THEORY AND MEASUREMENT OF VISUAL MECHANISMS

I. A Visual Discriminometer. II. Threshold Stimulus Intensity and Retinal Position

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I

A Visual Discriminometer

Various quantifiable properties of visually controlled response can be regarded as essentially expressions of a single functional process. The measurements depend fundamentally upon the performance of the organism in responding to a spatio-temporal pattern of at least two physically estimated luminous intensities. According to the particular conditions imposed we may be dealing with phenomena like "intensity discrimination," "flicker fusion," "visual acuity," or the time course of sensory adaptation. In the treatment of visual excitation as a sensory phenomenon there has been a pronounced tendency to discuss such manifestations as separable and distinct. The particular visible pattern to which the organism gives an index response, or expresses discriminatory decision, is, however, the only real distinction of any one of these "visual functions."[1] The pattern may be one which presents two intensities simultaneously, on different parts of a visual field, or they may succeed one another in time. One of the two intensities may be equal to zero. The two intensities may be "equal," but differ as to wavelength, or as to retinal area,

[1] Crozier, W. J., 1935–1936, *J. Gen. Physiol.*, **19**, 503. 1936, *Proc. Nat. Acad. Sc.*, **22**, 412.
Crozier, W. J., and Holway, A. H., 1937 *a*, *Proc. Nat. Acad. Sc.*, **23**, 23.
Holway, A. H., and Crozier, W. J., 1937 *b*, *Proc. Nat. Acad. Sc.*, **23**, 509.
Holway, A. H., 1937, *J. Opt. Soc. America*, **27**, 120.
Holway, A. H., and Hurvich, L. M., 1937, *J. Psychol.*, **4**, 309.
Holway, A. H., and Crozier, W. J., 1937 *a*, *Psychol. Rec.*, **1**, 170; 1937 *b*, **1**, 178.

or exposure time. The conditions may be such that time is brief and constant, or so long in special instances as to be without significance; presentation may be continuously uniform, or abruptly discrete and single, or cyclically repetitive; other parameters,—for example, retinal position,—may be involved, and in tests of different kinds each of the intensities concerned may be made to differ independently with respect to any of the other parameters. The organism itself may be permitted to vary or change,—as in a dark adaptation experiment. All of these various circumstances specifically circumscribe and delimit the conditions under which the discriminatory activity of the organism is called upon to exhibit its performance. A fundamental functional activity concerned throughout is that of *intensity discrimination.* The properties of this activity are to be defined by the manner in which its numerical measurements behave as functions of the conditions under which it is exhibited.

Certain general rules are now known to apply to the data of sensory discrimination, regardless of the particular set of conditions during a given kind of experiment. Thus if two intensities I_1 and I_2 are compared, I_1 being fixed and I_2 adjusted until just perceptibly greater than I_1, then the mean difference $\Delta I_m = \bar{I}_2 - I_1$, where $\bar{I}_2$ is the mean of the adjusted values of I_2, is found in all cases to be directly proportional to the standard deviation ($\sigma_{1\Delta I_1} = \sigma_{1I_2}$) of the distribution from which it is computed.[1] And the relation between ΔI and I_2 is in general of a simple and straightforward kind.[2] The analysis of various bodies of data shows [1, 3] that these relationships can readily be understood from the standpoint that the performance of the organism in executing the discriminatory act is essentially one exhibiting lawful fluctuation;[4] the indication is that σ_{I_2} *determines* ΔI_m, rather than the reverse.[5] The discriminatory performance, as measured, usually and characteristically involves the reacting organism as a whole. The immediately responsible nervous elements, however, are centrally

[2] *Cf.* Upton, M., and Crozier, W. J., 1936, *Proc. Nat. Acad. Sc.*, **22**, 417.
Crozier, W. J., and Holway, A. H., 1938, *Proc. Nat. Acad. Sc.*, **24**, 130.

[3] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1937, *Proc. Nat. Acad. Sc.*, **23**, 516. 1937–38, *J. Gen. Physiol.*, **21**, 17. 1938–39, in press.

[4] Crozier, W. J., 1935, Détérminisme et variabilité, Paris, Hermann et Cie, 56 pp.

[5] Holway, A. H., and Crozier, W. J., 1937, *Proc. Nat. Acad. Sc.*, **23**, 509.

situated; *i.e.*, are not the peripheral receptors. This makes it intelligible that the elementary rules for the data of sensory discrimination are identical (save for dimensional constants) whether one deals with photic excitation of the retina, auditory stimulation, pressure excitation, or tensive excitation of proprioreceptors.[1] It is thus also understandable that for a given type of excitation, as by light, the *form* of the rules required is in no way dependent upon the peripheral structure of the eyes in diverse animals.[1, 8] Area of a retina illuminated may enter as a complex factor owing to the morphological pattern of the distribution of the sensory cells;[6] the gross structure of the sensory field may introduce other secondary features;[6] but the character of the relationship between stimulating intensity and magnitude of sensory effect may be independent of the specificities of sensory structure.[1]

Sensory effect is measurable only in an indirect way: its magnitudes determine the size of the intensity difference ΔI which results from a given test of intensive discrimination. If for magnitude of sensory effect we write E, then the quantitative relation between E and I is the ultimate object of inquiry. We have to determine this relationship by means of the properties of ΔI; to a given value of $\Delta I_m = \bar{I}_2 - I_1$ there corresponds a quantity $\Delta E_m = \bar{E}_2 - E_1$; the problem is to determine the nature of this correspondence. The investigation thus becomes basically a study of the physiology of intensity discrimination. As such it *must* involve the physiology of the lawful variableness of organic performance, since this is a universal attribute of the basis of such measurements. This requires, as Helmholtz for other reasons clearly foresaw and emphasized,[7] a kind and a degree of care and precision in biological experimentation such as work upon the properties of non-living objects *per se* rarely requires. Without this, it becomes impossible to study for its own sake the test object's contribution to the distributions of the measurements.[4, 8]

[6] Hecht, S., 1937, *Physiol. Rev.*, **17**, 239.

Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1937–38, *J. Gen. Physiol.*, **21**, 223; 1938–39, in press.

[7] Helmholtz, H. L., 1924, Physiological optics, New York, Journal of the Optical Society of America, 3rd edition (translated by Southall), **2**, 77.

[8] Crozier, W. J., 1929, The study of living organisms, in Murchison, C., The foundations of experimental psychology, Worcester, Clark University Press, 45.

Stier, T. J. B., and Crozier, W. J., 1932–1933, *J. Gen. Physiol.*, **16**, 757.

One source of confusion can be avoided by refraining from the practice of averaging measurements from a number of individuals. The essential requirement has been defined[1] as homogeneity of the data to be used. In the absence of true homogeneity, mere increase of superficial statistical precision may serve only to obscure the fundamental phenomena one is seeking to explore. With human subjects, where age and relevant genetic composition are both significant variables, the criterion can be applied, in general, only in the case of series of observations obtained with the *same* individual. A particular advantage of the human subject lies in the fact that a greater variety of tests can be made than with any given type of lower animal thus far examined. The special importance of *visual* performance (as a type of sensory response) is that a greater range of intensity (some twelve logarithmic units) can be adequately explored experimentally than with other types of sensory excitation.

The demonstration of genetically determined differences in the reactive performance of animals[9, 3] gives a factual, empirical basis for the abandonment of the analytical effort to learn anything about the mechanism of excitatory processes by augmenting the number of (perhaps genetically unlike) subjects to be included in a series of observations in an attempt to obtain increased precision of numerical results. With certain lower organisms this can be done, because it is possible to obtain groups of individuals which are demonstrably equivalent for the purposes of a particular experiment.[3] Where many human subjects have been employed by others in the past no such criterion has been applied.

A parallel and equally important requirement of the investigation of the properties of the parameters of visual excitation is that the examination of the intensity discrimination response, under diverse conditions of its exhibition, should be made with the same source of light and with the same apparatus. The significance of this requirement is obvious if one considers the problem presented by the measurement of luminous intensities in absolute units, or in units which shall be comparable if frequency (wavelength) is caused to vary. It is equally important in other ways.

[9] Crozier, W. J., and Pincus, G., 1929–30, *J. Gen. Physiol.*, **13,** 57; 1935–36, **20,** 111.

These general requirements have been especially in mind in the design of the "discriminometer" which we now describe. It was sought to devise an instrument which would permit the precise and convenient investigation of properties of human visual response such as have been traditionally grouped under such rubrics as: intensity discrimination, flicker fusion, color mixture, sensory bisection, equal brilliance steps (distances), visual acuity, and the like. The requirements include the necessity of binocular as well as of monocular observations, under conditions such that the variation of critical illuminations can be investigated (and, when possible, the fluctuations in the excitability function as a whole); and the control of intensity, area, retinal location, wavelength, and duration of exposure. The work thus far done with it shows that the instrument is capable of producing highly accurate results and that it has the desired flexibility.

The optical system and a schematic plan of the visual discriminometer are shown diagrammatically in Fig. 1. The general plan may be outlined first. The lenses L_1 are the objectives of three collimators focussed at S_o, a common source of illumination. Parallel light is regularly reflected at 90° at P_1 to the lenses L_2 which bring the rays to a focus in the plane of S_1, the bilateral slits of the discriminometer. The three uniformly illuminated apertures S_1 now serve as three secondary light sources of equal intensity and essentially identical wavelength composition. Lenses L_3 constitute the objectives of another triple collimator system. Parallel light enters the head of the discriminometer (H) and then passes on through a large converging lens L_4. Light from the companion collimators passes directly into L_4; light from the other collimator is reflected 90° by the front-surfaced mirror in the center of the head and thence into the center of L_4. This lens terminates the second series of collimators and at the same time serves as the objective lens of a binocular telescope. The inclined body of a binocular microscope head (MH) and the eye-pieces E complete the general plan of the optical assembly.

The observer looking into one of the eye-pieces can see a tripartite pattern, the evenly illuminated images of the apertures S_1 (Fig. 2). An evenly illuminated circular "surround" (Maxwellian view) can be obtained simply and immediately by sliding any one of the lenses, L_3, so that its first focal point lies in the plane of L_2. Relative to S_1, the system MH and L_4 in conjunction with the lenses L_3 may be regarded either as a short-focus binocular telescope or as a long-focus compound microscope.

The primary light source (S_o) is housed in a special aluminum casting, built with fins to provide a highly radiating surface. The housing is of ample size (21×21×31 cm.) and can easily accommodate a 2000 watt Mazda lamp. A motor and fan tend to maintain a constant temperature by forcing a blast of cool air

through the chamber. The temperature at the cover of the lamp house, during operation, averages about 5° (or less) above that of the room. The force of the blower is regulated by a rheostat located on the base plate at the right of the discriminometer head (*cf.* Fig. 3). The removable top is so constructed as to permit continuous ventilation and easy access to the bulb. A stage, adjusted mechanically from outside the lamp house (vertical rack-and-pinion and plane-

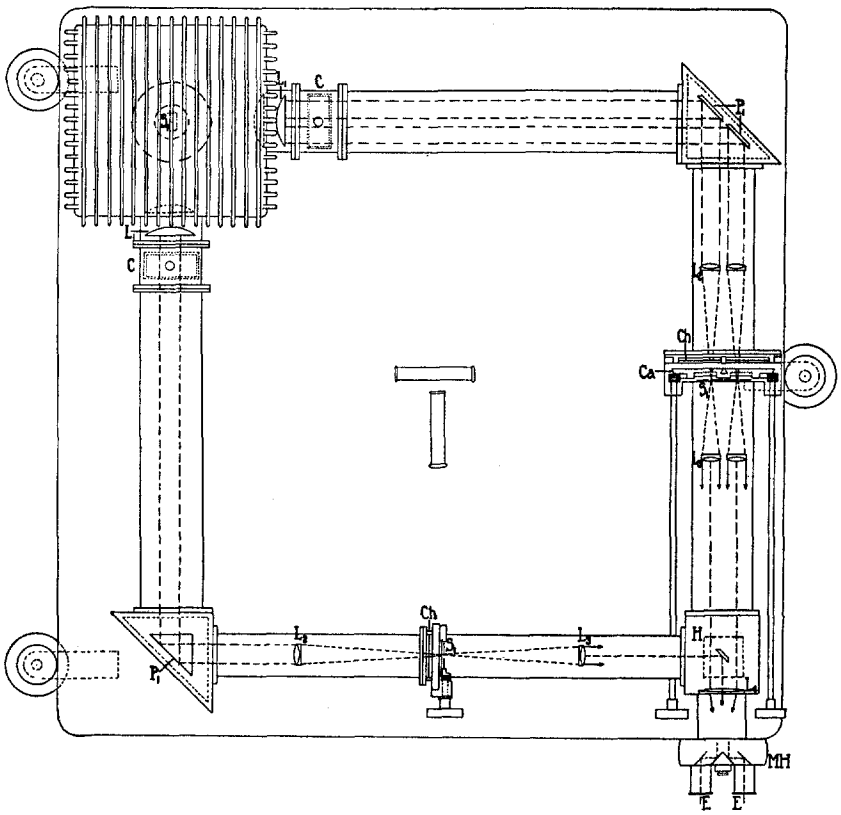

FIG. 1. Schematic plan view of the visual discriminometer. For description, see text.

horizontal controls are provided), supports the lamp and insures perfect centering of the wide ribbon filament.

The light paths of the optical system are indicated by dotted lines in Fig. 1. Light enters the first set of collimators *via* the two quartz objectives, L_1. These lenses are optically accurate and are mounted in movable ring-type holders. Cylindrical Christiansen cells (C) are located just behind the objectives. A

rectangular isosceles prism totally reflects the light in the single collimator at P_1, while front-surfaced chrom-aluminized mirrors reflect the beams in the twin collimator. Each mirror is supported individually by an adjustable stage. In all cases, the reflectors are placed at 45° to the incident light. Upon striking these surfaces, the beams are reflected at right angles into L_2, lenses that are independently mounted and appropriately stopped in cylindrical draw tubes. The draw tubes slide co-axially in body tubes and can be maintained in fixed positions by means of knurled thumb-screws. These adjustable lenses serve to place real, slightly magnified, and evenly illuminated images of the flat ribbon filament in the plane of each slit, S_1.

The slits are quadrilateral, each being formed between the knife-edges of two pairs of metal jaws which can be accurately and independently adjusted by means of fine-pitched screws. The edges are sharp and straight. To insure paral-

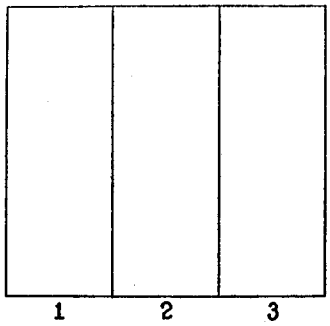

FIG. 2. The form and proportions of three contiguous light patterns which can be placed on either or both retinae of the observer. The uniformly illuminated images 1, 2, and 3, can be independently varied in intensity, wavelength, size, form, time relations, and retinal position; two of them, or all three can be made to overlap completely.

lelism of the slit opening, the jaws are fitted exactly into two parallel guides cut in a rectangular brass frame. The frame is screwed to a bed-plate of solid brass. The latter is attached to a strong support, is located in a plane perpendicular to the optical axis, and can be rotated and lifted or lowered for final alignment of the apertures in the field of view. A rectangular opening permits the passage of light through the bed-plate. To minimize the chance for side play, the lengths of the bearing surfaces are large relative to the size of the maximal, clear aperture. The jaws are bevelled and so placed that the flat edges face the source of light. All the elements of this assembly are uniformly black. The capstan-head screws actuating the jaws work in blocks fixed to the bed-plate support. In each instance, the screw passes through a pair of fixed nuts, one on the bed-plate, the other on the slide. The screws may be easily adjusted from the outside of the instrument, and can be secured in place by lock-nuts. Any one

of the three slits can be increased so as to produce a clear image which subtends a visual angle of approximately 40° on a side at the principal point of the eye when appropriate oculars are employed.

The slits S_1 also lie in the focal planes of the lenses L_3 which are identical with L_2 with respect to mounting and adjustment. Parallel beams from L_3 enter the head and then pass on to L_4. L_4 is screwed into a fixed mount, and converges all of the rays passing into the head of the inclined binoculars where the rays are equally divided, twice reflected at right angles, and finally enter the paired eye-pieces, E. Coupled with the eye-pieces, L_4 is thus the objective lens of a binocular telescope focussed for "infinite distance."

Each eye-piece may be supplied with a small camera lucida (Abbé type) which provides a movable fixation point in the dioptric focal plane of the observer's eye. Vertical adjustments permit the prisms of the cameras to be placed at the eye-point, and two concentric adjusting screws allow them to be independently centered. Small neutral tint filters between the eye-piece and the mirror regulate the intensity of the fixation point. Artificial pupils can be attached to the oculars. Ordinarily, however, such pupils are not necessary since the maximal diameter of the light beam at the eye-ring of our oculars is less than 2 mm.

The optical axes of the binoculars are parallel. A dial, graduated in millimeters, and conveniently located in the binocular head, is used to adjust the eye-points to the interocular distance for different observers and to reproduce settings with the same observer at different sittings. One of the ocular tubes is provided with a spiral screw to accommodate for slight differences in accommodation between the two eyes,—a very important matter for the measurement of *binocular* thresholds. A monocular head, body tube, and shield can be substituted for the binoculars when necessary. A Bausch and Lomb combination chin-rest and head-support is used to reduce extraneous movement.

All lenses are achromatic. Enclosing the body tubes of the collimators is a protective metal casing. The entire assembly is supported by vertical columns. Each of the supports is flanged at its base which *rests* on a smooth, heavy, cast-iron base-plate; the principle of the hole, slot, and plane is employed here and the supporting columns suffer no twisting or lateral strains. Spirit levels are mounted at right angles on the base-plate, and three levelling screws centered in circular bed-plates serve to maintain the base in a horizontal position. This accuracy in design and ruggedness in construction are necessary to insure rigidity and duration of alignment and adjustment under the severe routine of continuous use.

Control of Intensity and Wavelength.—To control intensity, each of the light paths is supplied with appropriate mounts and holders for a wedge, a balancer, and for filters. The intensity of any one of the three beams can be varied independently: (1) in stepwise fashion (neutral filters, diaphragms), or (2) continuously (wedges). The filters are clamped in small aluminum castings which fit snugly into chambers (*CH*) prepared especially to receive them. The same is true for the balancers. When necessary, filters may be placed in front of the objective lens L_4 in the head of the discriminometer.

The wedges are mounted in frames and fitted securely in brass carriages (*Ca*) which can be raised or lowered by means of a smoothly operating helical rack-and-pinion adjustment. The rack is strong; the pinion-gear spindles, heavy. Vertical movement is imparted to any one of the carriages remotely through a steel shaft actuated by a bronze knob or hand wheel at the operating end (*cf.* Fig. 3). The knobs are conveniently accessible and easy to manipulate. Tension just sufficient to prevent slipping is exerted against the wedge-carriage. The motion can be

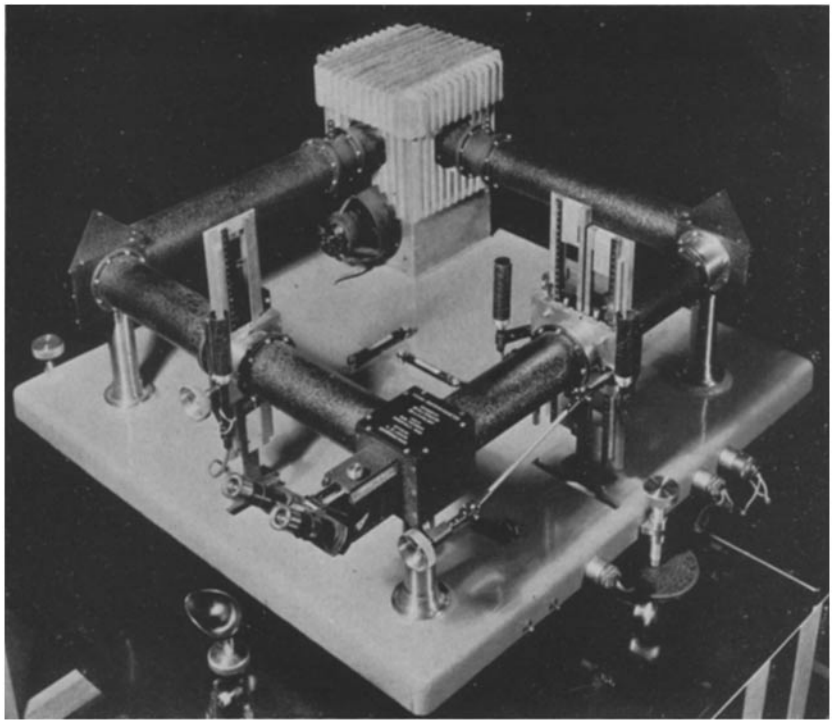

FIG. 3. Perspective view of the visual discriminometer. For description, see text.

stiffened or eased at will. Only slight tension is needed, however, since the area of the surfaces in contact is considerable. Universal joints remove unnecessary strain on the shafting, and the surfaces are provided with oil grooves. These factors in conjunction with the working of the helical pinion-gears insure smooth operation without backlash. Each carriage is supplied with a vernier scale and a shielded reading lamp. The collimator tubes are built in conveniently removable sections, and large Nicol prisms can be inserted to vary intensity or for other purposes.

Intensities are measured near the eye-point, either photometrically or in terms of radiant energy. The nature of the problem determines the method; this point will be discussed in subsequent reports. The range of intensities now being used extends from below the visual threshold up to a region which produces glaring and painful effects; *i.e.*, the entire range practicable for the study of visual intensities (about twelve logarithmic units).

For wavelength control, combinations of absorbing glasses and gelatin filters can be used in the filter holders. When an unusually narrow band of wavelengths (e.g. a "*line*") is necessary this purity can be obtained through the addition of proper absorbing solutions placed in the quartz cells (*C*) and used in conjunction with an intense "monochromatic" source. A calibrated spectrometer is provided and can be attached to either of the eye-tubes for reading the wavelength of the filtered light. An image of the resulting spectrum can be placed on either or both retinae of the observer. The intensity of this light (after calibration) can be controlled in the usual manner. Three beams of the same or of different wavelengths from a single source may thus be varied independently in intensity. By proper alignment of the apertures at the slits the images may be exactly controlled in the focal plane of either or both of the eyes to form an unusually accurate and useful color-mixer.

Control of Size, Form, and Position of Images.—The slits S_1 provide an accurate means for *continuous* variation of the area of rectangular images. However, provision is also made for apertures of fixed area of varied (*e.g.*, circular, annular) shapes. The various shapes are produced on quartz plates, the region surrounding the desired figure being optically stopped with a silver coating. A thin optically worked cover-glass cemented over the plate eliminates entirely the necessity for removing dust particles from the edges. These patterns can be cut to any desired form and size; the slides are readily substituted in place of the adjustable slits. The light patterns produced by these forms are sharply defined; they can be moved about and secured in any desired position within the 40° field of view. The linear or angular dimensions of these images are measured with the aid of a divided (objective) scale and filar micrometer.

Control of Exposure Time, Flashes, Flicker Cycle.—The sections at *C* are removable, and shutters placed in the openings can provide long or relatively brief exposures of any desired image. A catoptric pendulum can readily be installed for extremely short exposures (flashes). For flicker, front-silvered rotating sectors are moved into the plane of the reflector in the discriminometer head; the motor, reducing unit, and controls are held in place by a support which is independent of the discriminometer. This provides an accurate means for altering cyclically the intensity of a sharply defined image without in any way disturbing its form or position, and also for controlling the *amplitude* of the intensity cycle. An important aspect of the latter feature is that, by the use of the rectangularly disposed light beams in the apparatus, it permits the investigation of the hitherto neglected phenomena arising when two finite intensities are cyclically alternated in a systematic way.

By the substitution of a different type of binocular head, with *two objectives* focusing upon the slit-images in S, it is possible to investigate the properties of intensity discrimination under various conditions of difference of illumination in the two eyes, and of phase differences in flash cycles for the two eyes by binocular fusion.

Résumé.—A device has been constructed which permits the investigation of different aspects of human visual excitability over a wide range of luminous intensities, and under conditions such that various significant parameters of the visual response function are under precise control. The use of a single instrument for the investigation of superficially diverse types of visual performance contributes in a significant way to the homogeneity and comparability of the observational data.

We are under obligation to Mr. A. D. Jones and his Optical Company, of Cambridge, for excellent work on the optical parts of this instrument; and to Mr. Carl Heinrich, scientific instrument maker, of Boston, for his very superior execution of the mechanical design.

II

Thresholds and Retinal Position

Our discussion of the theoretical orientation from which quantitative visual data are to be interpreted has implied a divergence from a current and rather powerfully supported view. The measurable properties of visual performance are commonly regarded as giving information about the retinal excitatory process, including its photochemistry.[6] The development of this conception has been basically dependent upon the results of fitting curves by which it is attempted to correlate the properties of certain equations with numerical features of different aspects of intensity discrimination. Such equations are in fact non-specific. Without independent tests of the meanings of their contained constants, they are without real significance. In at least one case, these constants do not experimentally exhibit the necessary properties.[10] The method of fitting the photochemical equations to the data is usually highly arbitrary, and completely

[10] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1936–37, *J. Gen. Physiol.*, **20**, 393; 1937–38 *a*, **21**, 313; 1937–38 *b*, 463.

neglects the known properties of the variation present in the measurements. The resulting descriptions, for these different reasons, cannot be unique. We shall find it necessary to return to these matters in subsequent reports.

We are concerned now with an essentially qualitative point which is of special importance in the theory of photic excitation, namely the relations, if any, between numbers and kinds of excitable *peripheral* sense cells and the judgments of intensive discrimination. These relationships, and the amounts or rates of chemical changes supposedly associated therewith, have never been theoretically clarified. They are specifically important for the view that the data of visual excitability in an immediate, proportionate way reflect the physicochemical organization of the retina. The fact that the human retina ordinarily contains at least two classes of excitable elements, "rods" and "cones," permits a real test of certain aspects of this whole situation. Vertebrates generally which exhibit these two classes of visual cells provide visual response curves which are in two distinguishable parts or sections. This, of course, does *not* constitute proof that the peripheral two classes of primary neurons are the determining factors in this duplexity; nor does the fact that a vertebrate known to have only cones fails to show a duplex constitution of its visual response curve.[11]

For the human visual apparatus scotopic ("twilight") vision is conventionally considered to be associated primarily or exclusively with the excitation of the retinal rods,[5] and the magnitude of the absolute threshold stimulus (ΔI_o) for the dark adapted human eye has been taken to depend upon the excitation of a given number of rods,[11] as if a satisfactory basis for the interpretation of such results were to be found simply in the excitation of peripheral sense cells. An early paper by von Kries[11] shows that monocular ΔI_o for a small area *decreases* with increasing distance from the fovea, whereas the curves drawn by Kleitman and Piéron through their data purport to show that ΔI_o *increases* with increasing distance from the fovea.[12] Thus

[11] von Kries, J., 1895, *Z. Psychol. u. Physiol. Sinnesorgane*, **9**, 81; 1897, **15**, 327.

[12] Kleitman, N., and Piéron, H. (1928, *Ann. Psychol.*, **29**, 57) report data which at first sight seem to contradict this finding. Their results purport to give values of ΔI_o as a function of distance of the light image from the fovea, but at least two

in the two most complete available series of measurements bearing directly upon this question the indications are apparently contradictory, although the distances concerned differ; evidence for the evaluation of this matter is presented and discussed in the present paper.

Method and General Procedure

Two collimators of the discriminometer were used in the experiment. The slit opening at S was reduced in size until it presented a square light image. The size of the image was adjusted throughout the experiment so that it subtended at all times a visual angle of 4.8 minutes on a side at the nodal point of the observer's eye. A tiny aperture pierced in a thin sheet of aluminum foil, mounted in the adjacent slit base-plate, served as an adjustable fixation point. Both the image of the fixation point and that of the test source were located in the first focal plane of the eye-piece. A Wratten filter (No. 70), inserted at K (*cf.* Fig. 1), was used to color the image of the fixation point. The size of the test image and the distance separating it from the fixation image were measured directly with a filar ocular-micrometer. A calibrated camera shutter, centered and rigidly mounted in the head of the discriminometer, was employed to control the exposure time of the test image. Single flashes of constant duration ($= 0.20 \pm \sigma_{dist.} = 0.019$ second) were used throughout the experiment. For various reasons, which need not be fully gone into here, the variation of this exposure time (*ca.* 10 per cent) cannot be responsible for the observed behavior of the total variation in the values of the threshold intensities ($\sigma_{\Delta I_o}$) for retinal excitation; for example, there are persistent (and therefore organic) differences in the relative variation of ΔI_o for different observers in various series of measurements only a portion of which are used in the present paper (Tables I, II, and III); moreover, when the exposure time is lengthened its measured variation (with this shutter) of course increases, but ΔI_o declines and so does the value of $\sigma_{\Delta I_o}$. In the present series, mean $\sigma_{\Delta I} = 0.097\ \Delta I_o$; the proportionality constant is the same[1] as for other procedures in which ΔI is obtained for finite levels of I_1; so also is $\sigma_{\sigma_{\Delta I}}$; this emphasizes the intimate connection of ΔI with $\sigma_{\Delta I}$. The shutter was calibrated with the aid of a string galvanometer to which a high speed moving film

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corrections are required for their data. The first, the cosine correction, is readily made. As the eye is turned through an angle θ, the effective area of a constant pupil aperture (and therefore the intensity of the retinal image) is reduced by a factor very nearly equal to $\cos\theta$; even when an immobile eye is employed the intensity is probably diminished by $\cos\theta$ (–a correction on this basis has, of course, been applied to all our data). The second correction is more complex and, unfortunately, cannot be estimated. It involves the state of dark adaptation and (at extreme angles) also involves the effect of a varying stop (due to the observer's eyelid and eyelashes!).

camera was attached. A sinusoidal disturbance was impressed upon the string by alternating currents from a calibrated beat-frequency oscillator (GR type 613-A), —the amplitude of the vibrations being adjusted by means of a microvolter (WE type 509-W).

Absolute threshold stimuli were measured at eighteen different retinal positions along the 0–180° meridian for each of three practised observers. The observers were dark adapted for 45 minutes before the beginning of each experiment. Starting at an intensity well below the threshold stimulus, the intensity of the retinal light image was increased by small steps until the observer first reported the appearance of the light flash. The lamp color temperature was kept at 2050° K.

Ten measurements were taken at each retinal position during a single sitting. Five of the measurements at each position were made by beginning at the extreme temporal position on the retina and then proceeding inwards to and through the fovea. The remaining sets of measurements were secured in the reverse order,—by starting at the nasal aspect and continuing through the fovea until the last position in the periphery of the temporal aspect of the retina had been reached. The curves secured by these different procedures are essentially identical in form for any given observer, and for the present purpose only the averages at each position ($N = 10$) for each individual observer are required (*cf.* Table 1).

RESULTS

The results are given graphically in Fig. 4. This figure shows the general form of the function relating threshold stimulus intensity ($= \Delta I_o$, in photons) to the angular distance of the retinal test image from the fovea. For each observer, the curve falls as the distance from the center of the fovea is made greater. None of these curves is exactly symmetrical with respect to the fovea; each function possesses its own individual characteristics,—and a more thorough study (*e.g.* a study utilizing a closer spacing of positions on the retina) will probably reveal small but biologically real departures from the smooth curves drawn. The data basic to these curves, however, are nicely reproducible for each observer, and are entirely sufficient for our present purposes. (The magnitude of the absolute threshold intensity also declines in this characteristic manner for most wavelengths.[13]) For the positions on the meridian tested, our results demonstrate that the threshold intensity is a declining function of the retinal distance from the fovea,—a function which definitely tends to approach a minimal value in the periphery.[13] This fact has general implications for any theory of vision. It is of particular importance

[13] Crozier, W. J., and Holway, A. H., in preparation.

for the theory which attempts to account for such measurements simply in terms of retinal rod excitation.[14]

TABLE I

Data for *monocular* threshold stimuli, ΔI_o, in units of retinal illumination (photons) as a function of the angular distance of the test image from the fovea. Size of square test image = 0.08° on a side. Duration of flash = 0.20 second. Each entry is an average of ten measurements; $\sigma_{\Delta I_o}$ is the root-mean-square deviation of a single observation. Measurements on the *left* eye of A. C. S. H., and W. J. C.; *right* eye of A. H. H.

Angular distance from fovea along 0–180° meridian	Observers					
	W. J. C.		A. C. S. H.		A. H. H.	
deg.	log ΔI_o	log $\sigma_{\Delta I_o}$	log ΔI_o	log $\sigma_{\Delta I_o}$	log ΔI_o	log $\sigma_{\Delta I_o}$
32	$\bar{1}.537$	$\bar{2}.415$	$\bar{1}.905$	$\bar{2}.782$	$\bar{1}.221$	$\bar{2}.120$
29.5			$\bar{1}.943$	$\bar{2}.756$	$\bar{1}.215$	$\bar{2}.183$
27	$\bar{1}.528$	$\bar{2}.334$	$\bar{1}.981$	$\bar{2}.788$	$\bar{1}.215$	$\bar{2}.204$
24	$\bar{1}.501$	$\bar{2}.305$			$\bar{1}.220$	$\bar{2}.205$
21	$\bar{1}.522$	$\bar{2}.661$	$\bar{1}.941$	$\bar{2}.851$	$\bar{1}.149$	$\bar{2}.003$
19			$\bar{1}.972$	$\bar{2}.869$	$\bar{1}.177$	$\bar{2}.091$
16.5	$\bar{1}.763$	$\bar{2}.589$	$\bar{1}.983$	$\bar{2}.774$	$\bar{1}.200$	$\bar{2}.127$
13.5	$\bar{1}.724$	$\bar{2}.680$	0.016	$\bar{1}.145$	$\bar{1}.203$	$\bar{2}.138$
9.5	$\bar{1}.799$	$\bar{2}.873$	0.023	$\bar{1}.118$	$\bar{1}.182$	$\bar{2}.096$
6	$\bar{1}.878$	$\bar{2}.759$	0.124	$\bar{1}.216$		
5	$\bar{1}.924$	$\bar{2}.764$	0.142	$\bar{1}.138$	$\bar{1}.207$	$\bar{2}.316$
3.5	0.205	$\bar{1}.382$	0.504	$\bar{1}.629$	$\bar{1}.283$	$\bar{2}.366$
2	0.796	$\bar{1}.874$	0.719	$\bar{1}.827$	$\bar{1}.611$	$\bar{2}.712$
1					0.496	1.484
0	0.893	$\bar{1}.916$	1.178	0.106	0.799	$\bar{1}.829$
1					0.412	$\bar{1}.420$
2	0.720	$\bar{1}.739$	1.093	0.204	0.004	$\bar{1}.167$
3.5	0.156	$\bar{1}.221$	0.602	$\bar{1}.724$	$\bar{1}.575$	$\bar{2}.428$
5	0.077	$\bar{1}.006$			$\bar{1}.238$	$\bar{2}.133$
6.5	$\bar{1}.918$	$\bar{2}.883$	0.196	$\bar{1}.309$		
8	$\bar{1}.700$	$\bar{2}.647$				
10	$\bar{1}.683$	$\bar{2}.671$	0.101	$\bar{1}.227$	$\bar{1}.113$	$\bar{3}.993$

[14] *Cf.* the conditions in von Kries' experiments (footnote 11); the exposure time seems not to have been controlled here, and any "correction" would be of doubtful value. At any rate, a consideration of the conditions involved in von Kries' experiments shows clearly that at least a cosine correction needs to be applied to the data.

To evaluate this latter view, we may turn to a recent histological examination of the human eye (Østerberg, 1935).[15] This study gives the topography of the layer of rods and cones for practically the entire human retina. Thorough counts were made on very carefully prepared sections of the perfectly normal retina of a 16 year old male; the mean error for counts of rods and cones was about 1 per cent

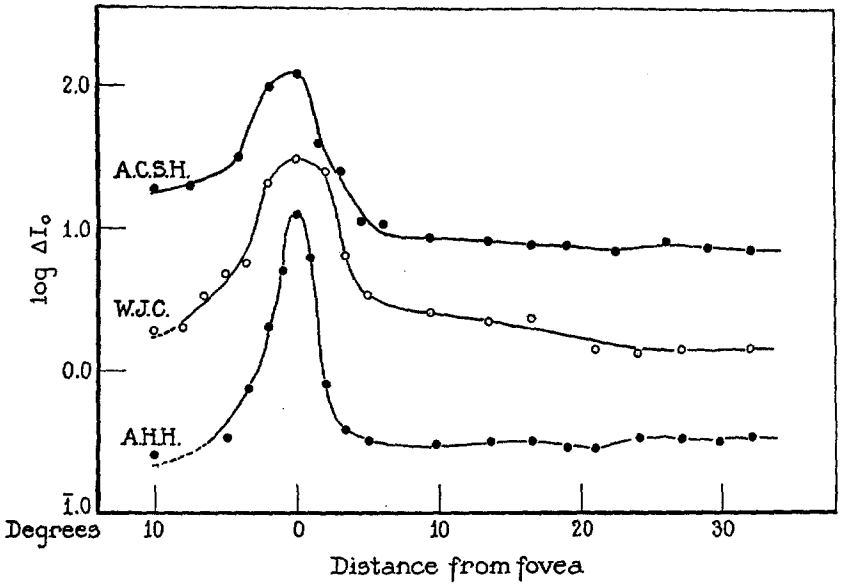

FIG. 4. Absolute mean threshold stimulus intensity (log ΔI_o, in photons) as a function of angular distance from the fovea, for each of three observers. Size of square test image = 0.08° on a side. Duration of flash = 0.20 second. Each plotted point is an average of ten measurements. The ordinate scale is correct for the A. H. H. curve; the measurements (Table I) for W. J. C. have been increased by 0.3 log unit, for A. C. S. H. by 0.6 log unit.

(or less). The count along the 0 −180° meridian is especially complete, and Fig. 5 is a plot based on Østerberg's counts along this meridian, extending from the quartered papilla to the ora serrata in the temporal aspect. The number of primary neurons per mm.^{2} (= *density*) is plotted as a function of the linear distance from the fovea.

[15] Østerberg, G., 1935, *Acta Ophthal.*, **13**, suppl. VI, 1.

The figure shows clearly that the number of *cones* per mm.^{2} decreases continuously as one proceeds peripherally from the fovea. The number of *rods* per mm.^{2}, on the other hand, at first increases, passes through a maximum, and finally declines, as one proceeds from the fovea toward the periphery along the horizontal meridian. The *total number* of primary neurons (rods *plus* cones) per mm.^{2} at any point along the same meridian, computed from Østerberg's tables, is shown by the broken line. This curve necessarily decreases at first,

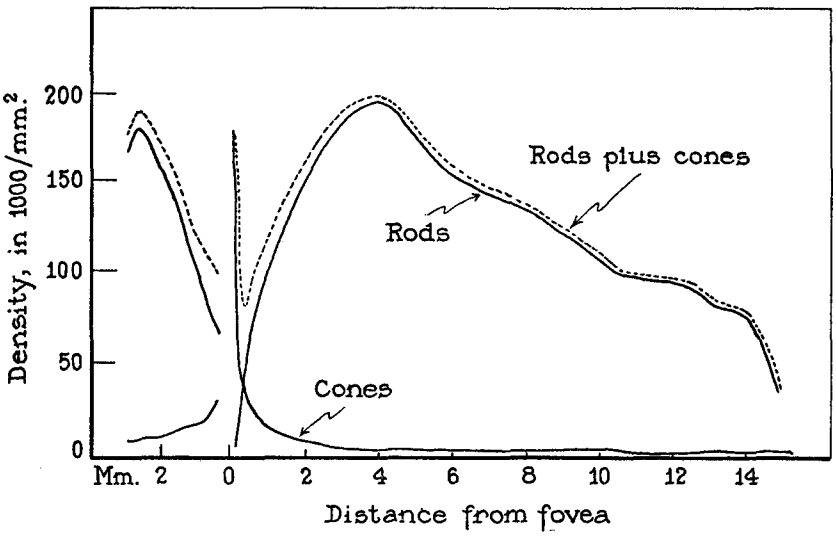

FIG. 5. Plot of Østerberg's[15] counts of visual cells along the 0–180° meridian of the human eye.

passes through a minimum, then increases, passes through a maximum, and finally declines.

If the behavior of ΔI_o were attributable exclusively to the rods, then under the assumptions ordinarily invoked to account for such results, the curves shown in Fig. 4 should exhibit an appreciable minimum at or near a visual angle equal to 16°, and on either side of this point the curve must rise. To compare Figs. 4 and 5, assume 1° = *ca.* 0.29 mm. Our results manifest no such minimum. Neither do the older results of von Kries.[14] As a matter of fact, the curves shown

in Fig. 4 tend to decline continuously even beyond a visual angle of 30° (32° being the limit set for our measurements), or to remain at a sensibly constant level. Unless we wish to introduce additional "supporting" assumptions (*e.g.* an assumption to the effect that the rods increase in sensitivity beyond 16°), then we are forced by the data to reject the notion that the rods alone are responsible for the magnitude of the absolute threshold stimulus for these and similar conditions of scotopic vision.[16] This type of argument, of course, leads immediately to a rejection of the cones *per se*, and also to the rejection of any notion like that which would simply correlate the magnitude of the visual threshold stimulus with the number of excited, primary retinal elements (rods *plus* cones).[17]

The rods and cones, however, are not the only nerve cells in the human retina, and we may turn to a consideration of the secondary (collector) neurons. Although no exact counts have been made as regards the number of these "ganglion" cells per unit area, it is known that the density of these cells tends to decrease as a function of distance from the fovea.[18] So also does the density of optic nerve cells associated with the ganglion fibers.[19] The ratio of the primary nerve elements (rods plus cones) to the number of optic nerve fibers tends in general to increase as one proceeds radially from the fovea toward the periphery of the human eye. If we assume that the intrinsic excitabilities of the nerve fibers concerned are (nearly enough) equally distributed, and if the physiological process critical for the eventuation of the required effect is located in the central nervous system, we have a sufficient basis for expecting that in a general way the threshold stimulus intensity will decline as a function of distance from the fovea.

Moreover, if the occurrence of the threshold response depends upon the eventuation in the central nervous system of a particular critical effect, then we certainly have reason to expect the threshold stimulus intensity for two eyes to be *less* than that for the more sensitive eye.

[16] von Kries, J., 1895, *Z. Psychol. u. Physiol. Sinnesorgane*, **9**, 81; 1897, **15**, 327.

[17] Wald, G., 1938, *J. Gen. Physiol.*, **21**, 269.

[18] Poljak, S. (personal communication). About one-half of these cells lie within a radius of 6° from the human fovea.

[19] Rochon-Dauvignaud, A., 1907, *Arch. anat. micr.*, **9**, 315.

And this, of course, is what was found long ago by Piper[20] to be a fact during the course of dark adaptation. More recently[21], the binocular ΔI_o has been shown to be related to the average of the ΔI_o for the left and right eyes singly by the factor 1:1.4. This fact at once suggests Piper's law, though the latter result was obtained for a large (= 12.5°) retinal image. We therefore find it of theoretical interest to test the implications of this result for a small image on different positions of the retinae.

For this purpose, light images were placed on corresponding points of the two retinae by means of the matched prism binoculars attached to the discriminometer head, and the experiment was carried out essentially as before. The barrels of the oculars were carefully adjusted until an image of S (*cf.* Fig. 1) was sharply defined on each retina. In securing data homogeneous in respect of the form of the function relating the magnitude of the binocular threshold stimulus to the mean angular distance from the foveae, results were secured from two dark adapted observers. Five measurements were taken at each position, beginning at an angular distance of 15° on the temporal aspect of the right eye and proceeding by fixed angular steps until a position equal to an angular distance of 15° on the temporal aspect of the left eye had been reached. The experiment was then repeated and five measurements were secured at each pair of retinal positions in the reverse order. In this way, ten measurements were obtained at every position for each mode of presentation (Table II).

Fig. 6 shows the magnitude of the binocular threshold stimulus (ΔI_o, in photons) as a function of the angular distance (in degrees) from the foveae along the equatorial meridian. Each observer was dark adapted 45 minutes before the measurements were taken. The measurements for each subject were secured at a single sitting, and the data are homogeneous in respect of the *form* of the function.

In general, the threshold is seen to decrease as the angular distance from the foveae is made to increase. Theoretically there need be but one exception to this rule; at about 12° on either side of the foveae (the region of the papilla, or "blind-spot"), the threshold function

[20] Piper, H., 1903, *Z. Psychol. u. Physiol. Sinnesorgane*, **31**, 161.

[21] Lythgoe, R. J., and Tansley, L. R., 1938, *J. Physiol.*, **91**, 427. *Cf.* also Graham, C. H., 1930, *J. Gen. Psychol.*, **3**, 494.

should manifest a slight (but significant) secondary maximum. The portion of the curve lying between these limits, however, is quite symmetrical. This fact by itself is clearly consistent with the idea that the physiological effect critical for the eventuation of the threshold response is central in locus, since the monocular curves (Fig. 4) are not so symmetrical.

TABLE II

Data from each of two observers for *binocular* threshold stimulus, ΔI_o, in units of retinal illumination (photons), as a function of the mean angular distance (degrees) of the test images from the foveae. Angular size of each square test image = 0.08° on a side. Duration of flash = 0.20 second. Each entry is the average of ten measurements; $\sigma_{\Delta I_o}$ is the root-mean-square deviation of a single observation. These data are homogeneous in respect of the *form* of the function relating ΔI_o and retinal position along the 0–180° meridian.

Angular distance from fovea along 0–180° meridian	Observers			
	A. C. S. H.		A. H. H.	
deg.	log ΔI_o	log $\sigma_{\Delta I_o}$	log ΔI_o	log $\sigma_{\Delta I_o}$
15	$\bar{1}.171$	$\bar{2}.021$	$\bar{1}.053$	$\bar{3}.994$
11			$\bar{1}.037$	$\bar{3}.912$
9	$\bar{1}.245$	$\bar{2}.162$		
4.5	$\bar{1}.651$	$\bar{2}.791$	$\bar{1}.461$	$\bar{2}.224$
2	0.108	$\bar{1}.033$	$\bar{1}.988$	$\bar{2}.789$
0	0.714	$\bar{1}.614$	0.912	$\bar{1}.920$
2	0.020	$\bar{1}.125$	$\bar{1}.821$	$\bar{2}.903$
3	$\bar{1}.774$	$\bar{2}.862$		
4	$\bar{1}.599$	$\bar{2}.482$	$\bar{1}.467$	$\bar{2}.293$
6	$\bar{1}.352$	$\bar{2}.406$	$\bar{1}.273$	$\bar{2}.315$
9	$\bar{1}.127$	$\bar{2}.016$	$\bar{1}.079$	$\bar{3}.899$
12	$\bar{1}.091$	$\bar{3}.971$	$\bar{1}.061$	$\bar{2}.000$

To determine quantitatively the relationship between monocular and binocular threshold stimuli, the procedure needs to be slightly altered. If the data are to be homogeneous, then the monocular and binocular measurements must be obtained under essentially identical physiological conditions. To approximate this ideal as nearly as possible, we used Piper's technique[20] of staggering the monocular and binocular measurements at each set of retinal positions. As before,

the oculars were adjusted so as to reduce to a minimum the accommodation differences existing between the left and right eyes of the observer. Failure to provide for this adjustment can completely invalidate results for *binocular* thresholds. (Under commonplace conditions, an individual tends to use his more sensitive eye.) The observers were (again) dark adapted for 45 minutes. The process of dark adaptation is, of course, not complete at the close of this time

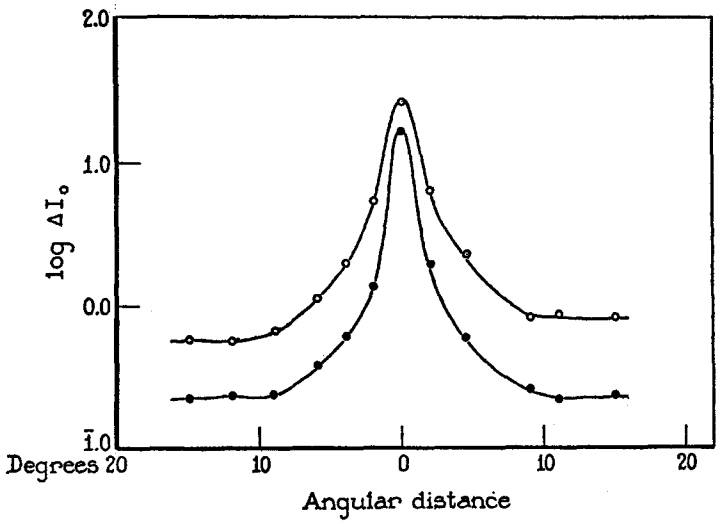

FIG. 6. Magnitude of binocular threshold stimulus (log ΔI_o, in photons) as a function of mean angular distance from the foveae for each of two observers. Size of square test image of each retina = 0.08° on a side. Duration of flash = 0.20 second. Each plotted point is an average of ten measurements. The data basic to the curves were obtained in such a manner as to make the functions homogeneous with respect to *form*. The ordinate scale applies for both curves.

interval, but its rate of change as a function of time in the dark is then slow enough to permit us conveniently to obtain reliable and strictly comparable results. At any given position, a single binocular measurement was taken first, next a monocular measurement was taken for one eye, and then one was secured for the other eye. This practice was continued systematically until finally a total of thirty measurements had been secured for each angular distance from the foveae.

The results are presented graphically in Fig. 7 and numerically in Table III. The half-shaded circles represent the monocular measurements: those shaded on the left are for the left eye; those shaded on the right, for the right eye. These data are not homogeneous in respect of form, but the curves are essentially similar to those shown in

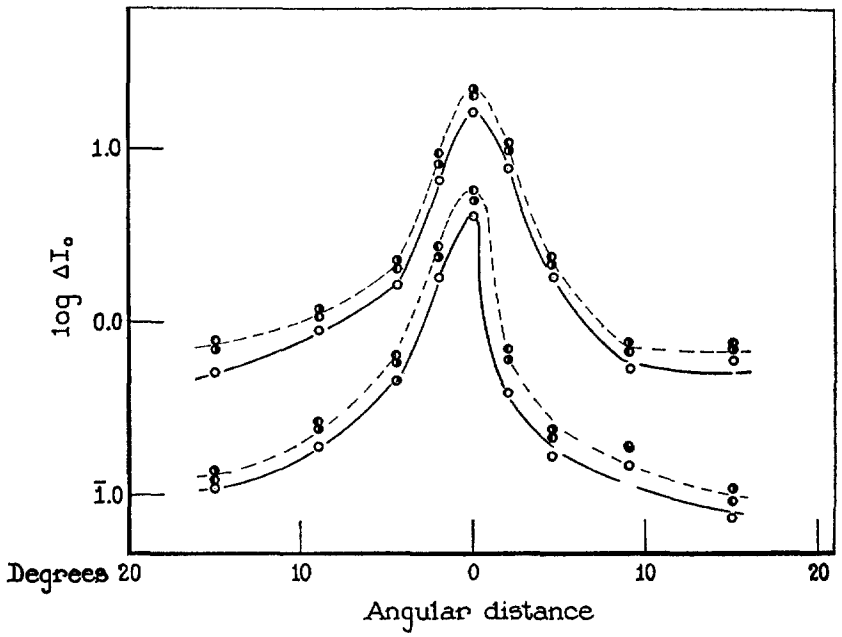

FIG. 7. Homogeneous data for two observers showing that the magnitude of the binocular threshold stimulus is *less* than the magnitude of the monocular threshold stimulus for the more sensitive eye. Each point is based on ten measurements. Since two eyes give greater sensitivity than either eye *per se*, the process responsible for the threshold response may definitely be localized in the central nervous system. See text.

Fig. 6. Table III shows the net result for all of the measurements as well as the measurements secured at each distance from the fovea. The binocular threshold is definitely lower than for the more sensitive eye, in each case. For each observer, the ratio of the binocular ΔI_o to the average of the monocular ΔI_o is, more frequently than not, and independently of retinal position, statistically equal to 1:1.4.

The ratio is thus nearly enough equal to $1/\sqrt{2}$ (*cf.* Piper's law), and hence appears to be independent of area (*cf.*[21]). These results are fully coherent with *a priori* expectation based on the assumption that the visual threshold finds its effective representation in *central* nervous processes. This situation may be a general one, since it applies for auditory excitation[22] as well, and for kinesthesis;[23] for

TABLE III

Data homogeneous for quantitative comparison between magnitudes of binocular and monocular threshold stimuli. Angular size of each square test image = 0.08° on a side. Duration of flash = 0.20 second. Each entry is an average of ten measurements; $\sigma_{\Delta I_o}$ is the root-mean-square derivative of a single observation. See text.

Angular distance from foveae along 0–180° meridian	Observers											
	A. H. H.						A. C. S. H.					
	Left eye		Right eye		Binocular		Left eye		Right eye		Binocular	
deg.	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$	$\log \Delta I_o$	$\log \sigma_{\Delta I_o}$
15	$\bar{1}.033$	$\bar{3}.891$	$\bar{1}.078$	$\bar{3}.952$	$\bar{2}.918$	$\bar{3}.813$	$\bar{1}.526$	$\bar{2}.463$	$\bar{1}.483$	$\bar{2}.577$	$\bar{1}.351$	$\bar{2}.428$
9	$\bar{1}.364$	$\bar{2}.294$	$\bar{1}.325$	$\bar{2}.464$	$\bar{1}.217$	$\bar{2}.192$	$\bar{1}.671$	$\bar{2}.785$	$\bar{1}.719$	$\bar{2}.738$	$\bar{1}.592$	$\bar{2}.616$
4.5	$\bar{1}.732$	$\bar{2}.666$	$\bar{1}.707$	$\bar{2}.871$	$\bar{1}.594$	$\bar{2}.389$	$\bar{1}.950$	$\bar{2}.927$	$\bar{1}.993$	$\bar{2}.944$	$\bar{1}.863$	$\bar{2}.845$
2	0.362	$\bar{1}.261$	0.327	$\bar{1}.183$	0.199	$\bar{1}.281$	0.617	$\bar{1}.720$	0.583	$\bar{1}.672$	0.461	$\bar{1}.661$
0	0.682	$\bar{1}.573$	0.643	$\bar{1}.582$	0.540	$\bar{1}.410$	0.982	$\bar{1}.936$	0.989	$\bar{1}.937$	0.830	$\bar{1}.829$
2	$\bar{1}.677$	$\bar{2}.799$	$\bar{1}.618$	$\bar{2}.690$	$\bar{1}.523$	$\bar{2}.627$	0.671	$\bar{1}.743$	0.637	$\bar{1}.724$	0.532	$\bar{1}.593$
4.5	$\bar{1}.276$	$\bar{2}.273$	$\bar{1}.302$	$\bar{2}.418$	$\bar{1}.159$	$\bar{2}.144$	0.012	$\bar{1}.214$	$\bar{1}.985$	$\bar{2}.993$	$\bar{1}.906$	$\bar{2}.947$
9	$\bar{1}.206$	$\bar{2}.163$	$\bar{1}.205$	$\bar{3}.998$	$\bar{1}.100$	$\bar{2}.035$	$\bar{1}.479$	$\bar{2}.493$	$\bar{1}.530$	$\bar{2}.622$	$\bar{1}.377$	$\bar{2}.520$
15	$\bar{2}.899$	$\bar{3}.714$	$\bar{2}.958$	$\bar{3}.835$	$\bar{2}.803$	$\bar{3}.951$	$\bar{1}.538$	$\bar{2}.629$	$\bar{1}.499$	$\bar{2}.555$	$\bar{1}.400$	$\bar{2}.503$

audition, the ratio of the ΔI's for excitation of a single peripheral sensory field to those for simultaneous symmetrical excitation of bilateral fields is not, however, equal to 1.4, but is greater (= *ca.* 2.0),

[22] *Cf.* Upton, M., and Holway, A. H., 1937, *Proc. Nat. Acad. Sc.*, **23**, 32. We have additional data for a further analysis of this matter, in preparation.

[23] Holway, A. H., Smith, J., and Zigler, M. J., 1937, *J. Exp. Psychol.*, **20**, 371.

—a fact which has considerable theoretical significance.[24] Piper's rule[25] for dark adapted eyes states that ΔI_o should be inversely proportional to $\sqrt{A}$, where A is the area of the test spot on a single retina. It will be noticed that we have in the present data, for fovea and for periphery, a rather precise demonstration of this rule,—but for the case in which area is doubled by applying the same area to corresponding points of two retinae.

We are under obligation to Mrs. Alice C. S. Holway for her patient collaboration as skillful observer in these experiments.

SUMMARY

Monocular threshold stimulus intensities (ΔI_o, photons) were measured along the 0–180° meridian of human retinae for three observers. The test image was small (= 0.08°) and of short duration (= 0.20 second). ΔI_o was found to decrease as the angular distance from the fovea was increased. Actual counts of the number of retinal elements per mm.^{2} along the 0–180° meridian (Østerberg[15]) were compared with the obtained results. No direct correlation was found to exist between visual sensitivity and the number of retinal elements.

Binocular threshold stimuli were also measured along the same meridian. The *form* of the function relating binocular visual sensitivity and retinal position was discovered to be essentially similar to that for monocular sensitivity, but is more symmetrical about the center of the fovea. The magnitude of the binocular measurement is in each case smaller than that of the monocular threshold stimulus intensity for the more sensitive eye. The ratio is statistically equal to 1.4 (a fact which suggests Piper's rule).

These results are shown to be consistent with the hypothesis that the process critical for the eventuation of the threshold response is localized in the central nervous system. They are not consistent with the view that the quantitative properties of visual data are directly determined by properties of the peripheral retina.

[24] We have also found, however, that over the whole workable range of intensities binocular ΔI, as a function of I_1, is less than monocular ΔI for either eye, but that for higher intensities the ratio is closer to 1.2 (Crozier and Holway, in preparation).

[25] Piper, H., 1903, *Z. Psychol. u. Physiol. Sinnesorgane*, **32**, 98.