

PRIBRAM, K. H. (1995) Brain in Perception: From Köhler's Fields to Gabor's Quanta of Information, *Proceeding of the 39th Congress of German Society for Psychology*, pp. 53-69.

Pribram

BRAIN IN PERCEPTION: FROM KÖHLER'S FIELDS TO GABOR'S QUANTA OF INFORMATION

Karl H. Pribram
Radford University, Virginia, USA

Just as now, at the time Wolfgang Köhler developed his theory regarding brain function in perception, the received view of the operation of the nervous system dealt mainly with the generation of nerve impulses and their transmission across connections between nerves. By contrast, Köhler based his Gestalt mechanism on the existence of neuroelectrical fields. I believe the time is ripe for a reconsideration of field theory as it applies to brain function, especially processing in the cerebral cortex. The data to be presented will support a view of neuroelectric fields considerably different from that presented by Köhler, somewhat more like that held by Karl Lashley, but based on the issues that deeply concerned them both.

I was fortunate to be able to partake in Köhler's explorations which attempted to demonstrate the existence of generalized direct current (DC) electrical fields in the brain. The experimental attack proved successful (Köhler, 1958). Such fields are restricted to the appropriate cortical region when an organism is stimulated through one or another sensory portal (Gummit, 1961). Further studies in my laboratory showed these fields to be correlated with the speed with which learning occurs (Stamm & Knight, 1963; Stamm & Pribram, 1961; Stamm & Warren, 1961), and the imposition of direct currents onto the cortex can retard or speed learning depending on the polarity of the imposed potential (Stamm, 1961). But Köhler was seriously disappointed when I expressed my uneasiness about the connection between these fields and perception. Later, when I had finished experiments (reviewed by Pribram, 1971, pp. 110-114) in which I had implanted aluminum hydroxide cream over the primary visual cortical surface of monkeys, we were once more in agreement. The experiments showed that discrimination of fine visual patterns remains intact despite marked disruption of recorded brain electrical activity. Köhler had never accepted experiments performed by Lashley (Lashley, Chow, and Semmes, 1951) in which gold foil was used to short circuit neuroelectric fields as evidence against his theory, nor did he yield to Sperry's crosshatches (Sperry, Miner, and Meyers, 1955) into which insulating mica strips had been placed. But when faced with the evidence from the aluminum hydroxide cream implantations he exclaimed: "that ruins not only my D.C. field but every other current neurological theory of perception."

Let me briefly indicate the evidence which has accrued since that conversation to dispel for me this dismal view of a field theoretical approach to the neurology of perception. Nerve impulse generation and transmission in neuronal circuits is but one of the important electrical characteristics of neural tissue. Another characteristic is the production of patterns of pre- and post-synaptic polarizations in axonal and dendritic arborizations. Though these polarizations are akin to Köhler's fields, they differ importantly in that they are not diffuse but sharply localized at the junctions between neurons or in dendrites where they may even be miniature spikes. However, such mini spikes, more often than not, immediately attenuate completely, precluding their ability to propagate. These pre- and post-synaptic patterns of polarization are produced everywhere in the brain cortex when nerve impulses arrive at synapses as a result of the fact that the impulses become attenuated due to decreased fiber size resulting from the branching of axons. Branching also assures that the consequent presynaptic polarizations are never solitary but constitute an arrival pattern. When polarizations are then induced postsynaptically in dendritic arborizations they also are often insufficiently large to immediately influence the pattern of nerve impulse

Pribram

generation which occurs at (or near) the axon hillock. Thus, the patterns of post-synaptic polarizations develop a design which resembles a wave front and can be described as a population vector. This design of polarizations is not some esoteric field, an epiphenomenal mirage superimposed known neural function it results from the arrivals of nerve impulses "awaiting" axonic departure.

Arrival and departure patterns thus conceived become a third alternative to the neural circuit versus "floating" field argument about the neurological process coordinate with awareness. The need for such an alternative was recognized by Lashley who was profoundly troubled by the problem:

Here is the dilemma. Nerve impulses are transmitted over definite, restricted paths in the sensory and motor nerves in the central nervous system from cell to cell through definite intercellular connections. Yet all behavior seems to be determined by masses of excitation, by the form or relations or proportions of excitation within general fields of activity without regard to particular nerve cells. It is the pattern and not the element that counts. What sort of nervous organization might be capable of responding to a pattern of excitation without limited, specialized paths of conduction? The problem is almost universal in the activities of the nervous system and some hypothesis is needed to direct further research (Lashley, 1942, p. 306)

Subsequently, he suggested that an interference pattern model would account for the phenomenon. When Lashley and I discussed these issues with Köhler, none of us had, as yet, conceived of it so obvious: that classical pre- and post-synaptic and dendritic polarizations could serve our purpose. This left Lashley's patterns both too much tied to the neuronal circuitry he found unsatisfactory and at the same time too disembodied as were Köhler's geometric fields. Nonetheless, both Köhler's and Lashley's insights have proved to be most incisive as I will try to show here.

Issues

Projection

Let me begin at the beginning: The study of behavior has provided indispensable tools for a study of psychological processes. However, if the concern of psychologists is to include awareness, the conscious mentality that we experience, inferences must be made from observable behavior. Köhler's interest, as was that of all of Gestalt psychologists, was in the operations of the mind rather than the organization of behavior whereas classical behaviorists focussed on behavior (for a clear statement of this issue see Pribram, 1962 and the Epilogue in Miller, Galanter and Pribram, 1960).

But the relation between mind and behavior concerns not only psychologists. Whether he be philosopher, humanist, politician, psychiatrist, neurologist or neurophysiologist, the mind-behavior relation becomes an issue for him sooner or later. Basically, we all must deal with each other by constructing a sharable world out of the variety of private experiences. Constructive demands that we behave verbally and nonverbally. Behavior organizes this sharable world, but in order to have this organization reflect inner experience, that experience must become projected into the sharable world.

Georg von Békésy performed a series of critical experiments that showed how such projection occurs.

Using touch, which is not ordinarily interpreted as distant, he creates conditions under which this "distant" interpretation is made:

Reflected light from an external object produces an image on the retina. The sensations exist only within our body, yet we localize the image outside the eye, even when we use only a single eye and look at an object far away. This localization beyond our perceptual system is of great importance for survival because it enables us to appreciate impending danger or objects of great necessity. This externalization is achieved without the slightest recognition of the optic image itself or the stimulation on the retina.

The same conditions hold for hearing. The sensations are produced by the action of stimuli on the basilar membrane of the cochlea. The cochlea is deeply imbedded in bone, but we do not localize auditory sensations there but usually refer them to a source somewhere in the environment. However, as we have seen, this external reference does not seem to be true for hearing with earphones.

This external projection has probably been learned early in life; certainly this is true for hearing and vision. But we have not acquired this kind of external projection for skin sensations, and so we have an opportunity to discover how stimulus projection in space is learned.

For this study a pair of vibrators stimulate two fingertips . . . Each vibrator is actuated by the same series of clicks, and their applied currents are varied to give equal magnitudes of sensation on each fingertip when the stimuli are presented separately. Also the setup includes a means of varying the delay time between the clicks of the two series. If a click is delayed for one finger more than 3 or 4 milliseconds, a person feels separate sensations in the two fingertips, as already described. If, however, the time between clicks is reduced to about 1 millisecond the two click series will fuse into one, and the vibratory sensation will be localized in the finger that receives each click the earlier. If the time delay is further decreased the sensation for a trained observer will move into the region between two fingers, and if then the time relation between the two click series is reversed the click will move to the opposite side . . .

The interesting point in this experiment is that for the condition in which there is no time delay the vibrations are localized between the two fingers where no skin is present. If the fingers are spread apart the same effect is found, and when the amount of time delay is varied the sensation will move correspondingly in the free space between the fingers.

Even more dramatic than this experiment is the one in which two vibrators are placed on the thighs, one above each knee. Here the vibrators can stimulate large skin surfaces and produce strong vibratory sensations. By training an observer first to note the localization of the vibration when the knees are together, he can be made to perceive a sensation that moves continuously from one knee to the other. If the observer now spreads the knees apart he will again experience at first a jumping of the sensation from one knee to the other. In time, however, the observer will become convinced that the vibratory sensation can be localized in the free space between the knees, and he will be able to experience a displacement of the sensation in this free space when an appropriate time delay between one stimulus and the other is introduced. This experience is a very peculiar one . . .

This manner of the external projection of vibratory sensations seems to be strange and hard to believe, yet it is well known in many fields. Every well-trained machinist projects his sensations of pressure to the tip of a screwdriver, and it is this projection that enables him to work rapidly and correctly. For most people this projection is so common that they are unaware of its existence. The same type of projection occurs in cutting with a knife, and our adjustments of the blade make use of sensations projected to its edge.

I found the localization of sensations in free space to be a very important feature of behavior. To study the matter further I wore two hearing aids that were properly damped so that the sounds could be picked up by means of two microphones on the chest and then transmitted to the two ears without change in pressure amplitude. Stereophonic hearing was well established, but a perception of the distance of sound sources was lost. I shall not forget my frustration in trying to cross the street during rush hour traffic while wearing this transmission system. Almost all the cars seemed to jump suddenly into consciousness, and I was unable to put them in order according to their immediacy. I should probably have required weeks of experience to become adjusted to this new type of projection. A small change in the amplification of one side was enough to cancel the whole learned adjustment. [Békésy, 1967, pp. 210-26]

A Dual Process

Békésy further observes that both his experience and behavior are organized by processes occurring in the sensory systems his monograph is entitled "Sensory Inhibition". To generalize this observation, a claim can be made that both awareness and behavior are organized by neural processes. However, only some of these processes lead to awareness; there are others that organize behavior of which we are not aware. In fact, instrumental (often automatized) behavior and awareness are to a large extent opposed the more efficient a performance, the less aware we

become. Sherrington (1906/1911) noted this antagonism, stating that between reflex action and mind there seems to be actual opposition. Thus, for the neuroscientist, the question becomes: What kinds of neural activity allow awareness to be inversely related to automatized action?

Patterns of synaptodendritic polarizations and nerve impulses are two kinds of processes that function reciprocally. A simple hypothesis states that the more or less persistent designs of dendritic field polarization patterns are coordinate with awareness (Pribram, 1971, Chapter 6). This view carries the corollary that circuits of nerve impulses per se and the behavior they generate are unavailable to immediate awareness. Even the production of speech is "unconscious" at the moment the words are spoken.

Nerve impulses arriving at synaptic junctions generate patterns of dendritic polarizations which compose a structured (that is, vector) field. The design of this structured field interacts with that already present by virtue of the spontaneous activity of the nervous system and its previous "experience." These interactions thus act as cross-correlation devices to produce new figures from which the patterns of nerve impulses are initiated. The rapidity of changes in awareness would reflect the duration of the correlation process.

What evidence suggests that the junctional electrical activities of the central nervous system are involved in awareness? Joseph Kamiya (1968) and others (Galbraith, et al., 1970; Engstrom, London, and Hart, 1971) have shown, using instrumental-conditioning techniques, that people can be taught to discriminate whether or not their brains are producing certain wave forms which repeat approximately 10 times per second, the so-called alpha rhythms, even though they have difficulty in labeling the difference in the states of awareness they perceive. Subjects who have been able to label the "alpha rhythm state" claim that it is one of pleasantly relaxed awareness. More experiments of this kind are now being carried out in my laboratory.

Equally important are some of Ben Libet's experiments (1966; 1994) that have explored a well-known phenomenon. Since the demonstrations in the 1880s by Gustav Fritsch and Eduard Hitzig (1969) that electrical stimulation of certain parts of man's brain results in movement, neurosurgeons have explored its entire surface to determine what reactions such stimulations produce. For instance, Otfried Foerster (1936) mapped regions in the post-central gyrus which give rise to awareness of one or another part of the body. Thus sensations of tingling or of positioning can be produced in the absence of any observable changes in the body part experienced by the patient. Libet has shown that the awareness produced by stimulation is not immediate: a minimum of a half second and maximum of five seconds elapses before the patient experiences anything. It appears that the electrical stimulation must set up some state in the brain tissue, and only when that state has been attained does the patient become aware.

The evidence for electrical fields

The Field/Spike Dual

In a comprehensive and critical examination of the evidence, D.S. Faber and H. Korn concluded in an article in *Physiological Reviews* (1989):

"that the major conditions that favor the generation of electrical field effects, [are] an increased extracellular resistivity [and] a regular pattern of neuronal orientation such as that found in laminar structures. [Thus] . . . we can predict that whenever the [extracellularly recorded potentials] are more than a few millivolts in amplitude they should . . . reflect electrical field effects. Obvious candidates would include cortical evoked potentials, which are associated with potential

gradients in the range of 4 to 30 mV/mm . . . In those conditions, as more excitatory inputs to a system are active, the growing extracellular fields and synaptic potentials would summate to recruit more postsynaptic neurons. (pp. 839-840).

Conversely, bundling of conical cell dendrites might [also] facilitate electrical interactions. In [such] regions large groups of neurons do not tend to fire synchronously, with the possible exception of certain sleep stages or in seizure conditions. Thus the background conditions may not be favorable for producing large widespread field effects. Rather, it may be that such interactions . . . are highly localized and will only be revealed . . . in conditions where small clusters of cells are

active synchronously." (p. 848).

These localizing conditions obtain when extracellular recordings show "bursts" of spikes (action potentials) created by adjacent clusters of neurons. Under these conditions we can separately record the bursts of spikes (as well as individual action potentials) with a high pass filter and simultaneously record the electrical field effects through a low pass filter. This procedure allows us to compare the time course of the recordings provided we have adjusted for the relative delay produced by the low pass filter. In our recording apparatus this delay amounts to 8-10 msec. Figures 1 and 2 show that the onset of the field effect precedes that of the initiation of spikes. Spike generation becomes most active just prior to the occurrence of the maximum amplitude of the depolarizing field and ceases as the field decays (Figure 3). Out of 2,369 recordings 1,573 or 61% showed this relationship; during sensory stimulation the ratio went to 75%. The remaining cases were made up of 796 instances where the field effect was recorded without any simultaneous spike activity; and where spikes were recorded independently of field potentials, 1,573 times.

To summarize the import of these findings: just as depolarization of axon membranes is a necessary precursor of the generation of action potentials, so also is the local build up of synaptodendritic field potentials a precursor to the recruitment of action potentials in post synaptic neurons.

Receptive Fields in Sensory Processing

For a half century, neurophysiologists have used extracellular recordings in extensive explorations of the functions of single neurons in sensory processing. The wealth of data obtained in these explorations has focussed on the properties - the features - of a sensory stimulus that would increase (or decrease) the number of action potentials (spikes) that was recorded in the presence of the inciting stimulus property.

However, axonal spike trains recorded from single electrodes reflect three separable processes: 1) those due to the sensory input per se, as is usual in feature analytic studies; 2) those that directly modulate the output of the axon hillock as determined by intracellular recording (Pribram, et al, 1981; Berger and Pribram, 1992); and 3) those that map the intrinsic response of the synaptodendritic field; and as shown when extracellular recordings are used to demonstrate the intrinsic configuration of the dendritic field of the neuron as it responds to sensory stimulation. This method of mapping the functional geometry of dendritic receptive fields was initiated by Kuffler (1953) and developed by Hubel and Wiesel (1959; 1968) for the visual system. Kuffler showed that he could map the geometry of the dendritic field of a retinal ganglion cell by recording from its axon in the optic nerve. Kuffler's is a simple technique for making receptive field maps, which is now standard in neurophysiology. By activating a receptor or a set of receptors with a variety of stimulus dimensions and using the density of unit responses recorded from axons, a map of the geometric organization of the synaptodendritic receptive field of that axon can be obtained. (See e.g. reviews by Békésy, 1967 and Connor and Johnson, 1992 for

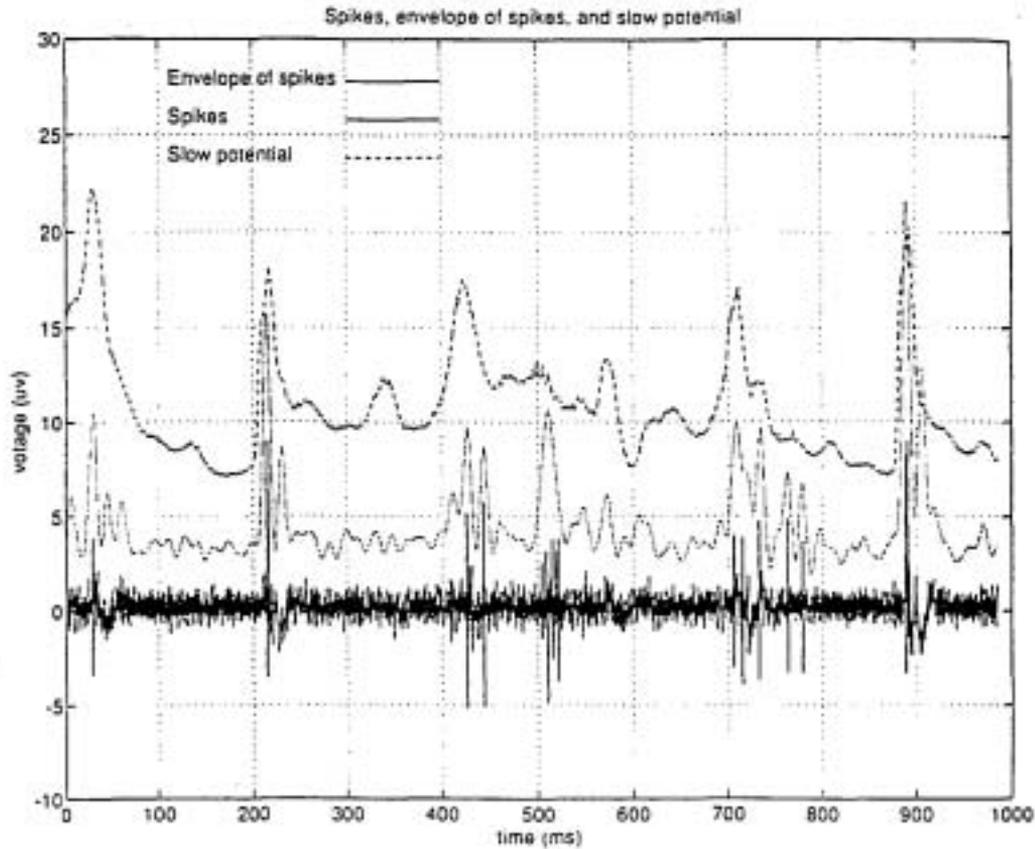


Figure 1. An example of the relationship between spikes and bursts of spikes to coincident slow potentials

somesthesia; and by Enroth-Kugel and Robson, 1966; and Rodiek and Stone, 1965 for vision).

Experiments by Barlow (1986) and by Gilbert and Wiesel (1990) have shown that sensory stimulation beyond the reach of a particular neuron's receptive field can, under certain conditions, change that neuron's axonal response. Synaptodendritic polarizations are thus subject to field effects produced in a more extended field of potentials occurring in neighboring synaptodendritic fields.

The Kuffler technique maps these relations among local field potentials occurring in extended overlapping dendritic arbors. The axon(s) from which the records are being made, sample a limited patch of this extended domain. As shown in the previous section, we can readily demonstrate the correlation between burst activity recorded from an axon and the local field potentials occurring in the synaptodendritic receptive field of that axon.

In the following study, we aimed to explore the relations among local field potentials by mapping receptive field organization using the Kuffler technique. The rat somatosensory system was chosen for convenience and because the relation between whisker stimulation and central

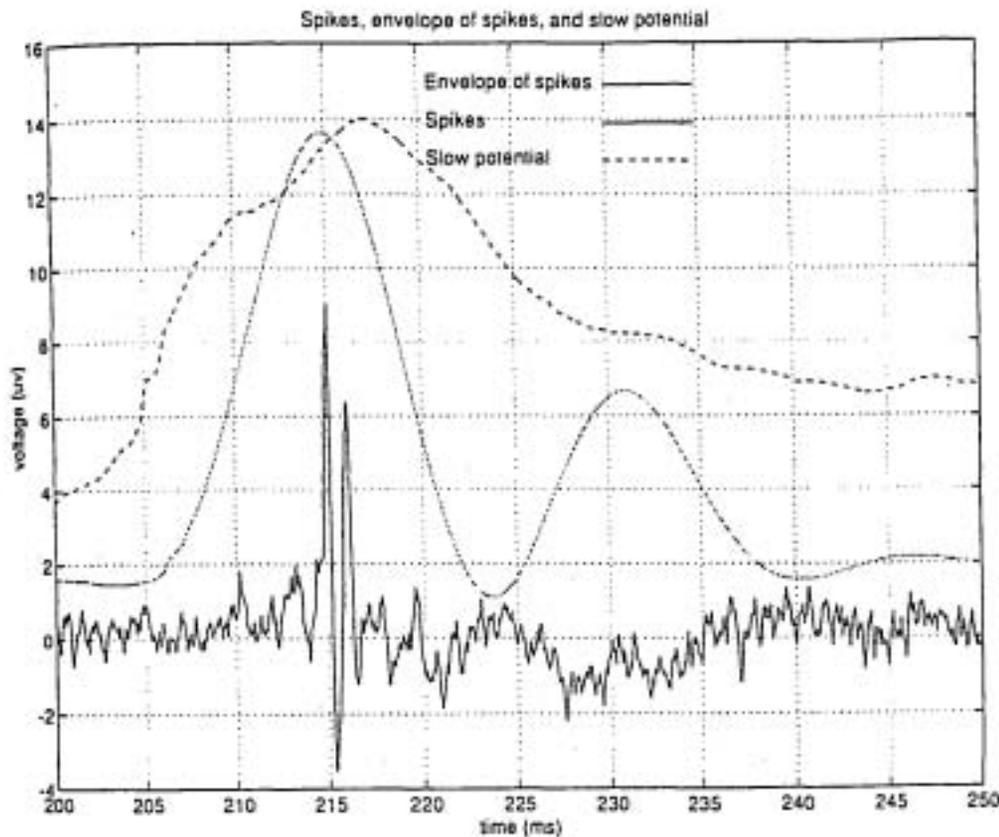


Figure 2. Enlargement of one example of the relationship shown in Figure 1.

neural pathways has been extensively studied (see review by Gustafson and Felbain-Keramidas, 1977). Whiskers were stimulated by a set of rotating cylinders, each grooved with equally spaced steps, the step width and adjacent grooves subtending equal angles. Three cylinders were used with their steps measuring 30 deg., 15 deg., and 7.5 deg., respectively. The cylinders were rotated at 8 different speeds, varying from 22.5 deg./sec. to 360 deg./sec. (The rotating cylinders were meant to mimic the drifting of gratings across the retinal receptors in vision.)

In most of our experiments an entire array of whiskers was subjected to contact with the rotating cylinders. This was done in order to bring the results of these somatosensory experiments into register with those performed in the visual system where an entire array of receptors is stimulated by the drifting grating.

In our experiments, sensory input is generated by the frequency with which the whiskers are stimulated. This frequency is a function of the stimulus as modulated by the spacings of the grooves on the cylinders and the speed with which the cylinders are rotated. The number of bursts or spikes generated at each recording location is thus determined by the spatial and

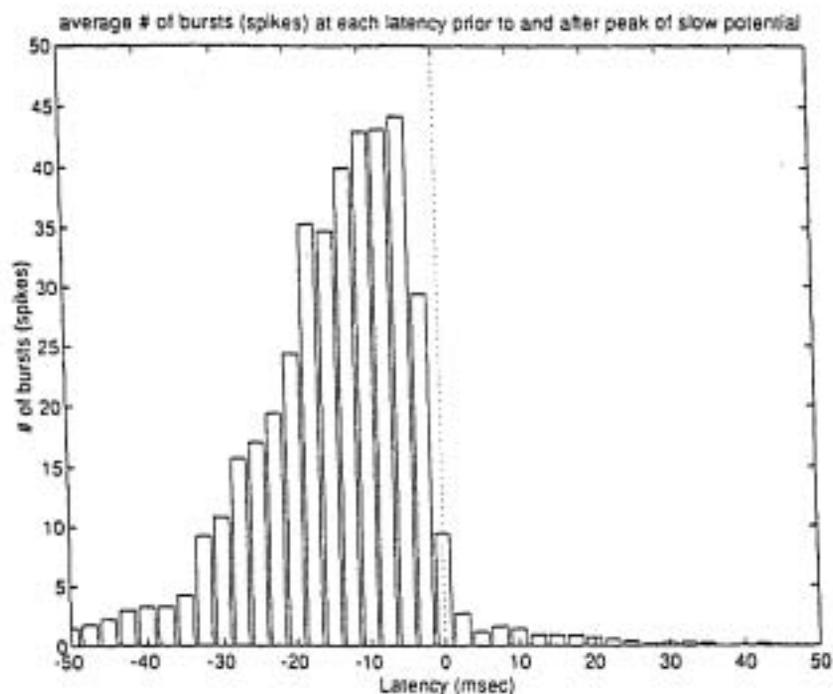


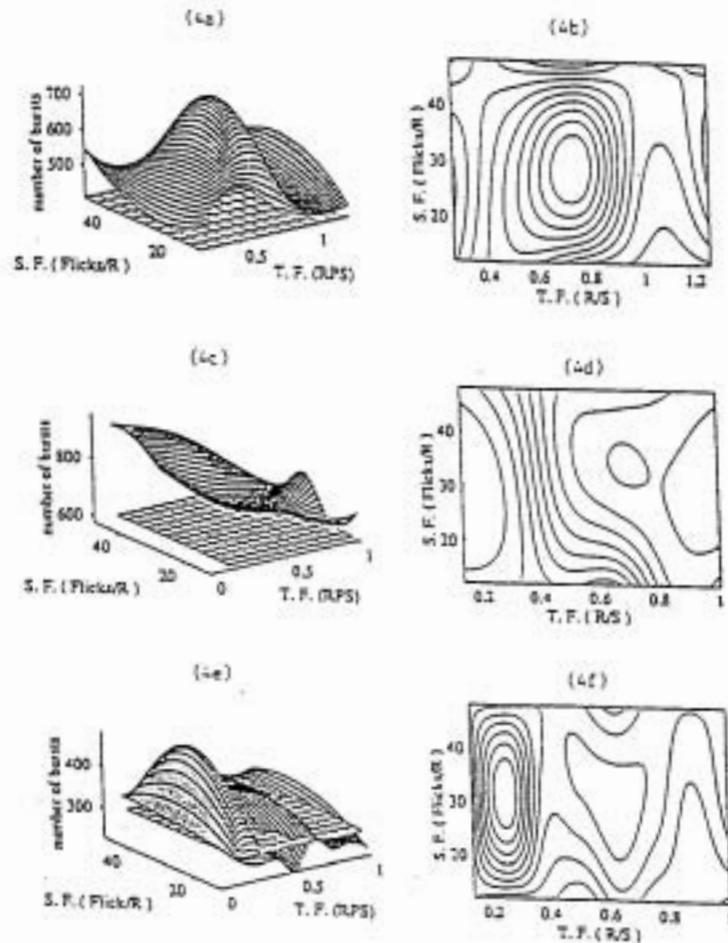
Figure 3. This figure demonstrates the average thirty data sets which include 11,715 bursts/spikes obtained under a variety of stimulations. Note that the peak of the slow potential is marked zero.

temporal parameters of the sensory input as they influence the frequency of stimulation (Figures 4a-f).

The activity above or below baseline which resulted from whisker stimulation is plotted as a manifold describing total number of bursts (or spikes) per 100 secs. of stimulation. Spatial frequencies are scaled in terms of grooves per revolution, while temporal frequencies are scaled in terms of revolutions per second. The density (or pure frequency) of stimulation of a whisker (or set of whiskers) is a function of both the spacings of the cylinder grooves and the speed with which the cylinder rotates. It is this density of stimulation per se which generates the map or manifold, the geometry of the receptive field. As this map is constructed in terms of pure frequency, it reflects processing in the spectral domain.

Simulation

According to signal processing theory, the general shape of a receptive field manifold is the same for each combination of spatial and temporal frequencies. However, a central peak, reflecting the density of response for that spectral location in the manifold, will be shifted within the field according to the particular spatial and temporal stimulation values.



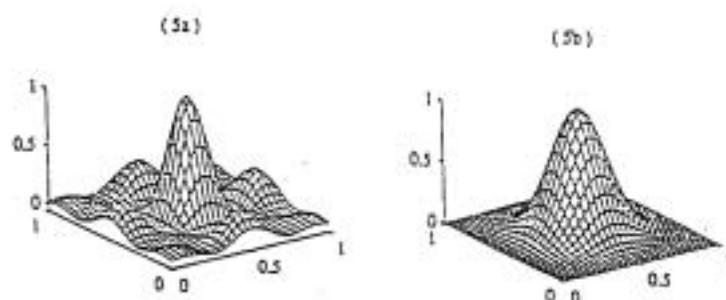
Figures 4a-f. Examples of receptive field manifolds and their associated contour maps derived by an interpolation (spline) procedure from recorded whisker stimulation. The contour map was abstracted from the manifold by plotting contours in terms of equal numbers of bursts per recording interval (100 secs.). Each figure shows baseline activity (no whisker stimulation) at a given electrode location as a gr-plane located in terms of number of bursts per 100 secs.

In order to discern whether, indeed, our data fit the requirements of signal processing theory, a simulation of the procedure was executed. The first stage of the simulation was to construct a putative receptive field manifold. Any extent of manifold generated by the frequency characteristics of the stimulus is best described formally by a truncated spectral function such as a constrained Fourier representation. Gabor (1946 p.431) defined such a function as follows: Let us now tentatively adopt the view that both time and frequency are legitimate references for describing a signal and illustrate this . . . by taking them as orthogonal coordinates. Its frequency is exactly defined [only] while its epoch is entirely undefined. A sudden surge or 'delta function'

(also called a 'unit impulse function') has a sharply defined epoch, but its energy is distributed over the whole frequency spectrum. Daugman (1990), MacLennan (1993) and Pribram and Carlton (1986), have extended this illustration to include, in addition to the time parameter, two spatial dimensions.

We chose a rectangular window in the spatiotemporal domain to constrain the two dimensional sinusoidal signal. The reasons for this choice are: First, that the resulting spectrum generates a number of side lobes surrounding a central peak. In the visual system a number of side lobes has been observed at the lateral geniculate nucleus, (Hammond, 1972; Pribram, personal observation, 1974) and at the cortex (Pollen and Feldon 1979; Pollen and Pribram, personal observation 1972). The second reason for the choice of a rectangular window is that it reflects the spatial and temporal constraints on the extent of the distribution of the signal: the spatial constraint reflects the limits on spacings of the grooves on our cylinders; its temporal constraint, the limits on their rotation speed.

In addition, the rectangular window allows for maximum resolution of frequencies (see Zeevi and Daugman 1981; and Oppenheim and Shafer 1989 esp. Chapter 11, for review). The use of such a window generates a sinc function in the spectral domain.



Figures 5a and b. 5a presents a stimulated manifold (mexican hat function) representing a spectral distribution induced by a single external stimulus (spatial and temporal frequency combination) across the cortical synaptodendritic field. 5b presents the second stage of the stimulation as a probe consisting of a band-pass filter formed by a Gaussian (exponential) function.

In our simulations (Figure 5a) each plot is a manifold of a spectral density function of a rectangular windowed continuous two-dimensional sinusoidal signal. When, in other experiments, only a single frequency of stimulation is used, a spatiotemporal connection matrix can be constructed from recordings made with multiple electrode arrays to represent the data (Barcala, Nicoletis and Chapin 1993). Our version of such a matrix represents the variety of spatially and temporally constrained spectral data gathered in our experiments as a sinc function, centered at the frequency of each stimulation pair, i.e.

$$F(\omega_1, \omega_2) = A \text{sinc}(\omega_1 - \omega_{01}) \text{sinc}(\omega_2 - \omega_{02})$$

where A is a scaling constant, ω_1 and ω_2 are spatial and temporal frequencies of the spectrum, and ω_{01} and ω_{02} are the spatial and temporal frequencies of the stimulation. The function $\text{sinc}(\omega)$ is defined as:

$$\text{sinc}(\omega) = \sin(\omega)/\omega$$

The second stage of the simulation uses as a probe, a Gaussian (exponential) function (Figure 5b). When this probe represents a single neuron it is limited by the spatial extent of the local field potentials fluctuating among that neuron's dendrites. When a burst manifold is modelled, the spatial constraint is assumed to portray a greater reach and is limited by the barrel (columnar) arrangement of the somatosensory cortex. Sampling is performed by the generative activity of the axon hillock, which, due to the upper and lower temporal limits of spike generation, functions as a bandpass filter of the response of the sensory system. This filter is multiplied with the sinc function to yield a display of the manifold.

Figures 6a-f depict manifolds and contours derived from these simulations. Note the close fit to the experimentally derived manifolds and contours shown in Figures 6a-f. A total of 48 manifolds were experimentally generated. Of those, three were essentially flat. Of the remaining 45, we simulated six; all but two of the remaining 39 have a shape that can be seen to be successfully simulatable with the technique described.

The similarity of these manifolds obtained by recordings made from the somatosensory cortex to the receptive field characteristics demonstrated in the primary visual cortex (DeValois and DeValois, 1988; Pollen and Taylor, 1974; Pribram and Carlton, 1986; Daugman, 1990) suggests that this process is ubiquitous in the cortical synaptodendritic network.

The manifolds derived from our data are constructed of two orthogonal dimensions: one dimension reflects the spatial frequency of the stimulus and the other its temporal frequency. Because spatial and temporal variables constrain the spectral density response, a Gabor-like rather than a simple Fourier representation describes our results. Thus the results of our experiments can be interpreted in terms of an information field composed of Gabor-like elementary functions, that is, of truncated two dimensional sinusoids.

An unconstrained spectral representation is globally holographic: the constrained spectral domain, as in patch or multiplex holography, is termed holonomic. (For the derivation of this nomenclature, originated by Hertz, see Pribram, 1991, p. 27.) Holonomic constraints quantize an essentially spectral process. Gabor called the elementary function described by the intersection of his spectral and time parameters a "quantum of information." His reason was that he could address the problem of the efficiency of communication across the Atlantic cable "in terms of the formulation of Heisenberg's principle of indeterminacy in 1927. This discovery led to a great simplification in the mathematical apparatus of quantum theory which was recast in a form of which use will be made in the present paper" (1946, p. 432).

A quantum information field theory of dendritic processing?

The formal, mathematical foundations of the computations which contribute to contemporary field theoretical concepts regarding brain function rest on a generalization of the application of the concept of a spectral domain: not only colors and tones can be analyzed into their component frequencies of oscillation. Processing of all exteroceptive sensations including those dependent on spatiotemporal configurations (such as the shapes of surfaces and forms) can be understood as

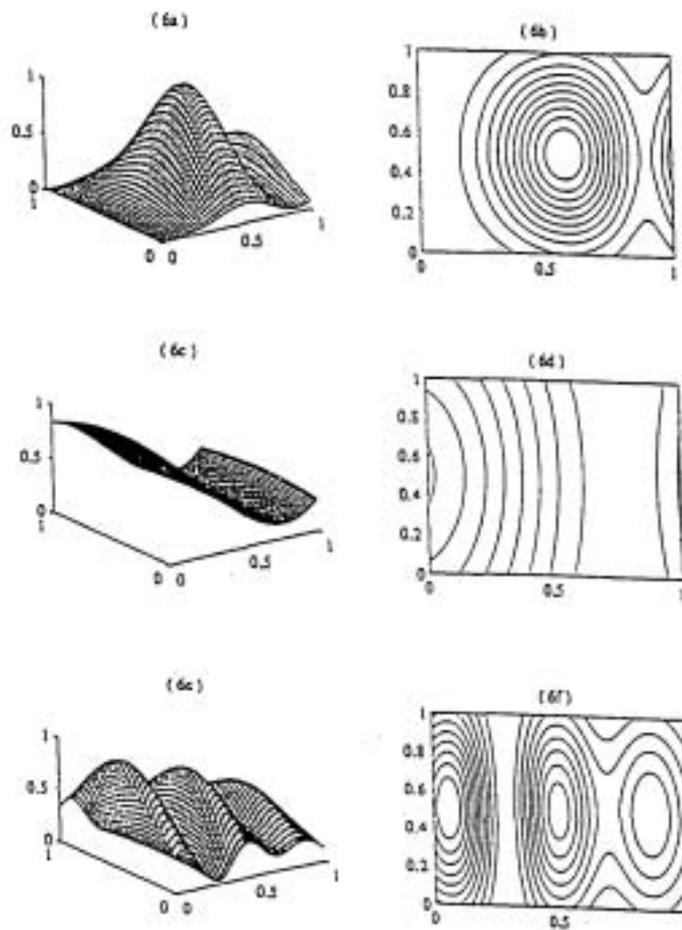


Figure 6. Examples of stimulated receptive field manifolds and their associated contour maps to be compared with the empirically derived maps presented in Figures 2a-f. Axes are normalized from 0.

amplitude modulations of these oscillations. In fact, due to the Fourier transformation, spectra enfold the ordinary conception of both space and time.

The mapping of dendritic receptive fields is based on the Fourier relationship. As noted, Fourier's theorem states that a pattern can be decomposed into components representing the relationships among sets of regular (i.e., periodic) oscillations each of which has been further decomposed into oscillations 90° out of phase. Components encode frequency, amplitude and phase (the relations between oscillations). These components are quantified as Fourier coefficients. The ensemble of such coefficients, when embodied in physical form, becomes palpable as an optical hologram. When coefficients of identical value are connected as in a contour map, the resulting schema is what in the holonomic brain theory is called a "holoscape." The contours

forming such a holoscape are embodied in the microprocess of polarizations occurring in dendritic networks thus constituting a sub- and transneuronal manifold.

Further, the Fourier theorem states that the original pattern can be reconstituted, reconstructed, by performing the inverse transform. It is this simplicity, its invertibility and linearity in analysis and (re-)synthesis, which is one of the attractive features of the Fourier theorem. There is, therefore, a computational gain leading to better understanding were brain processes to follow the rules of the Fourier relationship. Actuality is somewhat more complex.

Perceived patterns are ordinarily described in space and time. When the Fourier analytical procedure decomposes a spacetime pattern into an ensemble of components representing the frequencies of oscillations from which the pattern can be reconstructed, the decomposition is described as harmonic and the result, the spectrum of the pattern. Thus 1) spacetime, and 2) spectrum are differentiated by the Fourier procedure.

An additional concept derives from plotting spectral and spacetime values within the same frame. It turns out that when this is done there is a limit with which both frequency and spacetime can be concurrently determined in any measurement. As noted, this is the uncertainty relation was used by Gabor (1946) to describe a fundamental unit, a "quantum" of information. This unit differs from the unit of information defined by Shannon, usually taken as a bit, (a binary digit) i.e., a binary (Boolean) choice among alternatives (Shannon and Weaver 1949). However, Shannon also defined information as a reduction of uncertainty. This "uncertainty" relationship provides a link between Gabor's and Shannon's definitions and allows for an explicit convergence of "information processing" theories. Furthermore, the distinction between Gabor's and Shannon's formulations provide the basis of the distinction between configural and the cognitive aspects of perception (see Pribram, 1991).

Gabor became interested in describing a joint spacetime-spectral domain because he noted that there is a limit on the precision to which simultaneous measurement of spectral components and [space]time can be made. It is this limit, defined by residual bandwidth of frequencies and the probability of an occurrence within a range of spacetime, that proscribes the efficiency with which the system can operate. In effect, therefore, the Gabor relation describes the composition of a sensory channel, and the residual uncertainty defines the limits of channel processing span.

Processing efficiency was handled by Gabor in terms of a measure he termed the "Logon". Today we often refer to these Logons as "Gabor elementary functions." In Gabor's two dimensional scheme the Logon was a unitary minimum. This minimum describes an area surrounding the intersection of frequency and a temporal impulse function.

Gabor's mathematics paralleled that used by Heisenberg to describe experimental findings in the field of quantum physics. In essence, therefore, the mathematics found so useful in understanding relationships in quantum physics was generalized to deal with issues in psychophysics and Gabor termed the Logon a quantum of information. An ensemble of such quanta, processing channels, is dealt with by what mathematicians call a Hilbert space, as Hilbert originally devised the mathematics used by Heisenberg and Gabor.

In our experimental results, Gabor elementary functions are composed in dendritic arborizations, receptive fields of the neurons from which we are recording. Pollen and Ronner (1980) found adjacent neurons in the visual cortex to respond best to gratings 90 out of phase. These neurons make up a couplet, a quadrature pair. Thus in the visual system a module of receptive fields encodes the quadrature relation (essentially sine and cosine components that make up Fourier coefficients). Each logon, i.e. each such receptive field module, is a channel. According to Gabor, the ensemble of such channels is a measure of the degrees of freedom, the number of distinguishable dimensions or features (e.g., spatial and temporal frequency, degrees of orienta-

Pribram

tions, preferred direction, color). The minimum uncertainty relation expressed by Gabor elementary functions sets the limits on the information processing competence of each of these channels.

Coda

Given that an aspect of dendritic processing in the sensory cortex can be described in terms of quantum-like fields made up of Gabor channels, we are faced with a discrepancy: Such fields, composed of arrival and departure patterns of synapto-dendritic polarizations, are considered to be coordinate with perceptual awareness, which occurs within spacetime coordinates. Köhler did not have this problem with his more generalized fields which were deemed geometrically isomorphic not only with the physical sensory input but also with subjective experience.

Resolution of this discrepancy is beyond the scope of this address but has been dealt with in detail in Pribram and Carlton (1986) and in Lecture 6 of *Brain and Perception* (Pribram, 1991). Following the lead given by Poincaré, Helmholtz and Lie (see Pribram Epilogue, 1991), movement is given the critical role of organizing an inverse transform to produce our experience of entities such as objects in a spacetime frame. In visual processing, this organization is imposed by the peri- and prestriate cortical systems operating back (top-down) on the primary geniculostriate visual input.

Much has been made recently of the modular composition of mental (Minsky, 1986) and brain processes (Gazzaniga, 1985). This emphasis on neural systems which localize separate brain-behavioral relationships is vitally important to understanding such processes as memory retrieval (and has constituted the bulk of my laboratory research). However, equally important is the fact that these various systems not only relate to one another in a hierarchical manner but that the higher order systems operate on lower order systems by interpenetration. Thus, we ordinarily, immediately perceive named and categorized objects, not just sets of images (though we are capable of "imaging" by suspending the higher order processes). There is abundant evidence of such top-down penetration in the visual, auditory and somatosensory neural systems.

Mathematically, conformal (Lie) group procedures (Hoffman, 1966) are shown to describe this process. Frame effects are accounted for (Palmer 1988) as is the fact, in Poincaré's terms, that "objects are relations". Movement, whether actual or imaged follows a least action (or action integral) geodesic (Carlton and Shepard, 1990 I&II) described by vectors in the Gabor information processing domain.

A final question needs to be addressed. Why should the brain process go through a spectral transformation only to have to inverse transform in order to allow the organism to behave appropriately in a spacetime object(ive) world? The answer is that correlations are achieved much more parsimoniously when such transformations are employed. In statistical manipulations, the FFT (Fast Fourier Transform) has provided an incredibly useful tool to facilitate the computation of correlations. Medical applications of image processing such as computerized tomography (CT scans) and magnetic resonance imaging (MRI) have at their basis spectral domain transformations.

The evidence that brain processes partake of this computational simplification was not sought for but has accrued over the past two and a half decades serendipitously in various laboratories. The evidence is, at present, overwhelming that some such transformational brain process underlies perception: that Gabor-like synaptodendritic receptive *fields* are critical, fields that are sensitive to a multitude of chemical modulations but sufficiently robust to allow our experience of the world to be stable and predictive. The step in the process that needs more experimental evidence in various sensory modes is how the "inverse" transformation from field to action path

(for instance a vectorial representation of a geodesic, Shepard 1988, Pribram 1991) is effected. This step is the focus of our current research.

- Racala, L.A., Nicoletti, M.A.L., and Chapin, J.K. (1993) *Quantifying the connectivity properties underlying the dynamics of the rodent trigeminal network (Abstract)*, Society For Neuroscience Abstracts: 23rd Annual Meeting, Vol. 19, Part 1.
- Ratouf, H.B. (1986) Why Have Multiple Cortical Areas? *Vision Research*, 26, 81-90.
- Rubio, G. von (1967) *Sensory Inhibition*. Princeton: Princeton University Press.
- Singer, D.H. and Pribram, K.H. (1992) The relationship between the Gabor Elementary Function and a stochastic model of the inter-spike interval distribution in the responses of visual cortex neurons. *Biological Cybernetics*, 67, 191-194.
- Simon, E.H. and Shepard, R.N. (1990) Psychologically simple motions as geodesic paths: I&II, Asymmetric objects. *Journal of Mathematical Psychology*, 34(2), 127-188.
- Simon, C.E. and Johnson, K.O. (1992) Neural Coding of Tactile Texture: Comparison of Spatial and Temporal Mechanisms for Roughness Perception. *Vision Research*, 32, 3414-3426.
- Toussaint, J.G. (1990) An information-theoretic view of analog representation in striate cortex. In E. Schwartz (Ed.), *Computational Neuroscience*. Cambridge, MA: MIT Press.
- DeValois, R.L., DeValois, K.K. (1988) *Spatial vision*. Oxford psychology series No. 14. New York: Oxford University Press.
- Livingston, D.K., London, P., and Hart, J.T. (1971) EEG alpha feedback training and hypnotic susceptibility. *Nature*.
- Fattah-Kugel, C., Robson, J.G. (1966) The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology*, 198, 517-552.
- Faber, D.S., and Korn, H. (1989) Electrical Field Effects: Their Relevance in Central Neural Networks. *Physiological Reviews*, Vol. 69, No. 3, July, pp. 839-840, 848.
- Fierstein, O. Sensible cortical Felder in Bumke and Foerster (1936) *Handbuch der Neurologie*, Vol. 6: 358. Berlin, J. Springer.
- Flechsig, G., and Hitzig, E. (1969) On the electrical excitability of the cerebrum. In Pribram, K.H. (ed.) *Brain and Behaviour*, Vol. 2 *Perception and Action*. Baltimore: Penguin, pp. 353-64 (orig. Pub. 1870).
- Gabor, D. (1948) A new microscopic principle. *Nature*, 161, 777-778.
- Guthrie, G., London, P., Leibovitz, M.P., Cooper, C., and Hart, J.T. (1970) An electroencephalographic study of hypnotic susceptibility. *J. comp. physiol. Psychol.*
- Guazzarini, M.S. (1985) *The social brain: Discovering the network of the mind*. New York: Basic Books.
- Gülcher, C.D., and Wiesel, T.N. (1990) The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research*, 30, 1689-1701.
- Gurnea, R.J. (1963) The distribution of direct current responses evoked by sounds in the auditory cortex of the cat. *Electroenceph. clin. Neurophysiol.*, 13: 889-95.
- Gustafson, J.W. and Felbain-Kermadiaz, S.L. (1977) Behavioral and neural approaches to the function of the mystacial vibrissae. *Psychol. Bull.* 84, 477-488.
- Hammond, P. (1972) Spatial Organization of Receptive Fields of LGN Neurons. *Journal of Neurophysiology*, 35, 53-54.
- Helm, D.O. (1949) *The Organization of Behavior, A Neuropsychological Theory*. New York: John Wiley.
- Helm, D.O. (1955) Drives and the CNS (conceptual nervous system). *Psych. Rev.*, 62: 243-54.
- Hollman, W.C. (1978) The Lie transformation group approach to visual neuropsychology. In E.L.J. Leeuwenberg & H.F.J.M. Buffan (Eds.), *Formal theories of visual perception* (pp. 27-66). New York: Wiley.
- Hubel, D.H. & Wiesel, T.N. (1959) Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology*, 148, 574-591.
- Hubel, D.H. & Wiesel, T.N. (1968) Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215-243.
- Kataya, J. Conscious control of brain waves. *Psychology Today*, 1968, 1: 56-60. In *Readings in Experimental Psychology Today*. Del Mar, California: CRM Books, 1970, pp. 51-55.
- Kuffler, W. The present situation in brain physiology. *Am. Psychologist*, 1958, 13: 150.
- Kuffler, S.W. (1953), Discharge patterns and functional organization of mammalian retina. *Journal of Neurophysiology*, 16, 37-69.

Pribram

- Lashley, K.S. (1942) The problem of cerebral organization in vision. *Biological Symposia*, Vol. VII, *Visual Mechanisms*. Lancaster: Jaques Cattell Press, pp. 301-22.
- Lashley, K.S., Chow, K.L., and Semmes, J. (1951) An examination of the electrical field theory of cerebral integration. *Psych. Rev.*, 58: 123-36.
- Libet, B. (1994) Testable Field Theory of Mind-Brain Interaction. *Journal of Consciousness Studies: Controversies in Science & the Humanities*, September, vol. 1, no. 1.
- Libet, B. (1966) Brain stimulation and conscious experience. In Eccles, J.C. (ed.) *Brain and Conscious Experience*. New York: Springer-Verlag, pp. 165-81.
- MacLennan, B. (1993) Information Processing in the Dendritic Net. In Pribram (Ed.) *Rethinking Neural Networks: Quantum Fields and Biological Data*. INNS Publications New Jersey: Lawrence Erlbaum Associates.
- Minsky, M. (1986) *Society of Mind*. New York: Simon & Schuster.
- Morrell, F. (1961a) Effect of anodal polarization on the firing pattern of single cortical cells. In Furness, F.N. (ed.) *Pavlovian Conference on Higher Nervous Activity*. Ann. NY Academy Science, pp. 813-1198.
- Morrell, F. (1961b) Electrophysiological contributions to the neural basis of learning. *Physiol. Rev.*, 41: 643-94.
- Morrell, F. (1961c) Lasting changes in synaptic organization produced by continuous neuronal bombardment. In Delafresnaye, J.F., Fessard, A., and Konorski, J. (eds.) *Symposium on Brain Mechanisms and Learning*. Oxford: Blackwell Scientific Publications, pp. 375-92.
- Oppenheim, A.V., and Schaffer, R.W. (1989) *Discrete Time Signal Processing*. Englewood Cliffs: Prentice-Hall.
- Palmer, S.E. (1982) Symmetry, transformation, and the structure of perceptual systems. In J. Beh (Ed.), *Representation, and organization in perception* (pp. 95-144). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Pollen, D.A., Lee, J.R. and Taylor, J.H. (1971) How does striate cortex begin reconstruction of the visual world? *Science*, 173, 74-77.
- Pollen, D.A., and Feldon, S.E. (1979) Spatial periodicities of periodic complex cells in the visual cortex cluster at one-half octave intervals. *Investigations in Ophthalmology and Visual Science*.
- Pollen and Pribram (1972) Personal Communication.
- Pollen, D.A., and Ronner, S.E. (1980) Spatial computation performed by simple and complex cells in the cat visual cortex. *Experimental Brain Research*, 41, A14-15.
- Pollen, D.A., and Taylor, J.H. (1974) The striate cortex and the spatial analysis of visual space. In F.O. Schmin & F.G. Worden (Eds.), *The Neurosciences Third Study Program* (pp. 239-247). Cambridge, MA: The MIT Press.
- Pribram, K.H. (1962) Interrelations of psychology and the neurological disciplines. In Koch, S. (ed.) *Psychology: A Study of a Science*, Vol. 4, *Biologically Oriented Fields: Their Place in Psychology and in Biological Sciences*. New York: McGraw-Hill, pp. 119-57.
- Pribram, K.H. (1971) *Languages of the Brain: Experimental Paradoxes and Principles in Neuropsychology*. Englewood Cliffs, NJ: Prentice-Hall; Monterey, CA: Brooks/Cole, 1977; New York: Brandon House, 1982. (Translations in Russian, Japanese, Italian, Spanish)
- Pribram, K.H. and Carlton, E.H. (1986) Holonomic brain theory in imaging and object perception. *Acta Psychologica*, 63, 175-210.
- Pribram, K.H., Lassonde, M.C., and Pito, M. (1981) Classification of receptive field properties. *Experimental Brain Research*, 43, 119-130.
- Pribram, K.H., Nauer, M. and Baron, R. (1974) The holographic hypothesis of memory structure in brain function and perception. In R.C. Atkinson, K.H. Kranz, R.C. Luce, and P. Suppes (Eds.), *Contemporary Developments in Mathematical Psychology* (pp. 416-467). San Francisco, CA: W.H. Freeman.
- Rodieck, R.W., and Stone, J. (1965) Response of cat retinal ganglion cells to moving visual patterns. *Journal of Neurophysiology*, 28, 833-850.
- Shannon, C.E., & Weaver, W. (1949) *The mathematical theory of communications*. Urbana, IL: The University of Illinois Press.
- Shepard, R.N. (1988) The role of transformations in spatial cognition. In J. Sciles-David, M. Krichevsky, & U. Bellugi (Eds.), *Spatial cognition: Brain bases and development* (pp. 81-110). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Sherrington, C. (1947) *The Integrative Action of the Nervous System*. New Haven: Yale University Press (first published 1906)
- Simons, D.J. (1978) Response properties of vibrissa units in rat S1 somatosensory neocortex. *Journal of Neurophysiology*, Vol. 41, No. 1.

- Sperry, R.W., Miner, N., and Meyers, R.E. (1955) Visual pattern perception following subpial slicing and tantalum wire implantations in the visual cortex. *J. comp. physiol. Psychol.*, 48: 50-58.
- Stamm, J.S. (1961) Electrical stimulation of frontal cortex in monkeys during learning of an alternation task. *J. Neurophysiol.*, 24: 414-26.
- Stamm, J.S. and Knight, M. (1963) Learning of visual tasks by monkeys with epileptogenic implants in temporal cortex. *J. comp. physiol. Psychol.*, 56: 254-60.
- Stamm, J.S., and Pribram, K.H. (1961) Effects of epileptogenic lesions of inferotemporal cortex on learning and retention in monkeys. *J. comp. physiol. Psychol.*, 54: 614-18.
- Stamm, J.S. and Warren, A. (1961) Learning and retention by monkeys with epileptogenic implants in posterior parietal cortex. *Epilepsia*, 2: 229-42.
- Zeevi, Y.Y., and Daugman, J.G. (1981) Some psychophysical aspects of visual processing of displayed information. Proceedings of the Image II Conference, Phoenix, AZ.