A mathematical theory of optical illusions and figural aftereffects

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If it is assumed that spurious enhancement of receptive field excitations near the intersection of image lines on the retina contributes to the cortical determination of the geometry of two-dimensional figures, an equation based on the least-squares fit of data points to a straight line can be obtained to represent the *apparent* line. Such a fit serves as an *extremum* on the precision with which a data set can be represented by a straight line. The disparity between the *apparent* line and the actual line that occurs in the case of peripheral (and to a lesser degree in more central regions of the retina) vision is sufficient to produce the perceptual errors that occur in the Poggendorff, Hering, and Mueller-Lyer illusions. The magnitude of the Poggendorff illusion as a function of the line angle is derived and experimentally tested. Blakemore, Carpenter, and Georgeson's (1970) experimental data on angle perception are shown to fit this same function. The *apparent* curve is derived for the Hering illusion. The Mueller-Lyer illusion is found to be a variation of the Poggendorff illusion. The equations are further developed and used to derive Pollack's (1958) experimental results on figural aftereffects. The results involve only *one* experimentally determined coefficient that can be evaluated, within the limits of experimental error, in terms of physiological data. The use of these concepts provides a foundation for the abstract modeling of the initial phases of the central nervous system data reduction processes, including receptive field structure, that is consistent with the physiological limitations of the retina as a source of visual data, as well as with the findings of Hubel and Wiesel (1962).

I. INTRODUCTION

Optical illusions constitute errors or limitations that accompany the data reduction processes involved in pattern discrimination. As a consequence, they provide valuable clues to the processes by which the data stemming from neural excitations are handled by the central nervous system to produce a discriminatory response to the optical pattern.

The present paper will be concerned only with two classes of optical illusions—illusions of two-dimensional geometric figures involving intersecting lines and figural aftereffects. Other optical illusions may prove to be amenable to a treatment similar to that presented here. It is the intention of the present treatment to give a precise mathematical development of the origin of the *apparent* perceptual figures arising in the case of geometric optical illusions that is founded on physiological data, that is supported by the functional dependence of its parameters, and that is substantiated by the quantitative results of experiments. It may be pointed out that no prior theory succeeds in such an objective.

The literature on optical illusions has become too extensive to summarize fully here (Fisher, 1968; Green & Hoyle, 1964; Hoffman, 1971; Luckiesh, 1922; Weintraub & Virsu, 1971). Some comments concerning current theories are nevertheless called for.

The theories of Pressey (1967, 1970) and R. L. Gregory (1968) are sufficiently qualitative that appraisal of their adequacy depends as much on subjective determinants as do the illusions themselves. For example, to obtain agreement with the Orbisson illusion (Green & Stacey, 1966), R. L. Gregory's (1968)

perspective theory must introduce unconsciously perceived depth. In the words of Humphrey and Morgan (1965), "A theory which appeals to the idea of automatic compensation for unconsciously perceived depth is in obvious danger of being irrefutable."

Gillam (1971), after Filehne (1898) and Green and Hoyle (1964), has offered an interpretation of the Poggendorff illusion based on unconscious depth processing of two-dimensional figures as three-dimensional rectilinear perspective. The error is assumed proportional to the displacement from collinearity of the lines treated as three-dimensional perspective. The illusion is assumed to result from data reduction processes on retinal images. However, this data reduction process is not fully specified, most predictions of the theory being qualitative. Depth processing per se does not correctly resolve the findings of Lucas and Fisher (1969), that Poggendorff displacements occur in concrete three-dimensional situations. To accommodate this, Gillam "postulates automatic, often unconscious, perspective processing of oblique contours and not regression to the real object." Thus, the theory is not strictly a depth but an angle processing theory. In this, Gillam's treatment has commonality with the present approach. However, Gillam's experimental investigation of a perspective modification of the Poggendorff illusion did not yield (accurately) results predicted by the depth processing theory. We show below that the present treatment satisfies those experimental findings to the experimental accuracy.

The optical confusion theory developed by Chiang (1968) is an example of a theory that does allow for the quantitative treatment of the apparent perceptual figures as has been carried out by Glass (1970). However, the

Fig. 1. The Poggendorff illusion in which the two segments appear offset rather than collinear.

theory's basic concept, that optical blurring and physiological nystagmus are the cause of these illusions, has been shown to be unsatisfactory by Coren (1969) and Cumming (1968).¹

Neural confusion theories have been offered by Ganz (1966), Robinson (1968), and Blakemore, Carpenter, and Georgeson (1970). Ganz and Robinson suppose inhibitory effects to arise at the retinal level, while Blakemore, Carpenter, and Georgeson suppose these to occur at the cortical level. Strangely, none of these authors acknowledge that neural inhibition *per se* (as introduced in their theories) would give rise to perceptual distortions opposite to those necessary for an explanation of the illusions. This fact is particularly striking in the work of Blakemore, Carpenter, and Georgeson. While it is true that "two lines forming an acute angle should," as the result of inhibition, "appear to be shifted away from each other in orientation," it is false that as a consequence "the angle between them should seem to expand." The fact that the inhibitory shift, by their treatment, falls off with distance from the apex of the angle leads to a reduction in the apparent angle (for acute angles). The failure to recognize this fact must be attributed to the lack of any effort to formalize their theory in precise terms.

The present author's work (Walker, 1971) has pursued the development of a formal theory based on spurious neural excitation at the retinal level as manifest in line detection cortical functions. A corresponding dichotomy is to be found between the organization of receptive fields in the retina and in the visual cortex. In the cat's retina, one can distinguish two types of ganglion cells, those with *on-center* receptive fields and those with *off-center* fields (Kuffler, 1953). The lateral geniculate body also has cells of these two types (Hubel & Wiesel, 1961). On the other hand, the visual cortex contains a large number of functionally different cells. Arrangements of receptive fields in the cat's visual cortex studied by Hubel and Wiesel (1962) serve to discriminate line segment orientation. The theory in this paper is principally concerned with the process of line

orientation discrimination which, according to Hubel and Wiesel (1962), is cortically determined by receptive fields dependent on "the orientation of the boundaries separating the field subdivisions." In this process, patterns of neural excitations (*data points*) map the line element onto the cortical receptive field. Both excitatory and inhibitory impulses play a role in this overall process, but with regard to the generation of spurious *data points*, only spurious excitations will be introduced in the theory; in this way, the theory is maintained as a first-order theory requiring only one coefficient (see Eq. 33) to be determined either physiologically or experimentally. These *spurious data points* are neural excitations arising from receptive fields that give rise to an enhanced response due to excitation by one image line in the presence of the other (i.e., both lines fall on the receptive field).

Recent computer simulation studies carried out by Robinson, Evans, and Abbamonte² appear to confirm the contention that the illusions arise concomitantly with the data reduction involved in line feature discrimination (Walker, 1971).

By means of retinal excitatory enhancement arising from images of intersecting lines on the retina, spurious *data* are introduced into cortical line feature detection involved in pattern discrimination, producing the distortions in the *apparent* figure. The line discrimination is treated mathematically by the idealization of the least-squares fit which serves as a limit for the *class* of line detector theories. That is to say, the results of the theory are not dependent on the particular details of the data-handling functions at the cortical level that are involved in the determination of the occurrence of lines in the figure so long as the cortical process approaches the least-squares fit as a mathematical limit. More than this, the present theory takes cognizance of the real variation in the density of receptive fields on the retina in its formulation. It is pointed out further that a significant feature of geometric illusions is that the geometry of the figure is of necessity determined by the peripheral vision involving a low density of receptive fields or, when viewed centrally, subtends a sufficiently small angle for, again, the number of receptors involved in the discrimination of critical features to remain small.

A particularly elementary example of two-dimensional optical illusions is the Poggendorff illusion, in which two segments of a straight line interrupted by a band or two separated parallel lines lying at an angle to the segments (Fig. 1) do not appear collinear. The disparity between the geometry of the *apparent* figure and that of the real figure is large compared to the resolution we usually expect of our eyes.

One basic characteristic of such optical illusions is that the geometry must be determined largely by the peripheral vision of the eye. Although the *fovea centralis*

Fig. 2. Field distribution of neural excitations arising at the intersection of two lines. Receptive fields affected are indicated. The crosshatched sections represent the areas giving rise to spurious excitations.

can be used to examine any part of the figure (giving the illusion of having examined the geometry in detail), the geometry of the figure cannot be so examined. In the case of the Poggendorff illusion, an examination of one line segment with the *fovea centralis* leaves the other segment's orientation to be determined by the eye's peripheral vision. Looking directly at the second line segment does not resolve the question of the geometry of the figure, since the relation of the first segments to the rest of the figure must now be determined by the peripheral vision.

The density of neural excitations originating at receptors in the peripheral vision areas of the eye is rather low and probably becomes lower before cortical processing of geometrical relationships. The detection of geometrical elements immersed in a visual data set requires a process of identification and assignment of specific data points to the line elements discerned. The process of line element detection and data point assignment is handled as a single process; this fact is evident from the work of Hubel and Wiesel (1962). That a straight line exists as a pattern element of the figure must be determined from the information contained in a set of contiguous data points. If other pattern elements lie near this line, contiguous data points may be *spuriously* assigned to the set of data points that represent the line. Thus, in the initial stages of the pattern discrimination process, beginning in the plexiform layer of the eye and ending in the cortical regions of the brain,³ data from some of the receptors lying near the image of the intersection of the two lines may be spuriously generated and ascribed. The point we wish to consider is, assuming this to be the case, what will be the resultant distortion of the perceived geometry?

II. RECEPTIVE FIELD MODEL

For the purposes of this theory, many details of the behavior of the receptive fields will not be introduced since such added complexity is not called for in an elementary theory as will be given here. (A more

detailed model will be presented at a later point in the paper.) Let us define the *effective* receptive field to be the collection of receptors needed to produce one data point in the brain describing the geometrical relationships in the image. We take the effective receptive field representing one data point in the central nervous system to be circular with an angular radius (as measured from the corresponding principal point of the eye's optical system) r_o . With the receptor density on the retina given by σ , the number of receptors, ϵ , in an average receptive field will be given by

$$\epsilon = \pi r_o^2 \sigma. \quad (1)$$

The value of σ is a function of retinal position and will be so treated in the present paper.

Let us consider the way in which spurious data points arise in the case of the Poggendorff illusion (Fig. 1). Since the data points from Line A cannot be uniquely labeled, they may be assigned spuriously to B. The effect extends for some angular distance, λ , of the order of the angular diameter, $d_o = 2r_o$, of an effective receptive field. Thus, we write

$$\lambda = q d_o. \quad (2)$$

(The quantity q will be shown to have a value of about 5 from physiological data.) It is shown below that d_o is the diameter of the receptive field center, while λ is the diameter of the receptive field surround. Just how the surround can contribute to an enhanced response will become clear from the detailed treatment of the receptive field presented in the section on figural aftereffects. It is worth noting, however, that Enroth-Cugell and Pinto (1972a) have shown that the pure surround response of *off-center* receptive fields is similar in shape to the pure center response of *on-center* cells.

The data points upon which the determination of the presence and characteristic parameters of Line B in Fig. 1 will be distributed are shown in Fig. 2. The *apparent* line perceived will be slightly shifted, making

the angle, α , appear larger than it actually is. As a result, Lines B and C of Fig. 1 do not appear to join in a straight line but appear to be displaced.

The geometry of Fig. 2 will be used in the mathematical development in Sections II-V. A physiologically and mathematically more sophisticated postulate will be introduced for the treatment of figural aftereffects; its introduction at this point would, however, entail nonessential algebraic complications.

We will assume, therefore, that the spurious points come from an area lying between Lines A and B where the separation of the lines is less than or equal to λ , as shown in Fig. 2. Such an area occurs on each side of Line B. This area, $a(\alpha)$, is given simply by the expression

$$a(\alpha) = \frac{1}{4} \lambda^2 \cot \frac{\alpha}{2}. \quad (3)$$

From Eq. 3, we have for the number of spurious points

$$n = \frac{1}{4} \lambda^2 (\sigma/\epsilon) \cot \frac{\alpha}{2}. \quad (4)$$

For the following derivation, it will prove useful to use the *appropriate* average value for the τ, ξ coordinates (see Fig. 2) of these n spurious points. Here, *appropriate* refers to the use of first-order moments about the respective coordinate to give the average value of linear terms in the coordinate position, second-order moments of the points for quadratic terms in the coordinate positions, etc. Thus, for points distributed over the area included in the triangle on the acute-angle side of Line B, the first moment taken about the end of Line B in a direction perpendicular to B is

$$\lambda_{\xi} = \sum_{i=1}^n \xi_i \approx \frac{\int \xi \tau d\xi}{\int \tau d\xi} = \frac{1}{3} \lambda \cos \frac{\alpha}{2}. \quad (5)$$

That is to say, simply, λ_{ξ} is the average value of ξ for these n points.

The average value for the first moment of the supplementary area, λ'_{ξ} , is obtained by substitution of $\pi - \alpha$ for α in Eq. 5. (An explicit basis for the calculation of n and λ_{ξ}^2 is given in section VI, Eq. 65, and is used in Appendix A to replace Eqs. 4 and 5.)

The number of accurately ascribed data points arising from neural excitations along Line B having a length L when viewed from a distance D will be

$$N = L/d_o D, \quad (6)$$

which is simply the number of receptive fields crossed by the line projected on the retina.

To the extent that the data processing carried out upon the neural excitations by the retina and the central nervous system functions in the capacity of an ideal line detector (capable of extracting the line

characteristics in approximation to the mathematical limits imposed by the data set), these processes may be represented by the mathematics for the least-squares fit of the data to the equation of a straight line,

$$y = mx + b. \quad (7)$$

By approaching the problem in this manner, the greatest generality in the theory is achieved. More specialized line detector models may yield agreement with experimental findings through commonality with or approximation to this property, despite the employment of less general data-handling algorithms. Use of the most general approach avoids such a multiplicity of theories.

A least-squares fit requires that for each data point having coordinates (X_i, Y_i) , we form the deviation d_i given by

$$d_i = Y_i - mX_i - b. \quad (8)$$

The sum of the squares of the deviation for all data points yields the quantity $f(m, b)$

$$f(m, b) = \sum_{i=1}^{N+n+n'} d_i^2, \quad (9)$$

where there is a total of N valid points, n spurious points arising from the acute angle, and n' spurious points arising from the obtuse angle.

The valid points lie along the line

$$y = x \tan \alpha. \quad (10)$$

(The origin of the coordinates is chosen to lie at the intercept of Lines A and B, Line B serving as the abscissa.) They are assumed spaced a distance, $d_o D$, along the physical line or an angular distance, d_o (the diameter of receptive field centers), on the retina. There are a total of N such *data points*. A typical one, the N_i , has coordinates (starting from the intercept of Lines A and B)

$$X_i = N_i d_o D \sin \alpha, \quad (11)$$

$$Y_i = N_i d_o D \cos \alpha. \quad (12)$$

The resulting deviation, given by Eq. 8, is

$$d_i = N_i d_o D (\sin \alpha - m \cos \alpha) - b \quad (13)$$

and its square is

$$\begin{aligned} d_i^2 &= N_i^2 d_o^2 D^2 (\sin \alpha - m \cos \alpha)^2 \\ &\quad - 2b d_o D N_i (\sin \alpha - m \cos \alpha) + b^2. \end{aligned} \quad (14)$$

The sum of the squares gives

$$\begin{aligned}
 f_N(m,b) &= \sum_{i=1}^N d_i^2 = d_o^2 D^2 (\sin \alpha - m \cos \alpha)^2 \sum_{i=1}^N N_i^2 \\
 &\quad - 2bd_o D (\sin \alpha - m \cos \alpha) \sum_{i=1}^N N_i + \sum_{i=1}^N b^2 \\
 &= \frac{1}{6} N(N+1)(2N+1) d_o^2 D^2 (\sin \alpha - m \cos \alpha)^2 \\
 &\quad - N(N+1)bd_o D (\sin \alpha - m \cos \alpha) + Nb^2,
 \end{aligned} \tag{15}$$

where we have used the relations

$$\sum_{i=1}^N N_i^2 = \frac{1}{6} N(N+1)(2N+1), \tag{16}$$

$$\sum_{i=1}^N N_i = \frac{1}{2} N(N+1), \tag{17}$$

and

$$\sum_{i=1}^N b^2 = Nb^2. \tag{18}$$

The contributions to $f(m,b)$ arising from the spurious points at the acute angle, $f_n(m,b)$, total in number n points. For simplicity in the mathematics, these points are taken to be located at a position $(\lambda_\tau, \lambda_\zeta)$ in the τ, ζ coordinate system shown in Fig. 2 or at the point

$$X_i = (\lambda_\zeta \sin \alpha + \lambda_\tau \cos \alpha)D \tag{19}$$

$$Y_i = (\lambda_\tau \sin \alpha - \lambda_\zeta \cos \alpha)D \tag{20}$$

in the x,y coordinate system. This leads to the expression for the deviations arising at the acute angle

$$d_i = D\lambda_\tau (\sin \alpha - m \cos \alpha) - D\lambda_\zeta (\cos \alpha + m \sin \alpha) - b \tag{21}$$

and from the obtuse angle

$$d_i' = D\lambda_\tau' (\sin \alpha - m \cos \alpha) - D\lambda_\zeta' (\cos \alpha + m \sin \alpha) - b. \tag{22}$$

where λ_ζ' is a negative number. The contribution to $f(m,b)$ from the $n + n'$ points is

$$f_{n+n'}(m,b) = \sum_{i=1}^n d_i^2 + \sum_{i=1}^{n'} d_i'^2. \tag{23}$$

The sum of Eqs. 15 and 23 give $f(m,b)$:

$$\begin{aligned}
 f(m,b) &= f_N + f_{n+n'} \\
 &= \frac{1}{6} N(N+1)(2N+1) d_o^2 D^2 (\sin \alpha - m \cos \alpha)^2 \\
 &\quad - N(N+1)bd_o D (\sin \alpha - m \cos \alpha) \\
 &\quad + (N + n + n')b^2 + n\lambda_\tau^2 D^2 (\sin \alpha - m \cos \alpha)^2 \\
 &\quad + n\lambda_\zeta^2 D^2 (\cos \alpha + m \sin \alpha)^2 \\
 &\quad - 2n\lambda_\tau \lambda_\zeta D^2 (\sin \alpha - m \cos \alpha)(\cos \alpha + m \sin \alpha) \\
 &\quad - 2nb\lambda_\tau D (\sin \alpha - m \cos \alpha) \\
 &\quad + 2nb\lambda_\zeta D (\cos \alpha + m \sin \alpha) \\
 &\quad + n'\lambda_\tau'^2 D^2 (\sin \alpha - m \cos \alpha)^2 \\
 &\quad + n'\lambda_\zeta'^2 D^2 (\cos \alpha + m \sin \alpha)^2 \\
 &\quad - 2n'\lambda_\tau' \lambda_\zeta' D^2 (\sin \alpha - m \cos \alpha)(\cos \alpha + m \sin \alpha) \\
 &\quad - 2n'b\lambda_\tau' D (\sin \alpha - m \cos \alpha) \\
 &\quad + 2n'b\lambda_\zeta' D (\cos \alpha + m \sin \alpha)
 \end{aligned} \tag{24}$$

The least-squares treatment is such that m and b will be so chosen as to minimize this sum of the deviations. This is accomplished by setting the partial derivatives of f with respect to m and b equal to zero.

$$\partial f / \partial m = 0 \tag{25}$$

$$\partial f / \partial b = 0 \tag{26}$$

and solving for m and b . Substitution of Eq. 24 into Eqs. 25 and 26 yields simultaneous equations in m and b , which, being linear, are readily solved.

The resulting expressions are inconvenient to handle unless higher order terms, terms involving λ_ζ^2 , λ_τ^2 , $\lambda_\zeta \lambda_\tau$, and the corresponding primed (coordinate position averages for the n' points) terms, are dropped. The complete expressions are given in Appendix B. These expressions have been used to calculate certain of the results to appear below, where appropriate. The resulting expressions for m and b are

Fig. 3. The relationship of the real and *apparent* lines.

$$m = \tan \alpha \left[1 + \frac{3}{2d_o N^2} (n\lambda_f f + n'\lambda'_f f') \sec \alpha \csc \alpha \right] \quad (27)$$

and

$$b = -\frac{D}{N} (n\lambda_f F + n'\lambda'_f F') \sec \alpha \quad (28)$$

where

$$f = 4(N+1)/(N+4n) \quad (29)$$

$$F = 1 + 3f/4)/(1+n/N) \quad (30)$$

and f' is given by replacing n' for n in Eq. 29 and F' by replacing n', f' for n and f in Eq. 30. From Eqs. 1, 2, and 6, we can write

$$m = \tan \alpha \left[1 + K \left(f \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - f' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right) \sec \alpha \csc \alpha \right] \quad (31)$$

and

$$b = -\frac{8}{3\pi} KL \left(F \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - F' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right) \sec \alpha \quad (32)$$

where

$$K = \frac{q^3 \epsilon D^2}{8\sigma L^2} \quad (33)$$

The quantities L and D are experimental parameters, σ is physiologically determined. The quantity $q^3 \epsilon$ appears as

a single coefficient that will be experimentally evaluated, below and will be shown to be consistent with physiologically determined quantities.

The values of m and b given in Eqs. 31 and 32, when substituted into Eq. 7, yield the equation for the *apparent* line in terms of the physiological and physical conditions of the observation. The real line, that is, the actual physical line, is given by

$$y' = x' \tan \alpha. \quad (34)$$

Figure 3 shows the *apparent* line, Eq. 7, resulting from observation of the line given by Eq. 34. These two equations, (7) and (34), can be used to calculate the distance Δx shown in Fig. 3, which is the distance between the intercept points on the line at $y = -a$, i.e., Line D in Fig. 1, for the real and the *apparent* lines.

At $y' = -a$, x' will be

$$x' = -a \cot \alpha, \quad (35)$$

whereas the *apparent* intercept will be

$$x = -(a+b)/m. \quad (36)$$

The magnitude of the displacement Δx between the real and *apparent* intercept points is given by

$$\Delta x = x - x' = a \cot \alpha - (a+b)/m. \quad (37)$$

Substitution from Eqs. 31 and 32 yields, approximately,

$$\Delta x = a \cot \alpha \cdot \left[1 - \frac{1 - \frac{8KL}{3\pi a} \sec \alpha \left(F \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - F' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right)}{1 + K \sec \alpha \csc \alpha \left(f \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - f' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right)} \right]. \quad (38)$$

Since K is small compared to unity, we can linearize Eq. 38 to obtain

$$\Delta x = \frac{8KL}{3\pi} \csc \alpha \left(F \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - F' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right) + aK \csc^2 \alpha \left(f \cot \frac{\alpha}{2} \cos \frac{\alpha}{2} - f' \tan \frac{\alpha}{2} \sin \frac{\alpha}{2} \right). \quad (39)$$

Since the terms in the linearized expression for Δx vary as (see Eq. 33) L^{-1} and L^{-2} , respectively, Δx will decrease as the length of the line increases in accord with Robinson's (1968) observation. Notice that Δx varies inversely with the product of σ and the angular size of

the figure (through L and a). Thus, Δx varies [including the effects of changes in ϵ (see data in Webb, 1964)] approximately as the square root of the subtended angle (for angles below 10 deg). As a consequence, these illusions are not removed when viewed with the *fovea centralis*; the illusion is not restricted to, but arises primarily in, peripheral vision.

To test Eq. 38, an experiment was designed in which the Poggendorff illusion could be projected on a screen in such a way that Line B of Fig. 1 could be moved until the Ss indicated that Lines B and C were perceived to be collinear. A vertical (normal) orientation of the head was maintained. In all figures, the central band of the figure was horizontal, as in Fig. 1. A total of 20 Ss was employed for this test. The values of a, L, and D were selected to be 25 cm, 12.5 cm, and 6.25 m, respectively. Various values of α , from 30 to 90 deg, were used. The average value of Δx for $\alpha = 45$ deg was found to be 4.25 cm, or 0.339 L. Under the conditions of the experiment, the optimum angle subtended at the eye between the midpoint of Line B and the intersection point of C in the illusion is 3.81 deg. For an eye, 24.7 mm in diam, having a first principal point to retinal (on the optic axis) distance of 23.2 mm (see Webb, 1964), data for the density of cones on the retina yield a value of σ of 1.17×10^7 sterrad $^{-1}$. Using these data in Eq. 17, we obtain

$$q^3 \epsilon = 1,589. \quad (40)$$

(The value of $q^3 \epsilon$ is weakly dependent, by way of the higher order terms in the equation, on the choice of q , varying by a factor of three for an order-of-magnitude change in q .) Hubel and Wiesel (1960) give data for the size of the receptive fields for the spider monkey eye. The receptive field center varies from 4 min to 2 deg, the higher values occurring in the periphery. At 4 deg, their data give 4.6 min of arc, which, allowing for the smaller eye of the monkey but assuming the receptive field to be the same size in the human, gives us $d_o = 4.0$ min. The receptive field surround is found to be five times (at 31 deg from the *fovea*, Hubel and Wiesel give a center diameter of 1 deg and a surround of 5 deg) as large as the center. From Eq. 1, we obtain for $d_o = 4.0$ min, $\epsilon = 12.7$. This value for ϵ in Eq. 40 gives $q = 5.0$, in agreement with the physiological value. Thus, the experimental and physiological data are in complete accord. Since the number (Polyak, 1941) of optic nerve fibers (one eye) is about 10^6 while the total number of cones obtained by integrating the data of Webb (1964) is 6.89×10^6 (the value for the rods is 1.26×10^8), the average convergence of neuronal excitations from the retinal cones onto the optic nerve fibers is about 6.89. This value is close to the value of ϵ obtained above, and thus the value of $q^3 \epsilon$ can be obtained from physiological measurements.

The angular dependence of the theoretically derived value of Δx , Eq. 38, using Eq. 40 for the value of the

Fig. 4. Comparison of the theoretical angular dependence of Eq. 38 with the experimental data.

coefficient, is shown in Fig. 4, together with the results of the experiment described above.

Blakemore, Carpenter, and Georgeson (1970) have experimentally investigated the effect of one line on the orientation detection of a second line as a function of the included angle, using human Ss. While their explanation of the observed effect in terms of lateral inhibition is inconsistent with their experimental findings, these findings offer additional data for comparison with the present theory. In their experiment, a line subtending 1 deg ($D/L = 57.3$) lies at an angle to a second line. The S is required to adjust a third line 0.6 deg distant until it appears parallel to the first line. The angular error $\Delta\alpha$ in this adjustment as a function of α is given by their experiment in Fig. 5. The present theory gives the apparent slope of the line to be m , as obtained in Eq. 31. Thus $\Delta\alpha$ is given by

$$\Delta\alpha = \arctan m - \alpha. \quad (41)$$

Using 0.3 deg as the optimum angle subtended by critical parts of the figure in the determination of the orientation (for a fixation point between the adjustable and reference lines), we obtain a density of receptors $\sigma = 4.04 \times 10^7$ sterrad $^{-1}$. Using Eq. 40 for $q^3 \epsilon$ yields for the coefficient K a value of 0.016. Equation 41 is plotted in Fig. 5 using this value of K together with a plot for $K = 0.011$ ($q^3 \epsilon = 1.055$), which yields a slightly

Fig. 5. A plot of Blakemore, Carpenter, and Georgeson's data for two Ss, giving the displacement angle of the apparent line orientation as a function of the angle of the intersecting lines. Also shown are the theoretical curves plotted using Eq. 40 to obtain $K = 0.016$.

improved fit. (Notice that a variation in the values of q and ϵ of 11% between the mean values of the quantities for the 20 Ss used to obtain the value in Eq. 40 and for the two Ss reported on by Blakemore, Carpenter, and Georgeson is adequate to account for this adjustment in K .) The data give excellent agreement with the theory without requiring a significant adjustment of the coefficient.

A subtle aspect of the Poggendorff illusion is a very slight apparent bending in of Lines B and C in Fig. 1. A careful consideration of the apparent shape of these lines under conditions of the Poggendorff illusion reveals that it is not clear visually that the lines are straight. This effect may be understood as arising from the fact that the angular error is a function of the length of the line. For a long line, the error is not simply inversely proportional to L , as would be assumed from Eq. 39, which applies only to short (i.e., less than the size of the receptive field of the line element detector in the visual cortex, generally a few degrees) lines. Since N is proportional to L , the apparent error in the slope of the line is a function of L . For an observer having an attention set centered on a point located a distance L' along the line, the error in the slope of the apparent line will be inversely proportional to the square of L' , as may be seen from Eqs. 31 and 33. As a result, the overall effect is to produce the subtle illusion of a slightly curved line. Since this effect determines the slope dy/dx of the apparent curve, we obtain from Eqs. 31 and 33 the expression

$$\frac{dy}{dx} = m \approx \tan \alpha + \frac{q^3 \epsilon D^2}{2\sigma L^2} \sec^2 \alpha \frac{\cos^3 \alpha/2 - \sin^3 \alpha/2}{\sin \alpha/2 \cos \alpha/2}, \quad (42)$$

where we have taken $n/N \ll 1$, satisfactory except for small values of α . However, if L is not taken to be the length of the line but the length L' of the segment from

the intersection to the point of gaze, then

$$L' = x/\cos \alpha. \quad (43)$$

Substituting Eq. 43 into Eq. 42 and integrating from a point (x_1, y_1) sufficiently far out along the real line so that there is no apparent error due to the intersection point, we obtain

$$y - y_1 = (x - x_1) \tan \alpha - \frac{q^3 \epsilon D^2}{2\sigma} \left(\frac{\cos^3 \alpha/2 - \sin^3 \alpha/2}{\sin \alpha/2 \cos \alpha/2} \right) \cdot \left(\frac{1}{x} - \frac{1}{x_1} \right). \quad (44)$$

However, for large x_1 , the factor in $1/x_1$ tends to zero so that $y_1 = x_1 \tan \alpha$. Thus, Eq. 44 reduces to

$$y = x \tan \alpha - \frac{q^3 \epsilon D^2}{2\sigma x} \left(\frac{\cos^3 \alpha/2 - \sin^3 \alpha/2}{\sin \alpha/2 \cos \alpha/2} \right). \quad (45)$$

Using Eq. 40 for the product $q^3 \epsilon$, 40 cm, a nominal reading distance for D , 2.10×10^7 sterrad $^{-1}$ for σ corresponding to an angle of 1.43 deg (i.e., $L = 1$ cm at 40 cm), and setting $\alpha = 45$ deg, we obtain 0.049 (this value is obtained using the complete expression rather than the approximation in Eq. 42) for the coefficient of x^{-1} in Eq. 45. A plot of the real and apparent lines is shown in Fig. 6. (The scale of the effect is exaggerated in the plot.)

To show the validity of the curve in Fig. 6, the Poggendorff illusion has been corrected by introducing lines having the curvature necessary to compensate this effect; the result is shown in Fig. 7. The lines were computer generated using Eq. 45 with the sign of the second term on the right changed. The horizontal lines have also been corrected. The uncorrected Poggendorff illusion is shown for comparison.

III. DISCUSSION OF THE WEINTRAUB AND KRANTZ POGGENDORFF EXPERIMENTS AND THE WORK OF GILLAM

Weintraub and Krantz (1971) have concluded, based on a parametric study of the Poggendorff illusion, that a segment of one of the parallel lines, the part "forming an obtuse angle with the physically present transversal segment, produced the largest effect upon perceived orientation." There is the clear implication in their results that the acute angle appears to produce no (or possibly a reversed) effect in the absence of the obtuse segment. Were such the case, a strong argument would have been made against the present approach. Such an interpretation of Weintraub and Krantz' Experiments III and IV errs in that it does not incorporate the findings of Blakemore, Carpenter, and Georgeson (1970). Further, the altered figure introduces entirely new properties not present in the unmodified Poggendorff figure. It is not that the causative feature is removed, but that an exactly compensating effect arises in their modified figure that brings about the elimination of the illusion.

The present treatment of the Poggendorff illusion involves two principal steps vis-à-vis the brain's synthesis of the overall figure to extract the specific data that we measure.

(1) A reduction of the *data* to obtain a representation of Line Element B (in Fig. 1: the left transversal in the Weintraub-Krantz paper). This line is established not with respect to an absolute perception space but with respect to the immediate data field, in this case the closest of the parallel lines, Line A (in Fig. 1: the left parallel in the Weintraub-Krantz paper). This fact is substantiated by the treatment of figural aftereffects given below.

(2) A determination of the intercept of the extension of this line onto the second (Weintraub-Krantz right) parallel line. This requires a determination of the orientation of the second parallel line with respect to the

Fig. 6. A plot of Eq. 45. The apparent line is shown together with the real line.

Fig. 7. The corrected Poggendorff illusion together with the uncorrected figure shown for comparison.

first and a projection of Line B (left transverse) to an intercept with that line. (This decomposition of the steps could be carried out much further, but these two serve the present purpose.) In the standard form of the illusion, there exists sufficient data (obtained particularly from the free and clear end points of the parallel lines) for a determination of the relative positions of the two parallel lines, establishing their parallelism to an accuracy of about 1 deg. In this case, Step 2 becomes straightforward and is treated implicitly in the calculation of the intercept points in Eqs. 35 and 36. Step 1 thus leads to an angular displacement of some 7.8 deg (using Weintraub-Krantz's data) and a corresponding error in the apparent intercept point.

That Step 1 occurs and leads to a change in the apparent orientation of Line B even with Line A cut short (i.e., with the geometry of Weintraub-Krantz's Fig. 3, No. 2) is proved by the findings of Blakemore, Carpenter, and Georgeson (1970). (The geometry is sufficiently close to establish that fact and is consistent with the present theory.) Thus, the orientation effect must still be present in the figure studied by Weintraub and Krantz (Fig. 3, No. 2). The modification in which the left half of Line B (upper portion of the left parallel in the Weintraub-Krantz figure) is removed is a perturbation giving rise to *new* effects that render the figure distinct from the Poggendorff figure. Namely, the removal of that portion of the figure (or, for that matter, removal of the lower half of the left parallel in Weintraub-Krantz's Fig. 3, No. 3) greatly changes the reduction process of Step 2. The orientation of the truncated parallel is no longer accurately determined but contains errors of the *same magnitude* (about 7.8 deg) *but in the opposite direction* as for the transverse line segment, B. The resulting displacement is as shown in Fig. 8. That the displacement should be in the direction as shown, affecting the position of the truncated line as well as the orientation, follows simply from the same calculation used on Line Element B. Gillam (1971) gives a figure (her Fig. 10b) that clearly shows this effect, giving rise to *barrel-distortion* of the perceived image. The presence and importance of this effect can be seen by an examination of Fig. 7. This figure incorporates a change in the lines to compensate for the line distortion of the type shown in Fig. 6. Notice that the parallel segment nearest the transverse lines has been adjusted, as mentioned above. The effect of this displacement is

Fig. 8. Illustration of the effect on the Poggendorff illusion caused by the removal of part of one parallel line. The absence of that segment removes the reference orientation from Segment A. Spurious data at the apex shifts the apparent position of the line through an angle, $\delta\alpha$, to A'. Line B is also shifted through an equal but opposite angle to the position B'. As a result, both B and B' intercept the same point on the parallel line, C.

subtle when the remainder of the parallel line is present, but is necessary in order to prevent the parallel lines from appearing bent.

It should be noted that the results of Experiments 1 and 2 in the Weintraub-Krantz (1971) paper are fully (to first order) in agreement with the present treatment. Notice in particular the independence of Δx on the opposite angle, as noted by Weintraub and Krantz. On the other hand, the relation $\Delta x \propto a \cot \alpha$ is only an approximation that in fact omits some important features of the illusion (see below).

Let us turn our attention to the experimental results obtained by Gillam (1971). Assuming the Poggendorff illusion arises from rectilinear perspective processing of the figural elements, Gillam conducted tests in which two additional parallel lines were drawn connected to the far ends of the transverse lines. By adjusting their lengths and positions, the figures provide a three-dimensional perspective which, according to the depth processing theory, should remove the illusion. The modification, however, reduced the magnitude of the illusion by a factor of 0.45. Gillam states, "On the basis of the theory the failure to eliminate the illusion altogether must be attributed to a failure to eliminate sufficiently the equidistance tendency . . . Nevertheless,

a reduction by half is strong support for the theory." On the basis of the present theory, the presence of these additional lines provides eight additional data points for the data processing of the figural geometry. These points are particularly useful because of the large moment arms they provide. (That is to say, the construction from these points of the position of the common *vanishing point* allows one to determine the slope of the transverse much more accurately than in their absence, a fact that holds not only for the unaided eye but for the draftsman as well.) Taking $\sigma = 5.6 \times 10^6$ (sterrad) $^{-1}$ (for an angle of 8.3 deg scaled to the angular length of the line in Gillam's experiment and the above Poggendorff experiment yielding Eq. 40), $\epsilon = 12.71$ and $L/D = 2.5$ deg, we obtain $N = 32.6$ data points (receptive field excitations) for one transverse segment. The average angular moment arm for the eight end points in the modified figure is 3.36 deg, or 2.7 times that for the average point on the transverse line. As a result, the modification provides the equivalent of $N' = 54.1$ data points. The ratio $N/N' = 0.60$ gives the factor by which the displacement should be reduced. This is within one standard deviation of Gillam's result. [In addition, data of Hubel and Wiesel (1961) indicate that the receptive field size increases with angle from the *fovea*, making d_0 about 1.9 times larger. This would lead to $\epsilon = 21.0$ and $N/N' = 0.54$.] The present theory not only accounts for a change in the size of the illusion, but does so accurately.

Gillam's Fig. 8, giving an illusion to transverse lines that are normal to the parallels, is easily attributable to angle and line-element displacement. Figure 9a shows diagrammatically the apparent displacements giving rise to the illusion. The angle at the intercept point, p, appears increased so that the right portion of the figure is perceived as apparently displaced vertically. The illusion is reduced if Point p is drawn sufficiently far from the horizontal line elements and if these line elements do not lie so far in the peripheral vision. It should be noticed that in Gillam's figure, both horizontal line segments are so short and so widely separated that few receptive fields provide the data to the brain necessary for their identification as portions of the same line segment.

Figure 9b shows Gillam's original figure together with a modification of that figure (9c), implementing the concepts of the present theory to reduce the magnitude

Fig. 9. Gillam's altered Poggendorff illusion exhibiting displacement for normal transverse segments. (a) Schematic of apparent displaced figural elements. (b) Gillam's original figure. (c) Modified figure.

Fig. 10. The Hering illusion. The radial pattern of lines distorts the two superimposed parallel lines, making them appear convex.

of the illusion, specifically by increasing the horizontal line-element lengths and shifting the intercept point, p . The modified figure should show a greatly enhanced effect were depth processing the basis of the illusion. However, the illusion is nearly absent. Gillam's Fig. 11a, presented as a new illusion confirming the depth processing theory, is entirely consistent with the present theory based on receptive field data processing leading to angular shifts of the transverse line segments.

IV. THE HERING ILLUSION

A most surprising aspect of Eq. 39 is the fact that the error in extrapolating a line across an interrupting band of width a does not approach zero as the width of the band approaches zero. Because the density of receptors, σ , is quite high in the neighborhood of the *fovea centralis*, Δx becomes insignificant when the *entire* geometry can be examined by that region of the eye, as is possible when $a = 0$. Thus, we do not see a noticeable discontinuity at the intersection of two crossed lines when viewed directly; we do, however, see such a break when the lines are seen with peripheral vision. The presence of such an effect is rather evident in the data given by Weintraub and Krantz (1971, see their Fig. 1). Unfortunately, a measurement of the displacement for zero separation of the parallel lines (for peripheral vision) was not made by these authors. A zero displacement was *assumed* to obtain a linear fit to the data passing through the zero point. This nonzero effect for zero separation of the parallel line provides an adequate basis on which the Hering illusion can be understood. The Hering illusion is shown in Fig. 10. The parallel lines cutting across the radial pattern of lines appear to be convex. It may be noticed that a small break appears to be present at the intersection points near the periphery of the pattern (this is a subtle effect, however). Because of the apparent displacement of each segment of the parallel lines, each segment appears to be cocked at a slight angle. The cumulative effect of this is to produce the illusion of a curved line.

Let us now derive the shape of the apparent curve. For $a = 0$, Eq. 39 gives

$$\Delta x = \frac{8KL}{3\pi} \csc \alpha J(\alpha) \quad (46)$$

where

$$J(\alpha) = F \cos \frac{\alpha}{2} \cot \frac{\alpha}{2} - F' \sin \frac{\alpha}{2} \tan \frac{\alpha}{2}. \quad (47)$$

The component Δt of this displacement perpendicular to Line B (Fig. 1) is

$$\Delta t = \Delta x \sin \alpha. \quad (48)$$

Now the slope of any segment of length L lying between two adjacent lines in the Hering illusion will appear to be (see Fig. 11)

$$\tan \theta = -\Delta t/L. \quad (49)$$

If the angle from the vertical to one of the radiating lines is ϕ and γ designates the angle between any two adjacent radial lines, then length L of the segment they cut is given by

$$L = h[\tan(\phi + \gamma) - \tan \phi], \quad (50)$$

where h is half the distance separating the parallel lines, as shown in Fig. 11. For small values of γ , we can write simply

$$L = h\gamma/\cos^2 \phi. \quad (51)$$

Substituting Eqs. 46, 48, and 51 into Eq. 49 yields

$$\tan \theta = -\frac{q^3 \epsilon D^2}{3\pi \sigma h^2 \gamma^2} \cos^4 \phi J(\alpha). \quad (52)$$

Fig. 11. The apparent gap, Δt , occurring between two adjacent segments is shown for the Hering illusion. The quantities L , ϕ , γ , and θ are also illustrated.

Fig. 12. The integral of Eq. 55, showing the theoretical shape of the apparent line for the first quadrant of the Hering illusion. The dashed curve shows the results obtained for the Hering illusion using Eq. A-9.

Fig. 13. The Mueller-Lyer illusion. The shaft with arrowheads on each end appears shorter than one with reversed arrowheads. The quantities α_1 , α_2 , L , and x are also indicated in the drawing.

Now α is related to ϕ by

$$\alpha = \pi/2 - \phi, \quad (53)$$

and we can write for $\tan \theta$, approximately,

$$\frac{dy}{dx} = \tan \theta. \quad (54)$$

Using Eqs. 53 and 54, Eq. 52 becomes

$$\frac{dy}{dx} = -\frac{q^3 \epsilon D^2}{3\pi \sigma h^2 \gamma^2} \cos^4 \phi J\left(\frac{\pi}{2} - \phi\right), \quad (55)$$

where ϕ is related to x and y by

$$\phi = \arctan (x/y). \quad (56)$$

If we take, as before, $q^3 \epsilon = 1,589$, $D = 40$ cm, $h = 1$ cm, and $\gamma = 7.5$ deg (as in Fig. 10) and use the value of σ as a function of ϕ obtained from the data of Webb (1964) with the eye looking at the center of the figure (the eyeball is taken to be 2.47 cm in diam, 2.32 from first principal point to retina), the integral of Eq. 55 yields the curve shown in Fig. 12. It will be noticed that the magnitude of the effect is accurately given without evaluating any additional coefficients. Also, the general shape corresponds to what one observes in the Hering illusion. However, the inflection point in the curve occurs at about $\phi = 50$ deg rather than at about $\phi = 60$ deg as in the actual illusion (which is noticeable only in Hering patterns wider than those shown in Fig. 10).

V. THE MUELLER-LYER ILLUSION

Let us now consider the application of these results to the Mueller-Lyer illusion shown in Fig. 13. If we remove all the arrowhead lines in Fig. 13 except those labeled A, B, C, and D, we will have a figure similar to the Poggendorff illusion where a is zero. The fact that the lines are not collinear is of no importance; variants of the Poggendorff illusion employ noncollinear lines. If we apply Eq. 39 to each end of the two shafts shown in Fig. 13, we will obtain for the apparent difference in length Δx_{ML}

$$\Delta x_{ML} = \frac{2q^3 \epsilon D^2}{3\pi \sigma L} [\csc \alpha_1 J(\alpha_1) + \csc \alpha_2 J(\alpha_2)]. \quad (57)$$

The coefficient $q^3 \epsilon$ is given by Eq. 40, and the remaining quantities are all measurable.

The magnitude of Δx_{ML} does not depend explicitly on the length of the shafts, but does implicitly through the angular dependence of σ . In Fig. 14, the angular dependence of Eq. 57 with $\alpha_1 = \alpha_2$ is shown normalized to unity for $\alpha_1 = 45$. Experimental data points after R. L. Gregory (1968) are also shown; the probable error for the data points is not provided by Gregory, but, since 20 Ss were used, the probable error is likely to be similar to

that in Fig. 4. For this reason, the data may be considered consistent with theoretical results. Unfortunately, Gregory does not provide sufficient data about his experiment to allow us to check the magnitude of the effect against Eq. 57. However, for $D = 100$ cm, $L = 2$ cm, $\sigma = 1.17 \times 10^7$ sterad $^{-1}$ (corresponding to a shaft length of about 10 cm), $q^3 \epsilon = 1,589$ and $\alpha_1 = \alpha_2 = 30$ deg, we obtain $\Delta x_{ML} = 1.18$ cm as the combined effect for the two shafts.

VI. DISCUSSION OF GANZ'S THEORY OF OPTICAL ILLUSIONS

The question of the relationship of optical illusions and figural aftereffects has been raised by Ganz (1966). His theory, developed on the basis of the figural aftereffects experiments of Gibson (1933), Kohler and Wallach (1944), and Pollack (1958), assumes that inhibitory effects occur in association with retinal images that modify the response of other areas of the retina. As a result, areas of the retina between images are inhibited, reducing the response to the stimulus of light in those areas and causing such effects as the illusion of image displacement. (Ganz also gives an excellent review and criticism of previous theories concerning figural aftereffects.)

The present theory ascribes optical illusions to the spurious assignment of neural excitations coming from receptive fields in the retina, together with the effect this has on cortical line detectors. As a consequence, optical illusions are viewed as arising from the events occurring both in the retina and in the brain (A. H. Gregory, 1968).

Perhaps the central result obtained by Ganz is the derivation of his Eq. 4 to fit the data of Pollack (1958). However, his Eq. 4 involves the separate adjustment of two constants, though one of these is not adjusted a great deal (m is chosen to be 4 min of arc, although other measurements imply a value of 10 min of arc). Unfortunately, the other parameter, L , determines the magnitude of the effect. Finally, the shape of the theoretical curve is almost wholly dictated by Ganz's assumption of a normal distribution for the eye movement. The pertinence of his Eq. 3 is overshadowed by his assumption of the part played by eye movement and the absence of a separate determination of L . The eye movement considered by Ganz that consists of saccades is not introduced correctly into the mathematical treatment. The total time average of these saccades is used without consideration of the probability that such movement did occur during the figural display transition. Concerning eye movement, Riggs and Ratliff (1954) give the following data: "The retinal image is stationary for exposures up to 0.01 sec in duration. Exposures of 0.1 sec entail an average displacement of 25 sec of arc (a visual angle corresponding to the diameter of a single cone)." With regard to saccadic eye movement, Crovitz and Daves (1969) measure a

Fig. 14. A plot of the angular dependence of Eq. 57 with $\alpha_1 = \alpha_2$ and normalized for $\alpha_1 = 45$ deg. Data due to R. L. Gregory (1968) are also shown.

postexposure eye-movement latency greater than 1 sec in 70% of the trials conducted. Thus, saccadic movement is not rapid enough to be introduced without a weighting factor for the probability of eye-movement occurrence.

On the other hand, physiological nystagmus (the high-frequency motion of the eye) is too small in amplitude to serve the purpose in Ganz's theory. Moreover, if eye movement results in an integral averaging over retinal inhibitory effects (as appears in Ganz's treatment), it must be explained how the limits of visual acuity are as great as 2 sec of arc (Falk, 1956; Morgan & Stellar, 1950) and deal with the position widely held (Andersen & Weymouth, 1923; Falk, 1956; Weymouth, Andersen, & Averill, 1923) that "physiological nystagmus contributes to acuity" (see Falk, 1956, p. 116).

The theory presented in this paper can be used to derive Pollack's experimental results *without fitting any arbitrary parameters or functions*. It requires, however, that we first consider the receptive field structure in more detail.

VII. THE STRUCTURE OF THE RECEPTIVE FIELD AND THE PROBLEM OF FIGURAL AFTEREFFECTS

We begin by treating the problem of the organization of individual receptors into receptive fields. It is clear from the considerable size of receptive fields that large numbers of receptors contribute to the excitation of individual optic fibers. But, as pointed out earlier, the number of cones per optic fiber is rather modest, about seven, indicating that an individual receptor contributes to the excitation of several optic fibers and thus belongs

Fig. 15. Plot of data after Hubel and Wiesel (1961) for the reciprocal threshold luminance as a function of spot radius. The function S from Eq. 62 is plotted with $A = 50$, $B = 0.75$, and $b = 2.5$ (deg^{-1}). The scale of the ordinate is given in terms of the logarithm (base 10) scale for luminance, with unity representing $2 \times 10^{-2} \text{ cd/m}^2$. (See reference for additional illumination data.) Receptive field center and surround behavior are exhibited.

to several receptive fields. This is also clear from histological evidence (Kuffler, 1953). As such, the character of the receptive field should be expected to arise from the interrelation of the individual receptors and not the special interconnection of exclusive groups of receptors.

For simplicity, we will deal with only *on-center* receptive fields, *off-center* fields being nearly mirror images of the *on-center* fields. We know that the receptive field contains an excitatory center and an inhibitory influence from the surround. We assume, therefore, that any receptor transmits an excitation to a retinal ganglion cell that falls off exponentially with distance from the ganglion as well as varying logarithmically with the illumination it receives. Moreover, the excitation transmitted by the receptor is inhibited in proportion to the extent of the illuminated area around the receptor (see Enroth-Cugell and Pinto, 1972b, Fig. 10). [The origin of the exponential factors can be understood simply in terms of the probability of dendritic branching as a function of distance (see also the data of Hartline, 1940, and Kuffler, 1953).] Thus, we have for the excitation, E , transmitted to the ganglion by a given receptor

$$E = F_1(1 + F_2) \quad (58)$$

where

$$F_1 = A_1 e^{-b\xi_g}, \quad (59)$$

ξ_g being the distance between the receptor and the ganglion cell and A_1 being a measure of the log of the illumination. The function F_2 is

$$F_2 = A_2 e^{-b\xi_e}, \quad (60)$$

where ξ_e is the distance to the edge of an illuminated region and A_2 is a measure of the difference in the

logarithms of the illuminations across the boundary. The effect of the surround will therefore be basically multiplicative, i.e., the product $F_1 F_2$. That this is the case has been established by Enroth-Cugell and Pinto (1972a). The magnitude of the excitation signal received by a ganglion cell is the integral over all the neighboring receptors.

$$S = \int F_1(1 + F_2) d\xi d\zeta, \quad (61)$$

where ξ and ζ are simply Cartesian coordinates for the angular position of a receptor on the retina relative to the ganglion cell.

Receptive field geometries are generally explored using circular spots of light of varying diameter centered at the ganglion cell. If the radius of the circular spot of light is ρ_o , we have from Eqs. 58-61, using polar coordinates (where $d\xi d\zeta = \rho d\rho d\theta$)

$$\begin{aligned} S &= \int_0^{2\pi} \int_0^{\rho_o} A_1 e^{-b\rho} (1 + A_2 e^{-b(\rho_o - \rho)}) \rho d\rho d\theta \\ &= A\rho_o^2 e^{-b\rho_o} + B [1 - (1 + b\rho_o) e^{-b\rho_o}]. \end{aligned} \quad (62)$$

In Eq. 62, we have redefined the constants according to $A = \pi A_1 A_2$, $B = 2\pi A_1 / b^2$. Hubel and Wiesel (1961) give data for the illumination thresholds for an *off-center* geniculate cell as a function of spot diameters. Since Eq. 62 depends on the illumination by way of A_1 , their data can be used to exhibit the adequacy of Eq. 62 as a model of receptive field structure. This is shown in Fig. 15. The coefficients have been chosen to fit the data; however, further work should show their dependence on the physiological data, specifically the extent of dendritic connections and the response of individual receptors to illumination. (The dependence on illumination is not the purpose of the present paper and has not been pursued.) It will be seen that the region

inside about 1 deg appears to function as a receptive field center, while the region from 1 deg to about 4 deg exhibits the function of a surround, though no such separate functions or regions were introduced into the derivation.

It will be seen that $F_1 F_2$, the *cross term*, yields the effect of a boundary on the response of the field. The first term, F_1 , when normalized to the surrounding brightness in the vicinity (in the absence of a contribution from the cross term) determines the number of receptive field *data points* or excitations per unit area of a uniformly illuminated area. This allows us to treat the figural aftereffects phenomenon studied by Pollack.

In Eq. 2, spurious neural excitation contributions to cortical line detection depended in a very simple way on the distance between the lines. All neural excitations arising from receptive fields within a distance λ of the first line were assigned to that line and none beyond that distance. Such a treatment was satisfactory there. Since the figural aftereffect experiments involve figures separated by only a few minutes of arc, the detailed structure of the receptive field becomes important and must be introduced into the treatment. On the other hand, we find that the psychological data are useful in further understanding, by means of the present theory, the structure of the receptive field.

Based on the above treatment of the receptive field, we can state that a fraction $F(\xi)$ of the retinal receptors are activated when they lie within an angular distance $\xi = x/D$ from a line or edge of a figure. At $\xi = 0$, it is assumed that F will be unity. The number of receptors activated along a length, ℓ , of a line or of a contour viewed at a distance, D (angular length, ℓ/D) will be

$$n = \frac{\sigma \ell}{\epsilon D} \int_0^\infty F(\xi) d\xi. \quad (63)$$

For a line lying a distance s from the first line, the number, n' , of receptors activated will be

$$n' = \frac{\sigma \ell}{\epsilon D} \int_0^\infty F_2(\xi) [1 + F_1(\xi)] d\xi, \quad (64)$$

which is simply the normalized form of Eq. 61 for which the first integral has been carried over the distance 0 to $\xi = \ell/D$. The integral of Eq. 64 over the region between two boundary lines will yield the total activation n_2 . The additional activation due to the presence of the second line is obtained by subtracting Eq. 63 from the integral of Eq. 64:

$$\Delta n_2 = \frac{\sigma \ell}{\epsilon D} \int_0^\infty F_2 F_1 d\xi. \quad (65)$$

The results can be applied to the problem of figural aftereffects provided we take account of the basic

difference between figures such as the Poggendorff or Hering illusions and the aftereffect illusions considered by Ganz and Pollack. In the former, the lines actually intersect so that it is primarily the spurious line data points arising from the neural excitations due to the figures themselves that produce the illusion. In the latter, the figures do not touch; the illusion centers on the space separating the figures, which is determined on the basis of the *size* of the bounding areas that border the figure. The size of the border is distorted by the spurious neural excitations. As with most optical illusions, the brain is confronted with an ambiguity: the spurious points may indicate an additional brightening of the Mach bands or the spurious points may be interpreted as an additional separation of the test figure from the position of the induction figure. The latter solution is consistent with the otherwise uniformity of the background. Furthermore, normalization of the receptive field signal is generally required for area size determinations, but in the present case the region involved is probably too small for such a normalization to be carried out independently. The additional points, interpreted as an increase in the width of the border, yield an increase that is in proportion to Δn . The total number, N_ℓ , of receptors activated by light from the area separating the two objects in the figures, separated by a distance s , is

$$N_\ell = \sigma s \ell / \epsilon D^2. \quad (66)$$

The net angular increase, ψ , in the width of the separation gap (real separation distance s) is given by

$$\psi = -\frac{s}{D} \frac{\Delta n}{N_\ell}. \quad (67)$$

The net increase in the number of receptors assigned to the gap due to the combined effects of the inspection and test figures is given by Eq. 65. Substituting the appropriate normalized expressions for F_1 and F_2 ,

$$F_1 = e^{-b\xi}; \quad F_2 = e^{-b(s/D - \xi)}, \quad (68)$$

into Eq. 65 and integrating over the area in between gives

$$\Delta n = \frac{\sigma \ell s}{\epsilon D^2} e^{-bs/D}. \quad (69)$$

Thus, the angular displacement of the figures will be

$$\psi = -\nu e^{-b\nu}, \quad (70)$$

where

$$\nu = s/D. \quad (71)$$

Fig. 16. A plot of the theoretical curve given by Eq. 70 together with data for figural aftereffects displacement after Pollack (1958).

A comparison of Eq. 70 with the experimental results of Pollack is shown in Fig. 16. The constant $b^{-1} = 4$ min is obtained from the receptive field size data after Hubel and Wiesel (1960), adjusted for the eye size difference (i.e., between spider monkey and human eyes) and for the angle subtended by the Pollack display; Eq. 62 is used to relate receptive field center size to the constant b . The agreement achieved between Pollack's data for black figures on a midgray background and Eq. 70 is extremely good. The theoretical curve departs from the data only for $\nu = 0$. No explanation for this fact will be offered here, since it appears to be a higher order effect. The nonzero displacement for $\nu = 0$ is small, although apparently a real effect.

Pollack's data for black figures on a white background do not fall on the theoretical curve. In the present theory, we have not explored the illumination effects explicitly, but the value of A does depend on the illumination. Experiments of the type described in this paper to determine the value of $q^3\epsilon$ and of the type carried out by Pollack should be repeated under controlled illumination, relating both to the physiological data.

VII. CONCLUSIONS

Although neurophysiological excitatory processes form the basis of the present theory, it is perhaps best to describe the theory presented here strictly in terms of the mathematical statements. In its more general form, those statements are given by Eq. 65 for the spurious assignment of neural excitations as data points in cortical line detection together with the least-squares data-reduction formulation. Such a statement of the theory is explicit enough to allow the derivation of specific consequences that can be shown to be consistent with several experimental results. Because this analysis involves the concept of local or point-by-point data reduction, the present theory suggests that pattern perception, at least in its initial steps, involves quite simple local data-processing procedures, which largely

determine the character of certain optical illusions, an observation entirely consistent with physiological evidence (Hubel & Wiesel, 1962). This is perhaps rather in contradistinction to *Gestalttheorie*.

The recognition of the significance of the receptive field density, particularly in peripheral vision, to the creation of optical illusions is an integral part of the present theory. Perhaps without exception, optical illusion figures require greater data acquisition for their correct resolution than can be provided by the limited density of receptors, especially in peripheral vision. Because those figures involve extended geometries, the entire figure generally cannot be visualized at once by the *fovea centralis*. When they can be, the illusion is moderated or disappears, as has been shown by Hochberg (1968).⁴ A specific example of this is provided by the *impossible pictures* (R. L. Gregory, 1968; Hochberg, 1968) of Penrose and Penrose. Here the number of receptors involved in the determination of a critical line orientation is low, 40 for a 1-cm line 40 cm from the eye and 15 deg from the *fovea*. The number of receptors that may contribute to a distortion of the figures described by Eq. 65 under the same conditions is about 20. As a consequence, the contradictory information may be discriminatively weighted in the data-reduction processes of the central nervous system; this has also been pointed out by Hochberg (1968). Such a limitation is probably attendant to all later steps in the process of pattern discrimination carried out by the brain.

In the present theory, there are two basic processes, that modeled by the least-squares calculation and that involving the spurious generation and assignment of neural excitations (as representations of data points). The former very likely takes place in the central nervous system, while the latter may occur in the retina, in the cortex, or, more likely, both (Boring, 1961; Day, 1961; A. H. Gregory, 1968; Lau, 1925; Ohwaki, 1960; Schiller & Wiener, 1968; Springbett, 1961; Witasek, 1899).

The major significance of the present theory is that within a factor of about two, all the results have been obtained with no adjustable coefficients, all quantities being accounted for in terms of known quantities for the retina's structure. Furthermore, if the quantity $q^3\epsilon$ is measured experimentally, considerable agreement is obtained between the theory and several experiments. The fit between theory and experiment is not perfect but, recognizing this to be a first-order theory, the agreement is good. If further examination of these results substantiates this conclusion, a more precise formulation should be developed. Since this would likely necessitate additional coefficients, such refinements have not been explored here.

Modification of the present formulation to allow for the longer range of influence found by Hubel and Wiesel (1962) for complex cortical receptive fields should serve to explain certain other optical illusions within the present framework. Certain optical illusions, such as the

Ponzo figure, as well as many of the aftereffect figures of Kohler and Wallach (1944), involve comparatively large separation angles between figural elements that appear to influence one another. It is reasonable to expect that these involve higher order figural synthesis (Hochberg, 1968). Illumination and afterimage effects should also be introduced into the theory. Further, a differential formulation of the theory might prove more generally applicable than the present formulation that depends on integral expressions involving straight line elements.

Finally, it is perhaps noteworthy that in the present approach we have a meeting of physiological and psychological data; not only does the physiological data provide a basis for understanding fundamental psychological phenomena, but these phenomena as such lead us to a better approach to modeling physiological processes.

APPENDIX A

In Section II, Eqs. 4 and 5 were used as the basis for the calculation of the quantity $n\lambda_\xi$, which is the dominant term (except for small angles) in the least-squares fit leading to Eqs. 31 and 32. In that derivation, the results are not extremely sensitive to the detailed distribution of induced neural excitations, since the optical illusions being considered involve the total (or integral) effect over the area near line intersections. In Section VI however, our interest in certain figural aftereffect phenomena that depend on small angular displacements between the inspection and test figures required a more explicit basis. As a consequence, we used Eq. 65 as a postulate to supplant Eqs. 4 and 5 together with a simple calculation to normalize the new expression in terms of the earlier results. It behooves us now to show that these two assumptions are not independent. Let us therefore derive from Eq. 65 a quantity, Q , which replaces the previously assumed quantity $n\lambda_\xi$, where (see Fig. A-1)

$$Q = \iint \xi d_n^2, \quad (A-1)$$

which gives the first moment of the quantity $\sigma F_1 F_2$ about Line B in Fig. A-1. The quantity d_n^2 from Eq. 65 is

$$d_n^2 = \sigma F_1 F_2 d\xi d\tau, \quad (A-2)$$

where, from Eq. 68, we have

$$F_1 = e^{-b\xi_1}, \quad (A-3)$$

and

$$F_2 = e^{-b\xi_2}. \quad (A-4)$$

In Region I, i.e., for positive τ ,

$$\xi_1 = \begin{cases} (\xi - \tau \tan \alpha) \cos \alpha & \xi > \tau \tan \alpha \\ (\tau \tan \alpha - \xi) \cos \alpha & \xi < \tau \tan \alpha \end{cases} \quad (A-5)$$

Fig. A-1. Illustration of the quantities used to evaluate Q . The first moment of $\sigma F_1 F_2$ is taken about Line B.

and

$$\xi_2 = |\xi|. \quad (A-6)$$

In Region II, we take F_2 to be given by

$$F_2 = e^{-b\rho}, \quad (A-7)$$

where

$$\rho = (\xi^2 + \tau^2)^{1/2}. \quad (A-8)$$

Integrating Eq. A-1 over all space gives

$$Q = \frac{2\sigma}{b^3} \left[\frac{2 \cos \alpha (1 - \cos \alpha)}{\sin^5 \alpha} - \frac{\cos^2 \alpha}{\sin^3 \alpha} - I(\alpha) \right] \quad (A-9)$$

where

$$I(\alpha) = \int_{-\pi/2}^{\pi/2} \frac{\sin \theta d\theta}{[1 + |\sin(\theta - \alpha)|]^3}. \quad (A-10)$$

By setting

$$Q|_{\alpha=45^\circ} = n\lambda_e|_{\alpha=45^\circ} \quad (A-11)$$

we can evaluate b in terms of λ :

$$b = 1.344/\lambda. \quad (A-12)$$

If we use Eq. A-9 for the quantity $n\lambda_\xi$ to derive Δx for the Poggendorff illusion, we have

$$\Delta x = (1.355 q^3 \epsilon D^2 / \sigma L) \csc \alpha \left(\frac{3a}{L} \csc \alpha + 2 \right) \cdot \left[\frac{2 \cos \alpha (1 - \cos \alpha)}{\sin^5 \alpha} - \frac{\cos^2 \alpha}{\sin^3 \alpha} - I(\alpha) \right]. \quad (A-13)$$

The use of Eq. A-9 gives improved results when used to

Fig. A-2. The corrected Hering illusion in which Eq. A-9 has been used to calculate the displacement of each line segment needed to correct the illusion when the fixation point lies at the center of the upper horizontal line. Individual differences as well as limitations in the theory limit the perfection in the correction.

derive the Hering illusion. In Fig. A-2, Eq. A-9 is used to calculate a compensatory figure for the Hering illusion in which both the parallel lines and radial lines incorporate deviations opposite in sign but equal in magnitude to that given by the equation. While the corrected illusion is not perfect, it should be recognized that an entirely corrected Hering illusion is not possible, since the shape needed to correct for this illusion varies from person to person and depends on the gaze point. A gaze point located at the center of the upper horizontal line is assumed for Fig. A-2.

APPENDIX B

Equations 27 and 28 give approximate expressions for m and b . For certain cases, the complete expression is required. This is particularly so for small values of α . However, for small α , the terms arising from the obtuse angle can be neglected. For simplicity, therefore, we write the expressions for m and b , neglecting the terms arising from the n' data points. These terms, however, are easily restored since they are identical except that they involve the complementary trigonometric functions. We have

$$m = \tan \alpha (1 + T_n/T_d) \quad (B-1)$$

where

$$T_n = d_o \frac{nN(N+1)}{N+n} \lambda_f \sec \alpha \csc \alpha - 2n \left(1 - \frac{n}{N+n} \right) \cdot (\lambda_f^2 \sec^2 \alpha + \lambda_r \lambda_f \sec \alpha \csc \alpha) \quad (B-2)$$

$$T_d = d_o^2 \left[\frac{1}{3} N(N+1)(2N+1) - \frac{N^2(N+1)^2}{2(N+n)} \right] - 2d_o \frac{nN(N+1)}{N+n} (\lambda_r + \lambda_f \tan \alpha) + 2n \left(1 - \frac{n}{N+n} \right) (\lambda_r^2 + \lambda_f^2 \tan^2 \alpha + 2\lambda_r \lambda_f \tan \alpha), \quad (B-3)$$

while b , expressed in terms of m is

$$b = \frac{D}{N+n} \left\{ \frac{1}{2} N(N+1) d_o \sin \alpha + n \lambda_r \sin \alpha - n \lambda_f \cos \alpha - m \left[\frac{1}{2} N(N+1) d_o \cos \alpha + n \lambda_r \cos \alpha + n \lambda_f \sin \alpha \right] \right\} \quad (B-4)$$

The appropriate expression to be used for λ_f^2 is

$$\overline{\lambda_f^2} = \sum_{i=1}^n \xi_i^2 \approx \int \xi^2 \tau d\xi / \int \tau d\xi = \frac{1}{6} \lambda^2 \cos^2 \frac{\alpha}{2}. \quad (B-5)$$

The expressions for λ_r and λ_r^2 are

$$\overline{\lambda_r} = \frac{1}{3} \lambda \cos^2 \alpha \csc \alpha / 2 + \frac{1}{2} \lambda \csc \frac{\alpha}{2} \frac{\sin^2 \alpha - \frac{2}{3} (1 - \cos^3 \alpha)}{1 - \cos \alpha} \quad (B-6)$$

and

$$\overline{\lambda_r^2} = \frac{1}{8} \lambda^2 \csc^2 \frac{\alpha}{2} \left[\cos^3 \alpha + \frac{\frac{1}{3} - \cos^3 \alpha + \cos^4 \alpha}{1 - \cos \alpha} \right] \quad (B-7)$$

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NOTES

1. A mathematical similarity between the present theory and that of Chiang, as treated by Glass, accounts for that degree of success which was achieved by the optical confusion theory.
2. Robinson, D. O., Evans, S. H., & Abbamonte, M. Geometric illusions as a function of line detector organization in the human visual system. Institute for the Study of Cognitive Systems, Texas Christian University. Unpublished report.

3. In the treatment given here, it will be found most consistent to ascribe this process of the spurious data point generation to the data processing in the retina [i.e., not due to optical distortion as proposed by Chiang (1968)], while the spurious assignment of the data occurs concomitantly with the line element detection in the cortex. That this is the case will become clear from the values of certain quantities occurring in the theory.

4. Hochberg states: "With small distances between inconsistent corners" of the Penrose and Penrose figure, "the

figures do appear . . . relatively often, as a flat nested pattern. However, with increased distance," whereby the figures are viewed more with peripheral vision, "tridimensionality judgments are about as high as with completely consistent figures of the same dimensions."

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