

ON THE VARIABILITY OF CRITICAL ILLUMINATION FOR  
FLICKER FUSION AND INTENSITY DISCRIMINATION

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I

The properties of events constituting stimulation or excitation are established by measurement of aspects of excitation as functions of the exciting energy. This involves the averaging of measurements of response, or of energies associated with a chosen index of responsiveness, or of both. The real meanings of such averages may be quite different in the several instances, with regard to the uses to which it may be desired to put them. The averaging process itself may not be overt, but may be concealed in the method whereby the recorded observations are obtained.

When indices of the dispersions of the measurements entering into such averages can be given, additional information may be secured which is of distinct utility. It can provide criteria for the homogeneity of the assemblage of data. It also makes possible a functional analysis of variability of organic performance (*cf.* Crozier, 1935). And these indices of dispersion appear to have a very important bearing upon the interpretation and the use of the data of sensory discrimination; they have of course long been employed, in a sense, in connection with the so called psychometric functions, but it seems without adequate realization of certain of their properties. In the customary type of experiment, for example, two intensities of an exciting variable are judged just equal, but it is of course their *effects* which are seen not to be detectably different. The distinction is real and necessary; it is required to obtain independent but congruent information concerning the relation between intensity and effect before the basis for the distinction of two effects can be understood. A larger discussion of this matter will be undertaken elsewhere. We wish to deal now

with certain empirically determined properties of the data upon which the curves of some visual functions are based. These serve to extend the variety of cases in which the laws of organic performance are equally evident in the variation of the measurements and in the means (*cf.* Crozier, 1929; Crozier and Pincus, 1927-28; 1929-30; Wolf and Crozier, 1932-33; Crozier, 1935). The data to be discussed have it in common that they depend upon the comparison of alternately disposed stripes of equal width illuminated by two intensities, one of which may be zero. They also have it in common that they are based upon constant numbers of observations in each series. It is important to discover if the analysis of objective measurements possessing a certain homogeneity of character shows their properties to be similar to those of subjectively based judgments or decisions in similar tests. The comparison of findings and relationships in the present inquiry with those which result from the examination of properties of subjective judgments of just noticeable difference may be expected to provide an interpretation of the nature of such judgments as they are functionally dependent upon variables experimentally controlled.

## II

When intensity discrimination is measured in the eye of the bee (Wolf, 1932-33*a, b*) by using a moved background of alternating equally wide stripes respectively illuminated by intensities  $I_1$  and  $I_2$ , a threshold response is obtained from the bee when  $(I_2 - I_1)$  has a certain mean value for each magnitude of  $I_1$  and for stripes of a given width.  $I_2 - I_1$  defines a value of  $\Delta I$ , the "just detectable difference of intensity" characteristic of  $I_1$  (or of  $I_2$ ). It is sometimes overlooked that  $\Delta I$  is described not only by its mean value, but also by the properties of the frequency distribution of the measurements from which average  $\Delta I$  is computed. From the standpoint of demonstrating the propriety of deriving quantitative laws for the performance of biological systems, in the face of the variability which all properties of organisms manifest, it has been important to demonstrate that the variability of measurements of performance, for example of  $\Delta I$  regarded as a measure of excitability, is lawfully related to the independent quantity  $I$  responsible for the effects measured under the given conditions (*cf.* Crozier, 1935). It is also to be demonstrated

that the variability of such measured indices as  $\Delta I$  must be carefully considered in the light of the manner in which mean  $\Delta I$ 's emerge from the experimental procedure, before fully effective theoretical use can really be made of them.

From the data secured with the visual response of the bee (Wolf, 1932-33 *a, b*; 1933-34) it was possible to show (*cf.* Wolf and Crozier, 1932-33) that for intensity discrimination by the method described the curves obtained on plotting the "Weber fraction"  $\Delta I/I_1$  against  $\log I_1$  are of the same form as those given by  $\sigma_{(\Delta I/I_1)}$  against  $\log I_1$ , for each width of stripes employed (*i.e.*, for the various visual acuities called upon);  $\sigma$  = standard deviation of the mean; the number of observations entering into each average is the same for each value of  $I$ . This says that one can write

$$\delta(\Delta I/I_1) = \phi(I_1) = k\delta(\sigma_{\Delta I/I_1}).$$

By the procedure employed in obtaining these data  $I_1$  is fixed when each value of  $\Delta I$  is obtained. (When the method used involves simultaneously changing both  $I_1$  and  $I_2$ , but keeping the ratio constant, it may be impossible to undertake a satisfactory analysis of the observed variations in sensitivity. The reasons for this will be considered in detail elsewhere.) Hence  $\sigma_{(\Delta I/I_1)} = \sigma_{\Delta I}/I_1$ , and since  $\sigma_{\Delta I} = \sigma_{I_2}$ , we have  $d(\Delta I/I) = kd(\sigma_{I_2}/I_1)$ . In other words,

$$\Delta I = k\sigma_{I_2} + \text{const.}$$

This is directly illustrated in Fig. 1. The slope of  $\log \Delta I$  as a function of  $\log \sigma_{I_2}$  is constant, and is not distinguishably different from 1. The position of the graph on the coordinate grid differs slightly from one lot of bees to another in experiments made at different times, but is the same for the same lot, and  $k$  is independent of  $I$  and of the width of the test stripe. In Fig. 1,  $\log P.E._{\Delta I}$  is given as a function of  $\log \Delta I$ .  $P.E._{\Delta I} = 0.6745\sigma_{\Delta I}$ , and is the same as  $P.E._{I_2}$ . For Series *A* (Wolf, 1932-33 *a*), first set, there is a slight apparent difference in slope from that given by the measurements with other widths of stripe; the experiments were done a year before the others, and are shown separately. The upper limiting line has a slope of 1. Error in the setting of  $I_2$  at very low values might well make  $P.E._{I_2}$  there appear too high. The breadth of the band should be constant, since  $\sigma_{P.E._{I_2}}$  should be

proportional to  $P.E._{I_2}$ ; in Series *A* this seems not to be the case; at the upper end of the graph the breadth is that given by the other measurements; it is to be presumed that a larger number of determinations in this series would show the band broader at the lower end. A second set of tests (Wolf, 1932-33 *a*), also shown in the left hand graph (Fig. 1) supports this view. The relationship of  $\Delta I$  to  $\sigma_{I_2}$  is independent of the width of the stripes in the test pattern.

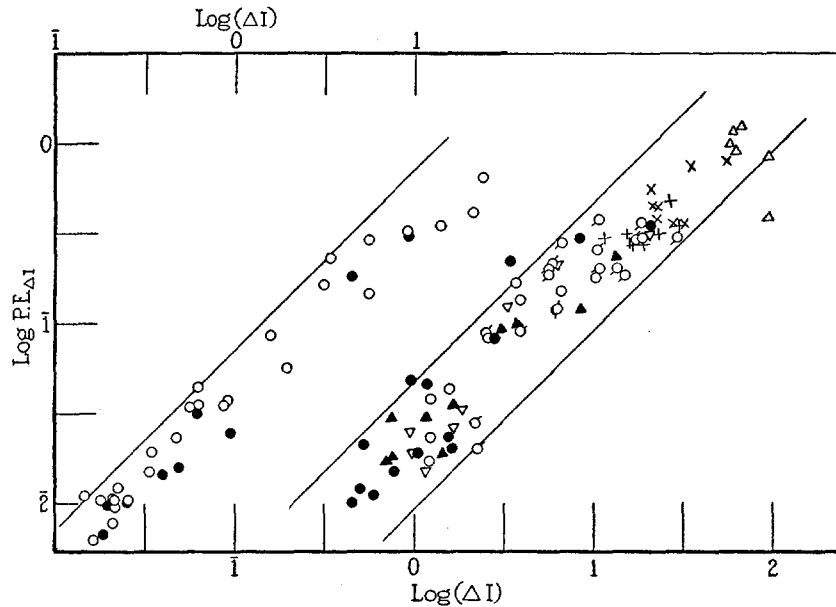


FIG. 1.  $\text{Log } P.E._{\Delta I}$  as a function of  $\text{log } \Delta I$ , from experiments on intensity discrimination by the bee (data in Wolf, 1932-33 *a, b*; Wolf and Crozier, 1932-33). Data from one series, the earliest (Wolf, 1932-33 *a*, "Series *A*") are shown separately at the left; see text.

The proportionality of  $\Delta I$  to  $\sigma_{I_2}$  (or  $\sigma_{\Delta I}$ ) has a very interesting bearing upon the problem of intensity discrimination. It is not our purpose to enlarge upon this at the moment. But it is of value to indicate that the rule is obeyed under conditions such that the bee's capacity to respond is changed, not by altering  $I$ , but by employing the animal's changing photic sensitivity during dark adaptation. In this case, the magnitude of  $I$  required to elicit a threshold response declines with

the length of time during which dark adaptation has taken place (Wolf and Zerrahn-Wolf, 1935-36*a*). The method here consists in having stripes (of maximum usable width) alternately illuminated by intensity  $I$  and dark; the same threshold response is employed, and values of  $I$  are found which give the threshold response at times  $t$ .

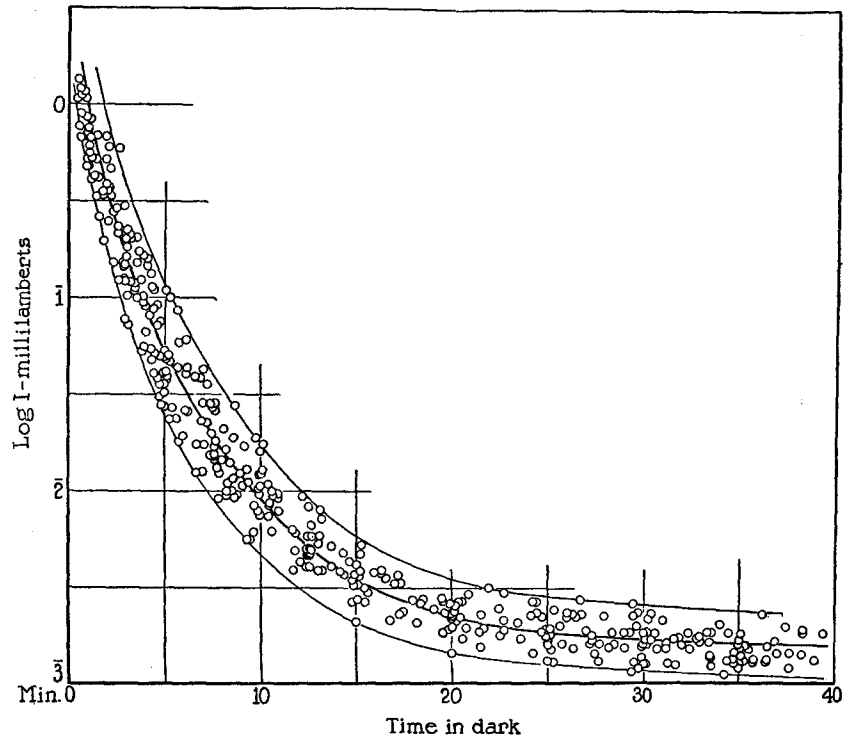


FIG. 2. Dark adaptation in the bee; individual determinations of photic intensity required to produce reaction to a stripe system after various periods in darkness subsequent to light adaptation; see text.

The single readings obtained in this way are scattered in a band with definite enveloping margins. When  $\log I_1$  is plotted as a function of time in the dark the curve is not hyperbolic (Fig. 2), but the line of central tendency corresponds quite precisely with that given by the equation

$$-\log(\log I_t/I_f) = kt + \text{const.}$$

where  $I_t$  = mean  $I$  and at time  $t$  and  $I_l$  = mean least intensity (Wolf and Zerrahn-Wolf, 1935-36a). The lowest intensity evoking response at time  $t$  is labelled  $I_a$ , the highest  $I_b$ . These must be estimated, in the

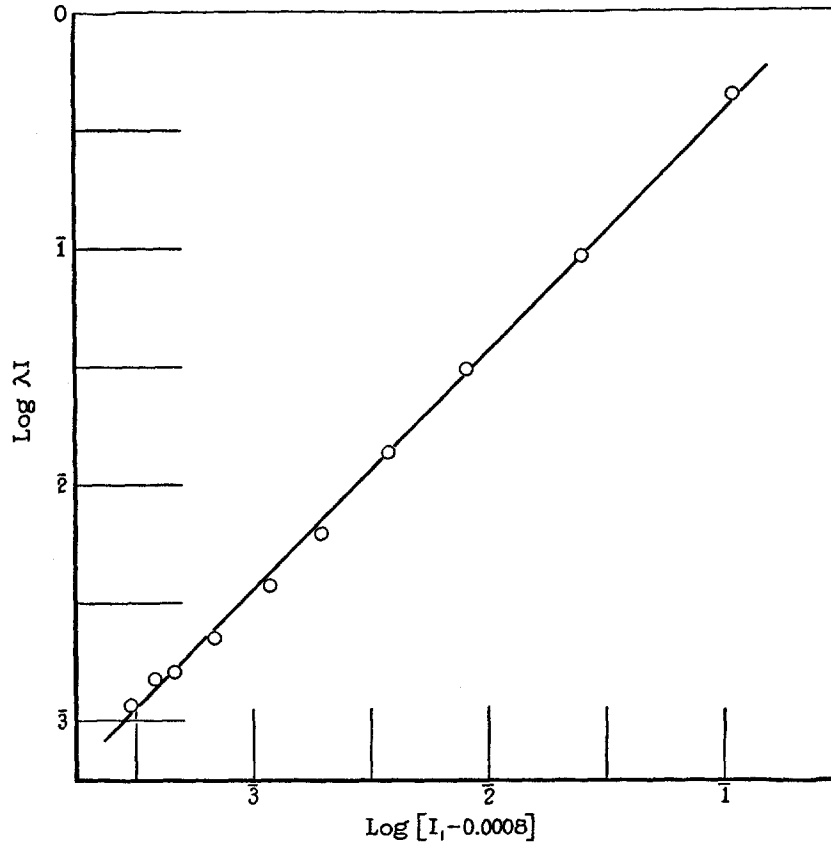


FIG. 3.  $\log \lambda I$ , the latitude of variation of intensity required for threshold response to a stripe system at various levels of dark adaptation, as a function of  $\log I_1$ , the lowest intensity giving the response at the respective levels of dark adaptation (*cf.* Fig. 2);  $\log \lambda I$  is directly proportional to  $\log (I_1 - \text{threshold } I)$ , and the slope = 1.

nature of the case, from the marginal envelopes fitting the array of plotted points. The latitude of variation, at fixed time  $t$  is  $(I_b - I_a) = \lambda I$ . The method of obtaining the threshold response is such that  $\lambda I$

corresponds in meaning to  $\sigma_{I_2}$  in the tests already considered, and in the experiments on visual acuity (mentioned subsequently),—provided equivalent care has been employed in making each separate measurement; the consistency of the behavior of  $\lambda I$  makes it clear that this requirement has been met.  $\lambda I$  is directly proportional to  $I_a$ , so that

$$\log \lambda I = \log [I_1 - 0.0008] + \text{const.},$$

(see Fig. 3). The constant 0.0008 corresponds to the fact that there is an upper limit of excitability, and consequently an asymptotic lower limit of  $I$  capable of evoking the response with stripes of the width used (*cf.* Fig. 2). Since the distribution of  $I$  is “normal,”  $(I_a + I_b)/2$  corresponds to the mean value of  $I$  ( $= I_m$ ) at each  $t$ ; hence  $I_m$  is directly proportional to  $\lambda I$ . In this respect the array of individual determinations is comparable to that seen in curves of frequency or speeds of vital activities as a function of temperature (Crozier and Federighi, 1924–25; 1925; Crozier and Stier, 1924–25; Crozier, 1929; 1935). In the present case, the latitude of variation of  $I$  is directly proportional to  $I$ . This indicates, among other things, that the variation in  $I$  is not fundamentally caused, at constant  $t$ , by fluctuations in the velocity of dark adaptation due to its being a complex process, otherwise  $\lambda I$  could scarcely follow the same law as  $I_m$ . The distribution of the determinations in a band of this sort shows the latitude of distribution of the probabilities, at each value of  $t$ , that a given bee will exhibit the index-response.

If two values of  $I$ ,  $I_1$  and  $I_2$ , were to be distinguished as just detectably different, at various levels of  $t$ , on the basis of a uniform statistical criterion applied to the system illustrated in Fig. 2, namely in terms of their abilities to call forth just threshold response at different levels of receptivity, it is clear that,  $I_1$  being fixed and  $I_2$  being adjusted,

$$\Delta I = I_2 - I_1 = k\sigma_{I_2} + \text{const.};$$

from what we have just seen,

$$\sigma_{\Delta I} = \sigma_{I_2} = k'I_2 + \text{const.},$$

and consequently  $\Delta I$  is directly proportional to  $I_2$ . It is clearly difficult to get a “ $\Delta I$ ” by this means directly, but its significance is impor-

tant. The understanding of this particular situation is made easier by the fact that one is not required to compare the magnitudes of a series of effects produced by each of two chosen intensities, but merely the probability distributions of occurrences in two sets of one constant effect—namely threshold response, at times  $t_1$  and  $t_2$  (for an analogous case, see: Crozier and Pincus, 1931–32*b* (p. 244, *footnote*); Crozier, 1935).

We may also consider that for threshold response in these tests  $I_2$  must be just distinguished from  $I_1 = 0$ . The visual angle of the stripes is kept constant, but the excitability increases with time in the dark. Hence the data give us values of  $I_2 - 0 = \Delta I$  at various levels of excitability;  $\Delta I$  is then  $= I$ , and  $\sigma_{\Delta I}$  is directly proportional to  $I$ . In either case, the result is the same as in the consideration of the data on intensity discrimination.

The limiting case of intensity discrimination is supplied by the measurements of visual acuity. Here (Hecht and Wolf, 1928–29) the width of the stripe is varied; the stripes are alternately illuminated and dark; for each width of stripe the illumination is determined which just evokes threshold response when the background is moved. It is not a question of matching two intensities on the basis of their effects;  $I_1$  is zero, and  $I_2 = \Delta I$ . Clearly, for this case also  $\Delta I/I_2 = 1$ . In terms of the preceding discussion we must expect to find  $\sigma_{\Delta I}$ , here the same as  $\sigma_{I_2}$ , to be directly proportional to  $I$ . This is best tested by plotting  $\log \sigma_I$  as a function of  $\log I$ ;  $\sigma_I$  was computed from the tabulated values of  $\log I$  in the paper by Hecht and Wolf (1928–29);  $\sigma_1$  is used in this case, since  $n$  is not the same throughout. It turns out that

$$\sigma_{I_2} = (I + 0.040)/5.02,$$

as shown in Fig. 4. The curve does not pass through the origin. When  $I = 0$ ,  $\sigma_I = 0.0079$ . This means that there is a residual variation of reaction, reflected in the variation of the settings of  $I$ , which is not fully accounted for by the influence of  $I$  upon the threshold reaction. This may well be due to the effect of transition of ommatidia from the illuminated to the “dark” state (or the reverse) (*cf.* Wolf, 1933–34; Wolf and Crozier, 1932–33; Wolf and Zerrahn-Wolf, 1934–35). In the visual acuity tests and in other tests by this method



involving the appearance of a threshold response, the frequency of such transitions is low, and small changes in this frequency are without effect upon mean  $I$  (*cf.* Wolf, 1932-33*a*); but variations in the effect of this factor would appear independently of changes (fluctuations)

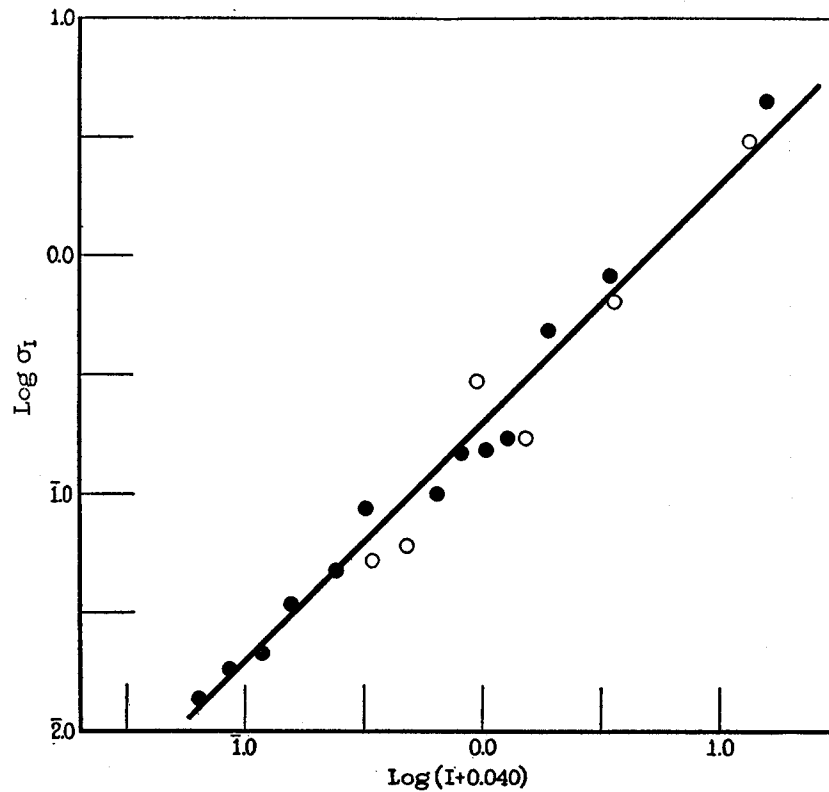


FIG. 4.  $\log \sigma_I$  as a function of  $\log I$  from data on visual acuity (bee); see text. The slope is 1. Data in Hecht and Wolf (1928-29). From the line drawn,

$$\log \sigma_I = \log (I + 0.040) - 0.70.$$

Solid circles, normal eyes; open circles, eyes opaqued on the anterior half.

in the effectiveness of  $I$ , and (since this factor is relatively without effect upon mean  $I$ ) should be detected as a constant value of  $\sigma_I$ , their presence being perceptible only through the measurements of  $I$ . The result given in Fig. 4, namely that  $\sigma_{I_2}$  ( $\equiv \sigma_{\Delta I}$ ) is directly proportional to  $I_2$  ( $\equiv \Delta I$ ), is the one already found in the data of intensity

discrimination (Fig. 1). The direct proportionality of  $\sigma_I$  to  $I$  makes it possible to fit exactly the same curve for visual acuity to  $\sigma_I$  and to  $I$ . This is shown in Fig. 5; the curve for  $\sigma_I$  is shifted laterally (by 0.720 units).

In the visual acuity tests a decrease in the width of the stripes is made up for by an inverse change in  $I$  so that a threshold excitation is

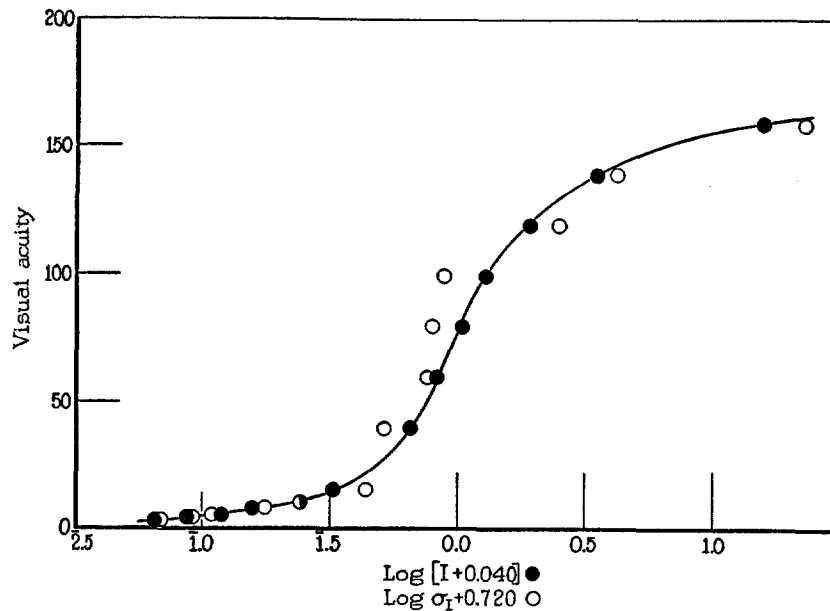


FIG. 5. The curve of visual acuity for the bee, expressed as a function of  $\log (I + 0.040)$ , also describes the relation of visual acuity to  $\log \sigma_I$ . (The fit is satisfactory in terms of the plus and minus deviations at fixed values of visual acuity; the deviations, in other words, have to be considered in the *abscissa* direction, and they are of about the same magnitude all along the curve.)

induced by movement of the visual field. It has been shown with the bees that the phototropic effects of two illuminated fields of similar contour but differing in area and in illumination become equal when the product of area by intensity is the same for both fields (Wolf and Zerrahn-Wolf, 1934-35). Moreover, to a flickered field, below the critical frequency of interruption, the reaction is greater than to a non-flickered field of the same mean intensity. It might then be

assumed that the total stimulation at the threshold for response must be taken as proportional to  $I$ , to  $V$ , and to  $1/V$ , where  $V$  is the visual angle subtended by a stripe, and  $1/V$  measures the frequency of transitions from dark to light. Hence the stimulation should be proportional to  $I$ . Variations in the threshold sensitivity would be reflected in variations of  $I$ . But since the same fraction of the field is illuminated with all stripe widths, namely 50 per cent, the total number of receptors functioning must be higher if  $I$  is higher, assuming a frequency distribution of intrinsic thresholds (Hecht and Wolf, 1928–29). But if a larger number of receptors is involved when  $I$  is higher, a lower frequency of excitation should suffice. One way out of this difficulty is to recognize that the threshold excitability of a receptor shows cyclic changes, but that the *average* excitability of all ommatidia is the same. It has not been found possible satisfactorily to rectify the curve connecting visual angle with  $I$  for threshold response (in the bee) in such a way as to show that visual angle and  $I$  are related reciprocally; that is,  $(V + m)(I + n) \neq \text{const.}$ , where  $m$  and  $n$  are constants. But when the area of the eye is reduced by painting over a portion of the ommatidial surface, the intensity required for response at a given visual acuity is increased. The same general rule, however, holds as with the normal eye;  $\sigma_I$  is again directly proportional to  $I$  (Fig. 4);  $\sigma_I$  might be expected higher, due to variations in the amount of eye surface blocked out in the different individuals, but the proportionality still to hold; this supplies an interesting check upon the differentiation between “experimental error” and variability by the method of expressing variation of  $I$  as a function of the measured intensity. It may be that the stimulation required for just detectable response is not the same for all levels of  $I$ , with this method. We know that the threshold response used as an indicator of excitation differs in at least one respect as threshold  $I$  increases, namely in that its sharpness and definiteness are augmented; but  $\sigma_I$  is greater as  $I$  increases, so that the mere relative sharpness of the response certainly cannot be held responsible for the change in  $\sigma_I$ . Our interest in these considerations is at the moment concerned with the essential equivalence of  $\Delta I$  and  $\sigma_{\Delta I}$ ; if the total excitation is the same at all levels of  $I$  for the index response, “ $\Delta I/I$ ” would necessarily be constant; but it does not appear obligatory to make this assumption.

The data here are entirely of the same sense as in the case of the curve of dark adaptation (Fig. 3); there, different levels of excitability are attained by altering the level of the stationary state of light adaptation; in each case,  $\Delta I$  is directly proportional to  $I$ , and  $\sigma_{\Delta I}$  is directly proportional to  $\Delta I$ .

### III

Flicker fusion depends upon the suppression of intensity discrimination. For the bee the relation of frequency of intermittence of a light and its critical intensity for response to flicker has been investi-

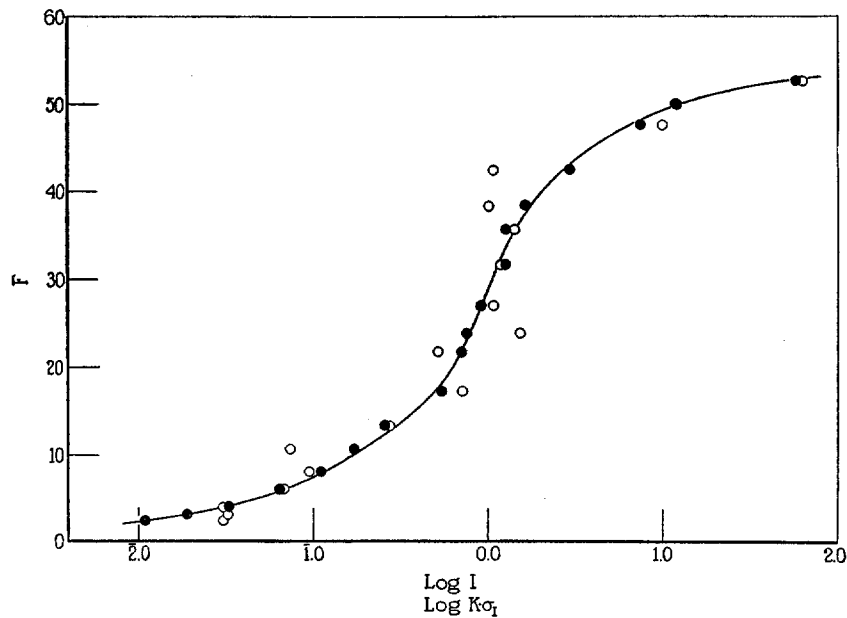


FIG. 6. Flicker frequency  $F$  and mean intensity  $I$  for flicker fusion, in the bee (data from Wolf, 1933-34); solid circlets,  $I$ ; open circlets,  $k\sigma_I$ .

gated (Wolf, 1933-34). The experiment involves measuring values of  $I$  adequate to produce fusion of the effects of flashes at fixed frequencies. The flashes are separated by equally long dark spaces. Fusion is indicated by failure of a response otherwise given to the field of successive light and dark sectors. For these measurements (*cf.* Wolf, 1933-34, Fig. 4).

$$\log \sigma_{I_2} = k \log I_2 + \text{const.};$$

$k$  is not certainly distinguishable from 1; hence

$$\sigma_{I_2} = mI_2.$$

(A better fit is obtained by adding a small constant to  $I_2$ .) As Fig. 6 shows, the curve connecting frequency of intermittence ( $F$ ) with mean critical illumination for response ( $I$ ) is duplicated by the relation of  $\sigma_I$  to  $F$ . As in Fig. 5, the *lateral* departures should lie within a band of constant width, if many determinations were available. Hence

$$d\sigma_I/dF = \phi(F) = k(dI/dF),$$

and

$$d\sigma_I/dI = K.$$

This is of course the result already given for the data upon intensity discrimination, dark adaptation, and visual acuity, and is to be interpreted in a similar way. We may say that the two intensities distinguished when flicker is reacted to are  $I_1$  ( $= 0$ ) and  $I_2$ , and again  $I_2$  is to be formally identified with  $\Delta I$ . If two mean intensities  $I_1$  and  $I_2$  were to be judged objectively as just significantly different, by means of the flicker curve, one of these intensities ( $I_1$ ) being fixed, then

$$\Delta I = k(\sigma_{I_2}) = k'I_2,$$

and

$$\Delta I/I_2 = k'.$$

The experiment is not usually made in quite this way. We shall see in a later connection that if  $\Delta I$  were to be determined by a comparison of mean values of  $F$  for two fixed magnitudes of  $I$ , the behavior of the  $\Delta I$  as a function of  $I$  would be found quite different.

#### IV

By a method similar in essentials to that used for the bees a "flicker curve" has been obtained for the sun-fish *Lepomis* (Wolf and Zerahn-Wolf, 1935-36 *b*). It has the general form found for the corresponding property of the human retina (Hecht and Verrijp, 1933-34 *b*) when  $\log I_m$  is plotted as a function of  $F$ . It has a lower segment of flat slope in the range of intensities where rod vision is

exclusively or predominantly concerned. The upper, steeper segment corresponds to the rôle of cone vision at higher intensities. This division permits a special kind of test of the notions here developed with regard to the analytical significance of the variation of  $I$  in such determinations. The measurements were made as with the bees, by

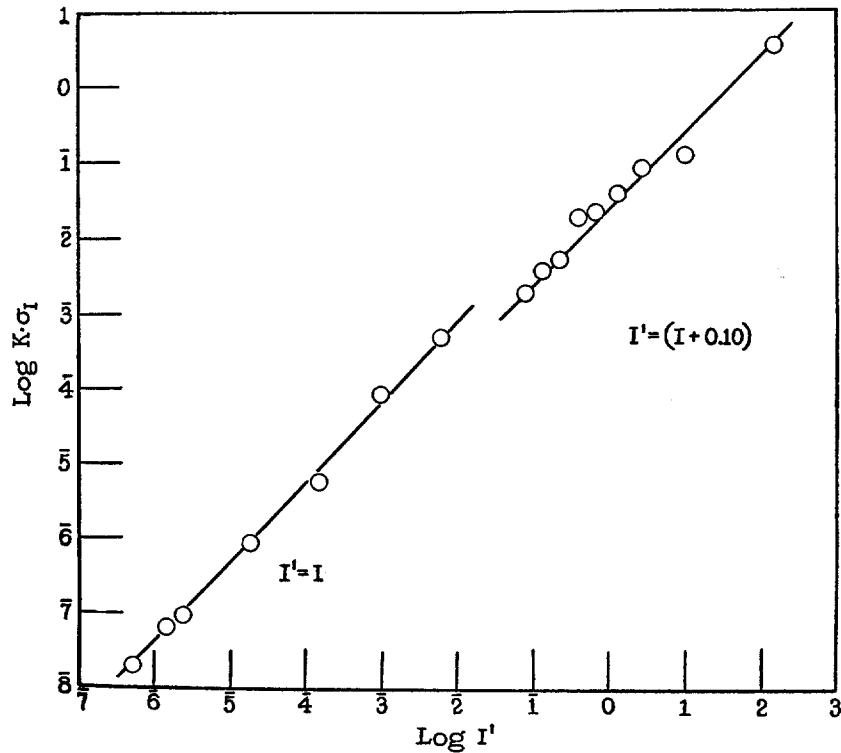


FIG. 7.  $\text{Log } \sigma_I$  as a function of  $\text{log } I$  for extinction of flicker with the sun-fish *Lepomis* (data in Wolf and Zerrahn-Wolf, 1935-36 *b*). The lower line refers to rod functioning, the upper to the cones; see text.

finding, for each of a number of fixed values of the frequency of intermittence ( $F$ ), the mean value of  $I$  which just gave threshold response to a moving background of equal stripes alternately black and illuminated by intensity  $I$ . The technic has been described in detail (Wolf and Zerrahn-Wolf, 1935-36 *b*).

For the rod section of the curve,

$$\log \sigma_I = k \log I + \text{const.},$$

and  $k$  is not certainly different from 1; in Fig. 7 the line is drawn with slope 1.05, but the difference from 1 is probably not significant. For the cone section (Fig. 7),

$$\log \sigma_I = \log (I + 0.10) + \text{const.}$$

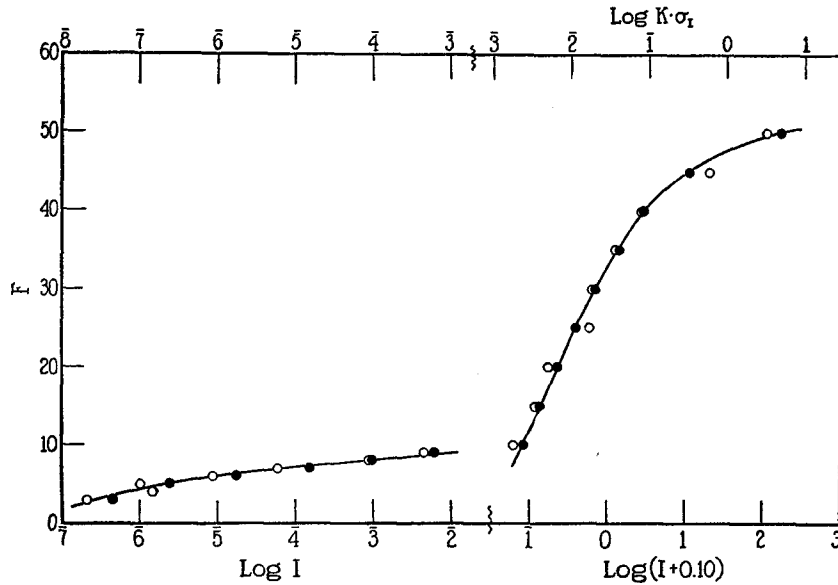


FIG. 8.  $\log I$  as a function of flicker frequency  $F$ , for rods (left) and cones (right); the curve of  $\log I$  is the same as that for  $\log \sigma_I$  (open circlets), when for the cones  $I$  is replaced by  $(I + 0.10)$ . See text.

The constant 0.10 means merely (as in the case of the bee visual acuity data) that  $\sigma_I$  is directly proportional to  $I$ , but that the line does not go through the origin. Since the cone segment of the curve is superimposed upon the rod segment,  $\sigma_I$  for the cones has to be diminished by an amount characteristic of the full excitation of the rods at the threshold  $I$  for excitation of cones; arithmetically this is the same as adding a constant to  $I$  for this portion of the curve.

It follows that the curve fitting  $\log I$  as a function of  $F$ , for the rods,

must also describe  $\log \sigma_I$  as a function of  $F$ . The left hand graph in Fig. 8 demonstrates this. For the cone portion,  $d(\log(I + 0.10))/dF$  must =  $d(\log \sigma_I)/dF$ . The right hand graph in Fig. 8 shows that the agreement is excellent.

The relationship found between  $I$  and  $\sigma_I$  for extinction of flicker is consistent with the results of intensity discrimination tests (p. 505). When the flickered light is just reacted to (threshold  $I$ ), it is a question of "recognizing"  $I_x$  (in the light sectors) as just different from  $I_x - \Delta I_x$ .  $I_x - \Delta I_x$  may be regarded as determining the apparent effect of the dark sectors. Here we must deal with  $I_x$  as the mean apparent intensity of the flickered light at the point of extinction of flicker (equivalent to the point of extinction's just failing). Whether this means that for the sun-fish the field is then one of continuous brightness corresponding to  $I_x$  is a question we need not discuss. At flicker frequencies above the critical, Talbot's law holds (*cf.* Hecht and Wolf, 1931-32). Apparently no measurements exist in the literature to show whether it holds at the critical frequency for fusion (or at the critical illumination), a matter which should be tested. We may assume that  $I_x = n I$ , as a first approximation. We have learned that  $\Delta I = k\sigma_{I_2}$ , for discrimination between  $I_1$  and  $I_2$  when  $I_1$  is fixed and  $I_2$  variable. Here,  $I_1$  and  $I_2$  both vary, although not independently;  $I_2 = I_x$ ,  $I_1 = I_x - \Delta I_x$ . Then  $\sigma_{\Delta I_x} = k'\Delta I_x$ . From the intensity discrimination case (p. 505) we also know that  $\Delta I = k\sigma_{I_2}$ , hence  $\Delta I_x = k\sigma_{I_x}$ , and since  $I_x$  is assumed =  $n I$ ,  $\Delta I_x = k''\sigma_I$ . From the data we learn that  $\sigma_I = K I$ ;  $\therefore \Delta I_x$  is directly proportional to  $I$ .

## v

Facts of the type here collected raise some curious problems of "curve fitting." The curve relating  $\log I_m$  to  $F$  for the vertebrate retina (man: Hecht and Verrijp, 1933-34 *a*; sun-fish: Wolf and Zerrahn-Wolf, 1935-36 *b*) contains two portions or segments, referring to the functional involvement of rods and of (rods and) cones respectively. These curves define the relationship  $d \log I/d F$ , where  $F$  is (in the cases we have considered) the independent variable. For a given value of  $F$ ,  $d \log I_x/d \log \sigma_{\Delta I_x}$  is constant, and obtains for all values of  $F$  under the given conditions (as to width of stripes, etc.) at the point where the flickered light is just not reacted to. We have seen that  $d \log I = d$



$\log \sigma_{\Delta I_x}$ , hence  $d \log I/d F$  is equivalent at each value of  $F$  to  $d \log \sigma_{\Delta I_x}/d F$ , assuming that  $I_x = k I$ . If we take the data as they stand in a table of  $F$ ,  $I$ , and  $\sigma_I$  we find that for the cones  $\log \sigma_I$  as a function of  $\log I$  is very nearly rectilinear, with a slope of about 0.81 (Fig. 9). We have already seen that a more reasonable treatment shows that  $\log \sigma_I$  is directly proportional to  $\log (I + 0.10)$  with a slope of 1, but the other formulation might easily be employed. It means that to a

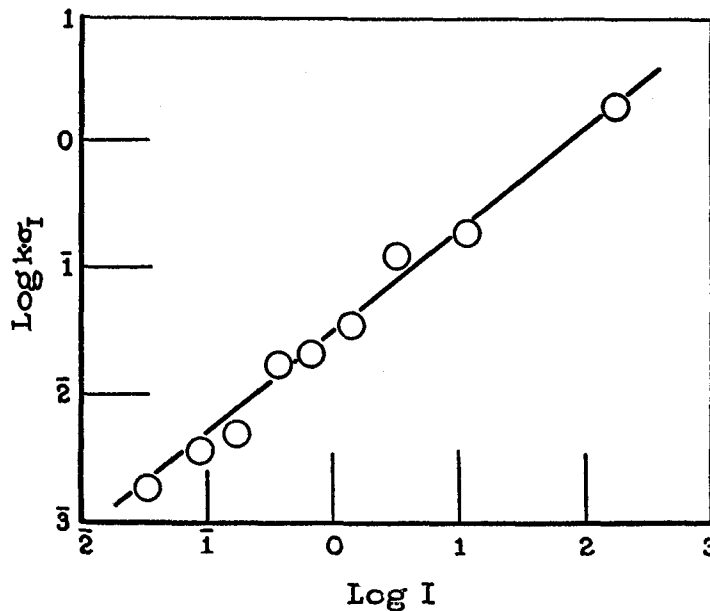


FIG. 9.  $\log \sigma_I$  as a function of  $\log I$ , cone portion of the flicker extinction curve (*Lepomis*), uncorrected for the rôle of the rods. The relationship is nearly rectilinear, with a slope of 0.81.

very fair approximation  $d \log \sigma_I = n d \log I$ . In terms of average  $I$  secured by this method, a significant increase in  $I$ , due to an increase of  $F$ , will be such that  $d \sigma_{I_x}/d I$  is really constant, but  $\sigma_I/I^n$  will appear constant, with  $n = 0.81$ . Therefore in fitting the cone curve of intensity discrimination to the data for critical illumination *versus* flicker frequency,  $I$  will seem to be in effect substituted for by a quantity ( $\Delta I$  or  $\sigma_{\Delta I}$ ) which is very nearly proportional to  $I^n$ . The suggestion is that the presence of an exponent such as  $n$  in the fitted curve (*cf.*

Hecht and Verrijp, 1933-34 *b*), may thus result merely from the fact that the cone portion of the curve is added to the rod portion and that  $\sigma_{IC}$  then contains the  $\sigma_{IR}$  associated with maximal rod function; this has formally the effect of making  $\sigma_{IC}$  seem proportional to  $I^n$ , in a way which is really accidental.

A related question concerns the form of the connection between (1) mean critical illumination for fusion of effects of flicker at fixed frequencies and (2) mean critical frequency of intermittence at fixed illuminations. It can be deduced from data of the sort we have considered that the two curves will not be identical. Let us take one example, the rod portion of the  $F - I$  curve for *Lepomis* (Wolf and

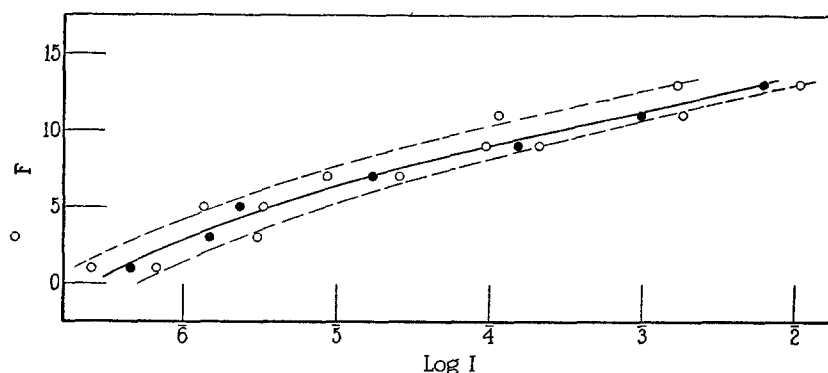


FIG. 10.  $\log I_m$ , and  $\log I_m \pm 10 \sigma_{I_m}$ , for the rod portion of the flicker extinction curve of *Lepomis* ( $10 \sigma_{I_m}$  is used merely for convenience in this case).

Zerrahn-Wolf, 1935-36 *b*). In Fig. 10,  $\log (I \pm k\sigma_I)$  is plotted as a function of  $F$ . The distribution of measured  $I$ 's at fixed  $F$ , measured by  $\sigma_I$ , gives the distribution of the threshold effects produced by intensity, at each value of  $F$ . The envelopes of these limits ( $\pm \sigma_I$ ) enable us to define the distribution of the threshold effects due to varying  $F$  at fixed levels of  $I$ . The experiment made in this way will be considered in another paper. It is obvious, however, that  $\sigma_F$  will follow a different law from that observed for  $\sigma_I$ , and that mean  $F$ 's at fixed  $\log I$ 's will give a curve detectably differing from that of  $\log$  (mean  $I$ ) at fixed  $F$ 's. (The problem is *formally* identical with the statistical one of fitting regression lines; the two problems need not

be the same from the standpoint of interpretation.) The importance of these considerations may be considerable, since they appear to apply quite generally.

## SUMMARY

From the data of experiments with bees in which threshold response is employed as a means of recognizing visual discrimination between stripes of equal width alternately illuminated by intensities  $I_1$  and  $I_2$ , it is shown that the detectable increment of intensity  $\Delta I$ , where  $\Delta I = I_2 - I_1$ , is directly proportional to  $\sigma_{I_2}$  ( $I_1$  being fixed). From tests of visual acuity, where  $I_1 = 0$  and the width of the stripes is varied,  $\sigma_{I_2} = kI_2 + \text{const.}$ ; here  $I_2 = \Delta I$ , and  $\Delta I/I_2 = 1$ . When the visual excitability of the bee is changed by dark adaptation,  $\lambda I \equiv k\Delta I$  ( $= k'\sigma_{\Delta I}$ )  $= k'' I + \text{const.}$  For the measurements of critical illumination at threshold response to flicker,  $\sigma_{I_2}$  ( $= \sigma_{\Delta I}$ )  $= k I_2 = k'\Delta I + \text{const.}$

The data for critical illumination producing threshold response to flicker in the sun-fish *Lepomis* show for the rods  $\sigma_{I_2} = K I_2$  for the cones  $\sigma_{I_2} = K'(I_2 + \text{const.})$ .

The data thus indicate that in all these experiments essentially the same visual function is being examined, and that the recognition of the production of a difference in effect by alternately illuminated stripes takes place in such a way that  $d(\Delta I)/d(\sigma_{I_2}) = \text{const.}$ , and that  $\Delta I$  is directly proportional to  $I$  (or " $I_2$ ," depending on the nature of the experiment).

It is pointed out that the curve for each of the cases considered can be gotten equally well if mean  $I$  or  $\sigma_I$  is plotted as a function of the independent variable involved in the experiment.

Certain consequences of these and related facts are important for the treatment of the general problem of intensity discrimination.

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