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ADAPTATION IN THE COMPOUND EYE AND INTERACTION WITH SCREENING PIGMENT

BY U. YINON

Vision Research Laboratory, Hadassah University Hospital, Jerusalem, Israel

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INTRODUCTION

Processes of light-adaptation and dark-adaptation in the compound eye have been described mainly in terms of amplitude changes in the electroretinogram (ERG) or in the receptor potential of retinula cells (Goldsmith, 1964, Mazokhin-Porshnyakov, 1969). The question whether there are latency changes in the electrical response during the adaptation processes has not yet been considered.

Another question was asked regarding light-adaptation and dark-adaptation, namely to what extent the absence of the screening pigments (present in most compound eyes) influences these processes. Adaptation is influenced by the screening effect of these substances which cause an increase in the sensitivity of the superposition compound eye under dim light or in dark conditions (Bernhard & Ottoson, 1960; Post & Goldsmith, 1965). How much the remaining pigment in the ommatidial area of the dark-adapted eye is effective is unknown. A 'residual effect' due to distally located pigment was confirmed by Höglund & Struwe (1970). Thus a question was asked: what is the net contribution of the screening effect to the electrical activity of the dark-adapted eye?

The above points, as well as some other electrophysiological aspects of the light-adapted and dark-adapted compound eye, have been studied in the present work.

METHODS

A tungsten lamp was used as an adapting stimulus and a xenon stroboscope (or tungsten lamp with a shutter) was used as a test light. The test light was operated by a photostimulator (or solenoid) triggering the oscilloscope and the camera. A photocell placed in the beam of the test light and time markers were used for timing of experimental procedures. Impulses from the eye were fed to a pre-amplifier leading to an oscilloscope or a pen recorder. For more details of the stimulation and recording techniques, see Yinon & Auerbach (1969).

In the first set of tests some stimuli were given randomly on dark background for control purposes. Then 7 min of dark-adaptation was allowed for standardization of the photochemical process. Following this, 16 min of light and 12 min of dark were given, on background of each period test stimuli were superimposed. In the second set of tests some selected aspects were examined for longer adaptation periods. Thus 10 min of dark-adaptation followed by 10 min of light-adaptation were given for standardization. Then the eye was stimulated under dark-adaptation for $\frac{1}{2}$ h or 1 h. The sequence of stimuli given is seen in Figs. 1 and 4.

Results were obtained from 42 normal and 10 mutant adults of the yellow mealworm beetle, *Tenebrio molitor* L. Eye mutants lacking the screening pigment (Ferwerda, 1928) were considered as the experimental group and normal animals as the control group.

RESULTS

The electroretinogram and spike discharges

During the adaptation processes some changes were found in the ERG pattern (Fig. 1). The ERG was distorted in the first 30 sec of dark-adaptation. Furthermore, irregular small potentials of high frequency were superimposed on the negative and positive components in the first 5 min. These potentials appeared for a shorter period when a lower light intensity was used as a pre-adapting stimulus (Fig. 1). The origin

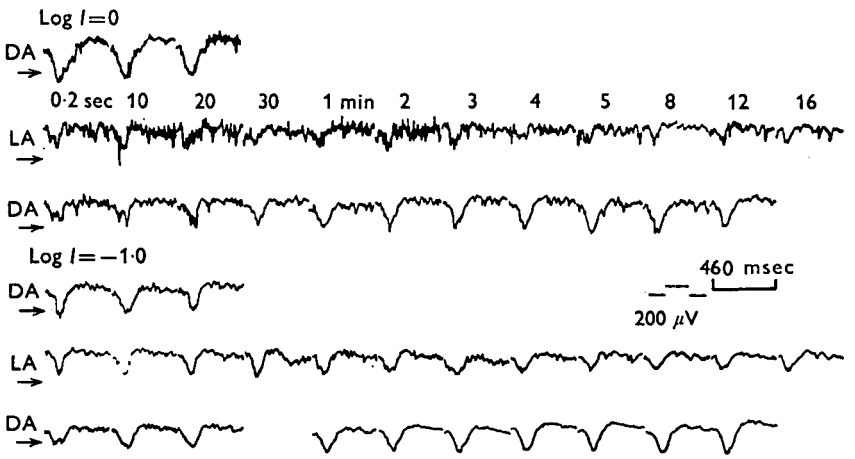

Fig. 1. The electroretinogram in light-adaptation (LA) and dark-adaptation (DA). Intensities given are of the light adaptation.

of the small potentials is difficult to assess owing to their irregularity. After the first 5–6 min in the dark the ERG pattern was normal. More small potentials and spikes appeared with light-adaptation for the whole experimental period. A very considerable decrease in their number was seen under a lower adapting light (−1·0 log unit) and the spikes disappeared. In dark-adaptation conditions spike potentials (300–600 μV) were superimposed on the ERG components (Fig. 2). They appeared 2 min after the beginning of dark-adaptation. No increase in their number was found during adaptation. They appeared in all the mutants and in a few normal specimens under the same conditions. (This is in agreement with the higher responses to light obtained for mutants [see below].) But no other differences were found between mutant and normal specimens in this respect.

Although the spikes were evenly dispersed on the ERG, in some cases they were not found on the negative component. In one case an 'off' unit was found; this was exceptional and no other 'on', 'off' or 'on–off' units were found (even if very long stimuli of 500–800 msec were given). As the spikes appeared more with

lower-intensity stimuli their appearance seemed to be inhibited under bright light. Therefore the origin of the spikes in most cases was in the visual system, probably in the optic ganglia.

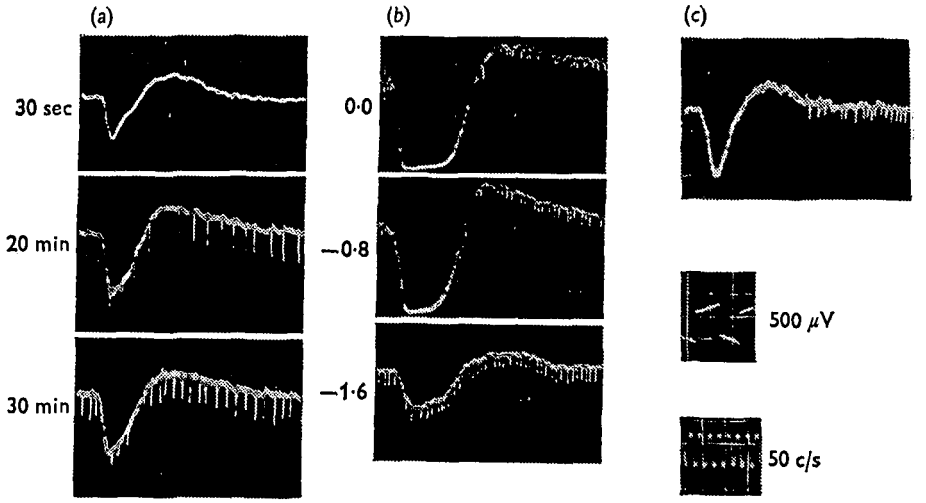

Fig. 2. Spike-potential discharges superimposed on the ERG, as function of (*a*) dark-adaptation and (*b*) light intensity (log units). An 'off' discharge is seen in (*c*).

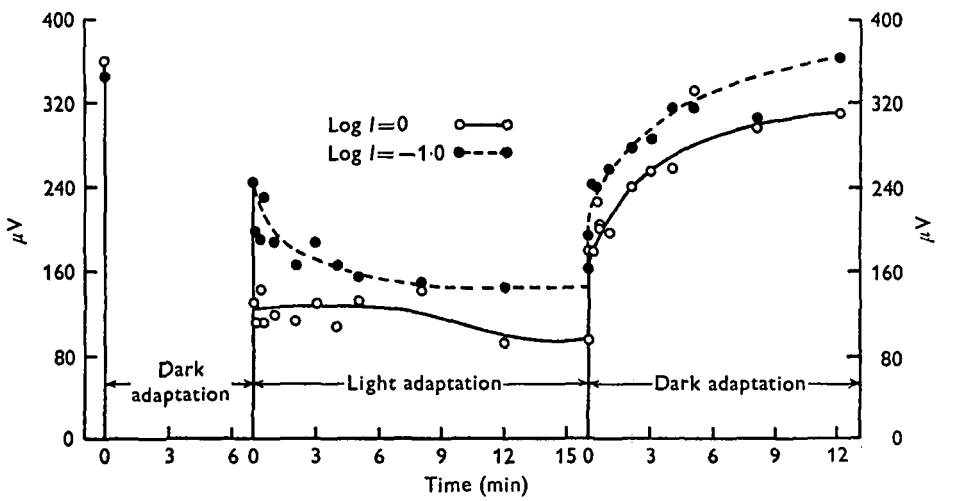

Fig. 3. Light-adaptation and dark-adaptation processes: changes in the amplitude of the negative potential (intensities given are of the adapting light stimulus).

Amplitude changes during adaptation

The changes in the amplitude of the principal negative potential as function of the adaptation process are shown in Fig. 3. The responses under light-adaptation reflect a bleaching procedure. The initial response dropped by 65%, and within 15 min gradually decreased to about one-quarter of the original level. When the

background light was lowered by one log unit, the initial response was 25% smaller than the control. It then showed a sustained level. Thus, the rate of bleaching is to a large extent determined by the light intensity.

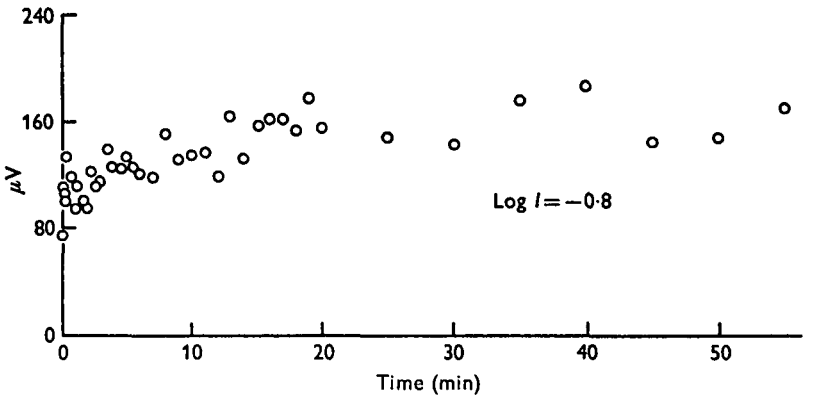

Fig. 4. Changes in the amplitude of the negative potential for a long duration of dark-adaptation.

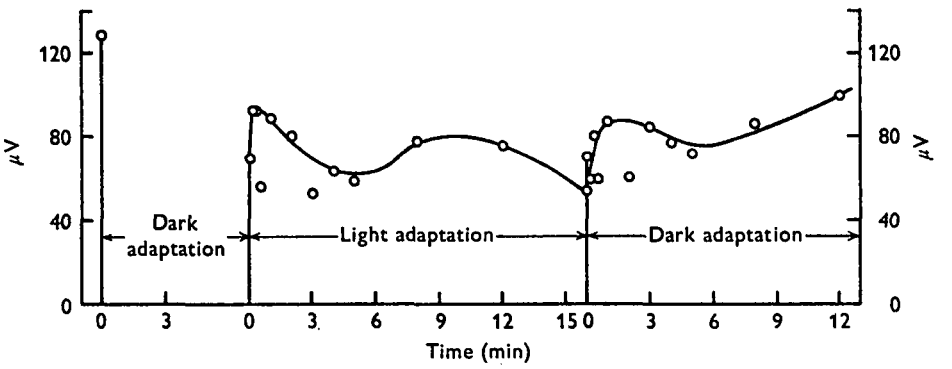

Fig. 5. The amplitude of the positive potential as function of light adaptation and of dark adaptation.

The rate of recovery during the dark-adaptation was rapid in the first 3 min, especially if a low-intensity (−1·0 log unit) pre-adapting light was used (Fig. 3). Looking at the dark-adaptation for a longer period (Fig. 4) we found that the response remained for 1 h at the same level as that established after the first 10 min.

The data for the positive potential of the ERG was less consistent than for the negative one (Fig. 5). However, it was in agreement with the results of the negative potential for the most effective periods, i.e. the first 1–2 min of both adaptation procedures.

Latency changes during adaptation

Very significant changes were found in the latency of the ERG as a function of the adaptation procedure. An initial sharp decrease in the latent period was seen under light-adaptation. It was even shorter under higher light intensity (Fig. 6). It remained at the same level even for an hour (Fig. 7). The rise time of the latency curve toward

the original value under dark-adaptation was very short, especially if in the pre-adapting light the eyes were exposed to a higher intensity. Thus, unlike the amplitude values, the latency curves obtained could not reflect the bleaching or the recovery processes for two reasons. First, the latency of the adaptation process showed an inverse relationship to the sensitivity of the visual system (i.e. the delay was longer when the sensi-

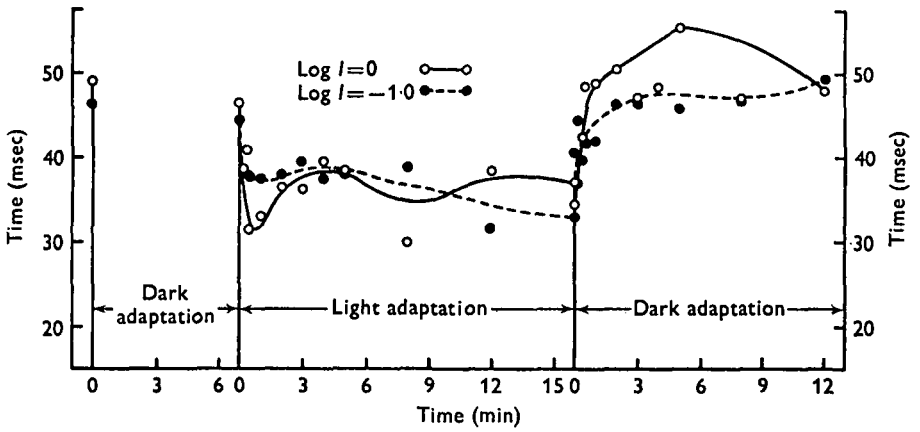

Fig. 6. The latency of the negative potential as function of light-adaptation and dark-adaptation (intensities are of the adapting light stimuli).

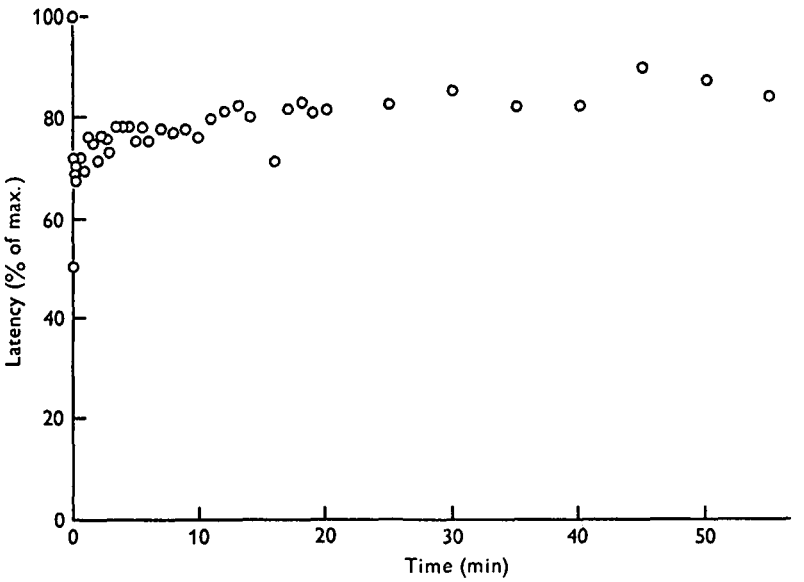

Fig. 7. The peak latency during long duration of dark-adaptation.

tivity was higher) in contrast to what was described previously for various intensities or wavelengths (Yinon & Auerbach, 1969; Yinon, 1971). Secondly, while there is a definite relationship between the degree of bleaching and recovery (see the ERG amplitude, Fig. 3), the latency results showed no such relationship (for the appropriate situations) (Fig. 6). As the sensitivity increased under dark-adaptation a shorter delay

was expected, but the opposite results were obtained, especially after lower pre-adapting light. The increase in the response after higher-intensity adapting light seen in the latency values may indicate the presence of an additional factor. This could be a process compensating for the fall in visual sensitivity under an excess of background

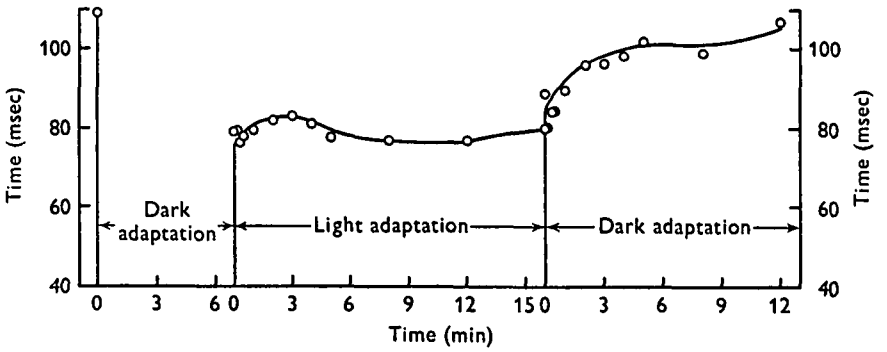

Fig. 8. The latency of the postive potential as function of light-adaptation and dark-adaptation

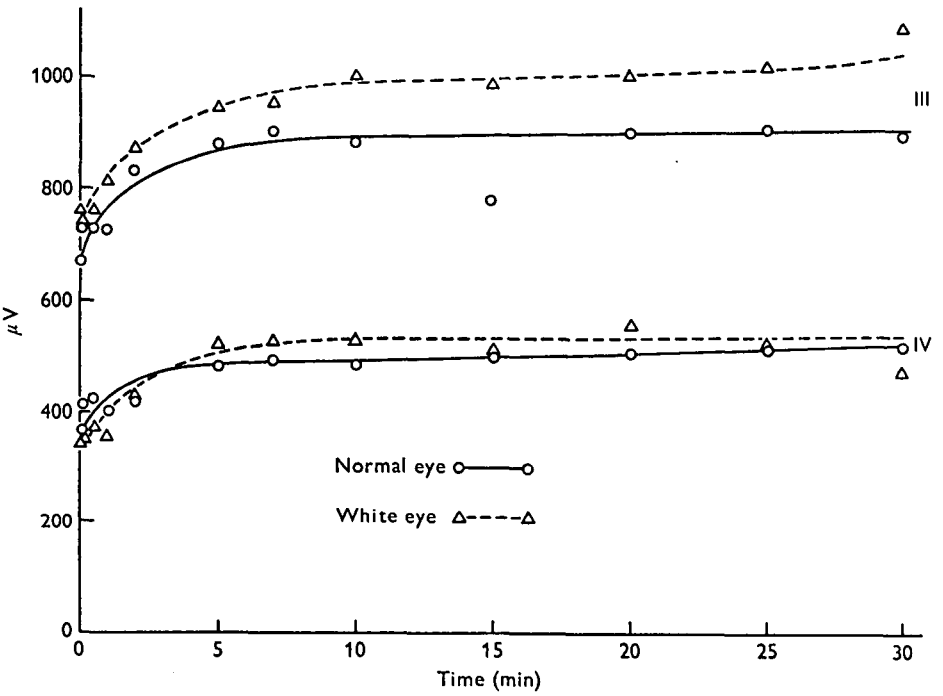

Fig. 9. Dark-adaptation curves for mutant (white) and normal eyes (III = negative potential; IV = positive potential).

light. It could be due to a change in the pupil size as found for *T. molitor* (Wada & Schneider, 1967), or an increase in the excitability of the retina (Höglund, 1966). Such a compensatory process could not be seen at all, or could be seen only partially, from the amplitude values in the above experiments since the threshold was not measured for various intensities of the adapting light.

The latency of the positive potential of the dark-adapted eye behaved in a similar way to that of the negative potential. In contrast, during light-adaptation there was an initial increase. Thus during light-adaptation the ERG spread along the time axis from peak to peak in the first 2 min (Fig. 8). We can assume that two populations of receptors contribute to the ERG; one gives rise to an earlier negative peak of the receptor potential with light-adaptation. Therefore, although the negative and the positive potentials are related to each other in their spectral response (Yinon, 1970*b*), they behave differently in this respect.

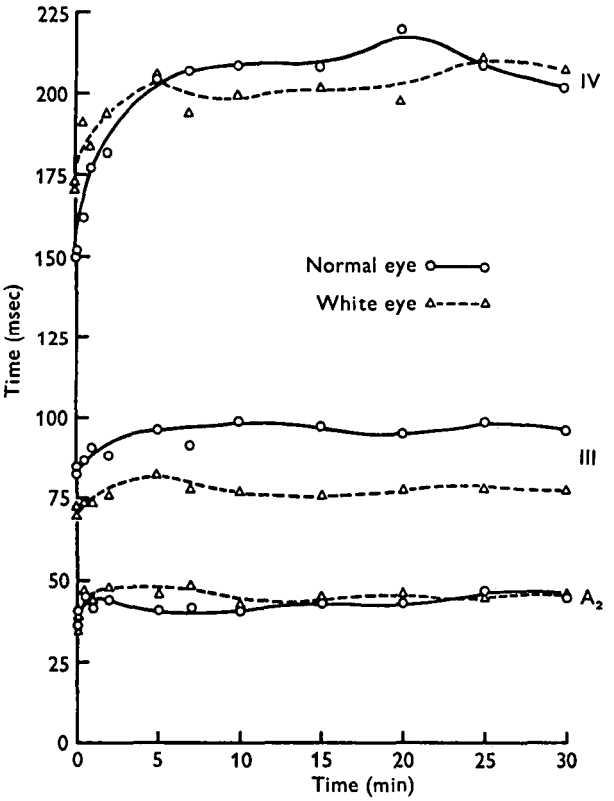

Fig. 10. The latency as influenced by dark-adaptation in mutant and normal eyes (A_2 = the latency of the negative potential; III = the peak latency of the negative potential; IV = the peak latency of the positive potential).

Adaptation and the screening pigment

The ERG pattern of mutant eyes lacking screening pigment was found to be the same as that of normal animals. This was also true for eyes stimulated by a monochromatic light instead of a white light (Yinon, 1970*b*). Thus there is no genetic mutation in the retinula or in the various neural levels of the visual pathways like that found in *Drosophila melanogaster* (Hotta & Benzer, 1969).

The light-adaptation curve obtained for mutants was higher than that for normal animals (Fig. 9). This is because the absence of the screening factor lowered the threshold sensitivity. Thus, under threshold conditions less light is needed to elicit

a visual response in the mutant than in the normal eye. Therefore, the difference between the curves of the normal and the mutant eyes shows the net effect of the screening pigment.

After exposing the eye lacking screening pigments to the adapting light, one would expect a slower recovery rate in the dark than in the normal eye, due to a stronger bleaching. The recovery rate of the unscreened eye after a weak bleaching should be faster than in the normal eye owing to the sensitivity increase. Therefore, there is a certain balance between the bleaching and the screening effects.

The latent periods of the ERGs in mutants during dark-adaptation were shorter than in normal animals, especially for the negative potential (Fig. 10). This was expected in view of the higher sensitivity shown by the unscreened eye.

DISCUSSION

Compound eyes have been classified into two groups with respect to their dark-adaptation processes (Autrum, 1948). In the 'fast-type' eye of the fly *Calliphora erythrocephala* no amplitude or latency changes were found in the principal potential of the biphasic ERG. In contrast, in the 'slow-type' eye of the cricket *Tachycines asynamorus* the height of the monophasic ERG as well as the latency were changed by dark-adaptation.

The adaptation process in *T. molitor* found in the present studies behaves similarly to the 'slow-type' but its ERG wave-form is like that of the 'fast-type' compound eye. Furthermore, changes mentioned by Autrum are seen in some details of the compound-eye ERG, but the general pattern is similar (Mazokhin-Porshniakov, 1969; Yinon, 1970*a*). In addition, the adaptation process is dependent mainly on the visual pigment which was found to be chemically similar in various species having compound eyes, either the 'fast-type' like the honey-bee (Goldsmith, 1958) or the 'slow-type' like the cockroach (Wolken & Scheer, 1963). The latency of response was found to behave systematically in the adaptation processes, which is in contrast to Autrum's findings for the 'fast-type' eye. Thus, Autrum's classification needs re-evaluation especially concerning the adaptation process.

Since scotopic and photopic components were not found in the adaptation patterns of the ERG, it seems as if there is no more than one receptor type in the compound eye examined. This is supported by the fact that the negative and the positive peaks have the same spectral characteristics in *T. molitor* (Yinon, 1970*b*). It is worth mentioning that even in compound eyes seeing colours which are known to have more than one receptor type, photopic and scotopic mechanisms have not yet been described.

The spectral response of compound eyes is distorted by screening pigments (Burkhardt, 1964). These pigments (isoxanthopterine and biopterine) were found in *T. molitor* (Harmsen, 1966). In the present studies the effect of this screening has been described. Under dark-adaptation the screening pigment in the compound eye migrates distally and an increase in sensitivity occurs, yielding a biphasic curve (Bernhard & Ottoson, 1964). The greater responses obtained in the present studies in unscreened eyes confirm this increase in the sensitivity as a result of partial or complete absence of the pigment. This is also in agreement with the behavioural results of Klingebeil (1938) that eye-mutants lacking screening pigments of the moth *Ephestia*

kühniella are more sensitive to light than in animals with normal eyes. The sensitivity of the compound eye depends both on the excitability of the photoreceptors and on the position of the light-screening pigment. Thus the retinular sensitivity cannot be measured by light passing through the dioptric area since it will influence the position of the screening pigment. By using direct techniques for stimulation and recording in the retinular area Höglund (1966) eliminated the effect of the screening pigment. In the present studies it has been shown that the net response was increased as a result of the absence of the screening pigment in the intact eye. A certain balance was suggested between the level of bleaching and of the screening effect. How much the absolute sensitivity of the eye is influenced awaits more investigation. In addition, although the screening effect has been found, the question of whether there is a pigment migration in the normal eye of *T. molitor* has to be answered.

T. molitor has an apposition eye which is characteristic for diurnal insects although it is a typical nocturnal insect (Cloudsley-Thompson, 1953). A large retinomotor effect in dark-adaptation (widening of the ommatidial pupil) was found in the *T. molitor* eye (Wada & Schneider, 1967). This effect is likely to occur in superposition eyes. It is probable that all of these characteristics interact with the dynamic processes of light-adaptation and dark-adaptation of the compound eye concerned.

SUMMARY

The electroretinogram pattern in the compound eye of *T. molitor* and the appearance of irregular small potentials and spikes superimposed on the ERG are influenced during dark and light adaptation procedures.

The amplitude of the principal negative potential reflects bleaching and recovery of the photochemical process. This is not true for the latency values. The delay of the electrical response increases in the dark and decreases in the light adapted eye. These changes were influenced by the intensity of the adapting light.

Mutant eyes only lack screening pigment and have normal visual neural pathways. The absence of this pigment lowered the threshold sensitivity of the unscreened eye in dark adaptation. The difference between the adaptation processes in mutants and normal animals has been suggested as a criterion for measuring the net effect of the screening pigment in the compound eye.

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