

THE INFLUENCE OF TEMPERATURE ON THE PHOTOSENSORY LATENT PERIOD.

By SELIG HECHT.

(From the Laboratory of Biophysics, Columbia University, New York, and the
Zoological Station,* Naples, Italy.)

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I.

Numerous researches on the photosensory properties of the clam, *Mya arenaria*, and the ascidian, *Ciona intestinalis*, have shown that the photoreceptor system is composed of at least two processes (Hecht, 1925). One way in which this is made evident is by the composition of the reaction time of these animals to light. A short exposure to light is sufficient to elicit the siphon retraction which is the typical response of these animals to illumination. However the response does not take place immediately, but only after a comparatively long latent period during which the animal may remain in the complete absence of light. With an illumination of 1000 meter candles an exposure of 0.01 second is enough to cause a siphon retraction in *Mya* after about 2.0 seconds of latent period. This is a ratio of 1:200 for the durations of exposure and latent periods respectively.

During the exposure period the light produces a photochemical change in a sensitive substance. Experiments to test the interrelations between intensity, time, wave-length, and various conditions of exposure and adaptation of the animals (Hecht, 1925, Piéron, 1926) have shown that this photochemical process is probably a reversible photochemical reaction of a comparatively simple type. Nevertheless the products of this photolytic activity do not directly release the impulse to the associated nerve endings which starts the very rapid train of nervous and muscular events culminating in the siphon

*The experiments here recorded were made in 1924-25 when, as Fellow of the International Education Board, I occupied the Jacques Loeb Memorial Table at the Zoological Station in Naples.

retraction. Between the photochemical effect and the siphon response there is intercalated an additional process which is represented by the latent period.

The long duration of the latent period in comparison to that of the exposure period would by itself indicate the different nature of the two processes. The same thing is evident from the different effects of temperature on exposure period and on the latent period. The former is hardly changed by an increase in temperature, thus corroborating its photochemical nature. The latter, however, in the case of *Ciona* and *Mya* at least, varies with temperature in a way similar to that of chemical reactions uninfluenced by light.

The two processes are intimately related. Conditions like time and intensity which control the photochemical reaction, exert a subsequent influence on the latent period of such a kind that its speed varies with the magnitude of the photochemical change. This has been interpreted as showing that the two processes form a coupled reaction of which the secondary, latent period reaction proceeds only in the presence of products from the primary, photochemical reaction. The mechanism which couples the two reactions may be a catalysis or a direct chemical relation.

The existence of such a coupled series of reactions is fairly common in the light reception of organisms, to judge only by the existence in the reaction time of a primary "light" period and a secondary "dark" period. In the heliotropic curving of plants such a division is of course well known, since the two parts are often widely separated in time, the turning (response) taking place a long time after the exposure. The primary reaction here is photochemical as Blaauw (1908) and Fröschel (1909) showed years ago. In the phototropic turning of sessile animals like *Eudendrium* there is a similar division of "light" and "dark" reactions (Loeb and Wasteneys, 1917). A secondary "dark" period in the phototropism of free moving animals is not often demonstrable, since the orientation of the animal ceases with the removal of the light (Minnich, 1919). Even here, however, Mast (1912) has shown that the fire-fly orients *after* the stimulating light has been extinguished. The latent period is thus an integral part of the process of light reception, and any information that will indicate its nature is relevant to an understanding of the photoreceptor process.

The effect of temperature on the duration of the latent period furnishes information of this kind. In *Mya* the relation between temperature and latent period may be described by the Arrhenius equation; the same is true of *Ciona*. The value of μ in the equation is different in the two cases. Since *Mya* and *Ciona* are the only animals in which the latent period has been studied in this way, I took the occasion of a stay in Naples to study the effect of temperature on the latent period of *Pholas dactylus*, an animal whose photosensory properties greatly resemble those of *Mya* and *Ciona* (Hecht, 1926-27).

II.

The procedure in these experiments is comparatively simple. An animal, in its rectangular dish, is placed in a large water bath where with the help of stirring, it quickly attains the temperature of the bath. Here it is left for about an hour in the dark, during which time it maintains its temperature constant by means of the gentle stirring created by its water current. Its reaction time is then measured after an exposure of 0.05 hm. (= hundredths of a minute) to an illumination of 2000 m.c. This involves taking the animal, in its dish, out of the thermostat and transferring it to the measuring table. The temperature to 0.1°C. is measured immediately before the exposure; but no difference is noted between the temperature then and in the thermostat, because of the volume of water in the dish in which the animal rests. After the exposure the animal is replaced in the water bath, the temperature of which is now rapidly changed. After a few minutes the sea water in the dish has reached the temperature of the bath, and the animal is at that temperature for an hour. Its reaction time is then again measured for the same exposure to the same light. After five such measurements, for a series of decreasing temperatures, five similar measurements are made at intermediate points with a series of increasing temperatures. Only one reading is made with each animal at each temperature.

All the manipulations are carried out in a dark room with the help of a very dim ruby lamp. By the light of such a lamp it is difficult to observe the siphon retraction which occurs some time after the exposure. The procedure is therefore adopted of watching the siphon

as silhouetted against the red light. In this way the very beginning of the retraction may be accurately timed with a stop-watch.

The temperature range over which the measurements are made is limited to about 10°. Below 10°C. the beginning of the siphon retraction ceases to be sharp enough for accurate measurement, while above 20°C. the reaction time becomes too short for timing with a stop-watch.

III.

The experiments were made with eight animals, all of which had been in the dark for about a week before the experiments were begun.

TABLE I.

Relation between the Temperature and the Photosensory Latent Period. Exposure Period is 0.05 Hm. (= Hundredths of a Minute) to an Illumination of 2,000 Meter Candles.

Temperature	Reaction time	Latent period, p	
		Measured	$\ln p = \frac{18,300}{RT} - 30.95$
°C.	hm.	hm.	hm.
10.5	3.93	3.88	3.75
11.3	3.51	3.46	3.43
12.7	2.94	2.89	2.94
13.3	2.84	2.79	2.75
14.6	2.43	2.38	2.37
15.3	2.24	2.19	2.27
16.2	2.05	2.00	2.00
17.3	1.84	1.79	1.77
18.3	1.64	1.59	1.59
18.4	1.63	1.58	1.57

The data secured are given in Table I, where each value of the reaction time is the average of eight measurements, one with each animal. Table I shows that the effect of temperature on the latent period is of the magnitude of that for chemical reactions. In this respect it resembles what has already been found for the latent period of *Ciona* and *Mya*; and thus supports the general idea of a coupled reaction underlying the photosensory process in these three animals.

To treat the data more quantitatively, I have supposed that the

latent period represents the duration of a chemical reaction which must produce a definite amount of its products in order to set off the stimulus to the sensory nerve. Therefore the reciprocal of the latent period is proportional to the velocity constant of the reaction, and may be used to determine whether the reaction follows the Arrhenius equation

$$\ln k = -\frac{\mu}{RT} + C \quad (1)$$

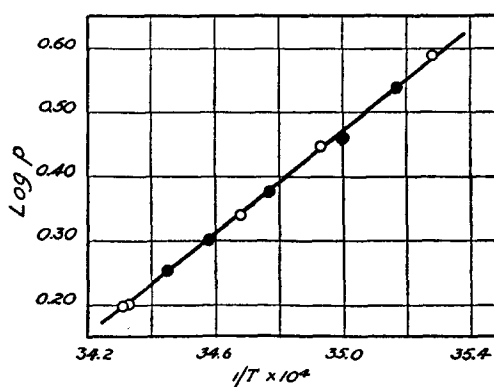


FIG. 1. Relation between the absolute temperature (T) and the latent period (p). The open circles represent measurements taken as the temperature was decreased; the solid circles, as the temperature was increased. The equation of the straight line is $\ln p = 18,300/RT - 30.95$.

for the relation between the temperature and the velocity constant of a chemical reaction. Let p be the duration of the latent period. Then $1/p$ may be substituted for k , and the equation becomes

$$\ln p = \frac{\mu}{RT} - C \quad (2)$$

which, when $\ln p$ is plotted against $1/T$, gives a straight line whose slope is μ/R . Fig. 1 shows the data of Table I plotted in this manner. It is clear that the Arrhenius equation describes the data with considerable fidelity. Here $\mu = 18,300$; R is the gas constant; and C , which equals 30.95, is merely an integration constant. To show the agreement between experimental and calculated values I have in-

roduced in Table I the values of the latent period computed in terms of the equation.

IV.

Two things follow from these temperature data on *Pholas*, *Ciona*, and *Mya*. The first is that the relation between temperature and latent period is expressible in the form of an equation applicable to many chemical reactions and to many biological processes. In terms of the previously suggested hypothesis, it may thus be supposed that the latent period represents the duration of a reaction $L \rightarrow T$ in which an inert substance L is converted into an active substance T , of which a definite amount is required to set off the stimulus to the associated nerve fiber. It is obvious that in such a system the Arrhenius equa-

TABLE II.

Values of μ for the Effect of Temperature on the Photosensory Latent Period of Different Animals.

Species	μ
<i>Ciona intestinalis</i>	16,200
<i>Mya arenaria</i>	19,700
<i>Pholas dactylus</i>	18,300

tion should apply with the same accuracy as in an isolated chemical reaction.

The second thing which the data show is that the value of the constant μ is different for each species. Table II gives the relevant information taken from the present data and from previous work (Hecht, 1918-19, 1925-28). Precisely what the specific values of μ mean is uncertain at present. The value $\mu = 19,700$ for *Mya* has been found in other instances (Crozier, 1925-26) but is apparently not associated with any definite group of biological or chemical processes. The very common value $\mu = 16,200$, found for *Ciona*, occurs in many cases where oxidations seem to be concerned, and is possibly related to the function of iron as catalyst (Crozier, 1924-25).

The value $\mu = 18,300$, found here for *Pholas*, is not uncommon in biological processes (Crozier, 1925-26). It is therefore not without interest to note its occurrence in purely chemical reactions in which

iodine is concerned. Plotnikow (1907) found $\mu = 18,400$ for the oxidation of HI in the dark. More recently Conant and Hussey (1925) studied the relations between the structure of a large assortment of organic halides and the speeds of their reaction with inorganic iodides like KI and NaI. They found that although the velocity of this metathesis varies enormously with the structure of the organic halide, the effect of temperature on the velocity can be uniformly expressed by the Arrhenius equation when $\mu = 18,400$. Similarly, Rideal and Williams (1925) found that the liberation of iodine from KI by ferric salts has a temperature coefficient of $\mu = 18,300$.

These similarities between biological and chemical behavior need not be taken as indicating identities. Nevertheless, the data are striking, and any theory which is to account for the effect of temperature on biological activities must be prepared to take them into account. For our present purposes they are significant in suggesting that the differences in μ value for the latent periods of the three species indicate a specific difference; and that the latent period reaction which has been formally expressed as $L \rightarrow T$ is most likely different in each species. In other words, though the organization of the photoreceptor process is the same for all, the materials which make up the reactions are different in the three animals.

SUMMARY.

1. The effect of temperature on the photosensory latent period in *Pholas dactylus* is accurately described by the Arrhenius equation when $\mu = 18,300$.
2. The adequacy of this equation has already been found for two other photosensitive animals, *Mya* and *Ciona*, which are very similar in behavior to *Pholas*. The value of μ is different for each of the three species studied.
3. This is taken to mean that though the organization of the receptor process is the same for the three species, the chemical materials concerned are very likely different.

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