

CRITICAL INTENSITY AND FLASH DURATION FOR RESPONSE TO FLICKER: WITH ANAX LARVAE

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(Accepted for publication, August 10, 1937)

I

To test the generality of the phenomena observed when the flicker response curve is obtained with differing proportions of light time to dark time in a flash cycle experiments were made with the larvae of *Anax junius* (dragonfly) in addition to those, already discussed, with the sunfish (Crozier, Wolf, and Zerrahn-Wolf, 1937-38*d*). The flicker curve ($F - \log I_m$) for *Anax* (1936-37*a, b*) is of special interest in that, while it is not complicated by the presence of two sorts of peripheral sensory elements, the convex surface of the eye mechanically introduces a distortion of the curve due to the comparative inefficiency of ommatidia at the margin of the eye (1937-38*b*). As a consequence, the probability integral which efficiently describes the flicker data in the case of vertebrates (1936-37*c*; 1937-38*a, c, d*; Crozier, 1937) is widely departed from by the *Anax* measurements at lower intensities. The discrepancy is explained by the results of blocking out parts of the eye (1937-38*b*). It was predicted that the departure from the probability integral would be reduced by increasing the proportion of light time to dark time t_L/t_D in a flicker cycle.

The procedure and apparatus have been described in the preceding papers. The *Anax* larvae used were of the same lot as those in our examination of the rôle of areas of eyes (1937-38*b*). Check experiments with $t_L/t_D = 1$, at 21.5° , gave close agreements in the values of I_m with those previously found under these conditions. The variation in I_1 agreed with that observed in other individuals of this group (1937-38*b*), but for both was lower than that in an earlier series (1936-37*b*). This is presumed due to differences in the groups of individuals.

The measurements are summarized in Table I and Fig. 1.

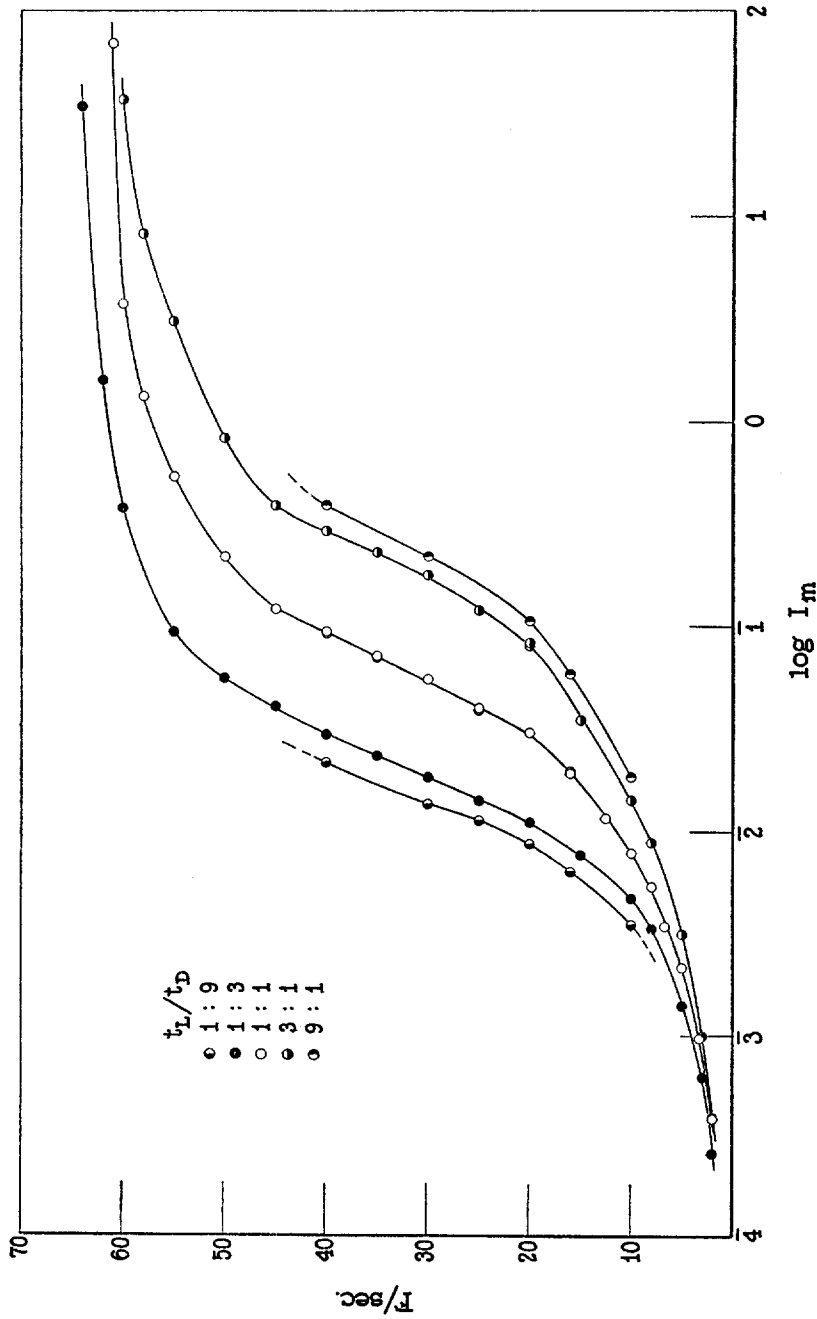


FIG. 1. Log I_m for response to flicker, as a function of flash frequency F , with different proportions of light time (t_L) to dark time (t_D) in a flash cycle, at 21.5° . Observations on larvae of *Anax* (data in Table I and, for $t_L/t_D = 1$, from Crozier, Wolf, and Zerrahn-Wolf, 1937-38). (Technical difficulties make it impossible to obtain complete curves for $t_L/t_D = 1/9$ and 9 ; consequently no values of F_{max} for these are estimated (cf. Figs. 2 and 3).)

II

Precisely as with the sunfish (1937-38*d*), increase in the light time fraction moves the flicker curve (Fig. 1) toward higher intensities and a

TABLE I

Mean critical illumination I_m in a flash and P.E._{1I₁} (millilamberts) as a function of flash frequency F per sec., for different percentages of light time (t_L) in a flash cycle, at 21.5°, for larvae of *Anax junius*. N = ten individuals, n = three observations on each, at every point. (Data on t_L = 50 per cent are given in Crozier, Wolf, and Zerrahn-Wolf, 1937-38*b*).

t_L , per cent	10		25		75		90	
	F /sec.	log I_m	log P.E. _{1I₁}	log I_m	log P.E. _{1I₁}	log I_m	log P.E. _{1I₁}	log I_m
2			$\bar{4}.4151$	$\bar{6}.9262$	$\bar{4}.5924$	$\bar{6}.8295$		
3			$\bar{4}.7950$	$\bar{5}.2716$	$\bar{4}.9997$	$\bar{5}.3510$		
5			$\bar{3}.1480$	$\bar{5}.5227$	$\bar{3}.4982$	$\bar{5}.9384$		
8			$\bar{3}.5233$	$\bar{4}.1065$	$\bar{3}.9451$	$\bar{4}.2405$		
10	$\bar{3}.5469$	$\bar{5}.8278$	$\bar{3}.6729$	$\bar{4}.2054$	$\bar{2}.1526$	$\bar{4}.7837$	$\bar{2}.2693$	$\bar{4}.8005$
15			$\bar{3}.8887$	$\bar{4}.3059$	$\bar{2}.5462$	$\bar{3}.1232$		
16	$\bar{3}.8064$	$\bar{4}.1433$					$\bar{2}.7697$	$\bar{4}.9593$
20	$\bar{3}.9454$	$\bar{4}.0409$	$\bar{2}.0500$	$\bar{4}.7641$	$\bar{2}.9219$	$\bar{3}.6695$	$\bar{1}.0290$	$\bar{3}.2700$
25	$\bar{2}.0680$	$\bar{4}.4736$	$\bar{2}.1535$	$\bar{4}.3479$	$\bar{2}.9069$	$\bar{3}.1232$		
30	$\bar{2}.1408$	$\bar{4}.4398$	$\bar{2}.2596$	$\bar{3}.1737$	$\bar{1}.0806$	$\bar{3}.2240$	$\bar{1}.3459$	$\bar{3}.8864$
35			$\bar{2}.3733$	$\bar{4}.9353$	$\bar{1}.2545$	$\bar{3}.6675$		
40	$\bar{2}.3434$	$\bar{4}.7634$	$\bar{2}.4765$	$\bar{3}.1222$	$\bar{1}.3659$	$\bar{3}.9155$	$\bar{1}.5036$	$\bar{2}.0622$
45			$\bar{2}.6129$	$\bar{3}.0641$	$\bar{1}.4695$	$\bar{3}.8191$		
50			$\bar{2}.7509$	$\bar{3}.2721$	$\bar{1}.5938$	$\bar{3}.9998$		
55			$\bar{2}.9779$	$\bar{3}.4729$	$\bar{1}.9201$	$\bar{2}.3090$		
58					0.4921	$\bar{2}.7746$		
60			$\bar{1}.5801$	$\bar{2}.1052$	0.9181	$\bar{1}.2591$		
62			0.2068	$\bar{2}.5982$	1.5704	0.4224		
63			1.5324	0.4835				

lower maximum.¹ The decrease in F_{max} is directly proportional to the increase in $t_L/(t_L + t_D)$, as seen in Fig. 2. The values given for

¹ In these experiments there is no sign of the effect found when two luminous intensities are flickered (as by reflection from light and dark sectors of a rotating surface). Under such conditions (Porter, 1898, *etc.*; cf. Piéron, 1935; Crozier, Wolf, and Zerrahn-Wolf, 1937-38*d*) F at fixed I in a flash passes through a maximum as t_L/t_D is increased. Apparently the same condition obtains with insects, for in tests involving the phototropic balancing of continuous light by a sectored

$F_{max.}$ are those found to give best rectilinearity of the upper parts of the curves upon a probability grid (Fig. 3). Accepting this formulation as fundamentally correct, and the departures at lower intensities as caused by mechanical disadvantage of the marginal retinal elements in the reception of light, the plots in Fig. 3 also show that the standard deviation of the $\log I$ distribution of $dF_p/d \log I$ is constant, where $F_p = 100 F/F_{max.}$ This is likewise true of the sunfish curves (1937-38*d*), and in each case is also found when temperature is varied (1936-37*b*; 1936-37*c*).

The intensity at the inflection of the ideal curve (straight lines in Fig. 3) is directly proportional (Fig. 8) to $t_L/(t_L + t_D)$, and conse-

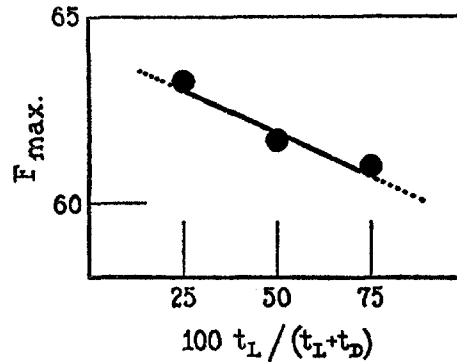


FIG. 2. $F_{max.}$ declines as percentage light time in the flash cycle is increased. (The rate of the decrease is less than with the sunfish (1937-38*d*).)

quently to $-F_{max.}$ (cf. Fig. 2). This again is found in the sunfish data.

The departure from a symmetrical curve for F vs. $\log I_m$ is clearly diminished as t_L/t_D is increased, as was predicted (1937-38*b*). With longer flashes, and higher mean flux of illumination at a given F , the chance of adequately involving disadvantaged ommatidia is naturally greater, although with larger t_L/t_D the frequency with which each of

beam of the same I the data of Mast and Dolley (1924) clearly show that F at the point of equivalence of the two beams passes through a maximum. The elaboration of experiments of this type holds the possibility of really deciding whether the events determining the form of the flicker function are primarily peripheral or central.

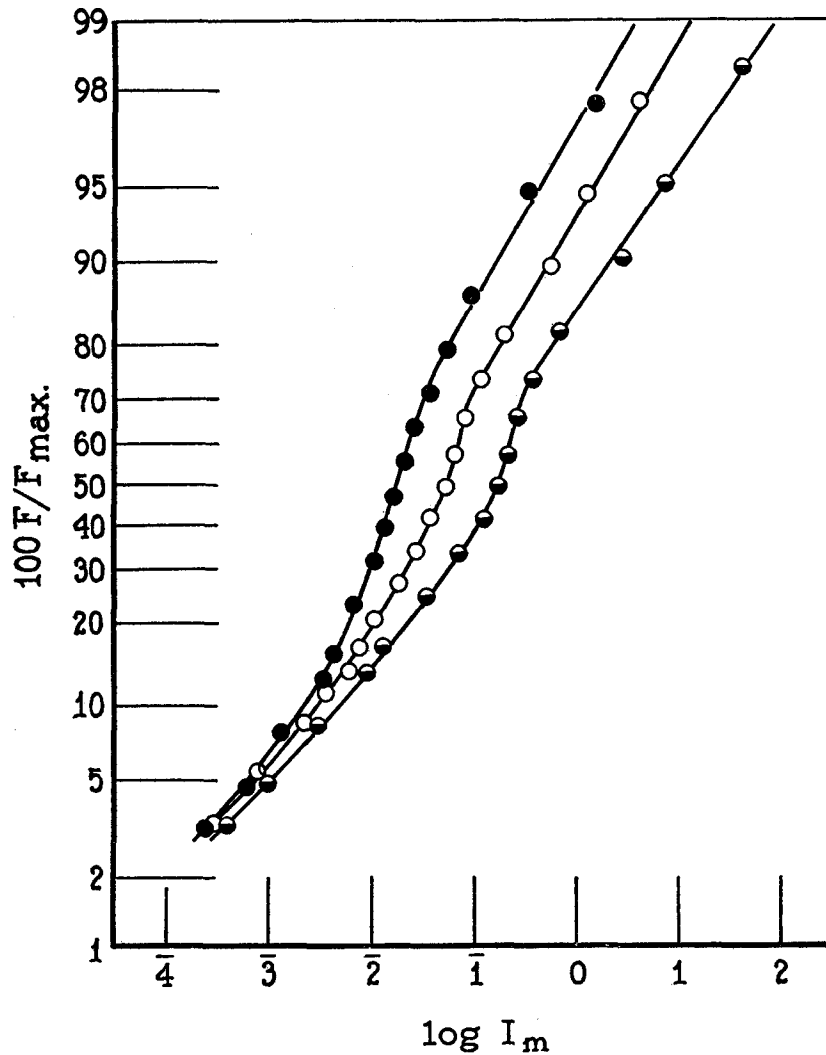


FIG. 3. $\log I_m$ vs. F on a probability integral grid ($F = 100 F/F_{max}$). The departure from rectilinearity, over the lower range of intensities increases as the proportion of light time is made larger. See text, and also Fig. 4.

these can be effectively excited is decreased. Thus while with the sunfish the shape of each part of the flicker curve is independent of t_L/t_D , a real change in shape is produced with $Anax$ (Fig. 4) in the

lower two-thirds of the curve. The maximum is not affected by this easier recruitment of peripheral units, because in any case the total of the potentially available elements is open to excitation long before F_{max} is reached.

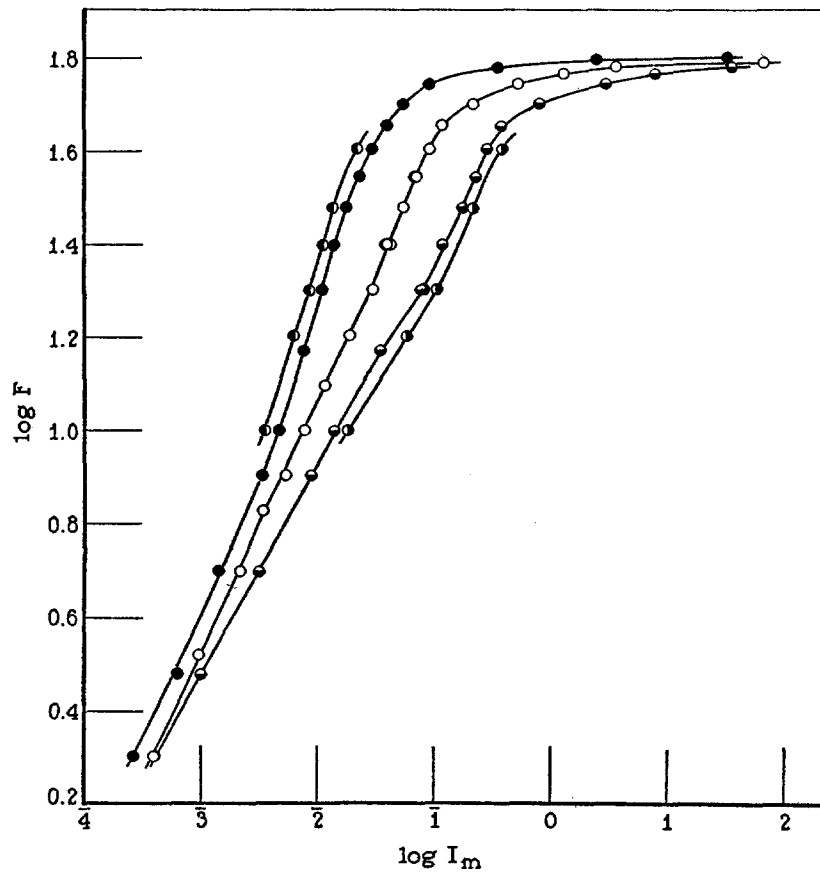


FIG. 4. $\log I_m$ vs. $\log F$, for different proportions of light time to dark time in a flash cycle, to show comparative shapes of the flicker contours.

The measurements with the sunfish showed that the direct proportionality between I_m and $P.E._{I_1}$ was identical at the various t_L/t_D ratios. Fig. 5 demonstrates that the rule holds for *Anax* as well.

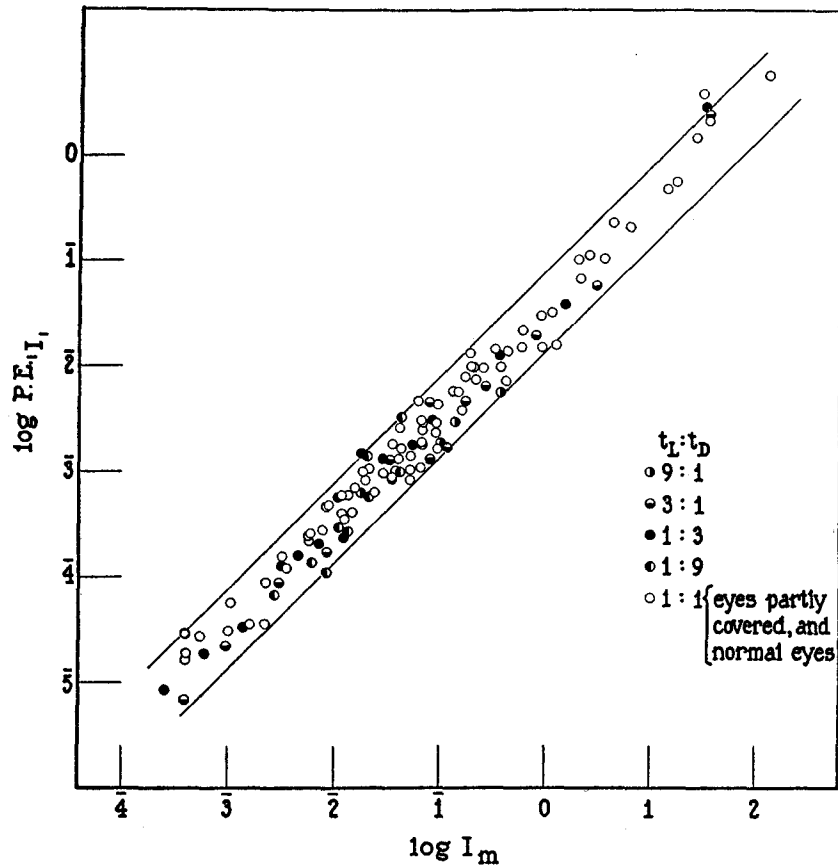


FIG. 5. The variation of I_1 (as $P.E._{I_1}$) and I_m are directly proportional (slope on log grid = 1). The proportionality constant is independent of visual area (open circlets, data in Crozier, Wolf, and Zerrahn-Wolf, 1937-38b) and of t_L/t_D (Table I).

III

The basic features of the flicker curve, as described by the parameters of a probability integral, are thus identical in their behavior with respect to changes in the ratio of light time to dark time in the two very different animals, sunfish and *Anax* larva. The different behavior of these parameters with reference to temperature is also

the same in both. A similar explanation may therefore be advanced in each case (1937-38*d*). It is based merely upon the dynamical properties of the behavior which has provided the measurements. These properties are defined by their quantitative relations to the experimental variables. Their meaning apparently is that F corresponds to a summated number of elemental effects, normally distributed as a function of $\log I$. Each I_m is the mean intensity required to produce this summation for a particular F , its variation (P.E. _{I}) is the intensity fluctuation corresponding to the natural fluctuation in excitability, which at each critical F is also measured by the ordinate $dF/d \log I$ since the number of elements in effective fluctuation will be proportional to the mean number marginally excited (1937-38*a*). The natural cycle of fluctuation in the excitability of each element is to be pictured as a relaxation-oscillation (*cf.* Hoagland, 1935) not affected by temperature, although the amount of excitation required for the response is increased by raising the temperature (1936-37*c*), so that F_{max} is unaffected. By shortening the time during which the light acts, in a cycle of fixed duration, it is possible for a succession of the flashes to act upon a larger number of elements before a magnitude of total summated effect is produced which will lead to forced recognition of flicker. F_{max} is then increased, in simple proportion to the percentage shortening of the light time (Fig. 2), because the succession of briefer flashes and longer dark times enables more elements to be "caught" in an excitable state, just as with larger visual areas. Since on this basis the same or additional elements of the same mean excitability can contribute more frequently to the summation required for critical F , $\log I_m$ at the inflection point ($= \tau'$) should decrease, but $\sigma_{\log I}$ should be the same (for a homogeneous receptor field). The frequency distribution, with area at 100 per cent, is merely moved to a lower position on the $\log I$ scale. These are the relations as found.

By comparison with the flicker curves for fishes (1937-38*a*) and for man (1937-38*c*) that for *Anax* is distinctly of an aberrant form. Such cases provide a valuable test of the general analysis, when the reasons for the unusual or less simple structure of the curve can be specified. For *Anax* this can be done, and in terms which are consistent with data on the visual performance of other arthropods

(1937-38*b*). The present results are in keeping with this. They indicate clearly that if t_L/t_D were to be reduced much below $1/9$ an even greater departure from the probability integral should be ex-

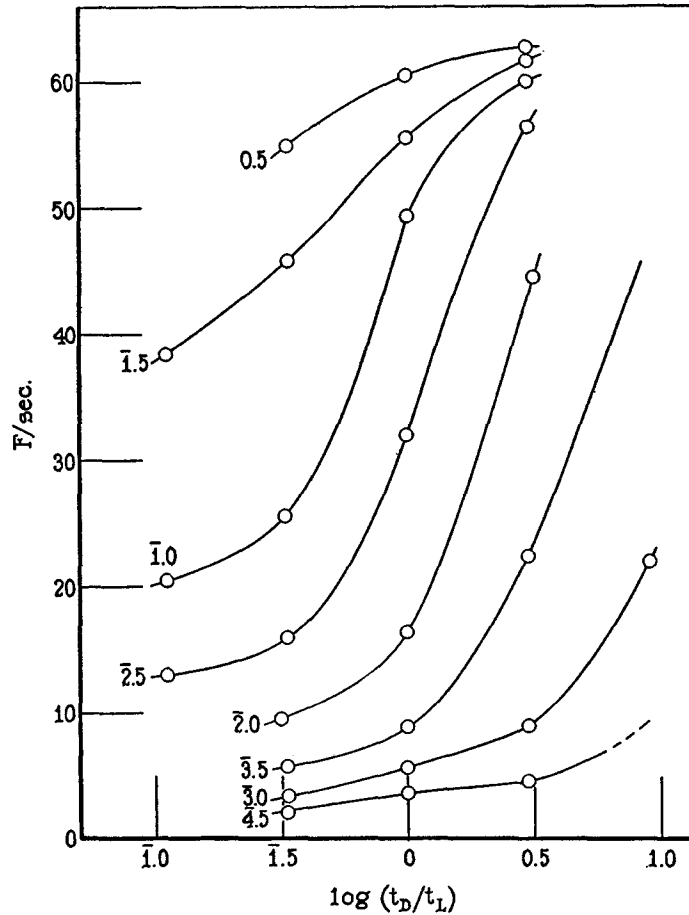


FIG. 6. F vs. $\log (t_D/t_L)$, for various values of $\log I_m$, as obtained from Fig. 1. For high values of F direct proportionality is more nearly approached. (This is also observed if calculations are made on the basis of I_{eq} , the mean equivalent flux of illumination at the point of the response.)

pected in the case of an arthropod with greatly convex eyes. This condition was employed by Sälzle (1932), and his flicker curve for *Aeschna* larvae is much more asymmetrical than any of ours (*i.e.*, the departure is greater).

This view obviously requires that changes of temperature should not modify the shape of the discrepancy in the *Anax* flicker curve, any more than they affect F_{max} . In fact on a probability grid the shape

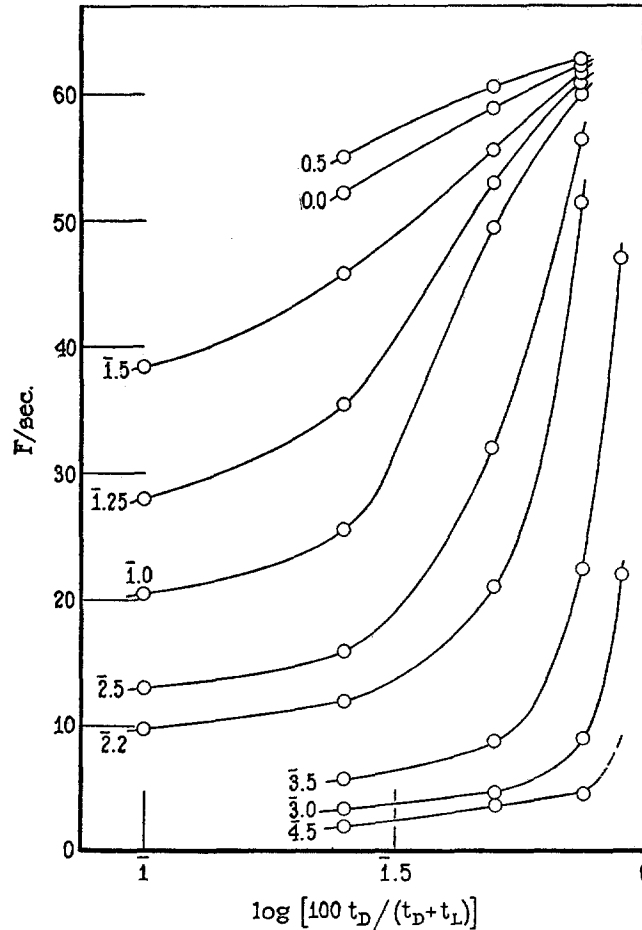


FIG. 7. F at different values of I_{eq} , as a function of the percentage dark time in the flash cycle.

is identical from 12.4° to 27.3° . Increasing t_L/t_D , however, decreases the discrepancy and lowers F_{max} . It is clear that conditions immediately affecting the reception of light (t_L/t_D , area) have a recognizably different effect upon the flicker curve than those primarily modifying

the central nervous mechanism of intensive discrimination (as, temperature).

Neither the curves for sunfish nor for *Anax* obey the rules which have been suggested for somewhat similar (but less complete) experiments with man. F at fixed I is not directly proportional to $\log(t_D/t_L)$ (Fig. 6) but follows a curve which is dependent upon the magni-

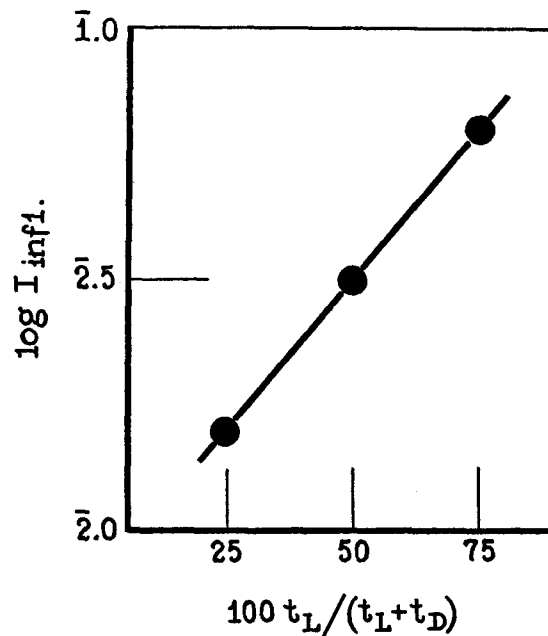


FIG. 8. For *Anax* larvae, as for the sunfish (1937-38*d*) $\log I$ at the inflection point of the flicker contour ($= \tau'$ in Fig. 3) is directly proportional to the percentage light time in the flash cycle.

tude of I . There is no clearer case to be made out if comparisons are made on the basis of $I_{eq.}$, the mean equivalent flux of illumination (Fig. 7). Talbot's law cannot be used to bring the several curves in Fig. 1 into coincidence. The simplest general fact of the situation, cleared of the structural complications, is that τ' , the $\log I$ at inflection of the ideal probability curve (Fig. 8), varies directly as the fraction of the cycle time occupied by light.

SUMMARY

Determinations of the flicker response curve ($F - \log I_m$) with larvae of *Anax junius* (dragonfly) for various ratios t_L/t_D of light time to dark time in a flash cycle provide relations between t_L/t_D and the parameters of the probability integral fundamentally describing the $F - \log I$ function, including the variability of I . These relations are quantitatively of the same form as those found for this function in the sunfish, and are therefore non-specific. Their meaning for the theory of reaction to visual flicker is discussed. The asymmetry of the *Anax* curve, resulting from mechanical conditions affecting the reception of light by the arthropod eye, is (as predicted) reduced by relative lengthening of the fractional light time in a cycle.

CITATIONS

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