THE EFFECT OF TEMPERATURE ON THE LATENT PERIOD IN THE PHOTIC RESPONSE OF MYA ARENARIA.

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I.

The purpose of this paper is to present an analysis of the relation between the temperature and the duration of a biological process. The numerous investigations which have already been published (Kanitz, 1915) have demonstrated that biological activities exhibit variations in rate at different temperatures. Usually the speed of the process is an exponential function of the temperature. Occasionally the relation between the two is linear. The latter phase has been particularly emphasized by Krogh (1914) and his colleagues.

However, no matter what the relation between the temperature and the rate may be, it fails to hold at higher temperatures. The rate of increase of the activity falls off decidedly. The velocity of the process soon reaches a maximum at a critical temperature. Above this so called optimum the activity declines or ceases altogether.

There has been much discussion as to the significance of these variations (Kanitz, 1915), and of the magnitudes of Q°, the temperature coefficient for 10°C. On the one hand, the value of the temperature coefficient, as usually found between 2 and 3, has been made to signify that the fundamental process underlying the activity is a chemical reaction. This is because of the well known van’t Hoff rule for the relation between the temperature and the velocity of ordinary chemical reactions. On the other hand, much effort has been spent to show that biological processes do not possess a constant temperature coefficient even for temperatures below the optimum (Krogh, 1914), and that consequently they do not obey the law
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of van't Hoff. The deviations above the optimum temperature are generally dismissed by attributing them to the destructive effect of heat on protoplasm.

As has been pointed out (Snyder, 1911), the lack of constancy of the temperature coefficient is no bar to a process being chemical in nature. This is simply because purely chemical reactions also fail to show a constant temperature coefficient. The emphasis is to be placed on the order of magnitude of the coefficient and not on its invariability.

The real difficulty, however, is that biological phenomena do not represent single chemical reactions. In order, therefore, that the variations shown by biological activities be properly understood, it is necessary to know the nature and number of the chemical reactions concerned, and also their interrelations. Osterhout (1917) has indeed emphasized this by assuming a wholly imaginary biological activity composed of two consecutive chemical reactions, and synthesizing the effect of temperature on their combined activity. An analysis of data actually secured in the study of a vital process has apparently never been made in any but the most approximate manner. This is especially true of the variations exhibited by vital processes at higher temperatures.

 Aside from the work of Blackman (1905), so vigorously criticized by Kanitz (1915, p. 22), the one significant contribution in this direction has been made by Pütter (1914). In the effect of temperature on the oxygen consumption of the leech, Pütter attributes the usual variations at higher temperatures to an increasing effect of an interfering process. For the estimation of this second factor, Pütter compares his actual results with those calculated on the basis of a constant temperature coefficient. The difference between the two is then shown to possess an approximately constant temperature coefficient of its own.

Pütter's idea, though correct in general conception, does not yield a quantitatively correct analysis. One reason for this is, as he realizes himself, that his data are not comparable at different temperatures; he measures the amount of oxygen consumed in a given time instead of the time for the consumption of a given amount of oxygen. In addition, we are wholly ignorant of the chemical and physical reactions involved in the process. Without such knowl-
edge it is impossible to apply the mathematical reasoning which is a prime essential for the proper comprehension of the data. The general idea, however, is a decidedly fruitful one; and, though arrived at independently, the analysis to be given in the present paper is really a quantitative application of just such a conception as developed by Püttier. The same idea has already shown its possibilities in the investigations of Tammann (1895) and of Duclaux (1899) on the effect of temperature on the activity of enzymes.

The case to be considered is the photic sensitivity of the mollusk Mya arenaria. Previous work (Hecht, 1919, a, b) has enabled us to propose an hypothesis to account for the photic behavior of this animal. The essential value of this hypothesis is its assumption of definite chemical reactions, the dynamics of which are known, and the interrelations of which are given. The effect of temperature on the photic behavior of Mya should therefore permit of a quantitative analysis in terms of the suggested hypothesis. The success of this analysis will then reciprocally furnish justification for the acceptance of the hypothesis.

II.

Mya responds to illumination by a rapid retraction of its siphons. Its reaction time is composed of two parts. The first is a sensitization period. This is the smallest interval of time during which the animal must remain exposed to the light in order to respond at the end of the usual reaction time. The second is a latent period during which Mya may remain in the dark. At the end of this period, the organism retracts its siphons exactly as if it had been exposed for the entire reaction time.

The sensitization period represents the duration of a photochemical reaction. This has been shown (Hecht, 1919, a) to consist of the decomposition of a photosensitive substance (S) into its two precursors (P and A), according to the reversible system

\[
\begin{align*}
S & \xrightarrow{\text{light}} P + A. (1) \\
S & \xrightarrow{\text{"dark"}} P + A.
\end{align*}
\]
The duration of the latent period is determined by the velocity of an independent chemical reaction

\[ L \rightarrow T \]  \hspace{1cm} (2)

in which an innocuous substance \((L)\) is changed into the stimulating substance \((T)\). The activity of this reaction is catalyzed by the presence of one or both of the precursor materials \((P\) and \(A)\) freshly formed during the sensitization period (Hecht, 1919, b). A slight fraction of the latent period represents the time for the conduction of impulses. This process, however, is very rapid, and may be entirely discounted in the comparatively large magnitudes of time concerned in the latent period.

The effect of temperature changes on the reaction time of \(M\) can therefore be considered as causing changes in the velocity of a photochemical reaction \((1)\) and of an ordinary chemical reaction \((2)\). It is well known that photochemical reactions suffer but slight changes with an alteration in the temperature. In fact, the sensitization process in \(M\) representing this photochemical reaction varies but slightly with the temperature. Data to be presented elsewhere give its temperature coefficient for \(10^\circ C\) to be about 1.3 or less. The latent period, however, representing an ordinary chemical reaction varies decidedly with the temperature. This may be demonstrated by determining the latent period at different temperatures as a result of a constant exposure period. Fig. 1 gives the data of one such experiment in which the exposure was for 0.078 second to an intensity of 400 meter candles. The latent period is the difference between the total reaction time and the exposure period of 0.078 second. It is therefore clear that the bulk of the variation in the reaction time resulting from a change in temperature is due to the alteration in the latent period. Consequently, by subtracting the sensitization period from the reaction time determined as a whole, it is possible to measure the exact relation between the temperature and the duration of the latent period.

The experiments thus resolve themselves into measuring at different temperatures the reaction time of an animal to a single intensity of light. Preliminary experiments showed that about 40 meter candles is the right intensity to use. This gives a reaction
Fig. 1. Temperature and latent period. The animals were exposed to an intensity of 400 meter candles for 0.078 second by means of a camera shutter. The latent period is the time during which the animals were actually in the dark. Since the exposure is so very short, the reaction time as measured with a stop-watch may be considered entirely as the latent period. The points represent single, individual readings for the three animals of this experiment.
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time sufficiently large to be measured comfortably. In addition, the sensitization period is quite small, averaging 0.21 second for the temperatures used. The actual manipulation is simple. An animal which has been in the dark for a number of hours is brought to the desired temperature using the ordinary precautions of stirring, etc. With the temperature constant, the reaction time is determined five times at 5 minute intervals. Readings are made approximately 5° apart, 20 minutes being allowed for the acquisition of the desired temperature.

The results which were obtained in six experiments are given in Fig. 2. Each point is an average of the five readings made at that temperature. The experiments were arranged to obtain a uniform distribution of determinations covering the range of temperatures to be investigated. In general the data are similar to those which have already been published. Considered in the usual way, it may be said that the temperature coefficient is approximately 2.5, being larger at lower temperatures and smaller at higher temperatures.

The data, however, possess much more meaning than this. Because of our knowledge of the chemical reactions underlying the reaction time, it is possible to make a quantitative analysis of the results. Such an analysis is significant not only of itself, but because it demonstrates the possibility of the quantitative treatment of biological data of this character.

III.

Arrhenius has long ago shown that the now biologically famous van't Hoff rule is not an exact statement of the facts (Arrhenius, 1912, p. 124). Moreover, even as an approximation it lacks the theoretical significance which is possessed by van’t Hoff’s equation relating the temperature and the equilibrium constant of a chemical reaction. Arrhenius has therefore derived, as a special case of the latter relation, an equation which relates the velocity constant of a chemical reaction with the temperature. If \( k' \) and \( k'' \) are the velocity constants at the absolute temperatures \( T' \) and \( T'' \), this equation of Arrhenius states that

\[
\frac{k'}{k''} = e^\left(\frac{\mu}{R}(\frac{1}{T''} - \frac{1}{T'})\right)
\]  

(3)
FIG. 2. Relation between temperature and reaction time. The reaction time minus 0.21 second gives the latent period. Each point is the average of five determinations on one animal. The heavy line is the theoretical expectation according to the Arrhenius formula when $\mu = 19,680$. The light line gives the general trend of the data above 21°.
in which \( e \) is the Naperian base, \( \mu \) is a quantity characteristic of a given chemical reaction, and \( R \) is the gas constant which may be put equal to 2.

Our hypothesis states that the duration of the latent period depends on the time required for the reaction \( L \rightarrow T \) to form a certain amount of the substance \( T \). If this is correct, the relation between the temperature and the latent period should be adequately expressed by equation (3). Since this equation requires only the ratio between the two velocity constants, it is permissible to substitute in their places the reciprocals of the time required to perform a definite amount of chemical work. The latent period is the time required for the formation of a definite amount of the material \( T \). Therefore the reciprocal of the latent period at different temperatures may be used in the equation of Arrhenius. The heavy line drawn in Fig. 2 is the curve for equation (3) when \( \mu = 19,680 \). In making the calculations it must be remembered that the latent period is the difference between the observed reaction time and the sensitization period. The average sensitization period for these temperatures, as already stated, was found to be 0.21 second.

The points in Fig. 2 are seen to be well represented by the theoretical curve from 13° to 21°. Above 21°C. the experimentally determined values deviate decidedly and increasingly from the expectation according to the Arrhenius equation. The experiments were performed at Woods Hole, Mass., during July and August, 1918. These are the hottest months of the year. During 1918 the mean water temperature for July was 20.2°C.; that for August was 21.7°C. The highest water temperature recorded was 23.0°C. for July 30. It is therefore apparent that the deviations of the experimental data from theoretical expectation begin to occur at temperatures above those to which the animal is normally subjected, even in the hottest days of the year. Below this normal maximum of approximately 21°, the data follow accurately the expectation that the latent period is conditioned by a single, simple chemical reaction.

The increasingly greater difference at higher temperatures between the calculated curve and the experimental data indicates clearly that a second factor has entered, the effect of which becomes more and more patent as the temperature increases. If we assume
that the substance $T$, formed during the latent period, is thermo-
labile, it is possible to account quantitatively for the activity of this
second factor. A certain amount of $T$ must be formed in order
that a response of $M\mu a$ may result. If some of this material $T$ is
destroyed at temperatures above $21^\circ$, the latent period reaction,
$L \rightarrow T$, must proceed longer in order to make up the amount of $T$
necessary for a response. As the temperature increases, the rate of
destruction of the thermolabile substance $T$ will also increase. Con-
sequently the latent period reaction will have to proceed longer in
order to make up the required quantity of $T$. The disparity between
calculated curve and actual results will therefore become greater and
greater.

If this reasoning is correct, it should be possible to determine
quantitatively not only the effect of this destructive second factor,
but the nature and dynamics of the process as well.

IV.

The work of Chick and Martin (1911) has demonstrated that the
rate of heat coagulation of hemoglobin and of egg albumin may best
be represented by the course of a reaction of the first order. More
pertinent, perhaps, are the experiments of Madsen (Arrhenius, 1915)
in which it was found that the spontaneous decomposition or inacti-
vation of many thermolabile substances also follows the course of a
monomolecular chemical reaction. It is therefore reasonable to as-
sume that the destruction of our thermolabile substance $T$ into some
ineffective material $N$ also follows the course of a monomolecular
reaction. For the sake of simplicity let it be further assumed that the
latent period reaction itself, $L \rightarrow T$, is also a reaction of the first
order. The duration of the latent period at temperatures above $21^\circ$
may thus be considered to depend upon two reactions,

$$L \rightarrow T, \quad T \rightarrow N$$

forming a catenary system. From this reaction system a certain
quantity of the substance $T$ must accumulate in the sense organ
before a response on the part of $M\mu a$ can result.

The quantitative relations of these two reactions may be illustrated
graphically. In Fig. 3 are drawn the isotherms of the reaction $L \rightarrow T$ at the temperatures indicated. In the construction of these isotherms the quantity of $L$ present at the beginning of the latent period is considered to be 1 gram-molecule, and the amount of $T$ necessary to accumulate in the sense organ is put equal to 0.10 gram-molecule. These quantities are chosen arbitrarily for convenience. They may be put at any value without changing the analysis in the slightest degree. The essential point is merely that the amount at the beginning and the amount necessary for the response must be the same at all temperatures. Accepting these quantities and knowing

\[ \text{TABLE I.} \]

Velocity Constants of the Latent Period Reaction, $L \rightarrow T$, at Different Temperatures. Values above 21° Calculated from the Arrhenius Equation when $\mu = 19,680$.

<table>
<thead>
<tr>
<th>Temperature, °C.</th>
<th>$k_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>0.0297</td>
</tr>
<tr>
<td>15</td>
<td>0.0376</td>
</tr>
<tr>
<td>17</td>
<td>0.0477</td>
</tr>
<tr>
<td>19</td>
<td>0.0565</td>
</tr>
<tr>
<td>21</td>
<td>0.0786</td>
</tr>
<tr>
<td>23</td>
<td>0.0948</td>
</tr>
<tr>
<td>25</td>
<td>0.117</td>
</tr>
<tr>
<td>27</td>
<td>0.144</td>
</tr>
<tr>
<td>29</td>
<td>0.178</td>
</tr>
<tr>
<td>30</td>
<td>0.215</td>
</tr>
</tbody>
</table>

the time interval during which the 0.10 mol of $T$ is formed, it is a simple matter to calculate the velocity constants ($k_i$) of the latent period reaction from the equation

\[ k_i = \frac{2.303}{t} \log \frac{a}{a-x} \]  \hspace{1cm} (4)

which represents the course of a monomolecular reaction. In equation (4), $t$ is equal to the latent period as given by the heavy line in Fig. 2; $a$ is equal to 1 mol; $x$ is 0.10 mol; and 2.303 converts Briggsian logarithms to the Naperian system. The velocity constants so obtained are given in Table I.
Fig. 3. Isotherms of the fundamental reaction, $L \rightarrow T$, of the latent period. Up to 21°, the reaction can accumulate without interference 0.10 mol of thermolabile substance in order to produce a response. Above 21°, the thermolabile substance is inactivated. The circles represent the time theoretically necessary to produce 0.10 mol *unhampered*. The triangles show the time actually required to produce enough thermolabile substance so that in spite of its inactivation there will still accumulate 0.10 mol of it in the sense organ. The vertical distance between the circles and the triangles gives the amount of thermolabile substance inactivated.
The table contains not only the values from the experimentally determined latent periods, but above 21°, also those calculated according to the Arrhenius equation (3) using $\mu = 19,680$. The constants given in Table I are used in making the curves of Fig. 3.

If the fundamental reaction of the latent period, as represented by the isotherms, were allowed to form the thermolabile substance $T$ undisturbed, enough of this material to produce a response would accumulate in the time indicated by the circles in Fig. 3. Below 21° this is the time as actually found in the results of Fig. 2. Above 21° the time is derived from the curve of Fig. 2 by extrapolation from the Arrhenius equation.

The action of the fundamental latent period reaction, however, cannot result in the accumulation of this amount of $T$ in the prescribed time, because $T$ is thermolabile, and above 21° is being inactivated all the time it is being produced. The experimentally determined data of Fig. 2 show for each temperature the time actually required for the accumulation of the necessary 0.10 mol of $T$. The triangles represent these values in Fig. 3. The reaction isotherms extending to these triangles show the amount of $T$ which must be formed by the reaction $L \rightarrow T$ before 0.10 mol of $T$ can accumulate.

The difference between the amount of thermolabile substance $T$ formed, and the amount allowed to accumulate (0.10 mol) gives the amount of thermolabile substance inactivated by the second reaction, $T \rightarrow N$, during the time of production. Graphically the quantity of inactivated material ($N$) is given by the vertical distance between the circles and the triangles in Fig. 3.

The quantities thus represented are in part a measure of the activity of the inactivating reaction $T \rightarrow N$. By no means, however, are they to be considered as the direct measure of this reaction, because the amount inactivated by the secondary reaction depends on one other condition besides its own speed. This other condition is the velocity of the fundamental reaction $L \rightarrow T$ which furnishes the pabulum for the secondary reaction. It is precisely this error of assuming the difference to be the direct measure of the inactivation factor, which vitiates the quantitative character of Pütter's (1914) explanation, as well as of the preliminary analysis given of the pres-
ent results (Hecht, 1919, c). In order to determine exactly the velocity of the inactivating reaction, it is necessary to utilize the dynamics of catenary reactions. This process does not lend itself readily to graphic representation, and must therefore be studied from certain mathematical considerations.

V.

We have to determine what happens in the case of the two consecutive monomolecular reactions

\[ L \rightarrow T, \quad T \rightarrow N. \]

It has been assumed that 1 mol of the substance \( L \) is present at the beginning of the latent period. At the end of the time \( t \) occupied by the latent period, let the reaction system contain \( x \) mols of \( L \), \( y \) mols of \( T \), and \( z \) mols of \( N \). Therefore

\[ x + y + z = 1. \quad (5) \]

According to the mass law the rate of diminution of \( L \) will depend on its concentration \( x \), and will proceed according to

\[ - \frac{dx}{dt} = k_1 x \quad (6) \]

where \( k_1 \) is the velocity constant of the reaction \( L \rightarrow T \). The rate of the formation of the indifferent material \( N \) will depend on the concentration \( y \) of the substance \( T \), and is

\[ \frac{dz}{dt} = k_2 y \quad (7) \]

where \( k_2 \) denotes the velocity constant of the transformation of \( T \) to \( N \). Therefore the rate at which \( T \) will accumulate in the sense organ will evidently be the difference between the rate of diminution of \( L \) and the rate of formation of \( N \); in other words,

\[ \frac{dy}{dt} = k_1 x - k_2 y. \quad (8) \]

The speed of the chemical system \( L \rightarrow T \rightarrow N \) is fully determined by these three simultaneous differential equations. The conditions
which govern the behavior of the four variables in the equations are well known, and have been subjected to experimental verification (Mellor, 1916, p. 434). Without going into the details of the mathematics of the matter, it is sufficient to say that by combining equations (5), (6), (7), and (8), and integrating under proper conditions, an equation is deduced which gives the amount \( z \) of the substance \( N \) formed in a given time \( t \) in the terms of the two velocity constants \( k_1 \) and \( k_2 \). This equation is

\[
z - t = \frac{k_2}{k_1 - k_2} \cdot \frac{1}{e^{k_1t}} - \frac{k_1}{k_1 - k_2} \cdot \frac{1}{e^{k_2t}} \tag{9}
\]

in which all the terms have their previous significance, and \( e \) is, as usual, the Naperian base.

### TABLE II.

**Velocity Constants of the Fundamental Reaction of the Latent Period, and of the Inactivation Reaction. Amount of Thermolabile Substance Inactivated above 21°, and the Time (\( t \)) during Which the Inactivation Actually Takes Place.**

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Latent period (sec)</th>
<th>( k_1 )</th>
<th>( k_2 )</th>
<th>( z )</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>1.30</td>
<td>0.0948</td>
<td>0.239</td>
<td>0.0161</td>
</tr>
<tr>
<td>25</td>
<td>1.22</td>
<td>0.117</td>
<td>0.500</td>
<td>0.0332</td>
</tr>
<tr>
<td>27</td>
<td>1.16</td>
<td>0.144</td>
<td>0.826</td>
<td>0.0540</td>
</tr>
<tr>
<td>29</td>
<td>1.13</td>
<td>0.178</td>
<td>1.22</td>
<td>0.0824</td>
</tr>
<tr>
<td>30</td>
<td>1.11</td>
<td>0.215</td>
<td>1.63</td>
<td>0.1125</td>
</tr>
</tbody>
</table>

We already know the values of \( t \), the actual latent period; these are given by the experimentally determined points of Fig. 2 and in part by the triangles in Fig. 3. The amount of \( N \) present in the system is the quantity \( z \) of thermolabile substance \( T \) which has been inactivated. This is also known from Fig. 3, and its value at different temperatures is given in Table II. Also, \( k_1 \) is known, its values having been given in Table I. The only unknown in equation (9), therefore, is \( k_2 \), the velocity constant of the inactivating reaction \( T \rightarrow N \). Equation (9) may then be solved for \( k_2 \), which will give us precisely the information we desire: the values of this velocity con-
stant at the different temperatures. Computation of equation (9) using the various values of \( t, k_1, \) and \( z \) yields the quantities plotted in Fig. 4, and given in Table II.

We are now in possession of the means of estimating the relation between the temperature and the speed of the inactivating reaction \( T \rightarrow N \). If our reasoning has been correct, these velocity constants should be related to one another according to the Arrhenius equation (3) previously given. Fig. 4 shows this to be true. The points are the logarithms of the velocity constants \( k_2 \), whereas the curve gives the theoretical expectation according to equation (3) solved for \( \log k_2 \) as follows:

\[
\log k_2 = \log k'_2 + \left[ \frac{1}{2.303 \cdot \frac{\mu}{T}} \left( \frac{1}{T'} - \frac{1}{T'} \right) \right]
\]

In making the computations, \( T' \) is put at 296° (=23.0°C.) and \( k'_2 \) is the value of \( k_2 \) at this temperature as given in Fig. 4. The factor \( \frac{1}{2.303} \) converts natural into common logarithms. For drawing the curve in Fig. 4, \( \mu \) is equal to 48,500. A much better agreement between observed points and the theoretical curve is hardly to be expected under the circumstances.

The fact that the hypothetical inactivation reaction, \( T \rightarrow N \), shows a constant value of \( \mu \) brings increased confidence in the reasons for its assumption. More convincing, however, is the order of magnitude of \( \mu \). In the table collected by Arrhenius (1915, p. 54) it is shown that ordinary chemical reactions such as saponifications and hydrolyses possess values of \( \mu \) between 10,000 and 20,000. This agrees well with our findings of \( \mu = 19,680 \) for the fundamental reaction of the latent period, \( L \rightarrow T \). However, the chemical reactions involved in spontaneous destructions and in heat coagulations have values of \( \mu \) which are rarely below 30,000, and are usually well above this figure. For the destruction of trypsin, \( \mu = 62,000 \); for the heat coagulation of hemoglobin, \( \mu = 60,100 \); for the inactivation of emulsion, \( \mu = 45,000 \); etc. It is therefore highly significant that the reaction \( T \rightarrow N \), postulated for the heat inactivation of the thermodabile substance \( T \), shows a value of \( \mu = 48,500 \), thoroughly in accord with those usually found for such processes.
Fig. 4. Relation between the temperature and the velocity constants of the inactivation reaction $T \rightarrow N$. The points are those computed from the experimental data. The curve is the theoretical expectation from the Arrhenius equation when $\mu = 48,500$. 
In considering the results of this analysis, it is necessary to reiterate a caution previously mentioned. This concerns the amounts of L and of T assumed in the quantitative treatment of the data. The assumption of 1 mol of L at the beginning of the latent period, and of 0.10 mol. of T at the end, in no way affects the analysis except in so far as it makes it possible to present the matter graphically. The actual quantities may be those represented, or, what is more probable, they may not. The results of the analysis, however, will be the same, as long as we accept the fundamental idea that a definite amount of the thermolabile substance T must accumulate in the sense organ in order to produce the inner stimulus for retraction of the siphons.

Considered in such general terms, the relation of the latent period to the temperature may be stated as follows. The duration of the latent period depends fundamentally on the accumulation of a certain amount of material as the result of a single, simple chemical reaction. The variations of this reaction with the temperature are adequately expressed by the Arrhenius equation (3) when $\mu = 19,680$. At temperatures above 21°C., however, this substance which accumulates in the sense organ is perceptibly inactivated by heat. The reaction expressing this inactivation is of the kind usually found for spontaneous destructions, and its relation to the temperature is also adequately expressed by the Arrhenius equation when $\mu = 48,500$.

We therefore have a destruction reaction, the velocity of which increases more than twice as rapidly with the temperature as does the fundamental reaction which produces the thermolabile substance. At temperatures slightly above 21°, a balance may be struck between destruction and production so that sufficient thermolabile substance will eventually accumulate to produce a response. Soon, however, the destruction reaction is more than fast enough to inactivate the thermolabile material as rapidly as it is formed. The result is that no thermolabile substance can accumulate in the sense organ. In Mya this happens at temperatures above 35°C., when no amount of exposure to light can result in a retraction of its siphons.
VII.

The analysis with which we have been occupied, though it accounts for the data in a simple way, is not the only one possible. Even in the terms of the hypothesis of photoreception which has been adopted for Mya, there is at least one other explanation, just as plausible but not as simple, which deserves to be mentioned. Without entering into details, I wish to present this alternative analysis in its barest outlines.

The reaction of the latent period, \( L \rightarrow T \), is catalyzed by the precursor material freshly formed during the sensitization period. Organic catalysts are enzymes, and enzymes are notoriously thermostable. Since the velocity of the latent period reaction is a linear function of the concentration of catalytic precursor (Hecht, 1919, b), the deviations of the latent period at higher temperatures may be considered as due to the destruction of some of this catalytic agent. The velocity of the latent period reaction becomes slower because of the decrease of catalyst. The time required to form a definite amount of \( T \) to produce a response is, therefore, lengthened beyond that required on the basis of the Arrhenius equation (3). Assuming that the destruction of the precursor catalyst follows the usual course of such spontaneous decompositions, it is possible to estimate quantitatively its velocity constant, and to express the entire process diagrammatically.

The actual mathematical considerations, however, are rather involved. The destruction of the precursor material must be estimated not only during the latent period after its production, but during the sensitization period while it is still being produced. The simpler analysis has, therefore, been given in detail because it fits the facts just as well. Certain deductions from the two explanations are, however, different for the two cases, and further experimentation will show which is more probably correct.

SUMMARY.

1. The effect of temperature on the reaction time of Mya to light is mainly confined to the latent period. The sensitization period, representing a photochemical process, is changed comparatively little.
2. The relation between the latent period and the temperature is adequately expressed by the Arrhenius equation, for temperatures below 21°C. Above this temperature, the latent period becomes increasingly longer than is required by the Arrhenius formula when \( \mu = 19,680 \).

3. These deviations, occurring above the highest environmental temperature of *Mya*, are explained on the assumption that the principal product formed during the latent period is inactivated by heat.

4. Calculation of the velocity of the hypothetical inactivation reaction at different temperatures shows that it also follows the Arrhenius rule when \( \mu = 48,500 \). This value of \( \mu \) corresponds to those generally found for spontaneous inactivations and destructions.

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