TEMPERATURE AND CRITICAL ILLUMINATION FOR
REACTION TO FLICKERING LIGHT

VI. Flash Duration Varied

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For animals with simplex, structurally uncomplicated, visual systems the dependence of critical intensity \( I \) upon flash frequency \( F \) in reaction to visual flicker is described by a single symmetrical probability integral in \( \log I \).\(^1\) Vertebrates with duplex visual systems exhibit two such segments, overlapping to various degrees. The parameters of the curve are known to be modifiable as functions of the form of the light-dark succession in the flash cycle, and the proportion of light time to dark time,\(^2\) the retinal area excited,\(^3\) the temperature,\(^4\) and the wave-length composition of the light,\(^5\) and the state of visual adaptation.\(^6\) The theory of the origin of this non-specific type of performance contour has been derived from the considerations that the magnitude of sensory effect \( E \) produced by the interrupted light at the point of response is proportional to \( F \) and is measured by the integral of a frequency distribution of \(-I \cdot d(1/I)\) and consequently of \( d \log I \).\(^7\) Sensory elements of excitability \( 1/I \) contribute to sensory effect \( E \)


\(^8\) Crozier, W. J., 1940, The theory of the visual threshold, in preparation.
TEMPERATURE AND RESPONSE TO FLICKER. VI

over the finite time involved in the determination of response with a magnitude which declines with the intensity.

The effects of altering (1) the percentage light time \( \frac{t_L}{t_L + t_D} \) in the flash cycle and (2) the temperature should give a direct test of this conception. An increase of dark time permits each flash to act on a larger number of non-refractory elements, because of greater chance of recovery during a longer dark time. Hence the total number of units of effect obtainable (==\( F_{\text{max.}} \)) should be greater, while a given level of effect is secured with a lower intensity. But since the neural elements concerned are the same, and their basic excitabilities, \( \sigma' \) (the standard deviation of the frequency distribution of effects produced, with \( F_{\text{max.}} = 100 \) per cent) should not be modified. These are the findings; \( F_{\text{max.}} \) and the abscissa of the inflection \( (\tau') \) of \( F \)-log \( I \) are each rectilinear functions of the percentage dark time in the flash cycle, but \( \sigma' \) is invariant. On the other hand, increasing the temperature merely increases the metabolic reaction velocities responsible for the capacity to be excited, \( \frac{1}{I} \); hence \( F_{\text{max.}} \) and \( \sigma' \) are not functions of temperature but \( \tau' \) is. These effects have been secured in animals of such morphological diversity that their origin and basis in the dynamical statistics of cellular assemblages, rather than in any other way, seem obvious and assured. The analytical form of the \( F \)-log \( I \) function is non-specific; its parameters are specific and determinate, since they are fixed by the genetic make-up of the animal\(^6\) and their magnitudes exhibit rational dependence on variables which may be used to control them.\(^4\)

One important point remains to be examined. The influence of temperature on \( \tau' \) has been studied\(^4\) with \( t_L = t_D \). The rôle of the light-time ratio has been studied\(^6\) with the temperature constant at 21.5°. If the kind of interpretation previously suggested is correct, it is required that the exact mode of dependence of \( \tau' \) on the temperature must be the same with \( t_L = 0.1 \) as with \( t_L = 0.9 \), and the \( F_{\text{max.}} \) and \( \sigma' \) must be independent of temperature at all values of the light-time fraction.\(^6\)\(^a\)


\(^a\) Cases do arise, however, in which the number of potentially excitable elements is a function of temperature. Such an instance is found, for example, in the relation of exposure time to current strength for production of a given size of action current in nerve (cf. Crozier, W. J., 1937, Proc. Nat. Acad. Sc., 23, 71); presumably the same situation can be presented by the time intensity relation for photic excitation, under certain conditions. In the case of nerve the law of the temperature effect on excitability can be
The requirements are exceptionally rigorous. The outcome of the tests is a definite verification of the several expectations mentioned. A further instance is thus provided of the analytical separation of the properties of metabolically determined $1/I$ and of the purely statistical (distribution) factors producing the form of the $F$-log $I$ contour; $\mu$ for $1/I$ has already been shown to be independent of the form of the curve. It is also of significance for the general theory of temperature dependence and of the origin of the invariance of temperature characteristics in the performance of biological systems.

II

For these tests the responses of young turtles, *Pseudemys scripta*, ssp., are especially advantageous. The $F$-log $I$ curve is simplex; the relation of $1/I$ to temperature (with $t_L = t_D$) exhibits a critical temperature at 29.5°, with a quite high $\mu$ from 12 to 30° ($\mu = 26,700$) and a much lower one (12,400) above 30°; the responses are sharp and precise, and individual differences in a lot of individuals provide internal evidence of the precision of the observations. The nature of the temperature function is such as to give a real chance to detect even slight alterations which might be due to change of $t_L/t_D$ were these to occur with this animal. Below 30° the $\mu$ plot is steep, and the presence of the "break" at 29.5° indicates that two distinct processes are involved in the control of $1/I$.

The procedure used and the methods of calculation have been described. A group of 10 numbered individuals (3.24 to 3.66 cm. carapace length) was taken from a larger number acclimated to laboratory conditions. These same 10 were used throughout the present experiments. At each temperature and light-time fraction three observations were made with each dark-adapted individual at each flash frequency used. The means ($I_L$) of the three readings of $I$ for the 10 individuals are averaged and entered as $I_m$ in Tables I and II. The P.E. of the dispersion of the individual obtained from the behavior of the value of log $t_{final}$ for the probability integral relating $1/c$ to log time, that is of the chronaxie $\tau$, provided $\sigma_{log t}$ remains constant—as it is observed to do. Otherwise, the Arrhenius plot for log $1/t$ vs. $1/T_{abs}$ cannot be rectilinear if $t$ is the time for excitation by a fixed magnitude of current.


means is also given. Certain properties of this variation are discussed subsequently.

The methods used to control temperature \(^4, \, 10\) and light-time fraction \(^3\) have been described. The temperatures employed were arranged in random order. Check observations assured that even at 36 ° and at 12° as extreme adaptation temperatures the effects were freely reversible. The behavior of the turtles in providing the response signifying the establishment of the critical intensity has also been discussed; \(^10\) it is to be added merely that with decreasing \(t_a\), as with rising temperature, the vigor and amplitude of the responses is found to increase. \(^12\) This has no effect on the variability of critical intensity (cf. Figs. 8, 9).

In all of these experiments we have found it necessary and important to begin each set of observations with dark-adapted animals. According to Birukow \(^10\) this is not required for the turtles Emys and Testudo. We have pointed out that, for crayfish and frog, light adaptation reduces the \(F\) range and increases the critical intensities. \(^14\) and that this produces a profound contrast in the \(F\)-log \(I\) curves gotten for frogs by Birukow \(^15\) and by our procedure. For man it is well known that the critical flash frequency is a very definite (and superficially complex) function of the level of photic adaptation. \(^18\) The point is easily demonstrated qualitatively for Pseudemys. Pseudemys were adapted for 30 minutes under light of ca. 6,550 ml. on a white background and surrounded by white walls. They were then tested for response at \(F = 20\). At this temperature (21.5°), \(\log I_o\) for the critical flash intensity = 2.204 when the animals are previously dark-adapted. When exposed for light adaptation the head was always extended and the eyelids open, so that full adaptation was assured. On transfer to the apparatus for testing flicker response the turtles are restless, but good responses by the standard procedure can be observed after 10 to 20 seconds. Successive readings of the critical intensity get gradually smaller as the effect of light adaptation wears off. Data on 4 individuals, giving successive measurements (log \(I\)) up to 2 minutes after removal to the apparatus, illustrate this:

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.90</td>
<td>2.86</td>
<td>1.05</td>
<td>1.08</td>
<td></td>
</tr>
<tr>
<td>2.87</td>
<td>2.70</td>
<td>2.85</td>
<td>1.02</td>
<td></td>
</tr>
<tr>
<td>2.75</td>
<td>2.68</td>
<td>2.72</td>
<td>2.86</td>
<td></td>
</tr>
<tr>
<td>2.63</td>
<td>2.65</td>
<td>2.56</td>
<td>2.78</td>
<td></td>
</tr>
<tr>
<td>2.65</td>
<td>2.49</td>
<td>2.38</td>
<td>2.67</td>
<td></td>
</tr>
<tr>
<td>2.45</td>
<td>2.34</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^{13}\) Birukow, G., 1939, Z. vergleich. Physiol., 27, 322.


FIG. 1. The apparatus producing flicker by rotation of a striped cylinder. A, a cylinder (inside diameter = 14.5 cm.); the one shown has 40 opaque stripes. The animal under observation is in a cylindrical dish of thin glass, within the cylinder. The cylinder in its holder B is driven through a gear system by the variable speed motor C; coarse and fine rheostats D and E adjust its speed. The precision magneto F is geared to the same shaft; the voltage it develops, read on the millivoltmeter G, gives the rotation frequency of the cylinder in terms of calibration charts for the different gear systems used. Light from a lamp on an optical bench is admitted through the square diaphragm at H, controlled at I; a vernier scale (illuminated by use of a foot switch) can be read in the telescope J to give the diaphragm-opening, and thus by way of calibration charts the intensity (within the cylinder) due to a flash. The light is reflected vertically by the plate mirror K and is then horizontally diffused by the oxide-coated cone L. The bench M is for recording and monitoring the cylinder speed. During observations the curtain N excludes light from red pilot lamps, there being no other illumination in the dark room. (Thermostat tanks for dark adaptation are immediately at the right.)

The effect of proper preliminary dark adaptation in stabilizing the critical intensity, and the direction of the shift under light adaptation, are therefore the same with Pseudemys as with other animals.
It is worth recording that on one occasion two successive sets of observations were found to be discordant by a small amount, about 0.1 log unit; this was traced to the previously unnoticed drift of the thermostat temperature owing to the "sticking" of the regulator, the amount being 0.3°. In another case a slight error in the construction of a particular striped cylinder was found to be responsible for a persistent 0.2 log unit shift in the value of $I_m$ for $t_L/t_D = 9/1$ at $F = 10$. Unconscious experiments of this sort illustrate the kind of precision possible in these experiments if rigorous attention is given to their details.

![Figure 2](https://example.com/figure2.png)

**Fig. 2.** Log mean critical intensity $I_m$ as a function of flash frequency $F$, at 21.5°, for several proportions of light-time ($t_L$) to dark-time ($t_D$) in the flash cycle—$t_L = 0.10$, 0.25, 0.50, 0.75, and 0.50 $\times t_L + t_D$; i.e., $(t_L + t_D) = 1/F$. See Table I. Data for $t_L = 0.50$ $t_D$ are from a previous paper; here the circlets with tags refer to measurements of $F_m$; several determinations at $t_L = 0.50$ with the animals of Tables I and II are included to show reproducibility. The curves are adjusted probability integrals (cf. Fig. 3).

For technical reasons it is difficult to obtain light-time ratios greater than 9:1 or less than 1:9, and with these the complete response contours cannot be measured. These limitations arise because of the difficulty of preparing striped cylinders with the necessary accuracy and because flash intensities above antilog 2.3 millilamberts cannot be controlled with precision in the apparatus (cf. Fig. 1). Since, however, the form of the $F$-log $I$ curve does not change with temperature we are able to use $t_L = 0.1$
and 0.9 at any fixed flash frequency $F$ (below $F = 35$) and thus obtain data at cylinder rotation speeds which are favorable for precise determinations at various temperatures. On the other hand the $F$-$\log I$ function can be gotten over essentially its whole range at 21.5° with $t_\ell = 0.25$ and 0.75. We shall consider these measurements first, since it is desirable to establish the generality of the rules already found for this matter with Anax (dragonfly nymph) and Enneacanthus (sunfish).

### Table I

Critical flash intensities (as log mean $I$, millilamberts) with P.E.$t_\ell$ for response of *Pseudemys* at 21.5°, for various flash frequencies, with the proportion of light-time ($t_\ell$) in the flash cycle at 10, 25, 75, and 90 per cent; values of $F_m$ at log $I = 2.000$. See Figs. 2 and 3.

<table>
<thead>
<tr>
<th>$F$/sec.</th>
<th>$t_\ell = 10$ per cent</th>
<th>25 per cent</th>
<th>75 per cent</th>
<th>90 per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\log I_m$</td>
<td>$\log P.E.$</td>
<td>$\log I_m$</td>
<td>$\log P.E.$</td>
</tr>
<tr>
<td>3</td>
<td>$\bar{4.193}$</td>
<td>$\bar{4.041}$</td>
<td>$\bar{4.046}$</td>
<td>$\bar{3.567}$</td>
</tr>
<tr>
<td>7.5</td>
<td>$\bar{4.956}$</td>
<td>$\bar{3.147}$</td>
<td>$\bar{3.270}$</td>
<td>$\bar{3.238}$</td>
</tr>
<tr>
<td>10</td>
<td>$\bar{5.059}$</td>
<td>$\bar{3.544}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>12.5</td>
<td>$\bar{5.069}$</td>
<td>$\bar{3.494}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>20</td>
<td>$\bar{5.069}$</td>
<td>$\bar{3.444}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>25</td>
<td>$\bar{5.069}$</td>
<td>$\bar{3.654}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>30</td>
<td>$\bar{5.069}$</td>
<td>$\bar{3.152}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>35</td>
<td>$\bar{5.069}$</td>
<td>$\bar{3.120}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
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<tr>
<td>40</td>
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<td>$\bar{2.337}$</td>
<td>$\bar{3.659}$</td>
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</tr>
<tr>
<td>45</td>
<td>$\bar{5.069}$</td>
<td>$\bar{1.112}$</td>
<td>$\bar{3.659}$</td>
<td>$\bar{3.923}$</td>
</tr>
<tr>
<td>52.06</td>
<td>±0.614</td>
<td>2.000</td>
<td>2.000</td>
<td></td>
</tr>
<tr>
<td>48.09</td>
<td>±0.460</td>
<td>2.000</td>
<td>2.000</td>
<td></td>
</tr>
</tbody>
</table>

Table I contains the measurements from which the properties of the *Pseudemys* $F$-$\log I$ contour in terms of the light-time fraction at constant temperature may be deduced. It is apparent from Fig. 2 that, as with Anax and Enneacanthus the abscissa of inflection ($\tau'$) is decreased and the maximum $F$ increased when the percentage light-time in the flash cycle is reduced. It is also clear, as in the previous cases, that $\tau'_{\log I}$ is not affected (Fig. 3). Fig. 6 shows that, again as before, $F_{\text{max}}$ and $\tau'$ are related rectilinearly when $t_\ell$ is changed. (For the abbreviated series with $t_\ell = 0.1$ and 0.9, $F_{\text{max}}$ was found with the help of Fig. 4, and from this the computed positions of the points in Fig. 3 were found to give rectilinearity with the values of $\tau'$ used in Fig. 4 and with the constancy of slope.
TE/~PEILATUILE A.N-D RESPONSE TO I~LICILER. VI

showing that \( \sigma' \log \tau \) is invariant.) The relations of \( F_{\text{max}} \) and \( \tau' \) to the percentage light-time are shown in Figs. 4 and 5. They are essentially rectilinear, as with \textit{Anax} and \textit{Enneacanthus}.\(^3\) The proportionality constants are not the same as in the other cases, however, indicating that these constants depend on the nature of the visual system in each instance—although the several proportionality constants for \( \tau' \) vs. \( 100 \frac{t_L}{(t_L + t_D)} \) do not differ very greatly.

IV

With \( t_L = t_D \) it was found that \( \log (1/I) \) at fixed \( F \) obeys the Arrhenius equation as a function of temperature.\(^4\) For certain fishes the same temperature characteristic \( \mu \) obtains over the entire usable range of temperatures;\(^5\) for other forms,\(^6\) including \textit{Pseudemys},\(^7\) an intermediate critical temperature is observed. The calculation of \( \mu \) is made from the slopes of the lines on plots of \( \log (1/I) \) vs. \( 1/T_{\text{abs}} \). Only in very rare instances are such plots curvilinear, then requiring further analysis.\(^8\) We have already indicated that if the chemical control of excitability is to demonstrate the operation of governing mechanisms with the properties of simple catalytic reaction velocities, then the slopes of the \( \mu \) plot for \( 1/I \) must be independent of the light-time fraction in the flash cycle. The data of Table II, plotted in Fig. 7, show that this requirement is satisfied.

In Fig. 7 \( \log (1/I_n) \) is given as a function of \( 1/T_{\text{abs}} \). It is apparent that in the immediate neighborhood of \( 30^\circ \text{C} \) there occurs in each series a sharp break in the graph, and that on either side of this point the slopes are identical for all three values of the percentage light-time. The magnitudes of \( \mu \) computed from the slopes are 12,400 cal. above \( 30^\circ \) and 26,500 cal. below \( 30^\circ \). These are identical with the results previously gotten\(^9\) for \( t_L = 0.5 \) at \( F = 20 \) and \( F = 30 \). With respect to \( t_L \) as with respect to \( F \), the temperature characteristics are invariant. If this were not the case it would follow either that the conceptions of the two different modes of action of \( t_L \) and of temperature on the morphology of the \( F\)-log \( I \) curve are imperfect or incorrect, or that the theory of the nature of temperature characteristics is inadequate,—if not both.

A special point involves the use for this test of a case in which, as in Fig. 7,

Fig. 3. The data of Fig. 2 on a probability grid, each series computed in terms of its own $F_{\text{max}}$. (cf. Figs. 4 and 6). The slopes are drawn equal; $\sigma_{\log f}$ is consequently constant and independent of the light-time fraction. (For $t_L = 0.5$, the line is taken from earlier work, with the fresh determinations added.)

Fig. 4. $F_{\text{max}}$ decreases rectilinearly as percentage light-time is increased.

Fig. 5. $\tau'$ increases rectilinearly as the percentage light-time in the flash cycle is increased.
there occurs a "break" in the Arrhenius plot. Theory here demands that there be involved two different, linked, processes which by virtue of some physical change associated with a critical temperature are respectively

![Graph](image)

**FIG. 6.** The asymptotic maximum ordinate \( F_{\text{max}} \) giving adjustment of each series of observations on the probability grid (Fig. 3) declines in rectilinear relation to the increase of the abscissa of the inflection point \( \gamma' \).

**TABLE II**

Critical flash intensities, as log \( I_m \) (millilamberts), with log P.E.1, for response of *Pseudemys* at flash frequency \( F = 25/\text{sec.} \), with light-times \( (t_L) = 10, 50, \) and 90 per cent of the flash cycle, at various temperatures \( (\nu_{\text{mm}} \) ); three observations on each of the same 10 individuals at all points. See Figs. 7 and 8. (Three sets from previous measurements \( \delta \) at \( t_L = 50 \) are given for comparison.)

<table>
<thead>
<tr>
<th>( \nu_{\text{mm}} )</th>
<th>10</th>
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<th>90 per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>( t_L = 10 )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>log ( I_m )</td>
<td>log P.E.1</td>
<td>log ( I_m )</td>
<td>log P.E.1</td>
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<tr>
<td>12.2</td>
<td>5.6696</td>
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<td>5.8231</td>
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<td>5.3388</td>
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in control on either side of the critical temperature. The reality of this break is amply evident in Fig. 7. It would not be surprising to find that the use of an additional variable, such as the light-time fraction, would shift the intercepts of the two segments of the graph to different extents.
Fig. 7. Log (1/I_m) as a function of 1/T_{abs.}, for three values of the percentage light-time, at one flash frequency (F = 25/sec.); see Table II. The slopes of the lines on either side of 29.5° give $\mu = 12,400$ and 26,500 cals. These slopes are the same with $t_L = 10, 50, \text{and } 90\%$.
An effect of this kind is quite obvious in the case of the data on the sunfish, the relative positions of the low and high temperature segments are not the same for the "rod" and "cone" portions of the duplex F-log I curve. Other instances are known. This could bring about a slight shift in the critical temperature as $t_c$ is altered, such as is seen in Fig. 7. It could also appear in a difference between different lots of individuals. While it is not our desire to emphasize in any way the slight differences found in Fig. 7, it is perhaps legitimate to suggest that by the systematic use of additional variables in other cases light might well be thrown on the nature of the phenomena operating at critical temperatures.) Before this can be evaluated, however, it is necessary to consider the variation of $I_1$ as a function of $t_c$ and of $T$. We have already shown that slight individual differences tend to persist in _Pseudemys_ for longer times than we have noticed with any other animals we have tested.

It was shown for the lot of _Pseudemys_ previously used that the variation of $I_1$, measured by P.E., was rectilinearly related to $I_m$, and was apparently independent of temperature. In earlier experiments with _Anax_ and sunfish it appeared that for any level of $I_m$ the variation of $I_1$ was slightly greater at an intermediate temperature than at the two extremes. It is not so in the present data, which may be due to improvement of technic or other causes. This can be tested more completely in the present data, with particular reference to the fact that independent evidence may be obtained as to the simplicity or complexity of the processes controlling $1/I$. Simplicity of the controlling process over a given range of temperatures is implied by the constancy of $\mu$ and by its invariance with respect to $t_c$. In a case where complexity of control is required by the inconstancy of $\mu$ the variation of $I_1$ is definitely not a constant percentage of $I_m$. This supplies an empirical test of the idea that constancy in the relative variation of performance, under changed values of experimentally independent variables affecting the measure of performance, necessarily indicates simplicity of the controlling process, since these independent variables must then be conceived to affect all the elements of the situation in the same proportionate way. The sort of organization making this result possible is to be defined operationally as simple, in virtue of its unitary character.

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$^{20}$ Cf. Crozier, W. J., 1934-35, _J. Gen. Physiol._, 18, 801; and experiments with the effects of low temperatures, as yet unpublished.
It also appeared, however, that the raw variation of $I_1$ was in part influenced by the fact that the individuals of the original lot of 10 tended significantly to maintain their relative excitabilities from day to day. The rôle of this property must be examined in the present case also. We will first consider the gross P.E. figures given in Tables I and II.

Fig. 8 shows that with temperature constant and the percentage light-time varied, the rule of direct proportionality between P.E.1 and $I_m$ is not distorted; the same is now shown in Fig. 9 for the variation of both $t_L$ and temperature. The bands are essentially identical; the proportionality factor $k$ in $I_m = k(P.E.1)$ is the same, and does not differ significantly from that already on record for the first lot of *Pseudemys* with temperature and $F$ as variables. Consequently the homogeneity of the process measured by $1/I$ as an index of excitability, with respect to the significant relations to flash frequency, light-time ratio, temperature, and critical intensity, is objectively confirmed.

When the relative sensitivities in the set of 10 *Pseudemys* are examined it is observed that, as before, these are not distributed at random. Individuals 5, 1, and 9 tend to be much more consistently at one end (5, 9) or the other (1) of the sensitivity rank order than do the others. Thus the mean rank order number of No. 5 in 36 sets of measurements with temperature and $t_L/t_D$ varied is 1.67; of No. 1 it is 8.26. (No. 5 happens to be the smallest individual, carapace length 32.4 mm; but for the others—32.8 to 36.6 mm.—there is no correlation with sensitivity.) With these two and No. 9 excluded, the rank order numbers of the others are practically random. The individual rank order numbers have no relation to the order of use in a series of readings. In the second lot of 22 sets of measurements, with $t_L/t_D$ varied at 21.5°, the mean rank order numbers for No. 5 and No. 1 are respectively 1.44 and 8.12. The differences of these numbers from the random mean 5.5 are 6 to 8 times the P.E. of the differences, and are consistently exhibited. For this lot, also, individuals 9 and 10 persistently retain their relative sensitivities. The others vary at random, so far as can be told within the small span of critical intensities, but Nos. 1 and 9 are consistently the least sensitive while 5 and 10 require the smallest critical intensities. If we take Nos. 1 and 5 for purposes of illustration we find (Fig. 10) that the $\mu$ plots for Nos. 1 and 5 are quite parallel, but that the junction of the two sections of the graph is slightly different. It is clear that if a large number of determinations were available for a single individual they would form a band with a bend centering at 29.5° or a little above. This explains why, with a small number of
FIG. 8. The constant proportionality of the mean critical intensity and its variation is maintained at constant temperature for different proportions of light-time in the flash cycle. The slope of the band log P.E._1 vs. log $I_m = 1$, and its width is statistically constant.

FIG. 9. The constant proportionality of $I_m$ and P.E._1 is unchanged when light-time fraction and temperature are varied; the proportionality constant is the same as in Fig. 8.
FIG. 10. Log $(1/I_1)$ vs. $1/T_{abs}$ for the two most distinctly different of the 10 individuals from which averages $(1/I_{as})$ are used in Fig. 7. See text.
determined points, the region from 28° to 36° is bound to be more uncertain, as in Fig. 7, than elsewhere. A further fact is of course that in the observations made on one day, at one temperature, there is a measure of consistency in the direction of departure of all the readings from the general line of central tendency (cf. Fig. 10). This may in part only be due to properties of the apparatus. The greater spread of the points at $t_c = 0.5$, incidentally, is consistent with the data in Fig. 8.

These considerations go some way toward accounting for the systematic departures, slight as they are, seen in the plots of $1/I_m$ (Fig. 7), but it is also to be recognized that the parameters of the $F$-log $I_m$ function also vary slightly from one animal to another. This has been illustrated before; the same kinds of minor differences appear in the detailed records of the present experiments.

VI

The theory of the meaning of the qualitative relations of the $F$-log $I$ curve to temperature and to the light-dark ratio respectively has been conceived in the following way.

The temperature controls the velocities of specific catalytic processes which govern excitability; the excitability is measured by $1/I_m$, where $I_m$ is the mean critical intensity for response; the sensory effect produced at this level is proportional to $F$; consequently, for $dF/d \log I$ constant, $1/I_m$ has the physically appropriate relation to temperature; the shape of $F$ vs. log $I$ is not a function of temperature, hence at any $F$ the same temperature characteristic holds for $1/I_m$. This means that in terms of the derivation of the form of $dF/d \log I$ the total number of potential elements of sensory effect involved is independent of the temperature, while the ease with which they can be aroused (in terms of intensity) is dependent on the temperature. In other words, we have to do with a frequency distribution of $-k' I d(1/I)$ in which $k'$ is independent of temperature but $1/I$ is not, for a given kind of animal. It is to be remembered that $I$ is the intensity for excitation, or rather that the number of elements in a particular $d \log I$ class gives the appropriate normal occurrence for this value of $I$—the number of units of effect produced in the interval $(1/I_a + d(1/I)) - (1/I_a)$, where $1/I_a$ is a function of temperature. Consequently $F_{\text{max}}$ and $\sigma_{\log I}$ are not affected by temperature.

On the other hand, when the light-dark ratio is altered it must be supposed that $k'$ is a function of the dark-time fraction. The frequency with which flashes of a given intensity, at the critical flash frequency $F$, serve to produce unit sensory effects in elements of excitability $1/I$ is greater...
the longer the dark-time fraction. Hence, at given \( I \), \( F \) is higher, and \( F_{\text{max.}} \) greater, in proportion to lengthening of the dark-time fraction. If this effect is one involving \( k' \), not \( 1/I \), then the temperature characteristics for \( 1/I \) must be the same for all levels of the light-dark ratio. This has been shown to be the case. On any other theoretical basis this kind of result is apparently impossible. It amounts to an analytical separation of the properties of the two factors involved in the production of the frequency distribution of the elemental sensory effects of which the \( F - \log I \) contour is the integral. The two factors have to do with the excitabilities of the effects, and with the frequencies of their occurrence as a function of intensity. It has been argued that the basic excitabilities form some sort of a frequency distribution of \( d(1/I) \), but that over a finite time interval the number of elemental effects gotten by critical intensity \( I \) from excitabilities momentarily in the class \([1/I_a + d(1/I)] - [1/I_a]\) will be a declining function of \( I_a \), such that this number = \(-k'I\), unless the conditions of excitation are changed. When they are changed by increasing the dark-time fraction the effects are exactly of the kind produced by enlarging the retinal area involved, as already emphasized. \( F_{\text{max.}} \) is increased, \( \tau' \) is decreased, but (for a homogeneous area) \( \sigma'_{\log \tau} \) is constant. The reason is that with a longer proportionate dark-time the chance of any flash encountering a potentially excitable unit in a non-refractory state is in this degree increased. The integral of \(-k'I \cdot d(1/I)\) is that of \( k'd \log I \). Clearly, it is with this \( k' \) that purely photochemical (or photoelectric) considerations must be primarily concerned, and curiously enough not with \( 1/I \). It is of course consistent with this that \( \mu \) for \( \tau' \) is constant and independent of the dark-time fraction, and that Talbot’s law does not apply to marginal flicker.

Parallel cases are provided by certain other properties of homogeneous cellular populations. Two may be cited briefly. When, with a given interelectrode distance, the strength-duration curve for excitation of a nerve is determined at two temperatures, the curve of \( 1/C \) vs. \( \log t \) is a probability integral in which the maximum value of \( 1/C \) is greater at the higher temperature and \( \tau' \) less, although \( \sigma'_{\log \tau} \) is the same. Increase of temperature makes more of the elementary excitability units available. (In this case enlargement of area by further separation of the electrodes does the same thing for \( (1/C)_{\text{max.}} \) and \( \tau' \), but increases \( \sigma'_{\log \tau} \) because of greater variability in the population of units.)

A second case is more obviously pertinent. The photosynthetic activity \( P \) of green plant cells, measured by the \( O_2 \) liberated in a fixed finite time, gives a log probability

If the intensity of illumination $I$ is increased, $P_{\max}$ increases and $\tau^\prime$ (i.e. log $[\text{CO}_2]$ at the inflection point) is decreased, in direct proportion to $I$. The higher intensity increases the frequency of work done by each element whose momentary threshold is in terms of $dl/[\text{CO}_2]$. On the other hand, when $[\text{CO}_2]$ is varied, the $P$-log $I$ contour merely changes its ordinate scale but $\tau^\prime$ is unaltered: the amount of work done by each element is then increased, not its frequency.\(^{28}\)

The proportionality constant $k^\prime$ has another ascertainable property bearing upon the notion that the effect of the dark-time ratio is to be taken as involving a frequency of excitation. This is most simply seen if we consider log $I$ at the inflection point (that is, our $\tau^\prime$). We have it experimentally that at constant temperature

$$\tau^\prime = -Ct_d (t_e + t_D) + C_1$$

(Fig. 5).

With $t_L/t_D$ constant we have

$$\tau^\prime = C_4/T + C_1$$

(Fig. 7).

We can therefore compare the efficacy of (1) the dark-time fraction and (2) temperature in producing the same kind of shift in $\tau^\prime$. For a given change $\Delta \tau^\prime$ the necessary change in the dark-time percentage is a declining rectilinear function of the change in $1/T$ required to produce the same change in $\tau^\prime$. This is the kind of relationship to be expected if the percentage dark-time is proportional to the logarithm of a frequency. This could easily be the result if the dynamic equilibrium in percentage of non-refractory units is the outcome of opposed unlike processes respectively due to excitation and recovery of units in which the intrinsic excitability fluctuates.

The problem here can be phrased in a slightly different form. Suppose that the task had been set to ascertain the temperature characteristics of the percentage light-time required to produce constant performance in the visual reaction system of \textit{Pseudemys}. If the flicker response contour were to be used, a natural reference point would be the inflection of the curve. We could then measure at different temperatures the value of the light-time fraction required to activate 50 per cent of the elements at the same fixed value of log $I$. The calculation is easily made graphically, or numerically, on the basis that the slope of $\tau^\prime$ vs. $t_L$ in Fig. 5 is known to be the same at all temperatures. It is obvious that under these conditions the temperature characteristics for $t_L$ ($t_e + t_D$) at $F = 0.5 \ P_{\max}$ must be identical.

\(^{28}\) A more complete account of these questions will appear in another place; \textit{cf.} \(^{22}\), footnote 5; and \(^{8}\).
in magnitude with that for $1/I$ at any fixed $F$ and $t_L/t_D$, since the light-time ratio is clearly a logarithmic quantity.

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**SUMMARY**

For the turtle *Pseudemys scripta* the temperature characteristics for excitability of the response to visual flicker are found to be independent of flash frequency $F$, flash intensity $I$, and proportion of light time in the flash cycle. The maximum $F$ to which the flicker response contour ($F$ vs. log $I$) rises, and the abscissa of its inflection, are rectilinear functions of the percentage light-time in the flash cycle, but $\mu$ for $1/I$ at any flash frequency is the same with different values of the percentage light-time (10 to 90 per cent).

These facts, together with the properties of the variation of the critical intensity, objectively demonstrate the essentially simple or unitary character of the controlling events in the mechanism governing the excitability. They also provide a means of further illustrating a procedure whereby certain statistical factors in the performance of a population of units may be analytically separated from excitability properties common to all of the individual units. In particular, it is of general significance that it can be seen how it is possible for biologically exhibited frequencies or rates of performance to provide simple and physically significant relations to temperature, despite the fact that this performance may involve, almost inevitably does involve, the integrated actions of many individual units.