THE NATURE OF THE LATENT PERIOD IN THE PHOTIC RESPONSE OF MYA ARENARIA.

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I.

The response of Mya to light involves the existence of a latent period. The stimulus consists of the exposure of the animal to the influence of light for a short interval. Following the exposure period, Mya may remain in the dark for a length of time which is usually greater than the exposure. At the end of this latent period it retracts its double siphon in response to the stimulus. The demonstration of the latent period may be easily accomplished by the use of a photographic shutter. By this means the animal is exposed for very short intervals. At intensities above 3,000 meter candles, an exposure of 0.01 second is sufficient to produce a response after a latent period of about 1.3 seconds.

The sensitization process occurring during the exposure period has already been shown to depend on a reversible photochemical reaction (Hecht, 1919, a). This consists of the decomposition of a photosensitive substance into its two precursors. The dynamics of the decomposition and regeneration of the sensitive material follows closely the peculiarities of the sensory behavior of the animal.

The significance of the latent period, however, is still unknown. Of course it must include the time for the transmission of impulses, and for the latent period of the contraction of the muscles used in the siphon response. These are, however, notoriously short intervals of time, and may be almost ignored in the face of a latent period which lasts at least 1.3 seconds, and may be as long as 3 or 4 seconds under certain conditions. In order, therefore, that the photosensory process in Mya be understood in its details, it is necessary to investigate the probable nature of the latent period by a consideration of some of its properties.
II.

During the exposure of *Mya* to light, a photosensitive material is decomposed into its two precursors. If these precursor substances are in any way concerned with the nature of the latent period, there should exist some relation between the quantities in which they are produced and the duration of the latent period. Experiments were therefore performed to determine the influence of the exposure period on the length of the latent period.

The reaction time of *Mya* under given conditions is quite a constant quantity, and is well over 1 second in length. Any significant changes in its duration can, therefore, be measured by means of an ordinary stop-watch. On the other hand, the exposure periods necessary to produce a response are very small, and must be measured in a much finer manner. This was done by means of a camera shutter loaned to me by Dr. A. C. Redfield, to whom I am greatly indebted.

Seven exposures were selected for use. They were calibrated by photographing a small white spot moving in a circle at a definitely known rate in front of a dead black surface. The photographs were made at noon of a brilliantly sunlit day, using the largest stop of a lens about 4 cm. in diameter. Therefore the angle subtended by the streak image on the photographic plate may be considered an accurate measure of the duration of the exposure. The seven exposure periods were found to cover a range from 0.015 to 0.257 second; their values are given in Table I.

<table>
<thead>
<tr>
<th>Exposure</th>
<th>Duration (sec.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.015</td>
</tr>
<tr>
<td>2</td>
<td>0.078</td>
</tr>
<tr>
<td>3</td>
<td>0.133</td>
</tr>
<tr>
<td>4</td>
<td>0.176</td>
</tr>
<tr>
<td>5</td>
<td>0.206</td>
</tr>
<tr>
<td>6</td>
<td>0.233</td>
</tr>
<tr>
<td>7</td>
<td>0.257</td>
</tr>
</tbody>
</table>
For the experiments, animals were used which had been in the dark for some time,—more than long enough for them to have become thoroughly dark-adapted (Hecht, 1919, a). Observations were made by the dim light of a ruby lamp to which the animals are practically insensitive. The reaction time to lights of different intensities and for different exposure periods was determined for twenty-two individuals.

Fig. 1. Individual determinations of the reaction time of four animals for different exposure periods. The points read to the nearest tenth of a second. The curve joins the averages for the different exposures.

All the experiments agree in showing that for a given intensity the reaction time varies inversely with the exposure, for exposure periods shorter than the sensitization period. Exposures for intervals greater than the sensitization period make no change in the duration of the reaction time. The sensitization period may thus be defined
as the minimum exposure necessary to produce the minimum reaction time.

In Fig. 1 are given the detailed results of one experiment with four animals. Each point represents an individual determination of the reaction time at the exposure indicated. The solid line joins the averages of the four readings for each exposure period. The figure shows, that though the experimental error is large, the changes in the reaction time for different exposures are well beyond the variations due to the experimental error. Data for four other animals are recorded in the points of Fig. 2. Each point is the average of the reaction time of the four animals, one determination having been made on each animal for every exposure.

The trend of all the experiments is sufficiently clear from those presented in the two figures. They all show that the longer the exposure, the shorter is the reaction time. The difference between

![Graph showing reaction time vs exposure time for different intensities.](image-url)
The latent period, being the interval during which *Mya* may remain in the dark, is certainly not a time during which “nothing happens.” The fact that it varies under certain conditions is reason enough against such an idea. We may, therefore, rest assured that a process takes place during the latent period, which in some way is a vital link in the chain of events between the incidence of the light and the appearance of the response. There seem to be three possibilities for the nature of this process. The first is that the precursor substances formed by the light exert their stimulating action at a place other than where they are produced. The latent period would thus represent the time for the diffusion of these substances. A second possibility is that the latent period represents the duration of a subsidiary chemical reaction. This results from the interaction of one or both of the precursor substances with some other materials present in the sense organ. The time for the formation of the product of reaction would account for the duration of the latent period. The third possibility is that the latent period is determined by an independent chemical reaction which is catalyzed by the presence of the freshly formed precursor substances.

In order to decide among these possibilities it is necessary to inquire quantitatively into the relation between the exposure period and the latent period. Fig. 3 shows this for the experiment given in Fig. 1. Each point is the reciprocal of the average latent period plotted against the exposure time. That the points form a straight line is undoubted. Fig. 4 gives the reciprocals of the latent periods of the experiments presented in Fig. 2. In spite of the rather large observational error, it seems clear that the points may best be arranged in straight lines.

The exposure time measures the amount of photochemical activity. For these extremely short intervals, the amount of precursor ma-
terials formed by this photochemical activity may be considered directly proportional to the length of exposure. Since the reciprocal of the latent period represents the rate of the process which determines it, the data of Figs. 3 and 4 show that the velocity of the latent period process is a linear function of the concentration of freshly formed precursor materials.

This at once rules out the diffusion explanation. There is one case in which the rate of diffusion is a linear function of the concentration. This is when the concentration of diffused material is maintained at zero or nearly zero by continually removing the diffused substance, or by allowing the diffusion to proceed into a comparatively large volume. This is obviously not the situation here, because it is essential that the precursor substances accumulate in sufficient quantity to initiate a response. An additional objection to the diffusion idea is the temperature coefficient of the latent period. The latent period shows a value of $\mu = 19,680$ (Arrhenius,
1915, p. 49) which corresponds to a temperature coefficient of between 2.5 and 3.0 (Hecht, 1919, b). This temperature coefficient is much too high for a diffusion process, and corresponds well with those observed for ordinary chemical reactions.

![Graph showing the reciprocals of the latent period]

**FIG. 4.** The reciprocals of the latent period are derived from the data of Fig. 2. The interpretation is the same as that of Fig. 3. The broken line of the second series is drawn roughly parallel to the other three. It shows that the points of the second series may fit fairly well around the parallel line, thus indicating a fundamental similarity in the relationship at the different intensities. This rough parallelism is found in the data of the other animals of these experiments not recorded in the figures.

The data, at first sight, seem compatible with the idea of a subsidiary chemical reaction utilizing the precursor substances. This conception, however, involves an inconsistency, in that it requires the disappearance of the precursor materials during the latent period.
This means an upsetting of the balance in the reversible reaction system

\[ S \rightleftharpoons P + A \]

previously established for the photic response of Mya (Hecht, 1919, a). Such a difficulty, however, might be surmounted by assuming the photochemical reaction to be pseudoreversible like the reduction of ferric oxalate (Sheppard, 1914, p. 213). As a result, the formation of an additional substance would have to be postulated in order to replace the one used up in the latent period reaction. Matters would thus become increasingly complicated, and the value of the hypothesis considerably lessened as a means of explanation.

All the data may, however, be accounted for very simply on the basis of the third possibility. This assumes that the latent period represents the duration of an independent chemical reaction which is catalyzed by the presence of one or both of the precursor substances formed by the light. In this manner none of the precursor material is used up, and the balance of the reversible photochemical reaction is maintained. The reaction of the latent period may be considered to be arranged in the dark, in that the reacting substances are all present. It requires merely the action of the light in the production of precursor materials to cause the reaction to proceed with an effective velocity due to the catalytic influence of the fresh precursor materials.

The two characteristics of the latent period find their explanation in this way, in harmony with the previously developed concepts of the mechanism of photosensitivity. The latent period is a chemical reaction; this agrees with the observed effect of the temperature (Hecht, 1919, b). The rate of the latent period process is a linear function of the amount of precursor substances formed during the exposure period. In explanation of this it will be remembered that it is a common characteristic of catalyzed reactions for the velocity of the reaction to be a linear function of the concentration of catalyst (Euler, 1912, p. 132).
IV.

In terms of the conception developed in the present paper, the latent period assumes a position of importance in the composition of the reaction time of *Mya* to light, coordinate with that of the sensitization or exposure period. There being no evidence to the contrary, it seems reasonable to assume that the processes underlying these two phases of the reaction time occur entirely within the sense organs. The events which happen in the sense organ of *Mya* when it is stimulated by light may, according to our findings, be expressed as follows. The photosensitive substance (*S*), originally formed from its two precursors (*P* and *A*—Precursor and Accessory), is changed back into them under the influence of light, both reactions being given by the expression

\[
\text{light} \quad S \xrightarrow{\text{light}} P + A.
\]

This happens during the exposure to light or during the sensitization period when the exposure is prolonged. One or both of the freshly formed precursor substances then immediately serve to catalyze the transformation of an innocuous material (*L*) into a stimulating substance (*T*). This occurs during the latent period. When a sufficient amount of the stimulating substance (*T*) has been accumulated, it acts on the nervous connections to the sense organ and initiates the retraction of the siphon. The entire sensory process may therefore be summed up in the two reactions:

\[
S \rightarrow P + A; \quad L \parallel P + A \parallel \rightarrow T
\]

in which the symbol \( \parallel P + A \parallel \) signifies catalysis by one or both of the precursor substances.

Two reactions related as are these correspond to a well known group of photochemical reactions classed by Weigert as “catalytic photochemical reactions in which the catalyst remains after the action of light.” Among these are included so familiar a process as the exposure of a photographic plate and the development of the image under proper conditions (Weigert 1911, p. 74).

The hypothesis of photoreception, here presented rather concretely, will undoubtedly have to be modified in one way or another
as the investigation of the photic sensitivity of Mya and other animals proceeds. The concreteness of the conception, however, should prove a useful tool in the acquisition of additional knowledge in this field.

**SUMMARY.**

The latent period in the response of Mya to illumination varies inversely as the duration of the exposure to which it is subjected. The reciprocal of the latent period, measuring the velocity of the process which underlies it, is a linear function of the exposure period. Since the duration of the exposure represents the amount of photochemical activity, it is concluded that the substances formed at that time act to catalyze a chemical reaction which determines the duration of the latent period.

This explanation is in accord with the previous work on the photochemical reaction and with the effect of temperature on the latent period. As a result of the combined investigations there is presented a concrete hypothesis for the mechanism of photic reception in Mya.

**BIBLIOGRAPHY.**


Euler, H., General chemistry of the enzymes, New York, 1912.

Hecht, S., (a) Sensory equilibrium and dark adaptation in Mya arenaria, *J. Gen. Physiol.*, 1918–19, i, 545; (b) An analysis of the relation between the temperature and the duration of a biological process, *Proc. Nat. Acad. Sc.*, 1919 v, 146.

Sheppard, S. E., Photochemistry, New York, 1914.

Weigert, F., Die chemischen Wirkungen des Lichts, Stuttgart, 1911.