

CRITICAL ILLUMINATION AND FLICKER FREQUENCY,  
AS A FUNCTION OF FLASH DURATION: FOR THE  
SUNFISH

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I

Interest of several kinds attaches to observations in which the relations of critical illumination ( $I$ ) and critical frequency of flashes ( $F$ ) for response to visual flicker are determined with varying proportions of light time to dark time ( $t_L/t_D$ ) in a flash cycle. Data of this kind should provide an important test of theories of visual flicker. The majority of reported experiments have employed a flicker cycle in which  $t_L = t_D$  (*i.e.*, 50 per cent dark time). Measurements with  $t_L/t_D$  varied have given results which are to first inspection strangely contradictory. Porter (1902) and Ives and Kingsbury (1916) found for the human subject that with constant intensity in a flash while  $t_L/t_D$  was varied, the critical fusion frequency  $f$  passed through a maximum at or near  $t_L/t_D = 1$ . Hecht and Verrijp (1933-34) were able to give an equation requiring this effect on the basis of the general equation proposed (Hecht and Wolf, 1932-33) for Talbot's law, which accordingly became a test for the theory of the flicker curve obtained on the basis of that equation.

On the other hand it has been known for some time (*cf.* Piéron, 1922) that if observations are made by a method in which flashing is produced by the interruption of a beam of light, rather than by viewing a surface part white and part black upon which light falls, as in the experiments of Porter and of Ives and Kingsbury, the increase of  $t_L/t_D$  is accompanied by a progressive increase in  $f$ ; the curve does not go through a maximum (Ives, 1922; Piéron, 1935). Moreover (Cobb, 1934), for "constant brightness at fusion"  $f$  de-

clines as  $t_L/t_D$  is increased, and for higher values of the ratio (and of  $I$ ) falls rapidly (*cf.* also Piéron, 1928). These curves cannot be derived from the mechanism proposed on the basis of the theory that the data are primarily determined by the photochemistry of the retina (Hecht and Verrijp, 1933; 1933-34; Hecht, Shlaer, and Smith, 1935). The difference is presumably due to the effect of reflection from the "black" portion of the sector disc. If this is correct, an adequate theory of the flicker function is required to account for (1) the increasing value of  $f$  as  $t_L/t_D$  is increased, with  $I$  constant, when flicker is produced by periodic cutting-off of light; and (2) the increase and decrease of  $f$  when  $t_D$  really represents time during which a lower intensity of light is acting, so that we have to do with cycles characterized by  $t_{I_1}/t_{I_2}$ .

From the standpoint of what may be called the intensity-discrimination theory of the marginal recognition of flicker (Crozier, 1935-36; Crozier, Wolf, and Zerrahn-Wolf, 1936-37*c, d*) the mechanisms in these two cases should differ significantly. When  $I_1$  and  $I_2$  are measurable intensities, and by reflection from a sector disc  $I_2 = k I_1$ , the conditions for discrimination are not those which prevail when  $I_2 = 0$ . The curve of  $I_c = \theta(f)$  is of the same form as that for  $I_c = \theta'(F)$ , as attested by experiments with the human eye in which  $t_L/t_D = 1$  (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 *b*).

Qualitatively it could be expected as reasonable, if the kinetics of light adaptation and dark adaptation, as directly measured, are immediately concerned in the determination of the flicker intensity contour, that raising the temperature and increasing the proportion of dark time in a flicker cycle should have the same direction of effect. For a given energy of flash, the extent of dark adaptation should be increased at a fixed  $F$ , and  $I_c$  could then be smaller. The detailed comparison of the  $F-I$  contours obtained with temperature and  $t_L/t_D$  as parameters permits the evaluation of this notion. It also tests the idea that Talbot's law really has anything to say about the properties of  $I$  and  $t$  for marginal flicker.

Observations at various temperatures have been made with lower animals, by a technique which when used with human observers gives the well known properties of the flicker curve (Crozier, Wolf, and Zerrahn-Wolf, 1936-37*c, d*; 1937-38 *b*). The same procedure is

easily adapted for experiments in which the ratio  $t_L/t_D$  is varied. The present paper deals with our experiments on the sunfish *Enneacanthus gloriosus*.

## II

The apparatus is essentially a glass cylinder with black and transparent alternating stripes (Wolf and Zerrahn-Wolf, 1935-36; Crozier, Wolf, and Zerrahn-Wolf, 1936-37*a*; 1937-38*a*). The cylinder encloses a small aquarium containing the reacting animal, is evenly illuminated from outside, and is rotated at a known speed. The number and the widths of the opaque stripes can be such that any desired proportion of light time to dark time is obtainable in a cycle passing a given point at the cylinder wall. It is not practicable to have  $t_L/t_D$  less than 0.1 or greater than 0.9, owing to mechanical difficulties in the precise adjustment of very narrow stripes.

The responses of the fishes have been discussed in preceding papers (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1937-38*a*, and earlier articles there cited). Ten individuals were used throughout the present series of observations. The method of treatment of the data has been described in the previous papers: three successive measurements of  $I_c$  with each individual are averaged to give  $I_1$ ; the mean of these ten =  $I_m$ ; P.E. <sub>$I_1$</sub>  is the P.E. of the dispersion of the ten. The  $t_L/t_D$  ratios used were 0.10, 0.25, 0.50, 0.75, and 0.90. At 0.50 a sufficient number of determinations were made to show that the sunfish of the present lot gave values of  $I_m$  very closely agreeing with those obtained from previous lots at the same temperature (21.5°). In Table I the entries under  $t_L/t_D$  not in bold-face type are taken from earlier papers. The variation of  $I_1$  is discussed in Section IV. The observations at each value of  $t_L/t_D$  were taken in one series. The same ten individuals were used throughout. No progressive changes in sensitivity were detectable.

Careful examination has shown that in the new series of measurements, as in the older sets, the behavior of  $\sigma_{I_1}$  is of a uniform nature: the between-animal variation, except at the very highest flash frequencies, exceeds the within-animal; the relative sensitivities of the ten fishes fluctuate at random from one set of readings to another. The graph of  $\log \text{P.E.}_{I_1}$  vs.  $\log I_m$  breaks at about the point where the declining rod function fades out; beyond this intensity the data can still be described as  $\sigma_{I_1}$  and  $I_m$  in direct proportion, but with a new origin (Crozier, 1935-36).

The absolute values of P.E. <sub>$I_1$</sub> , however, are *lower* than in our previous series at this temperature (21.5°). The reasons for this are unknown, but are probably found in the differences between the lots of sunfish. In Fig. 13 only the new data for  $t_L/t_D = 1$  are plotted (*cf.* Table I).

The device producing flicker has one theoretical defect: the inner face of each opaque stripe receives light from the transparent bars on the opposite side of the cylinder. The reflection coefficient of the flat-black paper is small, and the results demonstrate that under our conditions  $F$  does *not* go through a maximum as

TABLE I

$I_m$  (millilamberts) and P.E. $_{I_1}$ , as  $\log_{10} I$ , at different flash frequencies  $F$ , for various percentages of light time ( $t_L$ ) in a flicker cycle. Observations on the sunfish *Enneacanthus gloriosus*, at 21.5°. The  $\log I_m$  figures not in bold-faced type are from earlier experiments (Wolf and Zerrahn-Wolf, 1935-36; Crozier, Wolf, and Zerrahn-Wolf, 1936-37 a, d); for these,  $N = 12$  individuals,  $n = 3$  observations on each at each  $F$ . For the newer data (bold-faced),  $N = 10$ ,  $n = 3$ .

$t_L$ per cent	10		25		50		75		90	
	$\log I_m$	$\log$ P.E. $_{I_1}$	$\log I_m$	$\log$ P.E. $_{I_1}$	$\log I_m$	$\log$ P.E. $_{I_1}$	$\log I_m$	$\log$ P.E. $_{I_1}$	$\log I_m$	$\log$ P.E. $_{I_1}$
2							<b>7.7013</b>	8.4072	<b>7.9718</b>	8.4387
3			<b>7.5702</b>	8.4620	7.6555	8.8414	<b>6.0795</b>	8.7095	<b>6.3418</b>	8.6626
4			<b>7.7827</b>	8.3510	6.1784 <b>6.1735</b>	8.716 8.6610	<b>6.5971</b>	8.9070	<b>6.8577</b>	7.0827
5	<b>7.8308</b>	8.5348	<b>7.9616</b>	8.4294	6.3701	7.6010	<b>6.8326</b>	7.2014	<b>5.0892</b>	7.6229
6	6.9900 <b>6.5630</b>	7.1655 7.0445	<b>6.7816</b>	7.3249	5.2385 <b>5.2423</b>	6.4814 7.6163	<b>6.6573</b>	7.9987	<b>5.9262</b>	6.1052
7	<b>6.5327</b>	6.0983	<b>5.7569</b>	6.1436	4.1855	5.4456	<b>4.6172</b>	6.9682	<b>4.8685</b>	5.3430
8	<b>4.3877</b>	6.9813	<b>4.5210</b>	6.8914	4.9954 <b>4.9848</b>	4.2788 5.3952	<b>3.4002</b>	5.8909	<b>3.6690</b>	4.0378
9	<b>3.1744</b>	5.7345	<b>3.3708</b>	5.9442	3.7983	3.0934	<b>2.1967</b>	4.3681	<b>2.4501</b>	4.7668
10	<b>3.9263</b> <b>3.8736</b>	4.3495 4.2266	<b>2.0878</b>	4.6497	<b>2.6625</b> 2.5600	4.9225 3.8710	<b>2.9751</b>	3.2100	<b>1.2442</b>	3.7251
15	<b>2.2312</b>	4.9235	<b>2.5009</b>	3.2060	<b>2.9446</b> <b>2.9403</b> 2.9543	3.4175 3.3581 2.1004	<b>1.3768</b>	3.7309	<b>1.6314</b>	2.0934
20	<b>2.4935</b>	3.1380	<b>2.8211</b>	3.0342	1.2591	2.2480	<b>1.6739</b>	2.0390	<b>1.9080</b>	2.3130
25	<b>2.7090</b>	3.3662	<b>1.1017</b>	3.7359	1.5631 <b>1.5566</b>	2.7993 3.8779	<b>1.9696</b>	2.2721	<b>1.2180</b>	2.8904
30	<b>2.9588</b>	3.6142	<b>1.3870</b>	3.9046	1.8118	2.8639	<b>0.2405</b>	2.7498	<b>0.5254</b>	2.8024
35	1.2458 <b>1.2405</b>	3.7615 3.6220	<b>1.7123</b>	2.2949	0.1418	1.1106	<b>0.5537</b>	2.9262	<b>0.8751</b>	1.2978
40	1.6123 <b>1.5733</b>	2.2438 2.0874	<b>0.0173</b>	2.6572	0.4601	1.4487	<b>0.8733</b>	1.3724	<b>1.3055</b>	1.6356
45			<b>0.3714</b>	2.7937	1.0465	1.6180	<b>1.4486</b>	0.1038		
47							<b>2.2660</b>	0.3845		
50			<b>0.9297</b>	1.5120	2.2264	1.0618				
53			<b>2.2927</b>	0.4964						

$t_L/t_D$  is varied with  $I$  fixed. Hence the analysis of the flicker function can proceed without reference to this complication. This is true in our experiments with insects as well as for the sunfish.

## III

The observations are summarized in Table I. It is apparent that for a given  $F$  the intensity of a flash required for response *decreases* continuously as the flash duration is made less and the dark interval accordingly greater. At fixed intensity,  $F$  increases as  $t_L/t_D$  becomes smaller, and the maximum to which  $F$  rises is found to increase.

In Fig. 1  $\log I_m$  is plotted as a function of  $F$ . The whole curve is shifted to lower intensities with decrease of  $t_L/t_D$ , and the maximum rises slightly. The curves show the features of structure already seen for  $t_L/t_D = 1$  (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*; 1937-38 *a*). The *form* of the curve is not affected. Fig. 2 demonstrates that the cone portion of each graph is accurately described by a probability integral. This is also true for the rod sections (Fig. 3). The limitations of the apparatus are such that intensities greater than antilog 2.3 cannot be obtained, and on the other hand flash frequencies above  $F = 40$  could not be produced with adequate precision for  $t_L/t_D = 0.10$  or 0.90. Below  $\log I = 7.5$  the animals cannot be clearly enough seen in the apparatus to observe their movements accurately. The curves are therefore incomplete in these respects. By trial, however, values of  $F_{max.}$  are found for the cone parts which give an adequate description of the data (Fig. 2). The further properties of the parameters of these descriptions give a sufficient justification for the procedure. A striking feature is that on the probability grid (with  $F$  as per cent  $F_{max.}$ ) the slopes of the lines for the cone contribution are independent of  $t_L/t_D$ , and for the rod part also (Figs. 2 and 3). From the standpoint that  $dF/d \log I$  vs.  $\log I$  represents a frequency distribution, this means that  $\sigma'_{\log I}$  is independent of  $t_L/t_D$ , as it is of temperature (1936-37 *d*). In Fig. 4 the graphs of Fig. 2 have been moved on the  $\log I$  axis so as to coincide at  $F = 0.5 F_{max.}$  (*i.e.*, each value of  $I_m$  has been multiplied by a constant for each  $t_L/t_D$ ); the points form a band of statistically constant width on the  $\log I$  axis. The same procedure applied to the rod portions of the data is shown in Fig. 5; here the *relative* departures of the points are greater on the  $F$  axis, although their absolute magnitudes are no greater (the maximum departure in Fig. 5 is equivalent to 0.63  $F/sec.$ ) since the  $F$  scale is magnified about seven times by comparison with that in Fig. 4.

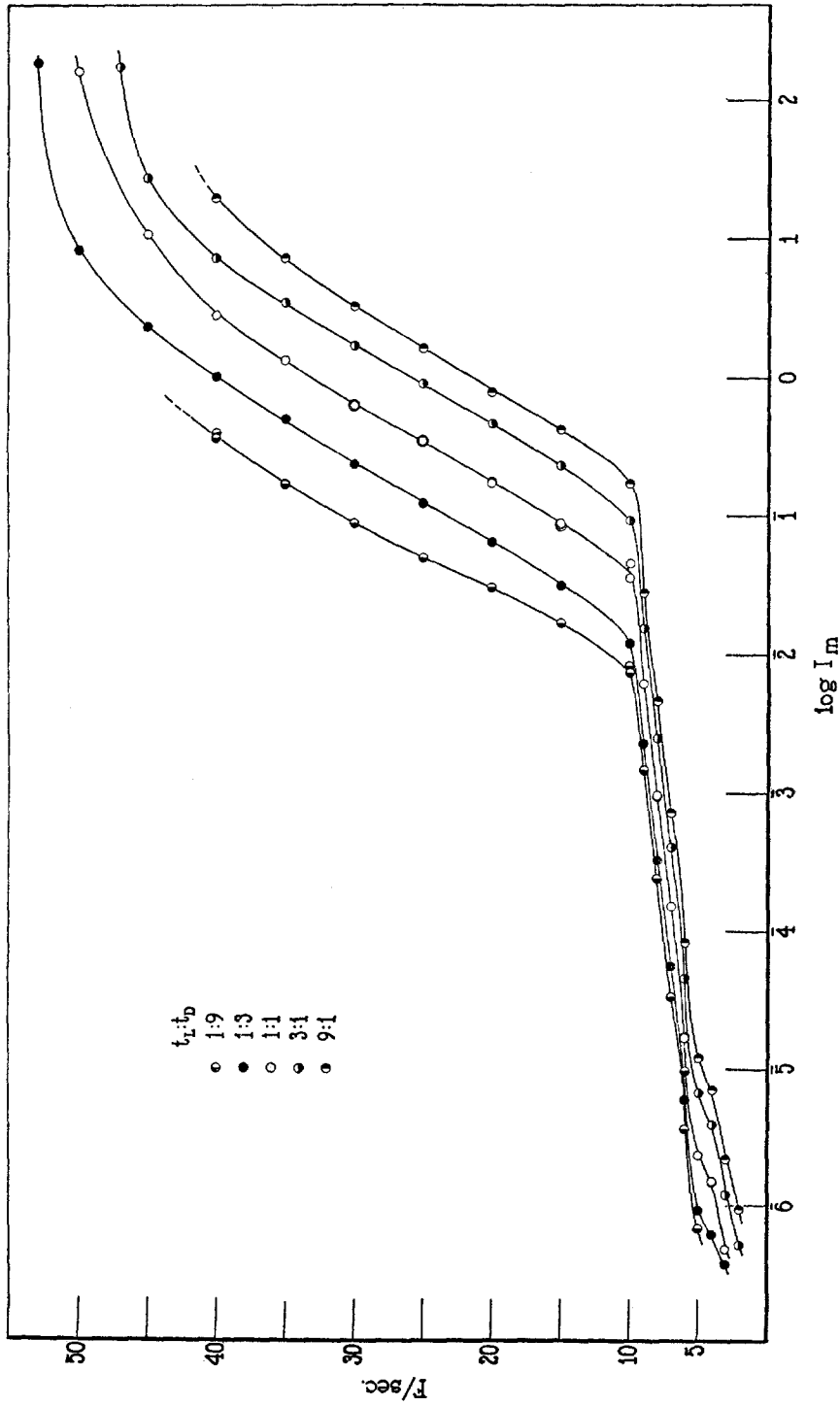


Fig. 1. Flash frequency and  $\log I_m$  for various percentages of light time in a cycle, increasing from left to right. Data on the sunfish *Emmeacanthus* (Table I).

The description of the  $F - \log I$  curve by means of a probability integral (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*; 1937-38 *a, c*; 1937; Crozier, 1937) has shown (1) that this function is adhered to by

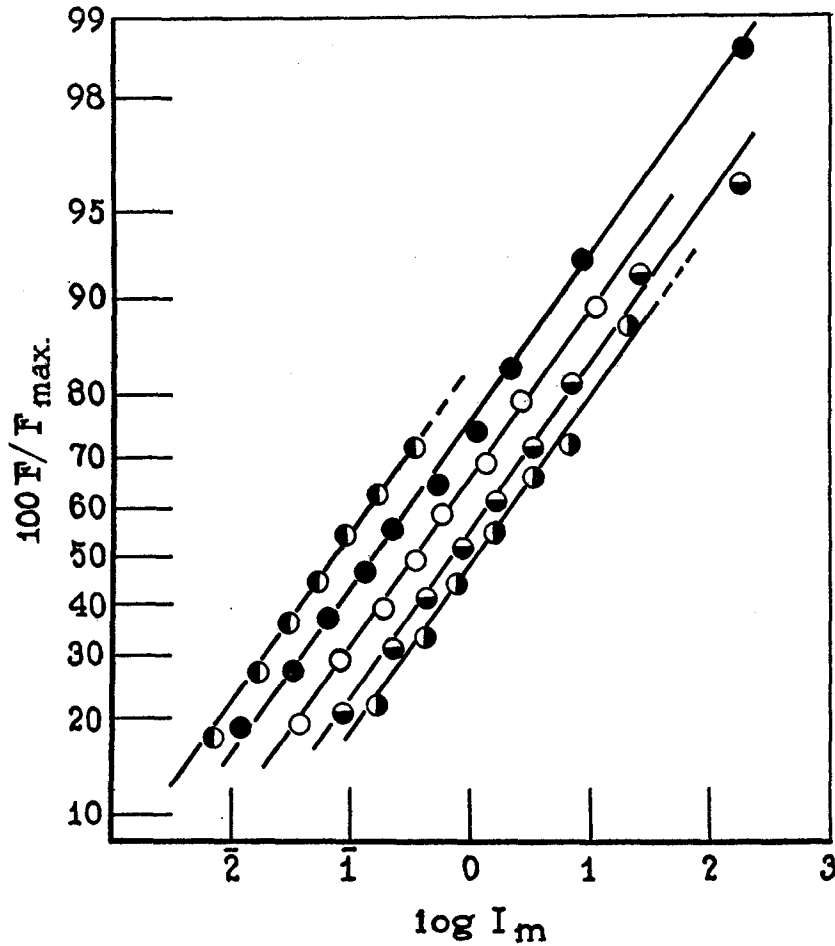


FIG. 2. The upper (cone) portions of the curves in Fig. 1 on a probability grid,  $F$  as  $100 F / F_{max}$ .

the data; (2) that systematic deviations from it, in the case of certain insects studied, are readily accounted for by structural conditions (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 *b*); (3) that it provides a

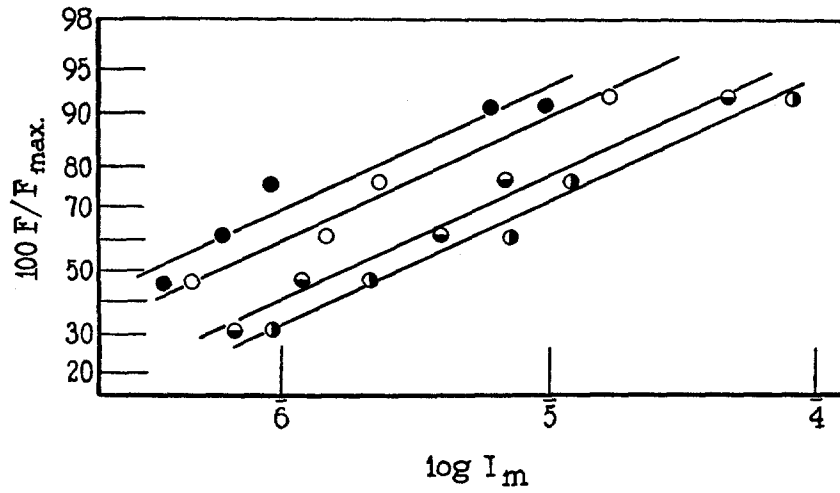


FIG. 3. The lower (rod) ends of the curves in Fig. 1 on a probability grid.

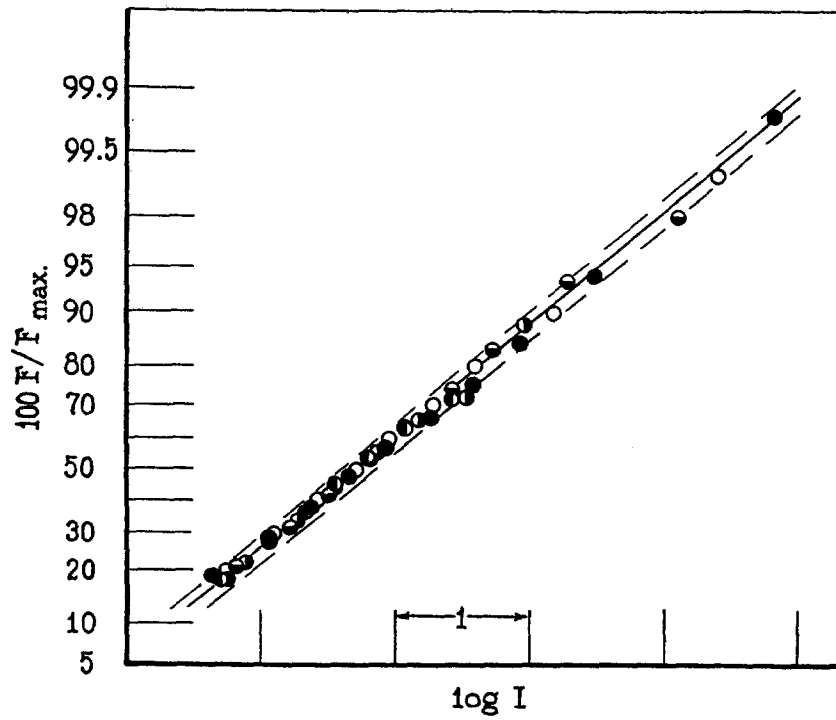


FIG. 4. The cone curves of Fig. 2 adjusted to the same value of  $\log I$  at the inflection point ( $F = 0.50 F_{max.}$ ); the slopes are the same.



rational dissection of the compound flicker curve for vertebrates; (4) that it is intimately connected with the intrinsic organic variability which is a basic feature of the data; (5) that its parameters bear the reasonably expectable relations to area and to temperature, which

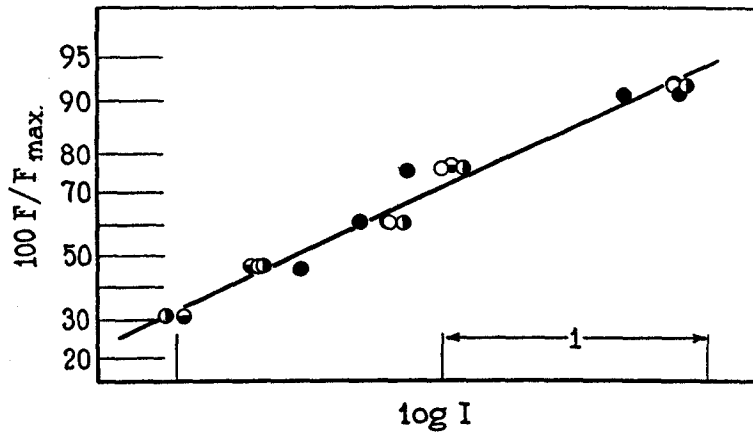


FIG. 5. The rod curves of Fig. 3 adjusted to the same value of  $\log I$  at the inflection point ( $F = 0.50 F_{max}$ ).

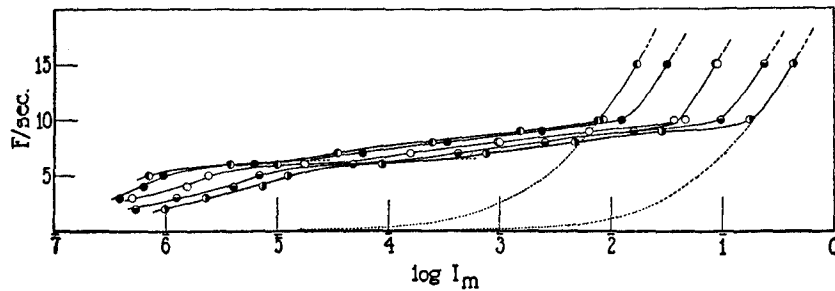


FIG. 6. The lower part of the  $F - \log I_m$  plot (Fig. 1), with the backward extensions of the probability integrals from Fig. 2 (shown in two cases only) to demonstrate the manner in which the extrapolation to the neighborhood of  $F = 0$  accounts for the shape of the graph resulting from the summation of  $F$  elements due to rods and to cones.

in the latter case would scarcely be looked for on other theoretical grounds; and (6), that the parameters in question are proved to have the nature of organic invariants determined by the composition of the organism (Crozier, Wolf, and Zerrahn-Wolf, 1937).

We may consider first with the present measurements the composite character of the flicker curve. The rod contribution, with the various fishes we have studied, is of much lower maximum  $F$  than the cone part, the proportion  $M_R/M_c$  being much smaller (*ca.* 0.13) than for man (*ca.* 0.2). The  $\log I$  separation of the rod and cone branch (Fig. 1) is also greater, and the cone curve is steeper ( $\sigma_{\log I}$  less). This brings it about that with the fishes there is a flat region in the curve, almost horizontal, on which a small hump signifies the entrance of the effects due to cones; with the human data the overlapping is much more complete (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*; 1937-38 *c*). Fig. 6 shows that, as for the curves at different temperatures (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*), and for various genetic types (1937-38 *a*), the extrapolation of the cone probability integral back toward  $F = 0$  accounts precisely for the beginning of the upward drift of the observations at different levels of  $t_L/t_D$ .

The difference curves obtained by subtracting the extended cone integral from the observations are also rectilinear upon a probability grid (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*; 1937-38 *a*).

#### IV

Upon the descriptive success of this formulation the contention rests that the theory of the marginal recognition of flicker must be derived from the properties of the parameters of the probability function. These properties are of two kinds. There are first the observable consequences of the fact that the curves (Figs. 2 and 3) describe the connection between  $F$  and *mean* values of  $I_c$ ; the nature of the *variation* of  $I_1$ , which is lawful (Crozier, 1935-36, etc.), and which can be established through its quantitative relations to experimental variables, is also to be accounted for by any acceptable theory. Second, there are the properties which can be measured by expressing these parameters as functions of area, wave length, temperature,  $t_L/t_D$ ,  $t_{I_1}/t_{I_2}$ , and other conditions. The necessary parameters are three:  $F_{max.}$ ,  $\sigma_{\log I}$ , and  $\log I_m$  at the inflection point ( $= \log I_{infl.}$ ). On a scale of  $F =$  per cent  $F_{max.}$ ,  $\sigma_{\log I}$  is  $\sigma'_{\log I}$ . It is already found that  $F_{max.}$  is decreased by decrease of visual area,  $\log I_{infl.}$  increased,  $\sigma'_{\log I}$  apparently unchanged (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 *b*). With increase of temperature (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *c, d*),

$F_{max.}$  and  $\sigma'_{\log I}$  are unaffected,  $\log I_{infl.}$  is decreased. By analogy with the case of electrical excitation (Crozier, 1937) we shall write  $\tau'$  for  $\log I_{infl.}$

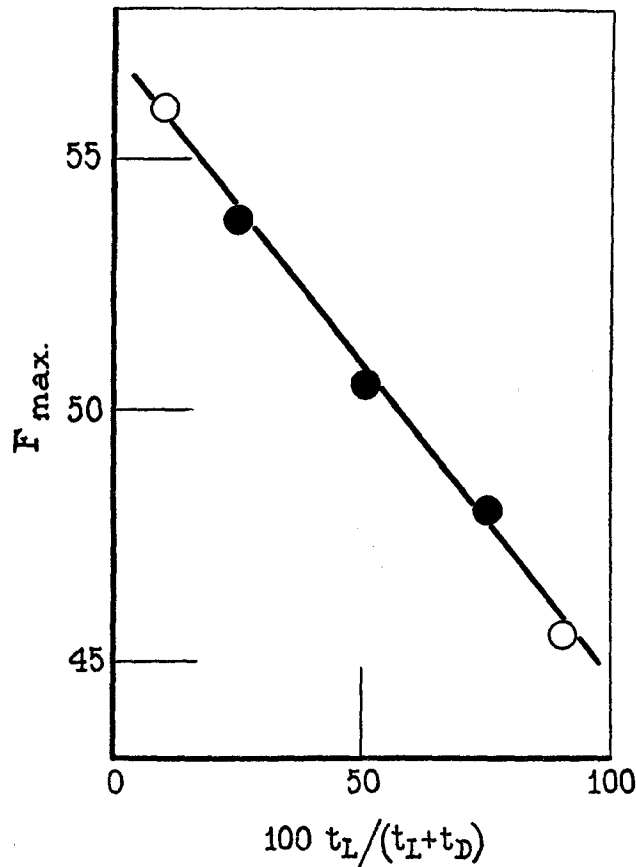


FIG. 7.  $F_{max.}$  (cones) is a declining rectilinear function of the percentage of light time in the flash cycle. (The points at 10 per cent and at 90 are estimated from the calculations in Fig. 2.)

With increase of  $t_L/t_D$  we find that  $F_{max.}$  is lowered (Fig. 1). The relationship is such that  $F_{max.}$  is a declining rectilinear function of the percentage of the flicker cycle time occupied by light (Fig. 7) (or, an increasing rectilinear function of  $t_D/(t_L + t_D)$ ). The effect is less

clearly evident with the rod curves, since a change in  $F_{max}$ . of the same proportionate amount (23 per cent of  $F_{max}$ . at  $t_L/(t_L + t_D) = 0.9$ ) would only be 1.6  $F$  units, and the detected change from 0.9 to 0.1 is less than this

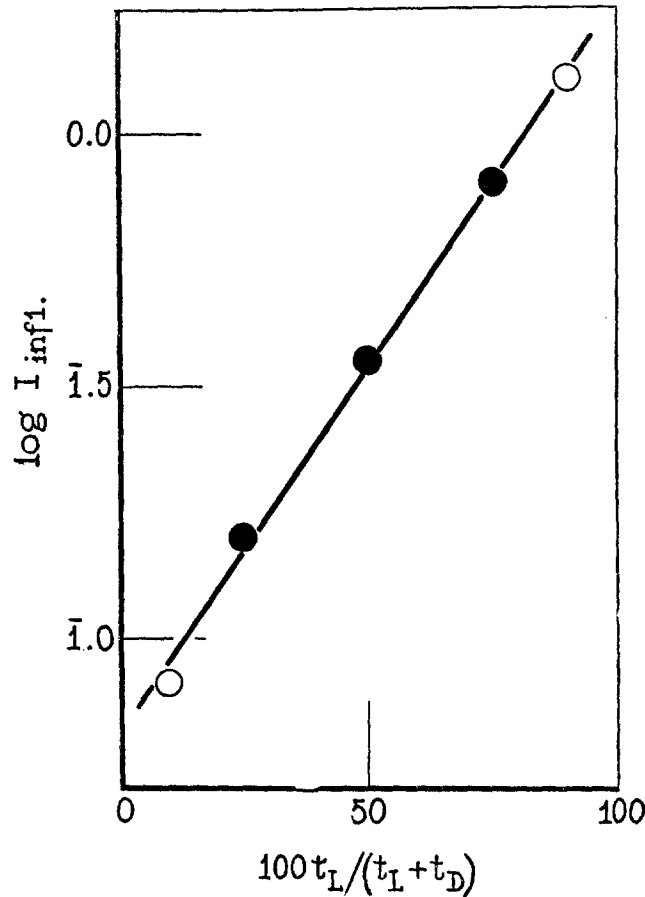


FIG. 8. The abscissa at the inflection point of the  $F$ ,  $\log I_m$  curves (cones) is a rectilinear function of the percentage light time.

The value of  $\log I_{inf1.}$  ( $= \tau'$ ) is a rectilinear function of  $t_L/(t_L + t_D)$ , for both rod and cone curves (Figs. 8 and 9). The proportionality constant is identical for the two sections; we may anticipate a subsequent report on similar experiments with *Anax* larvae to point

out that this relationship is discovered there also, but that the slope of the  $\tau'$  vs.  $t_L/(t_L + t_D)$  plot differs from that in Figs. 8 and 9.

We have thus a situation in which  $\sigma'_{\log I}$  is independent of  $t_L/t_D$ , area, and temperature, while  $F_{max}$  decreases directly with increase of  $t_L/(t_L + t_D)$  and  $\tau'$  increases in this proportion and decreases with rise of temperature; whereas  $F_{max}$  is independent of temperature. To reconcile these facts with the conception that  $F$  and  $I$  are interdependent by reason of the nature of a (homogeneous) photostationary equilibrium of light adaptation and dark adaptation in the retina appears to be impossible. Certainly it cannot be done on the assumption that liminal flicker depends upon constant or constantly propor-

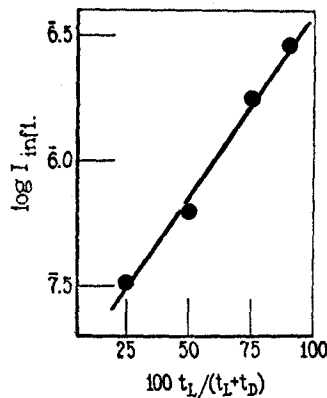


FIG. 9. The rule observed in Fig. 8 holds also for the rod portions of the flicker curves, and the slope constant is the same.

tionate differences in the amounts or rates of photochemical change produced by alternating intervals of light and darkness.

#### V

The  $F - \log I$  curves have been compared for various ratios  $t_L/t_D$  on the basis of the intensity of the illumination during a flash. If Talbot's law were applicable to a situation of this kind, comparisons might be instituted on the basis of the equivalent mean intensity flux ( $I_{eq}$ ) at the point of reaction for each  $F$ . Instead of being brought closer together, however, the curves in Fig. 1 are of course more widely spread apart when each  $I_m$  for  $t_L/t_D = 1/9$  is multiplied by 0.1, those for  $1/1$  by 0.5, and those for  $9/1$  are multiplied by 0.9;

while a transformation in terms of  $I \times t$  on the  $F$  axis inverts the order of the curves. Naturally, in discussing critical flicker frequencies, nothing can be said about equivalent brilliance in the case of lower animals, and nothing really justifies the use of Talbot's law at the critical flicker frequency.

Neither in terms of  $I_m$  nor of  $I_{eq.}$  does  $F$  exhibit a simple relation to  $t_D$ , logarithmic or parabolic (as *cf.* Piéron, 1935, etc.). As the

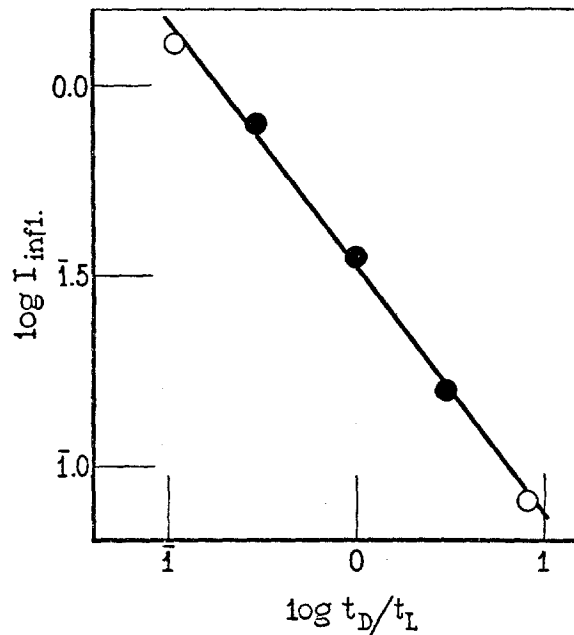


FIG. 10. For the cones,  $\log I_{infl.}$  is a rectilinear function of  $\log$  (dark ratio). This rule is not obeyed by the rod curves (Fig. 11), and is probably not a significant relationship. See text.

"dark ratio"  $t_D/t_L$  increases,  $F$  at fixed  $I$  also increases, but on a curve of which the shape depends on the magnitude of  $I_m$  or  $I_{eq.}$ . For higher intensities,  $F$  is more nearly a straight line function of  $\log (t_D/t_L)$ . The nearest approach to a valid relationship of this kind is given by the fact that (over the range considered)  $\tau'$  is very nearly a straight-line function of  $\log (t_D/t_L)$ , for the cones, so that  $I_{infl.}$  is a decreasing parabolic function of the dark ratio (or, increasing, of the

light-time ratio), as shown in Fig. 10. The case is not so good for the rods (Fig. 11). The same thing is found with  $Anax$ . Since (Figs. 7 and 8)  $F_{max.}$  is rectilinearly related to  $\tau'$ , the same relation must hold for it, with reversed sign (Fig. 12), and also for  $F_{infl.}$ ; with  $F_{max.}$  the slope is not far from 1, so that  $F_{max.} \cong 51 + \log_{10}(t_D/t_L)$ . In general the rule that  $F \propto \log(t_D/t_L)$  can be expected to hold only at the highest intensities, as a limiting condition.

These interrelationships at least indicate that the curves in Fig. 1 reflect merely a change in the scale of the  $F - \log I_m$  function when

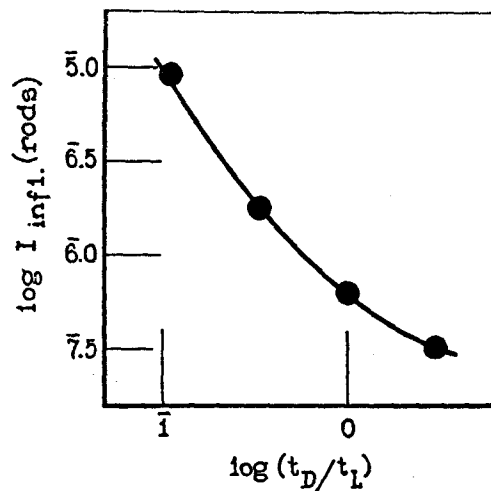


FIG. 11. For the rod curves  $\log I_{infl.}$  is not (as for the cones: Fig. 10) a straight-line function of  $\log t_D/t_L$ .

$t_L/t_D$  is altered. They are consistent with the idea that one is really dealing with a population of elements, the additive effects of which are proportional to  $F$ , and that the sum of effects producing the marginal response to flicker depends in a particular way upon the proportion of light time in a flicker cycle. When  $t_L/t_D$  is low, the total population of elements is larger, its sum being  $F_{max.}$ ; and as it grows, in direct proportion  $\tau'$  is augmented,  $F_{max.}$  and  $\tau'$  each being in rectilinear relation to the increase of the fraction of the total cycle occupied by light.

The reciprocal changes in  $F_{max.}$  and  $\tau'$  are consistent with expecta-

tion. When area is decreased,  $\tau'$  is higher and  $F_{max}$  less. This effect is to be looked for when the total available number of elements has been reduced. The legitimacy of considering  $F$  and visual area as equivalent in this way, that is, in terms of their significance for the magnitude of the sensory effect produced, is attested particularly by experiments below the critical flicker frequency: for the bee two flickering fields have the same phototropic effect if the product of flicker frequency  $\times$  area is the same; evidence of the same kind is provided by *Limulus* (Wolf and Zerrahn-Wolf, 1934-35; 1936-37). When  $t_L/t_D$  is increased it is reasonably supposed that the total number of

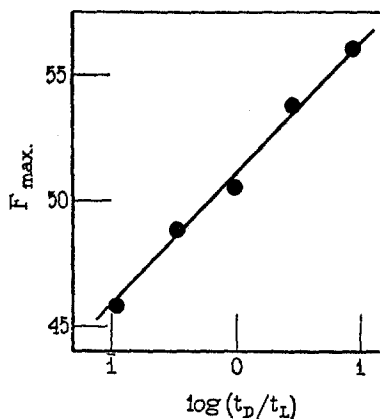


FIG. 12. The maximum  $F$  to which the flicker curve rises is directly proportional to  $\log(t_D/t_L)$ .

available elements is made less, because recovery of any one end-organ (rod or cone) from the effect of a flash will be less probable if the flash is longer and the dark period less, at given cycle time ( $1/F$ ). Hence to achieve a given effect ( $F$ ),  $I$  must be increased.  $\tau'$  is the measure of  $\log I_m$  required for activation of 50 per cent of all the available elements. It could therefore be expected to bear a simple relation to the fraction of the cycle occupied by light, and it is found to be directly proportional to this fraction (Figs. 8 and 9). If the sensory structures to be excited are the same, however,  $\sigma'_{\log I}$  should not be a function of the percentage of light time, any more than it is of temperature.  $F_{max}$  is independent of temperature because the



total number of available elements is not affected, although the mechanism whereby the action of flashes is balanced against their after-effects is influenced.

The latter mechanism has been taken to be essentially that operating in the discrimination of intensities. In the flicker experiment only one intensity is involved, the adjusted intensity  $\tilde{I}_2$ ; it is to be just discriminated from darkness,  $I_1 = 0$ , so that  $\Delta I = \tilde{I}_2 - I_1 = I_m$ . An essential attribute of  $\Delta I$  as obtained when  $\Delta I_m = \tilde{I}_2 - I_1$  is that  $\Delta I_m$  and  $\sigma_{I_2}$  are directly proportional (Crozier, 1935-36; 1936; Crozier and Holway, 1937; Holway and Crozier, 1937), and the ratio is not a function of area (*i.e.*, of number of sensory elements). In the data of critical flicker it has been shown that  $I_m$  and  $\sigma_{I_1}$  are in direct ratio (Crozier, 1935-36; Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *b, c, d*; 1937-38 *a, c*), and that the proportionality is independent of area (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 *b*). We here find also that it is independent of  $t_L/t_D$  (Fig. 13), and in *Anax* as well. The homologue for changes in  $t_L/t_D$  is found in certain experiments involving sensory discrimination of tension; the relation between  $\Delta W$  and  $\sigma_{\Delta W}$  is independent of frequency of the submission to tension, although increasing frequency decreases  $\Delta W$  (*cf.* Crozier and Holway, 1937).

The nature and the mode of action of the sensory elements concerned in this formulation can be investigated without assumptions as to their identity with single rods and cones. Elements are simply defined by  $dF/d \log I$ ; at given  $I_m$  their sum is  $F$ . Identification with the physicochemical properties of individual rods and cones is unnecessary, and indeed impossible. The mode of action in the sensory discrimination of flicker has been pictured (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*) as involving discrimination between (*a*) the central effects of the flashes of light and (*b*) the after-images of these effects. It can be supposed that the rate of decay of the after-effect of a flash depends upon the rate and the duration of the building up of the photic effect, and upon an intrinsic velocity constant. If the discrimination of light (flashes) from non-light intervals in cyclic succession depends upon the recognition of (reaction to) an efficient difference between (*a*) and (*b*), the relation of the  $F - \log I$  curve to temperature is easily explained and a reasonable account is obtained

of the behavior of the variability of  $I_1$ , as we have shown. These properties are exhibited by the responses of animals possessing very different eyes structurally, and, as in the case of other phenomena

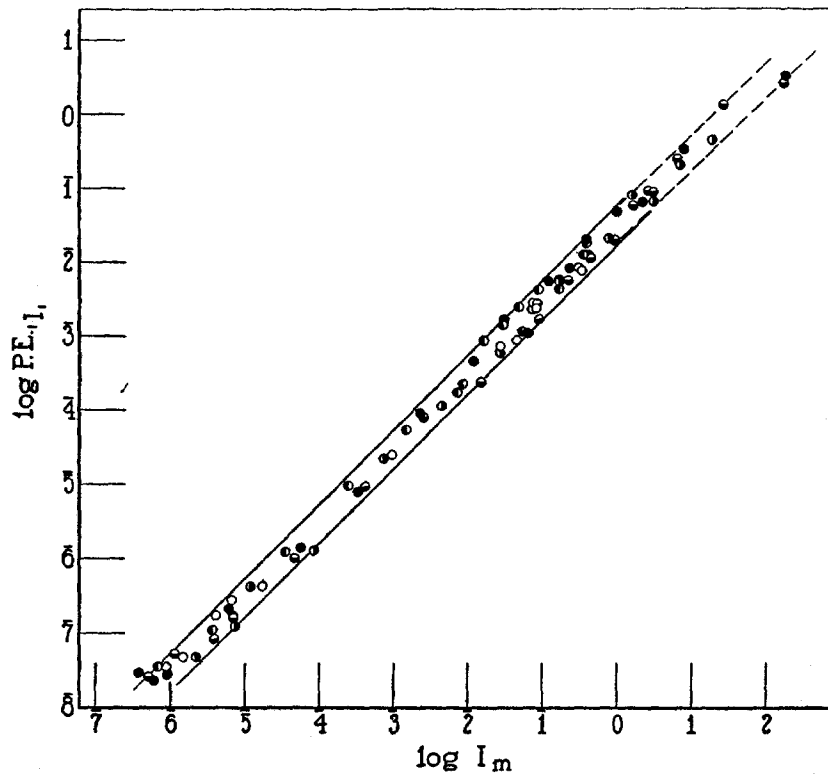


FIG. 13.  $I_m$  and  $P.E._{I_1}$  are directly proportional up to about  $\log I_m = \bar{1}$ ; above that, as in other data on vertebrates, the slope on the log grid is less than 1. The proportionality constant is quite independent of  $t_L/t_D$ . The symbols are as in Figs. 1, 2, etc.

of intensity discrimination, their essential dynamical features cannot be understood in terms of specificities of superficial structure.

To account for the changes in the  $F - \log I_m$  curve as a function of  $t_L/t_D$  in these terms is not especially difficult. In the diagram of Fig. 14 there has been indicated schematically the time course of development of the mean effect of a flash ( $A-B$ ) which for  $t_L/t_D =$

1 is critical for response to flicker. The effect  $E$  is due to the combined action of all the impulses peripherally produced during the action of

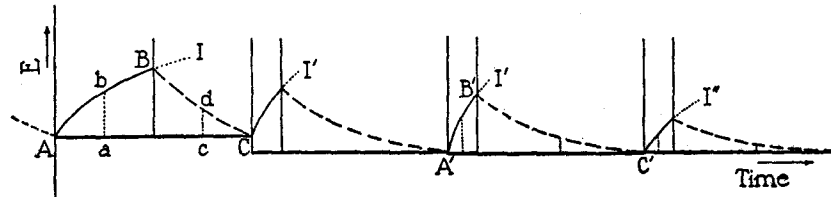


FIG. 14. Schematic theoretical representation of events in a flicker cycle, to show the way in which changes in the proportion of light time in a cycle can produce the observed changes in the  $F - \log I$  curve. The time curve for development of sensory effect of a flash has a velocity constant which is a function of  $I$  and of the number of excitation elements available; the decay curve for the after-effect at fixed temperature, has a fixed velocity constant.

$A B$  is the course of development of the sensory effect  $E$  of a flash, at the critical point for response to flicker;  $B C$ , the decline of its after-effect in an equally long dark interval. Between the mid-ordinates  $ab$  and  $cd$  (or the mean rates of change of  $E$ ) there obtains a certain difference which is necessary for response to flicker at this level of  $E$ .

If the cycle time ( $= 1/F$ ) be kept constant, and the intensity in a flash, and  $t_L$  is reduced, say to 15 per cent, a new position of balance  $A'B'C'$  is arrived at, at a lower mean  $E$ , although the velocity of increase of effect due to a flash is higher ( $I'$ ) with the same  $I$  because the number of elements of excitation is then larger (see text); but the difference between the mid-point ordinates is now greater, and flicker is recognized (by response). Only by lowering the intensity ( $I''$ ), producing a less rapid rise of the effect of a flash, can a balanced rise and fall of effect with constant mean  $E$  be achieved which will permit a just adequate difference between the mid-point  $E$  ordinates for the two parts of the cycle.

(Similarly, for constant  $I$  in a flash, the cycle time must be reduced for the same kind of adjustment.)

Thus, *with respect to the recognition of flicker*, when light and darkness alternate, *duration* and *intensity* in a flash do not have reciprocal significance. From the data of Table I plots can be made of  $\log I_m$  vs.  $100 t_L / (t_L + t_D)$  at each flicker frequency, and by interpolation we can get the values of critical  $I$  for different durations of a flash ( $t_L$ ) at constant dark time. The curve goes through a maximum, for long  $t_D$ , and its shape is a function of  $t_D$ . Talbot's law has nothing to say about the form of the critical flicker contour.

the flash. Its form must be primarily the result of the time and intensity-distribution of the excitabilities of the peripheral units *and* of their central representations.  $B-C$  is the course of the decay

of the after-effect (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*). For marginal response to flicker it matters little at the moment whether we take a critical difference between the areas under *A B* and *B C* or between the mid-ordinates as significant. When  $t_L/t_D$  is made  $< 1$ , the number of available units is larger, as indicated by the analysis already given, therefore *A B* rises faster; consequently, with *I* held constant, a smaller cycle time is required to give the same kind of difference between the mid-point effects of the light and the dark intervals. Similarly, for increase of  $t_L/t_D$  the number of potentially available elements is decreased, hence (at fixed *F*) *I* must be increased to give the same kind of balance. In the first case, however, with decreased light time, the mean level of *E* is then less than when the light ratio is higher (Fig. 14); this corresponds to the fact that the actual response, though "threshold," is weaker and less pronounced than when  $t_L/t_D$  is high. The elements concerned in the exhibition of the response are elements having to do with intensive discrimination, not directly with the magnitude of sensory effect ("brightness") at which the discrimination takes place; no difficulty therefore arises in the addition of elements due to excitation of rods and of cones, since the locus involved is presumably central, not retinal.

Certain features of the variability of  $I_1$  can on this theory be accounted for in the same general way as used for the data at different temperatures (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 *d*). At a given *F* a higher *I* is required for reaction the longer the proportion of light time in a flash. Therefore the greater the chance of moment-to-moment fluctuation in the mean effect produced by the flash. From the relationship

$$\sigma_p = K \sigma_I (dF/dI)$$

(*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1937-38 *a*) it can be seen that, for a given ratio  $t_L/t_D$ ,  $\sigma_p = K' dF/d \log I$ ; the proportionality constant  $K'$  must be independent of  $t_L/t_D$ ; consequently  $I_m$  and  $\sigma_{I_1}$  must be in the same proportion at all values of  $t_L/t_D$  (Fig. 13).

To what extent this should be true when not light and darkness but two intensities of illumination are flashed in succession awaits investigation. Measurements are needed in which  $I_1$  is not zero, but  $I_2$  and  $I_1$  are both finite intensities which are varied.

## VI

## SUMMARY

From the relations between critical illumination in a flash ( $I_m$ ) and the flash frequency ( $F$ ) for response of the sunfish to visual flicker when the proportion of light time to dark time ( $t_L/t_D$ ) in a flicker cycle is varied at one temperature (21.5°) the following results are obtained:

At values of  $t_L/t_D$  between 1/9 and 9/1 the  $F - \log I_m$  curves are progressively shifted toward higher intensities and lower  $F_{max}$ .  $F_{max}$  is a declining rectilinear function of the percentage of the flash cycle time occupied by light.

The rod and the cone portions of the flicker curve are not shifted to the same extent.

The cone portion and the rod region of the curve are each well described by a probability integral. In terms of  $F$  as  $100 F/F_{max}$ , the standard deviation of the underlying frequency distribution of elemental contributions, summed to produce the effect proportional to  $F$ , is independent of  $t_L/t_D$ .

The magnitude of  $\log I_m$  at the inflection point ( $\tau'$ ), however, increases rectilinearly with the percentage light time in the cycle.

The proportionality between  $I_m$  and  $\sigma_{I_1}$  is independent of  $t_L/t_D$ .

These effects are interpreted as consequences of the fact that the number of elements of excitation available for discrimination of flicker is increased by increasing the dark interval in a flash cycle. Decreasing the dark interval has therefore the same kind of effect as reducing the visual area, and not that produced by decreasing the temperature.

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