

# Making Sense of Brain Waves: The Most Baffling Frontier in Neuroscience

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## Abstract

Brains are characterized by every property that engineers and computer scientists detest and avoid. They are chaotic, unstable, nonlinear, nonstationary, non-Gaussian, asynchronous, noisy, and unpredictable in fine grain, yet undeniably they are among the most successful devices that a billion years of evolution has produced. No one can justifiably claim that he or she has modeled brains, but they are a flowing spring of new concepts, and they provide a gold standard of what we can aspire to accomplish in developing more intelligent machines. The most fertile source of ideas with which to challenge and break the restrictions that characterize modern engineering practice is the electroencephalogram (EEG). It was the action potential of single neurons that provided the foundation of neurobiology for the 20th century, and in its time it supported the development of digital computers, neural networks, and computational neuroscience. Now in the 21st century, the EEG will lead us in a remarkably different direction of growth for the computing industry, which will be dominated by highly parallel, hierarchically organized, distributed analog machines. These devices now exist in prototype form. They feed on noise in support of chaotic attractor landscapes, which are shaped by reinforcement learning through self-governed experience, not training by 'teachers', and they may solve many of the problems of interfacing between finite state automata and the infinite complexity of the real world.

## 1. Introduction.

Electroencephalographic (EEG) potentials are recorded from the scalp as aperiodic fluctuations in the microvolt range in humans and animals. They are also found within brains where they are often referred to as 'local field potentials', but they are manifestations of the same dynamics of populations of neurons. This report summarizes how they arise, why they oscillate, and what they

can tell us about brain function that will be useful for engineers to construct devices that can perform some of the functions that brains do very well, such as pattern recognition and classification, in contrast to existing machines.

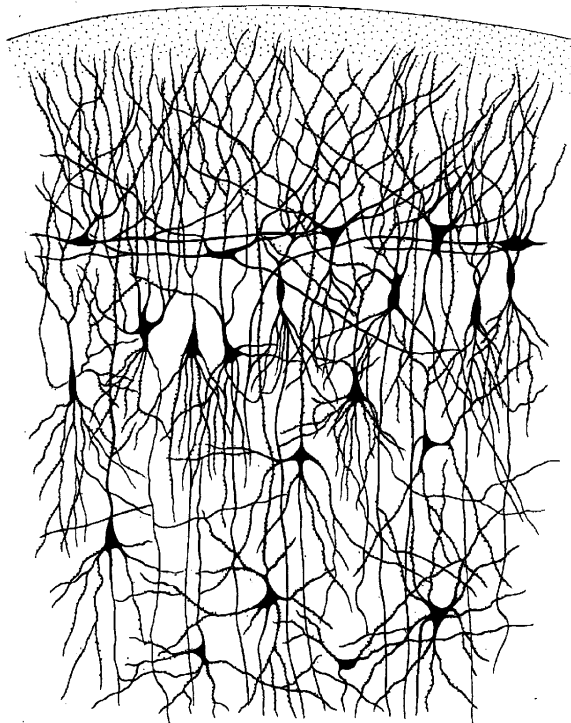
Neurons have two kinds of filaments by which they interconnect and interact. The transmitting filament, the axon, generates propagating pulses called action potentials or 'units', which serve to communicate information over short and long distances without attenuation. The receiving filament, the dendrite, converts pulses to graded waves of current that can be summed linearly both in time and space. The resultant sum is reconverted to pulses at rates proportional to dendritic current density in a biological form of pulse frequency modulation. Dendrites consume 95% of the energy that brains use for information processing, axons only 5%, so they are the principal determinants of the patterns that are observed in brain imaging with fMRI, PET and SPECT. They are also the principal source of electric currents passing across the extraneuronal resistance of brain tissue ( $\sim 300$  ohm.cm/cm<sup>2</sup>), creating the EEG. Most of what we know about sensory and motor information processing has come from studies of action potentials. The bridge that we need to understand the relations between 'unit activity' and brain images is provided by the EEG.

## 2. Relations between EEG and 'units'

Most EEG waves are generated by the cerebral cortex of the forebrain, for two reasons. First, the neurons are exceedingly numerous, and they are organized in layers with their dendrites in the main oriented parallel to each other (Figure 1), so their currents are also aligned in summation. Second, they interact synaptically in sparse but high density feedback. The reciprocal synaptic connections are by both positive feedback (mutually excitatory) leading to large areas of spatially coherent activity, and negative feedback (between excitatory and inhibitory populations)

leading to oscillations in the gamma range (20-80 Hz) that carry information content in wave packets [12]. Multiple types of feedback (including positive inhibitory feedback leading to spatial contrast enhancement) support lower frequency oscillations in alpha and theta ranges (3-12 Hz) at which wave packets are gated.

To understand how the information that is received at the dendrites is converged to the axon we need to understand the way the dendrites operate. The dendrites typically generate electric currents which are initiated at synapses packed over the entire tree (Figure 2).

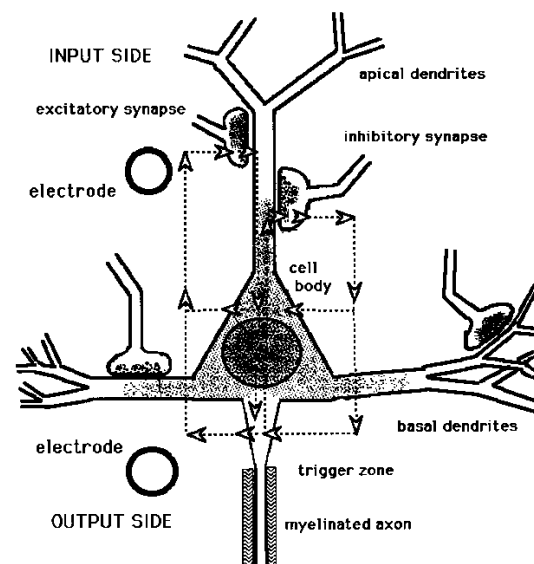


**Figure 1.** The filamentous structure of cortical neurons and their palisades in layers is shown by silver impregnation (the Golgi technique), selecting only 1% of the neurons in the field

Each synapse acts like a small battery with a high internal impedance, so that its current strength does not vary with external load. By Kirchoff's law, current always flows in a closed loop, so that current must flow in one direction across the membrane at the synapse and in the opposite direction across the membrane at other sites with impedance match to the crossing. The preferred current path is along the dendritic shaft toward the cell body. The loop currents from all synapses superimpose and are converge to the origin of all the branches at the cell body and pass across the membrane of the initial segment

of the axon where it originates from the cell body. Functionally, the initial segment of the axon is also known as the trigger zone.

Among the three kinds of chemical synapse, an excitatory synapse causes current to flow inwardly at the synapse, along the dendritic cable away from the synapse, outwardly across the membrane, and back to the synapse in the space outside the membrane (Figure 2). An inhibitory synapse causes a current loop with flow outwardly at the synapse and inwardly everywhere else. Each current causes a voltage drop across a high resistance in the trigger zone membrane. The inhibitory sum is subtracted from the excitatory sum of voltage differences.



**Figure 2.** Dendrites receive action potentials at synapses and convert the impulses to loop currents. The sum of current determines the rate of unit firing. The same current contributes to the EEG recorded with transcortical electrodes, but it sums with the current from all neurons in the neighborhood, manifesting a local mean field.

The inflow of current at one end of the neuron and the outflow at the other end create a source-sink pair, which gives a dipole field of potential. The amplitude falls roughly with the square of distance from the center, which explains how the EEG can be observed at the surface of the cortex and scalp, though at one thousandth the amplitude of transmembrane potentials, owing to the low specific resistance of extraneuronal fluid compared to that of the neural membrane.

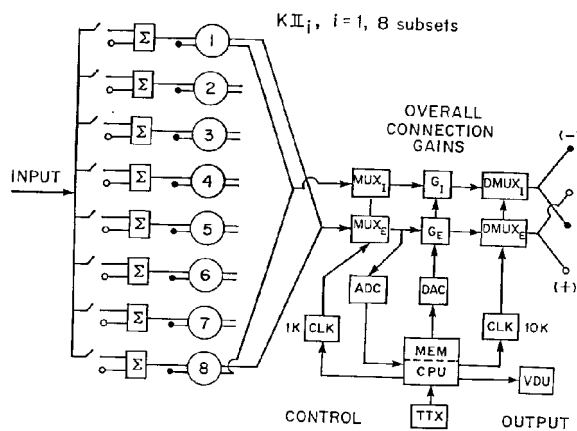
More generally, because the spread and summation of dendritic current conform to the

principle of superposition, they are described by a 2nd order linear ordinary differential equation, which is evaluated by fitting the sum of two exponentials to the impulse response.

$$d^2v/dt^2 + (a+b)dv/dt + ab v = k_{ij}G(p) \quad (1)$$

The minimal input to an excitatory synapse is an action potential, which is an impulse lasting about one millisecond. With a single impulse at the synapse the dendritic current rises at a rate of  $1/b = 1$  to 3 milliseconds and decays at a rate of  $1/a = 5$  to 10 milliseconds. At the cell body and trigger zone this brief electrical event is observed as an excitatory postsynaptic potential (EPSP). The impulse response of an inhibitory synapse has the similar form and decay time but opposite polarity and is called an inhibitory postsynaptic potential (IPSP). These two types of linear response are modeled in hardware with operational amplifiers and (for inhibitory synapses) inverters, and the combinations of multiple synapses are modeled with summing junctions. Summing at trigger zones takes place after synaptic amplification and sign reversal.

The third type of synapse, which is called modulatory, does not induce a loop current. Instead, it changes the strength of action of adjacent excitatory and inhibitory synapses. Neuromodulators are also released to diffuse through populations and enable alterations of their chemical states. Such multiplicative actions are modeled with variable resistors or a variable gain amplifier in circuits using time multiplexing to solve the connectivity problem (Figure 3).



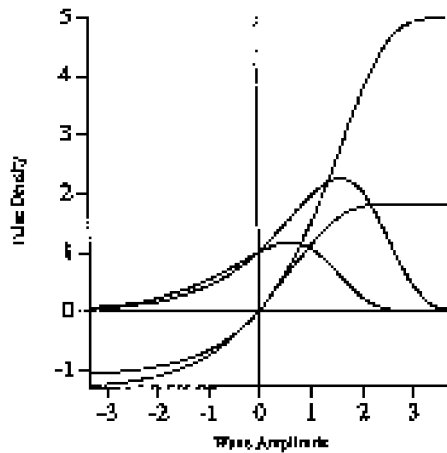
**Figure 3.** Time multiplexing is feasible because the bandwidth of EEG is much lower than that of 'units'. This reduces connectivity to  $2N$  instead of  $N^2$  for  $N$  nodes. Gain values are indexed to

connection pairs under digital control. Analog amplitudes simulate pulse density coding. Neuromodulation is used to normalize neural activity levels across distributed input, to perform logarithmic conversion and range compression on input, to change overall neuronal gain in respect to behavioral awakening and arousal, and to enable selective changes in synaptic strength during learning, either an increase in sensitivity during association or a decrease during habituation.

The architecture of dendrites reflects a key role that the dendrites perform, which is to convert incoming pulses to currents and sum them at the initial segment. Spatial integration at the cell body is important, simply because that is where all the axonal and dendritic branches originate. The integration of the dendritic currents is done there also across time. When stimuli are frequent enough, new current superimposes on old fading current to give temporal summation at the initial segment. The dendritic branches are poor electrical conductors with high internal resistance and high leakage across their surfaces. Effective dendritic currents can seldom be transmitted passively over distances longer than a few hundred microns because of the attenuation with distance. The critical function of the axon is to transmit the time-varying amplitude of current summed by the dendrites to distant targets without attenuation.

The neuronal stratagem is to convert the sum of currents into a pulse train, in which pulse frequency is proportional to wave amplitude. The pulse train is converted back to a wave function that is smoothed by the target dendrites. This is why the axonal "signal" is "analog" and not "digital". The energy for transmission along the axon is provided locally by the axon membrane as the pulse propagates, but the release of the energy takes time. It is not done with the speed of an electronic conductor. The price for axonal output that is free of attenuation and can be carried over large distances is threefold: nonlinearity; a delay in pulse transmission; and discretization in time. Thus dendrites which are short do not use pulses, and axons which are long do. Dendrites generate graded currents that are superimposable and distributed in time and space, whereas the pulses of axons are not superimposable. They are point processes in time and space.

In a neural population, activity densities are defined over spatial distributions of neurons in the two surface dimensions of the cortex orthogonal to the orientation of the dendrites. The transformation at trigger zones of dendritic wave density to axonal pulse density (Figure 4) has bilateral saturation. The function for single neurons is linear and time-varying; for populations it is nonlinear and static. Only populations of neurons have the smooth static "sigmoid" relationship between the two state variables. The reason that the curve is static stems from the fact that individual neurons in the population fire unpredictably, as shown by their Poisson interval distributions. They also fire in an uncorrelated manner with respect to each other. Hence the refractory period and adaptation of the single neuron do not appear directly as time variance in the ensemble average of activity of populations but set the upper limit on normalized pulse density,  $Q_m = (P - P_o)/P_o$



**Figure 4.** The asymmetric sigmoid curve is shown for two values of the asymptotic maximum,  $Q_m$ , the lower at 1.8 for rest, the upper at 5.0 for motivation and arousal as shown by the bursts in Figure 3. The equations are:

$$p = p_o (1 + \{1 - \exp[-(e^v - 1)/Q_m]\}), v > -u_o \quad (2)$$

$$dp/dv = u_o \exp[v - (e^v - 1)/Q_m] \quad (3)$$

Experimental demonstration of the sigmoid curve (Freeman 2000) is by calculating the pulse probability conditional on EEG amplitude in the same population. Cortical populations display activity when without stimulation that is seen as "spontaneous" or "background" activity at rest. The pulse activity of any one neuron averaged over a long time period is assumed by the

ergodic hypothesis to conform to the activity of its population over a brief time period. Its mean rate serves to represent the mean pulse density,  $P_o$  (Figure 4). In an excited population the pulse density increases up to a limit  $P_m$ , which is determined largely by potassium conductance,  $G_K$ , at trigger zones. In an inhibited population (hyperpolarization) the pulse density is bounded at zero. In awake subjects the ratio  $Q_m = P_m/P_o$  ranges from 5:1 to 12:1. In resting and sleeping states the ratio drops to 2:1, and under deep anesthesia it goes to zero, giving the open loop state for the impulse response.

Another characteristic of the trigger zones is that  $P_o$ ,  $Q_m$  and the slope  $dp/dv$  of the sigmoid curve (Figure 4) increase with behavioral arousal of a subject. This state dependence is expressed by a single variable  $Q_m$  in normalized coordinates, which probably reflects the operation on the cortex of a single neuromodulator chemical that is responsible for regulating cortical excitability during arousal in various behavioral states. This property is part of a more general pattern, in which each area of cortex receives modulatory input from several other parts of the brain. The modulation does not provide information-specific input, but it changes and adjusts the cortical state in such ways as "turn on", "turn off", "attend", "learn", "habituate", and so on by simultaneously operating on populations of cortical neurons. Neuromodulators may best be simulated in VLSI embodiments by sending control signals through the power lines of diodes and amplifiers.

The most important dynamic aspect of the biological sigmoid curve is the fact that it is asymmetric. Its maximal slope  $dp/dv$  is displaced to the excitatory side. This property reflects the fact that in a population most of the neurons most of the time operate near equilibrium and just below their thresholds for firing, where voltage-dependent  $G_{Na}$  increases exponentially with depolarization. As a result of this regenerative feedback the firing probability increases exponentially with depolarization, and this is reflected in the exponential increase of the concave-upward part of the sigmoid curve. The slope  $dp/dv$  is a main determinant of the forward gain of a population. Therefore, the gain is both state-dependent (on the degree of arousal) and input-dependent, giving a strong increase in gain on sensory excitation of the population. These gain dependencies are crucial for state transitions

of cortex during behavioral information processing. In particular, the nonlinear gain renders local areas of cortex unstable in respect to input, and the instability is enhanced with increasing arousal as in fear and anger.

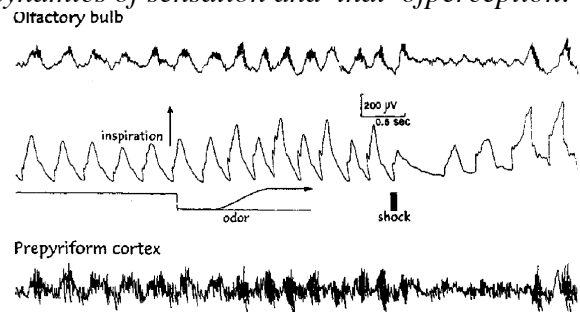
### 3. Three levels of hierarchical coding

There are three main levels of neural function in the pattern recognition performed by sensory systems, which are to be modeled with appropriately tailored state variables and operations. Microscopic activity is seen in the fraction of the variance of single neuron pulse trains (>99.9%) that can be correlated with sensory input in the form of feature detector neurons and motor output in the form of command neurons. Mesoscopic activity [20] is carried in the <0.1% of the total variance of each neuron that is covariant with other neurons in neuropil that comprise local neighborhoods. Collectively it is observed in dendritic potentials (EEGs). The interaction of multiple sensory cortices in different modalities together with association areas constitutes a macroscopic system [19]. That is the hierarchical level of organization of brain function that is revealed by present-day devices for brain imaging that rely on metabolic activity and blood flow.

The interactions by local negative feedback between excitatory and inhibitory neurons at the mesoscopic level support periodic oscillations manifesting limit cycle attractors. Multiple areas of neuropil comprising a sensory system interact by long feedback paths. Due to the facts that locally they have incommensurate characteristic frequencies, and that multiple local areas interact by axonal transmission imposing relatively long delays, together they maintain global chaotic states that are observed in aperiodic oscillations. The basal state without stimulus input is characterized by Gaussian distributions of EEG amplitude and by power spectral densities that conform to  $1/f^2$  linear decrease in log power with log frequency (brown noise).

On destabilization by sensory input the multipart system undergoes a state transition to a more narrowly constrained spectral distribution in the gamma range, which results from substantial increase in interactions of cortical neurons with each other, so that they no longer accept internal input. The neurons create a new pattern of activity following each sensory barrage (Figure 5). The contents of neural activity in brains are

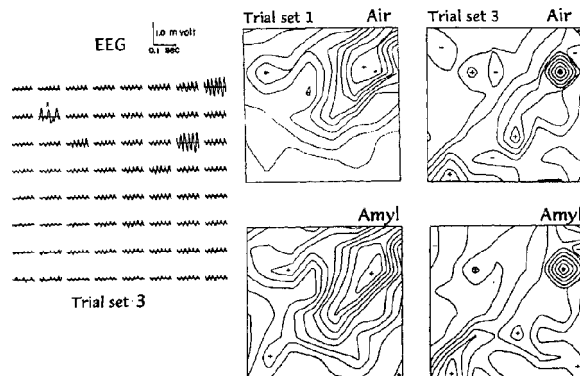
deduced from correlations of the amplitudes and frequencies of the observed activity with the ongoing behavior of animals. These correlations reveal a *profound difference between the dynamics of sensation and that of perception.*



**Figure 5.** An example from the olfactory bulb shows the EEG manifesting the short bursts of activity (top trace) constituting wave packets, the formation of which is by destabilization of the bulb by input, owing to the asymmetric nonlinear gain shown in Figure 4. The middle trace shows the pattern of driving by respiration that is under control by the limbic system. The bottom EEG is from the target of bulbar transmission.

Mesoscopic activity in sensory cortices is perceptual, not sensory. EEGs of nonlinear brain dynamics manifest internal self-organizing dynamics of newly created patterns emerging from cortical background noise destabilized under perturbation by sensory stimuli. Sensory and perceptual contents coexist in cortices. The former are extracted by time ensemble averaging over trials, the latter by spatial ensemble averaging of multichannel simultaneous recordings on single trials [3, 12, 15, 20].

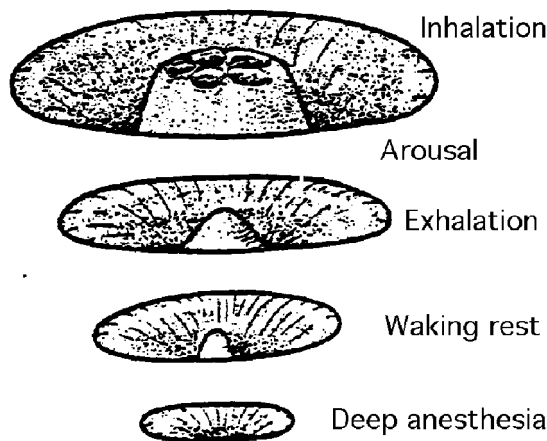
The contents of brain activity patterns are conveyed by wave packets of oscillatory activity recurring at rates in the theta range having the same aperiodic wave form observed throughout the entire population (Figure 6, left frame).



**Figure 6.** The left frame shows the carrier wave form of a single wave packet. The right frames show the changes in AM pattern with classical conditioning. The visual, auditory and somatic cortices have the same form of coding: a chaotic carrier wave spatially amplitude-modulated. This spatially coherent wave serves as a carrier for content by amplitude modulation in space (right frames). Because the AM patterns are created by interactions of neurons by synapses that have been modified by experience, patterns are not invariant with stimuli but reflect instead that experience. Hence the internal context of cortical responses to stimuli is carried in the spatial domain of cortical dynamics by spatial AM of the aperiodic carrier wave form [28].

During behavioral conditioning of an animal a new AM pattern emerges with each new stimulus the animal learns to discriminate [26], implying that the sensory system maintains an attractor landscape with a basin for each class.

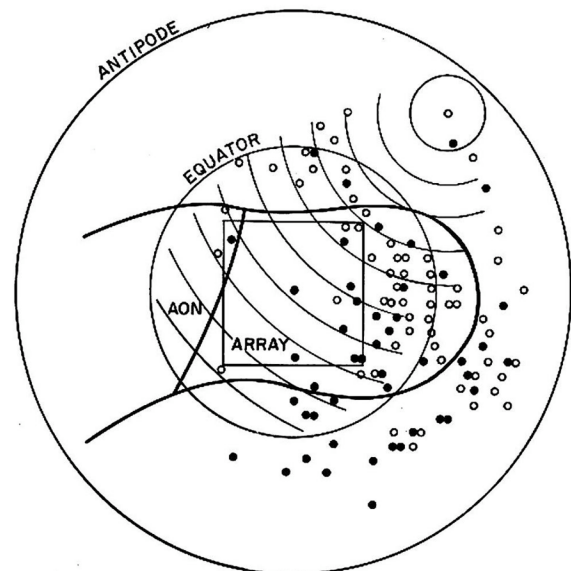
The basin of each attractor is defined by the stimuli in the learning set that is paired with reinforcement. Each basin is accessed by a state transition that is driven by a surge of input from sensory receptors, because the entire landscape is brought into play, then suppressed during exhalation to enable a new sample to be taken (Figure 7). The basin allows for many-to-one convergence that takes place when the animal generalizes over samples to identify the class to which a stimulus belongs. An important feature is that the chaos is a mesoscopic property. The microscopic neurons are governed by point attractors, not by chaotic attractors.



**Figure 7.** The state space of the olfactory system is schematized as it might appear from a high dimensional space projected into 2-space. The

attractor landscape appears with inhalation, and it dissolves with exhalation to allow the next stimulus to be classified.

The state transition is manifested by a conic phase gradient (Figure 8) of the aperiodic oscillatory event [21]. The apex of the cone demarcates the site of nucleation for each state transition, the location and sign of which vary randomly. The random variation in sign (extreme lead or lag) shows that the apex cannot represent the location of a pacemaker. The phase gradient shows the group velocity by which it spreads [21, 22, 24].



**Figure 8.** Phase distributions were measured with respect to the phase of the spatial ensemble average at the surface of the olfactory bulb and fitted with a cone in spherical coordinates. The sketch is a projection of the outline of the bulb as it would appear on looking through the left bulb onto the array on the lateral surface of the bulb. A representative set of isophase contours is at intervals of 0.25 radians/mm. The locations of the apices of the cones on the surface of the sphere (2.5 mm in radius) are plotted from the center of the array to the antipode. The square outlines the electrode array. The standard error of location of points was twice the radius of the dots.

Phase cones play a major role in determining the size of wave packets in neocortex, which is a continuous sheet of neuropil over each entire cerebral hemisphere. The delay that is imposed in the state transition from the site of nucleation by the conduction velocities of the axons that run parallel to the surface causes progressive phase difference with distance, eventually to the extent of going out of phase. This offers a solution to

the problem of how differing wave forms coexist in the same hemisphere. The phase gradient creates a soft boundary condition that is approximated by the half-power radius, implying that the modal diameter of neocortical wave packets is about a centimeter [23].

These two kinds of coding coexist in brains. The *microscopic* coding is characteristic of single neurons in the brain stem and spinal cord as well as in the peripheral nervous system, but also of cortical neurons. The microscopic pulse trains are described by means of stochastic point processes. The *mesoscopic* coding is found in the cortices as local mean fields of activity that constitute averages over many neurons. This activity has continuous distributions of neural activity, with time and space constants 1 to 2 orders of magnitude larger than those for single neurons. Though it appears random in time, this activity is spatially coherent and highly structured in phase and amplitude [17, 18]. Hence equations for describing neurodynamics have two forms: discrete and stochastic difference equations to model the microscopic input and output channels of cerebral cortex, and continuous integrodifferential equations for intracortical dynamics [12, 15]. While neural networks can be modeled with matrices that represent the dynamics of local integrate-and-fire elements connected globally, whether fully or sparsely, the dynamics of cerebral cortex is modeled with arrays of coupled oscillators in two spatial dimensions, with sparse but global internal connectivity to represent the architecture of the neural populations of cortex.

The distinction between digital and analog embodiments is focused on the difference between representing state variables with numbers *versus* voltages, not with discrete *versus* continuous variables. Brain function is neither analog nor digital, as these terms are defined for computer usage. Pulse trains that appear to be digital are in fact analog as a form of pulse frequency modulation. Analog integration is done with continuous variables in time, but usually with discretization by compartments in space and for segmenting for multiplexing (Figure 3) to solve the connectivity problem [11]. Sums of dendritic current are locally continuous distributions in time and space for short segments of time, but their spatial patterns are discretized by discontinuities imposed by 1st order state transitions (Figure 5) to form wave packets [12, 15, 16]. New brain models will be hybrid, not analog or digital.

Parallel networks of coupled oscillators in software [36] and hardware [11] serve to model the nonlinear dynamics of cortex. Solutions of ordinary differential or difference equations serve to model the chaotic wave forms of normal and abnormal brain activity, including the spatial coherence of broad-spectrum aperiodic activity that is so characteristic of EEG fields of potential over the cerebral cortex. The spatially coherent mesoscopic activity is extracted by the targets of cortical transmission through divergent-convergent axonal tracts that perform spatial integral transformations on cortical outputs. By this operation the cooperative, spatially coherent chaotic activity is extracted as signal, and the input-driven, spatially incoherent activity is attenuated as noise [20].

#### 4. Simulation of "background" activity

Unlike most neural network models, which remain at rest until given input, the cerebral cortex is ceaselessly active in sleep and wakefulness. The key to understanding the hierarchical organization of brain function lies in explaining the dynamical origin of this sustained endogenous activity. At the microscopic level, the background activity of single neurons in the absence of sensory stimulation can be accounted for by relaxation oscillation, which tends to give periodic or quasiperiodic pulse trains manifesting one or more limit cycle attractors, which is consistent with the performance of the "integrate and fire" models of single neurons.

In contrast, neurons embedded in neuropil typically generate aperiodic pulse trains [1, 2, 12, 24]. Their autocorrelations reveal their refractory periods but seldom clear characteristic frequencies. Their interval histograms conform to the Gamma distribution of order 1/2 at modest mean rates, tending toward the Poisson distribution (with a dead time) at low rates and the Gaussian distribution at high rates. Crosscorrelations between adjacent neurons are vanishingly small.

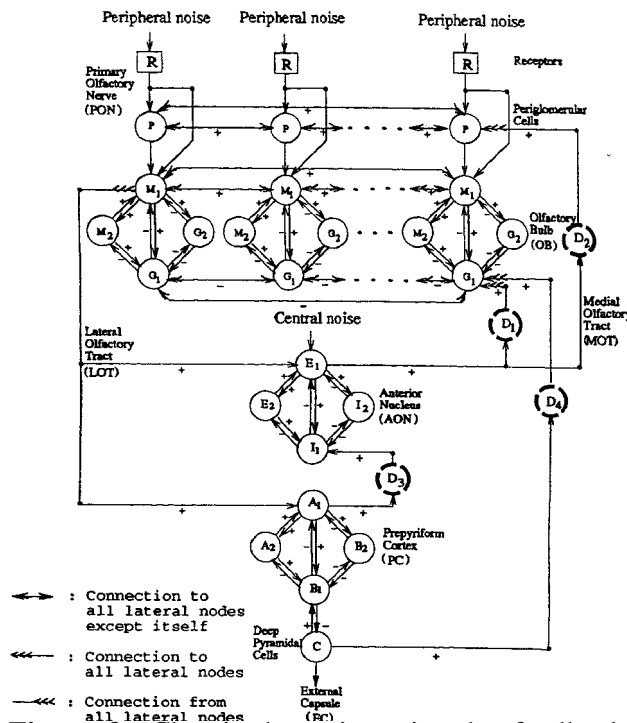
The background activity of neuropil, that is observed in the cortex at all levels, arises from mutual excitation within multiple populations of excitatory neurons. The governing point attractors are set by the mesoscopic states, which act as order parameters [31] that regulate the contributing neurons. The point attractors manifest a homogeneous field of white noise

[12]. These properties show that the activity arises by widespread synaptic interactions, and that it is maintained and governed by a mesoscopic point attractor based on the recurrent excitatory collateral axons of cortical neurons [5, 9] in neocortex and in populations of excitatory neurons [12] in the olfactory system (Figure 9).

The most detailed study is focused on the periglomerular neurons in the outer layer of the olfactory bulb, which form a densely interconnected population receiving input from the receptors and giving output to the mitral cells. Each neuron excites thousands of others in its surround and receives from them along innumerable connections with distributed axonal distances and successive synaptic delays. The feedback is modeled by a rational approximation for a 1-dimensional diffusion process with the Laplacian operator  $s$  in the expression,

$$\exp[-(sT)^{0.5}], \quad (4)$$

where  $T$  is a lumped, distance-dependent time constant [12]. This accounts for the randomization of activity on each pass through the loop for each neuron. Owing to the sigmoid nonlinearity [10, 20] in the feedback, the population has two stable points, one at zero and the other at a nonzero level [6].

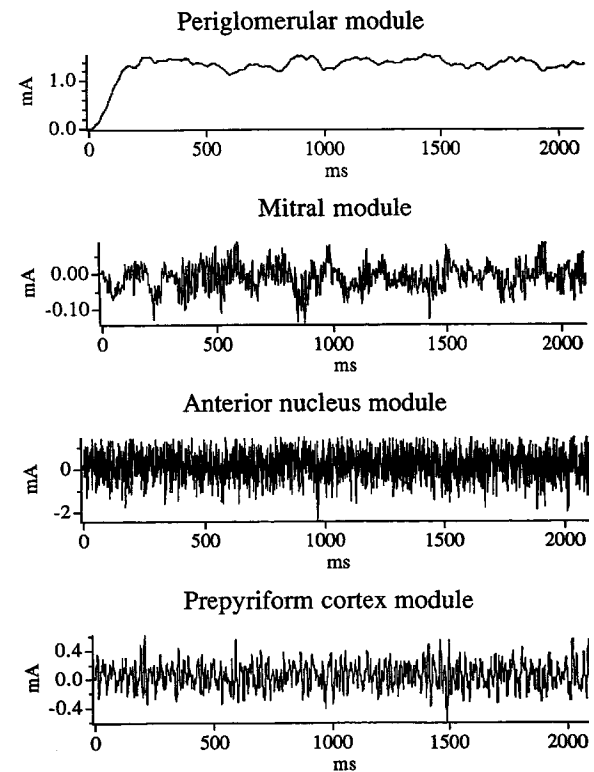


**Figure 9.** Chaotic dynamics arises by feedback with delay among 3 coupled oscillators having incommensurate characteristic frequencies. The

landscape is stabilized by additive noise. Each node is governed by equations (1) and (2). In digital models, noise serves to stabilize the chaotic attractors [25].

Thus, periglomerular pulse density is observed as noise at the microscopic level, but it is modeled as a d.c. bias that is stable under external perturbation at the mesoscopic level (top trace in Figure 10). The mechanism of stabilization of the point attractor by means of the sigmoid curve is shown in Figure 11, along with the amplitude histogram and power spectrum of periglomerular pulse density.

The bulb, nucleus and cortex interact by positive and negative feedback. The self-sustaining basal activity of the periglomerular neurons provides an excitatory bias to the mixed populations comprising the inner bulb, and also the cortices to which the bulb transmits. The three parts have characteristic frequencies in the gamma range (20-80 Hz) and feedback delays to each other as well as to the periglomerular neurons.

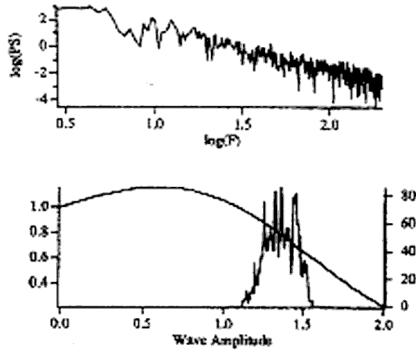


**Figure 10.** Simulations of output in the resting state by the KIII model are shown for activity patterns observed in 4 parts of the olfactory system in the rest state.

The inhibitory feedback between oscillators gives rise to negative or zero Lyapunov exponents. The excitatory feedback from the



anterior nucleus to the periglomerular neurons gives a positive exponent. Aperiodic activity is sustained by the system in the absence of input. The basal activity again exhibits a Gaussian distribution of amplitude (Figure 12), but the operating rest point at zero wave density is on the rising phase of the gain curve, reflecting the inherent bistability of the KII set in strong contrast to the periglomerular KI set [20].



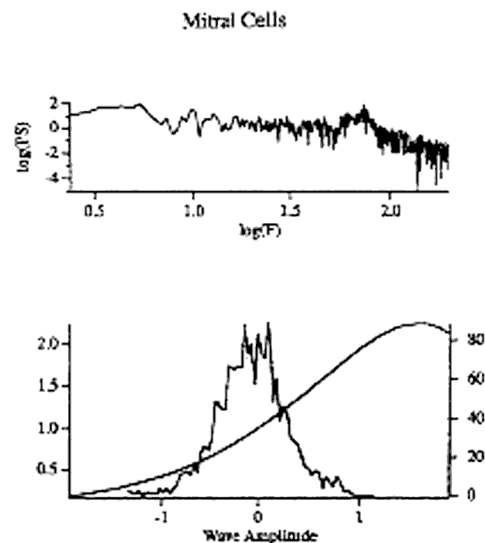
**Figure 11.** The stabilization of the KI set at the input layer of the olfactory bulb, PP, is on the right (upper) segment of the sigmoid curve, so that an increase in input amplitude leads to an increase in output amplitude, but the positive feedback gain is decreased, so the system returns to its nonzero rest level. That level is represented in a linear approximation by a real-valued root of zero, which corresponds to a pole at the origin of the complex plane. This pole governs the level of the background bias to the bulb and its targets of transmission.

**5. Microscopic coding and noise**

These observations in modeling the neuroanatomy and neurodynamics of olfactory cortex and simulating its spatiotemporal patterns of activity require inclusion of the distinction between high-dimensional "noise" at the microscopic unit level, low-dimensional chaotic "signal" at the mesoscopic EEG level [14], and the relations between them. The "noise" is essential for the maintenance of normal mesoscopic activity, for which it is a carrier, and the levels and spatiotemporal patterns of the "noise" are controlled by the mesoscopic activity acting as an order parameter [31] and as a "signal" [7, 17, 18, 25]. In turn, the mesoscopic activity of multiple mesoscopic domains organizes itself into macroscopic patterns that may occupy an entire cerebral hemisphere [19]. Microscopic neural coding is determined by recording pulse trains from single cells during

sensory stimulation and motor activation. The sensory code in all modalities is topographic from multiple receptor types distributed broadly and inhomogeneously over the receptor surface and extending their axons centrally as labeled lines. The intensity on each axon is conveyed by the pulse frequency.

Neural coding in cortical populations has been analyzed mainly from records of EEGs [13]. Corroborative evidence has been obtained by simultaneous recording of dendritic potentials and selected axonal potentials [12, 15]. The requirement has been imposed that (a) records be taken simultaneously from arrays of 16 to 64 electrodes placed on the cortical surface; (b) that the subjects be in the waking state and engaged in controlled sensorimotor behavior, such as performance of a conditioned reflex in response to conditioned stimuli; and (c) that brief epochs (on the order of 0.1 second) of EEGs be classified in respect to antecedent conditioned stimuli or consequent conditioned responses, solely on the basis of the spatiotemporal patterns of cortical activity that are extracted from sets of EEG traces [26, 28].



**Figure 12.** Spectrum and amplitude histogram of olfactory bulb simulation. The gain curve is from equation 3, the derivative of the sigmoid function. The negative feedback loops of the three oscillators are stabilized on the left (lower) side of the sigmoid curve, where an increase in input leads to an increase in output and also to an increase in gain, giving the input-dependent destabilization. This mechanism for conditional stabilization and bistability is characteristic of the limit cycle attractor.

The content is distributed over the entire sensory area, so that every neuron is involved in every discrimination. Local areas with high amplitude EEG are no more or less important than those with low amplitude EEG [26, 27]. The fields have the forms of interference patterns resembling holograms, except that their mechanism of formation is nonlinear and unstable involving state transitions and there is no inverse by which to recreate the input from the created patterns. The mean firing rates have no value as state variables, because it is the set of relations of every local amplitude to all others that defines the content.

The conversion of a sensory stimulus in the microscopic code on input axons to a mesoscopic code distributed over the whole of the sensory cortex depends on the conjunction of three factors. One is the prior formation through learning of a nerve cell assembly of strengthened associational connections at the synapses of excitatory neurons onto other excitatory neurons [9, 12]. The second is a motivated state of the subject that is expressed in a steep sigmoid curve. The third is a surge of input that is widespread over the cortex and that includes input not only to the learned nerve cell assembly but also to many other neurons in the bulb, whose response has been attenuated by habituation to uninformative, distracting, and ambiguous input.

In these circumstances the destabilized cortical mechanism is guided by the assembly into the basin in a chaotic attractor landscape for the entire cortex, which is expressed by the spatial pattern of the output of the entire cortex. That output is re-expressed in the microscopic form by the action potentials on the axons of the projection neurons that carry it to other areas of cortex or into the brainstem, where it has been shown to guide other interactive populations into basins of attraction formed in past learning experiences [4].

## **6. Chaotic attractor stabilization and classification enhancement by noise**

New techniques for large-scale parameter optimization enable simulation of these time series, as well as their spatial patterns of amplitude modulation following learning, with the solutions of networks of coupled ordinary difference equations having a static sigmoid

nonlinearity at the output of each node. The deterministic model is exquisitely sensitive to exceedingly small numerical changes in parameters, due to attractor crowding with basins of attraction shrinking to approximate the size of the digital numbers used for computation [35], and to lack of a shadowing trajectory [8, 30] due to the repeated destabilization and restabilization that requires translation of the real parts of the closed loop roots of the differential equations across the imaginary axis under piece-wise linearization [12, 20].

Considering that the olfactory system has both peripheral and central sources of noise, low-level Gaussian noise is added (Figure 9) at two significant points [7, 25]. This noise is designed to simulate the experimentally derived parameters of neurobiological noise: spatially independent and rectified at the input to simulate receptor input, and normally distributed with an excitatory bias but spatially coherent for the noise of central origin from other parts of the brain. The combined effect is to stabilize the model under input-induced state transitions and improves the simulations of EEGs and pulse densities from the olfactory system. Noise appears to do this by smoothing the landscape from digital representation in a nowhere differentiable manifold resembling rabbit fur to a smooth and well behaved landscape with a small number of large basins. These improvements are needed not only for EEG simulations but for optimizing the classification efficacy of the KIII model [32]. The Gaussian noise is simulated digitally with a random number generator, which supports robust and repeated access by repeated inputs to the learned basins of attraction in the simulated landscape through 1st order state transitions that are triggered by spatiotemporally patterned inputs given to the open nonautonomous KIII model, just as stimuli are received by brains that routinely function as open systems.

In using these data to model changes with associative learning a 2-D layer of 64 coupled oscillators is constructed to simulate the OB, and the simulated synaptic strengths between the coupled oscillators in the model are modified in accordance with modified Hebbian criteria [36]. The model also incorporates the biological property that the response energy during habituation to undesired input is not decreased, but is shifted from the gamma range to the theta range of cortical activity. Thereby the

"background" noise is not filtered out but is used to enhance the effectiveness of the microscopic "foreground" signal by contributing to the destabilization simulating the respiratory wave (Figure 5). With education by examples under selective reinforcement, the spatial pattern of amplitude modulation of the common carrier changes from a previous pattern and stabilizes in a new pattern, whenever an example is given as a member of the learned class of input. The report given by the system generalizes to the class of membership, which conveys the meaning of a stimulus, and not its form that is unique to each instance of stimulus presentation.

Each new stimulus that the model is trained to discriminate gives rise to a distinctive new spatial pattern of output that consists of 64 scalar AM values of the carrier wave, so that each output is a vector for a point in 64-space. The degree of similarity or difference between patterns is expressed by a Euclidean distance in 64-space. Classification is based on clustering of the points derived from measurement of individual responses in the biological system [26]. The effectiveness of the classification depends equally on each of the available measurements from a topographic array of input channels, which shows that the information density is distributed and spatially uniform, not localized as with the point processes of sensory displays. These properties replicate the dynamics of the olfactory system operating in the chaotic mode [13, 36]. The most effective performance of the KIII model in pattern recognition is achieved when it is operating in a chaotic domain that has been stabilized by optimal levels of noise [32], and in which the noise is further optimized in the manner of stochastic resonance.

## 7. Mesoscopic to macroscopic interface

This work is now in progress.

## 8. Summary.

The sensory input and motor output of brains is carried by action potentials at the microscopic level of brain function. The organization of the patterns of the 'units' that support behavior is done by large domains of the brain, as revealed by macroscopic brain imaging. The work of bridging between these levels is done at the intervening mesoscopic level by wave packets. These are spatially coherent domains of activity 1-2 cm in diameter, lasting 80-120 msec, and

recurring at 2-7/sec. They are manifestations of local mean field activities of millions of neurons, which self-organize spatial patterns of activity in the form of amplitude modulation of a common aperiodic carrier wave. They show the intrinsic bistability of areas of cortex at the mesoscopic level, comparable to the bistability of the axon at the microscopic level. A sensory cortex receives input from sensory pathways during a receptive 'diastolic' period, then transits to a transmitting 'systolic' mode by a 1st order phase transition, in which state it combines the features of the sensory input in the context of past experience fixed in the synaptic matrix of the cortex by past learning and the current brain state determined by the neuromodulators in which the cortex is bathed. The cortical output is broadcast in the form of a distributed interference pattern, which is selected by the targets in much the way that radio receivers can be tuned to specific broadcast stations, unlike point-to-point transmissions in telephone networks. All this mesoscopic action is detected, measured, and understood through recording the EEGs generated by the neurons comprising and enslaved by the wave packets. The EEG is not in itself the agent of cohesion of the neural activity; it is the noise made by the millions of neurons that contribute to it. Any attempt to inject electric current from electrodes placed in cortex so as to simulate the function of a wave packet would be like trying to fly a plane by playing a tape recording of the plane taking off from a loudspeaker set up beside the plane parked on a runway. The upshot is that the design of new electronic devices can best be undertaken with the aim of realizing in hardware the properties of wave packets, not merely of action potentials.

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## References

- [1] Abeles M (1991) *Corticonics: Neural Circuits of the Cerebral Cortex*. Cambridge UK: Cambridge University Press.
- [2] Aertsen A, Erb M, Palm G (1994) Dynamics of functional coupling in the cerebral cortex. *Physica D* 75: 103-128.
- [3] Barrie JM, Freeman WJ, Lenhart M (1996) Modulation by discriminative training of spatial patterns of gamma EEG amplitude and phase in neocortex of rabbits. *J. Neurophysiol.* 76: 520-539.

- [4] Bressler SL (1988) Changes in electrical activity of rabbit olfactory bulb and cortex to conditioned odor stimulation. *J. Neurophysiology* 102: 740-747.
- [5] Chang H-J, Freeman WJ (1996) Parameter optimization in models of the olfactory system. *Neural Networks* 9: 1-14.
- [6] Chang H-J, Freeman WJ (1998a) Optimization of olfactory model in software to give 1/f power spectra reveals numerical instabilities in solutions governed by aperiodic (chaotic) attractors. *Neural Networks* 11: 449-466.
- [7] Chang H-J, Freeman WJ (1998b) Biologically modeled noise stabilizing neurodynamics for pattern recognition. *International Journal of Bifurcation and Chaos* 8: 321-345.
- [8] Dawson S, Grebogi C, Sauer T, Yorke JA (1994) Obstructions to shadowing when a Lyapunov exponent fluctuates about zero. *Physical Review Letters* 73: 1927-1930.
- [9] Douglas RJ, Koch C, Mahowald M, Martin KAC, Suarez HH (1995) Recurrent excitation in neocortical circuits. *Science* 269: 981-985.
- [10] Eeckman FH, Freeman WJ (1991) Asymmetric sigmoid nonlinearity in the rat olfactory system. *Brain Research* 557: 13-21.
- [11] Eisenberg, J., Freeman, W.J. and Burke, B. Hardware architecture of a neural network model simulating pattern recognition by the olfactory bulb. *Neural Networks* 2: 315-325, 1989.
- [12] Freeman WJ (1975) *Mass Action in the Nervous System*. New York: Academic
- [13] Freeman WJ (1987) Techniques used in the search for the physiological basis of the EEG. In: Gevins A, Remond A (eds) *Handbook of EEG and clinical Neurophysiology Vol 3A, Part 2, Ch. 18*. Amsterdam: Elsevier.
- [14] Freeman WJ (1988) Strange attractors govern mammalian brain dynamics, shown by trajectories of electroencephalographic (EEG) potential. *IEEE Trans. Circuits & Systems* 35: 781-783.
- [15] Freeman, WJ (1992) Tutorial in Neurobiology: From Single Neurons to Brain Chaos. *International Journal of Bifurcation and Chaos* 2: 451-482.
- [16] Freeman WJ (1995) *Societies of Brains. A Study in the Neuroscience of Love and Hate*. Hillsdale NJ: Lawrence Erlbaum Associates.
- [17] Freeman WJ (1996) Random activity at the microscopic neural level in cortex ("noise") sustains and is regulated by low-dimensional dynamics of macroscopic cortical activity ("chaos"). *International Journal of Neural Systems* 7: 473-480.
- [18] Freeman WJ (1998) The regulation and use of microscopic neural noise by macroscopic chaos within populations of neurons in brains. pp. 89-105. *Proceedings, 19th Nihon University International Symposium "Order and Non-Order"*. Ito Y, Kawakami I, Konno K, Matunaga Y, Shimada I, Tsubokawa T (eds.) Singapore: World Scientific.
- [19] Freeman WJ (1999) *How Brains Make Up Their Minds*. London UK: Weidenfeld & Nicolson.
- [20] Freeman WJ (2000) *Neurodynamics. An Exploration of Mesoscopic Brain Dynamics*. London UK: Springer.
- [21] Freeman W J, Baird B (1987) Relation of olfactory EEG to behavior: Spatial analysis: *Behavioral Neuroscience* 101:393-408.
- [22] Freeman WJ, Barrie JM (1994) Chaotic oscillations and the genesis of meaning in cerebral cortex. In: Buzsaki G, Llinás R, Singer W, Berthoz A, Christen Y (eds.) *Temporal Coding in the Brain*". Berlin, Springer-Verlag, pp 13-37.
- [23] Freeman WJ, Barrie JM (2000) Analysis of spatial patterns of phase in neocortical gamma EEGs in rabbit. *Journal of Neurophysiology* 84: 1266-1278.
- [24] Freeman WJ, Barrie JM, Lenhart M, Tang RX (1995) Spatial phase gradients in neocortical EEGs give modal diameter of "binding" domains in perception. *Abstracts, Soc. Neurosci.* 21: 1649 .
- [25] Freeman WJ, Chang H-J, Burke BC, Rose PA, Badler J (1997) Taming chaos: Stabilization of aperiodic attractors by noise. *IEEE Transactions on Circuits and Systems* 44: 989-996. .
- [26] Freeman WJ, Grajski KA (1987) Relation of olfactory EEG to behavior: Factor analysis: *Behavioral Neuroscience*, 101: 766-777.
- [27] Freeman WJ, Van Dijk B (1987) Spatial patterns of visual cortical fast EEG during conditioned reflex in a rhesus monkey. *Brain Research*: 422: 267-276.
- [28] Freeman WJ, Viana Di Prisco G (1986) Relation of olfactory EEG to behavior: Time series analysis. *Behavioral Neuroscience* 100:753-763.
- [29] Freeman WJ, Yao Y, Burke B (1988) Central pattern generating and recognizing in olfactory bulb: A correlation learning rule. *Neural Networks* 1: 277-288.
- [30] Grebogi C, Hammel SM, Yorke JA, Sauer T (1990) Shadowing of physical trajectories in chaotic dynamics: Containment and refinement. *Physical Review Letters* 65: 1527-1530.
- [31] Haken H (1983) *Synergetics: An Introduction*. Berlin: Springer-Verlag.
- [32] Kozma R, Freeman WJ (2001) Chaotic Resonance: Methods and applications for robust classification of noisy and variable patterns. *International Journal of Bifurcation and Chaos*, in press, June 2001.
- [33] Singer W, Gray CM (1995) Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience* 18: 555-586.
- [34] Softkey WR, Koch C (1993) The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs. *Journal of Neuroscience* 13: 334-350.
- [35] Tsang KY and Wiesenfeld K (1990) Attractor crowding in Josephson junction arrays. *Applied Physics Letters* 56: 495-496.
- [36] Yao Y, Freeman WJ (1990) Model of biological pattern recognition with spatially chaotic dynamics. *Neural Networks* 3: 153-170.