ON CRITICAL FREQUENCY AND CRITICAL ILLUMINATION FOR RESPONSE TO FLICKERED LIGHT

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I

The examination of the data of intensity discrimination has demonstrated that a just detectable increase of illumination, $\Delta I = I_2 - I_1$ (I_1 fixed, I_2 adjusted), is directly proportional to its standard deviation in all homogeneous series of measurements for which data are available (Crozier, 1935–36). This fact is of fundamental consequence for the interpretation of the meaning of measurements of intensity discrimination. It has been shown that with suitable experimental procedures the data of visual acuity and of flicker fusion may be regarded from the same standpoint; both are based upon phenomena of intensity discrimination and σ_I here has the properties of σ_{I_1} $(=\sigma_{\Delta I})$ (Crozier, 1935–36). One consequence of these considerations leads to the prediction (Crozier, 1935–36) that a curve relating flicker frequency to mean critical illumination for threshold response to flicker will not be duplicated, with the same organisms, by the curve relating illumination to mean critical flicker frequency for the same response. This results from the fact that the regression of mean flicker frequency (F) upon illumination (I), as obtained from measurements of F as a function of I, is not of the same character as that for mean I upon F. Another way of stating this is, that the law according to which variation in flicker frequency depends upon I (or F) is not the same as the law according to which variation in I depends upon F (or I). Neither curve based upon averages gives an adequate formulation of the observed probability that a determination of F or of I at any point will possess the mean value recorded in the curve.

The importance of this situation for the theoretical utilization of measurements of intensity discrimination requires a direct examina-

tion of this particular case, which can be made more easily than that presented by direct tests of simple intensity discrimination, for purely technical reasons. The essential point concerned is that in the use to which the quantity ΔI must be put in deriving a physical theory of the excitatory process the actual dimensions of this quantity, as they arise in the experimental procedures employed, must not be lost sight of. A development of this matter will be found in a succeeding paper.

It is to be borne in mind that the predicted lack of agreement between the "flicker curves" determined in the two ways indicated involves not only the mere fact of their different positions upon the F, I grid, the curve for mean values of F being expected to fall above that for mean I's (Crozier, 1935–36), but implies also certain specific quantitative features of relationships between the indices of dispersion of the measurements. These we may consider more advantageously after the technical procedures have been discussed.

II

The reaction of a fish to a movement of a stripe system surrounding its container has been described previously (Lyon, 1904; Grundfest, 1931–32 *a*, *b*; Wolf and Zerrahn-Wolf, 1935–36) and has been used for the determination of sensitivity to visual stimulation.

For observation a fish is placed in a cylindrical glass jar, 10 cm. in diameter, containing 220 cc. of water. The container with the fish stands on a glass-topped table. It is surrounded by a glass cylinder on which black opaque paper stripes are pasted, leaving translucent spaces of equal width between them. The striped screen is mounted on an axle which can be driven by a motor at various speeds (*cf.* Fig. 1, Wolf and Zerrahn-Wolf, 1935–36).

The striped screen is viewed by the fish against a white reflecting surface. This is a hollow 45° cone made of sheet metal and painted with zinc oxide. The cone is illuminated from below. The light comes from a source consisting of 100, 500, 1000, or 1500 watt concentrated filament lamps, according to the brightnesses desired, and placed at different distances on an optical bench. The positions of the sources are fixed distances from a diffusing screen (D) at the end of the optical bench. Behind the diffusing screen there is placed a diaphragm which controls the size of the radiating area of the screen. The light then falls on a mirror which is inclined at an angle of 45° and reflects upward through the glass top of the table to the cone. The intensities of illumination at the eye of the fish are measured by a Macbeth illuminometer. With the different light sources and various distances from the screen, and the diaphragm, the brightness can be varied over a range of 5

logarithmic units. For low intensities we had to place in front of a 100 watt lamp in a fixed position Eastman Kodak neutral filters with transmissions of 1/10, 1/100, 1/1000, and 1/10,000, thus enabling us to have a total range of 9 logarithmic units of intensity.

In a previous paper (Wolf and Zerrahn-Wolf, 1935–36) the reaction of the sunfish *Lepomis* to flicker was studied by adjusting the speed of rotation of the striped screen so that certain constant flicker frequencies were obtained. A given flicker frequency was kept constant and the intensity of illumination was changed by increasing I until a threshold reaction of the fish became evident. For the present

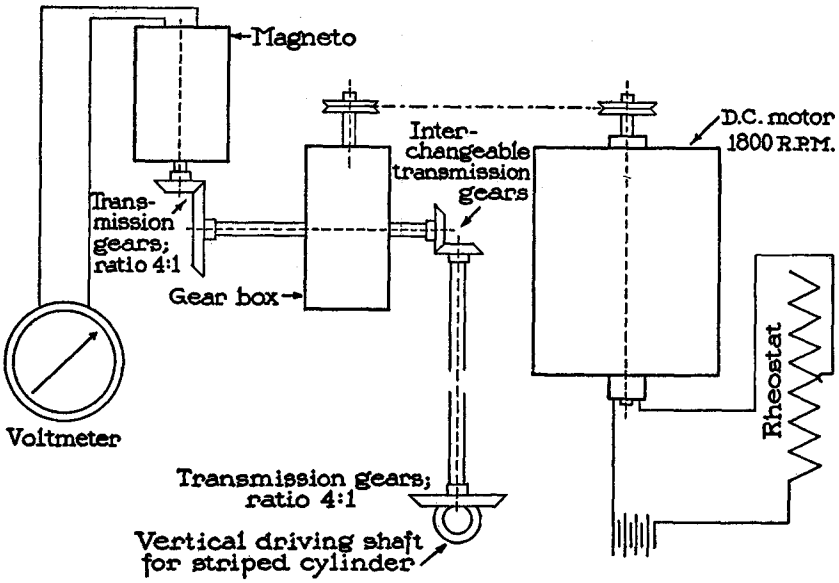

FIG. 1. Diagram of connections of driving motor with shaft for rotation of striped cylinder and with magneto for measurement of speed.

study it was desirable to take as the fixed intensities the mean values for threshold intensity of reaction from the previous experiments. The flicker frequencies were varied by decreasing the flicker frequency until a threshold response of the fish is obtained. The temperature throughout was 21° ± 1°.

For determination of threshold flicker frequencies at fixed intensities it is essential that (1) the transmission of motion to the striped screen be rigid, so that no slippage of belts in the transmission system may influence the flicker frequencies in an uncontrollable manner, and (2) instantaneous readings of flicker frequencies can be taken.

The striped cylinder is driven by a D.C. motor (1800 R.P.M.) the speed of which

is controlled by a rheostat (Fig. 1). The motor is belted to a reduction gear. The drive shaft of the gear box transmitting the reduced speed of rotation is on one side connected by a set of gears of ratio 1:1 to a shaft which transmits the motion through another set of gears of ratio 4:1 to the shaft turning the striped cylinder. The gears at the gear box junction can be interchanged for another set of ratio 2:1, to produce higher flicker frequencies in case they are needed. The gear transmission has no free play, and accurate settings of speeds of rotation are thus possible.

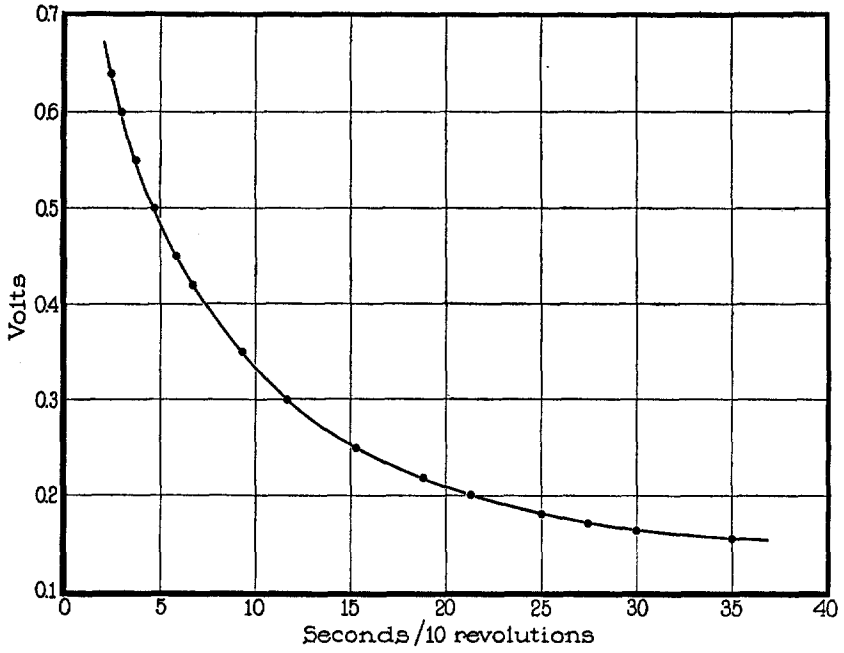

FIG. 2. Typical calibration curve—voltmeter readings from magneto as related to speed of rotation of striped cylinder.

The other end of the gear box shaft is connected with a second set of gears of ratio 4:1, transmitting the rotation to a magneto speed indicator system. The magneto is connected with a millivoltmeter from which by means of calibration curves the flicker frequencies can be read. In the tables the voltages have been rounded to the nearest 0.01 volt.

For calibration of the speed indicator the rheostat is set at a given position, the time for ten revolutions of the striped cylinder is determined by means of a stopwatch, and the voltmeter reading taken. Such determinations are made for a great many rheostat settings covering the entire range of speeds. The voltmeter

readings then are plotted as ordinates against the times for ten revolutions as abscissae (Fig. 2). We thus obtain a smooth calibration curve from which the flicker frequencies can be computed. Since for the entire range of flicker frequencies required, different striped cylinders have to be used (10, 20, and 40 stripes each) the total number of stripes passing in front of the fish's eye during ten revolutions must be divided by the values from the calibration curve read on the abscissa for any given mean voltmeter reading, to give the flicker frequency. For each set of gear ratios used a separate calibration curve is of course required. Only one of these is illustrated (Fig. 2). The different gear ratios are so chosen as to permit readings from the calibration curves in the region of maximum precision, rather than at either end of the curve (Fig. 2). In this way an approximately equal accuracy of instrumental estimate of flicker frequency is obtained over the whole range of frequencies used.

For experimentation twelve individuals which gave rather good reactions to moving stripes were selected. They were of the same batch from which the animals for the previous experiments (Wolf and Zerrahn-Wolf, 1935-36) were taken. Each animal is kept in a separate glass jar. For tests they are transferred into culture dishes 10 cm. in diameter and 5 cm. high. Each dish is filled with 220 cc. of clean tap water which was at room temperature before the fishes were put into it.

Before experimentation the fish are dark adapted for at least 2 hours. The first animal is then placed on the glass top of the table and left in the dark for a short time, so as to avoid any interference with our first reading by any effect of the handling. Then the striped screen is set into motion at a speed which is considerably higher than that at which the fish could be stimulated by the flicker produced. The light is turned on, giving an illumination previously adjusted to the desired intensity. As soon as the light is turned on the fish shows a slight light "shock" which consists in a sudden backward motion; after a few seconds it becomes quiet again. Then the position of the rheostat is changed (decreasing the flicker frequency) until the fish shows the first noticeable response. At this instant, the voltmeter reading is taken by another observer. Since the fish now is swimming forward with the stripes or backward against them, a shutter is closed reducing the light to a minimum. Then the speed is brought back to the original maximum level and as soon as the fish has become quiet again a second and a third test is made. With all animals and at all levels of intensity we took three successive readings, which agreed very closely one with another.

Since the transmission of rotation to the striped screen was done by a rigid gear system there is naturally some vibration of the jar in which the fish is kept. The fish therefore is never so quiet as when the transmission is by a belt system. The fish always shows active motions of the fins. It stays reasonably quiet, however, and the first jerk it gives with the visual stimulus produced by flicker is sharp enough to give repeatedly accurate settings for critical flicker frequencies. The various intensity settings were made in random order.

III

The analysis of the data obtained by measurements of mean critical illumination intensities (I_m) at fixed flicker frequencies showed that the dispersion of intensities (I_1) was related in a simple way to I_m; σ_{I_1} is directly proportional to I_m in the lower (rod) region of the curve, and directly proportional to (I_m-*const.*) in the upper (cone) section of the curve (Crozier, 1935–36). This result was brought into harmony with the results in tests of intensity discrimination, where in general σ_{I_2} ($=\sigma_{\Delta I}$) is directly proportional to I_2, on the basis that reaction to flicker involves an "intensity discrimination" between I_x and $I_x - \Delta I_x$, where $I_x - \Delta I_x$ (the brightness effect of the dark stripe) $\equiv I_1$, and $I_x \equiv I_2$. The data are properly described not by a curve but by a band, the width of which measures the probability that repetitive determinations of critical I will fall in a particular area; the margins of the band may be fixed by $I_m \pm \sigma_{I_1}$, or by $I_m \pm$ P.E.$_{I_1}$, or by σ_{I_m} or P.E.$_{I_m}$, since for each value of I_m the number of observations is kept constant. For the present purpose it is convenient to use $I_m \pm$ P.E.$_{I_1}$. The data are summarized in Table III. The horizontal width of the band has the properties of $k\,\sigma_I$. Its *vertical* width should predict the properties of σ_F if the experiment is made by determining F as a function of I. It is also apparent (Crozier, 1935–36) that the curve for mean F as a function of I should lie above that for mean I as a function of F (*cf.* Fig. 3)—unless the frequency distribution of measured F's or I's should be found to be of quite unexpected shape.

This might easily happen if it were correct to regard the observed variation of I as in the crude sense due to "experimental error"; error, that is, in the sense of variation introduced by the manipulation of the apparatus and of the organism with which the measurements are made. If this were correct, σ_I should be greater, absolutely, at low I's, and there would be no reason whatever for assuming that σ_I should be directly proportional to I, particularly since at high flicker frequencies (and high I) the reaction of the fish which is the basis of measurement is sharper, "cleaner", and easier to recognize quickly. The instrumental errors are thus in general to be expected to produce a type of dependence of σ_I upon I_m which is in fact the reverse of that actually encountered.

It might also be suggested, in line with a certain more or less traditional conception of the "interval of uncertainty", that at any moment a given tested individual fish will exhibit a zone of intensities within which it cannot distinguish intensities at fixed F, and *vice versa*; and that in consequence any single determination of critical I or of critical F represents an accidental overshooting of the true margin of this zone. Several considerations dispose of this view. If this were in fact the essence of the situation then the distribution of measured I's at fixed F, or of measured F's at fixed I, should be quite definitely skewed, heaped up at the *low* intensity side and at the *high* F side, owing to the way in which the end-point is approached. And it would be impossible to foretell from knowledge of the properties of σ_I anything whatever as to the properties of σ_F.

In opposition to this idea is the one which we employ, namely that a single determination of F_1 measures a state of the reacting system of the fish, which has a certain probability under the conditions imposed. The basis for this position requires brief consideration.

Prediction of the *properties* of σ_F is not to be confused with prediction of its absolute magnitudes. The manipulative process whereby critical I is measured is not the same as that by which critical F is ascertained. Each process must involve its own characteristic factor of procedural uncertainty. The method whereby I_1, F_1 and mean I, F are obtained reduces to a relative degree of insignificance the systematic distortions otherwise introducible from this source.

It is to be noticed, in the first place, that critical I is determined by increasing I to the point where reaction is obtained, while critical F is gotten by reducing F until reaction is given. The important feature of this is that the same reaction serves as indicator in both sets of measurements, and the same end-point is in each case approached in an equivalent manner. Using the terminology already employed, reaction is evidenced when I_x, the direct excitatory effect ("brilliance") of the illuminated stripe, reaches a critical value in relation to $I_x - \Delta I_x$. This effect is a function of I and of t, the duration of exposure to a stripe ($= k/F$). In measuring critical I, t is constant; in measuring critical F, I is fixed. Since $I_x = \phi\ (I, t)$, the critical excitation can be approached by increasing I or by decreasing F. It does not follow, however, that the mode of depend-

ence of the critical effect upon F is independent of I, and indeed there is good reason to expect that change of F would be less significant at fixed high intensities than at low (so that the *precision* of mean F at the highest intensities would be comparatively less than otherwise expected).

In these experiments, as already outlined, three determinations of critical flicker frequency were made with each fish at each intensity. The average of these was then taken, and the mean of the twelve

TABLE I

To illustrate nature of the data upon which mean critical flicker frequencies are calculated. The illumination I is fixed; cylinder with 40 stripes; the variation in mean flicker frequency from fish to fish greatly exceeds the variation in repeated determinations (voltmeter readings) with any single fish.

log I (millilamberts)	Fish No.	Voltmeter reading				Flicker frequency
					mean	
$\bar{1}$.8118	1	0.39	0.37	0.37	0.377	30.19
	2	0.38	0.38	0.37	0.377	30.19
	3	0.35	0.38	0.36	0.363	29.20
	4	0.39	0.37	0.39	0.383	30.89
	5	0.38	0.39	0.39	0.387	31.13
	6	0.37	0.39	0.38	0.380	30.53
	7	0.39	0.39	0.40	0.393	31.62
	8	0.40	0.40	0.39	0.397	32.13
	9	0.40	0.41	0.41	0.407	32.92
	10	0.38	0.39	0.40	0.390	31.50
	11	0.39	0.40	0.39	0.393	31.62
	12	0.39	0.40	0.39	0.393	31.62

individual averages used as the mean critical F. This procedure tends to eliminate the purely instrumental errors, and is manifestly a legitimate procedure since the scatter of the readings with any one fish is quite markedly less than the variation from fish to fish. Neither the raw single determinations of F_1, nor the individual means, are skewed in distribution. There is no basis for supposing that the readings represent "overshooting" of the margin of a zone of uncertainty. One set of typical results is given in Table I. An examination of the data on critical I's (*cf.* Wolf and Zerrahn-Wolf, 1935–36)

shows an entirely similar situation. The necessary presumption is that the different individuals represent, at any one time, an essentially random distribution of the capacity to be excited by the flickered light, as evidenced by the respective critical flicker frequencies obtained for each. This is amply substantiated by an examination of the relative positions of the twelve in tests at different intensities and at different times. The mean rank position (1 to 12) in terms of increasing critical flicker frequency for response was determined from

TABLE II

Relative sensitivities of twelve *Lepomis*, in terms of mean relative position in the series (1 to 12) of increasing critical flicker frequencies in twenty-three sets of determinations at various times and at different intensities.

Individual No.	Mean position
1	4.55
2	4.69
3	5.14
4	6.86
5	6.76
6	6.76
7	8.42
8	6.76
9	8.01
10	5.76
11	6.91
12	7.12
Mean.....	6.48 ± 0.846

twenty-three sets of measurements such as the one shown in Table I. The mean of these means was 6.48 (completely random = 6.5), the P.E. of a mean rank position 0.846, the maximum departure from the mean being 1.96 (see Table II). The difference between the extreme mean rank positions = 2.3 × its P.E. This is the relationship to be expected from a fluctuating chance distribution of relative reactiveness. The time fluctuation of reactiveness in one fish is of a totally different order of magnitude from that concerned in the narrower range of variation of F apparent in successive determinations with one individual at one intensity. The situation here is like that encountered

in measurements of geotropic orientation of rats (*cf.* Crozier and Pincus, 1931–32; Crozier, 1935): different individuals of one genetic composition represent at a given moment different states of performance of the same reacting mechanism; the fluctuation of reactivity is random in each of the several individuals, over a range of which the properties may be measured by the performance of the several representative states of reactivity in the sample taken at one time. For our present purpose the importance of this lies in the demonstration that the variation dealt with in the measurements is not instrumental error but is a property of the organisms and of the system of processes determining the effects measured. The use of a homogeneous population of tested individuals for all determinations in a series is merely a short-cut to the data which would be obtained by more protracted investigation of a single individual, involving an equal number of determinations. The variation indices secured therefore measure an essential aspect of the performance of the system under scrutiny.

It is of particular interest to examine experimentally the behavior of the index of dispersion of F_1 as it may be affected by purely instrumental errors. Four independent sets of determinations illustrate this. (1) The first determination of mean critical flicker frequency was made at an intensity of antilog $\bar{4}.9850$; it gave mean $F = 8.33$, but P.E.$_{F_1} = 0.336$. Subsequent determinations, after skill had been attained in repeated measurements, gave $F_m = 8.38$, with P.E.$_{F_1} = 0.188$. As pointed out subsequently, the latter determination is concordant with the position of this intensity in the whole series. (2) In a similar way, at a later date, it became necessary to change the gear ratio in the transmission system driving the striped cylinder; this entailed a new kind of practice on the part of the observer in using the rheostat controlling the speed of the driving motor; mean F from this series was 46.55 ± 0.929; after adequate training in the handling of the apparatus, a redetermination (Table III) gave $F_m = 46.46 \pm 0.436$; there is no question that the latter determination is a real measure of the variation effect. (3 and 4) We have described how in order to obtain an adequate range of flicker frequencies it was necessary to use cylinders with different numbers of opaque stripes; in two cases we have determined that when the number of stripes is

just barely inadequate to provide a sufficiently high flicker frequency to cover the range desired in the test, the mean flicker frequency obtained is, as would be expected, a little too low—for example at in-

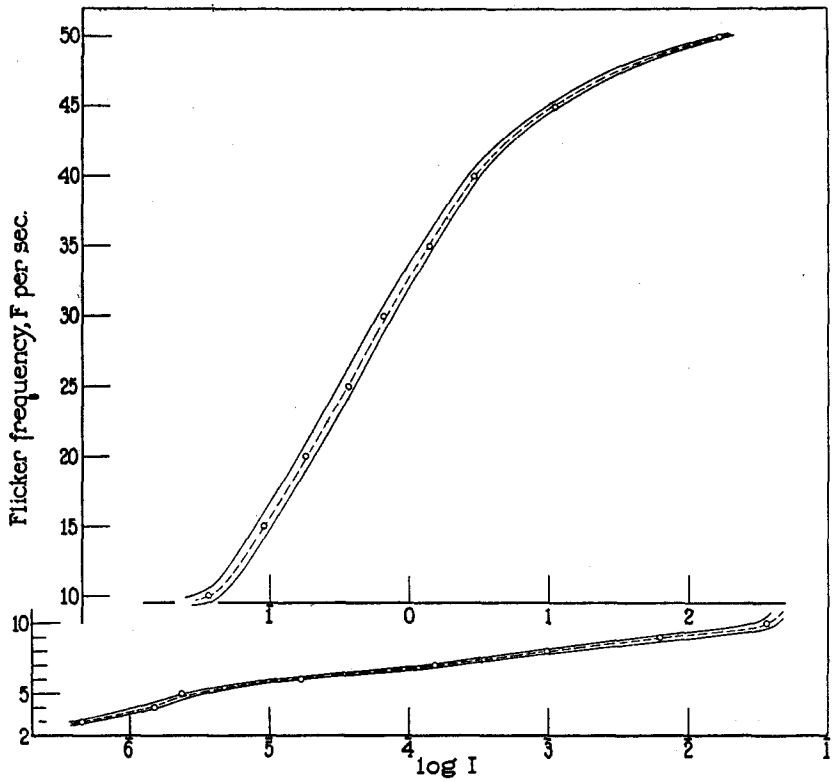

FIG. 3. Critical I_m as a function of F (data from: Wolf and Zerrahn-Wolf, 1935–36), plotted as $I_m \pm$ P. E.$_{I_1}$, to show form of the plot from which 2 P.E.$_{F_1}$ (the vertical width of the band) may be predicted as a function of I; see text. For convenience, the curve is shown in two sections, which are continuous (*cf.* Fig. 5); each point is the average of three determinations upon each of the same twelve individuals. The mid vertical points on this band give the "expected" values of F_m as a function of I.

tensity antilog $\bar{3}.7980$, F_m was 9.14 with a 10 stripe cylinder, known to be just barely inadequate, instead of 9.32, and at intensity antilog $\bar{1}.2591$, F_m was 20.51 with a 20 stripe cylinder, rather than 21.26 with an adequate (40 stripe) cylinder. Yet in each of these cases

P.E.$_{I_1}$ was definitely *low* when the cylinders contained too few stripes, —in the first case P.E.$_{F_1}$ = 0.244 rather than 0.253, and in the second case 0.210 rather than 0.388. The point is, that when the readings cannot be made by beginning with a flicker frequency definitely too high, and approaching the end-point by a sufficient decrease of flicker frequency, the only reactions which can be recorded as reactions to flicker are those of animals definitely in the less sensitive portion of their possible range; thus the effect of using a not sufficiently high

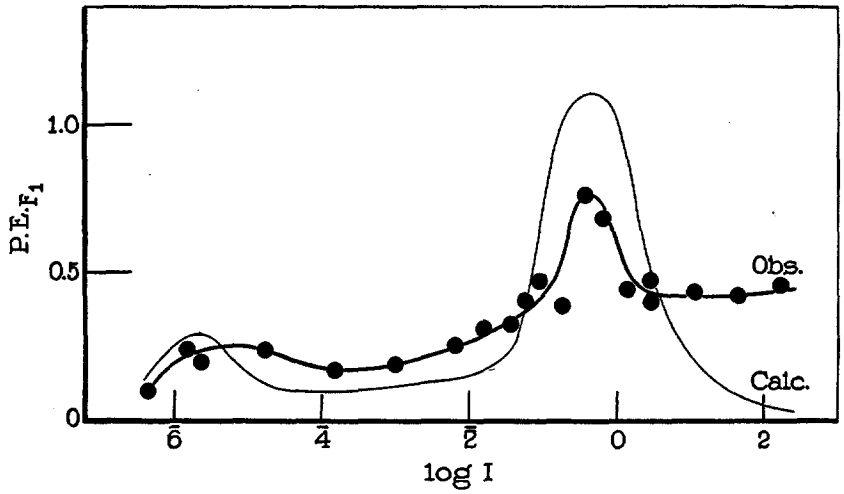

FIG. 4. The half-width of the band shown in Fig. 3, based upon P.E.$_{I_1}$, is taken as a measure of the expected dispersion (P.E.$_{F_1}$) of F. The solid circlets are the experimentally determined values of P.E.$_{F_1}$; each point is the average of three determinations upon each of the same twelve individuals.

range of possible flicker frequency is to produce an artificial kind of overshooting of the real critical frequency such as we have already commented upon in another connection; and it is significant that under such circumstances the index of dispersion of F_1 should be, as it is found, too small.

On this basis we may expect to be able to predict certain of the properties of the observable variation of F. In Fig. 3 the band drawn embraces $I_m \pm$ P.E.$_{I_1}$ as a function of F. The P.E.'s have been adjusted to the smooth curve by means of the relationships discussed

in the preceding paper (Crozier, 1935–36). One half the *vertical* width of this band, as a function of $\log I$, is shown in Fig. 4; it exhibits a minor and a major maximum. If the variation of I in determinations of critical illumination for response to flicker as a function of frequency reflects an organic property of the system excited, then the curve in Fig. 4 should be in all essentials duplicated by the direct determinations of the variation of F in measurements of critical flicker frequency as a function of intensity. In the analysis of the data now secured it is manifest that the prediction has been successful.

IV

The results of the determination of F as a function of fixed I are given in Table III. The curve of F_m (Fig. 5) is manifestly of the same general form as that secured by measuring I_m as a function of F, but it is definitely displaced upward, and the amount of the displacement is a function of I (or of F). The *form* of the displacement can be predicted by computation from Fig. 3. From Fig. 5 the extent of the displacement can be gotten directly. (The original plots are of course very much larger.) The two are compared in Fig. 6. Slight as the difference between the two curves may appear to be, it is thus none the less real and significant, since its somewhat peculiar major properties may be predicted. The separation of the two curves in Fig. 5 is of the order of $-\text{P.E.}_{I_1}$ at all intensities, but is about $-2.5 \times \text{P.E.}_{F_1}$; its consistency, however, removes this from the realm of accident. Moreover the form of the band (Fig. 4) given by the dispersion of F_1 (measured by $\pm k\,\sigma_{F_1}$) is clearly like that already found from the measurements of σ_{I_1} (Fig. 3). This is to be examined carefully, since it involves the prediction of the form of σ_{F_1} from the data of σ_{I_1} and reciprocally. From Fig. 3 the vertical width of the band may be computed; this should have the meaning of $2\,\sigma_{F_1}$. In Fig. 4 it is compared with σ_{F_1} as found experimentally. (It is obvious that the converse calculation must also give agreement with the form of the measurements of P.E._I.)

The chief source of disagreement between the curves drawn in Fig. 4 may quite reasonably be found in the general fact that the F_m curve was determined some time later than the I_m curve. It has been pointed out, however, that an additional feature was recognized in

the fact that the method of securing a variable flicker frequency introduced the possibility of arousing the fishes through slight vibration; this would be expected to make F_m a little higher than in the absence of vibration. It can be pointed out, however, that at the high intensity end of the curve P.E.$_F$ may be higher than predicted

TABLE III

Mean critical flicker frequency per second ($\mathbf{F_m}$) and the P.E. of a determination of F ($=$ $\mathbf{P.E._{F_1}}$) as a function of intensity (I), for the sunfish *Lepomis*. These determinations are compared with the data for the same organisms in which mean critical illumination (I_m) has been determined as a function of flicker frequency (F) (*cf.* Wolf and Zerrahn-Wolf, 1935–36; Crozier, 1935–36). Each mean F and mean I is the average of three determinations upon each of twelve individuals.

log I millilamberts	F_m	P.E.$_{F_1}$ ±	F	log I_m millilamberts	P.E.$_{I_1}$ ±
	per sec.		*per sec.*		
$\bar{7}.6550$	3.70	0.0981	3	$\bar{7}.6555$	0.694×10^{-7}
$\bar{6}.1750$	4.09	0.240	4	$\bar{6}.1784$	0.520×10^{-6}
$\bar{6}.3701$	5.22	0.196	5	$\bar{6}.3701$	0.399×10^{-6}
$\bar{5}.2300$	6.42	0.239	6	$\bar{5}.2385$	0.303×10^{-5}
$\bar{4}.1800$	7.41	0.165	7	$\bar{4}.1855$	0.279×10^{-4}
$\bar{4}.9900$	8.38	0.188	8	$\bar{4}.9954$	0.190×10^{-3}
$\bar{3}.7980$	9.32	0.253	9	$\bar{3}.7983$	0.124×10^{-2}
$\bar{2}.2000$	9.79	0.311			
$\bar{2}.5600$	10.69	0.327	10	$\bar{2}.5600$	0.743×10^{-2}
$\bar{2}.7600$	13.02	0.408			
$\bar{2}.9550$	16.12	0.471	15	$\bar{2}.9543$	0.126×10^{-1}
$\bar{1}.2591$	21.26	0.388	20	$\bar{1}.2591$	0.177×10^{-1}
$\bar{1}.5630$	26.68	0.764	25	$\bar{1}.5631$	0.630×10^{-1}
$\bar{1}.8118$	31.13	0.683	30	$\bar{1}.8118$	0.731×10^{-1}
0.1418	36.54	0.445	35	0.1418	0.129
0.4601	41.12	0.404	40	0.4601	0.281
	41.17	0.475			
1.0465	46.46	0.436	45	1.0465	0.415
1.6454	49.16	0.425			
2.2265	50.68	0.460	50	2.2264	11.53

because with high intensity and high flicker frequency a small change in F would be relatively less significant for excitation. One method of showing this is to consider the empirical equation which in general describes the course of such data; Hecht (1934) pointed out that the equation which may be written

$$KI = F^2/(C - F)^2$$

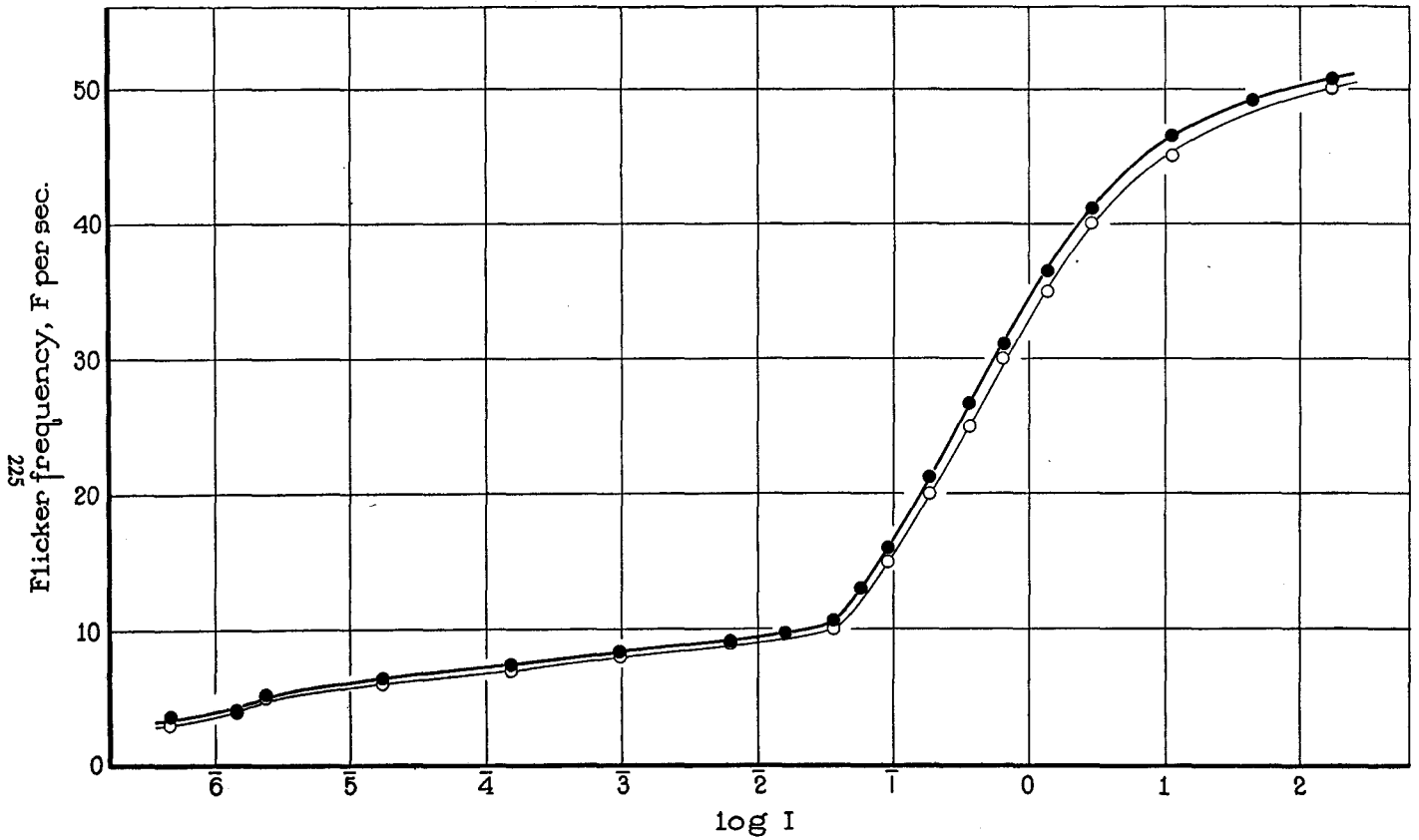

FIG. 5. The curve of mean critical flicker frequency for response of *Lepomis*, upper curve, compared with the (lower) curve of mean critical illumination.

describes well the relation between intensity and flicker frequency for flicker *fusion* (cones); when I is large, a given change in apparent K calls for a relatively larger change in F than in I; this means that measurements of F_m at the highest intensities would be relatively less precise. It is a curious fact, however, that within the limits of the curves, the areas under the two graphs in Fig. 4 agree to within 5 per cent. The only real agreement to be looked for, with regard to P.E.$_F$ observed and expected, is in the form of this quantity as a

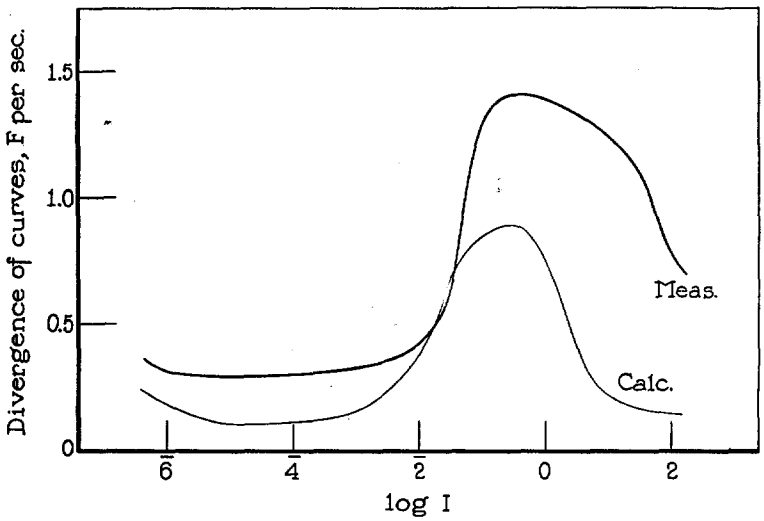

FIG. 6. Expected (*calc.*) and measured (*meas.*) divergences of the two curves shown in Fig. 5.

function of I (or of F); the different procedures necessarily involved upon the one hand in obtaining F_m and on the other in getting I_m must be expected to result in minor differences in absolute amounts of variation. It is a reasonable surmise that this may be the origin of the effect noticed in certain other series of measurements, in which changes in the dispersions of the data appear to be correlated with the use of different procedures in attaining the end-point (*eg.*, *cf.* Hecht and Verrijp, 1933–34, Fig. 1, and description in: Hecht, Shlaer, and Verrijp, 1933–34).

V

These considerations impose important restrictions upon the process of interpreting the theoretical meaning of a curve of thresholds for response to flickered light. In the first place, it is not correct to say that the *same* curve describes with sufficient precision the two sets of data obtained respectively by measuring mean flicker frequencies and by determining mean intensities. The quantities which may be calculated from such data and which may be used to test a theory of the visual excitatory process possess, and must retain, dimensions which describe properties of the reactions of the organism which are the basis of the measurements. The sensory phenomena, in terms of the index responses used for their estimation, are properly to be described by a formulation which embraces simultaneously the properties of σ_{F_1} and of σ_{I_1}; the dispersions of the measurements are properties of the reacting organism and not of experimental error. A quite general method of expressing this is to state that the law connecting flicker frequency and intensity, for threshold response, as found in the data, is to be represented as a band, *not* as a line or curve. The form of this band exhibits an essential property of the event whereby intensity discrimination is achieved. The use of this type of formulation in dealing with the prediction and the interpretation of other phenomena of photic excitation, and of comparable features of other kinds of excitation, will be considered in a following paper. A special feature of the data for response to flicker in the case of such a vertebrate as *Lepomis* is found in the superposition of effects due to excitation of cones upon those due to excitation of rods. The separation of these two effects presents certain complications. The whole situation may with profit be re-examined in the case of an organism in which these complications do not arise. A subsequent paper deals with the treatment of an analogous set of measurements made with such an organism.

VI

SUMMARY

The curve of mean critical flicker frequency as a function of illumination has been determined for the reaction of the sunfish *Lepomis* to flicker. It exhibits expected quantitative disagreements with the

curve of mean critical illumination as a function of flicker frequency in the same organism. The form of the dependence of the variation of critical frequency of flicker upon illumination can be predicted from a knowledge of the way in which variation of critical illumination depends upon flicker frequency. It is pointed out that these findings have an important bearing upon the interpretation of the data of intensity discrimination.

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