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THE EYE MUSCLE OF *CALLIPHORA VOMITORIA* L.

II. TRANSIENT RESPONSES TO CHANGES IN THE INTENSITY OF ILLUMINATION

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INTRODUCTION

The chief conclusion of the paper which forms a companion to this (Patterson, 1973) is that the eye muscle of *Calliphora vomitoria* L. is most probably concerned with the production of movements of the photoreceptive elements of the compound eye. These movements result in the scanning of the visual images produced by the corneal dioptrics.

Comparable systems in other animals are often responsive to a variety of visual stimuli. Optokinetic nystagmus can be produced in the eyestalk of the crab by the slow movement of vertical stripes in the visual field (Burrows & Horridge, 1968). In the more closely similar system found in the principal eyes of salticid spiders, saccadic movements are produced when the principal eyes are stimulated, and the retinae move so as to fixate the stimulating target. Tracking movements follow the movements of the target within the visual field (Land, 1969). Transient responses of the eye muscle of *Calliphora* can be elicited by changes in the level of illumination, by rapid, large-amplitude movements in the visual field and by the passage of air currents over the head (Burtt & Patterson, 1970). Van Barneveld (1971) has produced a brief account of the effects of changes in illumination and of movements in the visual field on eye-muscle activity in *Calliphora erythrocephala.*

This paper is concerned with a detailed description of the *transient* responses of the eye muscle to changes in the level of illumination in *C. vomitoria*. The long-term changes in the *resting* activity of light-adapted and dark-adapted preparations has been described previously (Patterson, 1973).

METHODS AND MATERIALS

Patterson (1973) gives details of the basic experimental methods. All experiments except those described in Fig. 1 were performed on dark-adapted, female *Calliphora vomitoria*. Electrophysiological recordings were obtained from isolated heads from which the ventro-lateral quadrat of the head had been removed to allow for the placement of a tungsten recording electrode in the vicinity of the eye muscle.

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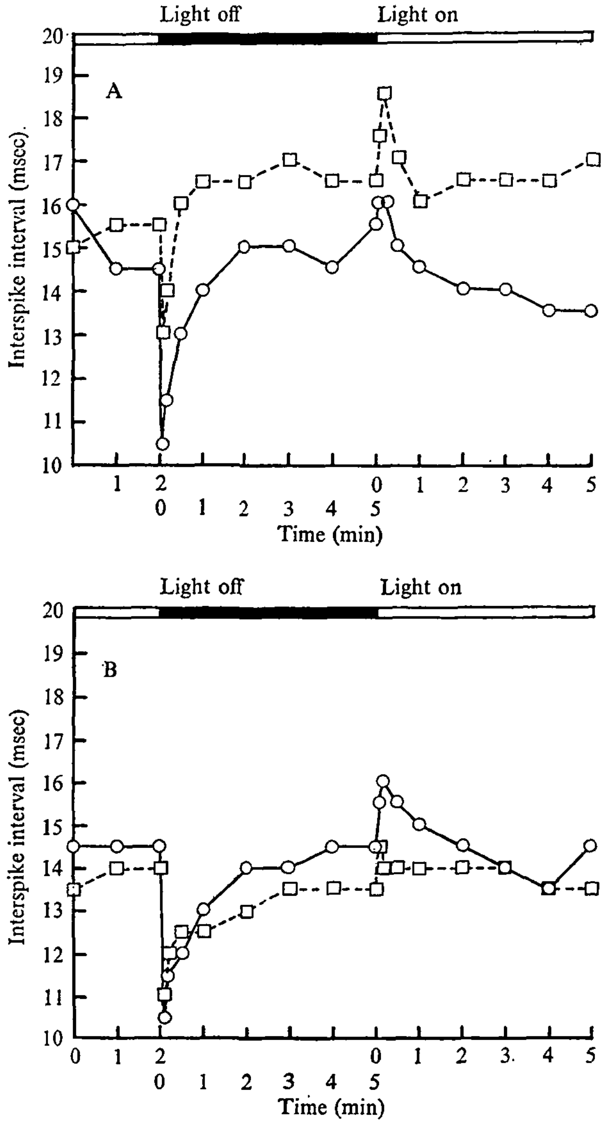

Fig. 1. 'Mean' interspike interval in milliseconds plotted as a function of time in minutes for two (A and B) female *Calliphora vomitoria* to show the effect of ocellar ablation on the transient responses of the eye muscle to changes in illumination between darkness and 5000 lux. Circles, responses obtained with intact ocelli. Squares, responses obtained after extirpation of the ocellar triangle.

RESULTS

Transient changes in eye-muscle activity with changes in illumination

Fig. 1 shows the effect of a 5 min period of darkness on the 'mean' interspike intervals (see Patterson, 1973, for explanation) of an eye muscle in two light-adapted (5000 lux) female *C. vomitoria*. The 'mean' interspike interval was measured 5, 10, 30 sec and 1, 2, 3, 4 and 5 min after each change in illumination. The circles show the responses of the intact head and the squares show, by way of a control,

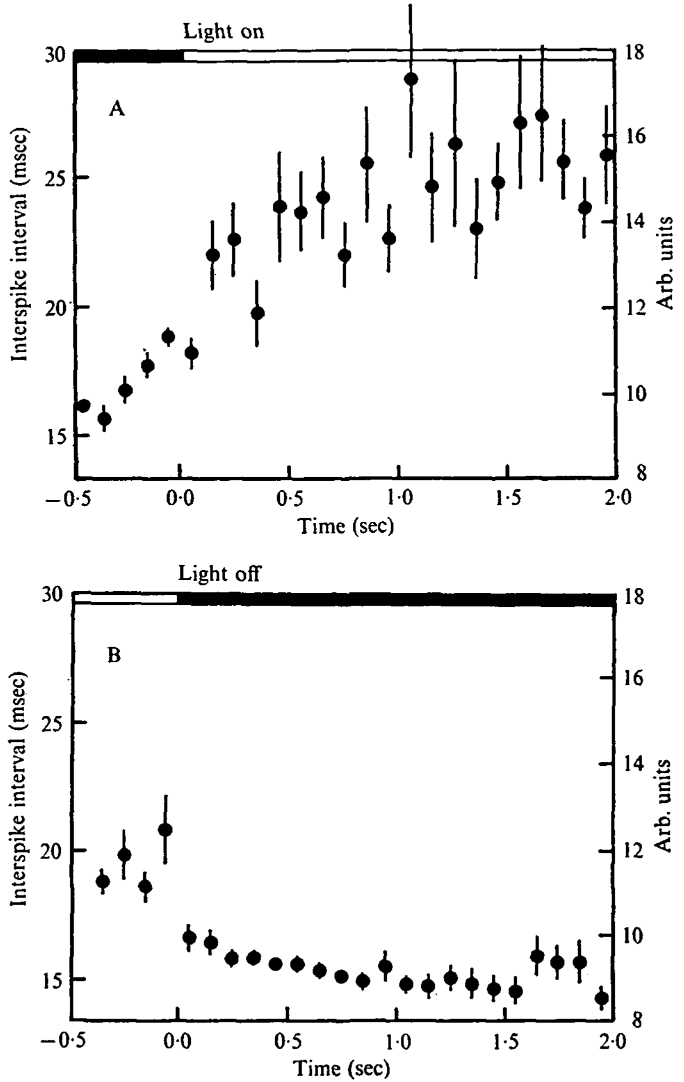

Fig. 2. True mean interspike interval in milliseconds plotted as a function of time in seconds to show the latency of eye-muscle responses to changes in illumination. The values are based on five animals in which the interspike intervals in each 100 msec period have been measured and averaged. (For explanation see text.) Bars indicate variance of the data expressed as ± the standard error of the mean. (*a*) Dark-adapted animals in response to light of 5000 lux intensity. (*b*) Dark-adapted animals in response to the onset of darkness after 30 sec of exposure to light of 5000 lux intensity.

the responses in the same preparations after the ocellar triangle had been dissected away. Experiments using light-guides to administer stimuli indicated that the responses are not a direct effect of illumination falling on the muscle and that the responses are indeed mediated primarily by the compound eyes. There is little difference between the response of the ocellate and anocellate preparations, and in both cases the onset of darkness results in a marked transient decrease in the interspike interval with a return to the pre-stimulus values within 30 sec to 2 min of the onset of darkness. Resumption of the adapting level of illumination results in a similarly transient response, an increase in the interspike interval on this occasion, with a similar recovery period.

Latencies of transient responses to changes in illumination.

To examine the latencies of the transient responses, five female animals were dark adapted and photographic records were obtained of the response of the eye muscle both to illumination of 5000 lux intensity and to a return to darkness after 30 sec of illumination.

Using the onset time of the stimulus as measured by a photocell as origin, the paper records obtained were divided into sections each of 100 msec duration. The duration of each interspike interval was measured in arbitrary units (mm) and the values for each 100 msec period were summed for the five preparations. From these data the mean interspike interval and standard error of the mean were calculated. Since each 100 msec period contained an inexact number of intervals, those intervals which overlapped the 100 msec divisions were pooled with the period which they occupied for the greater length of time.

The mean interspike intervals obtained in this way for each 100 msec period are plotted in Fig. 2. With 'light-on' (Fig. 2*a*) there is a small decrease in the mean interspike interval in the first 100 msec following the onset of the stimulus. The drift in the pre-stimulus values makes it unlikely that this decrease is significant. From the second 100 msec period onward there is a progressive increase in the interspike interval with an accompanying and marked increase in the variance about the mean, as evidenced by the standard errors of the mean which are plotted with the data.

With the return to darkness 30 sec after the onset of illumination (Fig. 2*b*) there is a noticeable decrease in the mean interspike interval within the first 100 msec of darkness. On this occasion there is a marked decrease in the variance of the data as compared to the pre-stimulus values.

The coefficient of variation of a system is defined as the standard deviation divided by the mean. Sample calculations of the coefficient of variation for the data associated with 'light-on' and 'light-off' indicate that with respect to the pre-stimulus values the variances about the means are respectively greater and less than those expected merely as a consequence of increased or decreased values for the mean interspike interval. In this respect the activity of the eye muscle is similar to that recorded from the units in the optic nerve of the *Limulus* compound lateral eye by Ratliff, Hartline & Lange (1968) although in the case of *Limulus*, decreases in the interspike interval are a consequence of illumination rather than of darkness, as is found for the *Calliphora* eye-muscle system.

For the eye muscle the changes in the interspike interval are sustained throughout the 2 sec period of observation, and the initial latency of the response is 100–200 msec. After this period there is a gradual growth in the magnitude of the response.

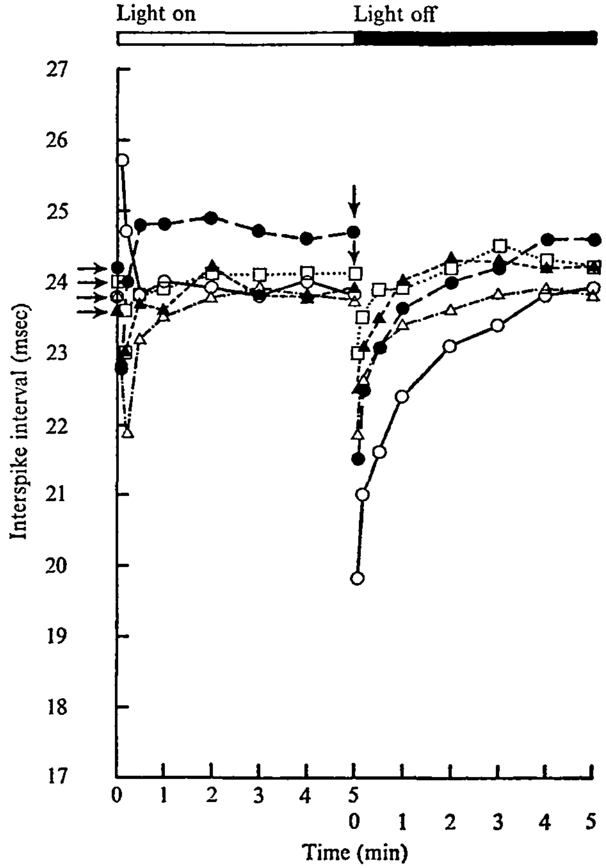

Fig. 3. 'Mean' interspike interval in milliseconds for eye-muscle potentials plotted as a function of time in minutes for dark-adapted female animals showing the transient responses obtained with changes in illumination of different intensities. All points are means of ten observations (ten animals). Mean temperature = 17·6 °C. Arrows indicate pre-stimulus values.

○ Darkness ⟶ 5000·0 lux ⟶ darkness
● Darkness ⟶ 500·0 lux ⟶ darkness
△ Darkness ⟶ 50·0 lux ⟶ darkness
▲ Darkness ⟶ 5·0 lux ⟶ darkness
□ Darkness ⟶ 0·5 lux ⟶ darkness

Transient responses to illumination of different intensities

The compound eye of arthropods, in common with many sense organs, shows a linear relationship between the magnitude of the evoked response and the logarithm of the stimulus intensity with a tail as the lower stimulus values are approached. This is the so-called Fechner line and has been discussed for the compound eye of the *Apis* drone by Naka & Kishida (1966). A series of experiments were performed to see whether a similar relationship is found between the transient responses of the eye muscle and the natural logarithm of the stimulus intensity.

The series of light intensities used formed a logarithmic series between 5000 and 0·5 lux and animals were presented with 5 min periods of each illumination intensity with 5 min of darkness separating each period of illumination. The stimuli were

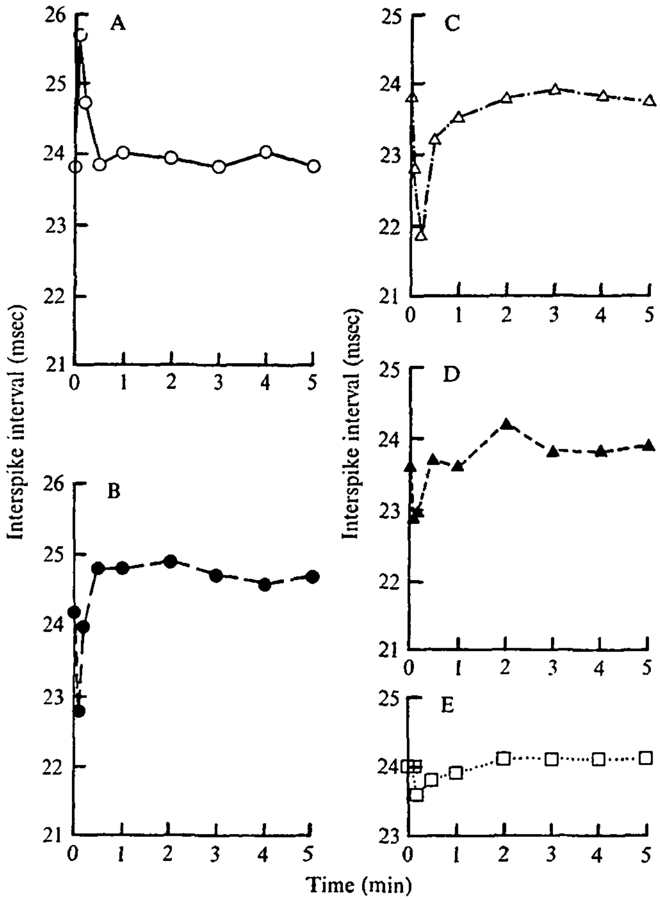

Fig. 4. Individual curves replotted from Fig. 3 for the responses of the eye muscle to 'light-on'. (A) Darkness ⟶ 5000·0 lux. (B) Darkness ⟶ 500·0 lux. (C) Darkness ⟶ 50·0 lux. (D) Darkness ⟶ 5·0 lux. (E) Darkness ⟶ 0·5 lux.

presented in decreasing order of magnitude to each of ten dark-adapted female *C. vomitoria* preparations. The stimuli were rotated by moving the starting-point one place down the series consecutively for each animal so that two complete rotations of each stimulus period relative to the time during the experiment occurred over the ten animals used. This technique was employed so that the effects of the gradual increase in the interspike interval which occurs during the first 20 min of an experiment (see Patterson, 1973) would apply equally to the data obtained from each stimulus intensity employed.

The 'mean' interspike interval was measured 5, 10 and 30 sec, 1, 2, 3, 4 and 5 min after each change in the level of illumination falling upon the preparation. The means of the values obtained from the ten animals are plotted in Fig. 3. The responses to 'light-on' are complicated and are replotted individually in Fig. 4.

The responses obtained from the eye muscle with 'light-off' form a graded series such that the greater the light intensity during the preceding 5 min the greater the decrease in the 'mean' interspike interval produced by the onset of darkness. The responses to the onset of illumination are, however, quite different. With the onset of light of 5000 lux intensity (Fig. 4A) there is an initial transient increase in the mean interspike interval. With light of 500 lux (Fig. 4B) there is initially a marked decrease in the 'mean' interspike interval, followed by an increase relative to pre-stimulus values after about 30 sec in the light. The remaining light intensities produce progressively smaller decreases in the 'mean' interspike interval with decreasing stimulus intensity. This experiment also illustrates further the time course of the transient responses and shows that the interspike interval has normally returned to near the pre-stimulus level within 30 sec of the stimulus onset.

To establish firmly the validity of the reversal in the direction of the 'light-on' response a second series of experiments were performed under slightly different conditions. Once again ten dark-adapted animals were used but the range of stimuli was reduced from 5000 to 5 lux. The number of stimulus intensities was increased by including intermediate values, and animals were presented with alternating periods of illumination and darkness of 30 sec rather than 5 min duration. The 'mean' interspike interval was measured 5 sec after each change in illumination. The stimuli were again presented in decreasing order of magnitude but no rotation of stimuli was employed; rather, the initial stimulus intensity of 5000 lux was repeated at the end of the series. The mean values for the ten animals are plotted in Fig. 5.

The values for the pre-stimulus 'mean' interspike interval shown as closed circles in Fig. 5(*a*) show the expected gradual increase which occurs during the course of the experiment – that is, with decreasing stimulus intensities. The values obtained 5 sec after 'light-on', plotted as open circles, show once again that the direction of the transient response reverses when plotted as a function of stimulus intensity. There is an increase in the 'mean' interspike intervals at high stimulus intensities, but below 500 lux the response is a decrease in the interspike interval. The graded decrease in the magnitude of the response with decreasing stimulus intensity is not marked as in the previous series of experiments.

The responses to 'light-off', plotted as closed circles in Fig. 5(*b*), all show a decrease in the interspike interval relative to the pre-stimulus values (open circles). The relationship between the post-stimulus interspike interval and the logarithm of the pre-stimulus light intensity is fairly linear over the range of stimuli employed.

Thresholds for transient responses to changes in illumination

Eye-muscle activity is recorded as a continuous train of tonically firing potentials so that the transient responses to the system are far from all-or-none effects. The fact that the responses of the muscle are graded with stimulus intensity suggests that the responses become progressively smaller as a 'threshold' change in light intensity is approached. The spontaneous fluctuations in the interspike interval constitute noise which can easily be confused with the small transient changes produced by a 'near-threshold' stimulus. 'Threshold' is therefore a difficult concept to apply to the system under investigation and so the following experiments were designed to show how the incidence of detectable changes in the interspike interval increases as the stimulus intensity is increased. Experiments of this nature were

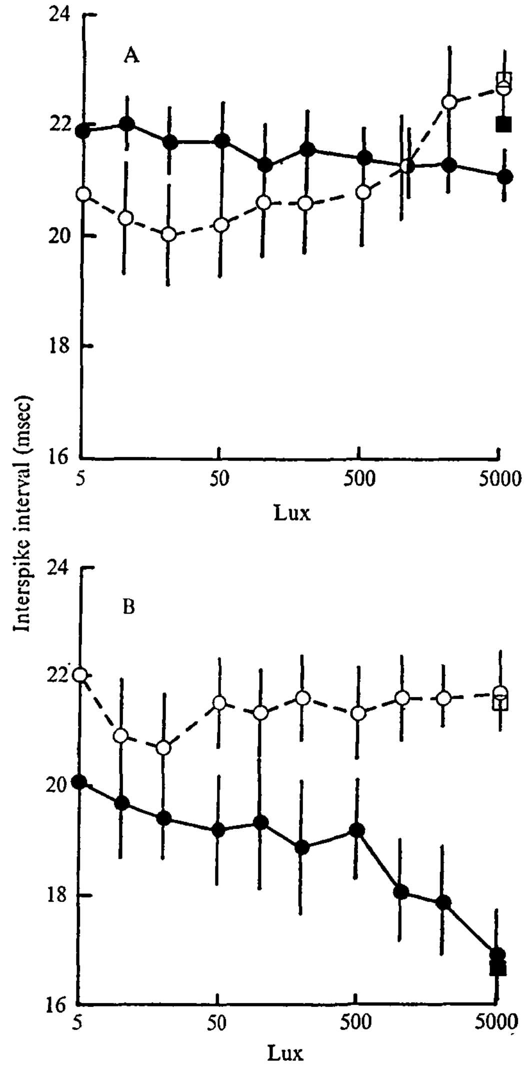

Fig. 5. 'Mean' interspike interval in milliseconds plotted as a function of stimulus intensity in lux for dark-adapted animals. All points are means of ten animals. (*a*) ●, Resting value (i.e. pre-stimulus). ○, 5 sec after 'light-on'. (*b*) ○, Resting values (i.e. 30 sec after 'light-on'). ●, 5 sec after 'light-off'. Bars indicate the variance of the data expressed as ± 1 standard error of the mean.

performed on groups of five female animals adapted to the following light intensities. A, 500 lux; B, 50 lux; C, 5 lux and D, darkness.

After a recovery period of 5 min at the adapting light intensity each preparation was presented with five separate series of stimuli. Each series consisted for A, B and C of ten equal logarithmic divisions of a light intensity ten times that of the adapting intensity; that is, 5000 lux for A, 500 lux for B and 50 lux for C. In each series the stimuli were presented in increasing order of magnitude. The starting-point was moved two steps (i.e. 0·2 log. units) along the series for each successive series. This procedure ensured that some degree of stimulus rotation was included

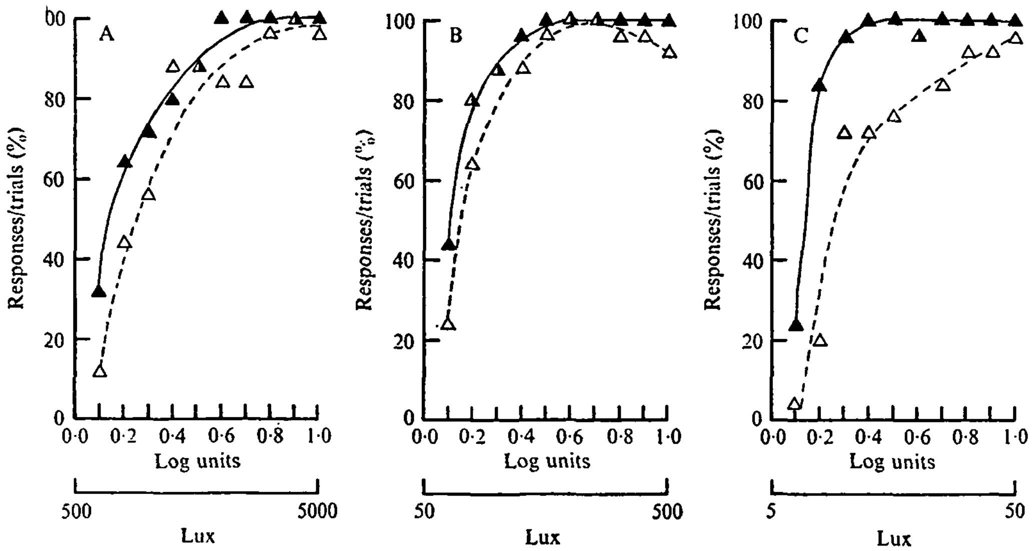

Fig. 6. Number of transient eye-muscle responses divided by the number of stimulus presentations (responses/trials) expressed as a percentage and plotted as a function of log stimulus intensity. Open triangles are the values obtained by an increase in illumination of a given value above adapting intensity. Closed triangles are the values obtained for a return from the increased light level to the adapting level. Each point represents the percentage of responses elicited from 25 stimulus presentations with five presentations made to each of five animals. (*a*) Adapting intensity, 500 lux. (*b*) Adapting intensity, 50 lux. (*c*) Adapting intensity, 5 lux.

in the data and also partially offset any consequences of always beginning with the lowest stimulus value. The starting-point was similarly rotated for each of the five animals in each experimental group.

For each stimulus value in each series an increase in the level of illumination was presented to the preparation for a period of 30 sec and was then withdrawn so that the preparation was returned to the adapting intensity for a period of 30 sec, after which the next stimulus in the series was presented. At each presentation or withdrawal of the stimulus any transient response of the interspike interval was noted but the magnitude and direction of the response were ignored.

The number of occasions on which each stimulus value elicited a response were summed over the five series and again summed over the five animals in each group. In this way the success of each stimulus in eliciting a response could be measured by expressing as a percentage the number of responses divided by the number of trials.

The results for groups A, B and C are presented in Figs. 6(A), (B) and (C) respectively; the open triangles are the values obtained with an increase in light intensity (presentation of stimulus) and the closed triangles are the values obtained when the intensity was decreased back to the adapting intensity (stimulus withdrawal).

A similar series of experiments were performed on a group of dark-adapted animals (group D) to determine the minimum 'threshold' stimulus for the responses of the eye-muscle system. An arbitrary maximum stimulus intensity of 0·5 lux was divided into a stimulus series covering 2 log. units giving a minimum stimulus

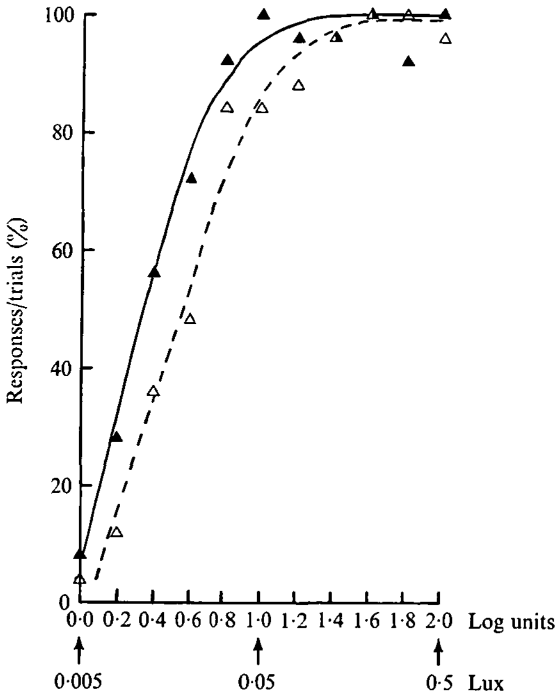

Fig. 7. As for Fig. 6 but for dark-adapted animals.

intensity of 0·005 lux. The stimuli were again presented for 30 sec with intervening periods of 30 sec in the dark. The results are plotted in Fig. 7 where the open triangles show the response of trial ratio for 'light-on' and the closed triangles that for 'light-off'.

All the curves in Figs. 6 and 7 have several features in common. As expected there is little sign of a marked 'threshold' stimulus value. At low stimulus intensities there is an initial phase in which the frequency of trials eliciting a response rises rapidly. This is followed by a plateau phase in which a 100% response/trial ratio is reached for the closed triangle data but not for the open triangles. Why the maximum is not reached for the open triangle data is puzzling and is unlikely to be due to an insufficiently high stimulus value, for the stimulus range was deliberately chosen to be quite wide. Notable also is the absence of stimulus values which totally fail to produce responses. This is possibly because the smallest stimuli were never 'subthreshold' although the confusion of small responses with the noise of the system offers an alternative explanation.

A further similarity shown between all the data is the consistently lower incidence of responses elicited by increases in illumination (or 'light-on') than that produced by decreases (or 'light-off') of the same magnitude. This hysteresis is such a common feature that one is tempted to say that the system responds more readily to decreases in the level of illumination than to increases. This suggestion is supported by the observations, shown above, that the magnitude of the responses to 'light-off' is normally greater than that to 'light-on'. The hysteresis is unlikely to be purely a consequence of preparations adapting to the increased level of

Table 1.

A. Light-adapted 50% response/trial stimulus values for *Calliphora* eye muscle responses at various adapting intensities of illumination

	50% response/trial stimulus			
	Open triangles data		Closed triangles data	
Adapting intensity (lux)	Log units above adapting	Lux above adapting	Log units above adapting	Lux above adapting
5	0·253	3·950	0·137	1·85
50	0·153	25·10	0·110	14·4
500	0·253	395·0	0·133	179

B. Dark-adapted

50% response/trial stimulus			
Open triangles data		Closed triangles data	
Log units above 0·005 lux	Lux above darkness	Log units above 0·005 lux	Lux above darkness
0·573	0·0187	0·347	0·0101

illumination during the 30 sec period which preceded the decrease to the adapting level. Such a process would normally be expected to decrease the magnitude and therefore to decrease the observed incidence of the responses to decreasing illumination rather than to increase it as in fact occurs.

Since neither the stimulus value which fails to elicit responses nor that which produces a response at every trial is readily measurable in these experiments, the stimulus value which produces a response/trial ratio of 50% was chosen for quantitative comparison of the data. The 50% response/trial stimulus values are plotted for each of the curves in Table 1. Table 1 B gives values for the minimum light intensity which will elicit a response in 50% of stimulus presentations to dark-adapted animals (open triangles) and for the minimum light intensity which produces a similar incidence of responses when the animal is returned to darkness after 30 sec in the light (closed triangles).

Table 1 A gives similar data for animals adapted to 5, 50 and 500 lux. The values of Table 1 A indicate, as the curves of Fig. 6 suggest, that the sensitivity of the system is modified with the adapting light intensity in a way which demonstrates the Weber–Fechner relationship, which like the Fechner line is a common feature of arthropod compound eyes and other sense organs (Naka & Kishida, 1966). To obtain a constant response, in this case a response on 50% of the occasions on which a stimulus was presented, the stimulus employed is a roughly constant fraction of the adapting intensity.

DISCUSSION

The simple stimulus of a change in the total intensity of the light falling on the compound eye is sufficient to produce marked changes in the activity of the eye muscle. If the proposed system of photoreceptor movement outlined previously

(Patterson, 1973) does in fact operate, then a change in the level of illumination initiates a feedback process which results in a scanning by the photoreceptors of the visual images produced by the corneal lenses of the compound eye.

Part of the interest of studying this type of system electrophysiologically lies in the information it yields concerning the way the nervous system integrates the initial visual input so as to modify the motor output to the eye muscle. Measurement of the latency of the response indicates that detectable changes in the 'mean' interspike interval occur possibly within 100 msec and certainly within 200 msec of the change in light intensity. It is difficult to find useful comparisons within the insect nervous system although visual interneurones in the locust optic lobe respond with latencies in the range 300–200 msec (Horridge *et al.* 1965).

The responses of the eye muscle to light stimuli of differing intensities show that where 'light-off' is concerned, the responses consist of a decrease in the 'mean' interspike intervals and the magnitude of the response is linearly related to the logarithm of the pre-stimulus light intensity. For the 'light-off' responses the eye muscle therefore shows similarities with the Fechner relationship between response magnitude and stimulus intensity which exists for the compound eye. This response-to-stimulus relationship is normally expressed in terms of the 'light-on' response for the compound eye, but the responses of the eye muscle to 'light-on' do not reflect the Fechner relationship. At high stimulus intensities (500–5000 lux) the eye muscle responds to 'light-on' with a transient increase in the 'mean' interspike interval; below 500 lux the response consists of a transient decrease.

The slow component of the electroretinogram (ERG) of the compound eye described by Burtt & Catton (1964) has a time course similar to that for the transient responses of the eye muscle. Experiments were performed with *C. vomitoria* (Patterson, 1972) to see whether the slow component of the ERG could be correlated with the reversal of the 'light-on' response of the eye muscle but no obvious relationship was found. Burkhardt (1954) describes a rhythmical potential originating in the optic lobe of *C. erythrocephala* which shows amplitude modulations with the onset of illumination with a similar time course to the transient changes in eye-muscle activity described here. It was found (Patterson, 1972) that these light rhythms were only larger than the background noise level with light of 500 lux or greater intensity. A clear relationship between the occurrence of light rhythms and an inhibition of eye-muscle activity was not established.

It remains a possibility that the reversal of the 'light-on' response of the eye muscle reflects a more general property of the insect nervous system. Two pieces of evidence encourage this idea. First, although the ocelli are not essential to the production of a normal muscle response at high light intensities (see Fig. 1) all other preparations allowed both compound eyes and ocelli to receive the light stimuli. Jander & Barry (1968) argue that in the behaviour of *Locusta* and *Gryllus* the ocelli act synergistically with the compound eyes at low light intensities and antagonistically at high intensities, and Cassier (1965) shows that in the positive phototactic behaviour of *Locusta* the accuracy of orientation increases until a light intensity of 50 lux is reached, above which the accuracy decreases again. Secondly, Hengstenberg & Götz (1966) show a reversal of the direction of a component which follows the 'on-effect' of the ERG in *Drosophila melanogaster*. This component was of the same sign as the 'on-effect' at low light intensities, reversing at high stimulus intensities.

Finally, experiments on the 'near-threshold' behaviour of the eye muscle indicate that the transient responses reflect the Weber–Fechner relationship between stimulus intensity, response magnitude and the adapting level of illumination found in the compound eye. In addition, it would appear that responses to 'light-off' or to decreases in the light intensity are more frequently elicited than responses to 'light-on' or to increases in the light intensity where stimuli of similar magnitude are employed.

A minimum stimulus of 0·0187 lux is required to elicit a response in 50% of presentations from a dark-adapted animal and a return to darkness after 30 sec at 0·0101 lux produces a similar response/trial ratio in the same preparations.

SUMMARY

1. Changes in the intensity of the illumination falling on the compound eye produce *transient* changes in the interspike interval of the tonic potentials generated by the eye muscle of *Calliphora vomitoria*. These changes are distinct and frequently different in direction from changes in *resting* activity produced by light and dark adaptation which have been described previously.

2. The effect of 'light-on' at high stimulus intensities is to produce a transient increase in the interspike intervals of the eye-muscle potentials. At lower intensities the result is a transient decrease in the interspike intervals.

3. 'Light-off' consistently evokes a decrease in the interspike interval, and the magnitude of the decrease is graded with the logarithm of the preceding light intensity.

4. With high-intensity stimuli changes in the interspike intervals occur within 200 msec of a change in illumination and continue to develop for at least 2 sec. The interspike intervals have returned to near to the pre-stimulus values within 30 sec to 2 min of the onset of the stimulus.

5. The behaviour of the eye-muscle system is described for 'near-threshold' stimuli and response 'threshold' is found to vary with adapting intensity in a way which illustrates a Weber–Fechner relationship.

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