Prolegomenon for a Holonomic Brain Theory

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"Before the connection of thought and brain can be explained, it must be stated in elementary form; and there are great difficulties about stating it. ... Many would find relief at this point in celebrating the mystery of the unknowable and the "awe" which we should feel. ... It may be constitutional infirmity, but I can take no comfort in such devices for making a luxury of intellectual defeat. ... Better live on the ragged edge, better gnaw the file forever!" (James, 1950 pp. 177-179)

"... it is entirely possible that we may learn about the operations of thinking by studying perception." (Rock, 1983 p. 1)

I. Aims and Origins of the Theory

"There is good evidence for the age-old belief that the brain has something to do with ... mind. Or, to use less dualistic terms, when behavioral phenomena are carved at their joints, there will be some sense in which the analysis will correspond to the way the brain is put together. ... In any case each time there is a new idea in psychology, it suggests a corresponding insight in neurophysiology, and vice versa. The procedure of looking back and forth between the two fields is not only ancient and honorable - it is always fun and occasionally useful." (Miller, et al., 1960 p. 196)

An Introduction

The explosion of data in the behavioral and neural sciences has made the study of the correspondence between the way the brain is put together and the carving behavioral phenomena at their joints even more intriguing and rewarding than when the first of the above quotations was written. The biological roots of behavior provide evidence for how experience becomes processed. When these roots are ignored, the experiential phenomena guiding behavior are found to be so richly structured, and carving can proceed in such a multitude of ways, that the result has often been a purely descriptive phenotypical science in which descriptions constitute a tower of Babel. This is especially true of perception which of necessity must come to grips with the simultaneity, subjectivity and relative privacy of what is being experienced.

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By constrast, as developed in this lecture, a neural systems analysis of the brain-behavior relationship, which takes into account processing levels, allows the perceptual experience to be analyzed into basic functional modules which are at the same time separable and interpenetrating.

However, care needs to be maintained when the functions of separate neural systems are identified. It seems deceptively easy, but is inadmissable, to completely identify neural system function with behavioral system function. The mistake of slipping into a category error plagues all of physiology. The function of the lungs is readily identified as respiration; but respiratory functions include those of red blood cells and the membrane exchange of O_2 and CO_2 as well as the lung's inspiratory/expiratory cycles which make the other aspects of respiration possible. The models that describe inspiration/expiration by the lungs are considerably different from those describing oxygen transport by the hemoglobin of red blood cells.

The issues are the same when it comes to relating the physiology of receptors and of the nervous system to behavioral functions including the ones reported as perceptions. There can be no simple model of "perception" or even "pattern recognition", which encompasses the functions of receptors, primary sensory receiving stations and those brain systems associated with them, any more than one can develop a simple model of "respiration".

In the current lecture these issues are handled in two ways: 1) an attempt is made to sharply distinguish models based on observations made at the behavioral level of psychophysics and perception from those at the neural systems, neuronal and subneuronal levels. The distinction is implemented according to whether models describe <u>what</u> is being processed or whether they describe <u>how</u> processing is carried out by the nervous system. 2) Whenever possible, transformations, transfer functions, are described that relate the models at different levels to one another. It is the specification of these transfer functions that distinguishes computational from earlier mathematical and general systems approaches. The nature of the transfer functions is adduced from data obtained in neuropsychological observations in which both the brain and the situational variables controlling the behavioral reports of perceptual experience are specified.

Neural Systems

When the neurophysiology of perception is considered, a set of processes emerges, each served by a separate neural system. These systems are shown to act in concert with other neural systems that are related to them anatomically and/or biochemically. Three major divisions can be discerned in the sets of primate brain systems relevant to perception. The division is made on the basis of sense modality. In the posterior convexity of the cerebrum, processing is anchored in visual and auditory inputs ("distance" processing); in the frontolimbic forebrain, processing is anchored in olfactory/gustatory and in pain/temperature stimulation (thermochemical processing); midway, surrounding the central (Rolandic) fissure, processing is anchored in somatic sensibilities that allow the organism to be in proximate <u>touch</u> with the environment and, even more important, to directly <u>act</u> on, and thus alter it.

Within each division, there is a core of projection systems connected extrinsically, rather directly, with the receptors of the modality. Surrounding these projection systems are perisensory systems which process the input by controlling movements related to that input. Beyond these systems are others that are intrinsic in their connections, i.e., they primarily receive their input from and operate back on the sensory-motor systems. The intrinsically connected systems themselves are hierarchically organized: in humans, the systems involved in language almost exclusively utilize other intrinsic systems, and have few direct connections with receptors and effectors.

Within the class of systems involved in figural perception, those involved in imaging can be distinguished from those involved in the perception of object-forms. But, as experienced in awareness, the systems responsible for extracting the invariances (constancies) that characterize object forms, interpenetrate in a top-down, corticofugal fashion, those systems responsible for imaging. This top-down interpenetration is implemented by parallel connections. Such connections, now at a new level in the hierarchy, are found again when systems responsible for stimulus sampling and categorizing are considered, and once more when the systems concerned with relevance and with inference are studied. The fact that each level of processing entails both feedforward and feedback operations accounts for the paradox of the separable yet unitary nature of the perceptual experience.

This characterization of the relations between brain systems differs from the traditional view which has been limited to bottom-up, forward propagation from sensory projections to higher order "associative" systems. Flechsig (1896) had suggested that cognitions are derived exclusively by a process in which input from various senses becomes associated in the cortex of the posterior cerebral convexity - thus the term "association cortex". Flechsig's view is still widely held despite overwhelming evidence against it. (See e.g., Mishkin, 1973; Luria 1973; Kuffler and Nichols, 1976; Shepherd, 1988.)

The alternative to the traditional view is that the results of computation at the later level of processing are fed back to the earlier levels. The present approach is based on evidence for such reciprocal connectivity between hierarchically ordered neural systems. The resulting theory accounts for both the top-down and bottom-up constraints on processing. Top-down constraints constitute controls on lower level processes, much as programs constitute controls on the operations of computational hardware. Psychophysical data and theories map in experiential and behavioral languages those relations that determine the phenomena that need to be examined at the neural systems level. At the same time, neural system properties set the constraints on processing at the subneuronal, synaptodendritic, level of investigation.

Mutual, reciprocal bottom-up and top-down determination of processing leads to a selection procedure in which input is matched against a resident microstructure (genetically or experientially produced memory). The result of the match acts as does a set point on a thermostat (or homeostat) to instruct further processing. Of course the set point is not a point or single number as it is on a thermostat; rather, a multidimensional complex, a temporary stable state often referred to as an Image (e.g., a "motor image"), is what guides processing. At the same time, the details of processing need not be specified in the match, a

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In such a reciprocally acting set of systems, input <u>triggers</u> an operation which at any moment is largely self-determining. Further, the larger the amount of experience stored in the systems operating in a top-down fashion, the greater the self-determination. Thus Beethoven could compose the late quartets and his eighth and ninth symphonies despite the fact that he was completely deaf at the time of composition.

In short, in systems characterized by bottom-up, top-down reciprocity, selection characterizes a microprocess in which sensory and central inputs are matched with a resident microstructure. The results of the match instruct further processing. In systems endowed with memory storage, these interactions therefore lead to progressively more self-determination. Momentary input serves to trigger rather than specify the process.

Neurons

Neurons are ordinarily conceived to be the computational units of the brain. Thus the majority of processing theories since the seminal contribution of McCulloch and Pitts (1943) have taken the axonal discharge of the neuron, the nerve impulse, as the currency of computation.

However, this framework for computational theory has led to considerable misunderstanding between neuroscientists and those interested in computational processing. Successful computational networks depend on highly - often randomly - interconnected elements. The more complex the computation, the more connections are needed: the law of requisite variety (Ashby, 1960). Neuroscientists know that neurons are connected non-randomly, often sparsely, and always in a specifically configured fashion [see Crick and Asanuma (1986) for a neuroscience view of connectionist computational theory). In short, current computational processing emphasizes a minimum of constraints in the processing wetware or hardware; in the current neuroscience framework wetware is highly constrained.

Misunderstanding is alleviated when the computational framework is broadened to include the microprocessing which takes place within dendritic networks. Not only are axonal-dendritic synapses that connect neurons subject to local influences in these networks, but innumerable dendrodendritic synapses provide the unconstrained high connectivity needed in computational procedures (Bishop 1956; Pribram, 1960; 1971; Schmitt et al., 1976). In fact, a large proportion of neurons - in some systems, such as cortex, as high as 50 percent - do not have any axons at all. Their processing capability (primarily inhibitory) is purely dendro-dendritic.

Junctions (axo-dendritic and dendro-dendritic) between neurons in the form of chemical synapses, electrical ephapses and tight junctions occur within overlapping dendritic arborizations. These junctions provide the possibility for processing as opposed to the mere transmission of signals. The term "neurotransmitters" applied to chemicals acting at junctions is, therefore, somewhat misleading. Terms such as neuroregulator and neuromodulator convey more of the meaning of what actually transpires at synapses.

Nerve impulse conduction leads everywhere in the central nervous system to such junctional dendritic microprocessing. When nerve impulses arrive at synapses, presynaptic polarizations result. These are never solitary but constitute arrival patterns. When post-synaptic hyper- and depolarizations are then generated in dendritic networks of the brain, the polarizations are insufficiently large to immediately incite nerve impulse discharge. The patterns of these postsynaptic polarizations are constituted of sinusoidally fluctuating hyper- and depolarizations.

The dendritic microprocess thus provides the relatively unconstrained computational power of the brain, especially when arranged in layers as in the cortex. This computational power is well described by linear dynamic processes, in terms of quantum field neurodynamics.

Neurons are thresholding devices that spatially and temporally segment the results of the dendritic microprocess into discrete packets for communication and control of other levels of processing. These packets are more resistant to degradation and interference than the graded microprocess. They constitute the channels of communication not the processing element.

Communication via neurons often consists of dividing a message into chunks, labelling the chunks so that they are identifiable, transmitting the chunked message and reassembling it at its destination. Neurons are labelled by their location in the network. Because of the essentially parallel nature of neuronal connectivities, this form of labelling is highly efficient.

Neuronal channels constrain the basic linear microprocess. These structural constraints can be topologically parallel, convergent and divergent. An instance of a combination of these forms of constraint is the connectivity between retina and cerebral cortex which is expressed as a logarithmic function of distance from the foveal center. Other constraints shape the time course of computations and lead to learning. Unveiling the manner in which constraints are imposed in the natural brain is the work of the neurophysiologist. Much of what is contained in this lecture describes the results of this work.

Dendritic Microprocessing

Recognizing the importance of dendritic microprocessing allows a coherent theory to be framed regarding the neural functions responsible for perception. As initially stated in Languages of the Brain (Pribram 1971 p. 104):

> "Any model we make of perceptual processes must thus take into account both the importance of Imaging, a process that contributes a portion of man's subjective experience, and the fact that there are influence on behavior of which we are not aware. Instrumental behavior and awareness are often opposed - the more efficient a performance, the less aware we become. Sherrington noted this antagonism in a succint statement: "Between reflex action and mind there seems to be actual opposition. Reflex action and mind seem almost mutually exclusive - the more reflex the reflex, the less does mind accompany it."

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Languages then proceed to detail the fact that nerve impulses in axons and junctional microprocessing in dendrites function reciprocally. A hypothesis was formulated to the effect that when habit and habituation characterize behavior which has become automatic, there is efficient processing of dendritic "arrival patterns into departure patterns". On the other hand, persisting designs of junctional patterns are assumed to be coordinate with awareness. The hypothesis is consonant with the view that we are cognizent of some of the events going on in the brain, but not all.

Nerve impulses arriving at junctions generate dendritic microprocesses. The design of these microprocesses interacts with that which is already present by virtue of the spontaneous activity of the nervous system and its previous "experience". The interaction is modulated by inhibitory processes and the whole procedure accounts for the computational power of the brain. The dendritic microprocesses act as a "cross-correlation device to produce new figures from which the patterns of departure of axonic nerve impulses are initiated. The rapidly paced changes in awareness could well reflect the [pace of] duration of the correlation process." (Pribram 1971)

Historically the issues were framed by Lashley, Kohler and Hebb. Donald Hebb (1949) summed up the problem by pointing out that one must decide whether perception is to depend on the excitation of specific cells, or on a pattern of excitation whose locus is unimportant. Hebb chose the former alternative: "A particular perception depends on the excitation of particular cells at some point in the central nervous system."

As neurophysiological evidence accumulated (especially through the microelectrode experiments of Jung (1961): Mountcastle (1957); Maturana, Lettvin, McCulloch, and Pitts (1960); and Hubel and Wiesel (1962) this choice, for a time, appeared vindicated: microelectrode studies identified neural units responsive to one or another feature of a stimulating event such as directionality of movement, tilt of line, etc. Today, textbooks in psychology, in neurophysiology, and even in perception, reflect this view that one percept corresponds to the excitation of one particular group of cells at some point in the nervous system.

Lashley, profoundly troubled by the problem, took the opposite stance:

> "Here is the dilemma. Nerve impulses are transmitted over definite, restricted paths in the sensory and motor nerves and in the central nervous system from cell to cell through definite inter-cellular 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 acitivities of the nervous system and some hypothesis is needed to direct further research." (Lashley, 1942 p. 306)

Wolfgang Kohler also based his Gestalt arguments on such "masses of excitation ... within generalized fields of activity" and went on to prove their ubiquitous existence in the decade after the publication of Hebb's and Lashley's statements. A series of experiments in which I was involved established the existence of generalized fields but showed that, although they were related to the speed with which learning took place, they were unrelated to perception as tested by discrimination tasks (see <u>Languages of the Brain</u>, Chap. 6, for a review of these studies).

Lashley was never statisfied with either Hebb's or Kohler's position. His alternative was an interference pattern model which he felt would account for perceptual phenomena more adequately than either a D.C. field or a cell assembly approach. He did not, however, have a clear idea of how the process might work. He never specified the fact that the interference patterns were generated by arrivals of nerve impulses nor how such patterns provide a computational scheme for perception. He thus never developed an argument for the existence of a dendritic microprocess responsible for the computational power of the neuronal mechanism.

According to the views presented here and in keeping with Lashley's intuitions, this computational power is not a function of the "particular cells" and the conducting aspects of the nervous system (the axonal nerve impulses) nor is it necessarily carried out within the province of single neurons. At the same time, the theory based on these views does not support the notion that the locus of processing is indeterminate. Rather the locus of processing is firmly rooted <u>within regions of dendritic networks</u> at the junctions between neurons.

As summarized by J. Szentagothai (1985 p. 40): "The simple laws of histodynamically polarized neurons ... indicating the direction of flow of excitation ... came to an end when unfamiliar types of synapses between dendrites, cell bodies and dendrites, serial synapses etc. were found in infinite variety ... . A whole new world of microcircuitry became known ... culminating in a new generalized concept of local neuron circuits (Rakic 1976; Schmitt et al. 1976)."

The ubiquity of such axonless local circuit neurons indicates that computation is strongly influenced by dendritic-dendritic interactions which modify the postaxonal dendritic processes. Perceptual processing depends therefore on network properties that extend beyond the purview of the dendrites of a single neuron. It is the synaptic event, rather than the neuron per se, that serves as computational element.

The sub- and superneuronal aspect of the dendritic microprocess, its potential to extend beyond the single neuron, provides explanatory power for both older and recently accumulating evidence that brain processes cordinate with perception are <u>distributed</u>. In a distributed process, perceptual events are represented not by single neurons but by <u>patterns of polarization</u> across ensembles of neurons. E.R. John, on the basis of his extensive studies (reviewed in Thatcher and John, 1977) has come to a similar conclusion:

> "The spatiotemporal patterning of these cooperative processes ... (involve) ionic shifts ... with extrusion of potassium ions and ionic binding on extracellular mucopolysaccharide filaments. If we focus our attention not only on the membranes of single neurons, but upon charge density distributions in the tissue matrix of neurons, glial cells, and mucopoly-saccharide processes, we can envisage a complex, three-

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Basic to this new view of the neurology of perception is the fact that propagated nerve impulses are but one of the important electrical characteristics of neural tissue. The other characteristic is the microprocess which takes place at the junctions between neurons. Hyper- and depolarizations of postsynaptic dendritic membranes occur at the junctions between neurons where they may even produce miniature electrical spikes. However, these minispikes and graded polarizations also differ from nerve impulses in that they do not propagate. The influence of these minispikes and graded polarizations on further neuronal acitivity is by way of "cooperativity" among spatially separated events. Cooperativity is mediated by the cable properties of dendrites and the surrounding glia (see e.g., Poggio and Torre, 1980). This type of interaction is called "non-local" because the effect is exerted at a distance without any obvious intervening propagation. By analogy the effect is also called "jumping" or "saltatory" as in saltatory conduction by myelinated nerve fibers. It is this saltatory nature of the interactions as captured by perceptual experience that fascinated Frank Geldard, experiences so clearly described in his inaugural MacEachron Memorial Lecture (1975).

Receptive Fields

The neurophysiologist can readily study the output - spike trains - of neurons when they act as channels, but he has only limited access to the functions of the interactive dendritic junctional architecture because of the small scale at which the processes proceed. A major breakthrough toward understanding was achieved, however, when Kuffler (1953) noted that he could map the functional dendritic field of a retinal ganglion cell by recording impulses from the ganglion cell's axon located in the optic nerve. This was accomplished by moving a spot of light in front of a paralyzed eye and recording the locations of the spot which produced a response in the axon. The locations mapped the extent of the responding dendritic field of that axon's parent neuron. The direction of response, inhibitory or excitatory, at each location indicated whether the dendrites at the location were hyperpolarizing or depolarizing.

The resulting maps of dendritic hyper- and depolarization are called receptive fields. The receptive fields of retinal ganglion cells are configured concentrically: a circular inhibitory or excitatory center surrounded by a penumbra of opposite sign. This center-surround organization has been shown to be due to the operation of axonless horizontally arranged dendritically endowed neurons which produce "lateral" inhibition in the neighborhood of excitation and vice versa. The center-surround organization thus reflects the formation of a spatial dipole of hyper- and de-polarization, an opponent process fundamental to the organization of the configural properties of vision.

Utilizing Kuffler's techniques of mapping, Hubel and Wiesel (1959) discovered that at the cerebral cortex the circular organization of dendritic hyper- and depolarization gives way to elongated receptive fields with definite and various orientations. They noted that oriented lines of light rather than spots produced the best response recorded from the axons of these cortical neurons. They therefore concluded that these cortical neurons were "line detectors". In keeping with the tenets of Euclidean geometry where lines are made up of points, etc., Hubel and Wiesel suggested that line detectors were composed by convergence of inputs from neurons at earlier stages of visual processing (retinal and thalamic) - which acted as spot-detectors due to the circular center-surround organization of the receptive fields. The Euclidean interpretation of neuronal processing in perception became what Barlow (1972) has called the neurophysiological dogma. The interpretation led to a search for convergences of paths from "feature detectors" such as those responding to lines, culminating in "pontifical" or "grandfather" cells which embodied the response to object-forms such as faces and hands. The search was in some instances rewarded in that single neurons might respond best to a particular object form such as a hand or face (Gross 1973). However, response is never restricted to such object-forms. Such "best" responses can also occur in parallel networks in which convergence is but one mode of organization.

About a decade after the discovery of elongated visual receptive fields of cortical neurons, new evidence accrued that discredited the view that figures were composed by convergence of Euclidean features. In our laboratory at Stanford University we mapped the architecture of cortical dendritic fields by computer and found cortical receptive fields that contained multiple bands of excitatory and inhibitory areas (Spinelli and Barret 1969; Spinelli, Pribram and Bridgeman 1970). In Leningrad similar observations were made by Glezer (Glezer, Ivanoff and Tscherbach 1973) who remarked that these cortical neurons responded more like "stripedness" (than line) detectors. The critical report, however, was that of Pollen, Lee and Taylor (1971) who interpreted similar findings to indicate that the cortical neurons were behaving as Fourier analyzers rather than as line detectors.

At the same time Campbell and Robson (1968), initially on the basis of psychophysical, and subsequently, also on the basis of neurophysiological exeriments, developed the thesis that vision operates harmonically much as does audition except that the visual system responds (by virtue of a Fourier process) to spatial frequencies. Here I want to introduce the critical difference between Euclidean based geometric and Fourier based harmonic approaches.

For those using the geometric approach, spots and lines are seen as elementary features that become combined in ever more complex forms as higher levels of the neural mechanism are engaged. When a harmonic analysis is taken as the approach, the elongated receptive field organization of cortical neurons suggests that neurons act as "strings" tuned to a limited bandwidth of frequencies. The ensemble of strings compose resonators or active filters as in musical instruments. Helmholtz, a century ago, proposed that sensory receptors are akin to a piano keyboard, that a spatially isomorphic relation is maintained between receptor and cortex as in the relation between keys and strings attached to the sounding board of the piano, but that each cortical "unit" responds (resonates) to a limited band width of frequencies much as do the strings attached to the piano's sounding board. From the

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The geometric and harmonic views differ significantly with respect to the composition of a percept. Irwin Rock (1983 p. 96) describes this difference as follows :

> "One confusion here may be with the meaning of "feature". A feature could refer to an identifiable part or unit that must first be extracted or detected, and then along with other features assembled into an overall pattern. Or "feature" could refer to an identifiable emergent characteristic of the form once it is achieved rather than as one of the parts that produces it."

The details of the neurophysiological data show that "features" such as lines are best conceived as identifiable emergent characteristics of form since they are already conjoined in the receptive field. Further such "features" become activated either by sensory input or by central process to configure a percept. This evidence makes the "resonating string metaphor" more reasonable than the feature detector approach. There are three critical reasons for preferring tuned frequencies to detected features: 1) neurons in the visual cortex respond to several "features" of sensory input and there is no evidence that the different features are represented separately in the output of the neuron, as would be required if it acted as a detector; 2) tuned frequencies provide a potentially richer panoply of configuration (e.g., texture), and 3) perceptual research has clearly shown that lines (and therefore line detectors) composing contours are inadequate elements with which to account for the configural properties of vision.

Rock (1983 p.43) summarizes the evidence and argument as follows:

> "The emphasis on contour detection is entirely misplaced because, as far as form is concerned, a contour simply marks or delineates a location. What matters for form perception is the set of all such locations; and if these can be delineated without contours, contours are not necessary. That is why, in addition to depth, we perceive regions of particular shapes in two random dot patterns viewed binocularly despite the absence of any physical contours (Julez 1971). Illusory contours ... also support this conclusion."

Rock provides the results of innumerable experiments to document: his insight that the configural properties of vision are due to a "process of directional integration" (p. 47). The most critical is the demonstration that "the perceived direction of a point with respect to ourselves ... is a joint function of retinal locus and eye position" (p. 46).

In summary, sensory cortical receptive fields are considered analogous to resonating strings in a piano. The functional relationship among strings (among the receptive fields of the sensory cortex) and with the keyboard (with the sensory receptors) is spatially organized and provides a macrolevel of perceptual processing. The functional relationship among resonant frequencies, characteristic of overlapping receptive fields of the cortical neurons, provides a microlevel of perceptual processing. It is this cooperative microprocess which allows one to assume that indeed a specific brain process is coordinate with the richness of experience that is perception.

Plasticity

Cooperativity, implemented in dendrodendritic synapses, makes possible parallel distributed processing of considerable flexibility within a single processing layer. Further, in multilayered networks *selective* modification can occur provided the *presynaptic* network becomes influenced by iterations of input. Such an arrangement is often referred to as the Hebb rule because Donald Hebb (1949) captured the imagination of the broad scientific community when he called attention to the fact that *selective* modification is dependent on presynaptic effects. The importance of this presynaptic requirement had been familiar to many neuroscientists for a half-century: e.g., Freud in his *Project for A Scientific Psychology* (1895/1966) ascribes selective learning to the restricted lowering of certain synaptic resistances by the absorption of energy (precathexis) at the presynaptic site due to repeated use. It is *the actual mechanism* by which such selective changes can occur that has taken a century to unravel (see e.g., Stent 1973; and discussion in *The Anatomy of Memory*, Ed. Daniel Kimble 1965).

The holonomic brain theory presented in the next section is based on a *radical* extension of this rule: a microprocess is conceived in terms of *ensembles* of mutually interacting pre- and postsynaptic events distributed across limited extents of the dendritic network. The limits of reciprocal interaction vary as a function of input (sensory and central) to the network - limits are not restricted to the dendritic tree of a single neuron. In fact, reciprocal interaction among pre- and postsynaptic events often occurs, is correlated, as in developing perceptual constancies, and is self-organizing. For other kinds of computation, structured constraints must be imposed on the networks. These constraints can come directly by way of sensory input or they can be imposed from within the brain. The centrally imposed top-down constraints are generated by a variety of brain systems which preprocess at the midbrain and thalamic level the input to the primary sensory cortex. These top-down preprocessing procedures, organized by prior experience, are those that constitute the cognitive aspects of perception.

Paralinearity

The cooperative stages of sensory processing are described in the theory of paralinear computations. Nonlinearities enter only as auxilliaries which sharpen the computational process. The locus of entry of nonlinearities can thus be identified without jeopardizing the advantages which accrue to the overall linearity of the operation of the brain systems involved in configuring percepts.

A beginning in making the distinction between overall linearity and the entry of nonlinearities comes from analyzing the relevant dynamics of neural processing. The input to the brain is in the form of modulations of nerve impulse trains, modulations initiated in receptor activity. Similarly, the output to muscles and glands is in the form of

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spatially and temporally patterned trains of nerve impulses. There are, of course many stages of processing intervening between input and output. At each of these processing stations, four types of transformation take place. Walter Freeman (1989 and private communication) has described these stages in the following passages:

> "At the first stage pulses coming in to a set of neurons are converted to synaptic currents, (patterns of hyper- and depolarizations) which we call waves. Second, these synaptic currents are operated on by the dendrites of the neurons. This involves filtering and integration over time and space in the wave mode. Third, the wave activity reaching the trigger zones is converted back to the pulse mode. Fourth, it then undergoes transmission, which is translation from one place to another, delay, dispersion in time, etc. The operations of filtering, integration and transmission can be described with linear differential equations. Pulse to wave conversion at synapses is commonly thought to be nonlinear, but in fact in the normal range of cortical operation it is linear. Multiplication by a constant suffices to represent the conversion from a density of action potentials (pulse density) to a density of synaptic current (wave (i.e. polarization amplitude)). But the operation of wave to pulse conversion is nonlinear, and the trigger zone is the crucial site of transformation that determines the neural gain over the four stages."

These passages contain the key elements of the holonomic brain theory presented in the next section, in which "the operations of filtering, integration and transmission can be described with linear differential equations" and "pulse to wave conversion at synapses is commonly thought to be non-linear, but in fact, in the normal range of cortical operation is linear." It is only at the axon hillock where nerve impulses are generated that "wave to pulse conversion is nonlinear." In the holonomic approach, the configural aspects of perception are coordinate with synaptic and dendritic processing; modelling can therefore take advantage of the attractive features of linearity. This leaves to conducted nerve impulse activity the role of imposing nonlinear constraints and of communicating the results of processing at one brain location to another such location. Signal transmission with its attendant gain control (as indicated by Freeman) necessitates the introduction of nonlinearities. But (again, as Freeman notes) pulse to wave conversion at synapses once more linearizes the system. Thus the unconstrained dendritic computational microprocess in perception is essentially linear.

Understanding the neural basis of the imposition of nonlinearities in constraining the basically linear junctional microprocesses is illustrated by the work of Poggio (1985). Poggio has come to the following views (p. 317):

> "(An) analog parallel model of computation is especially interesting from the point of view of the present understanding of the biophysics of neurons, membranes and synapses. Increasing evidence shows that electrotonic potentials play a primary role in many neurons. Mechanisms as

diverse as dendrodendritic synapses, gap junctions, neurotransmitters acting over different times and distances, voltage-dependent channels that can be modulated by neuropeptides and interactions between synaptic conductance changes provide neurons with various different circuit elements. Patches of neural membrane are equivalent to resistances, capacitances and phenomenological inductances. Synapses on dendritic spines mimic voltage sources, whereas synapses on thick dendrites or the soma act as current sources. Thus, single neurons or small networks of neurons could implement analog solutions ..."

When the constraints on processing are asymmetrical, as for instance, when excitatory and inhibitory inputs are spatially or temporally asymmetrical (Poggio and Torre, 1983) directional selectivity results. Such asymmetries impose nonlinearities on the basically linear analog microprocess.

The issue of linearity with regard to cortical processing in visual perception has recently been addressed in a comprehensive review by Shapley and Lennie (1985): "The idea (that within patches of receptive field, linearity is maintained) is an attractive one because it is consistent with the narrow spatial frequency tuning and spread of best frequencies of cortical neurons but is weakened to the extent that the neurons behave non-linearly" (p. 572). As noted, these nonlinearities are a function of the outputs of neurons which depend on gain control at the axon hillock. The nonlinearities are thus introduced primarily into the perceptual microprocess in the form of overall retinal to cortical mapping which is spatially logarithmic (Schwartz, 1977). However, in addition to the effects on the perceptual macroprocess, "... the nature of some of these nonlinearities suggests that they are precisely what make the cells highly tuned spatial frequency filters" (Shapley and Lennie 1985, p. 575).

The configurations (i.e., the internal architecture) of the receptive fields of visual cortical neurons can be described in terms of <u>spatial</u> frequency: Recordings of axonal impulse responses of the cortical neuron show that the stimulus which best engages these cortical neurons is a (sine wave) grating (composed of regularly spaced bars of widths equal to those of the spaces) which is drifted across the visual field. The spatial frequency of the gratings which engages the spatial frequency of the receptive field is determined by the widths of the bars making up the grating and the spacings between them. The range of spatial frequencies to which the cortical neuron responds determines the bandwidth of the tuning curve. This band width is approximately an octave (± 1/2 octave) (see review by DeValois and DeValois, 1980).

These experimental results have led to the view that the neural processes involved in spatial vision are akin to those involved in audition. Harmonic analysis is therefore an appropriate tool for developing a computationally realizable theory of the neural processes involved in the configural aspects of perception.

The simplest and most fundamental of the tools of harmonic analysis is the Fourier decomposition, which represents a spatial or temporal pattern by a set of regular oscillations differing in amplitude and frequency. Each regular oscillation is in turn decomposed into sine and cosine components, which differ only in that they are 90° out of

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phase. The phase of each of the regular oscillations with respect to the others differing in frequency, is encoded by a ratio which is called the Fourier coefficient. Computation of the Fourier representation of <u>oriented gratings</u> in terms of their coefficients has more successfully predicted the responses of cortical neurons, than has the display of oriented <u>single</u> lines or bars of various widths (DeValois, Albrecht and Thorell 1978). At the neural microprocessing level, the holonomic brain theory is thus not only computationally simpler, especially with respect to calculating correlations, than non-linear theory but is more accessible to test.

However, each of the sinusoidal Fourier components extends to infinity. Cortical receptive fields are bounded. The limit on the functional receptive field of cortical neurons is produced not only by the anatomical extent of the dendritic field of a single neuron, but also by inhibitory (hyperpolarizing) horizontal networks of dendrites that interpenetrate overlapping excitatory (depolarizing) fields.

These bounded receptive fields provide the data reviewed by Shapley and Lennie (1985) which were obtained using harmonic analysis. They note that the existence of nonlinearities has caused advocates of the Fourier approach "to propose that the spatial image may be analyzed into spatial Fourier components over small patches of visual field." This "patch" technique of Fourier analysis was pioneered for radioastronomy by Bracewell (1965) and then applied to neurophysiology by Pollen, Lee and Taylor (1971); Pribram (1971); Robson (1975) and Glezer (1985). For the brain cortex each patch is configured by a simple cortical receptive field.

State of the Art

Currently, several formalisms have been adopted to construct theories of perception similar in character to the holonomic approach taken in this lecture. For example Ginsberg (1971), Caelli (1984), Watson and Ahumada (1983), Hoffman (1984), Dodwell (1984), Cutting (1985), Cavanagh (1984, 1985) and Palmer (1983) have presented models which, however, are primarily psychophysical. These encoding schemas aim to explain in one model the full range of phenomena involved in pattern recognition by a variety of correlational methods (e.g., those of Anderson et al. 1977; Kohonen 1977), holographic filters (Cavanagh 1975; 1976), or Lie group manifolds (Hoffman 1984, Dodwell and Caelli 1984). The theories thus differ from the holonomic brain theory in that they do not address the variety of <u>brain systems</u> involved in perception.

Kronauer and Zeevi (1985) have independently summarized the essentials of the neural microprocesses upon which the holonomic brain and similar theories are based :

> "The operation in question obviously cannot be a global Fourier transformation or, for that matter, any simple harmonic decomposition scheme, since we are dealing with a space (position)- dependent system whose characteristics are inhomogeneous. At best, therefore, we may consider a possible "short distance" spectral decomposition analogous to the time-frequency domain spectrogram so widely used in speech analysis."

Flanagan (1972) and before him Gabor (1946) had shown that in a communication there is a tradeoff between accuracy in the spectral domain and accuracy in the time domain. In fact the unit they found to be most useful to represent and analyze a communication (e.g. speech) was a time-limited sinusoid, (repetitive waveform) of specified frequency. It is this unit which forms the basis of the holonomic brain theory.

For vision, the sinusoid is space-limited (as well as time limited). As space is at least two dimensional, measurement entails at a minimum two dimensions of "spatial frequency". But, as Kronauer and Zeevi (1985 p.99) point out, the tradeoff between space and frequency has consequences:

> "Thus, as every engineer well knows, sharpening up the spatial resolution results in a spread of the spatial-frequency characteristics, and vice versa. Does this conclusion, based on pure communication theory considerations, bear any relevance to better understanding of cortical engineering design and signal processing in the visual system? Recent studies indicate that, in fact, cortical neurons in area 17 respond in a way that is localized both in space and in spatial frequency (Maffei and Fiorentini 1973; Andrews and Pollen 1979; Tootell et al. 1981; Movshon et al. 1978), in the sense that a cell's stimulus domain exists in a certain well-defined region of visual space (the so-called receptive field) and is also localized in spatial-frequency to a limited range of luminance-periodicity-modulation. Proceeding from photoreceptors through ganglion- and LGN-cells to cortical simple cells, one finds a progressive loss in localizability of positional information (at the single cell level of operation) and a decrease in spatial frequency bandwidth."

This relationship between space and frequency is fundamental. A convenient way to picture it is to recall the previous metaphor of a piano as developed by Helmholtz (1863) and Ohm (1843) to describe the auditory system. At a macro level of organization, the keys of the keyboard (the receptors) are spatially arranged with respect to one another and this spatial arrangement is maintained in the connectivity between keyboard and the strings of the sounding board. It is at the micro level of individual strings (the cortical cells) that the frequency mode of response occurs: each string resonates at a limited bandwidth of frequency. We are well acquainted with the richness of sensory experience that can be generated by such an arrangement.

Further, Kronauer and Zeevi indicate, as above, that this micro level frequency response is carried out within the functional receptive field, i.e., the dendritic microprocess of junctional polarizations.

> "The response characteristics of a cortical simple cell can conveniently be described in terms of a receptive field profile (the cell's kernel) that specifies its excitatory and inhibitory substructures. Typically there appear to be two major subclasses of simple-cell receptive field profiles: bipartite ("edge" type) and tripartite. Careful analysis

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> of the receptive fields, reconstructed from spatial-frequency selectivity measurements, indicates additional "ringing" reminiscent of Gabor's elementary function (Andrews and Pollen 1979). Most interesting, however, is the finding that pairs of simple cells that are adjacent in the cortical tissue and have the same preferred orientation are tuned to the same spatial frequency and respond to drifting sine wave gratings 90 out of phase, spatially (Pollen and Ronner 1980). Thus, the fact that cortical neurons balance the position/frequency trade-off by possessing both some spatial retinotopic localization and, at the same time, a spatial frequency bandwidth of about one octave with matched sine and cosine (phase quadrature) cell pairs, suggests that important kinds of visual processing are going on in both domains (Zeevi and Daugman 1981)." (Kronauer and Zeevi, 1985 p. 100)

One of the advantages of processing in both spatial and frequency domains is economical coding. This is due to the efficiency of encoding when uncertainty with regard to frequency and place (in space and time) are minimized. Kronauer and Zeevi (1985 p. 100) point this out in the following passage:

> "Some recent theoretical studies have emphasized the principle of economical coding (minimal representation) for the cortex (e.g., Sakitt and Barlow 1982). In view of the high-functional multiplicity found in the cortex, this emphasis seems misplaced. Yet, it is true that, from several view points, the processing is economical. The receptive field patterns of simple cells come very close to minimizing uncertainty in the four-dimensional space comprised of two spatial and two frequency coordinates (Daugman 1980, 1984). Moreover, it seems that no two cells perform the same functions, so there is no wasteful redundancy in the simple sense."

This type of economical encoding is achieved by an <u>ensemble</u> of receptive fields. The advantages of such coding are critical: transformations between frequency spectrum and spacetime are readily accomplished since the transform is invertable. This makes the computing of correlations easy. In addition, the property of projecting images away from the locus of processing (as by a stereo system and by a hologram) and the capacity to process large amounts of information are inherent in holonomic processing. As these properties are also the ones that characterize figural awareness, they make a good point of departure for constructing a theory of brain organization in perception.

II. Outline of the Holonomic Brain Theory

> "Fourier's theorem is probably the most far-reaching principle of mathematical physics." (Richard Feynman 1963)

> "Linear systems analysis originated in a striking mathematical discovery by a French physicist, Baron Jean Fourier, in

1822 ... (which) has found wide application in physics and engineering for a century and a half. It has also served as a principle basis for understanding hearing ever since its application to audition by Ohm (1843) and Helmholtz (1877). The successful application of these procedures to the study of visual processes has come only in the last two decades." (DeValois and DeValois 1988 p.3)

Inception of the Formalism

In this section the holonomic brain theory is outlined. The theory has several roots. As noted previously, historically it developed from Lashley's (1942) concern that the specific connectivities of the nervous system cannot account for the observation that: "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" (p. 306). Lashley drew on suggestions by Loeb (1907) and Goldscheider (1906), that the configurations experienced in perception might derive from excitation in the brain resembling the "force fields" that determine form during embryogenesis. Goldscheider had suggested that lines of force are developed when sensory input excites the brain. Lashley noted that such lines of force would form interference patterns in cortical tissue. However Lashley remained perplexed regarding the neurophysiological origins of these interference patterns and how they might generate the configurations of the experiences and behavior under consideration.

The limitations of understanding the interference pattern model began to yield to further inquiry with the advent of optical holography. This invention made it possible to specify how interference patterns could account for image (re)construction and for the distributed nature of the memory store (Van Heerden 1963; Julez and Pennington 1965; Pribram 1966; 1971; 1975). A holographic hypothesis of brain function in perception was developed into a precise computational model of brain function on the basis of the mathematics which had made holography possible (see e.g. Barrett, 1969; Pribram, Nuwer and Barron, 1974). The computational promise and firm neurophysiological base of this model was perceived by many scientists as a starting point for what has become the "connectionist" parallel distributed processing approach to modelling brain function in perception and learning (e.g., Anderson and Hinton; Willshaw; both in Hinton and Anderson 1961).

Despite this acknowledgement of promise, objections, some more precisely stated than others, were raised regarding the holographic model per se. Certain initial objections were based on an incorrect analogy between the <u>paraphenalia</u> of early optical information processing techniques (such as coherent reference beams) though these were shown very early on to be unnecessary (Pribram, Nuwer and Barron 1974; Leith 1976). Other objections derived from a misidentification of the "waves" involved in holography as somehow representative of the brain waves recorded from the scalp. Macroscopic waves cannot possibly carry the amount of information necessary to account for the processing requirements involved in perception. On the other hand, spatial interactions among junctional microprocesses occurring in dendritic networks can provide the basis for extremely complex processing (Pribram 1971 Chap. 8).

A more germane objection came from the fact that the mathematics involved in holography as developed by Gabor (1948), centered on the Fourier theorem. In psychophysics, therefore, it was sometimes held that the transfer function computed by the sensory system was a global Fourier transform, thus spreading the input over large extents of cortex. This was shown to be an untenable position for psychophysics (Caelli and Julez 1979). However, the neurophysiologists who had initially formulated the hypothesis with regard to brain function had *always* noted that *the transfer functions involved are limited to particular receptive fields* and that more complex relations determine processing of ensembles of such fields (Pribram 1966; Pollen Lee and Taylor 1971; Pollen 1973; Pribram, Neuwer and Barron 1974; Robson 1975).

However, the fundamental difficulty for understanding has to do with the nature of the Fourier relation itself. The Fourier theorem holds that any pattern can be analyzed into a set of regular, periodic oscillations differing only in frequency, amplitude and phase. The Fourier transform of such a pattern is described as a spectrum composed of coefficients which represent the amplitudes of the intersection (quadrature) of sine and cosine components of the various frequencies present in the pattern. The medium of optical holography, the silver grains of the photographic film, encodes these coefficients. The effects of reinforcement and occlusion at the intersections among wave fronts are encoded, but not the wave fronts themselves. The sites of intersection form nodes of varying amplitude which are represented numerically by Fourier coefficients. Thus, the holographic model of brain function has to be described in terms of a complex spectral representation. Often description was made solely in terms of wave form per se; sometimes the spectral representation, because of its counterintuitive nature, was discounted.

Much of the confusion was due to confounding two dualities: a wave vs. particle duality, on the one hand, with a space-time vs. energy-momentum duality on the other. The Fourier transformation expresses the space-time vs. energy-momentum duality. The wave vs. particle duality is expressed by another transformation (the Lorenz-Einstein, as in the photoelectric effect): This transform is between energy expenditure per unit time and the momentum of a mass (particle) in space.

Dirac (1951) introduced a concept which in the hands of Feynman (1963) has proved a powerful instrument in relating these two dualities to one another. The concept is called the least action principle. This is an optimization principle. The principle claims that the *path* of a particle in a space characterized by relations among oscillations (which, as will become evident, is a phase space) will tend toward the least expenditure of energy (i.e., make waves of least amplitude). The reason for this is that energy and momentum are conserved in any physical interaction (the conservation laws).

Holographic theory is based solely on the "either-or" Fourier duality between spacetime and spectrum. The holonomic brain theory incorporates this duality but is additionally based on the delineation by Gabor of a "phase space" in which the complex of spacetime *and* spectrum become embedded. In such a phase space, spacetime considerations constrain an essentially spectral computation. It is in this complex coordinate space that the least action principle is applied.

The holonomic brain theory thus aims to go beyond the earlier formulations of the holographic hypothesis and to extend the scope of computability. The term holonomic was chosen to distinguish it from holographic and still connote that it is "holistic" and lawful (Webster's 3rd International dictionary defines holo = whole; nomic = having the general force of natural law, i.e., is generally valid). In mathematics the term "holonomic" was first used by Hertz. As such it referred to structural constraints by which a set of original coordinates can be expressed by more generalized (Lagrangian) coordinates. In this usage the term was applied only to space (and time) coordinates. Here usage is extended to include the spectral domain (which as noted is the Fourier transform of spacetime). In contrast to a purely holographic theory, therefore, the inclusion of spacetime coordinates in the holonomic theory incorporates the operation of structural constraints in processing.

The formal, mathematical foundations of the computations which contribute to the holonomic brain theory rest on four fundamental concepts and the relations between them. Only one of these basic conceptions is familiar - that of spacetime, and even here, only in the 20th century has it been formally realized that space and time are intimately related through movement. The second basic conception is 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 amplitude moduluations of these oscillations. As noted, it is this spectral aspect of processing that was the foundation of the holographic hypothesis of brain function in perception. In the case of surfaces and forms this aspect is described in terms of <u>spatial</u> frequencies of oscillation. In fact, due to the Fourier transformation, spectra enfold the ordinary conception of both space and time.

A third 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. This is <u>the uncertainty relation</u> as used by Gabor (1946) to describe a fundamental unit, <u>a "quantum" of information</u>. This unit differs from the unit of information defined by Shannon, usually taken as a bit (a binary digit), a Boolean choice between alternatives (Shannon and Weaver 1949). However, Shannon also defined information as a <u>reduction of uncertainty</u>. 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 provides the basis of the distinction between the configural and the cognitive aspects of perception.

The fourth concept basic to the holonomic brain theory emphasizes the manner in which optimization is achieved in perception. Dendritic microprocessing is conceived to take advantage of the uncertainty relation to achieve optimal information processing. The holonomic brain theory concerns the efficiency with which processing proceeds - efficiency based on spectral resolution obtained by sharpening the tuning of receptive field properties.

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The Holoscape: Spacetime, Spectra, and Quanta of Information

The holonomic brain theory 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. Reality 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 the spectrum of the pattern. Thus 1) spacetime, and 2) spectrum are differentiated by the Fourier procedure whereas in the Gabor relation they become two orthogonal sets of coordinates.

Gabor's interest in a joint spacetime-spectral domain stemmed from telecommunication. Whereas telegraphy depended on a Morse or similar code which was readily seen to be composed of discrete elements, telephone communication utilized the spectral domain. It took some time to realize that efficient communication in this domain entailed signals coded as Fourier coefficients. In addition, however, signal transmission takes time. Nyquist (1924) and Kupfmueller (1924) pointed out that there is a relation between the rate of transmission and bandwidth. Hartley (1928) formalized this relation by noting that to transmit a given "quantity of information" a product of bandwidth x time is required. Hartley's formulation not only anticipated Gabor but also Shannon: he proposed that information was selective in that communication depends on a pre-existing alphabet of possibilities, and further, that the selective process is logarithmic. (An excellent review of this history has been written by Colin Cherry, 1978).

Note that with Hartley, communication and process begin to merge: the processing of information depends on communication and communication depends on processing. In communications systems that depend on processing it is practical to ask how efficient a process can be in order to facilitate communication.

Hartley's law indicates that there is a tradeoff between bandwidth and the time taken to process/communicate a set of signals: the greater the number of frequencies utilized, the more densely the signals are packed per unit time, the less time (or distance along a medium) is required. This distance-density relation is fundamental to many levels of processing in the holonomic brain theory as will become evident.

Gabor (1946) noted that there is a limit to the efficiency with which a set of signals can be processed and communicated. This limit is due to 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 band width 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 communication/processing 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 (Dirac or delta) 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 phase space or "Hilbert space", as Hilbert originally devised the mathematics used by Heisenberg and Gabor.

There are, however, some pitfalls inherent in the Gabor approach. Gabor's use of the Hilbert space representation deals only with steady states, when what needs to be represented is a process. The holonomic brain theory avoids this pitfall by generalizing the Gabor function and adhering to the reality implicit in the Fourier relation: there is in fact good evidence (Pribram and Carlton, 1986) that the Gabor elementary function can be pushed toward the spectral domain (as in holography) or toward the spacetime domain (as in ordinary photography) almost, if not quite, to the limit. Iterations of successive applications of the Fourier transform, such as differences of offset Gaussians; Gaussians times Hermite polynomials and, in general, 4D informational hyperspaces are thus, in empirically determined situations (e.g., Stork and Wilson), a better representation of process than the Gabor representation (see e.g., Weisstein and Harris, 1980; Yevick 1975; Weisstein, 1980). Structural (spacetime) constraints can thus operate not only as initial conditions as in the Gabor representation, but also as ongoing operations constraining the dendritic microprocess (Daugman 1985).

The holonomic brain theory takes as its starting point the description of logons (Gabor elementary functions) which are composed of several receptive fields. As noted previously, 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 sine-cosine quadrature pair. Thus a module of receptive fields encodes the quadrature relation (i.e., the sine and cosine components that make up Fourier and Gabor coefficients). Each logon, that is, each such receptive field module, is a channel. According to Gabor, the ensemble of such channels is a measure of its degrees of freedom, the number of distinguishable dimensions or features (e.g., spatial and temporal frequency, degrees of orientations, preferred direction, color). The minimum uncertainty relation expressed by Gabor elementary functions

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The holonomic brain theory, by generalizing both the Gabor and the Fourier theorems, allows for the operation of a process. In addition, the theory further develops Gabor's insight, and goes on to encompass ensembles in which multiple minima must be achieved by uncertainty reduction. The theory thus converges on thermodynamic and Shannon (Shannon and Weaver 1949) information processing modes of explanation. The next sections discuss these relationships.

The Occam Network and the Boltzmann Engine

Given an ensemble of channels with logon properties, there are as many minima of uncertainty as there are channels. This provides the theory with an additional important root. Recently, Hopfield (1982) and also Ackley, Hinton and Sejnowski (1985) - who called their model a Boltzmann engine - proposed implementations of statistical mechanics and thermodynamics in computational models of parallel processing arrays. These implementations address the problems of learning, memory storage and retrieval. The thermodynamic processor is one of several current "connectionist" models which are implemented as content-addressable multilevel parallel processing arrays. They are thus similar to a content addressable network called Occam which was developed and implemented in our laboratory in the 1960's (Spinelli, 1970; Pribram, 1971).

Occam describes modules constisting of cortical columns each of which is composed of input and operator neurons, and of interneurons and test cells. An input to overlapping receptive fields of input neurons becomes distributed to the receptive fields of interneurons which in turn connect to those of operator neurons. The receptive fields of interneurons are tunable - i.e., they adapt and habituate, they have memory. Each interneuron thus acts like a bin in a computer that stores the averages of the part of the patterns of input to which it is exposed. The ensemble of receptive fields (bins) stores the averages pattern. Only when a pattern is repeated does structured summation occur - nonrepetitive patterns simply raise the baseline and average out. Thus the receptive fields of operator neurons, sensitive solely to patterns of averages, are activated only when input patterns are repeated.

This procedure provides a primitive implementation of the least action principle: the paths by which polarizations are matched become "shortened" as processing proceeds. This shortening of the processing path is enhanced by feeding the output from the operator neuron back onto the receptive fields of the input cells via test neurons that compare the pattern of neural activity in the input and operator neurons. When a match is adequate, the test cell produces an exit signal, otherwise the tuning process continues. In this fashion, each cortical column comes to constitute a region of minimum uncertainty, an engram (a memory trace), by virtue of its specific sensitivity to one pattern of neural activity.

Each cortical column is connected with others by horizontal cells and their basal dendrites, which are responsible for inhibitory interactions. Whenever these horizontal cells are activated asymmetrically, as they are by directional sensitive inputs, a temporary structure composed of several columns becomes functionally connected.

These extended structures on modules are thus dependent for their extent on dendritic hyperpolarizations in local circuit neurons which are axonless, and not on nerve impulse transmission in axons.

The current connectionist models have a similar, though more generalized architecture. They are also composed of three or more reciprocally acting layers. Most compute the pattern to be stored by taking the least mean square of the difference between the stored and the input pattern. This enhances optimization (the least action principle) by doing away with the necessity of raising a baseline as in the earlier model. The recent connectionist models are therefore error-driven and go a step beyong Occam in that Occam models only the initial template (the "adaptation level" of the response to input) which, in current connectionist procedures, becomes the "goal" of processing.

The thermodynamic version of the connectionist models consists of elements (conceived to be neurons interconnected by synapses) which constitute an array in which neighboring elements mutually influence one another in a more or less symmetrical fashion. Ordinarily, the generation of an impulse (a nerve impulse) is considered a "+" and the suppression of an impulse a "-". A more neurologically sophisticated version would identify the "+" with depolarization and "-" with hyperpolarization and the holonomic brain theory would place the entire computational structure in the synaptodendritic microprocess rather than in the interaction among pulsatile outputs of neurons. What is interesting, however, is that in the computations the "+" and "-" are identified as directional polarizations due to "spin".

With respect to a directional component in the polarizations occurring in the dendritic microprocess, Pribram, Nuwer and Barron (1974) presented a preliminary outline of a model that can profitably be enriched and extended on the basis of current knowledge.

Perturbation in the postsynaptic domain is a function of differences in distribution of hyper- and depolarizations produced by the arrival of input patterns. When neighboring spines become locally hyper- and depolarized, the effect is to produce a pair of vertically oriented electric dipoles at the surface of the dendritic membrane which becomes superimposed on the horizontal fields already present. The net effect is to produce electrical polarizations which can be conceived to display direction (somewhat akin to spin).

The likelihood that neighboring postsynaptic events form a dipole consisting of hyper- and depolarization is enhanced in those structures endowed with many axonless local circuit neurons such as the cerebral cortex. These neurons are responsible for "lateral inhibition" by way of ubiquitous connections interspersed among those provided by input neurons.

The contribution of any pair of synaptic dipoles is small, but when many identical effects througout the dendritic microprocess are summed, the physiology of the network is significantly affected. Not only adjacent but remote synaptic events sum cooperatively and the effects of such cooperative interactions have been computationally modelled. In the holonomic brain theory, the processing model holds that computations proceed in collective cooperative ensembles constituting a holoscape. The holoscape is composed of vertically oriented dendritic spine-produced polarization dipoles embedded in horizontal dendritic polarization fields. Each dipole is what in quantum physics is called

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a polaron; that is, a quantum element in the polarization field. The computations in the holonomic brain theory are therefore formally equivalent to computations in the quantum field theory and thus constitute quantum neurodynamics. Once again, however, the caveat: formal similarities do not necessarily imply that the processes at the neural level can be identified substantively with those described in quantum physics. The holonomic brain theory does not imply that neural processes are quantum mechanical, although this is not ruled out as indicated by specific suggestions such as those proposed by Hameroff (1987).

The computations in quantum neurodynamics differ somewhat form those developed in the thermodynamic models. In the thermodynamic models computations are driven by "the principle of least action" to energy minima (Hamiltonians) which comprise an equilibrium (Hamiltonian) state. In keeping with findings by Caelli and Hubner (1983), the holonomic brain theory substitutes entropy minima for energy minima. Experiments by Caelli have shown that the resolving power of the visual system is determined by its spatial frequency resolution and not by the amplitude modulation of the system.

Caelli and Hubner (1983) compared an original image with one that had been "filtered" in different ways by a computational procedure, a procedure used by Ginsberg (1978) to demonstrate the possible origins of a variety of perceptual illusions. In these experiments:

> "The Fourier transform is first applied. Average amplitudes are then determined for each of the specified low-dimensional frequency regions, and all composite frequency components are assigned this value. The inverse transform is then computed to result in a new image which should not be discriminable from the original - if the bandwidths are chosen to be consistent with the lower bounds ... of approximately 5 (orientation increments) and 1/8 octave (frequency bandwidth). From a psychophysical perspective, these lower bounds correspond to bandpass regions in the two dimensional frequency domain whose elements cannot be discriminated.
>
> We have computed these transformations for a variety of different bandwidths. Clearly as the bandwidth approaches zero, the approximation to the original image improves. Form our results with two images (texture and face) the 1/4 octave width and 10 orientation bandwidth result in an image almost impossible to discriminate from the original. (This despite the fact that) ... the amplitude coding reduction is considerable ... (The) amplitude (and so energy) coding reduction is 98.3 percent (!). - (This makes) the 1/4 octave 10 wide amplitude code ... approximately 60 times more efficient than the baseline (digital) frequency code (that of the original image)."

Such considerations of processing efficiency have led Daugman (1988) to reconstruct a remarkably realistic portrait from a complete discrete 2D Gabor transform network at only 2.55 bits/pixel. The network was composed of overlapping Gabor elementary functions - the entropy of the ensemble of pixels is "little different from that of noise with uniform density since it does not exploit their intrinsic correlation structure."

The results of these experiments clearly indicate that image processing is a function of the efficiency of the spectral resolution of ensembles of Gabor elementary functions based on bandwidth and not on the average amplitudes of the processes. Average amplitude is a statistical measure of the amount of energy it takes to drive the process, whereas the efficiency of spectral resolution (which utilizes amplitude coefficients for each bandwidth of frequency) is measured in terms of the amount of ordering of energy, i.e. entropy. It is reasonable, therefore, to suggest that efficiency or entropy, rather than energy, is the critical element in perceptual processing: that entropy (uncertainty) minima rather than energy minima characterize the computational terrain.

Energy, Entropy and Information

The relation between measures of efficiency and measures of information (i.e., entropy and negentropy) has been discussed at length by Shannon (Shannon and Weaver 1949), Brillouin (1962) and MacKay (1969). However, these authors came to somewhat different conclusions: Shannon equating the amount of information with the amount of entropy, MacKay and Brillouin with the amount of negentropy. A conciliation of these views comes from the holonomic modification of the thermodynamic model. The conciliation results in a definition of entropy as potential information: The reasoning is similar to that which motivated Shannon. The structure within which information processing occurs is called uncertainty. It is this structure which allows for a measured amount of information to emerge. Shannon's use of the term uncertainty can thus be seen to be equivalent to "potential information", the term used in the holonomic brain theory. The argument runs as follows:

Thermodynamic engines operate to produce a state of maximum efficiency, i.e., a Hamiltonian state characterized by energy minima. The thermodynamic engines are thus sensitive to the entropy in the system measured as an amount of noise (heat). Perhaps a more accurate statement is that the degree of efficiency is a measure of the amount of entropy in the system. In thermodynamics the amount of entropy interpreted as noise is measured as temperature. At zero temperature the thermodynamic system acts like a ferromagnet (it has, at best, 2 minima). If the temperature is too high, the system acts as a "spin glass" - i.e., there are multitudes of minima. For optimally efficient performance - i.e., for optimal information processing - a "window" or "bandwidth" of noise (measured as a rise in temperature) must be added in. The amount and bandwidth is decided upon on the basis of trial and error (simulated annealing, Hopfield 1982; Hinton and Senjowski 1986). In short, the system can be tuned to perform optimally in recognizing patterns to which it had previously been exposed. Efficient, information pattern matching, occurs in a region between total randomness and total organization.

Note that "informative pattern matching" is an active process. "Information" is a function of a participating processing agency, ordinarily a living creature or its surrogate. Information does not exist per se in the absence of such an agency any more than sound or

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(Shannon and Weaver (1949) and Gatlin (1972) have noted that the efficiency of information processing depends not only on redundancy reduction by virtue of pattern matching but by actively structuring the redundancies that characterize the process. Miller (1956) has called attention to the importance of such structuring, which he calls "chunking", in psychological processing. Evidence has accumulated to show that the frontolimbic portions of the forebrain are critically involved in structuring redundancy and thus in enhancing the efficiency of information processing.

In the same vein, the holonomic brain theory holds that efficiency in processing entails a "polarization pattern path" whose trajectory is determined by the least action principle. The Hamiltonians become <u>operators</u> (defining paths) in a Hilbert space. In this space the amount of entropy is described as the amount of uncertainty and thus as the amount of <u>potential</u> information. Therefore, the path of uncertainty reduction is described, as in Shannon's (1949) definition of an amount of information, by a content addressable match between two patterns of probabilities, two polarization pattern pathways. These patterns constitute two entropic domains where entropy is defined as an at least partially structured potential. The amount of uncertainty to be reduced is defined as by Shannon: the amount of entropy conceived as an amount of structured constraint, i.e., potential information not disorder. Only the unit of information is different: Alternatives are no longer under consideration when this basic level has been reached. When the amount of uncertainty reduction achieves the minimum possible uncertainty, this quantity is equivalent to an amount of least entropy in terms of Gabor's quanta of information. These quanta then form the basic units, the polarons, in the holonomic brain theory.

Two examples can help the exposition of this set of concepts which has posed such difficulty for thoughtful scientists. I have an evening of leisure and wish to catch up with my reading of books that have recently arrived. They are stacked "randomly". By this I mean that the order in which the books are placed fails to reflect any other order that might be currently relevant to me. Randomness does not reflect disorder, however. The books are structured elements and one might wish to select one "at random" - say one with a red cover. The attributes that make for a book, for a cover and for a color must all be present for me to make that "random" selection.

Einstein was wrong in expression, if not in intent, when he stated his view that God does not play dice with the universe. Indeed he does, and has six-sided cubes (numbered at that), or perhaps 10 dimensional superstrings to play with. Playing with marbles would only get him Hamiltonians: The marbles would accumulate in equilibrium structures composed of sinks of least energy. In my evening's search for relevant information, in Einstein's search for determinate structure, the books and dice are the initial conditions. Randomness is as much a consequence of the structure of these initial conditions as it is of the processes of shuffling the books or throwing the dice. What is perceived as disorder with respect to some particular activity ordinarily results however, from the shuffling and throwing process. On closer scrutiny, randomness could be seen to <u>reflect</u> the structure of the initial conditions as they become processed in shuffling, throwing or selecting (Pribram 1972, 1986).

In the holonomic brain theory these initial conditions and the continuing control procedures which constrain processing, are "certainties" in their own right, composing a structure which reflects the degrees of freedom ("uncertainties") characterizing potential for actions to be taken in the situation. It is in the process of shuffling different constraining structures that both Shannon's BITS of information (reductions of uncertainties) and Gabor's quanta of information (minimum uncertainties) are produced.

Thus, amount of uncertainty (amount of structure in the initial conditions) and amount of residual uncertainty (the result of uncertainty reduction by virtue of the matching procedure) are reciprocals of one another. If entropy is a measure of the amount of initial uncertainty, the initial degrees of freedom, then the amount of residual uncertainty is the maximum amount of information achievable. In the brain the process involves a match between an input pattern (structure) and a pattern inherent in the synaptodendritic network by virtue of genetic or learning experience. In the holonomic brain theory, both the input and inherent patterns provide initial conditions such that the polarization pattern path of the match between them is probabilistic. The realization of this probabilistic process is expressed as changes in the probability amplitude weighting functions of Gabor coefficients representing synaptodendritic polarizations.

By recognizing entropy as reflecting some deeper structure which provides a variety of potential paths for the reduction of uncertainty and thus for the accretion of information, an additional possibility is presented for convergence among theoretical formulations. This possibility can be described as follows: Shannon's definition of an amount of information is based on the reduction of uncertainty. Further, there is in Shannon's information measurement theory, the concept of requisite variety (Ashby, 1956). Requisite variety is an optimization principle which claims that the reduction of uncertainty devolves on a tradeoff between equivocation and information density. Equivocation is defined as the sum of noise and redundancy. For the holonomic modification of the thermodynamic process this would mean that not only noise but structure, as inherent in redundancy (Attneave, 1954; Garner, 1962; and especially Gatlin, 1972), can be added to the system in order to maximize efficiency. And redundancy can be structured by experience as e.g., in chunking. This indicates once again, that for information processing the measure of efficiency, i.e. entropy, denotes not only randomness but tacit structure.

Daugman (1988) has made some additional observations relevant to an information theoretical approach to figural peception. He points out that retinal and geniculate processing decorrelates the optical image. Daugman also notes that Gabor proved that one could completely represent any arbitrary signal by expanding it in terms of ensembles of elementary functions (although he could not actually prescribe a way to do this). Daugman's contribution has been not only to generalize Gabor functions to two dimensions (independently achieved by Carlton in Pribram and Carlton, 1986) but to find the method to accomplish expansion when the Gaussian envelope is scaled proportionally according to spatial frequency. He relates his implementation to sampling in the theory of oriented wavelet codes.

A final point: Hopfield uses Liapunov functions in his analysis of the development of stabilities in neural networks. These are the same

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functions used by Prigogine (1980) to model dissipative structures that more or less "spontaneously" develop stabilities far from equilibrium. As such these processes are represented by nonlinear equations. As Kohonen points out (Kohonen and Oja, 1987) this nonlinearity depends on an a priori assumption that the network connectivity be proportional to the wanted state (vectors). In its initial form the thermodynamic processor is therefore incomplete. Brain processes are to a considerable extent optimally self-maintaining and even self-organizing (a point also made by Maturana, 1969 and by Varela, 1979) - and not subject only to the vagaries of input organization nor to spontaneous, unpredictable organization. Of course, occasional spontaneous innovative reorganizations can also occur. In more ordinary circumstances, Kohonen notes, where sypaptic couplings are formed adaptively (thus continuously relating input and central state values), the output state can relax to the linear range or to saturation. In Kohonen's model (1972; 1977) learning takes place in the linearized mode. Modifications of the thermodynamic models by Hinton, McClelland, Sejnowski and Rumelhart (Hinton, McClelland and Rumelhart, 1986; Hinton and Sejnowski 1986) have used similar continuous feedback ("back propagation") processes to overcome the limitations of nonlinearity.

With respect to perception, these models point to the importance of successive iterations of the process. These successive iterations can readily serve an optimization principle. In the holonomic brain theory successive iterations are based on movement which produces polarization pattern paths in computational space that describe the efficiency with which perceptual processing occurs. These polarization pattern paths are described by the least action principle in terms of mathematical group theory.

To summarize: the thermodynamic models fit well into the frame of holonomic brain theory. However, a modification based on the Gabor relation needs to be made. In the Hopfield networks and the Boltzmann engine, computations proceed in terms of attaining energy minima, while in the holonomic brain theory computations proceed in terms of attaining a minimum amount of entropy and therefore a maximum amount of information. In the Boltzmann formulation, the principle of least action leads to a spacetime equilibrium state of least energy. In the holonomic brain theory the principle of least action leads to maximizing the amount of information, defined as an ensemble of minima of least entropy. Such minima, defined by isovalent contours representing junctional polarizations (polarons) of equal value, can compose a temporarily stable holoscape far from equilibrium. In short, the holoscape is a dissipative structure, composed of ensembles of logon channels, uncertainty minima. These ensembles serve as attractors which define the boundary conditions for further processing. (For review of the functions of attractors see Prigogine and Stengers, 1984.) At this point, especially for the cognitive aspects of perception, the theory departs sharply from linearity.

The holonomic brain theory thus can account for the fact that organisms such as primates and especially humans are, on occasion, information (i.e., entropy minima) seeking "informavores" (Miller, personal communication; Pribram, 1971).

Addendum:

These pages constitute the core of the first two Mac Eachran lectures given at the University of Alberta in 1986. The entire series of lectures is to appear in 1990 as a book entitled Brain and perception: Holonomy and Structure in Figural Processing, published by Erlbaum Associates. This prolegomenon to the series is included in the current proceedings because of the many convergences between the holonomic brain theory and synergetic theory. There are, however, also important differences between the two theoretical approaches and these differences provide substance for further inquiry and research.

Perhaps the major point of difference between the two theoretical approaches is with regard to linearity. Synergetics is primarily nonlinear while the holonomic brain theory attempts to remain linear over the range of sensory driven phenomena. Nonlinearities play the role of adjuncts that sharpen the basically linear process. Furthermore, linearity is often the result of cooperativity among sets of nonlinear phenomena. This is brought out in the formal mathematical treatment of the theory contributed by Kunio Yasue and Mari Jibu as a set of appendices to the complete series of lectures.

Formally the holonomic brain theory resembles quantum field theory which remains linear until choices are made with the ensuing "collapse of the wave function". With regard to brain processes, nonlinearities become manifest when perceived objects become categorized, i.e., become alternatives.

A second major difference between synergetic and holonomic theory is that the holonomic brain theory has been developed to account for the results of neurophysiological, neuropsychological, and psychophysical experiments. The theory accrued slowly to accommodate observation. By contrast in synergetics the theory often precedes observation: the experiments are frequently performed to test tenets of the theory. In short, the holonomic brain theory has developed largely as a bottom-up endeavor; synergetics has developed, for the most part, as a top-down enterprise. The current convergence of these two somewhat different approaches promises to fertilize both.

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