

The Cerebral Cortex as a Diffractive Medium

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ABSTRACT

Viewing the central nervous system exclusively in electrical field terms, the cortex may be considered a lens. The "minimum ray characteristic" in Herzian wave theory indicates that the absolute unit of information measurement can be undefinable. Thus, whereas in the auditory system, where signal frequency is readily detectable, a clearly definable "bit" of information is objectively available, in the visual system, where edge detection is not carried by wavelength, the absolute unit can only be defined physiologically.

The modulation of transmitted information in the cortex could be carried out by delay methods of conduction. For this to be true, frequency in the central nervous system must be coded in the time domain and represented by transcortical "arrival patterns." It is shown that only during positive dc activity in the cortex is input registered.

If a "perceived object" is defined exclusively in terms of degrees of freedom, then "object constancy" reduces itself as a problem to the question how degrees of freedom may remain invariant under transformations of amplitude and phase.

The "carrier" for cortical information is suggested to be an indigenous cortical rhythm triggered by thalamic input. Interferometry thus occurs between the sensory input and this indigenous activity.

INTRODUCTION

This article proposes to view the cerebral cortex at the level of molar electrical activity. As theoretical writing on the storage of information is much more advanced in the optical field than in the electrical field, it is

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worthwhile to draw analogies between the two fields to the benefit of the latter. The cortex is treated as a transfer function existing between a read-in function and a read-out function. Viewed in this manner, within the confines of electrooptical processing, there seems little reason not to consider the cortex as a lens. A study of the cortex at this level, therefore, reduces to a study of its diffractive properties.

It is possible to derive Huygens' principle from Maxwell's equations provided that the Huygens principle formulation applies only to the vicinity of the center of quasi-spherical image-forming wave fronts. The result has the form of a Fourier transform and may be expressed as: the complex amplitude of the electric field vector at a point in the image plane is equal to the Fourier transform of the distribution of complex amplitude of the electric field within the image-forming aperture. It is considered, here, that the image-forming aperture is the read-in to cortical receiving areas, while the image plane is the readout from these areas.

If $\Phi(w)$ is the spectral energy distribution in the input of a linear system, $R(w)$ is the response of the system, and $h(w)$ is the impulse response, then (the interdependency of) these three functions may be defined as follows.

$$\Phi(w) = \int_{-\infty}^{+\infty} \Phi(w_0) \delta(w_0 - w) dw_0,$$

$$R(w) = \int_{-\infty}^{+\infty} \Phi(w_0) h(w_0 - w) dw_0,$$

or

$$R(w) = \Phi(w) * h(w)$$

(the last is the basic equation governing the behavior of spectrometers.) By Fourier transformation (the Fourier transform of the convolution of two functions is equal to the product of the transforms of the two functions), we have

$$T(R(w)) = T[\Phi(w)] \cdot T[h(w)]$$

where, for electrical and optical systems, $T[h(w)]$ is the frequency response of the system.

Let $\Phi(w)$ describe the read-in to the cortex; then $T(h(w))$ must be the cross-cortical spread of gross potentials occurring after dendritic activity and across time, and $R(w)$ is the readout from the cortex. The frequency response function of an optical system is the transform of the diffraction

pattern; it is also the transfer function of an image-forming instrument and may be defined:

$$\tau(x, y) = [f_1 * f_1^*]_{-x, -y} = \tau[s(n, v)].$$

That is, the transfer function is equal to the autocorrelation function of the pupil function evaluated at $(-x, -y)$, and $s(n, v)$ is the spread function.

Assuming that the transfer function is proportional to the intensity of the light, and if the input V_0 to the system is made up of two vectorial components V_1 and V_2 , then τ has been shown [61] to be equal to

$$\tau = cV_0^2 = c(V_1^2 + V_2^2 + 2V_1V_2 \cos \beta)$$

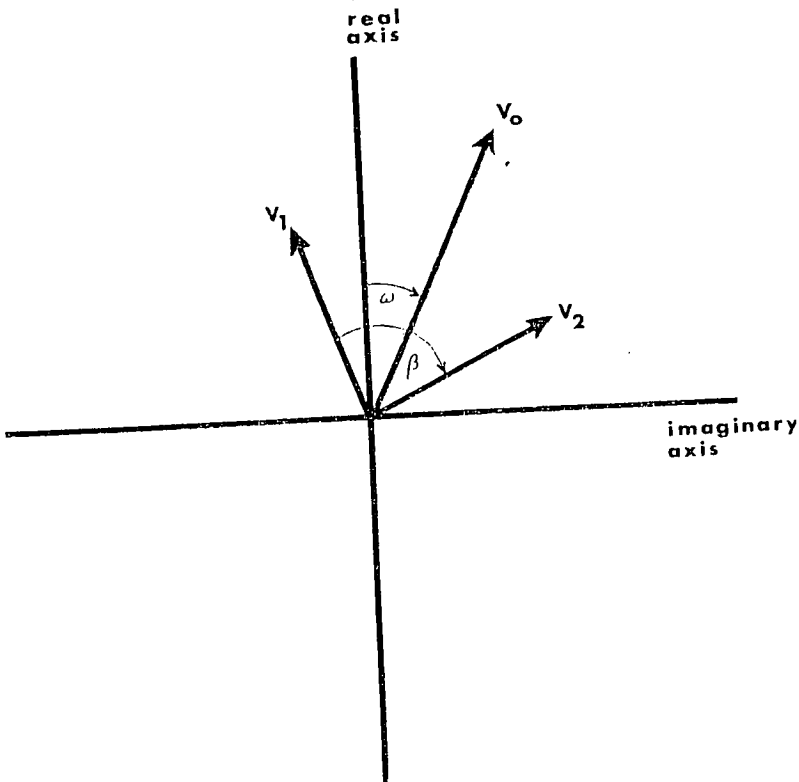


FIG. 1. Complex vector plane.

where

$$V = V_0 e^{i\omega t} \quad \text{and } c \text{ is a constant.}$$

Let us consider $\Phi(w) = V_1 e^{i\omega t}$; then

$$R(w) = V_1^2 e^{i\omega t} c(V_1^2 + V_2^2 + 2V_1V_2 \cos \beta)$$

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where

transmitted information: $V_1 e^{i\omega t} c(V_1^2 + V_2^2);$ (A)

ghost image of $V_2 + \text{noise}$: $V_2 e^{i\beta} e^{i\omega t} c V_1^2 2 \cos^2 \beta;$ (B)

noise: $V_2^2 \exp \left[i \left(\beta + \frac{\pi}{2} \right) \right] \exp(i\omega t) c V_1^2 2 \sin \beta \cos \beta.$ (C)

I will later show that in the cortex V_1 is produced by sensory input and V_2 by an indigenous cortical pacemaker triggered by thalamic input.

TRANSMISSION COEFFICIENTS TOGETHER WITH ROTATION COEFFICIENTS
UNIQUELY DEFINE INFORMATION-PROCESSING PROPERTIES, PERMITTING A
RIGOROUS DEFINITION OF PERCEPTION AND SENSATION

Gabor [18] has shown with his "expansion theorem" that information is not carried by rays but by certain tubes of rays, whose cross section remains invariant along the optical path. In wave optics, the *wavelength* is the natural unit of optical lengths and the suggestion is that the elementary

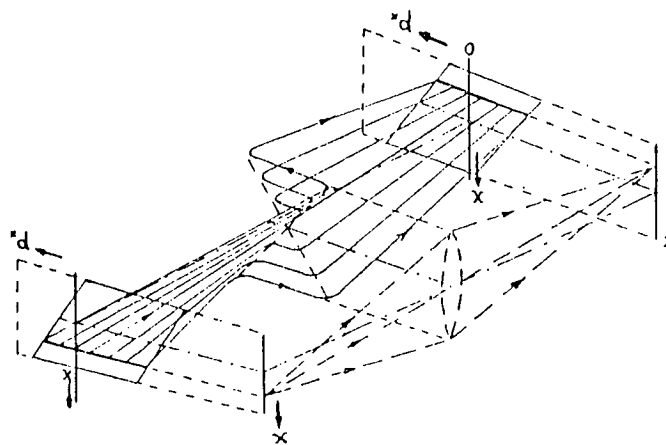


FIG. 2. One-dimensional imaging in configuration space and in phase space (from Gabor [18, page 19]).

tube must have a cross section λ^2 . Referring to Gabor's figure, in which the extra coordinate corresponds to the angle with the optic axis ($p_x = p \sin \theta$), the expansion theorem is as follows.

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Assume that the object area, large compared with the square of the wavelength, is limited by a black screen. Assume also that there is a similar limitation in an aperture plane, at a great distance from the object plane. Then, in the domain limited by these two black screens, there exist N independent solutions of the wave equation

$$\nabla^2 u + \left(\frac{2\pi}{\lambda}\right)^2 u = 0$$

that is to say solutions with $u = 0$ immediately behind the black screens and N is

$$N = \frac{1}{h^2} \int \delta_x \delta_y \delta(\cos \alpha) \delta(\cos \beta) = \frac{1}{h^2} \int \delta_x \delta_y \delta p_x \delta p_y \quad \left(p = \frac{h}{\lambda}\right)$$

Any progressive wave through the object area and through the aperture can be expanded in terms of these N eigensolutions, with not more than N complex coefficients [18, pages 20-21].

Thus energy fluxes in the object plane are additive. They must be additive in all planes, otherwise one beam would modulate the energy of another. The orthogonality of the elementary beams is, therefore, an invariant property, and the naive idea of "tubes of information" can be replaced by a set of orthogonal, elementary beams.

Gabor continues [18, page 25]: let P_1, P_2 be two points in a cross section of the optical tract, which is illuminated by a source Σ . Let I_1, I_2 be the intensities at these points, and u_1, u_2 the complex light amplitudes.

Then

$$\gamma_{12} = (I_1 I_2)^{-1/2} \int_{\Sigma} u_1 u_2^* d\sigma$$

is the coefficient of partial coherence.

Observing that

$$\gamma_{12} = \gamma_{21}^*$$

and that there exist only N elementary areas, an illumination matrix can be constructed that is also Hermitian, because $I_{ik} = I_{ki}^*$.

$$|I_{ik}| \equiv \begin{pmatrix} I_{11} & I_{12} & \cdots & I_{1N} \\ I_{21} & I_{22} & \cdots & I_{2N} \\ \cdot & \cdot & \cdots & \cdot \\ I_{N1} & I_{N2} & \cdots & I_{NN} \end{pmatrix}, \quad I_{ik} = \gamma_{ik} (I_i I_k)^{1/2}.$$

From the knowledge that in an optical system the amplitudes suffer linear transformations, it is suggested that the illumination matrix must transform like the outer product of two vectors, whose components are complex conjugates.

Gabor points out clearly the difference between communication theory

and optics. In communication theory a signal is an observable function of time; optics, on the other hand, is entirely in the quantum range, so phases are not readily observable. Thus it is necessary to utilize interference experiments to measure complex vector components. Gabor's final postulate is

All physical characteristics of practically monochromatic illumination can be represented by an *illumination ellipsoid* in the N -dimensional (complex) information space. All transformations of the illumination from plane to plane are (Hermitian) *rotations* of the ellipsoid in this space.

The principal axes of the ellipsoid are the square roots of the eigen-values of the matrix, that is to say the solutions of the characteristic equation

$$\|I_{ik} - \lambda^2 \delta(i, k)\| = 0$$

where $\delta(i, k)$ is Kronecker's unit tensor. We call the number of non-zero roots, that is to say of non-zero axes the *dimensionality* of the illumination. Fully coherent illumination has the dimensionality one; the illuminating ellipsoid degenerates to a vector. Fully incoherent illumination has the dimensionality N [18, pages 26-27].

Thus, the object effects a linear transformation in the complex amplitudes and must therefore be a *linear Hermitian operator*. Now, the operation consists of a deformation (transmission coefficients) and a rotation. Gabor defines the two operators into which the object operator was decomposed as (1) an amplitude contrast matrix and (2) a phase-contrast matrix.

Gabor indicates, but does not prove, that the general optical object in an optical system with N complex degrees of freedom is characterized not by $2N$ but by $\frac{1}{2}N(N + 1)$ real data and all of these can be determined from not more than N suitably designed experiments.

If this is correct, then the study of cortical structures should proceed along two lines: (1) amplitude changes; and (2) transcortical latency changes that would represent the relative time of arrival of impulses upon the cortical surface from inferior structures.

The analysis of Gabor [18] may be supplemented, however, as it would appear that there is no invariant of the transmitted information beside the number of degrees of freedom. This lack is remedied by Gamo [21], who concerns himself with the problem how, if a secondary image is obtained by transmitting through a given pupil the waves obtained by another pupil, the intensity matrix for the secondary image can be derived from one of the primary images. For simplicity's sake, Gamo concerned himself with the one-dimensional image-forming system where the magnification is unity.

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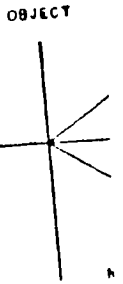


FIG. 3. Image of a secondary aperture

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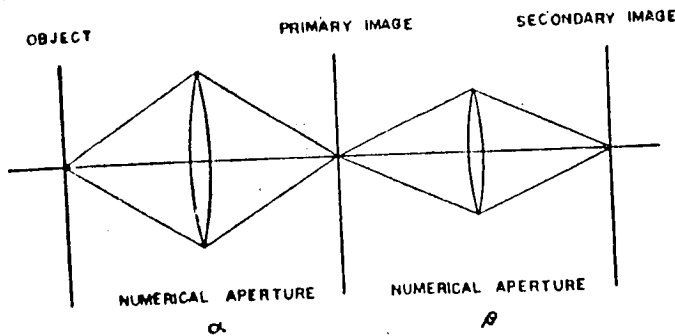


Fig. 3. Image waves from one pupil transmitted through a second for the formation of a secondary image (from [21, page 136]).

The intensity distribution of an image obtained by a pupil of numerical aperture α can be described by the Hermitian form

$$I(x; \alpha) = [\phi(x; \alpha), A\phi(x; \alpha)]$$

where A is intensity matrix of n, m elements,

$$A_{nm} = \iint \Gamma(X_1, X_2) E^*(X_1) E(X_2) u^* \times \left(X_1 - \frac{n\pi}{k\alpha}\right) u \left(X_2 - \frac{m\pi}{k\alpha}\right) dX_1 dX_2;$$

$\Gamma(X_1, X_2)$ is the mutual intensity of illumination or phase coherence factor multiplied by the amplitudes of waves at points X_1, X_2 in the object plane; $E(X)$ is the complex transmission function of an object; $u(X - n\pi/k\alpha)$ is the transmission function of a given pupil (i.e., complex amplitude of waves at the n th sampling point $n\pi/k\alpha$ in the image plane transmitted from the wave having unit amplitude at a point X and vanishing elsewhere in the object plane); $k = 2\pi/\lambda$; and λ is the wavelength. $\phi(x; \alpha)$ is a vector whose n th component is given by the n th sampling function for an image by a pupil of numerical aperture α .

$$\phi_n(x; \alpha) = \frac{\sin(k\alpha x - n\pi)}{(k\alpha x - n\pi)}.$$

The transmission function of the combined system is

$$\bar{u} \left(X - \frac{n\pi}{k\beta}\right) = \int_{-\alpha}^{+\alpha} u(X - \xi) u' \left(\xi - \frac{n\pi}{k\beta}\right) d\xi.$$

The matrix element of the combined system is

$$B_{nm} = \sum_k \sum_l T_{kn}^* A_{kl} T_{lm} \quad \text{or} \quad B = T'^* A T$$

where T is the "transmission matrix" and T'^* is a matrix equal to the complex conjugate of the conjugate transpose matrix of T .

Thus

$$I(x; \beta) = [\phi(x; \beta), T'^*AT\phi(x; \beta)]$$

and the intensity matrix A is invariant by the optical transmission, or

$$I(x, \beta) = [\psi(x; \alpha), A\psi(x; \alpha)]$$

where $\psi(x; \alpha) = T\phi(x; \beta)$. Thus, the intensity matrix is invariant by the optical transmission and the vector $\phi(x; \alpha)$ for the primary image is replaced by another vector ψ given by $\psi(x; \alpha)$.

Looking at the analyses of Gabor and Gamo, we must draw the conclusion that Gabor's bipartite classification into transmission coefficients and rotation coefficients leaves the transmitted invariant as degrees of freedom. *This is the case in organismic perception.* Gamo, on the other hand, leaves the transmitted invariant as intensity. *This is the case with organismic sensation.*

WOLTER'S ANALOGY BETWEEN OPTICAL LAMINATED MEDIA AND TRANSMISSION LINES IN SERIES

Wolter [59] indicates the analogy between laminated media of optics and electronic transmission lines in series. The analogy rests on the similarity of solution of

$$E(r; t) = E_0 \exp\left(i\omega t - i\omega \frac{n}{c} r \cdot f\right),$$

$$H(r; t) = H_0 \exp\left(i\omega t - i\omega \frac{n}{c} r \cdot f\right),$$

where r is a position vector, c is light velocity in a vacuum, n is the complex refractive index, ω is the angular frequency of the Maxwell equations for a plane wave that travels in the direction of the unit vector f , and of the solution

$$U(z; t) = U_0 \exp(i\omega t - \Gamma z), \quad J(z; t) = J_0 \exp(i\omega t - \Gamma z),$$

where z is a coordinate, t is time, which comes from the equations of telegraphy, likewise derived from Maxwell's equation, where Γ is a "propagation constant":

$$\Gamma = B + iA = [((R + i\omega L)(G + i\omega C))]^{1/2}.$$

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Line A is the phase measure, B the damping of the transmission line, G the cross conductivity, L the inductance, and C the capacitance, all per centimeter of the transmission line.

Wolter warns of the differences between the two media:

1. There is no separation into incident and reflected waves in telegraphy.
2. In optics, the input is considered to be only the incident wave, whereas the whole voltage is considered input in telegraphy.
3. In transmission lines the accent is upon departure from transversality, in contrast to the accent in optical waves of perpendicular incidence.

In the light of recent developments in laser communications [42], however, we may question whether these differences now still apply.

For our purposes the most interesting analogy is that between the optical image of a function of position by means of an optical system of *restricted aperture* on the one hand and the electronic distortion of a time function serving as a communication through a communication channel of *limited bandwidth* on the other.

The analogy exists between

$$U = ZJ$$

for the coupling of voltage and current in telegraphy and

$$E_{\parallel} = \frac{\mu}{n} H_{\perp}$$

for the coupling of an electric and a magnetic field component in optics, where μ is the magnetic permeability. It is to be noted that the field strengths themselves are not analogous to current and voltage.

The analogy in Fig. 4 between the surge impedance

$$Z \leftrightarrow \frac{\mu}{n \cos \varphi} \quad \text{for transverse } E \text{ waves}$$

and

$$Z \leftrightarrow \frac{\mu \cos \varphi}{n} \quad \text{for transverse } H \text{ waves}$$

shows the impossibility of a unique Z for the two polarizations unless $\cos \varphi = 1$, that is, unless the incidence is normal. Thus telegraphy permits transmitted waves of a single "polarization" and of a single "direction" of the multiplicity of a set

$$\{Z; -Z\}.$$

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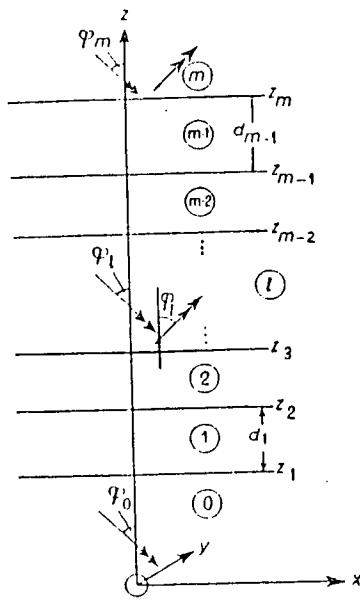
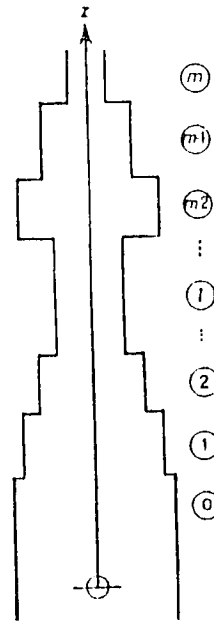


FIG. 4. Layer system in optics and conduction line in electronics (from [59, page 160]).



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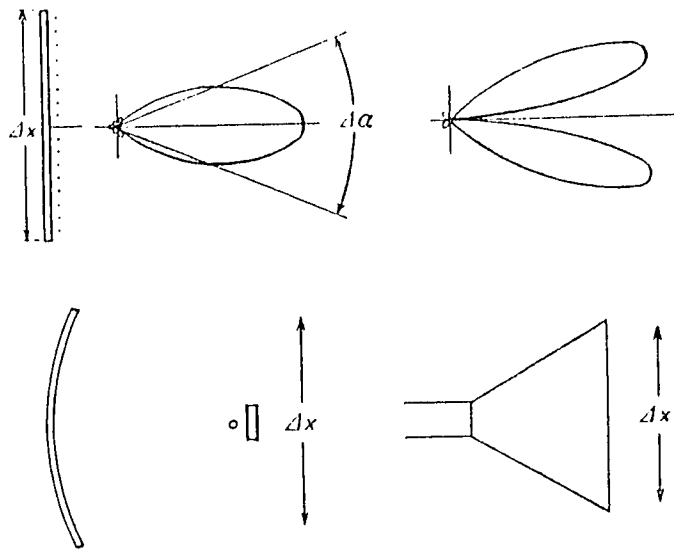


FIG. 5. a, b, c: Directional antennas; d: horizontal diagram of the directional antenna (a) by "maximum feeding;" e: a horizontal diagram of the same antenna by "minimum feeding" (from [59, page 181]).

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But an optical wave packet represents a two-dimensional continuum

$$\left\{ \cos \varphi; -\cos \varphi; \frac{1}{\cos \chi}; -\frac{1}{\cos \chi} \right\}$$

with $|\varphi| \leq \bar{\varphi}; |\chi| \leq \bar{\chi}$.

This two-dimensional continuum, of course, permits the transmission of phase relationships.

Wolter [59] draws the analogy between optical and Hertzian waves (cf. Figs. 5 and 6). He indicates that the rule according to which a group

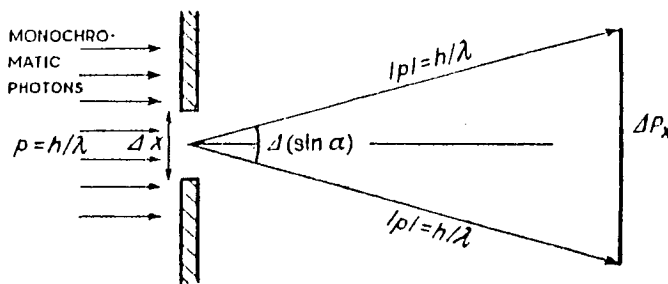


FIG. 6. On Heisenberg's uncertainty condition (from [59, page 182]).

dipole antenna can concentrate the radiation in an angular region of half width where Δx is the breadth of the group, namely,

$$\Delta x \Delta(\sin \alpha) \geq \lambda,$$

is analogous to the diffraction relation in optics:

$$\Delta x \Delta(\sin \alpha) \frac{h}{\lambda} \geq h,$$

which is related to Heisenberg's uncertainty relation because of the relation

$$\Delta p_x = p \Delta(\sin \alpha) = \Delta(\sin \alpha) \frac{h}{\lambda}$$

given for monochromatic photons of momentum $|p| = h/\lambda$, where h is Planck's constant.

It was considered that with $\Delta x \Delta(\sin \alpha) \geq \lambda$ the limit of information had been obtained. However, considering Hertzian waves, it is possible to make measurements of greater accuracy by using a minimum of the directivity diagram of the antenna than by using a maximum. As an

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example, Wolter gives the case that sharp "linear" zeros are obtained in the directional diagram if the two halves of the group are closely connected to the receiver with opposite phase. The analogy in optics is that if directions in space are not characterized by means of accumulations of photons but by surfaces in which the light intensity is zero, there exists no lower limit of their double width. This principle Wolter calls the "minimum ray characteristic."

It can be seen, therefore, that whereas in acoustics a clearly definable bit of information can be defined objectively (cf. [17] and [55]), in the case of the visual system the minimum ray characteristic leaves the absolute unit dependent on the resolution of the visual apparatus alone, that is, it may be defined only physiologically and biographically.

Wolter draws the analogy between Zernike's [60] method of making visible microscopic objects by changing phase differences into amplitude differences by means of intervention in the ray path (phase contrast method), and phase demodulation in communications.

If a phase grating lies in the object plane of a lens, the spectra of orders zero, first, minus first, second, and so on, appear in the focal plane of the object and each, in monochromatic light, consists of only one point. The spectrum of order m , which is produced at the angle α_m to the grating normal, is, according to Huygens' principle, the complex disturbance of light:

$$F_m = \frac{1}{g} \exp[i(\omega t + \Phi_0)] \int_0^g f(x) \exp\left(-2\pi i x \frac{\sin \alpha_m}{\lambda}\right) dx.$$

As the path difference of the ray deflected by the grating at the angle α_m at position x compared with the ray deflected at position 0 is $x \sin \alpha_m$, ω is the angular frequency of the light and Φ_0 a phase constant. The spectrum of order m for an angle α_m connected with the wavelength λ and the grating constant g are connected by

$$g \sin \alpha_m = m\lambda,$$

which, substituted in the previous equation, gives :

$$F_m = \frac{1}{g} \exp[i(\omega t + \Phi_0)] \int_0^g f(x) \exp\left(-2\pi i \frac{mx}{g}\right) dx,$$

which is the m th Fourier coefficient of the Fourier series

$$f(x) \exp[-i(\omega t + \Phi_0)] = \sum_{m=-\infty}^{\infty} F_m \exp\left(2\pi i \frac{mx}{g}\right)$$

and the representation of the object function is thus

$$f(x) = \sum_{m=-\infty}^{\infty} F_m \exp\left[i\left(\omega t + \Phi_0 + \frac{2\pi mx}{g}\right)\right].$$

As the image plane is traversed, the complex light disturbance is caused by interference of waves emerging from the point spectra in the back focal plane. By placing a Zernike phase plate in the focal plane of the object lens, at the point of the spectrum of order zero, a 90 deg phase shift of the side spectra occurs with respect to the rest of the plate. Thus phase differences become visible by their change into amplitude differences.

Turning to the communication analogy, the function

$$f(t) = a \exp(2\pi i v_0 t + i\Phi),$$

where a is "amplitude," v_0 is "carrier frequency," and the real Φ is "phase," may be subjected to amplitude modulation,

$$f_a(t) = a(t) \exp(2\pi i v_0 t + i\Phi_0),$$

or phase modulation,

$$\Phi_B(t) = a_0 \exp(2\pi i v_0 t + i\Phi(t)).$$

On rectifying the oscillation in a "demodulating link" and averaging with a time constant large compared with $1/v_0 = T_0$ but small compared with $\Phi(t)$, we find that the time function obtained from the previous equation is

$$|\overline{\text{Re } f_\Phi(t)}| = K a_0 \quad \text{where } K \text{ is a constant;}$$

that is, phase is lost. A phase-modulated communication must therefore be converted into an amplitude modulated communication before demodulation takes place. The following corresponds to the optical grating method.

$$\Phi(t) = \begin{cases} \Phi_1 & \text{for intervals of even numbers,} \\ 0 & \text{for intervals of odd numbers,} \end{cases}$$

which means that $f(t)$ is now

$$f(t) = \sum_{m=-\infty}^{\infty} F_m \exp\left[2\pi i t \left(v_0 + \frac{m}{T}\right)\right] = \exp(2\pi i v_0 t) \sum_{m=-\infty}^{\infty} F_m \exp\left(\frac{2\pi i t m}{g}\right).$$

Wolter points out the difference here between the optical representation and the communications representation: a genuine frequency $\omega/2\pi$ of light oscillation corresponds to the carrier frequency ν_0 in optics. In optics, however, "pseudofrequencies" m/g , which have the dimension of reciprocal length and not of time, correspond to the "side bands" of communication technique represented by the genuine frequencies m/T .

The communication appearing at the output of the apparatus causing the intervention is

$$f_B(t) = \sum_{m=-\infty}^{\infty} S_m F_m \exp\left[2\pi i t \left(\nu_0 + \frac{m}{T}\right)\right].$$

As absolute phase is irrelevant, either the side spectra or the carrier may be rotated by 90 deg in phase.

This method, of course, is possible only in the acoustical system, where phase is an objective stimulus, and not in the visual system, where phase is physiologically generated. The rotation of side spectra by 90 deg (by delay methods) could easily take place in the cortex (see below).

A FURTHER ANALOGY BETWEEN OPTICS AND ELECTRICAL TRANSMISSION

Leith *et al.* [32] have shown that the solution of Maxwell's equations, adapted from the theory of scattering of light by ultrasonic sound waves, is equivalent to the Kirchhoff formulation for calculating the relative intensities of the diffracted orders of three-dimensional gratings, as shown in Fig. 7 when $\theta_r = -\theta_s$.

It is assumed that the dielectric constant of the photographic emulsion is constant in space and time, and that the conductivity of the emulsion is a variable, $\sigma = \sigma_0 + \sigma_1 \cos qy$, where q is the radian spatial frequency of the recorded diffraction pattern.

The monochromatic plane wave incident upon the emulsion is $E = E_0 e^{i\omega t}$ where E_0 is the spatial variation of the electric vector inside the emulsion and ω is the radian frequency of the field.

If $\sigma_1 \ll \sigma_0$, then $\text{div } E_0 = 0$ and the wave equation to be satisfied is

$$\nabla^2 E_0 + k_1^2 E_0 = 0$$

where $k_1^2 = (\omega^2/c^2)[\epsilon + i(4\pi\sigma/\omega)]$, k_1 is the complex propagation constant, and the permeability μ is assumed to be unity.

Assuming that the incident wave of amplitude A is plane polarized

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FIG. 7. The fronts; θ_s constant d between the

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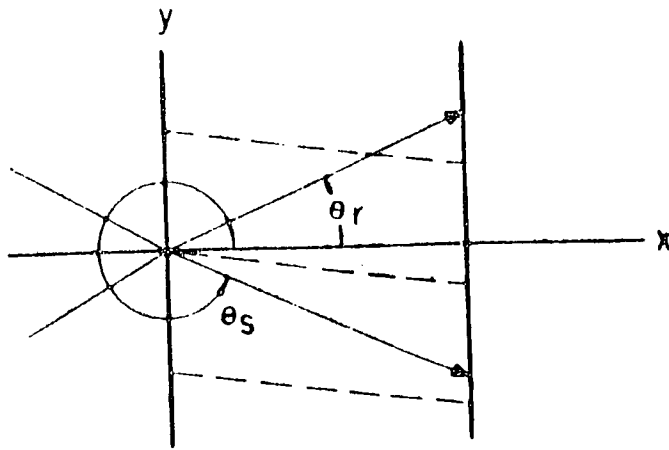


FIG. 7. The read-in process. The vectors designate the normals to the impinging wave fronts; θ_s and θ_r designate angles within the emulsion. The broken lines show the constant density surfaces produced within the emulsion as a consequence of interference between the two waves (from [32, page 1304]).

with its electric vector along the z direction, the E_x and E_y components of E_0 may be neglected, and E_z will be independent of the z coordinate.

The diffracted field may be obtained by solving the equation

$$\frac{\partial^2 E_z}{\partial x^2} + \frac{\partial^2 E_z}{\partial y^2} = -\frac{\omega^2}{c^2} \left[\epsilon + i \left(\frac{4\pi}{\omega} \right) (\sigma_0 + \sigma_1 \cos qx) \right] E_z.$$

Assuming solutions of the form

$$E_z = \sum_l V_l(x) \exp\{i[(k_1 \sin \theta_l + lq)y]\}$$

where $l = 0, \pm 1, \pm 2, \dots$, and θ is the angle (within the emulsion) that the incident, or read-out, wave makes with the x axis.

Using the grating equation $\sin \theta \pm (lq/k_1) = \sin \psi_{\pm l}$, where $\psi_{\pm l}$ is the angle (within the emulsion) that the diffracted orders make with the x axis, a solution for the first-order diffracted wave $V_{\pm 1}(x)$ is

$$V_{\pm 1}(x) = -k_1^2 A \left(\frac{2\pi\sigma_1}{\omega} \right) \frac{\sin[(\alpha_0)^{1/2} - (\alpha_{\pm 1})^{1/2}]x}{(\alpha_0 - \alpha_{\pm 1})/2} \times \exp\{i[(\alpha_{\pm 1})^{1/2} - (\alpha_0)^{1/2}]x\}$$

where $\alpha_{\pm 1}$ is defined as $\alpha_{\pm 1} = k_1^2 [1 - \{\sin \theta_{\pm 1} (lq/k_1)\}^2]$; l is either zero or one; $k = 2\pi n/\lambda$, the ordinary propagation constant inside the emulsion; n is the refractive index of the emulsion; and λ is the wavelength of the incident light.

The intensity of the diffracted wave emerging from the emulsion is found by taking $y = L$ (where L is the thickness of the emulsion) and obtaining

$$|V_{\pm i}(L)|^2 = S \left[\frac{\sin \frac{kL}{2} (\cos \theta_i - \cos \psi)L}{\frac{k}{2} (\cos^2 \theta_i - \cos^2 \psi)} \right]^2$$

where all the constants have been absorbed in S .

An equivalent solution can be found for the Kirchhoff formulation.

ON THE INFORMATION TO BE OBTAINED FROM A SOURCE

Gamo [20] has shown how the information on an object to be derived from an observed image is dependent on the nature of illumination, that is, the degree of coherence.

$$I(x) = \int_{\Sigma} J(y) |U(y - x)|^2 dy$$

where $I(x)$ is the intensity of an image at point x , $J(y)$ the intensity of the source, and $U(y - x)$ the complex amplitude of waves at point x in the image produced by a point source having unit intensity at point y in the source. The complex transmission function $U(y - x)$ is expressed by using the transmission coefficient of the object $E(x)$, the amplitude of incident waves at the object $A(y - X)$, and the transmission function of the pupil $u(X - x)$:

$$U(y - x) = \int A(y - X)E(X)u(X - x) dX.$$

As the Fourier transform of transmission function $u(X - x)$ is equal to the pupil function representing aberrations, and its frequency bandwidth is limited by a given aperture,

$$u(X - x) = \sum_{n=-\infty}^{+\infty} u\left(X - \frac{n\pi}{k\alpha}\right)u_n(x)$$

where the sampling function $u_n(x) = \sin(k\alpha x - n\pi)/(k\alpha x - n\pi)$, $k = 2\pi/\lambda$, λ the wavelength, and α the aperture constant. Thus

$$I(x) = \sum_{n=-\infty}^{+\infty} \sum_{m=-\infty}^{+\infty} u_n(X)A_{nm}u_m(x)$$

and

$$A_{nm} = \iint \Gamma(X_1, X_2)E^*(X$$

where the mutual intensity factor multiplied by the a This is the intensity matrix

This matrix is (1) elements are given by the sum of diagonal elements the image. (3) Any intensity transformation.

The fourth equation

$$I(x) = \lambda_j$$

where λ_n is the n th eigenvector of the intensity form as the entropy of

where λ_n is the n th eigenvalue for coherent illumination where N is the "degree of coherence" $4\alpha^2 S/\lambda^2$. $d = (D_0 - L)$ illumination.

Gabor [19] has shown that the Lagrange invariant is

a'

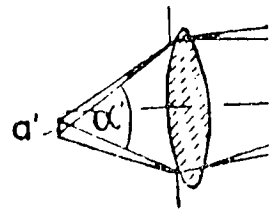


FIG. 8. The Smith-Lagrange invariant

and

$$A_{nm} = \iint \Gamma(X_1, X_2) E^*(X_1) E(X_2) u^* \times \left(X_1 - \frac{n\pi}{k\alpha} \right) u \left(X_2 - \frac{m\pi}{k\alpha} \right) dX_1 dX_2$$

where the mutual intensity $\Gamma(X_1, X_2)$ is equal to the phase coherence factor multiplied by the absolute values of amplitudes at points X_1 and X_2 . This is the intensity matrix.

This matrix is (1) positive, definite Hermitian. (2) Its diagonal elements are given by the intensities at sampling points, and the trace or the sum of diagonal elements is equal to the total intensity integrated over the image. (3) Any intensity matrix can be diagonalized by a unitary transformation.

The fourth equation may be expressed as

$$I(x) = \lambda_1 \left| \sum_i S_{i1} u_1 \right|^2 + \lambda_2 \left| \sum_i S_{i2} u_2 \right|^2 + \dots$$

where λ_n is the n th eigenvalue and S_{mn} is the m th component of the n th eigenvector of the intensity matrix. The following equation has the same form as the entropy of statistical mechanics.

$$D = - \sum_n \left(\frac{\lambda_n}{I_0} \right) \log \left(\frac{\lambda_n}{I_0} \right)$$

where λ_n is the n th eigenvalue, I_0 the trace of an intensity matrix. D is zero for coherent illumination and is $\log N$ for incoherent illumination where N is the "degrees of freedom" of an image of area S ; that is, $N = 4\alpha^2 S / \lambda^2$. $d = (D_0 - D) / D_0$ is the measure of "degree of coherence" of illumination.

Gabor [19] has sought the invariants of the imaging process, and these must be geometrical invariants. It is considered that only the Smith-Lagrange invariant is of this type (see Fig. 8).

$$a'\alpha' = a''\alpha'' \quad \text{or} \quad dS \cdot d\Omega = \text{inv.}$$

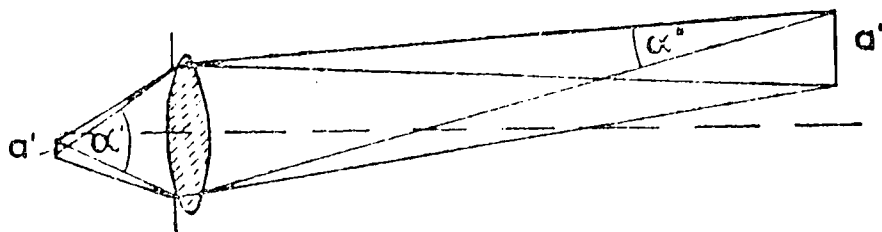


FIG. 8. The Smith-Lagrange invariant in geometrical optics (from [19, page 114]).

where $d\Omega$ is the solid angle of a very narrow cone of rays and dS is the projection of the area of a very small element viewed from the direction of the cone.

In the case of "scalar light" with amplitude u , the following wave equation must be satisfied.

$$\square u \equiv \left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2} - \frac{1}{c^2} \frac{\partial^2}{\partial t^2} \right) u = 0;$$

that is, light propagates in all directions with velocity c .

Gabor considers the wave

$$u_0 = \exp\left[2\pi i \left(\frac{z}{\lambda} - vt \right)\right];$$

immediately behind the object, that is

$$u(x, y + 0, t) = t(x, y) \exp(2\pi i vt).$$

If the transmission function is decomposed into its Fourier components, then

$$t(x, y) = \iint_{-\infty}^{\infty} T(\xi, \eta) \exp[2\pi i(x\xi + y\eta)] d\xi d\eta$$

where $T(\xi, \eta)$ is the Fourier transform of $t(x, y)$. This gives the result that those Fourier components whose period in the object plane is longer than a wavelength will be propagated as plane waves, while those with a shorter period will be continued as exponentially damped "evanescent waves," which means that they will be practically damped out in a matter of a few wavelengths at most. Thus light with a wavelength λ will under no circumstances carry with it information on detail below $\frac{1}{2}\lambda$.

Gabor shows that if the product of object area and Fourier area is of the order M , then the number of degrees of freedom can be given with an accuracy of $1/M$, for

$$F = 2 \times 2 \times \text{object area} \times \text{accessible Fourier area}$$

where F is number of degrees of freedom.

The first 2 factor is due to each term's having a complex coefficient equal to two real data, the second is due to the vector nature of light. If the object is moving, then as every degree of freedom can be considered a separate and independent communication line, which has $(2) \Delta\nu \Delta t$ degrees of freedom in a frequency interval $\Delta\nu$, and the time interval (observation time) Δt , with the factor (2) in brackets if "temporal phase" is measurable,

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then the degrees of freedom in the Fourier plane is

$$2 \cdot 2 \cdot (2)$$

If a Zehnder-Mach int

$$I =$$

if ϕ is the phase angle between the phase delay in the relation between the light

$$S =$$

Gabor assumes that the energy ξ_0 , because for s the root of the mean fluctuation

It is assumed that equal $s = \xi_0$, and therefore

Gabor makes the point that some size ξ_0 , which arrives at an average of S_0/ξ_0 arrivals can be made with less object.

I am suggesting the thalamic input. As for variations of Bishop [3] at positive phase of S_0 will potential elevations of indicating a synchronous response is obtained to of such rhythms, but surface-negative phase increase of the first few is, the response to stimulus spontaneous rhythm.

one of rays and dS is the area element viewed from the direction of

then the degrees of freedom of any light beam in the object plane and Fourier plane is

$$2 \cdot 2 \cdot (2) \iiint \iiint dx dy d\xi d\eta dv dt.$$

If a Zehnder-Mach interferometer is used, then the resulting image is

$$I = A_0^2 + a^2 + 2A_0a \cos \phi$$

if ϕ is the phase angle between the two depending on the optical paths and on the phase delay in the object. Similarly, there exists the following relation between the light sums.

$$S = S_0 + s + 2(S_0s)^{1/2} \cos \phi.$$

Gabor assumes that the experiment is bound to fail if the light sum s that has gone through the object element is smaller than a certain minimum energy ξ_0 , because for $s < \xi_0$ the interference term becomes smaller than the root of the mean fluctuation square of the background:

$$S_0s < (\delta S_0)^2.$$

It is assumed that equality (i.e., possible observation) is just achieved for $s = \xi_0$, and therefore

$$\overline{\delta \left(\frac{S_0}{\xi_0} \right)^2} = \frac{S_0}{\xi_0}.$$

Gabor makes the point that monochromatic light arrives in *quanta* of some size ξ_0 , which arrive at random, subject only to the condition that an average of S_0/ξ_0 arrives during the observation time. No observation can be made with less than one quantum passing through the observed object.

I am suggesting that S_0 is provided by a pacemaker triggered by a thalamic input. As for the quantity S_0/ξ_0 , we might point to the observations of Bishop [3] as indicative that only if s (input) arrives during the *positive* phase of S_0 will it be registered. Bartley [2] noticed that where the potential elevations of the spontaneous activity are of large amplitude, indicating a synchronization of many elements, cases occur in which a response is obtained to a shock that falls into the surface-positive phase of such rhythms, but no response occurs following a shock during the surface-negative phase. The response, when present, appears as an increase of the first few positive phases of the spontaneous rhythm. That is, the response to stimulation has the same frequency of repetition as the spontaneous rhythm. This situation may be compared to the responses to

two strong shocks [2] in a preparation where the spontaneous waves are low. The first response will produce the typical record; the second shock, if it falls in the surface-negative deflection following the first, is ineffective, but if it falls during the surface-positive deflection, a second train of responses occurs.

Winthrop and Worthington [57] have shown how the amplitude of Fresnel diffraction can be expressed as convolution in either direct or reciprocal space. A plane object of amplitude transmittance $t(r)$ is illuminated by a quasi-monochromatic point source $A\delta(r'_0 - r_0)$ of wavelength λ . Vectors r'_0 , r' , and r define points of the parallel planes of source,

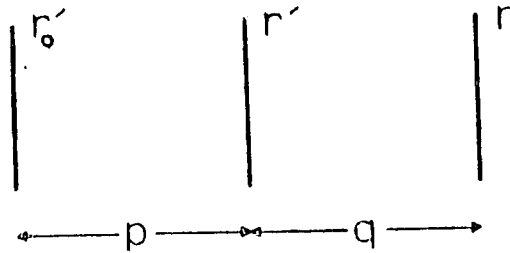


FIG. 9. The source is in plane r'_0 , the object is in plane r' , and Fresnel diffraction is observed in plane r (from [57, page 588]).

object, and observation. The planes are separated by distances p and q . The diffracted amplitude is given by the Fresnel-Kirchhoff relation $g(r, r_0)$ (cf. [6]). Adopting the approximation of parabolic wave fronts and omitting the obliquity factor, we write the diffracted amplitude as

$$g(r, r_0) = (i\lambda pq)^{-1} \exp\left[i2\pi\frac{(p+q)}{\lambda}\right] \int_{\text{object}} t(r') \times \exp\left[\left(\frac{i\pi}{\lambda p}\right)(r' - r_0)^2 + \left(\frac{i\pi}{\lambda q}\right)(r' - r)^2\right] d\sigma'$$

where $d\sigma'$ is the element of area in the object plane. This may be expressed in the form

$$g(r, r_0) = -\epsilon iB \int t(r') \exp[i\pi B(\rho - r')^2] d\sigma'$$

where

$$\epsilon = A(p+q)^{-1} \exp\left[i2\pi\frac{(p+q)}{\lambda} + i\pi\frac{(r-r_0)^2}{(p+q)\lambda}\right],$$

$$B = \frac{M}{\lambda q}, \quad \rho = \frac{r + mr_0}{M}, \quad M = 1 + m = 1 + \frac{q}{p}.$$

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The factor ϵ is the amplitude passed by a transparent object plane (an open aperture). The factor M describes the geometrical shadow magnification.

It is explained that the convolution of two functions $a(r)$ and $b(r)$ is written

$$a(r) * b(r) = \int a(r')b(r - r') d\sigma .$$

Fourier transform pairs are indicated by upper- and lowercase characters: $t(r) \rightleftharpoons T(R)$;

$$T(R) = \int t(r) \exp(-i2\pi r \cdot R) d\sigma,$$

$$t(r) = \int T(R) \exp(i2\pi r \cdot R) d\Sigma.$$

Vector r and the element of area $d\sigma$ refer to direct space, whereas vector R and the element of area $d\Sigma$ refer to reciprocal space (or Fourier space). The convolution theorem states that

$$a(r) * b(r) = \int A(R)B(R) \exp(i2\pi r \cdot R) d\Sigma$$

and $z(r)$ is called the Fresnel wave function, where

$$z(r) = iB \exp(i\pi Br^2).$$

The Fourier transform of $z(r)$ is $Z(R)$ where

$$Z(R) = \exp(-i\pi B^{-1}R^2).$$

Thus

$$g(r, r_0) = \epsilon t(\rho) * z(\rho),$$

which is the convolution in direct space. From the convolution theorem it can be written

$$g(r, r_0) = \epsilon \int T(R)Z(R) \exp(i2\pi \rho \cdot R) d\Sigma,$$

which is the Fourier integral form.

By expanding the exponential term in the integrand, $g(r, r_0)$ may be written

$$g(r, r_0) = \epsilon Z^*(B\rho) \int t(r')z(r') \exp(-i2\pi B\rho \cdot r') d\sigma',$$

and from the convolution theorem we can write

$$g(r, r_0) = \epsilon Z^*(B\rho)[T(B\rho) * Z(B\rho)].$$

The Fresnel wave function $z(r)$ has the property of self-orthogonality under the convolution operation:

$$z^*(r) * z(r) = \delta(r),$$

which follows from the Fourier transformation of $[Z(R)]^2 = 1$. Fresnel diffraction corresponds to optical Fresnel transformation and a Fresnel transformation applies to any function whose Fourier transform exists.

Cutrona *et al.* [13] have written that the matched filter, which has a transfer function that is the complex conjugate of the signal spectrum to which the filter is matched, maximizes the ratio of the signal squared to the root mean square noise, when the noise is white Gaussian. This criterion remains valid when the signals are two-dimensional and complex. This might be the mechanism whereby recognition may take place in any orientation.

Astigmatic systems can be multichannel optical computers capable of evaluating integrals of the form

$$f(x_0, y) = \int_{a(y)}^{b(y)} f(x - x_0, y)g(x, y)\exp(-j\omega_x x) dx$$

such that the mathematical operations presented in Table I can be performed with $\pm L$ representing the achievable aperture limits of the optical

TABLE I^a

$I(\omega_x, x_0, y)$	$f(x - x_0, y)$	$g(x, y)$	$\exp(j\omega_x x)$	$a(y)$	$b(y)$
Fourier transform	$f(x)$	1	$\exp(-j\omega_x x)$	$-L$	$+L$
Laplace transform	$f(x - x_0)$	$g(x)$	$\omega_x = 0$	$-L$	$+L$
Cross-correlation	$f(x - x_0)$	$f(x)$	$\omega_x = 0$	$-L$	$+L$
Autocorrelation	$f(x_0 - x)$	$g(x)$	$\omega_x = 0$	$-L$	$+L$
Convolution	$f(x)$	e^{-xy}	$\exp(-j\omega_x x)$	0	$+L$

^a From [13, page 395].

system. The information from a source, therefore, may be represented as either processed by an operator [19, 20] or convoluted with another function [13, 57].

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REPRESENTATIVE

Winthrop representation previously mentioned when comparing regions:

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TABLE II^a

Type of ho
Fresnel transform
Geometric shadowing
quasi-Fourier transform
Fourier transform

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REPRESENTATION OF INTERFEROMETRIC STRUCTURES

Winthrop and Worthington [58] have proposed a Fresnel transform representation of holograms and hologram classification. In their previously mentioned paper [57], they defined a characteristic length l that, when compared with the details of the object, defines three diffraction regions:

$$l = |B|^{-1/2} = \left| \frac{\lambda q}{M} \right|^{1/2}$$

Let the object occupy the region of the object plane $|r'| \leq a$; let the maximum spatial frequency of the object be $|R|_{\max} = R_0$. The diffraction regions are then defined by the following inequalities.

- $l < R_0^{-1}$ geometrical shadow region,
- $l > a$ far-field diffraction region,
- $R_0^{-1} < l < a$ Fresnel diffraction region.

They make the point that a hologram of a certain form may be produced in more than one diffraction region; also, different holograms may be produced by a single diffraction region. Hence, the terms Fresnel diffraction hologram and Fraunhofer diffraction hologram are ambiguous as terms of classification.

The conditions for production of the four special holograms are identical with the conditions under which the Fresnel interference transform \tilde{t} and its Fourier transform \tilde{T} reduce to the forms of Table II. For

TABLE II^a

Type of hologram	Form of $\tilde{t}(r)$	Form of $\tilde{T}(R)$
Fresnel transform	$t(\alpha r) * \exp(i\pi\beta r^2)$	$T(\alpha^{-1}R)\exp(-i\pi\beta^{-1}R^2)$
Geometrical shadowgram	$t(\alpha r)$	$T(\alpha^{-1}R)$
quasi-Fourier transform	$T(\alpha r) * \exp(i\pi\beta r^2)$	$t(\alpha^{-1}R)\exp(-i\pi\beta^{-1}R^2)$
Fourier transform	$T(\alpha r)$	$t(\alpha^{-1}R)$

^a From [58, page 1365].

each diffraction region there is a characteristic length that, when compared with the characteristics of the object, indicates the types of hologram

produced and specifies the arrangement of components.

1. Hologram recorded in the Fresnel region ($R_0^{-1} < l < a$); then

$$\begin{array}{ll} l_F < R_0^{-1} & \text{quasi-Fourier transform hologram,} \\ l_F > a & \text{Fresnel transform hologram,} \\ R_0^{-1} < l_F < a & \text{general hologram.} \end{array}$$

2. Hologram recorded in the geometrical shadow region ($l < R_0^{-1}$); then

$$\begin{array}{ll} l_{GS} < R_0^{-1} & \text{quasi-Fourier transform hologram,} \\ l_{GS} > a & \text{geometrical shadowgram,} \\ R_0^{-1} < l_{GS} < a & \text{general hologram.} \end{array}$$

3. Hologram recorded in a far-field region ($l > a$):

$$\begin{array}{ll} l_{FF} < R_0^{-1} & \text{Fourier transform hologram;} \\ l_{FF} > a & \text{Fresnel transform hologram;} \\ R_0^{-1} < l_{FF} < a & \text{general hologram.} \end{array}$$

The maximum spatial frequency of the object is easy enough to obtain in the auditory system. In the visual system it is impossible to tell; p and q could be defined with respect to the channel capacity of the system and the size of the object.

Ramberg [48] has classified the varieties of hologram into two categories. The hologram formed by a nearby object and a parallel reference beam is a Fresnel hologram with two conditions.

1. In a "Fraunhofer hologram" the reference source and (plane) object are placed in the focal plane of a lens and thus, effectively, at an infinite distance from the hologram plate. In the reconstruction, both the primary and the conjugate images are formed in the focal plane of a second lens, magnified or reduced by a factor equal to the ratio of the focal length of the two lenses.

2. In a Fourier transform hologram the parallel light beam originating from a point (x_j, y_j) of the object forms an interference pattern with the parallel reference beam (assumed perpendicular to the hologram plane). This pattern, in the hologram plane, corresponds to a sinusoidal intensity variation with a space period

$$\frac{\lambda}{\sin \theta_j} = \frac{\lambda f_1}{(x_j^2 + y_j^2)^{1/2}}$$

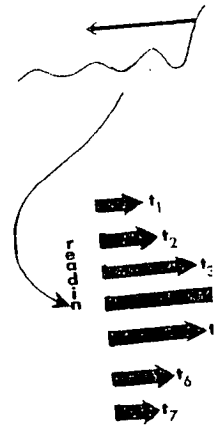
and an azimuthal direction

$$\phi_j = \arctan\left(\frac{y_j}{x_j}\right);$$

θ is the angle of incid point (x_j, y_j) . Thus uniquely on the hologi amplitude correspond point in question.

THE NEUROPHYSIOLOC

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θ is the angle of incidence on the hologram plane of the beam from the point (x_j, y_j) . Thus every object point in a half-plane is represented uniquely on the hologram by a two-dimensional Fourier component whose amplitude corresponds to the amplitude of the light wave emitted by the point in question.

THE NEUROPHYSIOLOGICAL ANALOGY

Considering the neurophysiological evidence, we can note that both amplitude and frequency changes in auditory stimulation find correlated changes in the cortex [56]. Neff *et al.* [41] and Neff and Diamond [40] showed that bilateral, though not unilateral, ablation of AI, AII, and EP in the cat leads to a severe deficit in the ability to localize sound in space. The ability to spatially localize in the auditory system, therefore, must be dependent on the transmission of phase relations between the stimulation at the two ears. To suppose an anatomical correlate of right and left in one hemisphere is unduly vitalistic. It is, of course, logically impossible to

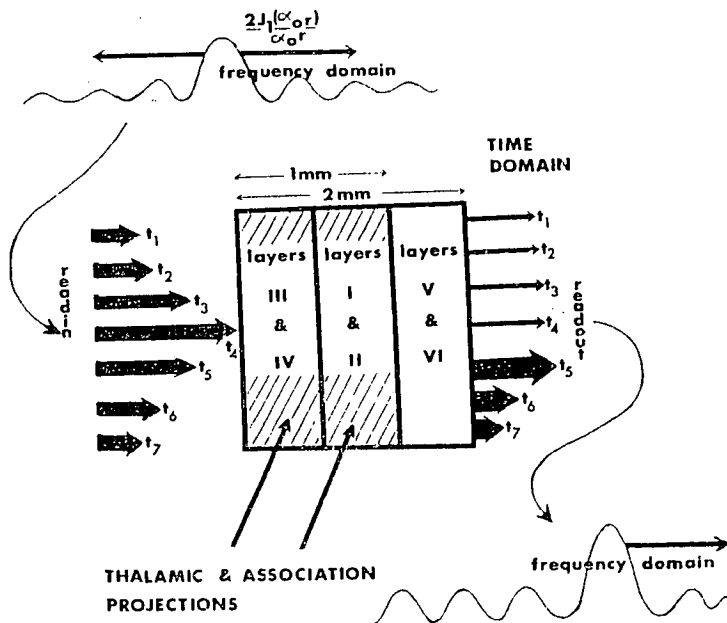


FIG. 10. Translation of frequency domain into time domain in the cortex. Arrow thickness indicates magnitude of potential. Cross-hatching indicates interferometry.

distinguish left from right in one hemisphere by intensity differences alone.

I am suggesting that the method used in the cortex to transmit and receive frequency and phase is a way of transferring the frequency domain of signals in the environment into a time domain (cf. Fig. 10). The transcortical waves, it will be noticed, are not generated transcortically but by "arrival patterns" upon the cortex from inferior structures. Thus any study that afflicts the cortex with knife cuts, wires, or any other interruption of horizontal conduction (cf. Sperry *et al.* [51]) and no behavioral deficit does not rule out the possibility of cortical arrival patterns from vertical elements.

It should be noted that although the transmission in the white matter is digital, the interactive processes within the cortex are considered analog; thus we have an analog-digital computer more advanced, presumably, than any available in technology. The wiring or anatomy of the digital elements is, of course, important, but must be secondary to that of the analog elements, which are host to the interactive processes. This monograph thus could be a eulogy on the dendrite at the expense of the much-studied axon.

POSSIBILITY OF INTERFEROMETRY IN THE CORTEX

Bishop [3] found in some cases, with the rabbit as subject, that even where the spontaneous potential rhythm of the cortex is low, weak shocks to the optic nerve are effective only when they fall in certain phase relationships with an inherent cortical rhythm that is not accompanied by a potential fluctuation in the record. An interval of about 0.2 sec or multiples of this can be found at which successive shocks will be equally effective. A slight change of *phase* relationships at the same frequency will alter the amplitude of the whole series of responses. A slight change of *frequency* will cause an alternating slow increase and decrease of successive responses in a manner strictly corresponding to beat frequency phenomena.

A single volley from the optic nerve synchronizes apparently cortico-thalamic circuits even if they are asynchronous and their summated responses then follow periodically as part of the cortical response to stimulation. Bishop remarks that the series of spikes that appears on the main cortical discharge may then represent the repetitive discharges of cortical *visual* elements; when not appearing as separate spikes, temporal

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THE CEREBRAL CORT

dispersion may fuse the

The evidence points, the afferent impulse alone is in the pathway, but it is able to facilitate the visual pathway a mechanism for vision is:

However effective the to the second is maximum an interval of 80-100 a second stimulus only through the successive facilitation by cortical synapses.

Thus two coincide the periphery and on the visual pathway to cause necessary cortical discharge triggered from the t: "carrier" of frequency duration.

In the sensorimotor thetized cat, spindle alternating excitatory their article, Jasper generated by the radiation of the synaptic activity these neurons, probably as judged by recorded with intracellular with microelectrode a modulating or "gating" In this study [29], cortical and somatic tract neurons with spindle waves of 50 msec duration were waves were inhibited excitatory (depolarized mV in amplitude.

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apparently cortico- nd their summated ortical response to that appears on the titive discharges of te spikes, temporal

dispersion may fuse them to a smooth elevation. He states ([3], page 313):

The evidence points, then, to a peculiar circumstance of cortical stimulation. The afferent impulse alone is in general unable to traverse the higher neurones of the visual pathway, but it is able to activate the parallel coordinating pathways which in turn facilitate the visual pathway to passage by afferent impulses. The significance of such a mechanism for vision is not apparent.

However effective the first maximal shock to the optic nerve, the response to the second is maximal only after a 0.2-sec interval, being absent during an interval of 80–100 msec after the first. The cortex is thus accessible to a second stimulus only after the first stimulus has completed the circuit through the successive elements of the cortex. Even with maximal stimuli; facilitation by corticofugal pathways is essential for passage of the critical synapses.

Thus two coincidental impulses are required to fire a synapse. One from the periphery and one from the cortex are necessary for input from the visual pathway to cause a response in the cortex. The frequency of the necessary cortical discharge is 5 per second and would appear to be triggered from the thalamus. This could serve as a coherent *temporal "carrier" of frequency* to nerve discharges of higher frequency and shorter duration.

In the sensorimotor cortex in the *cerveau isolé* or barbiturate-anesthetized cat, spindle waves recorded from the surface are composed of alternating excitatory and inhibitory postsynaptic potentials [29]; in their article, Jasper and Stefanis postulate that these potentials are generated by the radially oriented pyramidal neurons and that the location of the synaptic activity is along the extent of the apical dendritic shafts of these neurons, probably including the soma membrane and basal dendrites as judged by the large amplitude of postsynaptic potentials (PSPs) recorded with intracellular microelectrodes. Referring to other studies with microelectrodes [33, 34], the authors consider spindle waves to exert a modulating or "gating" action upon the excitability of cortical neurons. In this study [29], too, a dissociation was found between surface dendritic and soma membrane potentials. Increased firing of pyramidal tract neurons with slow positive shifts in potential occurred with spindle waves of surface-negative sign. Spontaneous slow waves of 300-msec duration were noted at a frequency of 3 per second. Slow surface waves were inhibitory and intracellular oscillations are composed of excitatory (depolarizing) and inhibitory (polarizing) components of 5–17 mV in amplitude. Stefanis and Jasper [52] stimulated axons in the pes

pedunculi and recorded the antidromic responses in cortical pyramidal tract neurons with intracellular microelectrodes. The antidromic inhibitory PSPs were found to originate mainly from synaptic sites of the soma membrane close to the spike trigger zone. Both excitatory and inhibitory PSPs could be recorded from the same neurons, indicating perhaps that collateral connections can be modified with respect to their excitatory or inhibitory effects.

Morison and Dempsey [14-16, 38] showed that both recruiting and augmenting waves increase the amplitude of cortical response to repetitive (5-10 per second) shocks to the thalamus. Jasper and Hanbery [24, 25, 28] have shown that the pathways for recruiting waves are independent of the specific projection nuclei. Thus, recruiting and augmenting waves represent different processes.

Recruiting waves are surface negative with long latency (ca. 15-30 msec) and with a smaller surface-positive phase occasionally preceding and often following. Complex polyphasic forms are common. Recruiting waves are most easily elicited by stimulation of the medial one third of the thalamus and occupy the upper dendritic layers of the cortex. They are maximally recorded in cortical regions other than the primary sensory projection areas with a distribution and morphology similar to that of spontaneous slow-wave "recruiting spindles" seen in barbiturate narcosis and sleep.

Augmenting waves have a latency of approximately 10-20 msec and follow repetitively elicited primary sensory responses to stimulation of thalamic radiations at the same optimum frequency for recruiting responses. An augmenting wave is an increasingly large negative wave with a peak 5-15 msec later than the peak of the specific response-negative wave.

Bishop *et al.* [5] recorded electrical activity between a surface electrode on the lateral gyrus and one in the subcortical white matter in the visual cortex of cat. The investigators consider the augmenting phenomenon to be correlated with stimulation of slowly conducting corticopetal fibers passing near to the lateral geniculate nucleus and mingling with radiation fibers to the cortex. When augmenting and recruiting waves were recorded from the same locus, augmenting waves could be occluded by preceding recruiting responses (possibly with some facilitation of the primary response), and vice versa. Both recruiting and augmenting waves occupy the same (0.4-1.0 mm) upper region of the cortex.

Jasper [26] found that auditory, visual, and somatosensory responses

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showed that both recruiting and the cortical response to repetitive stimulation. Jasper and Hanbery [24, 25], showing that inhibiting waves are independent of inhibiting and augmenting waves

with long latency (ca. 15-30 msec) and are occasionally preceding and augmenting waves are common. Recruiting waves of the medial one third of the cortex. They are larger than the primary sensory response. Morphology similar to that of waves seen in barbiturate narcosis

approximately 10-20 msec and are responses to stimulation of the cortex. Frequency for recruiting regularly large negative wave with the specific response-negative

between a surface electrode and white matter in the visual cortex. Augmenting phenomenon to recruiting cortical fibers and mingling with radiation waves were recorded. It can be occluded by preceding stimulation of the primary sensory cortex. Augmenting waves occupy the cortex.

1 somatosensory responses

evoked peripherally and in the relay nuclei were unaffected by reticular or medial thalamic stimulation, although the delayed waves after the primary response were usually suppressed. Jasper and Ajmone-Marson [27] showed facilitation of the surface-negative phase of the primary response to optic nerve or lateral geniculate stimulation by a simultaneous negative wave from the medial thalamus. The negative phase of the sensory response might be depressed by an "intralaminar response" and the latter might be depressed following the optic stimulus.

Landau *et al.* [30] investigated the interactions of several varieties of evoked responses in the visual and association cortex of cat. It was found that the optic response was practically always greatly facilitated during high-frequency (80-200 per second) intralaminar stimulation. Surface-positive current depressed the positive and exaggerated the negative phase of the specific response, surface-negative current doing the reverse. Tetanic stimulation of the medial thalamus induced large well-synchronized waves in the cortex but whose frequency bore no relation to the stimulus frequency. Posttetanic potentiation of the callosal response was accompanied by depression of the optic radiation or no change in it. The response in the lateral gyrus, however, was sometimes partially occluded by a tetanus (100-200 per second) to the optic radiation. Callosal, recruiting, and direct cortical responses all involve local graded activity in dendritic tissue, as only occlusive interactions were seen when any of these sites were stimulated.

The authors state that two general types of mechanisms appear to be involved, which can affect different regions of the same neuron. One is the specific sensory response, which is transmitted at and above the IV cortical layer to the lower poles of pyramidal cells. The second type of activity is generated via axons impinging directly on apical dendrites of pyramidal cells.

Their experiments suggest that the superficial layer of the cortex is a collecting net for various impulses from many loci. Any type of response activating apical dendritic terminals may show interactions with any other activity occupying the same dendrites, and all such activities should be capable of affecting the excitability of the axon spike generator.

If radiation afferents are stimulated and the cortex is directly stimulated [27] in appropriate time relations, the negative phase of the diphasic wave following stimulation of the specific thalamic radiation interferes with the simple negative wave response to antidromic synaptic activation of dendrites, and vice versa.

Clare and Bishop [11] have presented evidence of four groups of fibers activating cortical neurons:

1. conducting at 50 m/sec;
2. conducting at 25 m/sec; stimulation of both of these fiber groups results in responses initiated by spikes although they are superposed on a surface-positive wave and followed by a negative phase. Bishop and Clare [4] showed that these slow phases are of dendritic origin;
3. conducting at 8-10 m/sec;
4. conducting at 1 m/sec.

There is thus the wherewithal to effect delay methods for certain aspects of the input, for example, rotate side spectra by 90 deg, as suggested earlier in this monograph.

The authors propose the following reasons why the cortex is the locus for the functions determining the incremental character of the responses to repetitive stimulation. The exact locus is postulated to be the synaptic areas of dendrites.

1. Stimulation of white matter in the internal capsule or even immediately beneath the cortex induces recruitment quite as does thalamic nuclear stimulation.
2. The axons of most of the cells in the thalamus that might respond were directly stimulated, but there is no known way for nerve fibers to summate an effect over the successive intervals of recruitment.
3. Recruiting responses can still be obtained at a point on the cortex within $\frac{1}{2}$ mm of the stimulated point.
4. A cycle of excitability follows each response in a sequence of increasing responses. After a refractory period, a hyperexcitable phase occurs at one sixth to one eighth of a second from the start of each wave.
5. The interaction of a stimulated recruiting series or those set off by the one or more stimuli also indicates the operation of such a cycle in both these sequences.

Clare and Bishop [11] conclude that the essential features of central nervous system rhythmicity are predominantly functions of the excitability cycle of dendritic synapses, such as may be exhibited in relative isolation in the recruiting responses of apical dendrites of cortex.

THE CEREBRAL CORTEX: AN ISOTROPIC OR ANISOTROPIC MEDIUM?

Some of the structural details of the cortex remain the same in all mammals [37]. The arrangement of the synaptic articulations through

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PROBING MEDIUM?

remain the same in all articulations through

which nerve impulses are transmitted, that is, the plexuses of dendritic and axonal branches, remain constant. Indeed, axodendritic synapses would appear to exist in immature cortex [47]. Cell number, cell size, and form vary, however, and in the lower mammals there no longer appear certain types of cells found in monkey and ape.

Clare and Bishop [10] inferred the following sequence of firing: afferent radiation fibers immediately activate the short-axon cells of the fourth layer of cortex, which in turn activate a first group of pyramidal cells lying at about the same level. These pyramidal cells fire their axons, which leave the cortex by way of the subcortical white matter. Recurrent branches of these main axons ramifying within the cortex activate a second group of pyramidal cells. This alternate firing continues until a segment has run its course. The synaptic times between each pair of successive responses are less than 1 msec, which indicates that transmission is from axon to cell body.

Lorente de Nó [37] classifies cortical cells into four types:

1. Cells with descending axons often reaching the white substance to be continued by a fiber of projection or of association;
2. Cells with short axons ramified in the proximity of the cell body, often within a homogenous zone of the dendritic plexus;
3. Cells with ascending axons ramified in one or several cortical layers;
4. Cells with horizontal axons.

According to O'Leary [45], the essential anatomical characters of the cortex from the point of view of interpreting electrical phenomena are (1) The vertically oriented elements, each consisting of a pyramidal cell body, an ascending dendritic shaft, and a descending axon. (2) The chief intracortical connections are established through the collateral arborizations of the axons of pyramidal cells and the variety of short-axon arborizations that occur at different levels of the cortex. (3) In the sensory cortical areas the cortex is primarily activated through entering afferents that arborize at a level of the cortex corresponding to the granule layer (IV); in the precentral cortex the apparently but not necessarily equivalent afferent plexus arborizes at a more superficial level, probably articulating directly with superficial pyramids of medium size. (4) The activation of the whole cortex would appear to proceed through intracortical circuits arising from cells situated within the confines of the plexus of arborizing afferents. The arrangement of all contained elements is such that adequate records of cortical activity can only be expected from an intact cortex containing all of the various vertically disposed elements.

Functionally, therefore, there would appear no basis for considering the cortex as laminated. There is no layer for reception, nor for association, nor for projection. This is also the case with a lens. As the cortex appears to be able to pulsate at a regular rate from thalamic triggering, we might say that this pacemaker provides an isotropic medium. As, on the other hand, other sensory afferents may impinge on the specific receiving areas and modify discharge, the cortex is anisotropic.

THE VALUE OF A DIPOLE

Trabka and Roetling [54] have shown how objects of known shape may be detected in a slowly varying background by thresholding the cross correlation of the object seen with an aperture mask consisting of two narrow bands, one of positive transmittance and the other of negative transmittance, close to and on opposite sides of the object outline.

In present-day computers equipped with analog to digital conversion input-output devices, there is an absolute zero level given for the digital measurement that should be aligned with the absolute zero of the analog measurement. It is questionable, however, whether an analog measuring device is truly analog with an absolute zero. A dipole, however, would appear to dispense with an absolute zero and is a true analog measuring device with great flexibility.

Bishop and Clare [4] investigated the response of the cortex to direct cortical stimuli applied at different depths. Agreeing with Adrian's early work [1], the negatively responding elements acting at the surface were inferred to be either apical dendrites or horizontally oriented short-axon cells of the first layer. The positive component was assigned to the activity of elements deep in the cortex and the negative to elements near the cortical surface. This relation indicated propagation of activity upward from below in the normally activated response.

Two negative components were recorded in the response to stimulation. The earlier is weak but greatly accentuated by strychnine; when strychninized cortex is activated via the radiation, the usual positive wave precedes the exaggerated negative; when strychnine spikes occur spontaneously, the surface-negative spike may or may not be preceded by a positive corresponding to that of the specific response.

In the normal discharge to afferent stimulation, the earlier negative wave represents antidromic conduction along apical dendrites; this response is not usually maximal and strychnine accentuates it. The later negative

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wave of the specific response arises from below in the IV layer of the
cortex and may represent the response of the fusiform cells of layer VI.

When the suprasylvian cortex was stimulated on the surface, the upper
third of the cortex showed a surface-negative reaction. It was shown that
there is a failure of conduction of dendrites dromically; the speculation
is that decremental conduction must take place along apical dendrites
dromically, as practically all pyramidal cells have apical dendrites and
many dendrites from lower layers reach the surface.

Direct activation of the optic area gave the same results as obtained
from the suprasylvian gyrus, eliciting a surface-negative wave of 10-msec
duration. Stimulated below 0.5 mm, recording between surface and deep
electrodes, there occurred an initial positive spike superposed upon the
surface-positive phase of the diphasic response. With the stimulating
electrode at greater depth, a second spike followed the first, followed by a
third. The authors consider that the negative response to optic nerve
stimulation is assignable to conduction in apical dendrites. The surface-
positive phase is considered the activity of basal dendrites of pyramidal
cells and is nonconductive.

Clare and Bishop [9] consider apical dendrites to affect the cell body
electrotonically and the conduction downward to be decremental, local,
and not all-or-none. The conduction velocity in dendrites is slow:
Chang [8] reports 2 meters per second along the surface of the motor area.
In previous attempts to account for such slow wave phenomena, it was
noted that following a striate cortex response, the 5-per-second after-
discharge often broke up into bursts of shorter waves, the briefest of
which, approximately 15 msec in duration, corresponded to the duration
of the primary specific response.

For our purposes the interesting observation was made that since
apical dendrites exhibit no absolutely refractory period, a second response
initiated during the first sums with it. By repetitive stimulation a con-
tinuous negativity can be maintained. Thus modulation of stimulation
afferent to dendrites alone could induce potential wave forms of any
duration.

Clare and Bishop [10] showed that in the upper 0.3 mm of the cortex,
where there are few cell bodies and a high concentration of dendrites,
single electric shocks applied to the cortical surface give rise to surface-
negative waves of 15-msec duration. Below the cortical surface, the
electrode elicits a surface-positive wave succeeded by a surface-negative
wave. When cell bodies are reached, spikes are superposed on the surface

positively. At the base of the cortex, the record is the same as that of the cortical response to optic nerve stimulation.

The propagation of the dendritic impulse upward in the cortex is so slow that with a conduction distance of less than 2 mm, the surface of the cortex may remain positive for 5-10 msec before the dendritic impulse arrives to reverse the potential.

Following surface stimulation, the shallower of two recording electrodes becomes negative close to the surface, but the deeper lead fails to show any activity. Apical dendrites are capable of downward conduction under some conditions. When strychnine is applied to the optic cortex, its effect is to cause increased dendritic response to optic nerve stimulation, as well as sets of spontaneous waves (strychnine "spikes") assignable to the activity of dendrites.

A sequence of at least three prominent spikes indicated that three groups of cell bodies discharged successively. Recording at different depths within the cortex revealed that the cells involved are the pyramidal cells, and that the later groups to fire in the sequence are those that on the average lie shallow in the cortex.

Adrian's initial investigation [1] of the direct cortical response described two kinds: a "superficial response," surface negative and lasting from 10 to 20 msec, and a "deep response," surface positive, of the same duration or longer. The superficial response was thought to spread along either dendrites or Cajal cell fibers in the molecular layer. The deep response was thought to spread synaptically over neurons deeper in the cortex. The "dendritic response" spreads decrementally to a distance of 1 cm, which is a greater distance than the lateral maximum spread of dendrites—4 mm.

Ochs [43] found that a direct cortical response can be found on the far side of a cortical cut. This indicates that intracortical pathways are not necessary for the transmission of a response. As both stimulated site and responding site are intracortical, the linkage must be via a cortico-cortical neuron.

Ochs considers the response to be due to directly activated cortico-cortical fibers terminating on pyramidal cells in the responding area in two groups: an upper group on dendrites causing a surface negativity and a lower one on somas giving a surface positivity. The potentials are considered postsynaptic of the pyramidal cell.

Ochs and Suzuki [44] showed that the negative wave of the direct cortical response (DCR) is transmitted by neuronal elements present in

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the molecular layers. This was shown by a molecular layer preparation where the cortical layers below the uppermost layer and, in addition, the corticocortical fiber path below the cortex were cut. Such cuts did not block transmission of the negative wave. Another type of transmission link was shown after making cuts through the whole of the cortex. The responses transmitted were positive-negative DCRs with a longer latency and preceded by a small fast spike wave.

Landau *et al.* [31] analyzed evoked cortical potentials under the influence of polarizing currents. Although the major surface-positive wave is diminished by surface-positive polarization and increased by surface-negative polarization, the initial radiation spike is affected in the opposite way.

Using the isolated frog brain, Gerard and Libet [22, 35, 36] blocked synaptic conduction with nicotine but found electrical waves of regular shape still present in the cortex. Large caffeine waves, which travel at about 6 cm per second, were not abolished by nicotine and often not even by a complete transection of the entire cerebrum. They proposed that the cortical sheet behaves as does a polarized layer.

Morrell [39] showed that an auditory stimulus, which by itself evoked no response in rabbit cortex, produced a 0.5- to 1-mV steady potential (SP) shift if the auditory stimulus was followed by electrical stimulation of the center median nucleus.

Rusinov [50] reported the appearance of slow potential changes in the visual area when a light stimulus came to evoke a defense reflex. Rowland and Goldstone [49] demonstrated SP shifts of 100–200 mV to a 2-per-sec click or flash stimulation if the latter were reinforced by offering the animal food 2 sec after the sensory stimulus.

Bures [7] showed that the development of conditioned responses can be blocked by KCl-induced spreading depression in the cortex of the rat. Spreading depression was identified by the negative slow potential change, which is believed to reflect massive neuronal depolarization.

The data from strychnine studies should be viewed in the light that strychnine solution (10^{-2} – 10^{-3}) causes the cortex to become 200–300 mV negative to the ventricle or subcortical white matter. Negative aftermaths also follow spikes induced by surface application of curare.

O'Leary and Goldring [46] believe that all electrical phenomena can be gathered under the workings of the pyramidal cell, which presents a resting potential gradient along the length between its subsurface dendritic plexus and its soma. Be this as it may, the dipole offers great flexibility of analog measurement and of adaptation.

THE SPREAD OF ELECTRICAL ACTIVITY IN THE CORTEX

The case for electrotonic spread is weak. Hagiwara and Morita [23] have shown in the leech that two giant cells are connected by some electrotonic pathway. When a membrane potential is produced in one by a rectangular current pulse, there is developed synchronously a smaller potential in the other. Spike discharges are also induced. The conclusions of Gerard and Libet have already been mentioned.

The relation between EEG phenomena and dendritic activity finds some advocates; others see the relation between cellular discharge and the EEG. Creutzfeldt *et al.* [12] relate the origin of potential changes in different neuronal parts and the spread of potentials along the soma-dendritic membrane to the EEG.

They state that at the end of a high-frequency stimulation series in the specific thalamic nuclei, the EEG record may show a large positive swing that returns slowly, within 300–500 msec, to the base line. This positive swing is accompanied by a slow hyperpolarization of cellular membrane potentials that decreases with a similar time course.

A surface electrode located above the apical dendrites will “see” a potential that is the result of several mechanisms: a quick depolarization of the soma or near soma membrane (fast excitatory PSP after ventrolateral (VL) stimulation) will first be “seen” as a surface-positive potential and then change into a negative one, whereas a fast polarization (beginning of large synchronized inhibitory PSPs or repolarization after spike potentials) will be first “seen” as a surface-negative potential before the polarization changes the rest of the membrane.

The data of Suzuki and Ochs [53] support the authors’ suppositions. Weak surface stimulation produced a purely negative surface potential restricted to the superficial layers. Stimulation below 0.5 mm, however, produced a biphasic positive-negative response. This means, in the authors’ analysis, activation of apical dendrites in the former case, and of deep structures close to the soma in the latter case.

The primary surface negativity after VL stimulation is considered to be due mainly to the synchronous afferent volley; the primary excitatory PSP that appears on the crest of the primary positivity may add to the surface positivity if it is assumed that the specific afferents terminate mainly deep on the soma-dendritic membrane. The corticofugal spike discharge adds to the surface positivity. The primary negativity may be partly due to the electrotonic depolarization of the dendrites and is

enhanced by the secondary slow excitatory PSPs, which might even be due to the excitation of ascending recurrent collaterals.

The authors suggest that the beginning of the inhibitory PSP (fast transient localized on or near the soma) plays an important role in shaping the primary surface negativity during single stimuli. The primary surface negativity may be considered a mixture of transients from depolarization to polarization at or near the soma. The frequently observed late negative wave, especially during slow stimulation at 3-4 per second, can be explained by the slow tertiary excitatory PSP. In some cases the decay of the inhibitory PSP leading to relative negativity of the soma-dendritic membrane may lead to a surface negativity. The suggestion is that Adrian's [1] "superficial" response (the first negative potential) is correlated with excitatory responses in either the dendrites or soma-axon. The "deep" response (the ensuing positivity) corresponds to the inhibitory PSP.

CONCLUSION

Mathematical reasons have been given why transcortical arrival patterns should be studied if the methods of information storage in the brain are to be understood. The methods used are entirely topic-neutral and so do not represent a theory of brain functioning. Rather, their topic-neutrality compels a way of looking at the brain and implies a reason for experiments. The cortex, it is suggested, codes frequency in the time domain.

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