INTENSITY AND CRITICAL FREQUENCY FOR VISUAL FLICKER

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I

For the investigation of visual flicker in fishes, amphibians, and certain insects we have used[1] the procedure of exposing an animal in a space surrounded by a rotating cylinder upon which there alternate transparent and opaque vertical stripes. Light of adjustable, measured intensity is reflected through the transparent stripes. The critical illumination, I_c, is obtained which, for a given speed of rotation of the cylinder, results in forced reactions of orientation and movement by the organism tested. Alternatively, by adjustment of the speed of rotation of the cylinder, the critical flash frequency is obtained by test which, for a given intensity of illumination in a flash, forces the same response. The critical flash frequency, F_c, is given by the number of flashes passing a given point at the circumference of the cylinder in a unit time.

The relationships between F and the mean values of I_c ($= I_m$), and between I and the mean values of F_c ($= F_m$) have been discussed[1] from the standpoint that the response to the visual flicker, and to the direction of its movement, is homologous to the recognition of flicker in human visual experiments. For this position it can be said, in the first place, that the curves thus obtained for the relationship between F and I have the same general properties in various organisms[1] as are found for marginal suppression of human visual flicker; further, that the curve obtained with the bee[2] by means of a quite different technique[2] has again the same general properties.

[1] Wolf and Zerrahn-Wolf, 1935–36; Crozier, 1935–36; Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *a*, *b*, *c*, *d*; 1937–38 *a*.

[2] Wolf, 1934–35.

There arise in this connection certain special questions for the theory of critical flicker frequency. We are not now required to enter upon a detailed discussion of these particular questions, but their significance must be referred to; they will be more elaborately considered in subsequent papers.[3] One point we attempt to deal with now, because it is important for the general theoretical treatment: the question, namely, as to whether a valid homology may be held to obtain with respect to the flicker response data provided by lower animals on the one hand, as secured by the method outlined, and on the other hand the data of critical illumination as a function of flicker frequency for the human observer.

It is clear that the *general* form of the functional interrelationship of F and I, as it has been derived from different experiments, is the same for our measurements with fishes as in the case of the human observations.[4] Both exhibit the composite character attributable to the duplex constitution of the vertebrate retina;[5] and both (at least certainly, in really comparable data, for the cone portion of the curve) are adequately described by a probability integral in which log I is the abscissa. The human data, however, have been based essentially upon flicker *fusion*, while the data with lower animals are based upon threshold response signifying marginal *recognition* of flicker. It has been desirable to demonstrate experimentally that the two kinds of observations are comparable. By essentially comparable we of course mean that the form of the functional connection between F and I may be legitimately used to develop and to test the theoretical significance of such data for the interpretation of visual responses, with confidence that in the two sorts of cases the data have the same kind of meaning. A direct proof of the adequacy of this position is to be obtained by placing the eye of the human observer in the position occupied in our apparatus by a fish or insect larva. If under these conditions a technique and procedure essentially identical with that employed for other animals provides for human responses a flicker recognition curve basically identical with that known to be characteristic for flicker fusion in human visual reactions, the required demonstration is

[3] *Cf.* Crozier, Wolf, and Zerrahn-Wolf, 1937–38 *b*, *c*.

[4] Crozier, 1937.

[5] Hecht, 1937; Hecht and Verrijp, 1933–34 *a*, *b*; Hecht and Smith, 1935–36.

manifestly provided. In other words, it may be held with some confidence that what the lower animals are responding to is properly labelled "flicker."

The simple arrangement satisfying these conditions is illustrated diagrammatically in Fig. 1. The details of procedure have been varied in a number of ways, in different experiments. In tests with fishes and the like the practice has uniformly been[1] to obtain three readings of I_c or of F_c at one time upon each of ten (or twelve) individuals, the same individuals being used in securing the entire set of measurements for an $F - I$ curve. Tests must be applied to insure that the individuals thus treated together are objectively a homogeneous[6] group. Homogeneity thus defined means that the individuals concerned are essentially equivalent, and in a long series of observations could be interchanged. The average value of F_c or of I_c for an individual $= F_1$, or I_1; the mean of these numbers for the homogeneous group of individuals $= F_m$, or I_m respectively. The reasons for this procedure have been (1) that it reduces the influence of adventitious, irrelevant errors of observation and (2) that analysis of the variations of the individual magnitudes of I_1 (or F_1) in successive tests shows[7] that they correspond to natural fluctuations of excitability (responsiveness) in any one animal.

In experiments of this type[1] the determinations of I_c are made by slowly increasing the intensity of the flashing light until response of the organism tested is obtained at I_c; the same end-point is also approached, in other trials, by fixing the intensity and slowly reducing the flash frequency until the same end-point is signalled (F_c). Reasons have been discussed[8] (and tested[9]) for the contention that, under the conditions described, $F_m - I$ and $I_m - F$ curves cannot be expected to agree but must be found to differ in a predictable way. If observations of F_1 and I_1 (as already defined) are made at intervals upon a single organism this expectation is not in question, when the method of signalizing excitation during increase of I or decrease of F is being used. It is in point if the method of careful back-and-forth

[6] Crozier, 1936.

[7] *Cf.* Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *a*, *b*, *c*, *d*; 1937–38 *a*.

[8] Crozier, 1935–36.

[9] Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *a*, *b*.

adjustment to an apparent critical point is the procedure employed—as published data unmistakably signify[10] and as our own observations unequivocally demonstrate. The importance of these considerations is of two sorts. It has a bearing upon the process whereby theoretical interpretations are tested by the adjustment of curves to the observations; it has a more direct interest for the understanding of the way in which variability of responsiveness is involved in the determination of F_c or I_c.[11]

The procedure in the present experiments has been varied in order to throw light upon certain of these points, which will be amplified in subsequent papers. The technique has some manifest disadvantages for the precise investigation of the human visual response to flicker, but it has compensating advantages. We may repeat that our primary purpose in these experiments was to demonstrate whether the curves of "response to visual flicker" as we have analyzed them in the case of lower organisms[1] are essentially homologous to the data of human visual flicker. We have therefore employed the same apparatus for the determination of both. In the method used,[1] however, the opaque stripes necessarily reflect a certain percentage of the illumination used. Whether in our tests with the human eye this fact introduces complications of interpretation could be decided only by means of an elaborate series of experiments designed to make clear the influence of area, location, and form of test patch, and of wave length of light, upon the form of the $F - I$ curve, as well as of the fundamentally significant effect of modifications of the proportion of light time to dark time (t_L/t_D) in a flicker cycle. Our experiments with fishes and with insects[12] have shown that, with the apparatus and procedure we here employ, (1) the *form* of the $F - I$ curve is not affected by changes of (t_L/t_D) and (2) that the change of F_c as a function of I is not that which appears when reflection from the blackened surface of a sector disc is a factor, but is on the contrary that obtained[13] when flicker is produced by interruption of a beam of light. Since in any case we are concerned with the *form* of the function, these interest-

[10] Hecht, Shlaer, and Smith, 1935; Hecht and Verrijp, 1933–34 *a*; *cf.* Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *a*.

[11] *Cf.* Crozier, 1936; Crozier and Holway, 1937.

[12] Crozier, Wolf, and Zerrahn-Wolf, 1937–38 *b*, *c*; 1937.

[13] *Cf.* Piéron, 1922; 1936.

ing and theoretically important features of the case may therefore be ignored.

In one set of experiments we have, with each observer, systematically obtained ten successive determinations of I_c or of F_c at each of a number of levels of F or of I respectively, on different dates. The eye was adequately adapted to darkness, and then to the level of I being used; preliminary practice then assured absence of drift in successive readings. The corresponding mean values, I_m or F_m, obviously have mainly the status of I_1 or F_1 in our tests with other organisms.[1] It is clearly not to be expected that systematic differences should be apparent between F_m and I_m at equivalent levels, unless these values are obtained (with a given observer) *at the same time.* The *variation* in I_c or in F_c is of course still expected[1] to throw light upon the interpretation of the mechanism initiating the index response. It will be shown that the variation of F_c and of I_c respectively follows different rules, which are severally consistent with the indications already provided by experiments with other organisms.[1]

In another series of tests the procedure was adjusted to correspond more nearly with that followed in the experiments with fishes and insects. Three readings of F_c were obtained on each of five occasions at each of a number of intensities. The interpretation of these data will be discussed subsequently.

It has already been remarked that the instrumental procedure here used has certain theoretical deficiencies. One of its compensating advantages is that quite low flicker frequencies can be employed and maintained with relatively high precision. This has made it possible to extend the flicker curve to $F = 1$/sec. or below, and to demonstrate that its form in the region $< F = 10$ is like that observed with teleosts. A disadvantage is that very high intensities (log I for a flash > 2.5 millilamberts) cannot be obtained or varied with adequate precision. A knowledge of the kinds of complication legitimately to be expected in the flicker curve for a vertebrate, however, makes possible a useful analysis of the form of the function without an exact knowledge of the maximum to which the $F - \log I$ curve rises.[14]

[14] In any case, the observable value of the maximum may be adventitiously affected by decline phenomena influenced by "glare" and other factors in such a way as to be of minor analytical significance. Moreover, at very high values of F the precision of the apparatus is deficient in comparison with that obtaining (section II) at lower flash frequencies.

II

By means of two prisms and a short-focus telescope the line of sight from outside the rotating striped cylinder was focused upon the interior surface (Fig. 1). In effect, the human eye was thus put in the position of an animal located in an

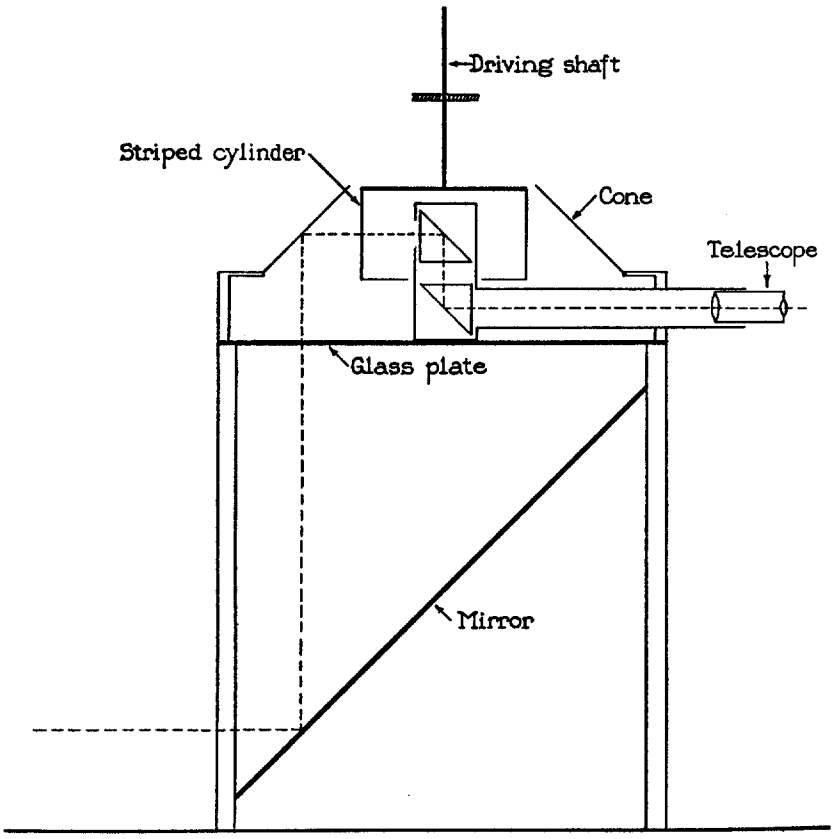

FIG. 1. The rotating cylinder device[1] (diagrammatic) as modified for measurements of human response to flicker. The apparatus is essentially the same as used for tests with lower organisms. By means of a set of two prisms and a telescope the observer views the striped cylinder in the position of an animal placed inside the striped screen. The visual field is square, with a visual angle of 14.3° on an edge.

aquarium inside the cylinder,[1] with the difference that only a patch of the surface was now exposed to view. Square diaphragms in the viewing tube (Fig. 1) delimited a square field with vertical edges parallel to the edges of the opaque

stripes on the cylinder. The visual angle of the field was about 14.3° on an edge. A large field (with central fixation) was employed partly in order to test a possible influence of the number of divisions between light and dark areas; using cylinders with different numbers of equally spaced stripes, and thus of different stripe widths, it was found that there was (within the range used) no effect due to the number of dark bars in the field.

A square field has disadvantages as compared with a circular one, since flicker at the corners may be apparent at an intensity below that which is critical for the center of the field. It is also clear that the method of transillumination of the cylinder allows light to be reflected from the inner surface of the opaque stripes. The complications arising in this way are of no consequence for our immediate problem, since the proportion of light time to dark time in a flash cycle was kept constant at 1 and we are concerned only with the form and structure of the curve.

Observations were made by the method used with lower animals. With a fixed illumination the speed of rotation of the cylinder was slowly reduced from a high level until the observer signalled the operator that flicker was recognized. In the converse test, with a fixed flash frequency the intensity was slowly increased from zero until flicker was signalled.

The intensities were obtained from calibration curves giving measured illumination at the eye piece of the telescope as a function of diaphragm opening.[1] No attempt was made to correct for pupil area. Cylinder revolution speeds were measured by means of milli-voltmeter readings from a magneto geared to the cylinder driving-shaft.[1] Speeds were adjusted with coarse and fine rheostats in the motor circuit.

Observations were taken in groups of ten successive determinations of the flicker response point (I_c, or F_c). The order of succession of levels of F, I was so arranged as to reveal any drift with time or practice. Fatigue of the observer was avoided as much as possible. In a few cases successive determinations of F_m and I_m were made at the same level.

Data secured with two observers, after preliminary practice on a number of days, are set out in Fig. 2. The curves are of the same type in the two cases, but exhibit interesting differences. The general form is that already found by other observers using rotating sector devices.[10, 5] There can be little doubt that the form of the flicker function has not been influenced by the fact that the opaque bars are moving across the field. The end-point used in the observations of Fig. 2 was a flutter of the field; a slightly higher intensity is required at each F to give definite response to the direction of movement of the bars, but there is no doubt that curves obtained with this end-point would have the same form.

The area of our square 14.3° field is a little less than that of the 19° circular field used by Hecht and Smith (1935–36). The curves have very much the same morphology: the maxima for rod and cone parts are about the same, and even the indication of a slight hump near $F = 35$ is also apparent in all these curves; the slopes of the practically rectilinear parts of the graphs are about 10.4 for E. W., 12.0 for

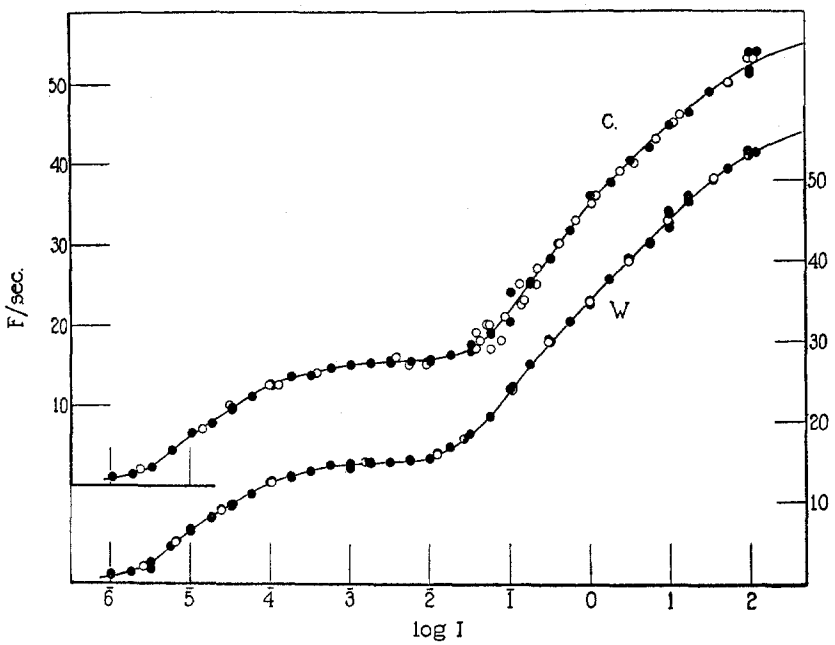

FIG. 2. The relation between critical flash frequency F and critical intensity I for human response to flicker. Solid circlets, F_m at fixed intensities I; open circlets, I_m at fixed F.

Upper curve, left eye of W. J. C.; lower, left eye of E. W. (F scale at the right).

The data shown are from homogeneous sets of measurements taken on a series of successive days, after considerable practice. Each plotted point is the mean of ten readings. Total number of observations: W. J. C., 1,220; E. W., 880.

W. J. C., and 12 – for E. L. S.; the separation of the rod and cone curve inflection points is identical, 3.45 log units in all three cases. These facts, together with others subsequently discussed, show that the curves in Fig. 2, obtained by the rotating cylinder method, represent the typical properties of the critical flicker mechanism for human visual excitation.

The corresponding curves for fishes[1] are very similar. They cover about the same intensity range, but (especially with allowance for the effect of temperature[7]) are on the whole situated at lower levels of intensity, despite the fact that the signalling response involves reaction to the direction of movement of the stripes; a further element in this case is the fact that the whole retina is excited by a field of unlimited extent. The cone curves for various fishes are usually steeper. The rod curve for fishes is of lower maximum F, and at a definitely lower intensity as a whole. Thus the extent of separation of the inflections in rod and in cone portions is definitely greater (about 5 log units) than in the human curves. The latter fact is of special interest for the analysis of the composite graph (section IV).

III

1. The variations in successive determinations of the flicker endpoint follow the general rules already obtained for motor reaction to photic flicker in lower animals.[1] The experiments were not specifically designed to examine all the properties of this comparison. In a later connection we expect to do this more critically, with apparatus designed for use with the human eye. One difference in the nature of the data is to be noted: the properties of the scatter of I_1 and of F_1 were, in the latter cases, obtained from the values of I_1 or F_1 as averages of three measurements each on each of a set of individuals, the several individuals being demonstrated to be equivalent. The reasons for this procedure have been described.[1] In the present instance, $P.E._{.1_I}$ and $P.E._{.1_F}$ are based upon a set of ten successive readings with one individual. They therefore correspond to the "within animal" variation which can be established as a mean value, by a variance test procedure, in the earlier series with *Anax* and fishes. If our readings are averaged in groups of successive 3's the means of these averages are correlated; consequently we cannot by this method obtain values of P.E. which escape the restriction of our present method. The two human observers give $F - \log I$ curves which are less alike than those of two individuals in our sets of *Anax* or of fishes, hence the data cannot be averaged.

The factors influencing the capacity to give variation in response (*i.e.*, the *variability*[15]) can probably be kept in a more uniform state,

[15] Crozier, 1929.

from time to time during a period of a month, in a carefully maintained set of the animals previously used than is possible with a human individual. The data show, however, that the relation of I_m to P.E.$_{1_I}$ (Fig. 3) is of the same kind as appears in the former cases. The curves for the 2 observers are the same, although the operators of the instrument were different. Up to about log $I_m = \bar{1}$ the two are directly proportional, and the proportionality constant (with P.E.$_{I_1}$ corrected

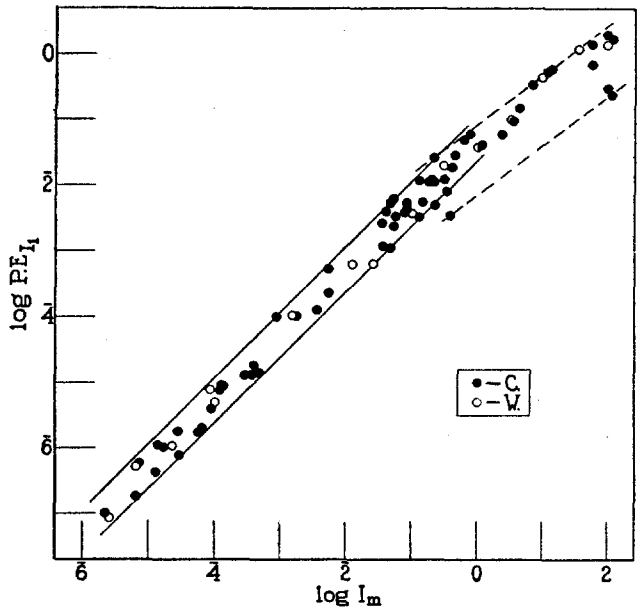

FIG. 3. The scatter of I_1 as a function of I_m. Solid circlets, W. J. C.; open circlets, E. W. Up to log intensity = *ca.* $\bar{1}.5$, I_m and P.E.$_{I_1}$ are directly proportional (slope on log grid = 1); see text.

for numbers) is about the same as with other organisms. At still higher values of F the slope on a log grid becomes less. The data on fishes show the same thing.[16] The human $F-I$ curve cannot be pursued to higher intensities with our apparatus, but presumably it would then show a continuation of this effect. For the two observers the course of the function is essentially the same. The lower portion, with slope = 1, gives P.E.$_{1_I}$ = *ca.* 5.4 per cent of I_m, about one-half

[16] *Cf.* also a subsequent paper on *Triturus*.

the value obtained with human visual intensive discrimination.[17] Where the slope becomes < 1 (about 0.76) the proportionality can be made direct by assuming a new origin (*i.e.*, adding a constant to I_m: *cf.* Crozier, 1935–36; Crozier, Wolf, and Zerrahn-Wolf, 1936–37*d*). The change in the curve (Fig. 3) shows that σ_{I_1}, rather than $\sigma_{\log I_1}$, is the significant measure. The vertical breadth of the inclusive band is about $1.6 \times$ P.E.$_{1_I}$, which when corrected for number of observations gives 5.06–a number larger than that obtained with fishes.[18] The vertical breadth of the band, a little > 0.6 log unit, is about the same as for human visual intensive discrimination[17] and less than that found with auditory and tension excitation. (These particular comparisons are merely intended to be suggestive: the interesting problems concerning the experimentally determinable properties of P.E.$_I$ and of P.E.$_{\text{P.E.}_I}$ require data of greater homogeneity before it can be decided if the proportionality between the two really has more than a simple and necessary statistical basis; the present indication is that it has.)

The variation in F_1 is a slightly more complicated matter. The between-individual variation, with *Anax* and with sunfish, rises to a maximum at each inflection of the $F - \log I$ curve. The mean *within*-individual variation also passes through a maximum, but at a definitely higher intensity. Beyond $F_m =$ about 70 per cent of $F_{max.}$, in each case,[19] the within-individual variation exceeds that between individuals. This curious result is also apparent in the data of geotropic orientation by rats (Crozier and Pincus, 1939), which are in several senses comparable to the data of visual flicker; its real significance is thus made more probable. The present measurements of P.E.$_{1_F}$ correspond to the indices of within-animal variation, and are on the whole lower than with the other organisms. But they are complicated by the fact that in successive sets of readings a given individual does not retain the degree of uniformity in variability which is assured in the experiments with *Anax* and sunfish. The result is that the scatter of P.E.$_{1_F}$, like that for P.E.$_{1_I}$, is absolutely and relatively larger in these human measurements. The comparison

[17] *Cf.* Crozier and Holway, 1937; Holway and Crozier, 1937 *a*, *b*.

[18] Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *d*; 1937–38 *a*.

[19] Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *c*, *d*.

can be made by considering the behavior of the extracted mean variation, in terms of σ_F', within animals, as calculated for the data[1] on sunfish. Each such value should carry with it a σ_{σ} proportional to its own magnitude (although it is possible that the proportionality factor is a function of the level of light intensity), so that on a log σ scale the vertical scatter of σ_F' should tend to be constant. Fig. 4 shows that the index of variation rises to a flat maximum in the neighborhood of log $I = \bar{5}.5$, and again at about log $I = \bar{1}.0$, and that at still higher intensities it again increases. This agrees with the indications given

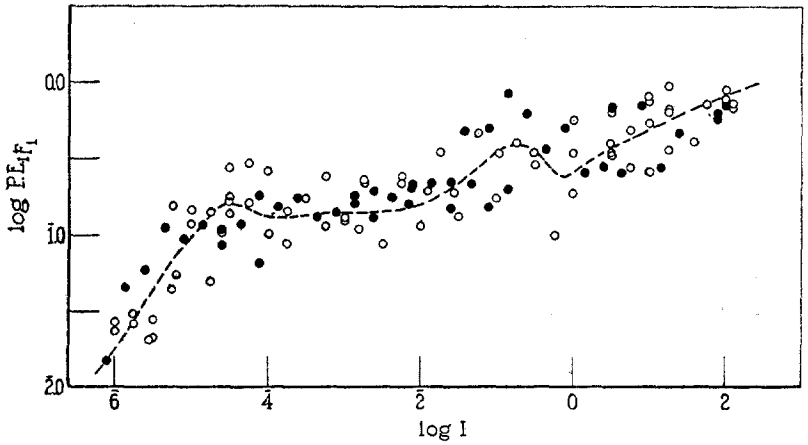

FIG. 4. P.E.$_{1F_1}$ as a function of log I. Solid circlets, W. J. C.; open, E. W. To facilitate comparison, the plot for C. has been moved 0.1 unit to the right and 0.25 units vertically on the log grid. The vertical width of the band should tend to be statistically constant, if the same shift is appropriate for the two parts of the curves. See text.

by σ_F' in the sunfish data, except that the terminal increase is greater. The final increase corresponds with the increasing introduction of purely experimental errors (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1936–37*a*, *b*) when the highest values of F are involved; it also depends upon increasing difficulty in the judgment of a consistent end-point, particularly with this apparatus in which slight lack of verticality in the cylinder holder tends to produce "ghost flickers." The fact that P.E.$_F$ tends to increase, at the highest intensities, while the relative increase in P.E.$_I$ becomes less, indicates, in view of the otherwise close

interconnection of the two, that purely instrumental errors there play an increasingly larger part. At the high end of each curve there is found a greater scatter of the points (Fig. 2), absolutely and relatively, although P.E.$_I$ increases relatively less rapidly; this indicates greater variation in the nature of the end-point actually used, but consistency in its use within each set of readings.

2. The conception that, in the absence of too large a proportion of instrumental errors, the values of P.E.$_{F_1}$ and P.E.$_{I_1}$ are intimately related and are produced as a consequence of the basic variability of the organism[1] gives rise to the prediction that the curves for F_m *vs.* I and for I_m *vs.* F will not be identical. If many measurements are made with one individual over a period of time, the two sets of determinations should however intermingle. A test of the prediction with one animal can really be made, therefore, only by comparing pairs of determinations of F_m and I_m made in succession. When single determinations of F and I are made by a process of careful adjustment by continued small changes until a satisfactory point has been achieved, the measurements then have, of course, the significance of internally averaged F_m and I_m (Crozier, 1936), and the differences between them become more immediately obvious. The expectation[1] is that if I_m is found at a given F, and then F_m is obtained at this value of I_m, F_m will be larger than F and $F_m - F$ will pass through a maximum at each region of inflection of the $F - \log I$ curve.

The pairs of determinations which are available for this test with our human data are plotted in Fig. 5. They show that the expectation is not contradicted by the present facts. Consecutive values of I_m, F_m show the expected differences, which separately measured pairs do not. Since the adaptation of the eye might be in a steadier state when F_m is being measured, by comparison with the condition when successive values of I_1 are taken, it is clear that the data have really not been influenced by differences in the mean level of adaptation.

It is therefore possible to state that the properties of P.E.$_I$ and of P.E.$_F$ are consistent with those observed with lower animals.

3. The nature of the variation of I_1 and of F_1 is such as to suggest rather definitely that it is the whole $F - \log I$ function which is randomly fluctuating. Whether its several parameters vary with time independently cannot be decided. The whole curve cannot be deter-

mined "instantaneously." But it is clear that in the low intensity part of the curve this kind of fluctuation is relatively more pronounced. Other sets of our measurements (on W.J.C.) show that data secured at a different time may follow a curve, in the rod region, in part separated by +0.2 log unit from that shown in Fig. 2 and rising to a slightly higher maximum. Fluctuations of this sort have been obtained by other observers (*cf.* Hecht and Smith, 1935–36). It is probable that at least part of this effect is due to fluctuation in the way in which the lower tail of the cone function is able to play a part in the response to flicker. In one of the teleost species we have

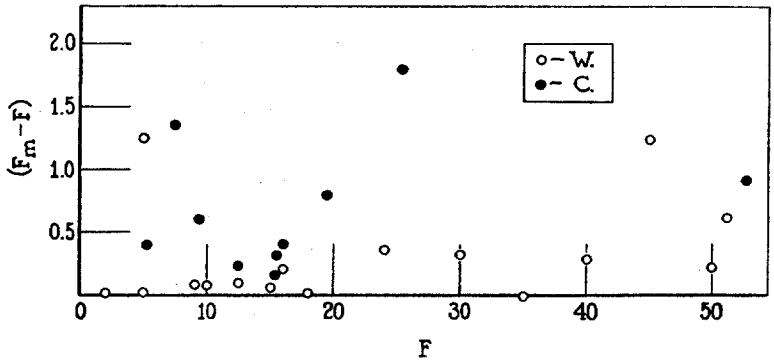

FIG. 5. The difference ($F_m - F$) between F and F_m at the value found for I_m at F, in series of this sort made in immediate succession, is positive. Only in the regions of inflection of the F – log I curve does it rise above 1.0. Its scatter should be greatest here also, and (for other reasons: see text) at the high end of the curve.

examined (Crozier, Wolf, and Zerrahn-Wolf, 1937–38*a*) an analogous effect was noticed; in the human curve the degree of overlapping of the rod and cone contributions is more extensive (Fig. 8), and the fluctuation in the rod part of the curve would be expected to be more pronounced.

It is consistent with this interpretation that considerable variation in I_m should be encountered at the intensity level deduced for the fading out of the influence of the rods upon F_c. This is at about log $I = \bar{2}.8$. The data in Fig. 2, and other measurements, confirm this expectation. It is probably significant that (Fig. 3), as in our experience with fishes (Crozier, Wolf, and Zerrahn-Wolf, 1936–37*d*; 1937–

38*a*), the "break" in the curve of log P.E.$_{I_1}$ *vs.* log I_m comes just beyond the point at which the declining rod curve stops.

IV

The flicker response curves (F, log I) for fishes have been resolved into two additively component probability integrals, respectively the contributions made by rods and by cones to the determination of F_c. The structure of the curves shows that beyond a certain intensity the effectiveness of the rods declines. The diminishing contribution

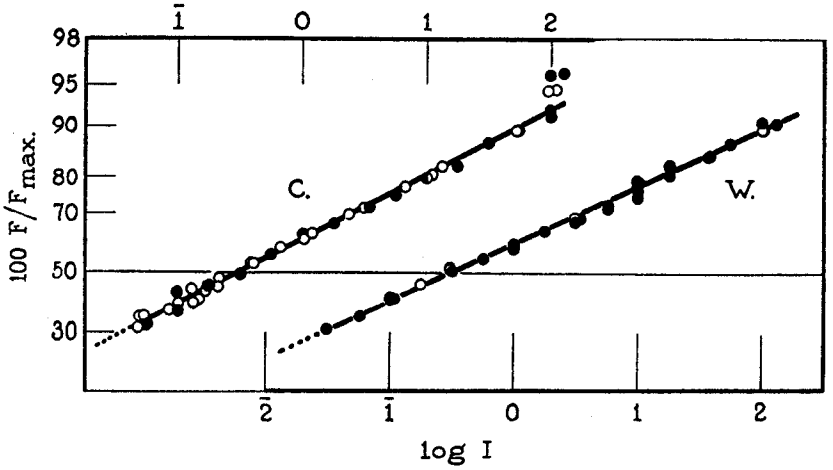

FIG. 6. F *vs.* log I on a probability grid. Solid circlets, F_m; open circlets, I_m; the data of Fig. 2, above F = 18. For C., $F_{max.}$ = 56.0; for W., 59.0. (The limits of horizontal scatter of the points agree with calculation on the basis of Fig. 3. The extreme departures at the upper end of the C. curve (3.8 per cent) are commented on in the text.)

of rod function follows a reversed probability integral.[1] Arthropods with large convex eyes give asymmetrical F, log I curves; the distorted probability integral form of these curves has been shown to be due to the mechanically disadvantageous location of the marginal ommatidia of the eye, reducing their contribution at lower intensities.[20] The data on human flicker fusion, in the cone part of the curve, are well described[4] by a probability integral. The separation of the centers of the rod and the cone sections of the human flicker curves is relatively less on the log I axis than with the fishes, and the total rod

[20] Crozier, Wolf, and Zerrahn-Wolf, 1937–38 *b*, *c*.

effect is larger. This brings it about that the overlapping of the zones of activity of rods and cones in human flicker recognition is more extensive, although with the fishes the decay curve for the rods is at a relatively higher intensity and more widely separated from the ascending rod curve.

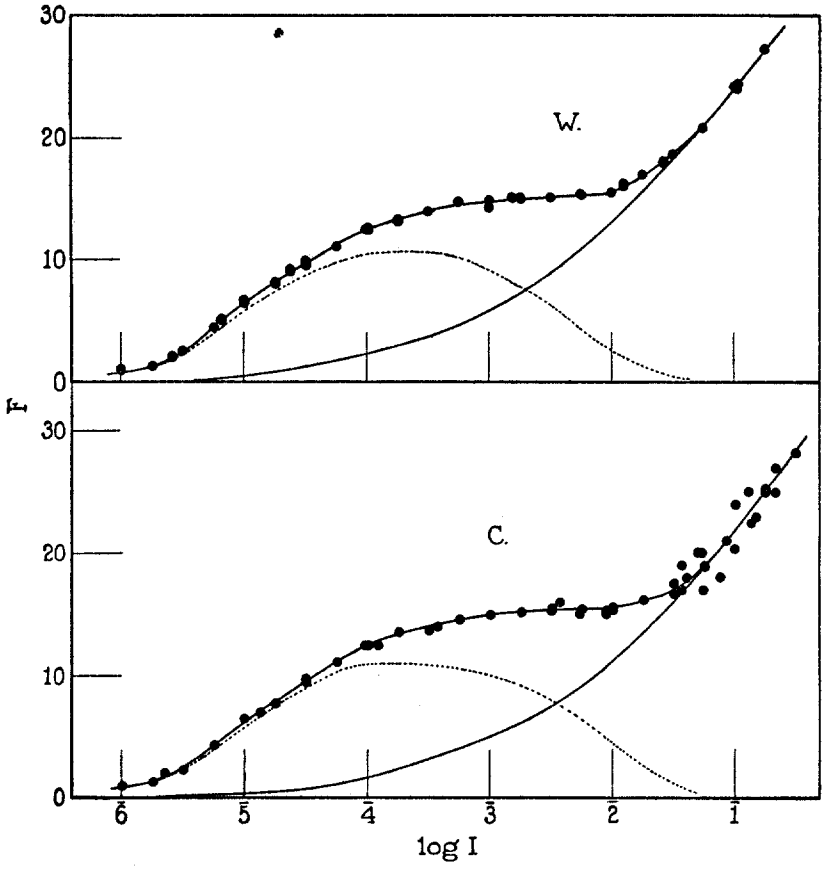

FIG. 7. The lower parts of the curves of Fig. 2. The probability integrals of Fig. 6, for the cone portions, have been extrapolated to $F = 0$. The difference curve is shown, dotted; its rising and falling branches are each fitted by a probability integral (Fig. 8).

The curves in Figs. 6, 7, and 8 show that this analysis gives an adequate description of the human flicker response measurements. The maxima $F_{max.}$ are found by trial: the experimental difficulties in the production of higher intensities, the effects of glare, and other

conditions make it impossible to complete the curves with this apparatus. There is very small latitude indeed, however, in the selection of $F_{max.}$ for a reasonably fitting curve. The test of a good fit is (1) that it obviously runs through the plotted points, (2) that it contributes adequately to the resolution of the composite graph, (3) that its parameters have the properties rationally expected of the standard deviation, maximum, and abscissa of inflection of a probability integral of excitation elements. The experiments with different kinds of organisms[4, 7] show that these criteria have been met fairly well.

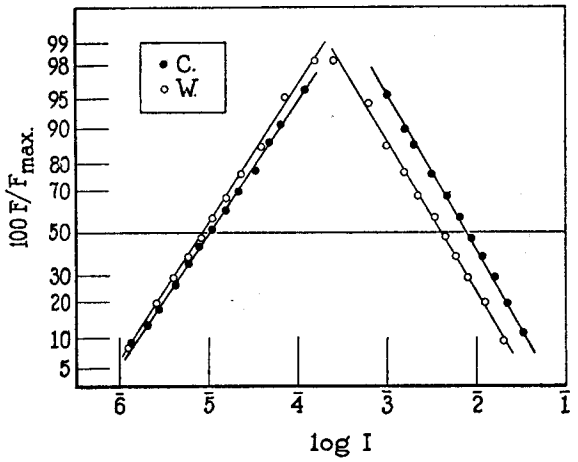

FIG. 8. The rising and descending portions of the rod contribution curve obtained in Fig. 7 are each described by a probability integral. See Table I. (The points are read from the curves in Fig. 7.)

The cone parts are well fitted, down to *ca.* $F = 18$ (Fig. 6). The extension of the probability curve to the log I axis gives by difference the (dotted) curve attributed to rod activity in the discrimination of flicker (Fig. 7). The ascending and the descending limbs of these curves are also well fitted by probability integrals (Fig. 8). In our measurements with fishes the separations of rod and cone components of the curves are so great that the entrance of cone activity produces a distinct bump on the flat intermediate part of the graph. This "anchoring point" for the extrapolation of the cone integral is not available in the human data. It has been pointed out[21] that in different organisms cases are to be expected in which the extent of over-

[21] Crozier, Wolf, and Zerrahn-Wolf, 1936–37 *d*, p. 430.

lapping of rod and cone curves varies. When overlapping is so complete as in Fig. 7, a test of the resolution by extrapolation of the cone curve can be made by seeing if the *uncorrected* rod data follow a probability integral. Tests prove that they cannot be rectified on a probability grid.

The curves for our two observers show the same kind of structure despite differences in the parameters of the rod and cone functions (Table I). The cone maximum and rod maximum differ independently (as proved, also, in our experiments with fishes[18]). But a higher maximum goes with a higher intensity (τ') at the inflection point and larger proportionate spread of the underlying frequency distribution of effects as a function of log I. This is also indicated by the data of other observers.[10] There is indicated throughout these comparisons a

TABLE I

Constants for the Flicker Response Curves of Figs. 2 and 8; F As Percentage of $F_{max.}$ vs. Log I. τ' = log I at Inflection of the Curve

Parameter	W.J.C.	E.W.
$F_{max.}$, cones	56.0	59.0
$F_{max.}$, rods	11.6	10.5
τ', cones	$\bar{1}.48$	$\bar{1}.50$
τ', rods	$\bar{5}.00$	$\bar{6}.93$
τ', declining rod curve	$\bar{3}.87$	$\bar{3}.61$
σ log I, cones	1.14	1.28
σ log I, rods	0.42	0.40
σ log I, declining rod curve	0.34	0.35

consistency with the expectations derived from the conception that the flicker response curve (F, log I) is essentially a probability integral of which the parameters are determined by the structural organization of the particular individual.[22] The properties of these parameters as functions of genetic composition, age, experimental treatments, and other factors, present numerous significant problems.

V

SUMMARY

Using the rotating striped cylinder device previously employed for determination of the flicker response function with lower animals,

[22] Crozier, Wolf, and Zerrahn-Wolf, 1937; 1937–38 *a*.

corresponding measurements have been made with human observers. The curves based upon the relation between critical flash frequency and critical intensity for the signalling of the recognition of flicker have the properties of human flicker fusion data as obtained by other methods. They also have the quantitative properties of the flicker curves provided by the motor responses of insects and fishes to the seen movement of flashes. This applies to the variation found in repeated measurements as well as to the nature of the analytical function describing the connection between flash frequency and intensity. The data for human visual flicker and those for the responses of lower animals are therefore essentially homologous.

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