DARK ADAPTATION IN THE EYE OF ERISTALIS TENAX

(One figure)

WILLIAM L. DOLLEY, JR.
Biological Laboratory, University of Buffalo, and Marine Biological Laboratory, Woods Hole, Massachusetts

INTRODUCTION

THE process of dark adaptation in photosensory organs has been studied in a few organisms: *Volvox* (Mast, 1911), *Amoeba* (Folger, 1925), three lamellibranchs, *Mya arenaria* (Hecht, 1919 and 1923), *Pholas dactylus* (Hess, 1910, and Hecht, 1927), and *Psammobia vespertina* (Hess, 1910), an ascidian, *Ciona intestinalis* (Hecht, 1918 and 1927), the snail, *Agriolimax campestris* (Crozier and Wolf, 1928), the cephalopod, *Sepia* (Hess, 1910), the molds, *Phycomyces nitens* (Tollenaar and Blaauw, 1921) and *Phycomyces blakesleanus* (Castle, 1929), the amphipod, *Atylus swammerdamii* (Hess, 1910), *Amphioxus* (Hess, 1910), the vertebrates, the chick (Honigmann, 1921), the tadpole (Obreshkove, 1921, and Hecht, 1927) and man (Piper, 1903; Nagel, 1911; and Hecht, 1920, 1921, and 1927). As yet this phenomenon has not been studied in an arthropod, except for the few observations of Hess on *Atylus*. It is important that adaptation be studied intensively in many of the large groups of organisms in the hope of unraveling the processes underlying it and in order to discover if these processes are similar throughout the world of living things.

This article is a first report upon adaptation to light in the eye of the drone fly, *Eristalis tenax*. This organism was chosen because it is an arthropod which can be secured in large numbers and which is especially adapted for experiments of this type owing to its size, hardiness, and uniformly highly positive reactions to light.

METHODS

The insects were collected in the vicinity of the laboratory at Woods Hole, Massachusetts, where they were feeding on various flowers. They were taken to the laboratory, where after their wings were clipped, they were kept in small wire cages containing cane sugar, privet pollen, and water.

Preliminary experiments showed that specimens with the two eyes unequally adapted to light do not behave in some respects as do animals with both eyes equally light adapted. When a normal specimen is exposed in a field of light formed by two horizontal beams of equal intensity crossing at right angles, it moves in general along the diagonal bisecting the angle formed by the two beams. When, however, a fly with one eye light adapted and the other dark adapted is placed in a similar field it does not move along the diagonal but deflects toward the side of the dark adapted eye, indicating that this eye is more sensitive than the other.[1] The extent of the deflection depends upon the relative sensitivity of the two eyes to light. In the experiments described below advantage was taken of this fact.

The method used in dark adapting one eye and light adapting the other was as follows: A small rectangular box was constructed out of thin sheet copper with the top and one end open. The box was about twice the length of the fly. Its depth and width were such that the insect could be placed in it completely and yet not be crowded. Out of the end of the box and down from the top a slit was cut of a width slightly larger than the width of the neck of the fly. A specimen was placed in the completed box with its body inside, its neck in the slit, and its head outside the end of the box. The organism was held without injury so that it could not move its head. Then over the whole box and insect a piece of tinfoil was wrapped, except that one eye was left exposed and an opening was left at the rear of the insect so that respiration was not interfered with. With a pair of fine forceps the edges of the tinfoil were pressed close around the covered eye. Another piece of tinfoil containing a hole of a diameter about the same as that of the insect's eye was placed around the covered box and fly with the hole in the tinfoil over the uncovered eye. Again the edges of the tinfoil were

[1] This is in harmony with the observation of Garrey (1918, p. 119) that the covering of one eye of the robber fly, *Proctacanthus*, with asphalt varnish causes this eye to become more sensitive to light than the uncovered eye.

pressed tightly around the covered eye. Frequently a third and fourth piece of tinfoil were similarly fastened around the insect. When the operation was complete respiration was not affected and yet one eye was completely covered so that no light could strike it while the other eye was completely uncovered.

Then the insect was placed in an adapting chamber. This was a box (45 by 45 by 270 cm.) made of beaver board and painted dead black inside. Near the center of this box was fastened vertically a 110 v. 150 watt lamp. The insect with only one eye exposed was placed on a horizontal support in the box level with the filament of the lamp. The distance from the filament of the lamp to the eye of the insect was 83.5 cm. The organism faced diagonally toward the light, the long axis being at an angle of 45 degrees with the rays of light. Thus during the exposure to light for the purpose of adaptation the image of the lamp fell on the same region of the retina as it did when the insect was oriented in the field of light consisting of two horizontal beams crossing at right angles.

It is assumed in this article that adaptation to light in one eye does not affect the other. Parsons (1924, p. 54) says, with reference to the human eye, "Dark adaptation of one eye has no effect upon the other."

Before describing these experiments I wish to express my appreciation of the aid of Professor S. O. Mast throughout the course of this work.

RESULTS

The procedure followed and the results obtained may be given by describing the reactions of a typical insect. This organism was collected, brought immediately into the laboratory, and left in a cage before an open window for an hour or more. Then it was taken into the dark room and left in darkness for an hour, after which it was tested in a field of light formed by two horizontal beams crossing at right angles, as described in previous papers (Mast and Dolley, 1924; and Dolley and Wierda, 1929). The luminous intensity of each beam at the center of the field of light was 52.9 m.c. In four trials it made an average deflection of 0.7 degrees toward the side of the left eye from the diagonal bisecting the angle formed by the two beams, its paths thus almost coinciding with the diagonal

(Table I, Exp. I). After this test the insect was placed again in a cage before an open window and allowed to remain there for an hour, i.e., until the eyes became thoroughly light adapted. Then the right eye was covered with tinfoil and the insect was placed in the adaptation chamber as described in the foregoing and left thirty minutes during which the right eye was dark adapted and the left eye light adapted in a luminous intensity of 52.9 m.c. The organism was now taken quickly from the adapting chamber, freed of its wrappings, and removed from the small metal box. The whole operation was done in dim red light and did not take more than 60 seconds. The fly was then tested again in the field consisting of

TABLE I

SENSITIVITY OF EYE OF *Eristalis tenax* TO LIGHT AFTER DARK ADAPTATION FOR 30 MINUTES*

EXPERIMENT	AVERAGE ANGLES OF DEFLECTION IN FOUR TRIALS					TOTAL AVERAGE ANGLE
	Designation of flies					
	a	b	c	d	e	
I	0.7 *l*	9.7 *r*	0.7 *r*	6.2 *r*	16.7 *l*	
II	25.2 *r*	24.0 *r*	17.0 *l*	23.0 *r*	20.2 *r*	
Corrected angle (I+II)	25.9 *r*	14.3 *r*	17.7 *l*	16.8 *r*	36.9 *r*	15.24 *r*

* *r*, deflection toward right; *l*, deflection toward left; Exp. I and II, tests in two horizontal beams crossing at right angles, illumination in each, 52.9 m.c. For procedure preceding each experiment see text.

two horizontal beams precisely the same as in the preceding tests. It now made an average deflection toward the side of the dark adapted eye of 25.2 degrees from the diagonal bisecting the angle formed by the beams (Table I, Exp. II), whereas with the two eyes equally light adapted it deflected 0.7 degrees toward the side of the left eye. Dark adaptation of one eye for 30 minutes consequently resulted in an increase in deflection toward the dark adapted eye of 25.9 degrees. Similar results were obtained in tests on four other specimens. These, together with those referred to in the foregoing, are presented in Table 1.

As is clear from the reactions of the typical insect described in the preceding, each fly before being tested in Exp. I (Table I) had been previously subjected to the following two experimental procedures: first, both eyes had been adapted to the bright light of the laboratory for 60 minutes or more, and then immediately afterward both eyes had been thoroughly dark adapted for 60 minutes. Immediately after the test in Exp. I and before the test in Exp. II each insect was subjected to the following two experimental procedures: first, both eyes were adapted to the bright light of the laboratory for 60 minutes, and then immediately afterward the right eye was dark adapted and the left eye was light adapted for 30 minutes in an illumination of 52.9 m.c.

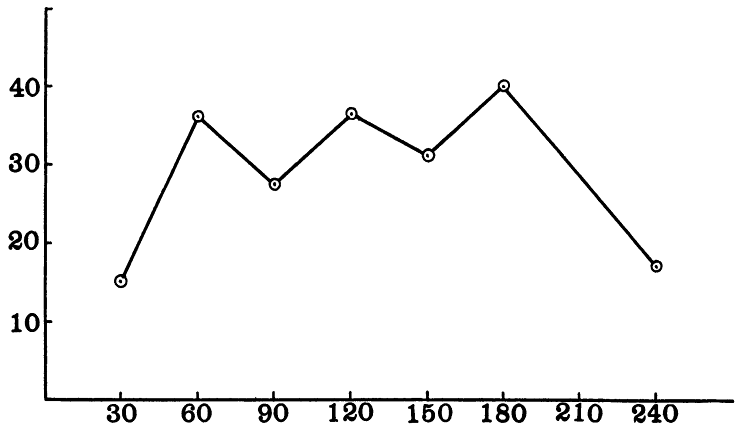

FIG. 1.—Relative sensitivity to light in eye of *Eristalis tenax* after various periods of dark adaptation. Ordinate, degree of sensitivity as indicated by the degree of deflection from the diagonal bisecting the angle formed by two beams of equal illumination, 52.9 m.c., crossing at right angles. Abscissa, duration of dark adaptation in minutes.

As is seen in Table I the five insects with one eye dark adapted and the other light adapted for 30 minutes made an average deflection from the diagonal bisecting the two beams of 15.24 degrees toward the side of the dark adapted eye.

In the same way six other groups of flies, five in each, were tested after having one eye dark adapted, but for various lengths of time. The results obtained in all these tests are presented in Figure 1.

As is shown in this figure, upon exposure to darkness sensitivity to light in the eye of *Eristalis tenax* increases to a maximum in about 60 minutes and remains at about the same level for the following 2 hours, after which it decreases rapidly. It is probable that the apparent variations after adaptation for 90, 120, and 150 minutes are not significant. The drop in the curve at 4 hours is significant, as is shown in the following experiment.

A normal insect with both eyes uncovered was tested in the field of light described in the foregoing after having previously been treated exactly as were the animals whose reactions have been described. In this test it made an average angle of deflection of 3.2 degrees toward the right eye. The left eye was then dark adapted for 60 minutes, and in the test after this period it deflected toward the dark adapted eye at an angle of 26.5 degrees. The left eye was again dark adapted for 60 minutes and in the test following it deflected at an angle of 21.7 degrees in the same direction. Three other tests were given consecutively in which the left eye had been dark adapted for 60 minutes before each test. In the first two the animal deflected toward the side of the dark adapted eye at angles of 13.2 and 10.5 degrees, respectively, while in the third it deflected in the opposite direction at an angle of 30.2 degrees. The results of this experiment support the conclusion drawn in the preceding, that the sensitivity of the eye to light drops rapidly following dark adaptation for 3 hours, and it indicates that the sensitivity of the dark adapted eye becomes even less than that of the light adapted eye.

The results presented do not however indicate the magnitude of the change in sensitivity correlated with dark adaptation. The following tests throw some light on this problem. Nine normal insects with both eyes uncovered were each given tests in the field of light described after having received exactly the same preliminary treatment given those flies used in Exp. I, previously described. The average angle of deflection of all these insects in thirty-six trials was 0.48 degrees toward the side of the left eye (Table II, Exp. III). After both eyes had been thoroughly light adapted for 60 minutes the right eye was dark adapted and the left eye light adapted for 60 minutes in an illumination of 52.9 m.c. The insects were then tested in a field of light in which the luminous intensity in the right beam was 52.9 m.c., while that in the left beam was 21.8 times as intense. Under these conditions the average angle of deflection for all the insects was 5.27 degrees toward the side of the left eye (Table II, Exp. IV). This angle is not greatly different from that made by the same insects with both eyes equally dark adapted in two beams of light of equal luminous intensity. This shows that it is necessary to increase the intensity of the left beam about twenty-one times in order to overcome the deflection toward the side of the dark adapted eye, indicating that the sensitivity of an eye dark adapted for 60 minutes is about twenty-one times that of the light adapted eye.

TABLE II

RELATIVE SENSITIVITY TO LIGHT OF LIGHT AND DARK ADAPTED EYES OF *Eristalis tenax**

EXPERIMENT	AVERAGE ANGLES OF DEFLECTION IN FOUR TRIALS									TOTAL AVERAGE ANGLES
	Designation of flies									
	f	g	h	i	j	k	l	m	n	
III	7.0 *r*	0.2 *r*	5.2 *l*	4.5 *r*	0.5 *r*	15.2 *l*	1.2 *l*	6.5 *l*	11.5 *r*	0.48 *l*
IV	8.0 *l*	11.5 *l*	14.0 *l*	2.0 *r*	15.5 *l*	9.5 *r*	10.5 *l*	2.0 *l*	2.5 *r*	5.27 *l*

* *r*, deflection toward right; *l*, deflection toward left: Exp. III, test in two horizontal beams crossing at right angles, illumination in each, 52.9 m.c.; Exp. IV, test in two horizontal beams crossing at right angles, illumination, right beam, 52.9 m.c., left beam, 52.9 by 21.8 m.c. For procedure preceding each experiment see text.

SUMMARY

During exposure to darkness sensitivity to light in the eye of *Eristalis tenax* increases in about 60 minutes to a maximum of about twenty-one times its sensitivity when adapted to a luminous intensity of 52.9 m.c., remains at about this level for 2 hours, then decreases rapidly to a point which is probably lower than that which obtains in light adapted eyes.

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