

PRIBRAM, K.H. (1994) Synapses not neurons as computational elements: how to reconcile real and artificial computing. *Hints from Life to AI, Artificial Neural Networks and Artificial Life Symposium* Middle East Technical University, Ankara, Turkey. Ugur Halici (ed.)

Hints from Life to AI, edited by Ugur Halici, METU, 1994

synapses not neurons as computational elements: how to reconcile real and artificial computing

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Neurons are ordinarily conceived to be the computational units of the brain, thus the majority of processing theories since the seminal contribution of Mc. Culloch 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. Current computational processing emphasizes a minimum of constraints in the processing wetware or hardware, but in the current neuroscience framework wetware is highly constrained. Misunderstanding is alleviated when the computational framework is broadened to include the microprocessing that takes place within dendritic networks, and recognizing importance of dendritic microprocessing allows a coherent theory to be framed regarding the neural functions responsible for perception.

I. 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 nonrandomly, often sparsely, and always in a specifically configured fashion 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 that takes place within dendritic networks. Not only are axonal dendritic synapses that connect neurons subject to local influences in these networks, but innumerable dendro-dendritic synapses provide the unconstrained high connectivity needed in computational procedures. (Bishop 1956, Pribram 1960, 1971; Schmitt, Dev&Smith 1976) In fact, a large number of neurons- in some systems, such as cortex, as high as 50%- do not have any axons at all. Their processing capability (primarily inhibitory) is purely dendro-dendritic.

Junctions (axodendritic and dendo-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. Term such as neuroregulator and neuromodulator convey more of 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. The patterns are constituted of sinusoidally fluctuating hyper- and depolarizations which are insufficiently large to immediately incite nerve impulse discharge. The delay affords opportunity for computational complexity.

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 can be 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, resembling it at its destination. Neurons are labelled by their location in the network. This form of labelling is highly efficient because of the essentially parallel nature of neuronal connectivities.

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.

2. Dendritic Microprocessing

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

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 influences 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 succinct 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."

Languages then proceeds 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 that 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 coordinated with awareness. The hypothesis is consonant with the view that we are cognizant of some, but not all of the events going in the brain.

Nerve impulses arriving at junctions generate dendritic microprocesses. The design of the 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 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, and so forth. Today, text books 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 at some point in the nervous system.

Profoundly troubled by the problem, Lashley (1942) 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 the 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 activities of the nervous system and some hypothesis is needed to direct further research.

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 established the existence of generalized fields but show that, although they were related to the speed with which learning took place, they were unrelated to the perception as tested by discrimination tasks.

Lashley was never satisfied with either Hebb's or Kohler's position. His alternative was an interface pattern model which he felt would account for perceptual phenomena more adequately than either a DC 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 provide a computational scheme for perception. Thus he 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 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 *within regions of dendritic networks* at the junctions between neurons.

As summarized by Szentagothai (1985) :

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, 1976)

The ubiquity of such axonless local circuit neurons indicates that computation is strongly influenced by dendritic-dendritic interactions that 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 the 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 coordinate with perception are *distributed*. In a distributed process, perceptual events are represented not by single neurons but by *patterns of polarization* across ensembles of neurons.

On the basis of his extensive studies E.R. John came 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 on the membranes of single neurons, but upon charge density distributions in the tissue matrix of neurons, glial cells, and mucopolysaccharide processes, we can envisage a complex, three dimensional volume of isopotential contours, topologically comprised of portions of cellular membranes and extracellular binding sites and constantly changing over time. Let us call this volume of isopotential contours or convoluted surfaces a *hyperneuron*.

Basic to this new view of neurology of perception is the fact that propagated nerve impulses are but of one of the important electrical characteristics of neural tissue. The other characteristic is the microprocess that 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 axonal nerve impulses in that they do not propagate. The influence of these minispikes and graded polarizations on further neuronal activity is by way of *cooperativity* among spatially separated events. Cooperativity is mediated by the cable properties of dendrites and the surrounding glia. This type of interaction is called nonlocal 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 MacEachran Lecture (1975).

3. 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 process 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 that produce 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, inhibitor or excitatory, at each location indicated whether the dendrites at that 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 that produce *lateral inhibition* in the neighborhood of excitation and viceversa. The center surround organization thus reflects the formation of a spatial dipole of hyper and depolarization, 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 the 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, planes by line and solids by planes. 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 neural 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 that 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

Furthermore 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 four critical reasons for preferring tuned frequencies to detected features:

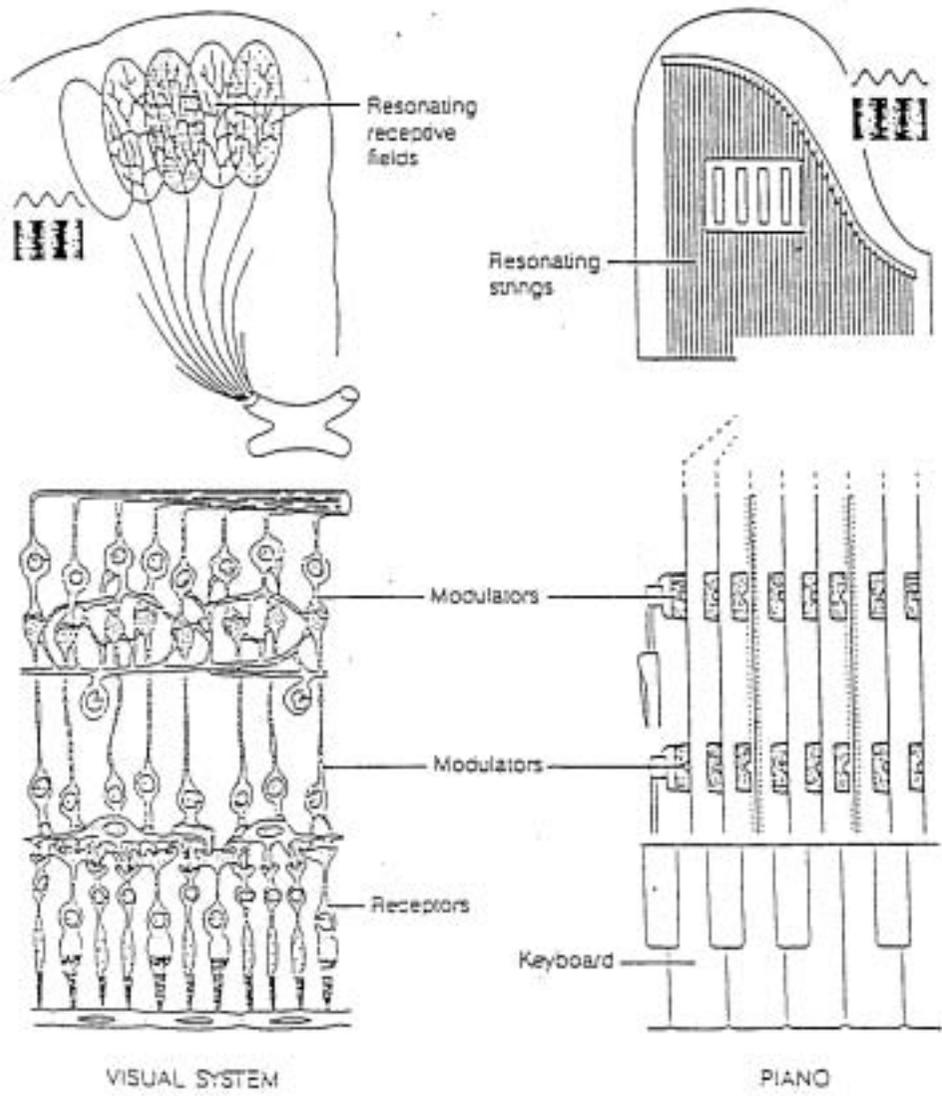
- (a) Neurons in the visual cortex respond to several features of sensory input and there is no evidence that the different features are represented by separate neurons, as would be required if it acted as a detector;
- (b) the receptive field properties of such neurons can be accounted for considering them as spatial and temporal differentiations of tuned frequency;
- (c) tuned frequencies provide a potentially richer panoply of configuration (e.g. texture, parallax), and
- (d) 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) summarized 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. Illusory contours also support this conclusion (pg.43).

Rock provided 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 which respect to ourselves... is a joint function of retinal locus and eye position* (pg.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, characteristics of overlapping functions of the receptive fields of the cortical neurons, provides a microlevel of perceptual processing. It is this cooperative microprocess that allows one to assume that indeed a specific brain process is coordinate with the richness of experience that is perception.



VISUAL SYSTEM

PIANO

FIG. 1. Diagram of essential connectivity of the initial stages of visual sensory processing and its similarity to the connectivity of a metaphorical piano to illustrate the principles of harmonic analysis.

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 called into question the view that figures were composed by convergence of Euclidean features. For instance, in the laboratories of Stanford University the architecture of cortical dendritic fields examined by computer and cortical receptive fields that contained multiple bands of excitatory and inhibitory areas are found. (Spinelli & Barret, 1969; Spinelli, Pribram & Bridgeman, 1973) In Leningrad similar observations were made by Glezer (Glezer, Ivanoff & Tscherbach, 1973) who remarked that these cortical neurons responded more like *stripedness* 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 Rabson (1968), initially on the basis of psychophysical, and subsequently, on the basis of neurophysiological experiments, developed the thesis that vision operates harmonically much as does audition except that the visual system responds to *spatial* frequencies. Here I want to introduce the critical difference between Euclidian-based and Fourier-based harmonic approaches.

When a harmonic analysis is taken as the approach, the elongated receptive field organization of cortical neurons suggest that neurons act as "strings" tuned to a limited bandwidth frequencies. The ensemble of strings compose resonators or active filters as in musical instruments. A century ago, Helmholtz 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 of a piano, but that each cortical "unit" responds to a limited bandwidth of frequencies as do the strings attached to the piano's sounding board. From the operation of the total range of such units, magnificent sounds (in the case of the piano) and sights (by means of the visual system) can become configured (Figure 1).

The geometric and harmonic views differ significantly with respect to the composition of a percept. Irwin Rock (1983) described 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 characteristics 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 oriented lines, movement and color are best conceived as identifiable emergent characteristics of form because they are already conjoined in the receptive field.