THE PHOTOCHEMISTRY OF THE SENSITIVITY OF ANIMALS TO LIGHT¹

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The stimulation of certain animals by light furnishes the opportunity for an objective and quantitative analysis of the underlying mechanism of photoreception. The reason for this is that both the stimulus,—light,— and the response of the animals,—a qualitatively invariable retraction reflex,—are capable of precise and easy control. Fortunately the characteristics of this sensitivity are not peculiar to these particular animals (a clam and an ascidian), but are to be found in one form or another generally distributed among animals possessing a light sense. The present analysis is therefore of broad application in its fundamental ideas.

The characteristics referred to are as follows. (1) A measurable interval, the reaction time, intervenes between the beginning of the application of the light and the beginning of the response. (2) A response is elicited only when the intensity of illumination has been increased. (3) Once a response has been given to a light, the continued application of the same intensity fails to produce any additional effect. (4) If, following this, the animal is placed in the dark, it soon recovers its sensitivity to the intensity which had become ineffective. The investigation of each of these characteristics has resulted in the formulation of certain principles and in the postulation of an hypothesis for their explanation.

A study of the reaction time shows first that it represents practically the time taken up in the sensory process alone, the conduction of the impulse and the early part of the response taking almost no measurable time in comparison. Second, it shows that the reaction time represents two definite intervals.

¹ Abstract of a paper delivered at the Symposium on General Physiology, held by the American Society of Naturalists on Dec. 30, 1920, at its Chicago meetings. The data on which this summary is based may be found in a series of articles in the *Journal of General Physiology* from 1918 on.

The first is the sensitization period, or the time during which illumination is actually necessary. The second is the latent period, or the time during which the animals may be in the dark, and at the end of which the animal gives its response as if it had been illuminated all the time. In the clam, *Mya arenaria*, the sensitization period may be 1/100 second or even less, depending on the intensity. The latent period, however, is constant, and lasts about 1.5 seconds. The discovery of the complexity of the reaction time opened up the field for quantitative investigation.

The action of light in the photosensory process is probably photochemical. Experiments show that this action possesses the ordinarily well-demonstrated properties of photochemical reactions. First, the relation between the intensity of illumination and the sensitization period, or time of necessary exposure, follows the Reciprocity Law of Bunsen and Roscoe. The product of the two variables is equal to a constant. Second, the temperature coefficient for the action of light on the sensory activity of these animals is very low, near 1 for a rise of 10° C. This is in contrast to the temperature coefficient of ordinary chemical reactions which is usually between 2 and 3. Therefore, no matter what the temperature, a definite quantity of photochemical transformation is required to produce a stimulating effect.

The light adaptation of these organisms is well marked. They fail to give more than a single response even to intense sunlight. Dark adaptation is equally prominent. Studies of the rate and course of dark adaptation furnish the clue to the photosensory mechanism. In the dark the quantity of light required to elicit a response is at first very large. Gradually the amount of light necessary for a response decreases, at first rapidly, then more slowly, until after a definite interval it becomes a constant minimum. This means that less and less photochemical decomposition is required during dark adaptation to produce the same response.

During light adaptation the light decomposes a sensitive substance, and at the same time causes a decrease in sensitivity. During dark adaptation it is possible that the return of sensitivity is the result of the formation of fresh sensitive material. If we

assume that the action of light is to break up a sensitive substance into its precursors, and that in the dark these precursors reunite to form the sensitive material, all the data acquired in these experiments may be explained in terms of the kinetics and dynamics of chemical and photochemical reactions whose general properties are well known and mathematically predictable.

The course of dark adaptation is found to follow with great accuracy the kinetics of a bimolecular chemical reaction. There are therefore *two* precursors (*P* and *A*,—precursor and accessory) uniting to form the sensitive material (*S*). The reversible photochemical reaction is then

and all the results fit this stoichiometric equation remarkably well. Moreover, certain predictions which can be made from it, have been tested, and have been verified on a number of occasions. For example, the "dark" reaction, $P + A \rightarrow S$, is an ordinary chemical reaction. Its temperature coefficient should therefore be between 2 and 3 for 10° C. This reaction represents the process of dark adaptation, and experiments show that dark adaptation in these animals has a temperature coefficient of 2.4.

The phenomena so far considered are those concerned with the sensitization or exposure period. But these animals possess a very definite latent period which very frequently is of longer duration than the sensitization period. A study of the latent period shows that it represents the duration of a process closely connected with the products formed by the primary photochemical reaction. The velocity of this process turns out to be a linear function of the concentration of precursors, *P* and *A*, formed by the light.

From this and other evidence the following explanation of the latent period has been proposed. During the latent period an inert material, *L*, is changed into a chemically active substance, *T*, which then acts on the nerve to produce the outgoing sensory stimulus. This reaction, $L \rightarrow T$, is catalyzed by the presence of

the freshly formed photochemical decomposition products P and A .

Thus the latent period reaction becomes really the principal reaction in the sensory process. It is all set and ready to go, and requires only that the light change S into P and A so that the latter can catalyze the transformation of L into T . The whole photosensory mechanism may then be summed up in the two reactions

in which $\parallel P + A \parallel$ means catalysis by one or both of the precursors. The first reaction occurs during the sensitization period; the second during the latent period.

This rather concrete hypothesis has proved to be a useful tool in getting further knowledge, because of experiments designed to test it in various ways. A few of these tests may be briefly mentioned. The latent period is supposed to be a simple reaction, perhaps an oxidation. Its behavior with the temperature should therefore follow the equation deduced by Arrhenius for the relation between the velocity constant and the absolute temperature. Experiments show that the reaction $L \rightarrow T$ does follow this prediction accurately. Moreover, the value of the constant $\mu = 19,680$, found for the reaction is in accord with those usually found for hydrolyses, oxidations, etc. in pure chemistry.

Another test concerns the interrelations between the exposure and the latent period. If the intensity of the stimulating light is constant, the velocity of the latent period reaction is found to be directly proportional to the time of exposure. On the other hand, if the time of exposure is kept constant, and the intensity varied, the velocity of the latent period reaction is found to be proportional to the logarithm of the intensity. If now both time and intensity are varied, the velocity should be proportional to the product of the time and the logarithm of the intensity. Experiments prove this to be true.

A perhaps more significant application of the hypothesis has been made to the dark adaptation of the human eye. A proper analysis of the dark adaptation data has shown that

the process in the human eye is fundamentally similar in principle to the process occurring in the clam and the ascidian. As a result there has been opened up a new field of investigation in retinal photochemistry which may some day enable us to possess a reasonable theory of vision.

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