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13 Localization and Distribution of Function in the Brain

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INTRODUCTION

Throughout his research career, Karl Lashley remained puzzled by the relationship between brain, behavior, and experience. On one hand, his experiments showed the brain to be put together with exquisite anatomical precision, which was to some degree reflected in the separation by behavioral function of the several sensorimotor systems and even regional differences within the so-called association areas. On the other hand, results of other experiments and observations made it clear that engrams, memory traces, could not be localized and that perceptual images and motor patterns displayed constancies and equivalences for which it was difficult to conceive *any* permanent "wiring diagram." Lashley is best known for his continuing attention to these nonlocalizable aspects of brain function that he formalized in the laws of mass action and equipotentiality. But it should be remembered that these aspects were puzzling to Lashley in large part because he was so keenly aware of the anatomical precision of the connectivity that gave rise to nonlocal characteristics in function. Had the brain been shown to be essentially a randomly connected network (as was so often assumed by those then working in the field of artificial intelligence), the problem might not have loomed so insurmountable.

In this chapter I present data that fill out a theoretical frame that was proposed by Lashley as a possible resolution of the localization/nonlocalization puzzle. These data have accumulated during the quarter century that has intervened since his last paper. The data have been gathered without reference to the frame, and the frame itself was derived, not from brain-behavior studies, but from the

problems posed by morphogenesis during embryological development: Structural theories based on the principle of chemical gradients and resonances that "tune" specific locations in cytoplasm as inductors for organelles have been influential in embryology since before the turn of the century (see, e.g., Jacques Loeb, 1907; and Paul Weiss, 1939). In 1906, Goldscheider suggested that the structures of perception and memory might be similarly constructed by resonances among wave fronts created by sensory inputs in brain, especially cortical, tissue. In 1942, Lashley adopted this view as an alternative both to Köhler's field theory and to a localizationist view in which one percept or engram is matched to one neuron or neuron assembly. Lashley was never satisfied with this adoption because he could not envision the specific mechanisms that would give rise to resonant (and interfering) wave fronts in brain tissue and, equally important, how these, in turn, might be responsible for the structures that comprise perception and engram. He nonetheless held to the view that neither field nor localization (as, e.g., in the sophisticated development of Hebb, 1949) could account for the complex relationship between brain anatomy and phenomenal experience or could deal adequately with the encoding of memory.

Today a resonance theory *can* be detailed with high precision. Such a theory is thoroughly grounded in the structures and functions of the microanatomical connectivity of the nervous system and provides a mathematically sophisticated formulation of the relationship between anatomy and the images of perception, and also between anatomy and memory structure. Further, instantiations of this mathematical formulation in hardware have made possible in vitro observations that allow the exploration of the range and limits of the formulation. Finally, in vivo experimentation has provided a wealth of neurophysiological data that can be used to test the theory against alternative formulations.

THE NEURAL MICROSTRUCTURE

A fundamental observation concerning the structure and function of the nervous system is the fact that the relationship between locations that characterize peripheral receptors and effectors is reflected in the organization of the input to and output from the brain cortex. The peripheral relationship may become distorted through convergence in the pathways to synaptic way stations that are intercalated between periphery and cortex and by divergence from those way stations, but enough of the relationship is maintained to be recognizable as a mapping of periphery onto cortex. In order for such cortical mapping to be possible, signals must be transmitted from and to specific locations in the periphery by way of pathways of nerve axon systems in which impulses are generated and propagated.

A second fundamental fact about the organization of the nervous system is

that these peripheral-cortical axonal pathways are interlaced at every station—that is, in the periphery (e.g., in the retina), in central nuclei (e.g., in the lateral geniculate nucleus), and at the cortex (e.g., in the striate cortex)—with cells that possess either very short, fine-fibered axons or no axons at all. Such cells, called "local circuit neurons" (Rakic, 1976), are incapable of maintaining and transmitting action potentials, the nerve impulses, that convey signals over distances. Instead, these local circuit neurons are characterized by profusely branching dendrites that intersect with others from adjacent neurons. The electrical potential changes in such dendritic structures tend to be graded rather than impulsive, and when impulses are generated they are small in amplitude, decay rapidly, and thus are not conducted over any considerable distance (Rall, 1970; Shepherd, 1974). In sum, the potential changes in these dendritic arborizations are most often hyperpolarizing and thus inhibitory (e.g., Benevento, Creutzfeldt, & Kuhnt, 1972; Creutzfeldt, Kuhnt, & Benevento, 1974).

The interaction between vertical (i.e., periphery to cortex) axonal transmission pathways and the interlaced horizontal dendritic networks has been worked out in several sensory systems by extracellular recordings made from the separate neurons composing the axonal transmission pathways. In essence, the interaction leads to a center-surround organization when a discrete stimulus excites the neuron. A center-surround organization is one in which the spatial extent of the signals transmitted becomes enveloped in a penumbra of signals of opposite sign. This center-surround organization often displays the characteristics of a waveform in that several excitatory and inhibitory bands surround the center much as ripples are formed in a pond when the surface is excited by a pebble. Precise mathematical descriptions of such center-surround organizations have been given by Bekesy for the auditory and somatosensory systems (1959) and Hartline (1940) and by Rodieck and Stone (1965) for the visual system (see also the review of early formulations by Ratliff, 1961). The data obtained from the olfactory system appears somewhat more complicated (Shepherd, 1974), but mathematical treatment has been successfully achieved by Freeman (1975).

The results of these studies have in common the finding that whatever the nature of the inciting stimulus to receptor excitation, such excitation and its subsequent processing can be readily formulated in terms of a calculus describing the microstructure of a network of hyper- and depolarizations. This formulation shows that the principle of superposition applies to the local spatial interactions between excitation (depolarizations) and inhibition (hyperpolarizations). Superposition indicates that the system is linear within the ranges examined and that a waveform interpretation of the data is useful. This does not necessarily mean that the dendritic potentials actually make up discernible wave fronts; what it does mean, at the minimum, is that the center-surround data describe transfer functions by which a matrix of discrete polarizations is related to an exciting input, functions that can readily be treated by linear wave equations.

Holography

These mathematical treatments of the data obtained from recordings of potentials of single neurons in the nervous system are akin to those that spawned holography. In 1948 Dennis Gabor devised a mathematics showing that image reconstruction might attain greater resolution if, instead of intensity, the pattern of wave fronts generated on a photographic film by an exciting electron or photon were recorded. Gabor addressed his mathematics to electron microscopy, but in the early 1960s optical holography succeeded in implementing this image-processing technique in such a way that the properties of holograms became readily demonstrated (Leith & Upatnicks, 1965). The essential properties are as follows: (1) The holographic store is distributed; (2) vast amounts of storage can be concentrated in a small holographic space; (3) image reconstruction is three-dimensional, displaying constancies and parallax, and is highly textured; (4) images do not appear coextensive with the holographic store; they are projected away from the film surface; (5) the hologram has associative properties; when it is made by the reflected light of two objects, subsequent illumination of the stored hologram by light reflected from only one object will reconstruct a ghost image of the missing object.

These properties of holograms are so similar to the elusive properties that Lashley sought in brain tissue to explain perceptual imaging and engram encodings that the holographic process must be seriously considered as an explanatory device. In doing this, however, it must constantly be remembered that it is the mathematics of holography and brain function that needs to be compared and tested, not the optical holograms or computer instantiations of holography.

The essentials of this mathematics can best be summarized by reference to a particular form of holography—the construction of a Fourier hologram. The Fourier theorem states that any pattern, no matter how complex, can be decomposed into a set of component, completely regular, sine waves. The Fourier transform of an image is formed by encoding these component waveforms. Thus, in the transformed record, each point indicates the presence of a particular component waveform rather than the corresponding local intensity, as in an ordinary record. Take for comparison an ordinary photograph and a Fourier-transformed record. The ordinary photograph is made up of a mosaic of points of varying intensities, the intensity of each point corresponding to the intensity of a point of light reflected from a specific location on the object being photographed. In the Fourier-transformed record, by contrast, each point represents the amount of energy present in a waveform component of the entire array of light reflected from the object. The bandwidth of that component may vary; the resolving power of the transform is in part dependent on this bandwidth.

To make a (Fourier) hologram, two such Fourier-transformed records must be linearly superposed. Mathematically, this is performed by the transfer function in which one record is convolved with the other and then the resultant complex

conjugate stored. In essence, convolving consists of "adding" the waveforms together. Now each point in the record contains this "addition"—that is, the resultant of superposing the energy contained in two waveform components derived from the entire array of reflected light. A holographic record can be made by superposing the Fourier transform of the light reflected from two (or more) objects or by using the transform of a nonreflected reference. When two or more objects are used, the light reflected from each serves as a reference for the other(s). This accounts for the property of associative recall already noted. In addition, since parts of objects as well as whole objects serve as sources of reflection and thus as references for other parts, constancies are generated when images are (re)constructed. Constancies are therefore the result of the fact that the transformed "view" of any part of the objects acts as a reference for every other part.

It is these enfolding properties of holograms that make them so counterintuitive. Within the holographic domain, geometry as we sense it disappears and is replaced by an order in which the whole becomes enfolded and distributed into every part—thus the term *hologram*—but from each part, the whole can again be reconstituted. This is due to another property of the Fourier theorem: Applying the identical transform inverts the waveform domain back into the image! The process (the Fourier transfer function) that converts images into waveforms can therefore also accomplish the inverse and convert waveforms into images.

This parsimony in processing raises the question of utility. If image and waveform domain are so readily transformed into each other, why bother? The answer to this question is that correlations are much simpler to accomplish in the waveform domain; they essentially entail superposition, addition. That is why the Fast Fourier Transform (FFT) has proved so useful in computer programming—for instance, when image reconstruction by CAT scan in X-ray tomography is desired. It is this power of the Fourier domain that the brain can exploit.

In the introduction it was noted that there really have been only three classes of neural mechanisms proposed to explain the properties of perception. The three may, for convenience, be labeled: field theoretic, feature correspondent, and holographic. A review of currently available data regarding each of these classes follows:

DEFINITION AND EVIDENCE: FIELD THEORY

Wolfgang Köhler proposed that direct current (DC) fields were set up in the brain cortex by sensory stimulation and that these fields were isomorphic with—that is, had the same shape as—the phenomenally perceived stimulus. Köhler showed that, in fact, sensory stimulation did result in DC shifts (Köhler & Wegener, 1955), and in our laboratory we showed that such shifts were accompanied by

desynchronization of the electrocorticogram (Gumnit, 1960). However, several experiments that throw doubt on the relationship between such shifts and perceptual performance were performed by Lashley, Sperry, and Pribram. In these experiments gold foil was placed over the surface of the cortex (Lashley, Chow, & Semmes, 1951); the cortex crosshatched the mica insulating strips inserted (Sperry, Miner, & Myers, 1955); and aluminum hydroxide cream injected in minute amounts into the cortex to produce gross abnormalities (Kraft, Obrist, & Pribram, 1960; Pribram, 1951; Stamm & Knight, 1963; Stamm & Pribram, 1960, 1961). See Figs. 13.1 and 13.2.

In none of these experiments did the animals show any change in their ability to discriminate among cues; gross alteration of the cortical DC field was not accompanied by any gross change in perceptual performance. These findings take additional meaning from the fact that the aluminum hydroxide cream implantation produced a fivefold retardation of learning and that imposing direct currents across cortex impairs (when cathodal) and enhances (when anodal from surface to depth) learning (Stamm & Rosen, 1972). Direct current fields are thus shown capable of biasing learning rate; and at the same time such fields seem to be unrelated to the structuring of percepts.

DEFINITION AND EVIDENCE: FEATURE CORRESPONDENCE THEORY

Field theory and feature correspondence concepts either explicitly or implicitly imply a brain-perceptual isomorphism. In the case of feature correspondence, isomorphism is thought to be established when a particular cell or cell assembly responds uniquely to a feature of the phenomenally experienced image; that is, a
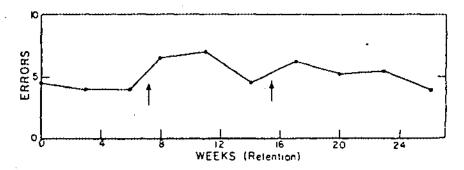

FIG. 13.1.   Record of *retention* of a visual discrimination performance (+ vs. □) *before and after* implantation of aluminum hydroxide cream (first arrow) in primary visual cortex and the subsequent development of electrical seizure patterns (second arrow). Note that no deficit has occurred. The same result was obtained when the implantations were performed in inferotemporal, parietal, and frontal cortex.
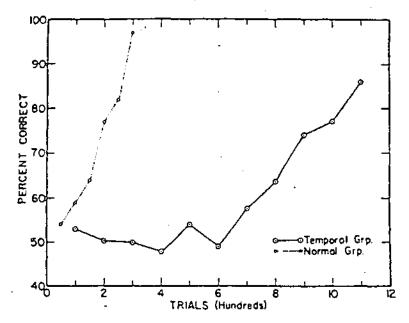
FIG. 13.2. Record of *learning* the same visual discrimination *after* the development of electrical seizure patterns. Note the prolongation of the "period of stationarity"—the flat part of the learning curve prior to its rise.

feature of the imaged object is detected. It is then assumed that the organism's response to the total object is composed by convergence of the outputs from a set of feature selective elements onto a higher-level neuroperceptual unit—a "pontifical" cell or cell assembly (Hebb, 1949) composed of like elements ("cardinal" cells; Barlow, 1972).

In the late 1950s and early 1960s, Hubel and Wiesel (e.g., 1962) discovered that the center-surround organization of the dendritic microstructure of cells (their receptive fields) in the peripheral visual system became elongated at the cortex. Further, they presented indirect evidence that this enlongation might be due to convergence onto the cortical cells of fibers from cells with center-surround receptive fields. Their demonstration emphasized that cells in the visual cortex responded best to bars of light presented in specific orientations. It was easy to generalize these findings into a Euclidean geometry of brain function—points to oriented lines, to curves and planes, to complex figures of all sorts. The search for feature detectors was on.

The results of the search were by no means meager. For instance, one cell in monkey cortex was found to respond maximally to a monkey's hand (Gross, Bender, & Rocha-Miranda, 1969); another cell was shown to respond best when a stimulus was repeated six times (Groves & Thompson, 1970); still others appeared to be activated largely by vocalizations of their own species (Maurus & Ploog, 1971).

Such specific selectivities can be misleading, however, if they are interpreted as showing that the cells in question function as feature detectors. To serve as a detector, the output of the cell must uniquely reflect the input feature, and this is only occasionally the case. More often a cell responds to a variety of feature triggers. In the visual system, for example, a cell that responds selectively to a bar in a specific orientation will modify that response with a change in luminance, with the direction of movement of that bar and the velocity of such movement (Pribram, Lassonde, & Ptito, 1981; Spinelli, Pribram, & Bridgeman, 1970). Furthermore, that very same cell may show a differential response to color and even be tuned to a specific auditory frequency (Spinelli, Starr, & Barrett, 1968). Finally, the number of bars, their widths, and spacings also influence the response of the cell, which suggests that "stripes" rather than "bars" form the critical stimulus dimension for their orientation selectivity (DeValois, Albrecht, & Thorell, 1978; Glezer, Ivanoff, & Tscherbach, 1973; Movshon, Thompson, & Tolhurst, 1978; Pollen & Taylor, 1974; Schiller, Finlay, & Volman, 1976). More of this in a moment.

Findings such as these, and they are equally true of other systems (e.g., see Evans, 1966, for cells in the auditory cortex), make untenable the view that these cortical cells are simple detectors of features. Nonetheless, each cell is selectively responsive to a variety of highly specific stimulus dimensions, the "feature triggers." Some of these dimensions appear to be mapped into recognizable patterns in adjacent cells; for example, orientation selectivity has been related to the columnar structure of cortex (Hubel & Wiesel, 1977), and selectivity to bar width and spacing has been reported to be a function of cortical layers (Maffei & Fiorentini, 1973). Other stimulus dimensions, such as the tuning of cells in the visual cortex to auditory frequencies, are distributed without any apparent regularity over much wider expanses of cortex. These distributed forms of organization become especially evident when recordings are made from groups of neurons when problem solving is being investigated (Gross, Bender, & Gerstein, 1979; John, Bartlett, Shimokochi, & Kleinman, 1973; Pribram, Spinelli, & Kamback, 1967).

The view obtained from the results of these studies is that rather than feature detection by single neurons, some sort of feature selection is effected by neuron networks. Some features seem to relate a structured network response; these same features and others may, however, under other conditions, elicit a more widely dispersed response. Furthermore, features are not always what they initially seem to be, and little attempt has yet been made to classify features systematically in such a way as to relate their phenomenal to their neural response characteristics. An exception to this has been the experiments of DeValois on the color system of primates, which can serve as a model for studies of feature analysis by neural networks (DeValois, 1960).

Feature selection by neural networks may be considered a form of feature correspondence. As noted in the previous paragraphs, however, the nature of the

features responded to by a neural network property is often considerably different from their perceived phenomenal nature. Perception is only under very restricted circumstances limited to bars of certain width and spacings, or to a limited range of tonal frequency. With the exceptions of color and species-specific vocalizations, the phenomenal-neural correspondence seems at best strained in view of the multiple selectivities of most cells and the fact that these multiple selectivities fail, for the most part, in any cell or cell assembly to map coherently phenomenally experienced psychophysical characteristics. In the case of color and that of species-specific vocalizations, however, such mappings show that feature correspondence can be abstracted from the multiple selectivities of neurons and neuron assemblies. The question of how this abstraction is accomplished remains.

DEFINITION AND EVIDENCE: HOLOGRAPHIC THEORY

One possibility for abstraction lies in the powerful correlational facility of holographic transformations. The idea that the neural network performs holographic transformations on sensory input must be clearly distinguished from both field theory and feature correspondence theory. In a holographic transformation, the various stimulus dimensions become enfolded into every part of the transform domain; a set of neural signals is transformed, and transfer functions, often readily dealt with by waveform mathematics, describe the transformation. However, statistical mathematical procedures have proved equally useful, and a combination of waveform and statistical approaches has been found to be most powerful (e.g., see Julesz, 1971, for the visual system; Flanagan, 1972, for the auditory system). Transformation of a set of signals into an enfolded order is very different from simply generating a DC field in cortex by the arrival of neural signals. Holographic theory is therefore not a field theory, although it is related to field theory in that wave mechanical descriptions are relevant and holistic, rather than point-to-point, analysis is emphasized.

Holographic transformations also resemble feature correspondence theory to some extent, although once again they can be sharply distinguished. The similarity comes from the fact that, as already noted, performing a transform a second time will reinstate the image (with all its features) from the transform domain. The difference between holographic transformation and feature correspondence is that the transform domain is recognized and, in the strongest form of the theory, is recognized as *the* domain in which neural networks operate. The finding of multiple feature selectivities of most brain cells and cell assemblies is compatible with such a view. As we shall see, however, this strongest form of the theory does not account for all the available data, thus necessitating some specifiable modifications. In either the strongest or modified version, *features are generated, constructed, when the encoded transform domain is addressed*

through additional sensory input or by "reference" from other neural processes such as sensitivities to internally produced stimulation.

There is thus no brain-perceptual isomorphism in the holographic theory as there is in the field and the feature correspondence theories. Rather, phenomenal experience is generated when sensory or internally derived inputs activate a holographic process or store. There is therefore no necessary identity between brain structure and phenomenal experience, just as in an optical hologram there is no identity between the structure of the photographic film and the image produced when that film is properly illuminated. Even a functional identity between phenomenal experience and brain processes becomes suspect if this means ignoring the input to senses from the world outside the organism and the input to other receptors from within the body.

What, then, are the transfer functions that describe the transformations of sensory and bodily inputs into a brain holographic process? And what are the limits of explanatory power of such transfer functions with respect to the data at hand? The first suggestion that brain processing might involve a Fourier analysis was made a century ago for the auditory system by Ohm, the same Ohm who formulated Ohm's law of electricity. This suggestion was adopted by Herman von Helmholtz, who performed a series of experiments that led to the place theory of hearing—essentially a view of the cochlea as a piano keyboard whose keys, when struck by acoustic waves, would initiate nerve impulses to the brain, where resonant neurons were activated. This view was modified in this century by Georg v. Bekesy (1959), whose experiments showed the cochlea and peripheral neurosensory mechanism to operate more like a stringed instrument, sensitive to superposition of acoustic waveforms. Good evidence has accrued to the effect that a major effect of initial auditory processing can be described in terms of a Fourier transform of the acoustic input (Evans, 1974).

Bekesy (1959) then went on to make a large-scale model of the cochlea composed of a set of five vibrators arranged in a row. The model could be placed on the forearm and the phase of the vibrators adjusted. At particular adjustments the phenomenal perception produced by the model was that of a point source of stimulation. When two such model "cochleas" were properly adjusted and applied, one to each forearm, the point source appeared, at first, to jump alternately from one forearm to the other, then suddenly to stabilize in the space just forward and between the two arms. In short, the stimulus was "projected" away from the stimulating source and receptive surface into the external world.

Both macro- and microelectrode studies have shown that multiple vibratory stimulations of the skin also evoke unitary responses in cortex (Dewson, 1964; Lynch, 1971). The electrical potentials evoked fail, therefore, to reflect the actual physical dimensions of the stimulus. Instead, they reflect the fact that the sensory process has transformed the physical stimulus according to some transfer functions. Bekesy noted that sensory inhibition, effected by lateral inhibitory dendritic networks of neurons, might be the responsible agent in the transformations.

Evidence is therefore at hand to indicate that the input to the ear and skin becomes transformed into neural patterns that can be described by sets of convolutional integrals of the type that Gabor (1969) has suggested as stages in achieving a fully developed Fourier holographic process. In the olfactory (Freeman, 1975) and visual systems, as well, such transformations have been described by Rodieck (1965) as convolving input with retinal receptive field properties as recorded from units in the optic nerve. See Figures 13-3a and 13-3b.

The manner in which such a stepwise process occurs is best worked out for the visual system. A second step in the process occurs at the lateral geniculate nucleus, where each geniculate cell acts as a peephole, "viewing" a part of the retinal mosaic. This is due to the fact that each geniculate cell has converging
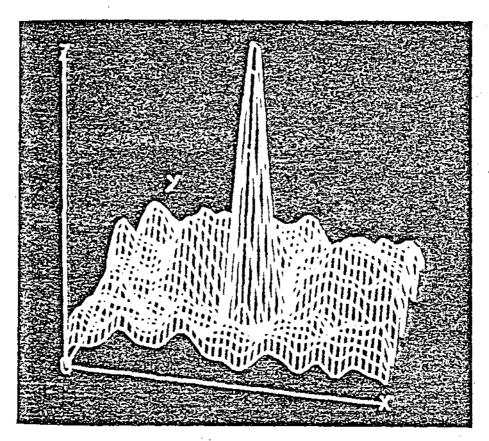

FIG. 13.3a.   Three-dimensional computer-generated reconstruction of the receptive field of a neuron in the lateral geniculate nucleus. Note the "Mexican hat" configuration where the height of the crown (z axis) reflects the number of impulses generated by the cell in response to a moving light displayed over the reach of the x-y plane represented as the brim of the hat. A similar, though not as completely regular, receptive field configuration is found when cells in the optic nerve are plotted.
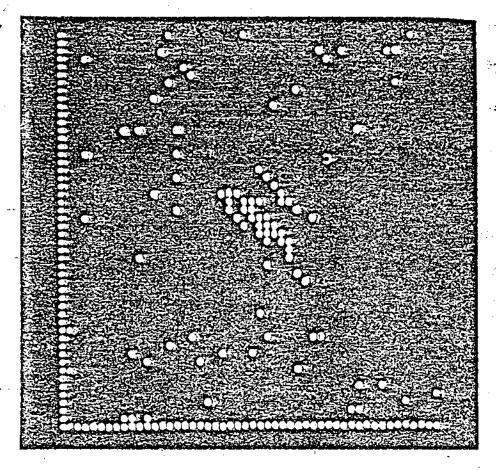
FIG. 13.3b.   Cross section of a receptive field of a cell in the visual cortex. Now the three-dimensional reconstruction would resemble a homburg rather than a Mexican hat because the receptive field has become elongated. Note the sidebands (inhibitory and excitatory) which suggest that the cell's best response might not be produced by a single line but rather by multiple lines (gratings). Note also the orientation selectivity of the receptive field which is a consequence of its elongation.

upon it some 10,000 optic nerve fibers originating in the ganglion cells of the retina. The receptive field of the geniculate neuron is composed of a center surrounded by concentric rings, each consecutive ring of sharply diminishing intensity and of sign opposite that of its neighbors (Hammond, 1972). This type of organization is characteristic of units composing a near-field Fresnel hologram (Pribram, Nuwer, & Baron, 1974).

At the cortex the transformation into the Fourier domain becomes complete. Beginning with the work of Campbell and Robson (1968); Pollen, Lee, and Taylor (1971); Maffei and Fiorentini (1973); and Glezer, Ivanoff, and Tscher-
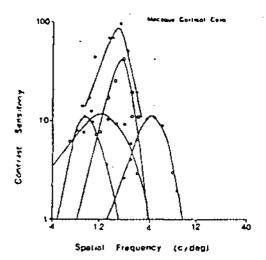
FIG. 13.4.   Graph of tuning curves of five individual adjacent neurons in the vivisual cortex of a rhesus macaque monkey exposed to a range of gratings of various spatial frequencies (widths and spacings). These tuning curves were obtained at threshold (when the grating contrast was just sufficient to elicit a constant response). Results such as these are interpreted to indicate that the visual system performs a spectral analysis on the patterns of light and dark distributed across space that make up the visual scene. In a very basic sense, therefore, the visual system can be said to operate somewhat like the auditory and somatosensory systems where spectral analyses of sound patterns and vibratory patterns are performed. (From ``Cortical Cells: Bar and Edge Detectors, or Spatial Frequency Filters?'' by R. L. De Valois, D. G. Albrecht, & L. G. Thorell. In S. J. Cool & E. L. Smith (Eds.), *Frontiers in Visual Science*. New York: Springer-Verlag, 1978, p. 548.)

bach (1973), investigators using gratings as stimuli (e.g., Pribram et al., 1981; Schiller et al., 1976) have repeatedly confirmed that the cells in visual cortex are selectively tuned to a limited bandwidth of spatial frequency of approximately an octave (½ to 1½ octaves). The spatial frequency (or wave number) of a grating reflects the widths and spacings of the bars making up the grating. When such widths and spacings are narrow, the spatial frequency is high; when widths and spacings are broad, the spatial frequency is low. See Fig. 4. Ordinarily the term *frequency* implies a temporal dimension; in the case of spatial frequency, this temporal dimension can be evoked by successively scanning across the grating (e.g., by walking across the path of illumination of a projection of a slide of such a grating). Conversion to the temporal dimension is, however, not necessary. The grating is a filter whose characteristics can be expressed either as spatial or temporal or both.

The difference between a feature correspondence and a holographic transform approach has recently been brought into sharp focus by tests of hypotheses devised to contrast the two. In the visual cortex the center-surround orgainzation
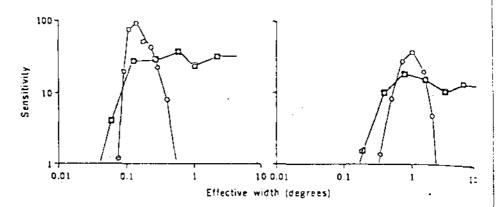
FIG. 13.5.   Selectivity functions for bars (squares) and gratings (circles) of two
striate neurons: (Left) macaque monkey simple cell; (Right) cat complex cell.
There is little selectivity for bars and essentially no drop in the sensitivity as bar
width increases. In contrast, the cells are sensitive to only a limited range of spatial
frequencies and are therefore selective for gratings. (From "Visual Cortical
Neurons: Are Bars or Gratings the Optimal Stimuli?" by D. G. Albrecht, R. L. De
Valois, & L. G. Thorell. *Science*, 1980, *207*, 88.)

of visual receptive fields that obtains in the geniculate nucleus gives way to an
elongated receptive field with sidebands of opposite sign. In their original dis-
covery of this change, Hubel and Wiesel (1959) emphasized that lines presented
at specific orientations were the most effective stimuli to activate units with such
receptive fields. They also presented evidence that the elongated fields might be
composed by convergence from geniculate cells with spotlike concentric fields.
The feature hierarchy Euclidean view of feature correspondence grew naturally
from these early results and their interpretation. More recently it has been shown,
as noted earlier, that these cells with orientation-selective, elongated receptive
fields also vary their output with changes in luminance, movement of lines across
the receptive field, the direction of that movement, its velocity, and the number
and spacings of such lines (gratings of various spatial frequencies). In addition, it
has been shown that changes in the width of single lines have little effect on the
responses of these cells (DeValois et al., 1978; Henry & Bishop, 1971). See Fig.
5. Finally, in a direct confrontation of feature correspondence theory, DeValois,
DeValois, and Yund (1979) showed that the complex stimulus such as a plaid or
checkerboard had to be rotated in such a way that the axes of the Fourier
transform, rather than the edges per se of the stimulus pattern, would engage the
orientation selectivity of the cell. Every cell examined responded maximally
when the plaid or checkerboard pattern was rolated to the degree and minute of
visual angle predicted by the Fourier (and no other) transform of the pattern as
determined by computer (using the Fast Fourier Transform—FFT). See Fig. 6.
the cortical cells were thus shown to respond holistically (i.e., to the Fourier
transform of the entire pattern) rather than feature by feature. In another elegant
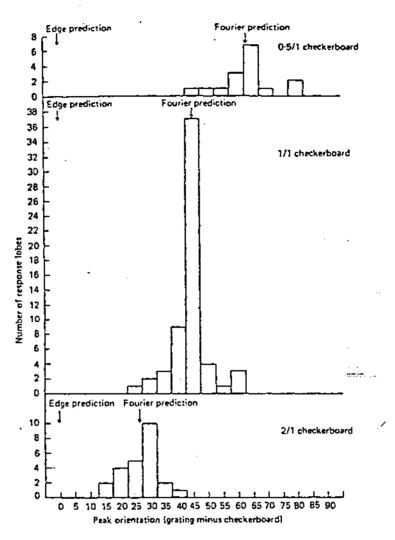
FIG. 13.6. Histograms of the differences between optimum orientations for gratings and for the various checkerboards. Our entire cell sample from cat and monkey is included. The arrows indicate the difference predicted on the basis of the orientation of the edges of the checks in the patterns (edge precipitation) and the difference predicted on the basis of the orientations of the patterns' fundamental Fourier components (Fourier prediction). The mean orientation shifts, compared with the Fourier prediction, for each of these patterns are as follows: 2/1 checkerboard 26.9° (Fourier prediction 26.6°); 1/1 checkerboard 44.3° (predicted 45°); 0.5/1 checkerboard 63.9 (predicted 63.4°). (From "Responses of Striate Cortex Cells to Grating and Checkerboard Patterns" by K. K. De Valois, R. L. De Valois, & E. W. Yund, 1979.)

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experiment, Movshon et al. (1978) has detailed the complementarity between the spatial profile of the receptive fields of these cells and the Fourier transform of the stimulus giving rise to that profile. That cells in the visual cortex encode in the Fourier domain is thus an established fact.

These findings do not, however, mean that the visual system performs a global Fourier transform on the input to the retina (see also Julesz & Caelli, 1979). The moving retina decomposes the image produced by the lens of the eye into a "Mexican hat" receptive field organization that can be described as convolving retinal organization with sensory input (Rodieck, 1965). But the spread function, as such convolutions are called, does not encompass the entire retina; rather, it is limited to the receptive field of a retinal ganglion cell. Similarly at the cortex, full-fledged encoding in the Fourier domain is restricted to the receptive field of the cortical neuron. This patchy organization of the Fourier domain (Robson, 1975) does not impair its holographic characteristics. The technique of patching or stripping together Fourier-transformed images has been utilized in radio astronomy by Bracewell (1965) to cover expanses that cannot be viewed with any single telescopic exposure. The technique has been further developed by Ross (see Leith, 1976) into a multiplex hologram to produce three-dimensional *moving* images when the inverse transform is effected. Movement is produced when the Fourier-encoded strips capture slightly different images—for instance, when adjacent frames of a motion picture are used as the image base for the Fourier transformation.

In the multiplex hologram, spatial relationships among the Fourier-transformed patches or strips become important. Thus, this form of hologram is a hybrid from which movement can be derived. Recall that a simple hologram is characterized by translational *invariance;* that is, the image that results from inversion is essentially stationary and appears the same from different vantages except for changes in perspective (object constancy). The hybrid multiplex form has therefore considerable advantage for moving organisms.

Suggestions have been made that the orientation-selective, elongated receptive fields that compose the visual cortex are arranged in Fibonacci spirals along the axes of cortical columns (Schwartz, 1977). Such an arrangement of the spatial relationships among the Fourier-transformed patches of receptive field would enhance still further the power of the transform domain in that three-dimensional movement (and therefore the resultant space–time relationship) would be readily explained. At present evidence for this sort of helical arrangement is not firmly established; on the other hand, the suggestion is consonant with what is already known.

Perhaps more important is the well-established fact that there is a topographic correspondence between receptor surface and its cortical representation in cortical columns (Edelman & Mountcastle, 1978; Hubel & Wiesel, 1977). Thus, the holographic patches have an overall arrangement that corresponds to the sensory surface of the organism. Therefore in coarse grain (i.e., between receptive

fields), the sensory mechanism is represented; in fine grain (i.e., within receptive fields), a holographic representation becomes manifest. The situation is not altogether different from that in physics. At a certain grain of analysis—the ordinary—the principles of mechanics operate. At a finer grain (where electrons and photons come into focus) quantum principles come into operation with their complementarities, such as between locus and moment and between wave and particle.

David Bohm (1971, 1973) has pointed out that we can begin to conceptualize these complementarities in quantum physics if we realize that concepts about particles devolve from the use of lenses. Lenses built into the objectives of our telescopes (to deal with photons) and microscopes (to deal with photons and electrons) objectify by *focusing* electromagnetic energy. The result is that we experience objects, particles, things. If, on the other hand, we should peer at the universe through gratings of various spatial frequencies, Bohm suggests, we would experience a holographlike universe of interfering waveforms (which, in physics, is what results in double-slit experiments and the like).

Take this formulation and apply it to the brain. The ordinary coarse-grained representation of receptor surfaces provides a lenslike mechanism for processing input. With this mechanism we can "make sense" of the universe in terms of images of objects because we sense it through lenses and lenslike structures (the cochlea, the skin, as in Bekesy's experiments). But at the same time, a finer-grained—quantum level—process operates to provide a different sort of order, a holographlike, distributed, and enfolded order superior in correlating and in storing and in computing. Is this order best described in wave or in statistical terms or both? The Fourier approach has been extremely successful; but are we in the brain sciences about where physics was when Schrödinger proposed his encompassing wave equation?

COUNTERPOINT

The multiplex hybrid nature of cortical holographic organization serves as a warning that any simply conceived "global-Fourier-transform-of-input-into-cortical-organization" is untenable. Furthermore, the multiple selectivities of cortical cells in the visual (Morrell, 1972; Spinelli, Pribram, & Bridgeman, 1970; Spinelli, Starr, & Barrett, 1968), auditory (e.g., Evans, 1974), and somatosensorimotor (e.g., Bach-y-Rita, 1972) projection areas clearly indicate that such cells serve as nodes in neural networks in which the Fourier transform is only one, albeit an important, process. Several attempts have been made therefore to characterize more fully such cortical networks in terms of their essential properties. Thus, Longuet-Higgins (see Willshaw, Buneman, & Longuet-Higgins, 1969) proposed an associative-net model, and Leon Cooper (1973) has developed this model into a self-organizing distributed net whose mathematical

description contains as a special case the Fourier transform hologram. Julesz (1971), Uttal (1978), Borsellino and Poggio (1973), Poggio and Torre (in press), and (in our laboratories) Sutter (1976) have taken a more statistical stance. Thus, for instance, Uttal emphasizes spatial autocorrelation functions, whereas Poggio and Sutter rely on Wiener polynomial expansions. In addition, Poggio treats the dendritic potential microstructure in terms of the Volterra solution of cable equations. His carefully worked out proposal includes a stage of Fourier analysis and another in which the Laplace transform occurs. David Marr, Tomaso Poggio, and Whitman Richards (Marr, 1976a, 1976b; Marr & Poggio, 1977; Richards, 1977; Richards & Polit, 1974) are developing a model based on repetitive convolving of Laplacians of a Gaussian distribution. E. Roy John speaks of "hyperneurons" constituted of the distributed system of graded potentials he records from the brains of problem-solving animals. Such organizations have been described in terms of Lie groups by Hoffman (1970), vector matrices by Stuart, Takahashi, and Umezawa (1978), and tensor matrices by Finkelstein (1976) in which the tensors represent multidimensional Fourier transforms. Finally, Edelman & Mouuncastle (1978) have proposed a degenerative group model, also based on an essentially random connectivity.

On looking over these various proposals, one finds commonalities and distinctions that can be summarized as problem areas that need further inquiry: (1) To what extent is the idealization warranted that the brain cortical connectivity is essentially random? This issue was discussed earlier in this chapter. In addition, the models proposed by Hoffman and by Poggio clearly opt for nonrandomness, whereas the others are either explicitly or implicitly based on the assumption that an idealized random connectivity is not too far from actuality. (2) To what extent can brain systems be treated with linear (and reversible) equations, and to what extent must nonlinearities be introduced to explain the available data? Good evidence is at hand that the primary sensory systems (as discussed throughout this chapter) and primary motor systems (see, e.g., Granit, 1970) are essentially linear in most of their overall operations despite many local nonlinearities. Overall nonlinearities are apparently introduced into the system when decisions have to be made—decisions involved in discriminating between inputs, in performing this rather than that action. Decisional operations have been shown to be local functions of the intrinsic (association) systems of the brain (Pribram, 1972a, 1972b, 1974, 1977a, 1977b). Thus, the question is raised as to how these nonlinearities relate to the essentially linear sensorimotor functions. (3) Nonlinear decisional operators can enter the system in two ways: They can be imposed by a parallel corticifugal process upon the sensorimotor systems (Christensen & Pribram, 1979; Pribram, 1971a, 1974; Pribram, Spinelli, & Reitz, 1969; Ungerleider & Pribram, 1977), or the decisions can be attained by a serial processing hierarchical abstraction of the relevant variables (see, e.g., Gross, 1973; Mishkin, 1973; Weiskrantz, 1974). It is, of course, also possible that the hierarchical serial process operates during learning (as, e.g., suggested by Hebb,

1949) while parallel corticifugal operators determine momentary perceptions and performances. (4) These nonlinear decisional operators are localized to one or another brain system. Two major classes of such operators can be distinguished. One is a set of sensory-specific processes that involve the posterior cerebral convexity (inferotemporal cortex for vision; superior temporal for audition; anterior-temporal for taste; posterior parietal for somesthesis). In addition, a set of higher-order, executive—that is, context-sensitive—processes has been identified to involve the frontolimbic portions of the forebrain (see, e.g., reviews by Pribram, 1954, 1969, 1973).

When these decisional processes operate on the distributed memory store, they re-member an input that had on earlier occasions become dismembered. The sensory-specific operators deal with recognition and with the processing of referentially meaningful information. The frontal lobe executive operators deal with recall and with the pragmatics of processing context-sensitive, episode-related instances (for review, see, e.g., Pribram, 1971a, 1977a).

The persistent puzzle that brain functions appear to be both localized and distributed is thus resolved. Memory storage is shown to be distributed; decisional operators involved in coding and retrieval are localized. These operators can be conceived as separate brain systems, genetically inherent in their function but dependent on sensory input from the environment to trigger and shape their development (see, e.g., Chomsky, 1980; Pribram, 1971b). In short, there are "boxes in the brain," each "box" corresponding to a "faculty of mind." But these "boxes" operate on a distributed matrix that is nonlocal and therefore available to all.

Perhaps the easiest way to conceptualize this "model" of brain function is in terms of states and operators on those states. At present it appears reasonable to continue to search for linearities in the state descriptions of sensory perception, highly practiced skilled action, and memory storage processes. The greater part of this manuscript has been devoted to detailing problems inherent in such state descriptions. Only in this final section have we briefly dealt with the abundant evidence that these states come under the control of localized nonlinear operators whenever discriminate decisions (e.g., recognition) or selective (planned) actions are involved. Whether these nonlinearities are abstracted serially and hierarchically from the states or whether they are imposed corticifugally by a parallel process—or both—continues to be an active area of investigation.

CONCLUSION

There is a considerable intellectual distance between Lashley's despair in finding a localized engram in 1950 and the richness of data and theory on cerebral localization and distribution in 1980. To his credit, Lashley recognized the problem and specified it in sufficient detail so the generation of investigators

standing on his shoulders could deal effectively with it. That so much progress has been made reflects the support given by society to the brain and behavioral sciences during this 30-year period. Should this support continue, the issue of localization-distribution that has mobilized such differing views over the past two centuries may yet be resolved before the end of the twentieth.

REFERENCES

Albrecht, D. G., de Valois, R. L. & Thorell, L. G. Visual cortical neurons: are bars or gratings the optimal stimuli? *Science*, 1980, *207*, 88-90.

Bach-Y-Rita; P. *Brain mechanisms in sensory substitution*. New York: Academic Press, 1972.

Barlow, H. B. Single units and sensation: A neuron doctrine for perceptual psychology? *Perception*, 1972, *1*, 371-394.

Bekesy, G. v. Synchronism of neural discharges and their demultiplication in pitch perception on the skin and in hearing. *Journal of the Acoustical Society of America*, 1959, *31*, 338-349.

Benevento, L. A., Creutzfeldt, O. D., & Kuhnt, U. Significance of intracortical inhibition in the visual cortex: Data and model. *Nature New Biology*, 1972, *238*, 124-126.

Bohm, D. Quantum theory as an indication of a new order in physics. Part A. The development of new orders as shown through the history of physics. *Foundations of Physics*, 1971, *1*(4), 359-381.

Bohm, D. Quantum theory as an indication of a new order in physics. Part B. Implicate and explicate order in physial law. *Foundations of Physics*, 1973, *3*(2), 139-168.

Borsellino, A., & Poggio, T. Convolution and correlation algebras. *Kybernetik*, 1973, *13*, 113-122.

Bracewell, R. *The Fourier transform and its applications*. New York: McGraw-Hill, 1965.

Campbell, F. W., & Robson, J. G. Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, 1968, *197*, 551-566.

Chomsky, N. *Rules and representations*. New York: Columbia University Press, 1980.

Christensen, C. A., & Pribram, K. H. The effect of inferotemporal or foveal prestriate ablation on serial reversal learning in monkeys. *Neuropsychologia*, 1979, *17*(1), 1-10.

Cooper, L. N. A possible organization of animal memory and learning. In F. Lindquist & S. Lindquist (Eds.), *Proceedings of the Nobel symposium on collective properties of physical systems*. New York: Academic Press, 1973.

Creutzfeldt, O.D., Kuhnt, U., & Benevento, L. A. An intracellular analysis of visual cortical neurones to moving stimuli: Responses in a cooperative neuronal network. *Experimental Brain Research*, 1974, *21*, 251-272.

DeValois K. K., DeValois, R. L. & Yund, E. W. Responses of striate cortex cells to grating and checkerboard patterns. *Journal of Physiology*, 1979, *291*, 483-505.

DeValois, R. L. Color vision mechanisms in monkey. *Journal of General Physiology*, 1960, *43*, 115-128.

DeValois, R. L., Albrecht, D. G., — Thorell, L. G. Cortical cells: Line and edge detectors, or spatial frequency filters? In S. J. Cool and E. L. Smith (Eds.), *Frontiers in visual science*. New York: Springer-Verlag, 1978.

Dewson, J. H., III. Cortical responses to patterns of two-point cutaneous stimulation. *Journal of Comparative and Physiological Psychology*, 1964, *58*, 387-389.

Edelman, G. M., & Mountcastle, V. B. *The mindful brain*. Cambridge, Mass.: MIT Press, 1978.

Evans, D. C. Computer logic and memory. *Scientific American*, 1966, *215*, 74-85.

Evans, E. F. Neural processes for the detection of acoustic patterns and for sound localization. In F.

O. Schmitt & F. G. Worden (Eds.), *The neurosciences third study program*. Cambridge, Mass.: MIT Press, 1974.

Finkelstein, D. Classical and quantum probability and set theory. In Harper W. L. & Hooker C. A. (Eds.), *Foundations of probability theory, statistical inference, and statistical theories of science* (Vol. III). Dordrecht, Holland: D. Reidel, 1976.

Flanagan, J. L. *Speech analysis, synthesis and perception*. Berlin: Springer-Verlag, 1972.

Freeman, W. *Mass action in the nervous system*. New York: Academic Press, 1975.

Gabor, D. A new microscopic principle. *Nature*, 1948, *161*, 777–778.

Gabor, D. Information processing with coherent light. *Optica. Acta*, 1969, *16*, 519–533.

Glezer, V. D., Ivanoff, V. A., & Tscherbach, T. A. Investigation of complex and hypercomplex receptive fields of visual cortex of the cat as spatial frequency filters. *Vision Research*, 1973, *13*, 1875–1904.

Goldscheider, A. Uber die materiellen veranderungen bei der assoziationsbildung. *Neurologische Zentralblatt.*, 1906, *25*, 146.

Granit, R. *The basis of motor control*. New York: Academic Press, 1970.

Gross, C. G. Inferotemporal cortex and vision. In E. Stellas & J. M. Sprague (Eds.), *Progress in physiological psychology*. New York: Academic Press, 1973.

Gross, C. G., Bender, D. B., & Gerstein, G. L. Activity of inferior temporal neurons in behaving monkeys. *Neuropsychologia*, 1979, *17*, 215–229.

Gross, C. G., Bender, D. B., & Rocha-Miranda, C. E. Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, 1969, *166*, 1303–1305.

Groves, P. M., & Thompson, R. F. Habituation: A dual-process theory. *Psychological Review*, 1970, *77*, 419–450.

Gumnit, R. J. DC potential changes from auditory cortex of cat. *Journal of Neurophysiology*, 1960, *6*, 667–675.

Hammond, P. Spatial organization of receptive fields of LGN neurons. *Journal of Physiology*, 1972, *222*, 53–54.

Hartline, H. K. The nerve messages in the fibres of the visual pathway. *Journal of the Optical Society of America*, 1940, *30*, 239–247.

Hebb, D. O. *The organization of behavior: A neuropsychological theory*. New York: Wiley, 1949.

Henry, G. H., & Bishop, P. O. Simple cells of the striate cortex. In W. D. Neff (Ed.), *Contributions to sensory physiology*. New York: Academic Press, 1971.

Hoffman, W. C. Higher visual perception as prolongation of the basic lie transformation group. *Mathematical Biosciences*, 1970, *6*, 437–471.

Hubel, D. H., & Wiesel, T. N. Receptive fields of single neurones in the cat's striate cortex. *Journal of Physiology*, 1959, *148*, 574–591.

Hubel, D. H., — Wiesel, T. N. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, 1962, *160*, 106–154.

Hubel, D. H., & Wiesel, T. N. Functional architecture of macaque monkey cortex. *Proceedings of the Royal Society of London Series B* 1977, *198*, 1–59.

John, E. R., Bartlett, F., Shimokochi, M., & Kleinman, D. Neural readout from memory. *Journal of Neurophysiology*, 1973, *36*(5), 893–924.

John, E. R., & Morgades, P. P. The pattern and anatomical distribution of evoked potentials and multiple unit activity elicited by conditioned stimuli in trained cats. *Communications in behavioral biology*, 1969, *3*(4), 181–207.

Julesz, B. *Foundations of cyclopean perception*. Chicago: University of Chicago Press, 1971.

Julesz, B. & Caelli, T. On the limits of Fourier decompositions in visual texture perception. *Perception*, 1979, *8*(1), 69–73.

Köhler, W., & Wegener, J. Currents of the human auditory complex. *Journal of Cellular and Comparative Physiology*, 1955, *45*, 25–54.

Kraft, M. S., Obrist, W. D., & Pribram, K. H. The effect of irritative lesions of the striate cortex on

learning of visual discriminations in monkeys. *Journal of Comparative and Physiological Psychology*, 1960, *53*, 17-22.

Lashley, K., Chow, K. L., & Semmes, J. An examination of the electrical field theory of cerebral integration. *Psychological Review*, 1951, *58*, 123-136.

Leith, E. N. White-light holograms. *Scientific American*, 1976, *235*(4), 80.

Leith, E. N., & Upatnicks, J. Photography by laser. *Scientific American*, 1965, *212*(6), 24-35.

Loeb, J. *Comparative physiology of the brain and comparative psychology*. New York: Putnam, 1907.

Lynch, J. C. *A single unit analysis of contour enhancement in the somesthetic system of the cat*. Ph.D. dissertation, Stanford University, May 1971.

Maffei, L., & Fiorentini, A. The visual cortex as a spatial frequency analyzer. *Vision Research*, 1973, *13*, 1255-1267.

Marr, D. Analyzing natural images: A computational theory of texture vision. *Cold Spring Harbor Symposium Quant. Biol.*, 1976, *40*, 647-662. (a)

Marr, D. Early processing of visual information. *Philosophical Transactions of the Royal Society of London Series B*, 1976, *275*, 483-524. (b)

Marr, D., & Poggio, T. From understanding computation to understanding neural circuitry. *Neurosciences Research Program Bulletin*, 1977, *15*, 470-488.

Maurus, M., & Ploog, D. Social signals in squirrel monkeys: Analysis by cerebral radio stimulation. *Brain Research*, 1971, *12*, 171-183.

Mishkin, M. Cortical visual areas and their interaction. In A. G. Karczmar & J. C. Eccles (Eds.), *The brain and human behavior*. Berlin: Springer-Verlag, 1973.

Morrell, F. Visual system's view of acoustic space. *Nature* (London), 1972, *238*, 44-46.

Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. Receptive field organization of complex cells in the cat's striate cortex. *Journal of Physiology*, 1978, *283*, 79.

Poggio, T., & Torre, V. A new approach to synaptic interactions. In H. Palm (Ed.), *Approaches in complex systems*. Berlin: Springer-Verlag, in press.

Pollen, D. A., Lee, J. R., & Taylor, J. H. How does the striate cortex begin the reconstruction of the visual world? *Science*, 1971, *173*, 74-77.

Pollen, D. A., & Taylor, J. H. The striate cortex and the spatial analysis of visual space. In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences third study program*. Cambridge, Mass.: MIT Press, 1974.

Pribram, K. H. Some aspects of experimental psychosurgery: The effect of scarring frontal cortex on complex behavior. *Surgical Forum*, 1951, *36*, 315-318.

Pribram, K. H. Toward a science of neuropsychology: Method and data. In R. A. Patton (Ed.), *Current trends in psychology and the behavioral sciences*. Pittsburgh: University of Pittsburgh Press, 1954.

Pribram, K. H. The amnestic syndromes: Disturbances in coding? In G. A. Talland & M. Waugh (Eds.), *The psychopathology of memory*. New York: Academic Press, 1969.

Pribram, K. H. *Languages of the brain: Experimental paradoxes and principles in neuropsychology*. Englewood Cliffs, N.J.: Prentice-Hall, 1971. (a)

Pribram, K. H. *What makes man human*. James Arthur Lecture, New York American Museum of Natural History Monograph, 1971. (b)

Pribram, K. H. Association: Cortico-cortical and/or cortico-subcortical. In T. Frigyesi, E. Rinvik, & M. D. Yahr (Eds.), *Corticothalamic projections and sensorimotor activities*. New York: Raven Press, 1972. (a)

Pribram, K. H. Neurological notes on knowing. In J. R. Royce & W. W. Rozeboom (Eds.), *The second Banff conference on theoretical psychology*. New York: Gordon & Breach, 1972. (b)

Pribram, K. H. The primate frontal cortex-executive of the brain. In A. R. Luria & K. H. Pribram (Eds.), *Psychophysiology of the frontal lobes*. New York: Academic Press, 1973.

Pribram, K. H. How is it that sensing so much we can do so little? In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences third study program*. Cambridge, Mass.: MIT Press, 1974.

Pribram, K. H. Modes of central processing in human learning and remembering. In T. J. Teyler (Ed.), *Brain and learning*. Stamford, Conn: Greylock Press, 1977. (a)

Pribram, K. H. New dimensions in the functions of the basal ganglia. In C. Shagass, S. Gershon, & A. J. Friedhoff (Eds.), *Psychopathology and brain dysfunction*. New York: Raven Press, 1977. (b)

Pribram, K. H., Lassonde, M., & Ptito, M. *Intracerebral influences on the microstructure of visual cortex: I. Classification of receptive field properties. Experimental Brain Research*, 1981 (in press).

Pribram K. H., Lassonde, M. & Ptito, M. Classification of receptive field properties in cat visual cortex. *Experimental Brain Research*, 1981, *43*, 119-130.

Pribram, K. H., Nuwer, M., & Baron, R. The holographic hypothesis of memory structure in brain function and perception. In R. C. Atkinson, D. H. Krantz, R. C. Luce, & P. Suppes (Eds.), *Contemporary developments in mathematical psychology*. San Francisco: Freeman, 1974.

Pribram, K. H., Spinelli, D. N., & Kamback, M. C. Electrocortical correlates of stimulus response and reinforcement. *Science*, 1967, *157*, 94-96.

Pribram, K. H., Spinelli, D. N. & Reitz, S. L. The effect of radical disconnexion of occipital and temporal cortex on visual behaviour of monkeys. *Brain: A Journal of Neurology*, 1969, *92*(2), 301-312.

Rakic, P. *Local circuit neurons*. Cambridge, Mass.: MIT Press, 1976.

Rall, W. Dendritic neuron theory and dendro-dendritic synapses in a simple cortical system. In F. O. Schmitt (Ed.), *The neurosciences second study program*. New York: Rockefeller, 1970.

Ratliff, F. Inhibitory interaction and the detection and enhancement of contours. In W. A. Rosenblith (Ed.), *Sensory communication*. New York: Wiley, 1961.

Richards, W. Stereopsis with and without monocular cues. *Vision Research*, 1977, *17*, 967-969.

Richards, W., & Polit, A. Texture matching. *Kybernetick*, 1974, *16*, 155-162.

Robson, J. G. Receptive fields, neural representation of the spatial and intensive attributes of the visual image. In E. C. Carterette (Ed.), *Handbook of perception, Vol. V: Seeing*. New York: Academic Press, 1975.

Rodieck, R. W. Quantitative analysis of cat retinal ganglion cell response to visual stimuli. *Vision Research*, 1965, *5*, 583-601.

Rodieck, R. W., & Stone, J. Response of cat retinal ganglion cells to moving visual patterns. *Journal of Neurophysiology*, 1965, *28*, 833-850.

Schiller, P. H., Finlay, B. L., & Volman, S. F. Quantitative studies of single-cell properties in monkey striate cortex. *Journal of Neurophysiology*, 1976, *39*, 1288-1374.

Schwartz, E. L. Spatial mapping in the primate sensory projection: Analytic structure and relevance to perception. *Biological Cybernetics*, 1977, *25*, 181-194.

Shepherd, G. *The synaptic organization of the brain—An introduction*. New York: Oxford University Press, 1974.

Sperry, R. W., Miner, N., & Meyers, R. E. Visual pattern perception following subpial slicing and tantalum wire implantations in the visual cortex. *Journal of Comparative and Physiological Psychology*, 1955, *48*, 50-58.

Spinelli, D. N., Pribram, K. H., & Bridgeman, B. Visual receptive field organization of single units in the visual cortex of monkey. *International Journal of Neuroscience*, 1970, *1*, 67-74.

Spinelli, D. N., Starr, A., & Barrett, T. W. Auditory specificity in unit recordings from cat's visual cortex. *Experimental Neurology*, 1968, *22*, 75-84.

Stamm, J. S., & Knight, M. Learning of visual tasks by monkeys with epileptogenic implants in temporal cortex. *Journal of Comparative and Physiological Psychology*, 1963, *56*, 254-260.

Stamm, J. S., & Pribram, K. H. Effects of epileptogenic lesions in frontal cortex on learning and retention in monkeys. *Journal of Neurophysiology*, 1960, *23*, 552-563.

Stamm, J. S., & Pribram, K. H. Effects of epileptogenic lesions in inferotemporal cortex on learning and retention in monkeys. *Journal of Comparative and Physiological Psychology*, 1961, *54*, 614–618.

Stamm, J. S., & Rosen, S. C. Cortical steady potential shifts and anodal polarization during delayed response performance. *Acta Neurobiologiae Experimentalis*, 1972, *32*(2), 193–209.

Stuart, C. I., Takahashi, Y., & Umezawa, H. On the stability and non-local properties of memory. *Journal of Theoretical Biology*, 1978, *71*, 605–618.

Sutter, E. A revised conception of visual receptive fields based on pseudorandom spatio-temporal pattern stimuli. In P. Z. Marmarelis & G. D. McCann (Eds.), *Proceedings 1st Symposium on Testing and Identification of Nonlinear Systems*. Pasadena, Calif.: California Institute of Technology, 1976.

Ungerleider, L. G. & Pribram, K. H. Inferotemporal versus combined pulvinar-prestriate lesions in the rhesus monkey: Effects on color, object and pattern discrimination. *Neuropsychologia*, 1977, *15*, 481–498.

Uttal, W. R. *The psychobiology of mind*. Hillsdale, N.J.: Lawrence Erlbaum Associates, 1978.

Weiskrantz, L. The interaction between occipital and temporal cortex in vision: An overview. In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences third study program*. Cambridge, Mass.: MIT Press, 1974.

Weiss, P. *Principles of development: A text in experimental Embryology*. New York: 1939.

Willshaw, D. J., Buneman, O. P., & Longuet-Higgins, H. C. Non-holographic associative memory. *Nature*, 1969, *222*, 960–962.