

## THE VARIABILITY OF INTENSITY DISCRIMINATION BY THE HONEY BEE IN RELATION TO VISUAL ACUITY

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It is necessary to produce an intensity of illumination ( $I + \Delta I$ ) in one component of a series of alternating bars differently illuminated, the intensity of illumination of the other set being  $I$ , in order to call forth a response in a creeping bee when the visual field so composed is moved to one side. With wide stripes the variability of ( $I + \Delta I$ ) depends upon the intensity of illumination  $I$  in exactly the same manner as does ( $I + \Delta I$ ). When  $I$  is high, and thus  $\Delta I$ , the standard deviation of  $\Delta I$  is high; it decreases as a simple power function of decreasing  $I$ , until a very low intensity is reached (*cf.* Wolf, 1932–33*a*). These determinations were made with one particular width of bars (20 mm.) constituting the illuminated pattern in the substratum upon which the bee creeps (Wolf, 1932–33*b*). It is important to consider the manner in which the variability of  $\Delta I$  may be affected according to the widths of the bars of light. Variability is defined as the quantitative dependence of the scatter of the determinations upon the magnitudes of the independent variable—in this case, the illumination  $I$  (*cf.* Crozier, 1929; Crozier and Pincus, 1931–32; etc.).

Clearly, the variability of the measurements, considered in this way, has an intimate bearing upon the automatic demonstration of internal self-consistency in the data, thus providing a control upon the consistency of the observer's performance; and, since it gives a means of estimating the variability of responsiveness of the tested organism, it is also important for questions as to the rôle of "pattern," "form discrimination," and several related topics. In this case, the pattern is simple and its properties may be suggestive. The excitation of the bee by movement of or in its visual field is clearly and definitely apparent by a reaction—a change of direction of the bee's path—when the animal is creeping geotropically upon an inclined surface. The

immediate cause of the response is given not by the movement of the bee, but by a movement of the diversely illuminated pattern above which it creeps. The bee does not react to motion of the stripes if it is not moving.

Excitation must depend upon the passage of a certain number of ommatidia from the less excited to the more excited state (or the reverse, or both) while the bee is creeping. This must depend largely upon the sizes of the alternate bars illuminated in a contrasting manner. Since the total area of the field respectively covered by the brighter and by the less bright bars which alternate in position is independent of the width of the bars, the excitation must be a function of the frequency of occurrence of divisions between the two areas, since the greater frequency of such divisions per unit area the greater the chances of a given ommatidium passing from less excited to more excited state. We found previously (Wolf, 1932-33*a*) that the variation of  $\Delta I$  increased as a power function of  $I$ , with given constant width of stripe (20 mm.). With bars of narrower width one must then expect that at given intensity of illumination the excitation must be higher—the visual angle being smaller—and consequently the variation of  $\Delta I$  must be expected to be higher, reducing with continuing increase of illumination to a certain magnitude dependent upon maximal excitation of all the ommatidia. With still narrower bars, this process must be expected to continue. This would of itself be enough to show that the observed variation of  $\Delta I$  is connected with a property of the bee, rather than a matter of “experimental error.”

It was found with bars of 20 mm. width that the P.E. of  $(\Delta I/I)$  declined hyperbolically with  $\log I$ . In terms of the reasoning thus far outlined, we expect this relationship to be apparent with stripe systems of narrower widths, but that with successively narrower stripes the curve of hyperbolic descent of P.E.  $(\Delta I/I)$  with increasing  $\log I$  should move successively toward higher values of  $\log I$ . For the present series of measurements (Wolf, 1932-33*b*) Fig. 1 demonstrates that this relationship is indeed obeyed. The data are contained in the preceding paper by Wolf (1932-33*b*). As there explained, the readings are averages of ten determinations of  $\Delta I$ , and the probable errors of these averages. Since the number of observations is constant in each set, the use of a probable error of the mean is merely a matter

of convenience, and in no way affects quantitatively or qualitatively the character of the subsequent reasoning; we are quite well aware that other methods of expressing the scatter of observations might be preferable for other purposes. P.E. ( $\Delta I/I$ ) decreases with increasing  $I$  in precisely the same manner as does  $\Delta I/I$  itself (Wolf, 1932-33*b*). It was concluded previously (Wolf, 1932-33*a*) that the quantitative

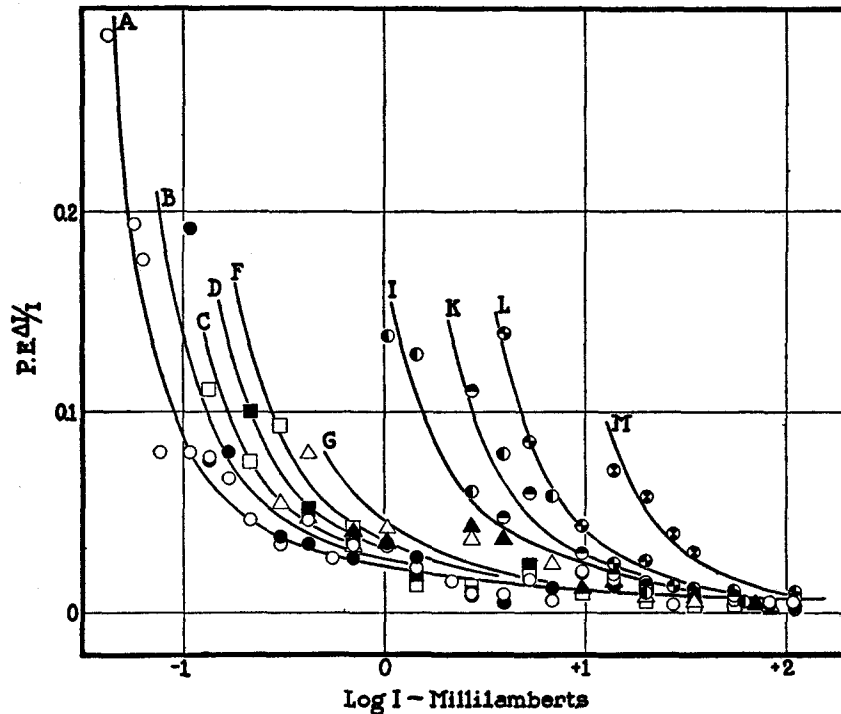


FIG. 1. Probable errors of the ratios ( $\Delta I/I$ ) as a function of  $\log I$ , for stripes of different widths,  $A$  to  $M$ , progressively narrower. The widths of stripes, and the corresponding visual angles, are given in an accompanying paper (Wolf, 1932-33*b*).

level of intensity discrimination—with stripes of given width—determines or limits the variation in the measure of this discrimination. From Fig. 1 it is apparent that with stripes of narrower and narrower widths the P.E. of ( $\Delta I/I$ ) is higher and higher at given intensity of illumination; put in another way, the narrower the stripe, the higher the intensity of illumination required to produce a given variation in

( $\Delta I/I$ ). This is completely consistent with the thought that the general intensity of excitation directly determines the magnitude of the variation in reactivity for the threshold response which is the basis of the measurements.

In one sense, this is more simply seen if one considers that, at given magnitude of  $I$ ,  $\Delta I$  is inversely proportional to the visual angle subtended by the width of one of the stripes—that is, by the distance between the lines of division of the illuminated areas (visual angle is of course the reciprocal of the visual acuity); the curve relating  $\Delta I$  with visual angle is almost exactly hyperbolic, so that  $\Delta I$  is almost directly proportional to the visual acuity. At given magnitude of intensity, P.E.  $\Delta I$  increases with  $\Delta I$ , that is, with decreasing visual angle. This is consistent with the idea that the observed variation of  $\Delta I$  tends to be progressively restricted as the fineness of discrimination (decreasing value of  $\Delta I$ ) becomes greater.

For the stripes of greatest width used (20 mm., *A*, Fig. 1)  $\Delta$  (P.E.  $\Delta I$ )/ (P.E.  $\Delta I$ ) is directly proportional to  $\Delta I/I$ , until, at a very low level of intensity, P.E.  $\Delta I$  increases somewhat, owing presumably in part to lack of nicety in the adjustment of the apparatus (that is, of  $I + \Delta I$ ) by the observer. With narrower illuminated bars (Fig. 2) this secondary source of increase in P.E.  $\Delta I$  naturally appears at higher and higher intensities, until, beyond the inflection point in the curve for visual acuity at any intensity of illumination (*cf.* Wolf, 1932–33*b*; Fig. 2), the curvature of the departures of P.E.  $\Delta I$  from the limiting line connecting  $\log$  P.E.  $\Delta I$  with  $\log I$  assumes a somewhat different form. With stripes of still narrower widths, the visual acuity at given intensity of illumination becomes higher and declines less rapidly for a given increase of illumination; consequently, the curves for departure of  $\log$  P.E.  $\Delta I$  from the limiting line descend less rapidly to this line.

A fundamental problem arising in relation to the sensory effects, or the effects upon behavior, of the seen movement of a patterned field, has to do with the question as to whether effects induced are of purely peripheral, that is, sensory, origin; or whether the character of the pattern as a pattern is intrinsically significant. This question can be determined most directly, not by the consideration of picturesque differences in forms of pattern, but by the close analysis of the influence of simple changes in pattern of which the possible sensory consequences

may be determined and checked. In the present instance we have to do with a visual field in which the differences experimentally produced concern, not modifications of the relative amounts of brighter and less bright surface, but changes in the frequency per unit area of divisions

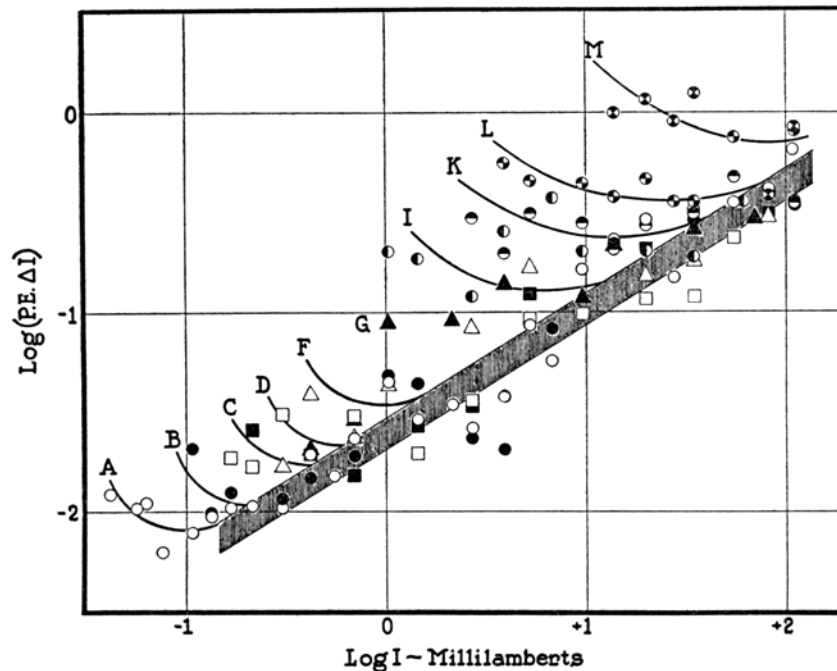


FIG. 2. Probable error  $\Delta I$  considered as a power function of  $I$ . For stripes of greatest width (*A*) the wide bar gives the limiting line (*cf.* Wolf, 1930; 1932-33*a*); with stripe systems of progressively narrower widths, to *M*, departures from this limiting line are increasingly more extensive. This is discussed in the text. For the stripes of a width corresponding to the location of the inflection point in the curve for visual acuity (Wolf, 1932-33*b*) the variation is much more extensive than in the data obtained with the other stripes; for these observations, *G*, no curve is drawn.

between brighter and less bright; this means, that with given frequency (that is, with the total number) of demarcation lines encountered by the ommatidial surface, the excitation of an ommatidium, so far as concerns the elicitation of the threshold response which is the basis of measurement, must depend upon the passage of ommatidia from

a condition of illumination by the brighter or the less bright bars to the reverse. The visual acuity curves determined by this method, and the intensity discrimination curves upon which they are based, can be understood on the assumption (*cf.* Hecht and Wolf, 1928–29) that excitation is determined at given intensity of illumination by the number of ommatidia stimulated, and fundamentally by the distribution of thresholds for photic excitation as a function of intensity among the total population of ommatidia. We find here that not only do the data upon intensity discrimination retain a consistent character regardless of the width of stripe (that is, detail of the pattern) but, what is more surprising, that the variation in the measurement of  $\Delta I$ , considered as a function of  $I$ , can also be understood completely as to its form, on the assumption that the relative change of the standard deviation of  $\Delta I$ , when  $I$  is altered, is fundamentally directly proportional to the relative change of intensity, but with a modification of the fundamental limiting graph from which this statement is derived which becomes apparent when, with narrower and narrower illuminated bars, the increasing frequency of excitation, due to the increased frequency of transitions from brighter to less bright illuminations upon the bee's eye, determines at a given intensity of illumination a higher intensity of excitation. It is conceivable that, from the character of these departures from the limiting line in the graph of P.E.  $\Delta I$  against  $I$ , estimation could be made of the manner in which narrowing the widths of bars to the point beyond the inflection point in the visual acuity graph serves to bring about increased excitation; in other words, narrowing the bars increases the frequency of excitation (over a relatively gross interval of time); increasing  $I$  increases the total intensity of a single excitation. It is to be remembered, again, that in these measurements one deals with a threshold response, which does not depend upon the speed of the translational displacement of the seen pattern, at least within rather wide limits not exceeded in securing the actual readings.

#### SUMMARY

Variation in the determined magnitudes of the difference in brightness between alternating members of a system of stripes requisite for the elicitation of a threshold response in bees shows that the intensity

of excitation, as a function of width of stripe and of intensity of illumination, is determined by the intensity of illumination and by the frequency of occurrence of divisions between bright and less bright bars. The variation of  $\Delta I$  is limited by the intensity of excitation, so that the curves relating P.E. ( $\Delta I/I$ ) have the same form in relation to  $I$  as do the curves for  $\Delta I/I$ . The limiting rule according to which P.E.  $\Delta I$  is a power function of  $I$  for stripes of maximum usable width is departed from more and more markedly, for lower intensities, as narrower stripes are employed.

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