References and Notes

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2. J. Moor-Jankowski and K. S. Brown, *Exptl. Med. Surg.*, in press.
3. To avoid ambiguity, symbols for blood factors and their corresponding antibodies are printed in boldface type, symbols for genes and genotypes are printed in italics, and symbols for agglutinogens, phenotypes, and blood group systems are printed in regular type.
4. J. Buettner-Janusch [*Ann. N.Y. Acad. Sci.* **97**, 9, (1962)] has also observed that baboon red cells do not agglutinate in anti-**A** or anti-**B** sera, but he made no attempt to A-B-O group his baboons by testing their saliva and serum.
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9. A. S. Wiener, M. Baldwin, E. B. Gordon, *Exptl. Med. Surg.*, in press.
10. The tests carried out in the Serological Laboratories of the Office of the Chief Medical Examiner of N.Y. City were aided in whole by U.S. Public Health Service grant GM-09237-02. The collection of primate blood samples was greatly facilitated by Dr. Willard H. Eyestone, Chief, Animal Resources Branch, National Institutes of Health.
11. A more complete listing of published data can be found in the review by P. Kramp, in *Primatologia, Handbook of Primatology*, H. Hofer, A. H. Schultz, D. Stark, Eds. (Karger, Basel, 1960), vol. 3, No. 2, pp. 88–162.
12. A. S. Wiener, *Transfusion* **3**, 173 (1963).
13. The paper of Landsteiner (*6*) quotes two orangutans of group O, but comparison with his previous paper [K. Landsteiner and C. P. Miller, Jr., *J. Exptl. Med.* **43**, 853 (1925)] indicates that this is a typographical error and that the orangutans were really group A. Therefore, they are entered in Table 1 as group A.
14. There is a considerable confusion in the baboon taxonomy; the animals described here have been classified for this study by Dr. W. T. Roth, General Curator, Smithsonian Institution, National Zoological Park.

18 July 1963

Visual Responses in the Eye of the Dragon Fly

Abstract. *Responses to illumination recorded from cells in the eye of the dragonfly are similar to responses of cells in the eye of* Limulus *and are affected in the same manner by currents through the cell membrane. It appears probable that visual responses are brought about by the same processes in the two species.*

The compound eye of the dragonfly consists essentially of a few thousand ommatidia, each of which possesses its own dioptric system in the form of a cone-shaped lens. The ommatidia are thin, elongated structures packed in a regular array along the radii of the eye. Each ommatidium contains four transparent cells which join, along one of their long edges, to form a complex structure called a rhabdome. As in other compound eyes, the rhabdome is thought to contain the photosensitive pigment and, therefore, to be responsible for the initiation of responses to light.

When the eye is sectioned along an appropriate plane, a layer of ommatidia is exposed, and individual ommatidia (but not individual cells) can be clearly seen under a dissecting microscope. It is then possible to introduce a microelectrode into an ommatidium, under visual control.

Some features of the responses recorded from visual cells of dragonflies by means of intracellular electrodes have been described by Naka (*1*). He found that ommatidial cells are electrically polarized (with the negative pole inside) and that steps of light evoke depolarization in two phases—a high, transient and a lower, steady-state phase.

Work on the visual cells of dragonflies (suborder Anisoptera) was extended, in the experiments reported here, to include studies on the relationship between the intensity of the stimulating light and the size of the response, and also the effects of electric currents on the responses to light.

In confirmation of Naka's (*1*) re-

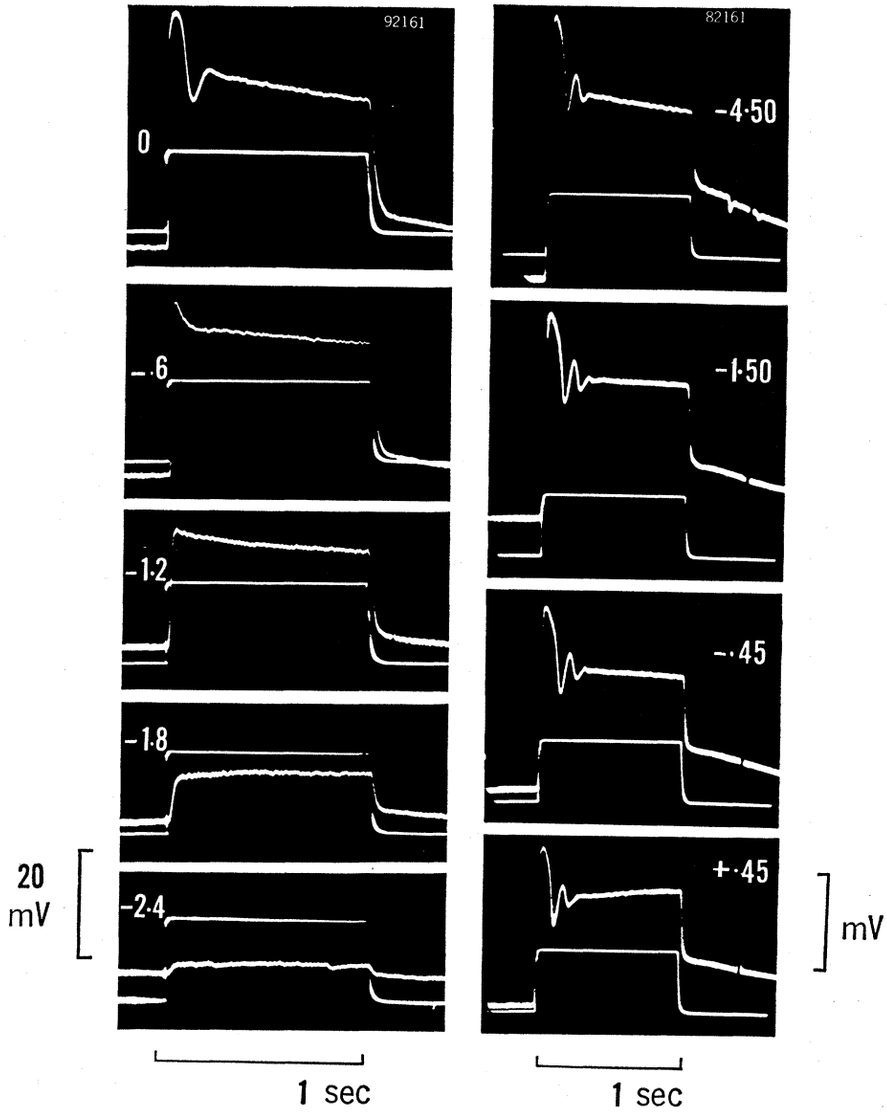

Fig. 1. Responses to illumination with steps of light of 1-second duration. (Left) Figures at left are the logarithm of relative light intensity. One beam measures duration (but not intensity) of the step of light and the other beam measures the intracellular potential change evoked by light. Temperature, 20°C. (Right) Recordings from a different preparation. Figures at right indicate the intensity, in nanoamperes (1 na $= 10^{-9}$ amp), of a steady current passed through the intracellular microelectrode and thus through the cell membrane. The steps of light are all of the same intensity. It may be seen that the change in potential is increased by hyperpolarizing (—) currents and decreased by depolarizing (+) currents. Temperature, 20°C.

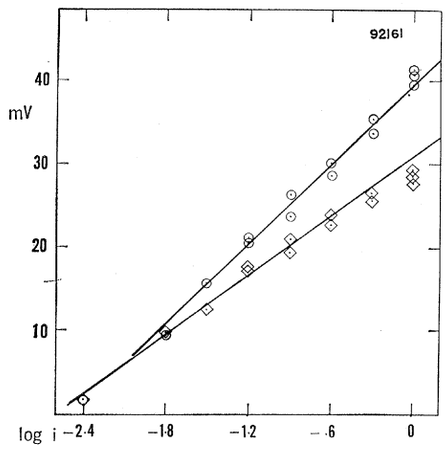

Fig. 2. Relation between the height of response and the light intensity. Data are from the experiment of Fig. 1, left. (Circles) Height of early peak; (diamonds) height of response 900 msec after initiation of the illumination. The figures along the abscissa are the logarithm of relative light intensity.

sults, it was found that when an ommatidium is penetrated by a microelectrode, a steady resting potential (usually 30 to 60 mv, with the negative pole inside) is recorded, and that this potential difference is reduced by illumination. Figure 1, left, illustrates responses obtained after illumination with steps of light of different intensity. It may be seen that, with weak light, the response is approximately "square-shaped," but that, with increasing light intensities, a higher transient response develops at the onset of illumination and an oscillation becomes apparent at the transition between the early, transient and the later, steady-state phases. Both at the beginning of the response and 1 second after the onset of the illumination, the amplitude of the voltage change is an approximately linear function of the logarithm of light intensity, as shown in Fig. 2.

Qualitatively, the features of the responses described are similar to those that occur in visual cells of *Limulus* (*2*, *3*). The most striking difference is that, whereas nerve impulses are usually recorded from cells of *Limulus*, no signs of impulse activity could be recorded in the dragonfly. In addition, the threshold for the first detectable response is higher in dragonflies than in *Limulus*, and the oscillation which occurs with bright light is less damped in dragonflies.

When currents are passed through the microelectrode, a drop in potential occurs across the membrane of the cell. It was found in *Limulus* that hyperpolarizing currents increase the size of the potential change evoked by light (*2*), and this finding was explained by the assumption that the voltage drop produced by the current across the cell membrane is less during illumination than it is when the membrane is at rest. Thus, it was concluded, membrane resistance is decreased during illumination, and it was suggested that the change of voltage recorded after illumination is a consequence of this decrease in membrane resistance. Similar results were obtained when the same method was applied to responses recorded from dragonflies. As Fig. 1, right, shows, steady hyperpolarizing currents increase the voltage change evoked by a given intensity of light, while depolarizing currents decrease it. The relation between the current intensity and the size of the voltage change is approximately linear, both during the early phase of the response and in the steady state (Fig. 3). That membrane conductance changes as a result of illumination can be confirmed by the bridge-balance method. If the potential drop evoked by pulses of current is balanced in darkness, unbalance, revealing increased conductance of the arm that includes the cell membrane, occurs during illumination, just as it is observed in *Limulus* (*2*).

It appears from these results that the arguments proposed for interpreting the responses evoked by light in cells of the eye of *Limulus* may apply, in essence, also to the dragonfly. Thus, it seems likely that light evokes increase of conductance of the membrane of visual cells of dragonflies and that the decrease in membrane potential that occurs as a result of illumination is a consequence of the change in conductance. The similarities between *Limulus* and the dragonfly in their responses to steps of light and in the relation between amplitude of response and light intensity suggest that essentially the same mechanisms operate in the two species.

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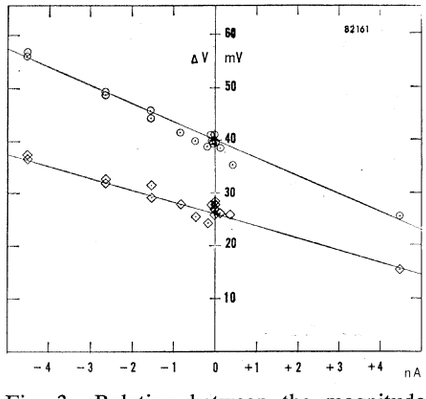

Fig. 3. Relation between the magnitude of the voltage change evoked by light and the intensity of a steady current through the cell membrane. Data are from the experiment of Fig. 1, right. (Circles) Height of early peak; (diamonds) height of steady-state response. Slope of straight lines is —3.4 Mohm for peak measurements and —2.3 Mohm for steady-state measurements (see text).

References and Notes

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16 August 1963

Aversive Stimulation of the Rat: Long-Term Effects on Subsequent Behavior

Abstract. *One year after exposure to intense electric shock, rats were punished with shocks of lesser intensity. The previous exposure increased the suppressive effects of the punishment during both the initial encounter with punishment and over the course of a 7-day test period. Rats that had not been previously exposed to shock recovered during continued shock punishment.*

When a mature animal is exposed for a brief period to experiences of intense aversive stimulation, its reactions to fear-producing stimuli in subsequent test situations are drastically modified (*1*). The results of a number of recent studies have been consistent with the hypothesis, originally proposed by Kurtz and Pearl (*2*), that prior experiences of intense fear serve to sensitize an organism, predisposing it to react with "increased fearfulness" during later encounters with aversive stimulation. For example, such prior treatment results in increased resistance to extinction of an acquired-fear response (*2*), greater disruptive effects during an approach-avoidance conflict task (*3*), and an increase in the suppressive effects of punishment on both conditioned (*4*) and unconditioned (*5*)