

TEMPERATURE AND CRITICAL ILLUMINATION FOR REACTION TO FLICKERING LIGHT

I. ANAX LARVAE

By W. J. CROZIER, ERNST WOLF, AND GERTRUD ZERRAHN-WOLF

(From the Biological Laboratories, Harvard University, Cambridge)

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I

Properties of measurements of the relationship between illumination and flicker frequency for response ("recognition of flicker") show that the theory of the relationship must be based upon something more than curves of critical frequency or of critical intensity. Such measurements are not adequately described by their average values.¹ The data really describe the probability that, with a given illumination (I) a certain flicker frequency (F_m) will be found, for a given organism; or conversely, with a given value of F , the probability that a certain critical illumination (I_m) will be found to obtain. The probabilities may be measured by the standard deviations of the observed values of F_1 or of I_1 . The indices of dispersion of the observations, with constant numbers of observations, are expressions of a property of the reacting system, and under suitable conditions are not in any sense measures of "experimental error" as ordinarily understood; their primary properties show them not to result from inadequacies or irregularities of technic or of observation. From a knowledge of (1) $I_m \pm \sigma_{I_1}$ as a function of F , the curve (2) of $F_m \pm \sigma_{F_1}$ as a function of I can be predicted in its essential differences from (1). The law connecting F and I for critical response is thus to be regarded not as a curve, but as a band defining a region within which there is a certain probability that observations of marginal recognition of flicker will occur. This band may not be very broad, so that it might be considered that a curve could be put through it which adequately char-

¹ Crozier (1935-36); Crozier, Wolf, and Zerrahn-Wolf (1936-37a, b).

acterizes the underlying processes responsible for the occurrence of response to flicker. The nature of σ_{r_1} and of σ_{r_2} as functions of I (or of F) makes it impossible, however, to employ the same method of determining an adequate fit of curve to data in the 2 cases (determinations of $F_m = \phi_1(I)$ and of $I_m = \phi_2(F)$, respectively); so a choice becomes arbitrary, and since a number of curves may be made to fit a given set of measurements equally well any final decision must rest upon the dimensional properties of the constants which the selected curve contains. This applies with the same force to equations derived from any relevant theory and to purely empirical curves.

Equations have been derived which describe with admirable formal fidelity the relationship between mean values of I_1 as a function of F (*cf.* Hecht, Schlaer, and Smith (1935)). We have found it necessary to inquire into this matter, because it is important for the theory which seeks to provide a generally applicable procedure for the unifying treatment of the data of sensory discrimination (Crozier (1935-36)). The position taken is that discrimination depends upon comparison of effects in two excited populations of nervous elements. These elements may be centrally situated or peripheral; presumably they are central, at least in the meaning that primary receptor cells are not immediately concerned in the comparison upon which the manifestation of response (reaction or recognition) rests. The comparison or competition which results in the signaling reaction is essentially upon a statistical basis and behaves as if dependent upon the standard deviations of the effects produced by these populations of elements. The two sets of effects may originate in two discrete sensory fields, or may correspond to successive states of the same peripheral field and its central nervous representation.

With flickered light, at the level of marginal recognition of flicker, a distinction is just made between the effects of light flashes and the effects associated with the alternating intervals in which no light is delivered (*cf.* Fick (1879); Grünbaum (1897-98)). We deal with cases in which the light and the dark interval are equal. In an interval of no light the after effect (positive after-image) of a flash decays. The rapid cycle of flashes and interruptions provides a large number of these intervals. Critical response to flicker involves marginal discrimination between the two "populations" of effects. The action of a

light flash, in terms of the effect produced as concerned in the determination of response, unquestionably fluctuates; it must be supposed that the after effect also fluctuates, in part independently. In this way it can be understood that I_m and σ_{I_1} , at various fixed levels of F , are rectilinearly proportional and depend upon phenomena of intensity discrimination (Crozier (1935-36)).

The equations describing flicker fusion as a function of intensity, for human visual effects, have approached the matter in another fashion, assuming that the critical frequency f is proportional to the concentration x of photoproduct at the steady state determined by the intensity I ; and that at flicker fusion the velocity of formation of x is balanced by the velocity of its "dark" removal. Hence

$$2Ik_1/k_2 = x^n/(a-x)^m = f^n/(f_{max} - f)^m, \quad (1)$$

where

- k_1 = velocity constant for photochemical production of x ,
- k_2 = velocity constant for thermal regeneration of photosensitive material from x ,
- m = order of the photochemical reaction,
- n = order of the dark process.
- m and $n = 2$ for human cones,
- $m = 2$ or 1 , $n = 1$ for human rods.

The descriptive adequacy of this conception for the human reactions (Hecht, Shlaer, and Smith (1935)) and for those of the fish *Lepomis* (Crozier, Wolf, and Zerrahn-Wolf (1936-37 b)), successful also in giving an explanation of the basis of Talbot's law (Hecht and Wolf (1931-32)), does not necessarily justify the assumptions leading to its derivation, as we have already pointed out (Crozier, Wolf, and Zerrahn-Wolf (1936-37 b)). When $n = m$, equation (1) is in fact identical in form with the logistic

$$F = \frac{F_{max.}}{1 + ce^{-z \log I}},$$

with $z = 0.5$ for $n = m = 2$; for $n = m = 1$, $z = 1.0$; for $m = 2$, $n = 1$, $c = 1/\sqrt{F}$ and the curve of F vs. $\log I$ is asymmetrical.

While this could be made consistent with the population notion, the significance of equation (1) must be determined by the

properties of its contained constants. The simplest test of their meaning is obtained by varying the temperature. In this case we must expect from (1) that since the temperature coefficient of k_1 must be small while the critical increment for k_2 should be large, the effect of lowering the temperature must be to decrease critical I if f is fixed and if f_{max} is not affected (Crozier, Wolf, and Zerrahn-Wolf (1936–37 b)). The actual result is quite the opposite. Moreover, if in a vertebrate the rod and cone portions of a flicker curve require different values of k_1/k_2 and of m and n , a change of temperature should not affect the two portions in the same way or to the same extent; but experiment shows us that they are affected in just the same degree.²

This experimental finding is readily reconciled with the intensity discrimination theory of recognition of flicker, and is indeed predicted by it. This interpretation also accounts rather fully for the phenomena of variation, which the customary method of treatment ignores completely or dismisses as an unfortunate concomitant of observation. As has been indicated, however, the variation of I_1 and of F_1 is an essential property of the reacting organism, and the lawful character of this capacity to exhibit variation in the magnitude of critical I_1 or

² In the formulation originally proposed (Hecht and Verrijp (1933–34)), where the case $m = 1$, $n = 2$ was discussed, the stationary state conception led to the expression

$$\frac{KI}{2c} = \frac{f}{\frac{a}{c} - \sqrt{f}},$$

where $K = k_1/k_2$, $a =$ total amount of photosensory material (100 per cent), $f =$ critical frequency, and $c = \sqrt{2c'/k_2}$, where $c' = \Delta x =$ the constant quantity of x involved in the fluctuation from dark to light at flicker fusion. This, rewritten, is

$$\frac{k_1 I}{\sqrt{8} c' k_2} = \frac{f}{\frac{\sqrt{a k_2}}{2c} - \sqrt{f}},$$

which gives an increase of I at constant f if the temperature falls; but it necessarily implies a value of f_{max} which is a function of temperature, for which there is no evidence. On the other hand, if c' is also taken as a function of temperature, f_{max} should still rise with rising temperature but one is further left in doubt as to the kind of function to assume for c' ; no definite prediction would be possible concerning the direction of change of I_m with change of temperature.

F_1 must be accounted for; after all, the dispersions of the measurements are one of their primary attributes—to ignore them is scarcely just, and may be simply willful.

We discuss first the relation between temperature and the shape and position of the curve for mean critical illumination as a function of flicker frequency with the larva of the dragonfly *Anax junius*. The measurements have been restricted to determinations of I_m and of σ_{I_1} ; we have earlier described the relation between these measurements and those of F_m and of σ_{F_1} as a function of I for these larvae, at one temperature, $21.5^\circ \pm 0.4^\circ$ (Crozier, Wolf, and Zerrahn-Wolf (1936–37 b)). The new determinations were made at $12.4^\circ \pm 0.4^\circ$ and at $27.3^\circ \pm 0.2^\circ$. Physical limitations precluded for the moment making concurrent determinations of F_m . Our main purpose was to investigate the change in position of the $F - I_m$ curve with altered temperature in an animal with which the complication of two sets of receptor elements (rods and cones) would not be encountered. The presumptive effect of the “mechanical disadvantage” of the marginal ommatidia of the eye in the reception of photic excitation (Crozier, Wolf, and Zerrahn-Wolf (1936–37 b)) should not in this respect interfere with simplicity of outcome, although it introduces complications in the use of equation (1) for this animal.

The results are also of interest as indicating how an obscure and peculiar relationship to temperature may be obtained in the case of a biological process the measurements of which are intrinsically complex from this standpoint and unsuitable for the determination of temperature characteristics (*cf.* Crozier (1935)). A subsequent paper contains the outcome of similar experiments with the sunfish *Lepomis* (*cf.* Wolf and Zerrahn-Wolf (1935–36 b); Crozier (1935–36); Crozier, Wolf, and Zerrahn-Wolf (1936–37 a)).

II

Procedure and technic have been described in our preceding papers (Wolf and Zerrahn-Wolf (1935–36 a, b); Crozier (1935–36); Crozier, Wolf, and Zerrahn-Wolf (1936–37a, b)). We have used the larvae of *Anax junius* employed in the earlier work (Crozier, Wolf, and Zerrahn-Wolf (1936–37b)). One of the 12 individuals used died at the beginning of this experiment. Another died in the course of it. The previous determination of the relationship between critical illumination (I_c) and critical flicker frequency (F_c) was made at temperature $21.5^\circ \pm 0.4^\circ$. At

fixed flicker frequencies (F) mean values of I_c , labelled I_m , were now found at $t = 12.4^\circ \pm 0.4^\circ$ and at $27.3^\circ \pm 0.2^\circ$. The average value of I_c was obtained for each larva from three readings of the intensity just required to force it to move with the direction of the system of revolving stripes; the mean of these values, I_1 , was then averaged for all individuals and recorded as I_m . P.E. _{I_1} is the P.E. of the dispersion of the individual values I_1 , and is independent of the number of individuals if this number is large enough and if the relative sensitivities of the individuals are distributed at random. The reasons for this procedure have been considered at some length (Crozier, Wolf, and Zerrahn-Wolf (1936-37b)).

The relative sensitivities of the larvae used are examined by considering their rank-order numbers in the various sets of measurements. The mean values for the 10 individuals used throughout the experiment are randomly distributed and have the same properties as in the series previously analyzed. Tests were made usually with two flicker frequencies on one day. The correlation between individual rank-order position class in the first of two such tests and the mean value of the rank position in the second test is of the sort already found in comparing sensitivities in successive determinations of relative sensitivity among larvae of one lot in which I_1 and F_1 were found on the same day (Crozier, Wolf, and Zerrahn-Wolf (1936-37b)). Rank-order positions on successive days show no correlation whatever, as found previously. We are justified in regarding the populations of I_1 at the various F 's as indicating fluctuations in a property of the reacting system responsible for the larva's reaction.

The larvae were kept at a desired temperature, for 27.3° , 0.5° above and for 12.4° , 0.5° below that at which a determination of I_m was to be made, in individual jars in a well regulated thermostat. With some control of the temperature of the dark room only a slight change of temperature occurred in a jar when it was placed upon the exposure stage of the apparatus for the length of time required for a measurement. This was ascertained by control runs in which the jar contained a thermometer. The series at 12.4° was run first, then that at 27.3° . These are at about the most extreme temperatures with which it is possible to obtain reliable results.

III

The data are collected in Table I. In Fig. 1 the curves of I_m as a function of F at $t^\circ = 12.4^\circ$ and 27.3° are compared with that gotten with these larvae at $t^\circ = 21.5^\circ$. It is to be noticed that points on the curve at 21.5° are repeatable after an interval of some weeks.

The data show, rather surprisingly, that the maximum flicker frequency, where the $F - I_m$ curve has flattened off, is independent of temperature. They also indicate that the intensity at which threshold response occurs is practically independent of temperature when maximum flicker frequency is attained.

The direction of the orderly shift in the $F - I_m$ curve with change of temperature is not that which the use of the stationary state equation calls for (*cf.* Crozier, Wolf, and Zerrahn-Wolf (1936-37 *b*)). The animal should be relatively in a more dark adapted state the higher the temperature, since it must be presumed that the temperature coefficient of the "dark" process, k_2 in equation (1), is greater than that for the photochemical velocity constant k_1 . Hence at given intensity I_m F should on this basis be found lower the higher the temperature; but

TABLE I

Mean critical illuminations at various frequencies of flicker (F), at three temperatures. *Anax* larvae. Each mean is derived from the average of three determinations on each of the same 12 or 10 larvae. (At 21.5° a number of values of I_m were determined at other frequencies; these are given in our preceding paper (Crozier, Wolf, and Zerrahn-Wolf (1936-37 *b*)) and are plotted in Fig. 1.)

F <i>per sec.</i>	log I_m , millilamberts, with log $P.E.I_1$					
	12.4° ± 0.4°		21.5° ± 0.4°		27.3° ± 0.2°	
2	4.8530	5.4433	4.5884	5.3209	4.4153	6.9744
5	3.5267	4.3462	3.3367	4.4797	3.0997	5.5904
10	2.1173	4.6830	3.8982	4.9282	3.7160	4.3111
16	2.5437	3.2573	2.2830	3.1593	2.0795	4.8849
25	2.8461	3.5250	2.6019	3.4682	2.4613	3.1790
35	1.0795	3.9446	2.8592	3.4166	2.6885	3.4732
45	1.3109	3.6035	1.0874	3.6669		
50	1.5417	2.4440	1.3438	2.0245	1.1501	3.7608
55	1.9751	2.6973	1.7356	2.4538		
60	0.6106	1.2586	0.5759	1.2390	0.5339	2.9784
61	1.8532	0.0738	1.8407	0.8341		

the reverse is true. From equation (1), moreover, if F_{max} is independent of I , then at fixed F , I must decrease when k_1/k_2 is increased by lowering the temperature. Since the shift is in the opposite direction the constant k_1/k_2 cannot have the meaning which equation (1) calls for. We have obtained a precisely similar result in experiments with the fish *Lepomis*, discussed in a following article. The finding has therefore an apparently general significance.

The shape of the $F - I_m$ curve is not greatly different at the several

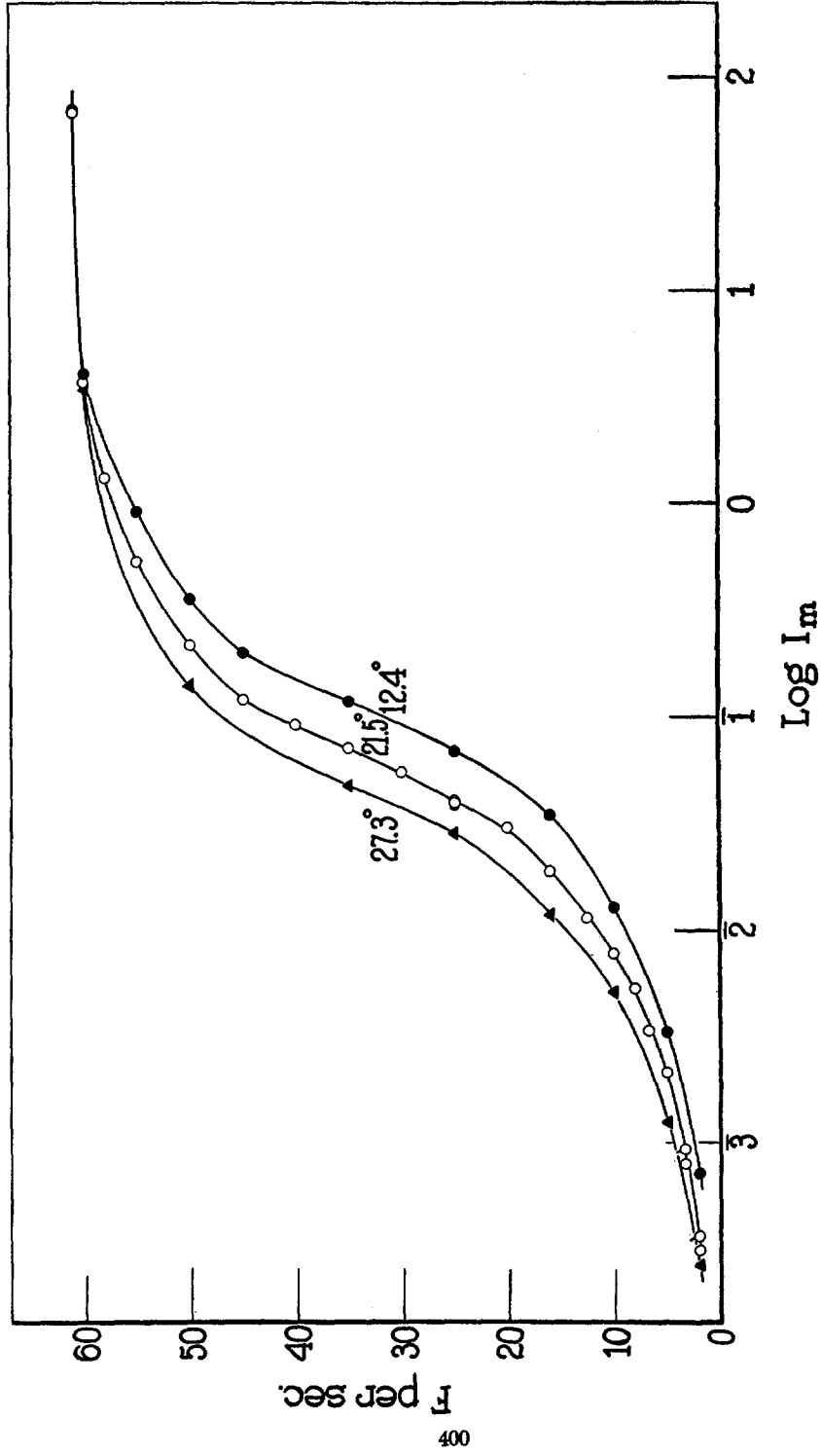


FIG. 1. Mean critical intensities for response of *Anax* larvae to flickering illumination, plotted as $\log I_m$, as a function of frequency of flicker (F), at three temperatures (Table I). Data for 21.5° taken from a preceding paper (Crozier, Wolf, and Zerrahn-Wolf (1936-37b)).

temperatures. Without undue violence to the data the portion of the curve from $F = 2$ to $F = 20 +$ may be regarded as rectilinear upon a logarithmic grid (Fig. 2); the slope is about the same at each temperature ($F = AI_m^{0.524}$). The small deviations from this rule, suggested by the continuous lines drawn through the plotted points, are conceivably consistent and are perhaps real. Above $F = 20$ the curvature is of a different sort and depends upon the temperature, being less

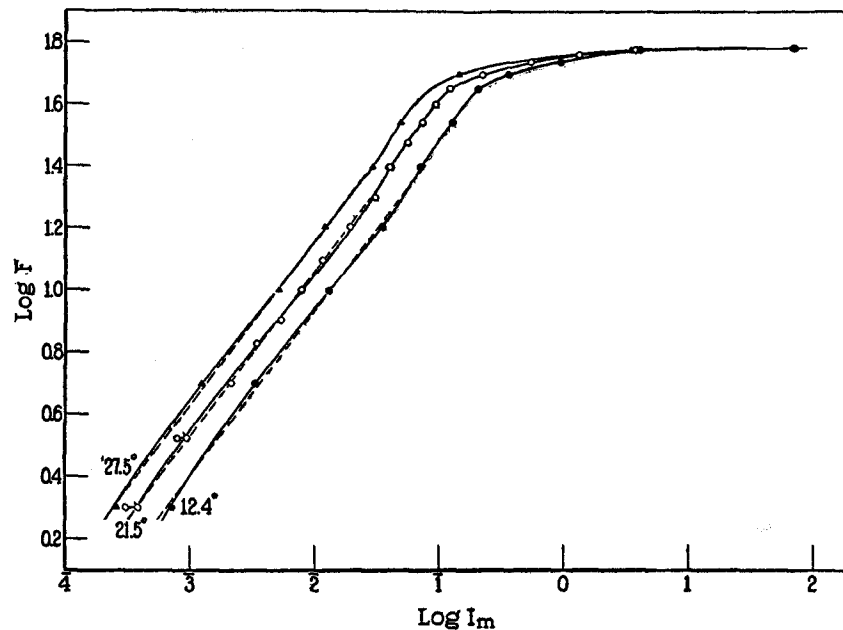


FIG. 2. $\log I_m$ as a function of $\log F$. The broken lines indicate that up to about $F = 25$ the data may be regarded as signifying that $d \log F / d \log I_m = 0.524$. As the continuous lines suggest, however, the deviations may be systematic. Above $F = 20$ the curvature depends on the temperature.

abrupt the lower the temperature. These relationships also appear when F is plotted against I arithmetically.

In the analysis of these effects it might be tempting to regard response at a fixed value of F as corresponding to a constant level of effect achieved by the stimulating agent. It is clear, however, that this is not permissible in any simple sense. The complexity of the matter is shown by the fact that the temperature coefficient of I_m is a

function of F above $F = 20$ and declines as F increases; below this level it is approximately constant, with an apparent temperature characteristic for $1/I_m$ of $\mu = 11,000$, but a value of μ for F at constant I is only 6,000. The temperature characteristic plot, moreover, is not rectilinear in any case, and the apparent temperature characteristic is a function of the temperature.

At constant I , F is increased as the temperature rises; the time required for a given intensity to build up an effect such that its decay in an equal period of no light is not detectable, is thus reduced. Similarly, at fixed F , I is reduced as the temperature is increased. But this is not to be taken as evidence that the effect produced by light of given intensity in a fixed time has an appreciably high temperature coefficient. The basis for a *detectable* difference between light flashes and intervals of no light is also a function of the temperature.

That up to $F = 25 \pm$, $d \log F/d \log I$ is approximately constant (Fig. 2), with the value 0.52, independent of temperature, follows simply from the fact that the logistic formulation of the curve (Crozier, Wolf, and Zerrahn-Wolf (1936-37b)) fails in this portion although approximately obeyed if $\left(\frac{100 F}{F_{\max.}}\right)^{0.5}$ be substituted for $100 F/F_{\max.}$.

This disturbance we have suggested as due to the fact that at low intensities, up to $F = 20$, within the time allowed for reaction to flicker according to the activity of the most effective ommatidia, the marginal ommatidia are perhaps at a disadvantage in the reception of light, owing to their angular separation (*cf.* Baldus (1926)). Increasing F and using the same criterion for the value of I_c results in using higher intensities; the assumption is that then the effective area of ommatidia involved in the threshold recognition of flicker is increased, because, even with the same duration of a flash, the higher intensity employed can act upon a sufficient number of ommatidia in such a way as to be significant for the determination of the response. For the portion of the flicker curve, then, for which $F = AI_m^{0.52}$, the value of A may well appear as a function of the temperature; it increases as the temperature falls, because the thresholds for photic excitation for the marginal and other ommatidia at fixed F presumably rise with lowering of temperature—since this must bring about a relative enhancement of the stationary state condition in terms of light adaptation.

The magnitude of $\frac{dI}{dF} = k \frac{F}{I}$ (Fig. 2) should be inversely proportional to I at constant F and independent of t° if the action of the light depends upon a purely photochemical effect.

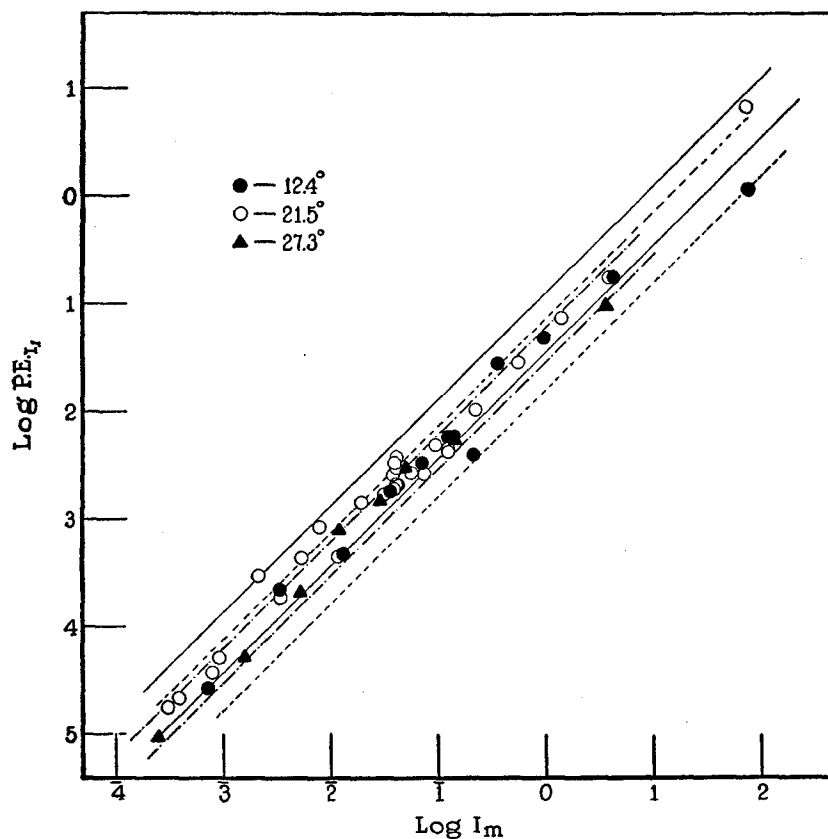


FIG. 3. The variation of I_1 , measured by $P.E.I_1$, is a rectilinear function of I_m at each temperature (the slope on the logarithmic grid = 1). The value of the constant B in $P.E.I_1 = BI_m$ changes slightly as the temperature is altered; this scatter of the determinations, which is proportional to $\sigma_{P.E.I_1}$, is discussed in the text.

IV

The variation of I_1 obeys the same general rules as in our earlier series. $P.E.I_1$ is a rectilinear function of I_m ; $\log P.E.I_1$ is a straight line

function of $\log I_m$, with a slope of 1 (Fig. 3). The value of B in the equation $P.E._{I_1} = BI_m$ depends to some extent upon the temperature; estimated from the lines of central $P.E._{I_1}$ at $\log I_m = 0$, B is 23.4 at 27.3° , 40.5 at 21.5° , 21.0 at 12.4° , and thus appears to go through a maximum at intermediate temperature. The spread of the values of $P.E._{I_1}$, estimated from the vertical widths of the bands in Fig. 3, is a measure proportional to $P.E.P.E._{I_1}$, and is thus equivalent to $a \frac{P.E._{I_1}}{\sqrt{n}}$ where a is a constant and n is the number of I_1 's (constant at each temperature). With correction for n , this spread has at $I_m = 1$ the

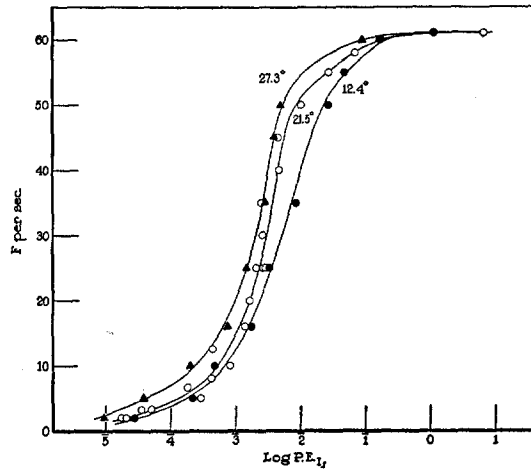


FIG. 4. $P.E._{I_1}$ as a function of F . See text.

approximate values 0.107 at 27.3° , 0.222 at 21.5° , 0.204 at 12.4° . The proportionality constant for the relation of $P.E.P.E._{I_1}$ to $P.E._{I_1}$ has therefore values in the ratios 4.22:8.99:2.52 at these temperatures. With all allowance for the difficulty of accurately determining the widths of the bands in Fig. 3 it is apparent that the "spread coefficient" is less at the highest and lowest temperatures. In consequence of this, $P.E._{I_1}$ is also an inverse function of temperature at constant flicker frequency (Fig. 4), but the displacement of the curve of $P.E._{I_1}$ vs. F with change of t° is not quite of the same form. In this respect also, then, the law of the connection between F and I_m is equally apparent in the relation of $P.E._{I_1}^f$ to F (Crozier (1935-36)).

In addition to demonstrating anew the lawful character of the variation in the determinations of I_1 the additional features suggested by the complex relationships to temperature will require consideration in any theoretical discussion of the basis for discrimination of flicker. This is reinforced by the fact that similar relationships appear also in our data on *Lepomis*.

We have already commented upon the fact that at higher intensities of illumination the sharper reactions of the animals do not reduce $P.E._{I_1}$ (Crozier, Wolf, and Zerrahn-Wolf (1936-37 *a, b*)). A similar conclusion is apparent from the examination of the data at high and low temperature. At any given intensity the movement of the larva which constitutes the threshold response is less sharp and easy to note promptly the lower the temperature; this is in no way correlated with the changes in $P.E._{I_1}$ at constant I . The relation $P.E._{I_1}$ to the 2 variables I and t° therefore gives no support to the idea that $P.E._{I_1}$ is an expression of "error of observation;" it is consistent with the idea that $P.E._{I_1}$ measures the fluctuating capacity of a larva to exhibit the discrimination of flicker, and that this fluctuating capacity is an elementary property of the mechanism of the discrimination.

V

The change in the curve of I_m as a function of F when the temperature is altered can be accounted for qualitatively on the basis that distinction of flicker requires a discrimination between (1) the effects of flashes and (2) the after effects consequent upon the action of these flashes. It cannot be accounted for quantitatively from the form of the $F-I_m$ curve alone, although progress in this direction can be made by taking into account the variation of I_1 ; additional information is required as to the effect of varying the proportion of "light time" to "dark time" in a flicker cycle, to be obtained in subsequent experiments.

We assume that the building up of the effect of a single flash of light does not occur instantaneously, but with a speed which is significant and is a function of I and of the level of light adaptation (*cf.* Bills (1920)); that the magnitude of the effect produced at the termination of the flash is essentially a function of the intensity and of the duration of the light period; and that the I process is primarily photochemical and has a small temperature coefficient. The after effect of a flash

is assumed to be the result of a "dark" process with typically large temperature coefficient for its velocity of decay (Fig. 5). It is not required at the moment to correlate these assumptions (Crozier, Wolf, and Zerrahn-Wolf (1936-37 *b*)) with the suggestive and presumably relevant observations on the building up and decay of retinal potentials, optic nerve discharges, and cortical potentials (*cf.* Adrian and Matthews (1928); Hartline (1925); Granit and Davis (1931); Granit

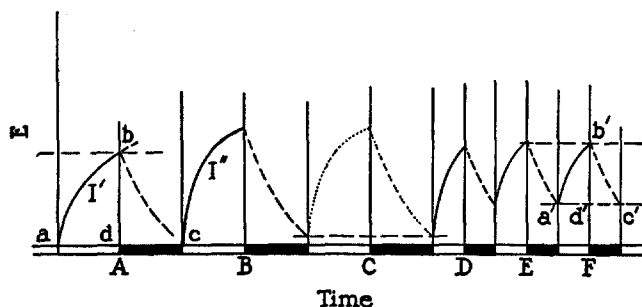


FIG. 5. When flicker is just recognized (*A*) the action of a flash (*a-d*) of intensity I' is represented by the curve *a-b*; (*a-d*) = $1/2 F$ seconds; *E* is a scale of effect produced. In the succeeding dark interval, of equal length, the effect at *b* decays. Recognition of flicker is assumed due to a certain proportionate difference between areas *a b d* and *b d c*. The curves *a b* and *b c* are assumed first order for convenience. If F is kept constant and I' is increased to I'' (*B*), a condition is attainable in which *E* fluctuates between the same levels (dotted lines, *C*), but only at the expense of a larger discrepancy between the "light" and "dark" areas—the flicker is more pronounced. This can be brought back to a condition of marginal response to flicker only by reducing $1/2 F$ —that is, by increasing F (as at *D*); when a new condition of balance is attained (at *F*) the same kind of difference between *a'b'd'* and *b'd'c'* can be established as in the base of *a b d* and *b d c* at *A*. This corresponds diagrammatically to the fact that as F is increased, I increases also.

(1935); Bartley (1934), etc.). The apparently fixed character of the maximum flicker frequency, and its comparative independence of intensity at different temperatures, presents a special problem. It is a curious fact that in various forms which have been investigated (man, *Lepomis*, bee, *Anax*) F_{max} has values which range only from about 50 to 61 per second. This suggests an interval of about 0.009 second as a general minimum time for photochemical action of a repeated flash permitting recognition of flicker when the light and dark

intervals are equal; above an intensity characteristic of the type of eye briefer flashes are not then reacted to as flickering. The value of F_{max} is, however, dependent upon the area of the flicker field on the retina (Hecht and Smith (1935)) and upon wave length (Hecht and Shlaer (1935)), so that interpretation in terms of anything resembling "implicit time" would appear to be quite dubious. Two additional assumptions are required for the formulation of a mechanism to account for the observed effects. These are (1) that the "after image

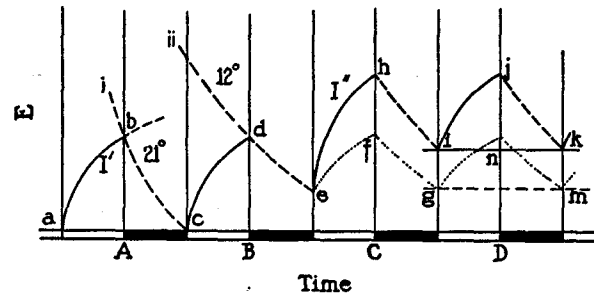


FIG. 6. At A a relation between I' and F is depicted, at a higher temperature, such that (cf. Fig. 5) flicker is just reacted to on the basis of the difference between the "light" area and the "dark" (as a function of the "light" area). The temperature is then lowered (at B); the velocity constant of the dark process governing the decay of E is then lowered, giving a curve of form ii in contrast to i ; keeping I' the same a new condition of constant rise and fall of E (dotted lines) can be attained (at D), but the areal difference is then insufficient for recognition of (reaction to) flicker. If, however, the intensity is increased to a value I'' (at C), a condition of balance is obtainable in which the difference between $ij n$ and $jn k$ is great enough, in terms of $ij k$, to permit recognition of the difference. (If I' were retained, the same result is to be obtained by lowering the flicker frequency.) These relationships are consistent with the experimental findings.

process" does not proceed during a light flash, but that its decay begins when delivery of light is interrupted, and (2) that for marginal recognition of flicker only the increase and decrease of effect are significant. These ideas are embodied in the diagrams given in Figs. 5 and 6. Fig. 5 shows how for marginal recognition of flicker on this basis, a balance between the effect of a flash (the area $a b d$) and the effect during the dark interval (area $d b c$) requires a certain difference between the two areas. We may consider that the difference should be a certain fraction of $a b d$. If now the intensity be increased from I' to I'' , the

areal difference at balance (C) will be too large, unless (at F) the flicker frequency is raised (time of a flash shortened). The curves are assumed to be first order, for simplicity; the rate constant for the I curve must be assumed less (in these cases only very slightly less) the higher the level of E , to account for the effect of the state of adaptation.

In Fig. 6 the effect of change of temperature is illustrated. There is necessarily demanded by this formulation an increase of intensity at constant flicker frequency if the temperature is lowered, if the average integrated effect of a flash is just to be distinguished from the average integrated after effect.

With higher intensity (and F), at fixed temperature, a given small change of intensity will produce a smaller absolute and relative change in the area $a b d$ (Fig. 5) and in the difference $(a b d) - (b d c)$; consequently a larger variation in I will be tolerated and will appear in the measurements.

When the temperature is lowered, at fixed F , I_m is higher. But the natural fluctuation in the decay constant of the after effect process will be expected to be less the lower the temperature—as measurements of velocities of biological processes as a function of temperature uniformly show (Crozier (1935)). Hence with fall of temperature we expect at constant I_m (and thus with falling F) that the tolerated variation of I_1 for recognition of flicker will pass through a maximum, as we have seen is indicated; with decreasing F (= increasing time of a flash), the area $a b d$ will increase, and a given change of I will produce a larger absolute effect; but as the temperature falls this will stand less and less chance of being cancelled by intrinsic variation in the velocity of the after effect decay.

It is not difficult, on this basis, to account for the behavior of $P.E._{F_1}$ as a function of I (Crozier, Wolf, and Zerrahn-Wolf (1936–37 *a, b*)); but this need not be gone into in detail here, since we do not yet have direct information as to the changes of $P.E._{F_1}$, as a function of I , as the temperature is altered. But we may point out that at fixed t° as I is increased, and F , $P.E._{F_1}$ passes through a maximum (Crozier, Wolf, and Zerrahn-Wolf (1936–37 *a, b*)); consequently a fixed deviation in F , δF , must be relatively constant in its effect in a mid-range of I and of F and must be of relatively greater consequence at the two ends; at high I and F (brief time) it should be easier to detect since it would

(in terms of its influence upon the area $a b d$ in Fig. 5) be more significant and less likely to have its effect cancelled by the action of spontaneous variation in the velocity constant of the light excitatory process, and at low I and F we should expect to find δF more influential owing to its there producing an effect comparable to slight change in I . With information to be obtained from experiments in which the proportion of light time to dark time in a cycle is varied, it should be possible to make a closer approximation to the forms of the curves in Figs. 5 and 6, and thus to account precisely for the variability relationships discovered.

V

SUMMARY

The curve of mean critical illumination (I_m) for response to flicker as a function of flicker frequency (F) for the larvae of the dragonfly *Anax junius* is progressively shifted toward higher intensities the lower the temperature. The maximum flicker frequency (one half the cycle time of light and no light) and the maximum intensity with which it is associated are very little if at all affected by change of temperature.

These facts are in agreement with the requirements of the conception that recognition of critical illumination for reaction to flicker involves and depends upon a kind of intensity discrimination, namely between the effects of flashes and the after effects of these flashes during the intervals of no light. The shift of the $F-I_m$ curve with change of temperature is quite inconsistent with the stationary state conception of the determination of the shape of the curve.

The dispersion (P.E. _{I_1}) of the measurements of I_1 is directly proportional to I_m , but the factor of proportionality is less at high and at low temperature than at an intermediate temperature; the scatter of the values of P.E. _{I_1} is also a function of the temperature. These facts can also be shown to be concordant with the intensity discrimination basis for marginal recognition of flicker.

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