upper traces of Fig. 4.
L.A.: Light adaptation D.A.: Dark adaptation.
In all figures the upper traces represent the ERG from the right eye, the lower from the left eye.
Time in the dark (in minutes) on top of recordings in all figures.

and 3rd elevations (arrows) are the scotopic 4th and 5th positive potentials. The latter potentials gradually increase in amplitude during the process of dark adaptation until they dominate the ERG (recordings at 8.00, 12.00 and 27.15).

Use of medium-intensity stimuli to demonstrate mainly the photopic potentials

In order to demonstrate the three photopic positive potentials clearly a higher stimulus intensity had to be used (Fig. 3, recordings not marked by black arrows). In the recording taken within 50 msec. after switching off the adapting light (labeled 0.0) the overall amplitude of the ERG has increased by about 50% as compared to the ERG in the light. Ten seconds later the amplitudes of the three positive photopic potentials have increased to such an extent that they are approximately of equal height. After the first minute in the dark the 1st positive potential (white arrows) begins gradually to decrease in amplitude until it becomes part of the negative

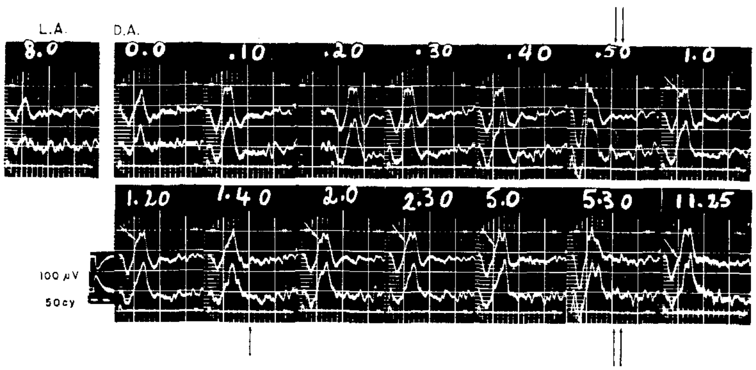

Fig. 3

The ERG during dark adaptation. A higher stimulus intensity than in the experiment in Fig. 2 was used here; medium-intensity stimuli clearly produce the first three positive potentials which build up the 1st elevation (all recordings except those marked by black arrows).
The white arrows indicate the decrease in the amplitude of the 1st positive potential during dark adaptation.
The single black arrow below the recording at 1.40 indicates an ERG produced by a low-intensity stimulus. The 1st and 2nd positive potentials appear on the ascending limb of the positive wave group.
The two black arrows above the recording at .50 and below that at 5.30 indicate ERGs produced by a much stronger stimulus than for the other recordings. At .50 the 1st positive potential is of greatest amplitude, while later in the dark (at 5.30) the 2nd positive potential is the largest. Consider mainly the upper traces of the recordings since due to a slight shift of the subject's head the light entered the left eye under a different angle.

wave group (at 11.25). Thus the stimulus strength used here, although it sufficed to elicit the 1st positive potential during the first few minutes of dark adaptation, later on became subliminal for this potential. (This stimulus intensity is called in the text 'medium').

The recordings in the same experiment at .50 and 5.30 (2 black arrows) show ERGs produced by high-intensity stimuli, and at 1.40 (one black arrow) an ERG produced by a low-intensity stimulus. In the former recordings the least sensitive 1st positive potential was maximally increased after 50 seconds in the dark and the other potentials were relatively suppressed while the 2nd positive potential was maximally increased later in the dark (at 5.30). In the latter case, the 1st and 2nd positive potentials were only partly elicited by a low-intensity stimulus, and appeared on the ascending limb of the positive wave group whose peak is formed by the 3rd positive potential.

THE EFFECT OF SLOW INTERMITTENT STIMULATION ON THE ERG

Trains of repetitive stimuli were delivered at rates from one per second to one every 30 seconds.

One medium-intensity flash every 10 seconds

The recordings in Fig. 4 are taken from an experiment in which the two eyes were at different states of dark adaptation. An adapting light shone

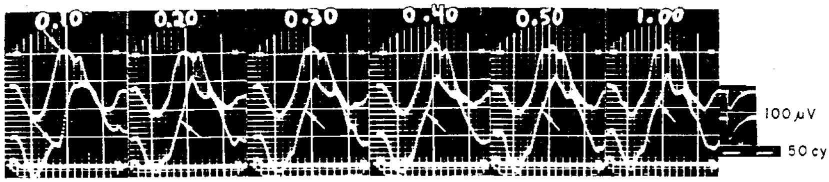

Fig. 4

Upper traces indicate the ERGs after light adaptation.
The white arrow points to the 1st positive potential.
These recordings correspond to those in Fig. 3 (note that the sweep speed was greatly increased).
Lower traces indicate the ERGs taken after 20 minutes in the dark. The time in the dark (on top of each recording) refers therefore only to the right eye.
The white arrows indicate the 1st positive potential. In the first recording it is part of the negative wave group. At a flash rate of one every 10 seconds it appears on the ascending limb of the positive wave group, gradually increasing in amplitude and becoming more marked. With the increase of the 1st positive potential only the 1st and 2nd negative potentials are left.

into the right eye only, while the left eye was light-tightly covered. The adapting light was then turned off and binocular recordings with stimuli of medium intensity were made. The ERGs obtained from the right eye (upper traces) were thus taken during the photopic phase of dark adaptation. They are characteristic for this phase and for the stimulus intensity used. The positive wave group is comprised of the first three positive potentials which are of about equal amplitude, whilst the negative wave group shows the first two negative potentials only. These recordings are therefore very similar to those presented in Fig. 3 (note that the sweep speed in the oscilloscope was increased for the recordings in Fig. 4).

Prior to the recordings the left eye had been in the dark for about 20 minutes, and was therefore already in the scotopic phase of dark adaptation. This accounts for the apparent shift of the positive wave group to the right in the ERG of the left eye (lower traces) as compared with the photopic ERG from the right eye (best seen in the recordings labeled 0.10). There is, however, not a real shift of the positive wave group since the shape of the ERG is due to the fact that the 1st positive potential is missing and an additional 4th positive potential has appeared. At this phase of dark adaptation the 1st positive potential has already decreased in amplitude (see 'introductory remarks' above) and appears in the negative wave group in response to medium-intensity stimuli (the white arrows at 0.10 of Fig. 4 indicate the 1st positive potential). The negative wave group displays the 1st and 3rd negative potentials, the 2nd being not visible in this ERG.

When a stimulus is applied every 10 seconds, the 1st positive potential in the left ERG is raised and appears as a slight hump on the ascending limb of the positive wave group and gradually increases in amplitude (arrows in the lower traces), while the negative wave group is left with the 1st and 2nd negative potentials. The 2nd positive potential also increases in amplitude while the amplitude of the 4th positive potential slightly decreases. The 3rd positive potential has become invisible in the slope between the 2nd and the 4th positive potentials.

Despite the slow rate of one every 10 seconds at which the stimuli were delivered, the ERG taken from an eye in the scotopic phase of dark adaptation did not maintain its initial pattern, and successive stimuli gradually built up an increasing response.

One flash per second

a. Medium-intensity stimuli

The first recording of Fig. 5 (at 21.45) demonstrates an ERG at a steady state in the dark attained under the experimental conditions. The 1st

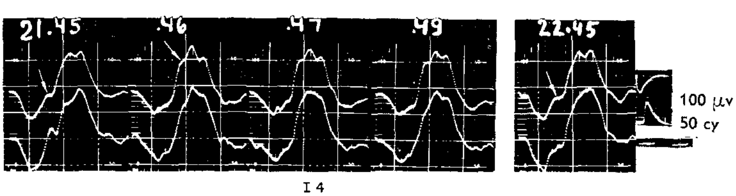

Fig. 5

Repetitive stimulation of medium-intensity at a rate of 1/sec. The white arrows indicate the 1st positive potential. After the initial response at 21.45 only three responses to repetitive stimuli are presented. The others show essentially the same. The white interspace between .49 and 22.45 indicates the interruption of repetitive stimulation.

positive potential appears as part of the negative wave group (arrow). The consecutive recordings, excepting the last (at 22.45), are responses to stimuli of medium intensity applied at a rate of one per second. The second stimulus of the train evokes a response which is markedly different from the first. The change is maximal, the wave pattern attained in the second response being maintained as long as the stimulus rate and the intensity of the stimulating light is not altered. The following changes are discernable in the response to the second stimulus. The amplitude of the 1st positive potential is greatly increased (arrow at .46) which leaves the negative wave group only with the 1st and 2nd negative potentials. The amplitude of the 2nd positive potential is also increased but to a smaller degree although being more sensitive than the 1st, whilst that of the last positive potential is decreased both showing the suppressing effect of the consecutive stimulus on the slower and more sensitive components of the ERG. To reestablish the initial state of the ERG at the beginning of the train, an interruption of the intermittent stimulation of at least 30 seconds

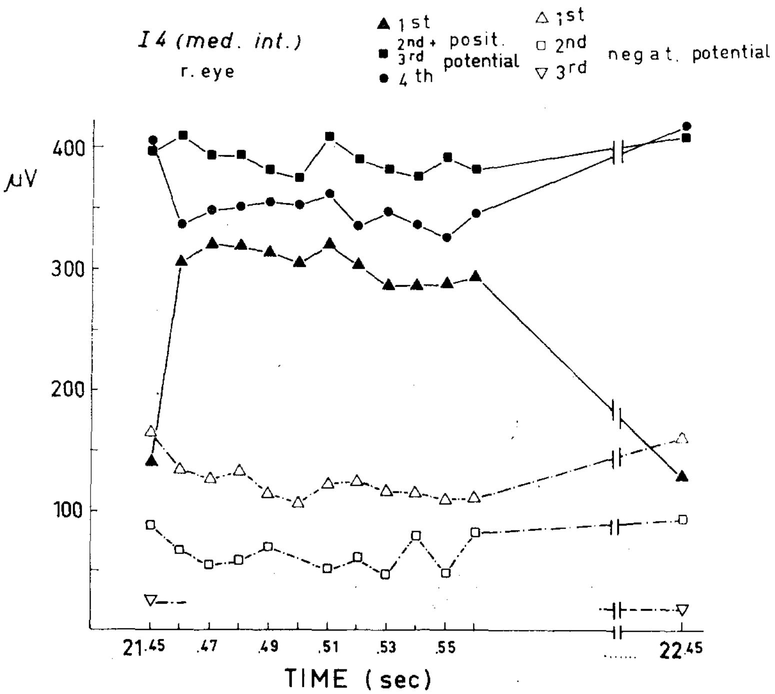

Fig. 6

The change in the amplitudes of the ERG as a function of time (to Fig. 5).

was necessary (compare the ERG at 22.45 with that at 21.45). Fig. 6 shows graphically the results of Fig. 5.

This phenomenon can also be demonstrated with different stimulus intensities, which will be illustrated by the two following examples.

b. Medium- and high-intensity stimuli in series

Fig. 7 shows the responses to two successive trains of stimuli of different intensities. The recordings in the upper row (labeled 25.00 to 0.11) de-

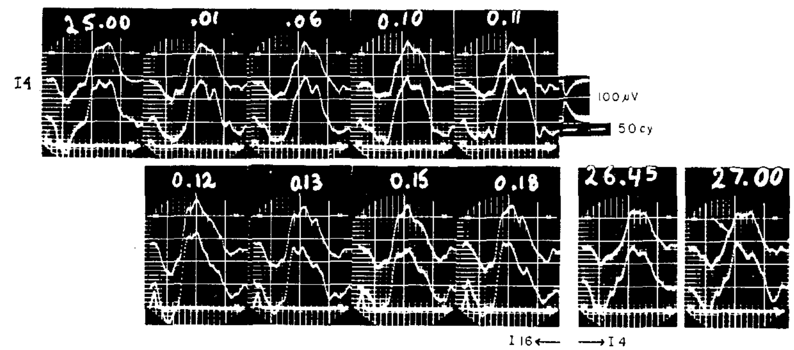

Fig. 7

The ERGs produced by repetitive stimulation at a rate of 1/sec. The upper row shows responses to stimuli of medium intensity. The lower row from 0.12 to 0.18 shows responses to stimuli of high intensity. After the interruption of repetitive stimulation (white interspace) follow responses to stimuli of medium intensity (at 26.45 and 27.00). The white arrow at 27.00 points to a small hump on the ascending limb of the positive wave group formed by the 1st positive potential.

monstrate the responses to medium-intensity stimuli, and the recordings in the lower row (labeled 0.12 to 0.18) demonstrate the responses to high-intensity stimuli. The responses in the upper row show essentially the same picture as those in Fig. 5. The response to the first high-intensity flash of the stimulus train (at 0.12) is characterized by an increase in all amplitudes as compared with the response to the lower stimulus intensity train shown in the upper row. A steady state was also here established with the response to the second stimulus of this intensity (at 0.13). This steady state is, however, characterized by a decrease in the amplitude of all positive potentials due to the high intensity of the repetitive stimuli. A solitary stimulus of medium intensity following the train of stimuli after an interval of at least 30 seconds shows the initial status reestablished (compare 26.45 with 25.00). If a stimulus follows after an interval shorter than 30 seconds, such as after 15 seconds, the 1st positive potential is raised again in amplitude and appears as a slight hump on the ascending limb of the positive wave group (arrow at 27.00). Fig. 8 shows the results of Fig. 7 graphically.

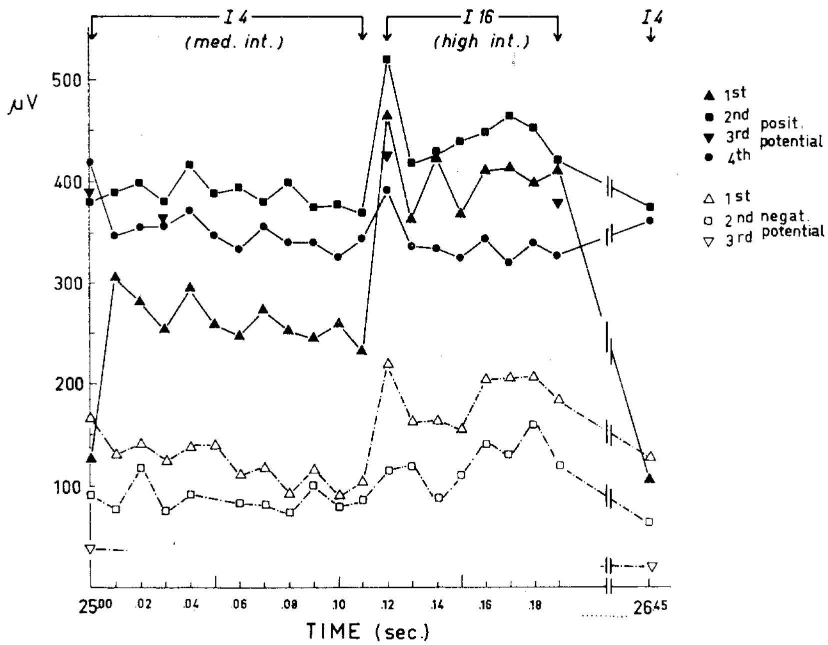

Fig. 8

The change in the amplitudes of the ERG as a function of time (to Fig. 7).

c. *Low-intensity stimuli*

Intermittent stimulation of low intensity (Fig. 9) shows essentially the same phenomenon, i.e. the changes attained in the response to the second flash were maintained during intermittent stimulation. A solitary stimulus, and for that matter the first stimulus of the train, of the intensity used here produces a response whose positive wave group consists of the 3rd, 4th and 5th positive potentials. It does not produce the 1st and the 2nd positive potentials as part of the positive wave group. They appear within the negative wave group which consists then of four negative potentials. Repetitive stimuli do not raise the amplitude of the 1st positive potential. The stimuli are therefore of a strength below the threshold of this ERG component even if repeated. However, the 2nd positive potential, although

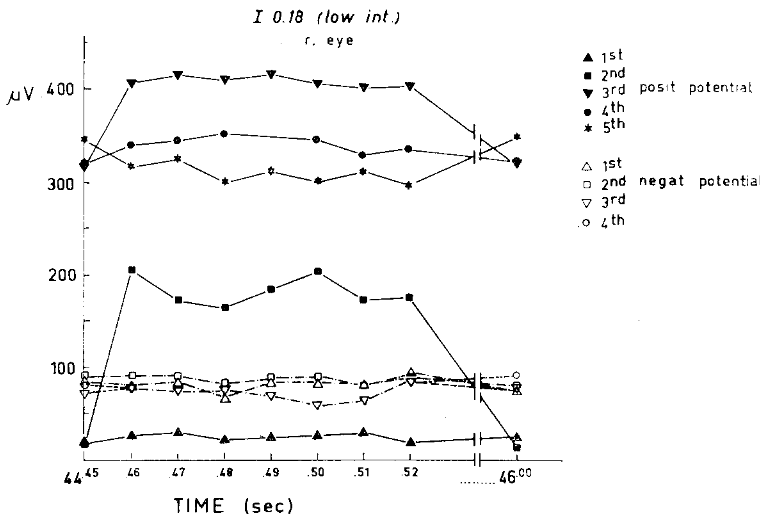

Fig. 9

The change in the amplitudes as a function of time in ERGs produced by repetitive stimuli of low intensity at a rate of 1/sec.

subliminal for the first stimulus of the train, is greatly raised by the repeated stimulus and only the first three negative potentials are left.

The 3rd positive potential although more sensitive than the 2nd increases in amplitude to a smaller degree than the 2nd positive potential. The amplitude of the 4th positive potential increases still less and that of the 5th positive potential is even decreased. The effect produced by the repeated stimulus is thus apparently the greatest on the last positive potential which is the most suppressed component. The initial status is reestablished after an interval of 30 seconds. The behavior is very similar to that described with stimulation of medium-intensity, except that the least sensitive 1st positive potential remains unaffected by the repeated low-intensity stimuli.

Other stimulus rates

Examples of responses to repetitive stimulation at a rate of one flash per second and at a rate of one flash per 10 seconds have been given. In the first case there was a characteristic change in the response to the 2nd stimulus of the train which was maximal and maintained for the duration of consecutive stimulation. In the second case, the successive stimuli gradually built up an increasing response. An effect similar to the first case was obtained when the intervals between stimuli were increased up to three or four seconds except that the change became gradually smaller with the increase of the intervals between stimuli. If these intervals were increased beyond 4 seconds, there was a gradual transition to the effect described in the second case. The increase of the intervals between stimuli beyond 15 seconds still resulted in a small effect on the ERG, and a further increase beyond 25 seconds did not display any detectable change in the pattern of the ERG.

DISCUSSION

These experiments, performed at an advanced stage of dark adaptation, reveal the following:

1. The effect on the electrical response of a solitary stimulus needs a certain period of time to disappear (about 25 seconds). If a second stimulus is applied within this period, the response to it shows certain characteristic differences from the response to the first stimulus.
2. Within the range of the stimulus rates used, the effect of a stimulus upon the electrical response is increased when it is repeated. The increased effect on the electrical response of a consecutive stimulus is a function of the stimulus strength; potentials increase in amplitude or become suppressed.
3. The effect on the ERG is gradually diminishing when the intervals between stimuli are increased. With the shortest rates used in these experiments, one per second up to one every three to four seconds, the effect is largest and already found to be maximal in the response to the second stimulus. A steady state is then established and maintained as long as the stimulus rate and the stimulus strength are not changed.

The increase of the electrical response which is obtained by a consecutive stimulus is unlikely to be caused by a photochemical reaction alone. If a photochemical reaction alone was responsible, one would expect the electrical responses to be in a direction opposite to that obtained in these experiments. The first stimulus, and for that matter a solitary stimulus, may possibly increase the excitability of the neural layers of the retina which gradually diminishes during the following 25 seconds. This period of time is, however, too long to account for a purely neural effect and partly contradicts this assumption.

Note on evaluation procedure used

The method used here for the measurements of the amplitudes of the potentials is in accordance with general usage. This method is, however, appropriate strictly speaking only for the measurement of a simple wave pattern built upon one component. In a complex pattern such as the ERG, which is the result of the superimposition and summation of a number of components, it can certainly not represent the elementary components upon which the ERG is built, and therefore not illustrate the true nature of the underlying physiological phenomena responsible for the pattern changes. What the method *does* represent is merely a demonstration of the visible changes in the overall pattern of the bioelectrical responses resulting from changes in physical and physiological parameters. The profit of the method used may be doubtful for a quantitative evaluation of the results and may indeed in this respect be misleading. However, at present no other method has proved more suitable for demonstrating the changes of the various potential differences, for example, the increase in the amplitude of the 'first positive potential' during the initial state of dark adaptation and its subsequent decrease as described in the introductory section in Results.

Misgivings regarding the suitability of the method of measurement used have, however, not much bearing on the graphs presented in this paper which demonstrate the effect of repetitive stimulation. Any method of measurement is suitable which shows graphically the establishment of a steady state attained by a certain rate of stimuli, and the return to the initial state.

CONCLUSIONS

1. A description of the pattern of the normal ERG including the recovery of the individual potentials following light adaptation is given.
2. The effect of slow intermittent stimulation on the potentials of the ERG in advanced dark adaptation is demonstrated, using ranges from one per second up to one every 30 seconds.
3. With the increase of the interval between stimuli the effect on the ERG produced by successive stimuli becomes smaller.
4. Stimuli at intervals from one second to four seconds produce a maximal effect on the potentials of the ERG with the second stimulus. A steady state is established during the continuance of the train of stimuli.
5. Successive stimuli at intervals beyond about four seconds up to about 15 seconds gradually build up an increasing response.
6. The changes in the electrical responses described are not detectable if the interval between stimuli is more than 25 seconds.
7. The relationship of these findings to a photochemical and a neural effect in the retina is discussed.

Summary

The ERG changes in the human eye at an advanced state of dark adaptation were measured as a function of slow intermittent stimulation at rates ranging between one per second up to one every 30 seconds.

The description of the findings is preceded by an introductory section dealing with the wave pattern of the ERG and the mode of recovery of the individual potentials following light adaptation. This section is a brief account of a study which will be reported elsewhere in detail and explains the criteria used.

With the shortest stimulus rates used (from one per second up to one per three or four seconds) the effect on the ERG is largest and is already maximal in the electrical response to the second stimulus. The steady state thus established is maintained as long as both stimulus rate and intensity are unchanged.

With the increase in the interval between stimuli beyond four seconds up to about 15 seconds, the establishment of a steady state during intermittent stimulation is delayed, and the successive stimuli gradually build up an increasing response.

When the interval between stimuli is increased beyond 25 seconds, there is no difference visible in the pattern of the electrical responses.

The relationship of these findings to photochemical reactions and to an increase in the excitability of the retinal neural layers is briefly discussed. The latter is assumed to be caused by a solitary stimulus and to decline during about 25 seconds.

Résumé

Les changements de l'ERG ont été examinés dans l'oeil humain pendant l'adaptation à l'obscurité comme fonction d'une stimulation intermittente et lente. Les intervalles entre les stimuli étaient d'une seconde jusqu'à trente secondes.

La description des résultats est précédée par une introduction sur les critères employés ici et qui seront publiés en détail ailleurs. Cette introduction traite les différents aspects ('Pattern') des ondes de l'ERG et la mode de rétablissement des potentiels individuels après un adaptation à la lumière.

Avec des intervalles de la stimulation les plus brèves utilisées ici (1-4 sec.) l'effet sur l'ERG est le plus fort et est déjà au maximum dans la réponse électrique du second stimulus. Une condition stable ('steady state') est ainsi établie.

Avec la prolongation de l'intervalle entre les stimuli au delà de quatre secondes jusqu'à environ 15 secondes, l'établissement de 'steady state' pendant la stimulation intermittente est retardé et les stimuli successifs déclenchent graduellement une réponse agrandissante.

Quand l'intervalle entre deux stimuli est prolongée au delà de 25 secondes, il n'y a pas de différence visible dans le 'pattern' des réponses électriques.

La relation de ces résultats avec des réactions photochimiques et avec une augmentation de l'excitabilité des couches nerveuses de la rétine est discutée brièvement. Il est supposé que la dernière est le résultat d'un seul stimulus et baisse progressivement pendant les 25 secondes suivantes.

Zusammenfassung

Die Potentialänderungen im ERG des menschlichen Auges bei fortgeschrittener Dunkeladaptation wurden als Funktion von langsam intermittierenden Lichtreizen gemessen. Die Reizintervalle waren zwischen einer Sekunde and 30 Sekunden.

Der Beschreibung der Befunde geht ein einleitender Abschnitt über die hier verwendeten Kriterien voraus, dessen Inhalt an anderer Stelle im Detail veröffentlicht wird. Er behandelt die Wellenform des ERG und den Erholungsverlauf der einzelnen Potentiale nach Lichtadaptation.

Die hier verwendeten kürzesten Reizintervalle (1-4 Sek), lösen den stärksten Effekt auf das ERG aus. Dieser Effekt ist ausserdem schon in der Antwort auf den zweiten Lichtreiz maximal (steady state).

Mit der Verlängerung der Reizintervalle über vier Sekunden bis ungefähr 15 Sekunden verzögert sich die Ausbildung eines 'steady state' und die einzelnen Antworten vergrössern sich stufenweise zu Beginn der intermittierenden Belichtung mit jedem folgenden Lichtreiz.

Bei Reizintervallen von mehr als 25 Sekunden sind keine Unterschiede mehr in den Antworten festzustellen.

Die Verbindung dieser Ergebnisse mit einem photochemischen Prozess und mit einer Erhöhung der Erregbarkeit der neuralen Schichten der Retina ist kurz besprochen. Es wird angenommen, dass die letztere durch einen Einzelreiz ausgelöst wird und während der folgenden 25 Sekunden absinkt.

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