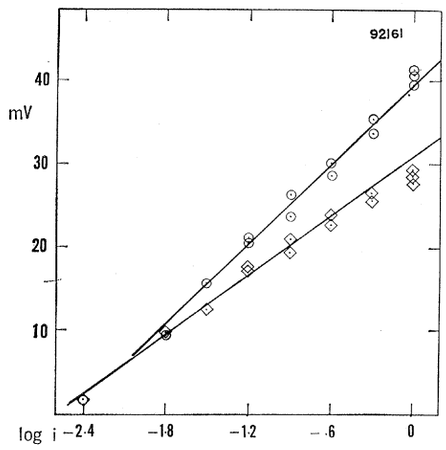

Fig. 2. Relation between the height of response and the light intensity. Data are from the experiment of Fig. 1, left. (Circles) Height of early peak; (diamonds) height of response 900 msec after initiation of the illumination. The figures along the abscissa are the logarithm of relative light intensity.

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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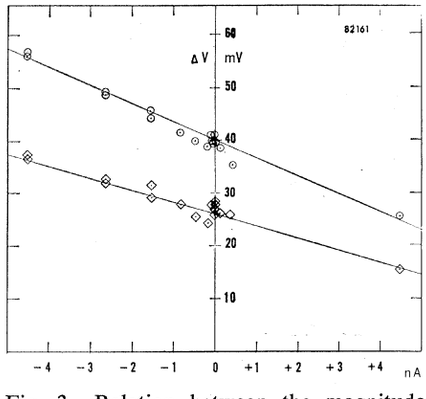

Fig. 3. Relation between the magnitude of the voltage change evoked by light and the intensity of a steady current through the cell membrane. Data are from the experiment of Fig. 1, right. (Circles) Height of early peak; (diamonds) height of steady-state response. Slope of straight lines is —3.4 Mohm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

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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*)

activity. One of the major questions which remained unanswered in these studies was whether such treatment merely produces a transient change in the organism's fear reactions or results in a more enduring modification.

We confined 14 albino rats, approximately 50 days old, individually in small compartments with grid floors through which shock could be delivered. The animals were divided into two groups. Group A (seven animals) received ten unavoidable shocks of approximately 1.50 ma intensity, as measured with the rat in series with a constant-current source. Each shock lasted 5 seconds and was given, without warning and at irregular intervals, on the average of one shock every 2 minutes. After this treatment, each animal was returned to its regular cage and was reared under normal laboratory conditions. The remaining seven animals (group B) received no shocks, but in all other respects they received the same treatment.

One year after the original treatment, all animals were placed on a 23-hour schedule of food deprivation and trained to press a lever to receive a pellet of food weighing 0.45 mg. Upon completion of preliminary training, each animal was given a daily 10-minute session in the apparatus for five consecutive days. During this period the animal procured a food pellet each time it pressed a lever. The chamber used during training and testing was different from the one in which shock had been administered.

On the day after the last training session, each animal was placed in the test chamber as before; but now, each time the lever was pressed, the animal received punishment in the form of a 0.20-ma shock of 0.20-second duration. The metal lever served as one pole and the grid floor as the other. The shock source was triggered automatically by the animal at the same time the food magazine was activated; hence the animal did not receive a shock unless the magazine was activated. The animal was rewarded by a food pellet each time it pressed the lever. Each experimental session lasted 10 minutes, and a total of seven daily sessions was given.

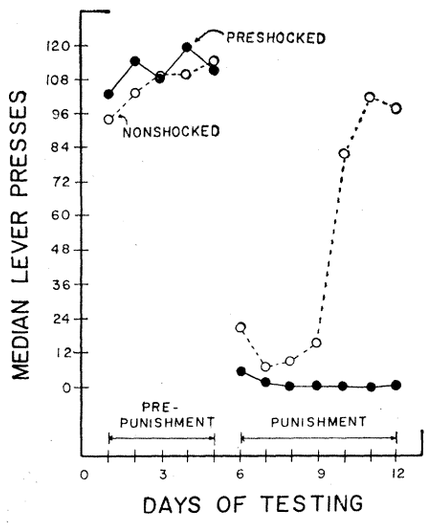

Fig. 1. Rates of response (median number of lever presses during each 10-minute session) in tests before punishment (left) and tests accompanied by punishment (right). Animals in group A (solid lines) had received shock 1 year before; animals in group B (broken lines) had not received those shocks.

As shown in Fig. 1, there was no appreciable difference between the two groups in the rates at which they pressed the lever until after they were subjected to punishment. This result confirms previous findings (*3*, *4*).

While the lever-pressing activity on the first day of punishment was low in both groups, the rate was significantly higher in group B (U of 0; $p < .01$) (*6*). There was no overlap in the response rates of the two groups on this day; the ranges were: group A, 3 to 9; group B, 12 to 32. An overall comparison of the distributions of response rates shown in Fig. 1 during the seven test days showed that the rate in group A remained significantly lower than that in group B (U of 5; $p = .01$). This finding was confirmed by separate analyses of results from the two groups, for each of the seven test days (U's ranged from 0 to 7; p's from $< .01$ to .03). By the last day of testing, group B had attained rates of lever pressing approximately equal to those they had attained before they were punished.

These results are consistent with the results of previous studies in which the intervals between the shocks and the punishments were much shorter (*2–5*). Our work indicates that prior exposure to intense electric shock has an enduring effect upon the organism. (*7*). By contrast, the control group (B) demonstrated recovery from the disruptive effects of shock punishment. The recovery during punishment of a previously suppressed response is not a unique finding, having been reported by other investigators who used special training conditions. Azrin (*8*) studied the effects of shock after each response during a variable-interval schedule of food reinforcement in pigeons. Although the initial introduction of punishment produced a marked depression in the rate of response, the pigeons often displayed complete recovery even though punishment was maintained. Azrin also reported that the intensity of shock was an important variable, with little or no recovery at very high intensities. Preliminary studies in our laboratory, with test conditions identical with those described here, support Azrin's finding that recovery of a punished response is dependent on the intensity of the shock (*9*).

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References and Notes

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29 July 1963