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A neurobiological theory of meaning in perception.

Part 1. Information and meaning in nonconvergent and nonlocal brain dynamics

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Abstract

The aim of this tutorial is to document a novel approach to brain function, in which the key to understanding is the capacity of brains for self-organization. The property that distinguishes animals from plants is the capacity for directed movement through the environment, which requires an organ capable of organizing information about the environment and predicting the consequences of self-initiated actions. The operations of predicting, planning acting, detecting, and learning comprise the process of intentionality by which brains construct meaning. The currency of brains is primarily meaning and only secondarily information. The information processing metaphor has dominated neurocognitive research for half a century. Brain certainly process information for input and output. They pre-process sensory stimuli before constructing meaning, and they post-process cognitive read-out to control appropriate action and express meaning. Neurobiologists have thoroughly documented sensory information processing bottom-up, and neuropsychologists have analyzed the later stages of cognition top-down, as they are expressed in behavior. However, a grasp of the intervening process of perception in which meaning forms requires detailed analysis and modeling of neural activity that is observed in brains during meaningful behavior of humans and other animals. Unlike computers brains function hierarchically. Sensory and motor information is inferred from pulses of microscopic axons. Meaning is inferred from local mean fields of dendrites in mesoscopic and macroscopic populations. This tutorial is aimed to introduce engineers to an experimental basis for a theory of meaning, in terms of the nonlinear dynamics of the mass actions of large neural populations that construct meaning. The focus is on the higher frequency ranges of cortical oscillations. Part 1 introduces background on information, meaning and oscillatory activity (EEG). Part 2 details the properties of wave packets. Part 3 describes the covariance structure of the oscillations. Part 4 addresses the amplitude modulations, and Part 5 deals with the phase modulations. The significance of a theory of meaning lies in applications using population neurodynamics, to open new approaches for treatment of clinical brain disorders, and to devise new machines with capacities for autonomy and intelligence that might approach those of simpler free-living animals.

1. Introduction

The predominant view of brain function among neuroscientists is that brains have evolved to process information. According to this hypothesis neurons form networks that receive, store and manipulate information in the form of representations of objects and events in the environment. A keystone of this view is information theory, which Shannon [1948] devised by divorcing information from meaning:

"The fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point. Frequently the messages have meaning; that is they refer to or are correlated according to some system with certain physical or conceptual entities. These semantic aspects of communication are irrelevant to the engineering problem" [p. 1, Claude Shannon, 1948].

Yet information has less survival value for humans and other animals than does meaning. From a biological perspective a theory of meaning might be far more useful in understanding brain function than a theory of information. However, there are significant problems in devising such a theory. There is no widely accepted definition of meaning by which to express it in a set of state variables in a model. It is not subject to quantitative measurement, prediction and description with mathematical and statistical tools. It cannot be transmitted using information as a carrier. Books, articles, graphs, paintings, icons, and other human artifacts are designed to elicit meaning in observers by information transmission, but the meaning that results is observer-dependent:

"I have already explained what I think of literal representation; but one cannot insist enough on this: *there is no true meaning of a text*. No author's authority. Whatever he may have wanted to say, he wrote what he wrote. Once published, a text is like an implement that everyone can use as he chooses and according to his means: it is not certain that the maker could use it better than someone else" [p. 1,597, Paul Valéry, 1957].

Clearly meaning is constructed within each brain following search for and reception, through the senses, of the requisite information. Proof of this statement is in this paragraph. Every reader on reading it will have a distinctive understanding from the information in the letters, that will depend on background and expectation, but no understanding will be entirely congruent with that of the author or any other reader, nor will any reader remember the sequence of letters. Evidently meaning is a closed system in each brain, that the brain expresses by forming external representations. It uses the body to make gestures, words, icons, and other symbols to broadcast or channel its internal states of meaning.

Meaning derives from intention, which is the creation and projection by the brain of alternative future states, desired or feared. These hypotheses are constructed in attractor dynamics by extrapolation from past experience, and they serve to control choices and directions of actions in the present. The projections are tested by actions into the environment and are evaluated and updated from the sensory consequences of the actions. This process of intentionality raises the unsolved referential "symbol grounding" problem in information processing [Harnad, 1990,

2001], which is the difficulty in establishing the semantic relations between the symbols in a logical calculus and the objects and events in the world that they represent [Searle, 1992]. Formation of the meanings of the symbols requires that brains, and devices, act into the world and learn from the consequences of their intentional actions [Steels & Brooks, 1996; Clark, 1996; Hendriks-Jansen, 1996; Freeman, 2001].

These are sufficient reasons to explain why discussion of meaning is common among philosophers [Parkinson, 1968; Stonier, 1997] but is seldom considered in the context of neurobiology [Fischer, 1993; Tsitolovsky & Babkina, 2002]. However, even the brains of simpler animals such as those in cats and rabbits, which can be regarded as electrochemical machines, have the capacity to construct meaning. Computers do not, and contemporary robots can act and learn but cannot intend. Successful simulation of animal intelligence could lead to an entirely new kind of artificial intelligence, for example, robots that could operate autonomously in unfamiliar environments, evaluating local conditions and making decisions to optimize their performance without need for immediate and continuous supervision. In brief, small mammals provide a biological proof of the possibility of constructing machines that can intend and construct meaning.

2. Toward a theory of meaning

A foundation in physics for a theory of meaning was laid by James Barham [1996] in terms of nonequilibrium thermodynamics and the nonlinear dynamics of coupled oscillators self-governed by attractors in phase space. He proposed that biological systems can be characterized as generalized nonlinear oscillators, which are stabilized through successive phase transitions by effective interaction with high energy environmental oscillators serving as constraints (e.g., sources of food). Information inheres in low energy environmental energy fluxes that are correlated with the high energy fluxes so as to serve as signals of distal events (e.g. odors of prey). Effective interaction comes with thermodynamic engagement of the inner and outer high energy oscillators (e.g., with attack and consumption). He called the inner counterpart of an outer low energy system an "epistemon" and identified it with a chaotic attractor in a sensory system. He interpreted the meaning of the information as the "prediction of successful functional action" [p. 235]. In biological terms the meanings of stimuli for an organism are demonstrated by the uses to which they are put in successful adaptation to environmental constraints through the action-perception cycle [Piaget, 1930; Merleau-Ponty, 1945]. In engineering terms the meaning of low-energy environmental constraints will be observed in the successful adaptation of autonomous robots to environmental challenges without observer intervention.

Recent advances in technology have made it possible to for neurobiologists to observe the electrochemical oscillations of energy that enable brains to maintain their states far from equilibrium and at the edge of stability. Masses of neurons constitute nonlinear oscillators that generate what Tsuda [2001] has called "itinerant trajectories" through successions of attractors that dissolve into "attractor ruins" as soon as they are accessed. Measurement of the autocorrelation functions, spectra, and statistics of these nonconvergent oscillations makes it possible to construct models of brain dynamics using networks of ordinary differential equations in software [Kozma & Freeman, 2001; Kozma, Freeman & Erdí, 2002] and hardware VLSI

[Principe et al., 2001] to generate simulations. The physiological evidence has been gathered from electroencephalograms (EEG) [Barlow, 1993] recorded with high density electrode arrays, intracranially on or in the brains of cats, rabbits, and neurosurgical patients, and from the scalps of normal volunteers. Signal identification and pattern classification have been done with high temporal resolution using wavelets [Freeman & Grajski, 1987] and the Hilbert transform [Freeman & Rogers, 2002].

Behavioral correlation has shown that, unlike the patterns of action potentials derived by stimulus-locked averaging, the EEG patterns lack invariance with respect to learned stimuli, and instead depend on experience, context and reinforcement contingencies. This independence from stimulus specificity and dependence on experience is a necessary attribute for any brain activity that is to be related to meaning. Modeling with nonlinear ordinary differential equations indicates that the EEG patterns form by a 1st order phase transition [Abeles et al., 1995; Freeman, 1995, 2000a; Tsuda, 2001; Freeman & Rogers, 2002], resembling condensation of a gas to a liquid, or a subcritical Hopf bifurcation. Recent evidence suggests that percepts, the vehicles of meaning, occupy large areas of each cerebral hemisphere in animals and humans. They recur by repeated global phase transitions, with timings that are independent between the two hemispheres. Frame rates appear to decrease from a state of rest (alpha) to a state of intentional action (theta), when the brain engages sensory input, indicating the amount of extra time that is required for the human brain to construct meaning from sensory information.

Metaphorically speaking, a starting point is to visualize the receptor input from the retinas that enables a person to recognize a familiar face breaking into a smile. Sensory receptors are selective for types of environmental energy, not for information. The cortex must receive an enormous barrage of action potentials, that induces in the visual cortex an explosion of action potentials from all of the motion, edge, and color detectors in the visual field. Experimental evidence summarized here indicates that heightened activity can destabilize the cortex and induce the formation of a sequence of brief spatial patterns of neural activity. The phenomenon resembles the formation by fish, birds and insects of schools, flocks and swarms [Edelstein-Keshet et al., 1998]. Individuals synchronize their activities to conform to the whole, yet they retain their autonomy. In the sensory cortices the patterns bind only a small fraction of the total variance of the neural swarm, so the patterns are not observable in recording from one or a few neurons. They can be observed by multichannel EEG recording with high density arrays of electrodes placed epidurally over the cortex. This is because the main source of EEG potentials is the sum of the dendritic currents of the neurons in local neighborhoods that control the firing rates of the action potentials. That sum is accompanied by extracellular potential differences that give access to the local mean fields of activity governing the collective behavior [Freeman, 1992, 2001, 2003].

An important caveat is that no physical or chemical measurement of brain activity is a direct measure of meaning. Meaning can be experienced subjectively in oneself, and one can infer it in other from the behavioral context in which measurements are made, but one cannot measure it. An equally important caveat is that no measurement of brain activity makes sense unless the investigator has sufficient control over the behavior of a subject to be able to infer the teleology of the subject, whether animal or human, at the time of measurement, that is, the history, intention, expectation, motivation, and attentiveness of the subject. For this reason, all of the

data on brain function described in this tutorial have been accumulated from studies in which the subjects were carefully trained or coached to enter and maintain overt states of normal behavior that could be reproduced and measured, along with the measurements of brain activity.

Barham's thermodynamic theory of meaning posits low and high energy fluxes. The difference spans many orders of magnitude, for example, between a few molecules of an odorant and the mass of skeletal muscle in a predator or prey. The description of brains must be hierarchical, from molecules to the brain and body as a functioning unit in perception, which is the process of constructing meaning. The lowest level is the quantum mechanical description of the energy and information transfers that occur between environmental molecules and macromolecular assemblies in the membranes of sensory receptor cells. The next is the biochemical description of the positive feedback loops by which the energy of the information is amplified by 10^4 [Lancet et al., 1982] and transduced to trains of action potentials for transmission into the brain. There in cortex the meaning is constructed in perception with further amplification by 10^4 [Freeman, 1992]. The neurodynamics of perception in populations occurs in three levels, with both upward and downward interactions across the two interfaces. The first level is microscopic. Observers measure the trains of action potentials of neurons one at a time in behaving animals. The second level is mesoscopic. Observers measure the summed dendritic potentials of masses of neurons and acquire evidence of local mean fields (LMF). The third level is macroscopic. Observers use imaging techniques such as fMRI [Buxton, 2001] to measure activity patterns in whole brains. Descriptions of the observations made at each level fill many journals, monographs, and textbooks.

Much less well documented are the energy transforms at the two interfaces. My views on the first interface, between microscopic and mesoscopic, have been presented in several reports in this journal [Freeman, 1992, 1999, 2000, 2003; Chang & Freeman, 1998, 1999; Kay, Shimoide & Freeman, 1995; Kozma & Freeman, 2001] and are summarized here in Part 1. The bulk of this tutorial addresses the second stage in perception, in which construction of meaning occurs bidirectionally across the mesoscopic-macroscopic interface.

3. The information hypothesis: Neural networks

In the main stream view of experimental and theoretical neuroscientists, cortex processes information that comes from objects in the environment delivering space-time patterns of energy to sensory receptors. The receptors encode the information in trains of action potentials for transmission into the brain and thereafter between neurons. The brain builds dedicated neural networks ("assemblies") to process the information by modifying the synaptic connections among cortical neurons. The environmental information in the energy patterns is corrupted by thermal noise and other inadequacies and limitations of the biological mechanisms of transduction. It is fragmented by conversion to pulse trains, which are point processes that represent discontinuously the continuous gradations in the incident energy. It is further distorted by delay, temporal dispersion, and spatial divergence in the axon tracts that topographically map the body organs and surfaces (skin, retina, cochlea, tongue and nose) onto the sensory cortices. Above all, the information from objects is overlain by environmental noise, clutter and background. Sensory receptors respond nonselectively to all incident energies within their

domains of specialization. The task of cortex is to identify and respond preferentially to that portion of the information inflow, the foreground, that is relevant to the survival of the organism.

In this prevailing view information is inherent in the "features" of objects, such as the contours of a face, the phonemes of a word, and the chemical constituents of an odor. Each feature is matched by a cortical neural assembly with synaptic connections that have been strengthened or weakened by learning in past experience [Hebb, 1949]. The assembly constitutes a memory of that feature. A match is signified by a burst of firing of the "feature detector" neuron. Its pulse train is a representation of the feature. The set of features belonging to an object, such as its color, shape, consistency and weight, induce the simultaneous discharge of an assembly of feature detector neurons. When the pulse trains of that assembly are coordinated in firing times, they match the environmental coordination of the features, and the collective firing constitutes a representation of the object. This operation of combining the firing of the feature detectors is known as "feature binding" [von der Malsburg, 1983].

Multi-unit recording and time ensemble averaging of action potentials has indicated that the probability of spike occurrence for many feature detector neurons oscillates at frequencies in the gamma range. Evidence in each sensory modality has often shown phase locking of multiple spike trains at a shared frequency. These findings have suggested that the "binding" of feature detector neural activity may occur by linear vector summation to form representations of sensory stimuli [von der Malsburg, 1983; Singer & Gray, 1995; Roelfsema et al., 1997; Singer et al., 1997]. Models have been offered by Schillen & König [1994], Traub et al. [1996], and Whittington et al. [2000] to explain how synchrony might be achieved at the microscopic level despite obligatory conduction delays [Freeman, 2000b]. This linear approach been criticized on diverse grounds [e.g., Tovée & Rolls, 1992; Hardcastle, 1994; Ghose & Freeman, 1997]. Yet there is a basic validity in the concept of synchronization that needs more sophisticated reformulation [Quiroga et al., 2002]. Some other approaches at the microscopic level include "synfire chains" [Abeles et al., 1995]; self-stabilizing "phase-locked pulse trains" [Aertsen, Diesmann & Gewaltig, 1996; Diesmann, Gewaltig & Aertsen, 1999; Fries et al., 2001]; multineuronal firing in motor cortex constituting "vector codes" for movement [Georgopolis, Schwarz & Kettner, 1986]; and maintenance of representations in local neuronal netlets by "reverberations" that form short term memories [Amit, 1989; Miyashita, 1993, 1995]. Hoppensteadt and Izhikevich [1998] and Izhikevich [1999] proposed that neurons and columns of neurons function as quasi-periodic oscillators having multiple spikes in their spectra. Even if the oscillators are connected synaptically, they can only interact at resonant frequencies. Mean firing rates identify the channels of communication. Information is carried by modulations in interspike intervals about the mean frequencies, as it is in radio FM between transmitter and receiver tuned to the same carrier frequency.

The correlated action potentials of an assembly are thought to be carried by converging axons to higher order neurons. Successful information processing occurs when a higher order neuron fires a burst that represents the object or, better yet, the class to which the object belongs. Evidence for the existence of what might be called "object detector" neurons and "object binding" takes the form of the highly selective responses of neurons in association cortex of awake, behaving animals to complex objects such as faces, hands, or words. A widely cited version of this model [Engel et al., 1999] holds that "dynamic binding by transient and precise

synchronization of neuronal discharges" serves as "some form of attentional mechanism ... that selects relevant information and enhances its impact on subsequent processing stages" [pp. 130-131]. "The prediction is that neurons which respond to [selected features of] the same sensory object might fire their action potentials in temporal synchrony with a precision in the millisecond range", thereby "providing an efficient mechanism for selection of assemblies for further processing ... because precisely synchronized spikes constitute highly salient events which can be detected by coincidence-sensitive neurons in other brain areas" [p. 132], so that the output of an assembly is " ... 'routed' [targeted] to appropriate processing centers downstream" [p.145] by the transmitting area of cortex containing the assembly.

The ensuing steps in developing the information processing hypothesis, yet to be taken, are conceived as integrating representations of objects into neural firing patterns that will represent frames, and then into temporal sequences of frames that will represent actions such as search, speech and dance. The penultimate goal is to model the cognitive processes that brains use to recognize objects against varied backgrounds, predict the sequellae that are implicit in incoming information, and select the appropriate motor responses to the processed information. Mainstream neurobiologists aim to understand the neural basis for these steps by generalizing the network concept. They conceive of cortex as a network of modules [Calvin, 1996; Bressler, 1996; Taylor, 1997; Bruns et al., 2000; Eckhorn et al., 2001]. Each module contains the local assemblies that are required to extract and process the information to represent features and objects. Just as neural networks are adapted by learning to match features, the modular networks are conceived to form collections of episodic memories by modification of the synapses sustained by long axons between cortical modules. The preferred mode of learning is by reinforcement.

Functional evidence for networks of modules has been derived in part from recording pulse trains of multiple neurons in diverse cortices [e.g., Abeles, 1995; Aertsen et al., 1996; Vaadia, 2000], but more often from other techniques: the EEG [e.g., Bressler, 1996; Haig et al., 2000], the magnetoencephalogram (MEG) [Joliot, Ribary & Llinás, 1994], event-related potentials (ERP) [Gevins et al., 1989], and imaging of regional changes in cerebral metabolism and blood flow by several methods [Roland, 1993]; Buxton, 2001]. With these techniques the modules appear as areas of high neural and/or metabolic activity, blood flow or oxygen deficit ("hot spots") in association with standardized forms of behavior. Notably, the meaning of information is seldom discussed.

4. Difficulties encountered by the information hypothesis

The information processing model is indispensable for describing sensory function, when the number of neurons is kept low by the experimental conditions. What fails is the attempt to up-scale network modeling beyond the number of neurons that are accessible for simultaneous recording. Human cortex has billions of neurons and trillions of synapses, yet most of the supporting evidence for the network hypothesis has come from recording pulse trains of neurons one at a time. The limitations on microelectrode technology presently allow simultaneous recording from a few hundred neurons at most. The difficulties in scaling stem from various features of cortex, ten of which are listed here for didactic purposes. First, the Golgi technique that is used to visualize neurons in networks stains only about 1% of the neurons in a slice, if it is

successful, for otherwise the slices are interpretable [Sholl, 1956]. This gives a sample biased to the larger neurons, and by abstraction it presents a picture of cortex as a network rather than a tissue. Second, each cortical neuron receives synaptic input from roughly 10^4 neurons and transmits to about 10^4 other neurons, not merely the number that can be recorded. Third, cortical connectivity is sparse. Each cortical neuron connects with only 1% of the 10^6 neurons within the diameter of its dendritic tree [Braitenberg & Schüz, 1991], and the likelihood is one in a million of reciprocal connections between any pair of neurons forming symmetrical Hebbian synapses. Fourth, a remarkable 85% of the input to a cortical neuron is from other cortical neurons, and the greatest portion by far of those synapses is excitatory. Only a small proportion of cortical synapses is maintained by axons that relay input from sense organs. Fifth, whereas topographic order is characteristic of sensory and motor pathways, intracortical and intercortical pathways tend to divergence-convergence. Each neuron transmits to many and receives from many. This is especially well documented for the olfactory system [Freeman, 1975]. While cortical input from sensory arrays is mapped from the body surface in a way that preserves the spatial relationships of receptors, cortical output undergoes spatial integral transformation that selects cortical activity having spatial coherence (a common instantaneous temporal frequency over a distribution of neurons) [Freeman, 2000a]. Owing to the relatively small number of long axons connecting remote cortical areas, no cortical neuron is more than 4 or 5 synapses from any other, raising possibilities for small world effects [Watts & Strogatz, 1998].

Sixth, action potentials serve mainly to transmit pulses without attenuation over distances greater than can be reached by diffusion or analog dendritic current [Häusser, Spruston & Stuart, 2000]. Many small neurons are "non-spiking"; they have no detectable pulses. In any case neural integration is not done with pulses. It is done only after conversion of the pulses to synaptic currents. The weighted sum of dendritic current, not the number of incoming action potentials, determines the relative rate of firing or the timing and likelihood that a neuron will fire. Conventional artificial neural networks avoid this problem by modeling average rates of firing, not the pulse trains [McCulloch & Pitts, 1943; Rosenblatt, 1962]. Pulsed neural networks simulate the precise timing of spike trains by transforming axonal pulses at synapses to dendritic current summed at trigger zones [Ermentrout, 1994; Chapeau-Blondeau, 2001]. Networks of simulated pulsing neurons [Maass & Bishop, 1998] are small and do not scale up to millions of neurons, because the simulated interactions are very complex.

Seventh, the input at a single excitatory synapse generates on the order of 1% of the current required to reach firing threshold, so that even in the unlikely condition of zero inhibitory input, the coincidence of on the order of 10^2 incoming action potentials in each ms is required to reach threshold [Amit, 1989]. This exceeds the number of feature detectors that are accessible to recording for experimental proof. Eighth, the background firing rates of cortical neurons seldom exceed 1 to 10 pulses/s. In time windows on the order of 0.1 to 0.2 s, which are typical for the frame durations of cortical events, any one neuron may contribute only one pulse if any [Abeles, 1991; Tovée & Rolls, 1992], so that mean firing rates have little meaning in networks. Barlow [1972] has proposed equivalence among "a college of cardinal cells" to avoid postulating Sherrington's [1940] "pontifical cell", perhaps in support of time-multiplexing, but this lacks experimental verification. Ninth, the pulse interval histograms of cortical neurons typically show an exponential decay after an initial refractory period [Freeman, 1975]. This form is consistent with a Poisson process having a dead time. The correlations of firing times of a

neuron with those of other neurons in the neighborhood are vanishingly small [Abeles, 1991]. The pulse trains appear largely as independent aperiodic point processes. Tenth, cortical neurons are continually active in the absence of sensory input. The seemingly random "spontaneous" activity in the form of pulse trains cannot be modeled with single integrate-and-fire neurons having random input [Gabbiani & Koch, 1996]. The spectra of EEG waves rarely show spikes other than artifacts at 50 or 60 Hz. They do not conform to the flat spectra of white noise but instead to $1/f^\alpha$ (linear decrease in log power with increasing log frequency with slope α) [Barrie et al., 1996; Hwa & Ferree, 2002]. This form is very difficult to simulate with digital computation owing to numerical instabilities [Freeman et al., 1997; Chang & Freeman, 1998, 1999].

Extension of the information processing hypothesis from neural networks to multicortical modular networks is problematic also on three conceptual grounds. First, complex physical, chemical and social systems having immense numbers of autonomous components are commonly viewed as hierarchically organized. They have multiple levels of description, each level with its own scales of time and space, its own state variables, and its unique perspective on events that take place across all levels simultaneously. The network concept with its token action potential lacks scaling above 10^2 neurons to 10^6 neurons and beyond.

Second, information is defined within the conceptual frame of the investigator and not that of the subject under investigation. Time-locked averaging of neural responses to stimuli reinforces this view, because averaging extracts the stimulus-induced component of cortical activity, while attenuating the intrinsic activity that individualizes the performance of the subject. That intrinsic activity is self-organized with its own times of onset. Owing to "jitter" [Tallon-Beaudry et al., 1998; Quiroga, Kreuz & Grassberger, 2002] in cortical activity and reaction time with respect to the time of stimulus onset, the intrinsic component is diminished by time ensemble averaging of cortical responses and is usually lost from view. The remaining information conforms to that which the investigator introduced through the sensory receptors. The comparison of output with input can measure the information loss through a channel, but the ratio cannot measure the information increase that surely must take place when the subject interprets and assigns meaning to the incoming information, because that increase has been attenuated or deleted by time-locked averaging.

Third, brains normally control their sensory input so as to admit only the information that is relevant to the goals of the organism. Information processing is channeled by expectancy, attention, and habituation, which are governed by the teleology of intention. That dynamic screening is suppressed by anesthesia, whereby stimulus-response relations are simplified. In awake subjects the S-R relations are far more complex [Nicoletis et al., 1998]. Interpretations require manipulation of the goal-states through reinforcement learning, but the neural mechanisms of goal formation and implementation through action are not readily addressed by information processing.

5. The meaning hypothesis: A neural continuum

A long-standing tradition outside the main stream has been that of holists. They have held that cerebral cortex functions as a unified tissue. Holists recognize that the modules identified in the

network view are essential for introducing processed information into the cortical mantle during sensation and feedback muscle control, but a network of modules does not suffice to support the higher order functions of perception and cognition. The debate on modular vs. global function of cortex has lasted well over a century without resolution [Young, 1970]. Among several conceptions of holist function, the better known are the field theory of Wolfgang Köhler [1940] based in Gestalt psychology, the equipotentiality of cortex of Karl Lashley [1960] based on his fruitless 50-year search for the "engram", the "holographic" memory model of Karl Pribram [1971], the Papez circuit of "emotionality" [Maclean, 1969], and the "global workspace" of Bernie Baars [1997]. These are top-down psychodynamic models from neuropsychologists are based on studies of human and animal behavior, both in normal subjects and in subjects after brain damage from experimental surgery, trauma or disease. They are in contrast with bottom-up neurodynamic models, that depend on measurements of neural activity in the brains of humans and animals that are engaged in normal behavior. Neurodynamic models must face the difficulty of defining a neural basis for meaning.

The ten features that have been listed open a new pathway to understanding cortical dynamics by turning them to advantage. They support models of cortical neurons operating in collective modes with continuous state variables in the form of pulse densities and dendritic current densities [Freeman, 1975; Wilson & Cowan, 1973; Nunez, 1981; Ingber, 1995; Wright & Liley, 1996; Robinson, Wright & Rennie, 1998]. This move to a hierarchical view is the reverse of the move in physics from a macroscopic thermodynamic treatment of fluids to a microscopic statistical mechanical description of molecules and atoms [Lindley, 2001]. In brain science the approach requires more than a change in state variables; it requires new scales of measurement in time and space, new properties of the architectures of connections (e.g., divergent-convergent projections vs. topographic mapping), and new equations to describe the transforms of pulses to waves at dendrites (state-dependent coefficients vs. the Nernst equation) and of waves to pulses at trigger zones (the sigmoid curve vs. the Hodgkin-Huxley equations) [Freeman, 2000a]. The number of hierarchical levels must be chosen, and the relations between state variables in each level to those above and below must be described. In this tutorial there are three hierarchical levels. The microscopic is that of the neuron and of neural networks with short scales (microns and milliseconds). The mesoscopic is that of the sensory, association, and motor cortices corresponding to the modules of network theory (millimeters and <0.1 second). The macroscopic is that of the lobes comprising each cerebral hemisphere (>10 cm and >1 second). The primary task is to define the spatiotemporal patterns within each of the three levels, particularly the reciprocal conversions between wave and pulse densities at synapses and trigger zones. The more difficult task is to describe the manner in which neural activity during normal behavior is related over the two interfaces — microscopic-mesoscopic and mesoscopic-macroscopic — in the construction of meaning.

The necessary conditions for the formation of an assembly were described by Ilya Prigogine [1980]: a large number of autonomous elements; distributed feedback interactions among them; nonlinear input-output functions of the elements; and an unlimited source of energy and sink for waste heat and entropy, so that the assembly operates far from thermodynamic equilibrium. These conditions are met by the immense number and relative autonomy of nerve cells, their broad synaptic connectivity, the nonlinearity in their pulse generating ionic mechanisms, and the role of the arterial supply of metabolic energy and venous disposal of waste heat and entropy.

Hermann Haken [1983] described the interactions of particles within a system in terms of "circular causality": the creation by an ensemble of an "order parameter" that regulated ("enslaved") the particles from which it emerged by bifurcation. His prime example was the transition in a laser from incoherent to coherent light output with the addition of sufficient energy to drive it far from equilibrium. Pulse densities (approximated by multiunit recordings) and wave densities (manifested in EEGs) from extracellular recordings of neural activity in local neighborhoods are obvious candidates for measurements of order parameters, because they are statistically (though not causally) related to the rates and time intervals of pulse trains from members of the neural populations [Freeman, 1975].

An operation is required by which to average the microscopic measurements of the intervals of neural pulse trains, in order to estimate the mesoscopic pulse density of neurons in the neighborhood of a measured neuron. This operation is done by assuming stationarity and invoking the ergodic hypothesis, that a representative neuron, if observed for a long enough time, will take all of the states of the neurons in the population at any one time. Experimentally a long recording is made simultaneously of pulses and waves, and the probability of pulse occurrence conditional on the amplitude of the wave density is calculated [Freeman, 1975]. A microelectrode is used with a high pass filter and a high threshold to record the pulse train of the single neuron, and a macroelectrode with a low pass filter and RC coupling is used to record the extraneuronal dendritic potential difference across cortex that is created by the flow across the cortical tissue resistance of the sum of dendritic current over the neighborhood. This measure of dendritic wave density is the "local field potential" (LFP) and the EEG. It is important to distinguish between the LFP and the "local mean field" (LMF). The mere summation of dendritic current does not create an interactive population. The population is formed by the synaptic interactions among the neurons based on the action potential, not by the extracellular dendritic current. The LFP is an epiphenomenon that manifests the LMF, only to the extent that the neurons are interacting, and only then does the LMF (EEG) serve as an index of an order parameter. The percentage of the total variance of the pulse train that is covariant with the local mean field is estimated to be on the order of 0.1% [Freeman, 2000a], so that the LMF is inaccessible by single unit recording. This small fraction indicates that cortical neurons are largely autonomous and can be involved with multiple order parameters and participate in multiple populations simultaneously. However, the LMF signals from those populations sum and overlap in the LFP, and they can only be untangled with reference to independent variables derived from measuring intentional behaviors.

Bak, Tang & Wiesenfeld [1987] proposed that a complex system such as a brain develops by self-organization to a critical state at the edge of chaos, by which it maintains a readiness to adapt rapidly to unpredictable changes in its environment and thereby maintain its integrity in accord with Barham's [1996] postulate. The adaptation is done by repetitive phase transitions; the space-time patterns of its state variables re-organize themselves abruptly and repeatedly. His prime example was the performance of a sand pile, in which a steady drip of grains of sand onto the central peak gave the pile the shape of a cone. The slope of the cone increased to a maximum that was maintained by repeated avalanches as sand continued to pour onto the apex. The avalanches had fractal distributions in size and time intervals. He called this a state of "self-organized criticality" (SOC), and he characterized it by the fractal distributions and the $1/f^\alpha$ form of the temporal spectra of the avalanches with α as the critical exponent. He concluded

that the $1/f^\alpha$ spectra were explained by the self-similarity of the recurrent events over broad scales of time and space. The $1/f^\alpha$ form has been repeatedly demonstrated in both temporal spectra [Barrie, Freeman & Lenhart, 1996; Hwa & Ferree, 2002; Srinivasan Nunez & Silberstein, 1998] and spatial spectra [Freeman & Baird, 1987; Barrie, Freeman & Lenhart, 1996; Freeman et al., 2000] of EEG recorded intracranially in animals and neurosurgical patients. Although EEG and EMG (the electromyogram from the action potentials of scalp muscles) appear to be similar in their time series, they differ significantly, because the spectrum of EMG tends to be flat like that of white noise, not $1/f^\alpha$ of EEG [Freeman, Holmes, Burke & Vanhatalo, 2003]. However, the temporal spectra are usually accompanied by prominent peaks in the clinical bands of theta (3-7 Hz), alpha (7-12 Hz), beta (12-30 Hz), and gamma (30-80 Hz), so that SOC cannot explain all of cortical dynamics. In particular, inclusion of the limbic and thalamic controls of cortical function are essential for modeling brain function [Taylor, 1997; Destexhe, 2000; Robinson et al., 2001; Steriade, 2000, 2001], but the focus here is on the intrinsic macroscopic properties of cortical activity, that which is being controlled.

6. The mesoscopic wave packet

The most important clue for constructing a neurodynamic theory of meaning was found by measuring the neural correlates of conditioned stimuli (CSs) that were recorded in the primary sensory cortices. For the information hypothesis the correlates were the features of the CSs, as they were defined and presented by the experimenter. For the meaning hypothesis the correlate was the state of the subject, prior to the stimulus and revealed in the history, context, and performance as the subject acted into the stimulus. These aspects constituted the meaning of the stimulus for the individual at the moment and circumstances of presentation. This difference was first revealed by analysis of the spatial patterns of EEG on recording from the surface of the olfactory bulb in rabbits trained to discriminate simple odorant chemicals serially [Freeman & Schneider, 1982]. The spatial patterns were observed by simultaneously recording 64 channels of EEG from an 8x8 array, giving a 4x4 mm window onto the bulb. With each inhalation a brief episode of oscillation occurred in the high beta and gamma range (20-80 Hz) that had everywhere in the bulb the same instantaneous frequency, but with spatial amplitude modulation (AM) of the shared wave form [Fig. 1]. The AM pattern in each event, whether calculated by PCA, FFT or simply RMS after temporal band pass filtering, was expressed in a 64x1 column vector giving a point in 64-space. The event was named "wave packet" [Freeman, 1975].

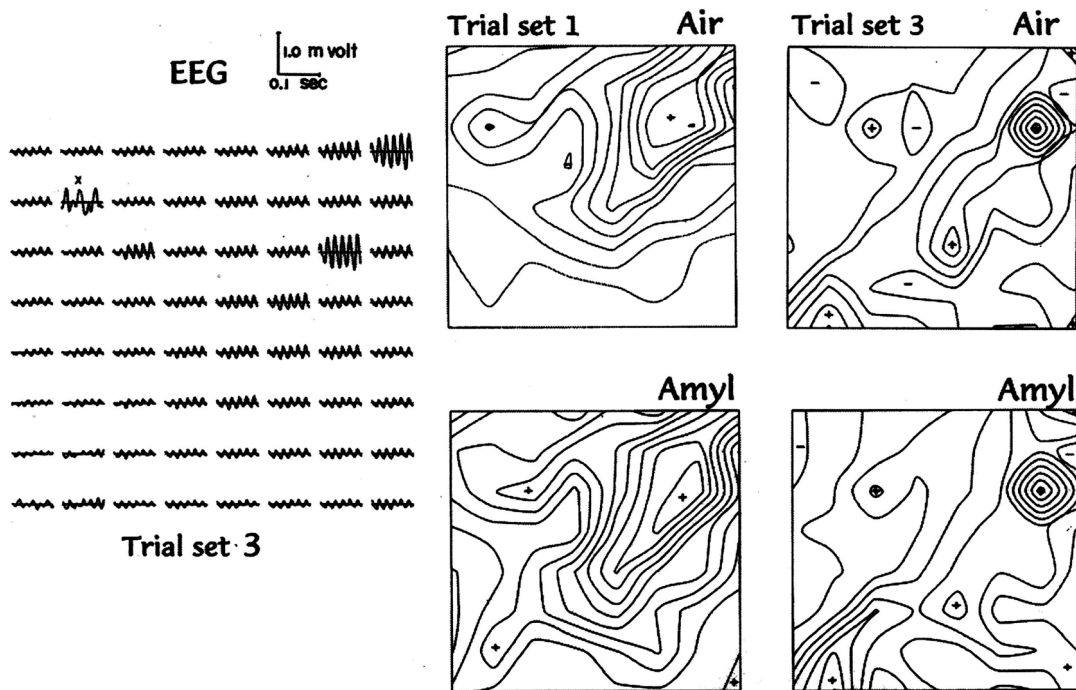


Figure 1. Left: The 64 EEG traces were band pass filtered in the gamma range and segmented to display an oscillatory burst with inhalation. the "x" marks a bad channel replaced with an EEG from the prepyriform cortex. Right: Contour plots show the amplitude modulation (AM) patterns with air and a conditioned stimulus (amyl acetate) on the first day of training and two weeks later with the same CS and control. From Freeman & Schneider, 1978.

The rabbits were trained to respond selectively to reinforced stimuli (CS+) and not to unreinforced stimuli (CS-). EEG patterns accompanying the two discriminated odorants and the background input formed three clusters of points in 64-space, which were displayed by projection into 2-space [Fig. 2]. The class of each pattern was defined by the location of the center of gravity of its cluster and its radius of 2 standard deviations (SD). The difference between classes was defined by the Euclidean distance between centers in units of SD. Classification of each individual pattern was by the shortest Euclidean distance to a center of gravity. The results showed that the discriminative AM patterns in the EEG lacked invariance with respect to the CSs [Freeman & Viana Di Prisco, 1986]. The AM patterns changed with training to new stimuli, or with switching the reward or punishment between CSs (reinforcement contingency reversal), or with other alterations in the context and history of recording. The AM patterns were unique for each individual, reflecting their dependence on unique experience. The efficacy of classification was dependent on the signal from every electrode equally, irrespective of its amplitude or variance. This test demonstrated that the information from measurement of the EEG patterns was uniformly distributed over the recording area in respect to its utility for the classification. This finding was contrary to the prediction of the information hypothesis, according to which the information being processed for each stimulus would be localized to the

bulbar neurons receiving the action potentials sent by the activated receptors by topographic mapping [Lettvin & Gesteland, 1965]. In effect, all neurons in the bulb responded to every odor in forming the mesoscopic AM patterns, with varying degrees of relative excitation or inhibition in the manner of interference patterns.

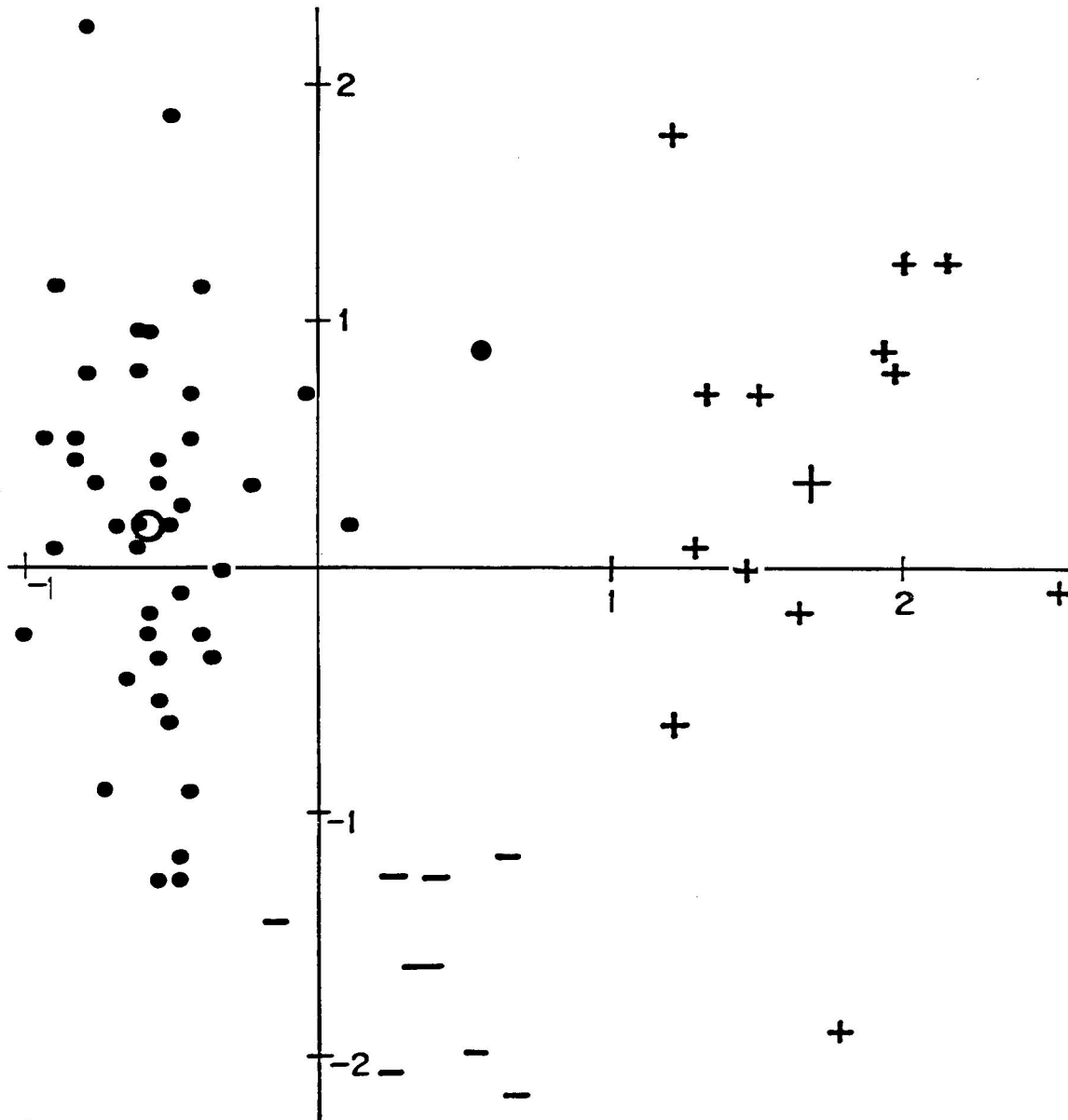


Figure 2. The AM pattern of 64 root mean square amplitudes in each burst determined a 64×1 column vector and a point in 64-space. The AM patterns with CS+, CS- and control formed three clusters, each with a center of gravity. Classification was by Euclidean distance to the nearest center. Display was by nonlinear mapping into 2-space. From Freeman & Grajski, 1987.

The manner of formation of the AM patterns was disclosed by investigation of the phase of the gamma oscillation in wave packets. Although the wave forms were aperiodic with broad spectra, in a short time window the spectrum of each wave packet had maximal power at one frequency in the gamma range. The phases of the 64 EEG segments was calculated by the FFT with respect to the phase of the spatial ensemble average. The first prediction, in accord with the information processing hypothesis, was that each wave packet in the olfactory bulb would have a planar phase gradient with the maximal slope downward in the anteroposterior direction of the axons coming from receptors in the nose, and with a phase gradient in radians/mm determined by the axons. The gradient was converted to phase velocity in m/s with the frequency at which the phase was calculated and was found to equal the slow conduction velocity (.42 m/s) of the action potentials on the unmyelinated axons from the receptors. The bulbar oscillation evoked by an electrical stimulus to the axons was expected to have a distance-dependent delay in onset comparable to the waves evoked in a field of grain by a puff of wind. This gradient was found by measurement of the impulse response of the bulb by fitting the brief oscillation with a damped cosine [Freeman, 1975].

This prediction did not hold for the EEG. The slope and direction of the phase gradient in the burst of gamma oscillation triggered by inhalation did not conform to the direction and conduction velocity of the incoming axons. When the phase gradient in radians/mm was converted to m/s using the frequency at which the phase was defined, it was equal to the mean conduction velocity (1.82 m/s) of action potentials on the myelinated axons originating in the bulb and running parallel to the bulbar surface, not to that of the incoming axons. The direction was fixed in each burst and varied at random from each wave packet to the next. On the one hand, a pacemaker could not account for the bulbar oscillation, because it was not compatible with the variation in direction and frequency [Freeman and Baird, 1987]. On the other hand, the phase gradient was compatible with a 1st order phase transition analogous to a subcritical Hopf bifurcation, in which the AM pattern formed by self-organization [Freeman, 1999]. The phase velocity was sufficient to extend the phase transition over the entire bulb in under a quarter cycle of the peak gamma frequency of oscillation, so that phase dispersion in the wave packet oscillation under a spatial integral transform was less than $\pm 45^\circ$, which defined the half-power radius of the wave packet ($\cos^2 \pm 45^\circ = .5$).

The same basic EEG properties were found in the primary visual, auditory and somatosensory neocortices with subtle but significant differences. The 8x8 array windows were larger (6x6 mm) to accommodate the larger surface areas of the neocortices. High covariance was again found among channels before and after band pass filtering in the gamma range. However, the low frequency activity was not correlated with the respiratory rhythm. The theta and alpha ranges had high power but seldom had sharp peaks. The $1/f^\alpha$ pattern was pronounced in both temporal and spatial spectra [Barrie, Freeman & Lenhart, 1996]. The rabbits were trained to discriminate visual, auditory, or somatosensory stimuli in the modality corresponding to the location of the array in each subject. Gamma AM patterns were correctly classified with respect to CSs. The patterns recurred intermittently at mean rates in the theta range (3-7 Hz) of the EEG [Fig. 3], which indicated that, as with olfaction, the other sensory systems for distance reception were systolic. The sensory areas received sensory input during a period of diastole and transmitted a wave packet during systole. The AM patterns differed among individuals and lacked invariance with respect to the stimuli under reinforcement contingency reversal, showing

that they were related to the context and history of the subjects. The goodness of classification was again diminished by deletion of contributions from individual electrodes in proportion to the number deleted, but no channel was any more or less important than any other. In contrast to the prediction of the network hypothesis, the AM patterns were nonlocal and distributed, analogously to the interference patterns of a hologram [Pribram, 1971], but with no inverse transform for recovery of an initiating sensory pattern. Comparable results were found with arrays of 35 electrodes on the visual cortex of a rhesus monkey [Freeman & van Dijk, 1987] trained to detect visual flicker, and 18 electrodes placed over the auditory cortex of Mongolian gerbils [Ohl, Scheich & Freeman, 2001]. The gerbils were trained to discriminate ascending from descending FM tones at one center frequency, and then to generalize to other center frequencies. When the behavioral capability for category discrimination abruptly emerged by "insight", nonlocal AM patterns related to the categories ("up-ness" vs. "down-ness") appeared having no tonotopic specificity.

Varying phase gradients were again found in association with the AM patterns, with phase velocities equivalent to the distribution of conduction velocities on intracortical axons running parallel to the surface [Freeman & Barrie, 2000]. As a result, the modal half-power diameter (15 mm) and the 95% upper inclusion range (28 mm) were substantially larger than the bulbar surface (10 mm) [Fig. 4]. Unlike the bulbar EEG in which the phase velocity was invariant with gamma frequency [Freeman & Baird, 1987], in the neocortical EEG the phase velocity co-varied with gamma frequency, but the half-power diameter did not. The conclusion was drawn that visual, auditory, somatosensory, and olfactory receiving areas had the capacity for input-dependent gain increase leading to destabilization. Emergence of self-organized mesoscopic patterns was by a 1st order phase transition that was completed within 3-7 ms depending on the center carrier frequency. The location, time of onset, size and duration of each wave packet were demarcated by the phase, and its perceptual content was expressed in an AM pattern, which appeared within 25-35 ms of the wave packet onset [Freeman, 2003]. The content, as defined by classification with respect to CSs, was context-dependent, unique to each subject, and it was nonlocal over delimited domains of both the cortical surface and the gamma spectrum.

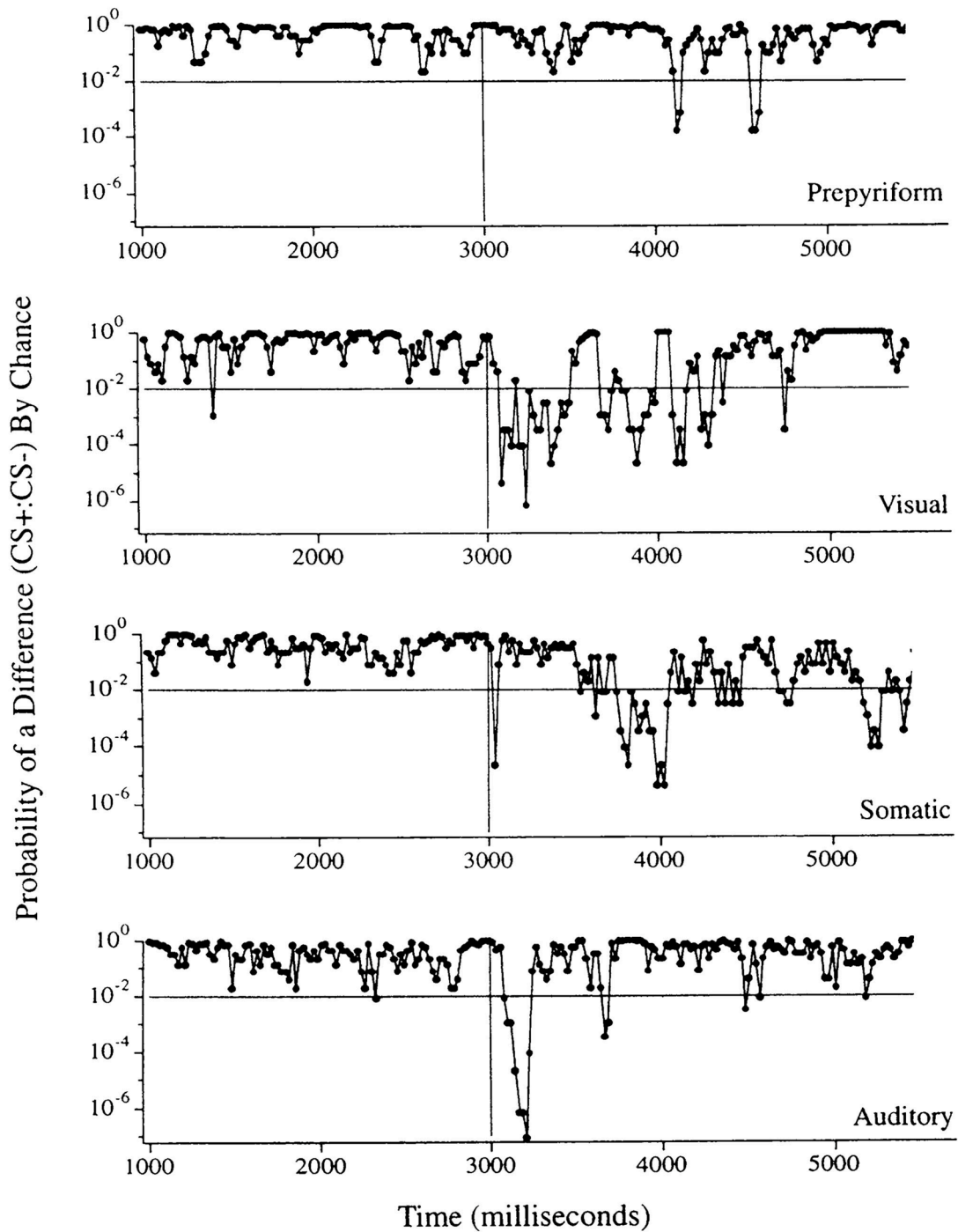


Figure 3. The probability of correct classification with respect to CS+ and CS- was calculated in a moving window both pre- and post-stimulus arrival at 3000 ms. Separation of AM patterns with CS was found in all areas examined intermittently only after CS onset and before CR onset. From Freeman & Barrie, 1996.

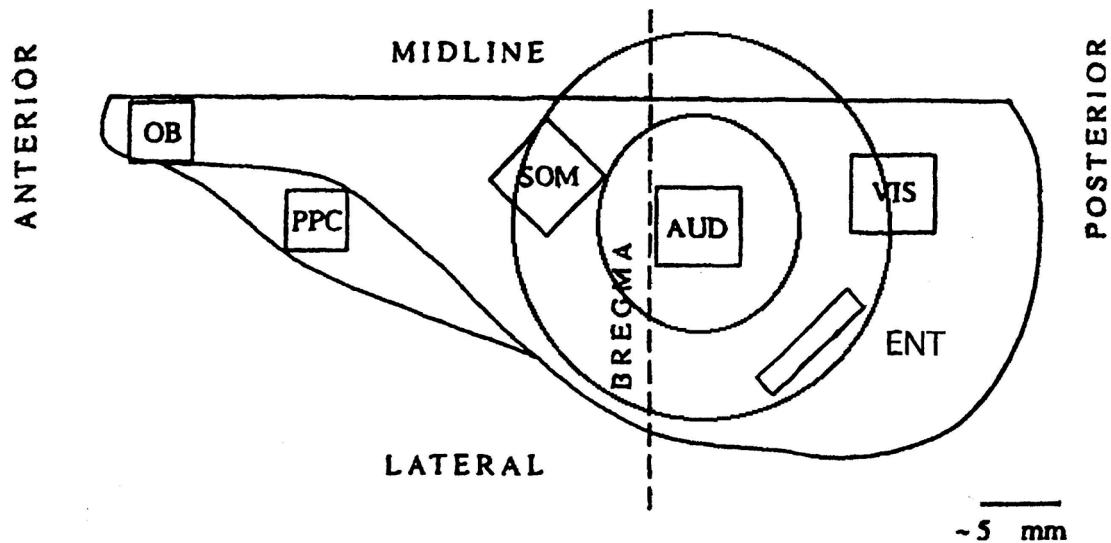


Figure 4. The rectangles superimposed on the left cerebral hemisphere of the rabbit show sizes and locations of the 8x8 arrays on the visual (VIS), auditory (AUD), somatosensory (SOM), prepyriform (PPC), and olfactory bulb (OB) areas and a 2x8 array on the entorhinal cortex (ENT). Patterns of phase modulation (PM) revealed radially symmetric gradients having circular isophase contours. The modal half-power diameter (inner circle) was 15 mm. The 95% inclusion diameter was 28 mm. Modified from Barrie, Freeman & Lenhart, 1996.

The high phase velocities were of exceptional interest, because they greatly exceeded the group velocities of serial synaptic transmission across the bulb and neocortical sensory areas. For example, the modal radius of the axon collaterals parallel to the surface from bulbar excitatory neurons was about .5 mm, and the time for transmission of an impulse input by synaptic relay over the entire bulb (about 10 mm) by convolution would require about 100 ms, about 20-fold greater than the observed time required [Freeman, 1975]. A comparable distinction is made between group velocity and phase velocity in media that conduct light [Hecht & Zajac, 1974, p. 42 and p. 205]. The transmission of energy and information in such media can never exceed the speed of light, but when the frequency of the carrier light is close to an absorption or resonance band of a medium, the phase velocity can appear to exceed the group velocity. The excess in apparent velocity above the speed of light manifests "anomalous dispersion". It does not carry information. By analogy, the maintenance in cortex by self-organized criticality of a resonance band might correspond to an absorption band in light media. Whereas the group velocity would correspond to the average rate of serial synaptic transmission of information by action potentials from one cortical area to another, the phase velocity would correspond to the spatial rate of spread of a phase transition across the cortex. Anomalous dispersion in the bulb or neocortex could not carry information at the phase velocity exceeding the limiting velocity of group (serial synaptic) transmission, but it might trigger the expression of information previously stored in synaptic weights into the spatial AM patterns of gamma oscillations, with negligible time lags between widely separated areas. The phase transitions clearly involve thalamic controls [Destexhe, 2000; Robinson et al., 2001; Steriade, 2000, 2001], but the global coordination of the

timing and content of beta and gamma oscillations, even over the entire extent of both cerebral hemispheres, may be an intrinsic property of the neocortex viewed as an integrated tissue. These aspects are considered in Part 4 in relation to new experimental data [Freeman, Burke & Holmes, 2003].

7. Postulates on macroscopic events leading to perception

Wave packets are sufficiently large to encompass the primary and multiple secondary areas of the sensory cortices. They offer a solution to the "feature binding" problem by explaining the manner in which foreground information about the features of objects, having been injected into the sensory cortices by afferent action potentials, is locally integrated with past experience in the context of coexisting background input. However, the wave packet can not explain multisensory convergence and the construction of an integrated Gestalt as the basis for meaning. The sensory cortices operate autonomously in processing information, but they operate collectively in constructing meaning. A critical contribution to every sensory system is made in every vertebrate brain by a network of neural populations comprising the limbic system [Fig. 5]. The key structure within this system is the hippocampus. Just as every other area of cortex has a unique contribution to the whole, the hippocampus provides for temporal orientation by "short term memory" and for spatial orientation by a "cognitive map" [O'Keefe & Nadel, 1978]. For example, the whiff of a few molecules of an odorant substance does not in itself reveal the location of its source in the environment [Freeman, 2001]. The direction and distance of a predator or prey must be inferred by the subject from multiple sensory frames (sniffs) that are gathered and integrated over a pattern of searching behavior that is expressed by movements of the body in the action-perception cycle [Piaget, 1930; Merleau-Ponty, 1945].

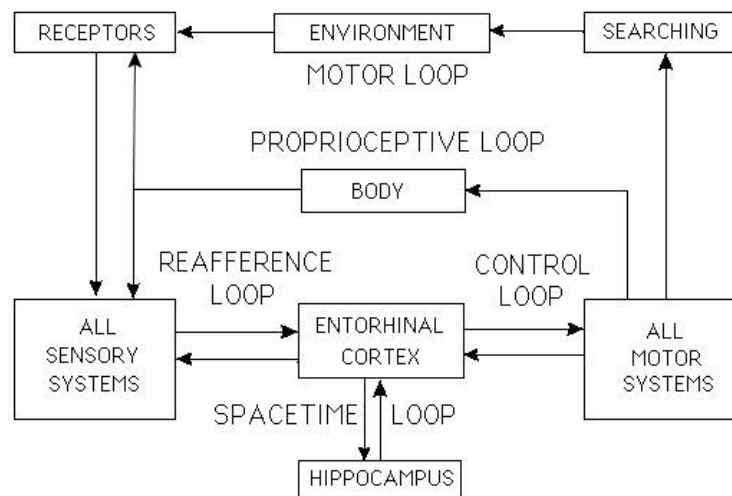


Figure 5. A schematic shows the flow of neural activity in the construction of meaning, with emphasis on two main structures in the limbic system. From Freeman, 2001.

In mammals the hippocampus is located centrally within the brain, and the greater part of its input is provided by the entorhinal cortex [Buzsáki, 1996]. All sensory cortices are connected by

axonal projections with each other, usually through multiple synaptic relays. They all include projections into the entorhinal cortex, which provides the main gate into the hippocampus. The output of the hippocampus goes in smaller part into motor systems such as the amygdaloid nucleus and in larger part back to the entorhinal cortex. This recurrent connection is summarized in Fig. 5 as the "space-time loop". The entorhinal cortex sends its output back to all sensory cortices by serial synaptic relays, as summarized by the "preaffference loop" [Kay & Freeman, 1998]. This is a feedback system entirely within the cerebral hemisphere for anticipating and compensating for the effects of action on sensory inflow. This system differs in this respect from the motor control loop that extends outside the forebrain through the brain stem and cerebellum for forward control of movement, the proprioceptive loop that extends through the body for feedback control, and the exteroceptive loop that extends through the environment. Though the definition, components, connections, and functions of the limbic system are matters of continuing controversy in basic neuroscience [Lopes da Silva, 1990], the importance of the entorhinal cortex and the hippocampus are universally acknowledged. As an indication, the perforant path that carries entorhinal activity into the hippocampus degenerates markedly in Alzheimer's disease, so that the catastrophic dementia is sometimes referred to as a 'disconnect' syndrome.

For the information hypothesis, perception begins with sensory input, and the eventual result is expressed in a motor response. For the meaning hypothesis, perception begins with the formation of a goal-seeking state through the participation of the limbic system with the neurochemical nuclei in the brain stem that express and directly control the state of the organism, body and brain [Panksepp, 1998]. Perception unfolds by the selection of an appropriate goal-directed action that is intended to reach the goal, and that is expressed in motor commands sent into the brain stem and spinal cord. Efference copies (corollary discharges) of the command are sent to the sensory cortices to prepare them for the changes in sensory input that will shortly occur as a consequence of the intended action. As the action evolves, the impact of the altered sensory input to the receptors is conveyed by action potentials to the sensory cortices in a diastolic receiving state. The sensory input under central control by the limbic system destabilizes each cortex. The resulting phase transition activates an attractor landscape in each sensory cortex [Skarda & Freeman, 1987]. The landscape has already been established by long-term learning and is modulated immediately before input by the corollary discharges from the limbic system. The sensory information selects an appropriate basin of attraction in every modality. Then it is mostly discarded. The selected attractor takes control of the cortical dynamics and constructs a systolic wave packet. The cortex broadcasts this activity pattern through the forebrain by coordinated action potentials on divergent pathways to a wide array of targets. Reception is determined by the receivers, not the transmitter.

The process of perception continues with multisensory integration of the wave packets. The most important site of convergence of wave packets is in the outer layers of the entorhinal cortex. The combined event passes through the hippocampus for assignment of spatial orientation and preparation for memory, then back to the inner entorhinal layers. From there the entorhinal cortex sends divergent feedback to all sensory areas in preaffference. That integrated activity enables multisensory percepts to incorporate past experience, current context, and future expectation. The percepts re-shape the attractor landscapes and up-date them. This comprises a proposed neural mechanism for the construction of meaning in brains.

The experimental basis for investigating the neural mechanisms that are required to assemble wave packets from all of the sensory cortices into a unified event is the topic of this tutorial, based on research on macroscopic integration in the cerebral hemisphere. Part 1 here summarizes the information processing hypothesis and its shortcomings. The theory of meaning is outlined. The main steps of construction are reviewed, based on published data from experimental animals. Part 2 summarizes observations on intracranial EEGs from sensory cortices by means of high density electrode arrays to deduce the properties of wave packets. Part 3 presents evidence for mechanisms by which zero time lag synchrony is achieved over wide areas of the brain, as a necessary prelude to global pattern formation [Freeman, Gaál & Jörsten, 2003]. Part 4 gives evidence for the construction of multisensory percepts in spatial patterns of amplitude modulation (AM) of gamma activity that include widely distributed brain areas [Freeman & Burke, 2003]. Part 5 details evidence from the Hilbert transform for global phase transitions of SOC in each cerebral hemisphere [Freeman & Rogers, 2003] that manifest the timing of its systolic mode of operation in perception, each frame contributing to an evolving state of meaning.

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REFERENCES

- Abeles, M. [1991] *Corticonics: Neural Circuits of the Cerebral Cortex*. (Cambridge U.P., Cambridge UK).
- Abeles, M., Bergman, H., Gat, I., & Meilijson, I. [1995] Cortical activity flips among quasi-stationary states. *Proc. Nat. Acad. Sci. USA* **92**: 8616-8620.
- Aertsen, A., Diesmann, M. & Gewaltig, M.O. [1996] Propagation of synchronous spiking activity in feedforward neural networks. *J. Physiol.-Paris* **90**: 243-247.
- Amit, D.J. [1989] *Modeling brain function: The World of Attractor Neural Networks*. (Cambridge U.P., Cambridge UK).
- Baars, B.J. [1997] *In the Theater of Consciousness: The Workspace of the Mind*. (Oxford U.P., New York)
- Bak, P., Tang, C. & Wiesenfeld, K. [1987] Self-organized criticality: an explanation of 1/f noise. *Phys. Rev. Lett.* **59**: 364-374.
- Barham, J. [1996] A dynamical model of the meaning of information. *Biosystems* **38**: 235-241.
- Barlow, H.B. [1972] Single units and sensation: A neuron doctrine for perceptual psychology? *Perception* **1**: 371-394.
- Barlow, J.S. [1993] *The Electroencephalogram: Its Patterns and Origins*. (MIT Press, Cambridge MA).
- Barrie, J.M., Freeman, W.J. & Lenhart, M.D. [1996] Spatiotemporal analysis of prepyriform, visual, auditory and somesthetic surface EEG in trained rabbits. *J. Neurophysiol.* **76**: 520-539.
- Βραυτενβεργ, ζ. & Σχημαζ, Α. [1991] *Ανατομψ οφ τηε Χορτεξ: Στατιστιχοσ ανδ Γεομετροψ*. (Σπρινγκερ-ζεορλαγ, Βερολιν).
- Βρεσσλερ, Σ. Α. [1996] Ιντερορεαλ σψνχηρονονιζατιον ιν τηε πιασαλ χορτεξ. *Βεηαπ. Βροιν Ρεσ.* **76**: 37-49
- Bruns, A., Eckhorn, R., Jokeit, H. & Ebner, A. [2000] Amplitude envelope correlation detects coupling among incoherent brain signals. *NeuroReport* **11** 1509-1514.
- Buxton, R. B. [2001] *Introduction to Functional Magnetic Resonance Imaging: Principles and Techniques*. (Cambridge U. P., New York).
- Buzsáki, G. [1996] The hippocampal-neocortical dialogue. *Cerebral Cortex* **6**: 81-92.
- Calvin, W.H. [1996] *The Cerebral Code. Thinking a Thought in the Mosaics of the Mind*. (MIT Press, Cambridge MA).
- Chang, H.-J. & Freeman, W.J. [1998] "Biologically modeled noise stabilizing neurodynamics for pattern recognition," *Int. J. Bifurc. Chaos* **8**: 321-345.
- Chang, H.-J. & Freeman, .WJ. [1999] Local homeostasis stabilizes a model of the olfactory system globally in respect to perturbations by input during pattern classification. *Int. J. Bifurc. Chaos* **8**: 2107-2123.
- Chapeau-Blondeau, F. [2001] Comparison between spike and rate models in networks of integrate-and-fire neurons. Ch. 11 in: Poznanski, R. R. (ed.) *Biophys. Neural Networks*. (Ann Liebert Inc., Larchmont NY).
- Clark A [1996] *Being There. Putting Brain, Body, and World Together Again*. (MIT Press, Cambridge MA).
- Destexhe, A. [2000] Modelling corticothalamic feedback and the gating of the thalamus by the cerebral cortex. *J. Physiol.-Paris* **94**: 91-410.
- Diesmann, M., Gewaltig, M.O. & Aertsen, A. [1999] Stable propagation of synchronous spiking in cortical neural networks. *Nature* **402**: 529-533.

- Eckhorn, R., Bruns, A., Saam, M., Gail, A., Gabriel, A. & Brinksmeyer, H.J. [2001] Flexible cortical gamma-band correlations suggest neural principles of visual processing. *Visual Cognition* **8**: 519-530.
- Edelstein-Keshet, L., Watmough, J. & Grunbaum, D. [1998] Do traveling band solutions describe cohesive swarms? An investigation for migratory locusts. *J. Math. Biol.* **171**: 515-549.
- Engel, A.K., Fries, P., König, P., Brecht, M. & Singer, W. [1999] Temporal binding, binocular rivalry, and consciousness. *Consciousness & Cognition* **8**: 128-151.
- Ermentrout, G.B. [1994] Reduction of conductance-based models with slow synapses. *Neural Comp.* **6**: 66678-695.
- Fischer, R. [1993] From transmission of signals to self-creation of meaning: Transformations in the concept of information. *Cybernetica* **36**: 229-243.
- Freeman, W.J. [1975] *Mass Action in the Nervous System*. (Academic Press, New York).
- Freeman, W.J. (1992) Tutorial in Neurobiology: From Single Neurons to Brain Chaos. *Int. J. Bifurc. Chaos* **2**: 451-482.
- Freeman, W. J. [1999] Noise-induced first-order phase transitions in chaotic brain activity. *Int. J. Bifurc. Chaos* **9**: 2215-2218.
- Freeman, W.J. [2000a] *Neurodynamics. An Exploration of Mesoscopic Brain Dynamics*. (Springer-Verlag, London UK).
- Freeman, W.J. [2000b] Characteristics of the synchronization of brain activity imposed by finite conduction velocities of axons. *Int. J. Bifurc. Chaos* **10**: 2307-2322.
- Freeman, W.J. [2001] *How Brains Make Up Their Minds*. (Columbia U.P., New York).
- Freeman, W.J. [2003b] A neurobiological theory of meaning in perception. Part 2. Spatial patterns of phase in gamma EEG from primary sensory cortices reveal the properties of mesoscopic wave packets. *Int. J. Bifurc. Chaos* **13**: 2513-2535.
- Freeman, W.J. & Baird, B. [1987] Relation of olfactory EEG to behavior: Spatial analysis. *Behav. Neurosci.* **101**: 393-408.
- Freeman, W.J. & Barrie, J.M. [2000] Analysis of spatial patterns of phase in neocortical gamma EEG in rabbit. *J. Neurophysiol.* **84**: 1266-1278.
- Freeman, W.J. & Burke, B.C. [2003d] A neurobiological theory of meaning in perception. Part 4. Multicortical patterns of amplitude modulation in gamma EEG. *Int. J. Bifurc. Chaos* **13**: 2857-2866.
- Freeman, W.J., Burke, B.C. & Holmes, M.D. [2003] Aperiodic phase re-setting in scalp EEG of beta-gamma oscillations by state transitions at alpha-theta rates. *Human Brain Mapping* **19**: 248-272.
- Freeman, W.J., Burke, B.C., Holmes, M.D. & Vanhatalo, S. [2003] Spatial spectra of scalp EEG and EMG from awake humans. *Clin. Neurophysiol.* **114**: 1055-1060.
- Freeman, W.J., Chang, H.-J., Burke, B.C., Rose, P.A. & Badler, J. [1997] Taming chaos: Stabilization of aperiodic attractors by noise. *IEEE Trans. Circuits Systems* **44**: 989-996.
- Freeman, W.J., Gaál, G. & Jornten, R. [2003c] A neurobiological theory of meaning in perception. Part 3. Multiple cortical areas synchronize without loss of local autonomy. *Int. J. Bifurc. Chaos* **13**: 2845-2856.
- Freeman, W.J. & Grajski, K.A. [1987] Relation of olfactory EEG to behavior: Factor analysis. *Behav. Neurosci.* **101**: 766-777.
- Freeman, W.J. & Rogers, L.J. [2002] Fine temporal resolution of analytic phase reveals episodic synchronization by state transitions in gamma EEG. *J. Neurophysiol.* **87**, 937-945.

- Freeman, W.J. & Rogers, L.J. [2003e] A neurobiological theory of meaning in perception. Part 5. Multicortical patterns of phase modulation in gamma EEG. *Int. J. Bifurc. Chaos* 13: 2867-2887.
- Freeman, W.J., Rogers, L.J., Holmes, M.D. & Silbergeld, D.L. [2000] Spatial spectral analysis of human electrocorticograms including the alpha and gamma bands. *J. Neurosci. Meth.* **95**: 111-121.
- Freeman, W.J. & Schneider, W. [1982] Changes in spatial patterns of rabbit olfactory EEG with conditioning to odors. *Psychophysiol.* **19**: 44-56.
- Freeman, W.J. & Van Dijk, B. [1987] Spatial patterns of visual cortical fast EEG during conditioned reflex in a rhesus monkey. *Brain Res.* **422**: 267-276.
- Freeman, W.J. & Viana Di Prisco, G. [1986] Relation of olfactory EEG to behavior: Time series analysis. *Behav. Neurosci.* **100**: 753-763.
- Fries, P., Reynolds, J.H., Rorie, A.E. & Desimone, R. [2001] Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**: 1560-1563.
- Gabbiani, F. & Koch, C. [1996] Coding of time-varying signals in spike trains of integrate-and-fire neurons with random threshold. *Neural Comp.* **8**: 44-66.
- Georgopolis AP, Schwartz AB, Kettner RE [1986] Neural population coding of movement direction. *Science* **233**: 1416-1419.
- Gevens, A., Bressler, S. L., Morgan, N., Cutillo, B., White, R., Greer, D. & Illes, J. [1989] Event-related covariances during a bimanual visuomotor task. *Electroenceph. clin. Neurophysiol.* **74**: 58-75.
- Ghose, G.M. & Freeman, R.D. [1997] Intracortical connections are not required for oscillatory activity in the visual cortex. *Vis. Neurosci.* **14**: 963-979.
- Ηαγ, Α.Ρ., Γορδον, Ε., Ωριγητ, Θ.Θ., Μεαρεσ, Ρ.Α. & Βαηραμαλι, ΗΒ. [2000] Σψνχηρονουσ χορτιχαλ γαμμα-βανδ αχτιπιτψ ιν τασκ-ρελεπαντ χογνιπιον. *ΝευροΡεπορτ* **11**: 669-675.
- Haken, H. [1983] *Synergetics: An Introduction*. (Springer-Verlag, Berlin).
- Häusser, M., Spruston, N. & Stuart, G.J. [2000] Diversity and dynamics of dendritic signaling. *Science* **290**: 739-744.
- Hardcastle, V.G. [1994] Psychology's binding problem and possible neurobiological solutions. *J. Consciousness Studies* **1**: 66-90.
- Harnad, S. [2001] Grounding symbols in the analog world with neural nets - A hybrid model - Target article on symbolism-connectionism. *Psychology* 12: 1-14.
- Harnad, S. [1990] The symbol grounding problem. *Physica D* 42: 335-346.
- Hebb, D.O. [1949] *The Organization of Behavior*. (Wiley, New York).
- Hecht, E. & Zajac, A. [1974] *Optics*. (Addison-Wesley, Reading MA), pp. 38-42, 205-205.
- Hendriks-Jansen H. [1996] *Catching ourselves in the act: Situated activity, interactive emergence, evolution, and human thought*. (MIT Press, Cambridge, MA).
- Hoppensteadt, F.C. & Izhkevich, E.M. [1998] Thalamo-cortical interactions modeled by weakly connected oscillators: could the brain use FM radio principles? *BioSystems* **48**: 85-94.
- Hwa, R.C. & Ferree, T. [2002] Scaling properties of fluctuations in the human electroencephalogram. *Physical Rev. E* **66**: 021901.
- Ingber L. [1995] Statistical mechanics of multiple scales of neocortical interactions. pp. 628-681 in: Nunez, P.L. (ed.) *Neocortical Dynamics and Human EEG Rhythms*. (Oxford U.P., New York).

- Izhkevich, E.M. [1999] Weakly connected quasi-periodic oscillators, FM interactions, and multiplexing in the brain. *SIAM J. Appl. Math.* **59**: 2193-2223.
- Joliot, M., Ribary, U. and Llinás, R. [1994] Human oscillatory brain activity near 40 Hz coexists with cognitive temporal binding. *Proc. Nat. Acad. Sci. USA* **91**: 11748-11751.
- Kay L.M. & Freeman, W.J. [1998] Bidirectional processing in the olfactory-limbic axis during olfactory behavior. *Behav. Neurosci.* **112**: 541-553.
- Kay, L.M., Shimoide, K. & Freeman, W.J. [1995] Comparison of EEG time series from rat olfactory system with model composed of nonlinear coupled oscillators. *Int. J. Bifurc. Chaos* **5**: 849-858.
- Köhler, W. [1940] *Dynamics in Psychology*. (Grove Press, New York).
- Kozma, R. & Freeman WJ [2001] Chaotic Resonance: Methods and applications for robust classification of noisy and variable patterns. *Int. J. Bifurc. Chaos* **10**: 2307-2322.
- Kozma, R., Freeman, W.J. & Erdí, P. [2003] The KIV model - Nonlinear spatio-temporal dynamics of the primordial vertebrate forebrain. *Neurocomputing* **52**: 819-826.
- Lancet, D., Greer, C.A., Kauer, J.S. & Shepherd, G.M. [1982] Mapping of odor-related neuronal activity in the olfactory bulb by high-resolution 2-deoxyglucose autoradiography. *Proc. Nat. Acad. Sci. USA* **79**: 670-674.
- Lashley, K. S. [1960] *The Neuropsychology of Lashley; Selected Papers*. Beach, F. A. et al. (eds.). (McGraw-Hill, New York).
- Lettvin, J.Y. & Gesteland, R.C. [1965] Speculations on smell. *Cold Spring Harbor Symp. Quant. Biol.* **30**: 217-225.
- Lindley, D. [2001] *Boltzmann's Atom. The Great Debate that Launched a Revolution in Physics*. (Free Press, New York).
- Lopes da Silva, F.H., Witter, M.P., Boeijinga, P.H. & Lohmann, A.H.M. [1990] Anatomic organization and physiology of the limbic cortex. *Physiol. Rev.* **70**: 453-511.
- Maass, W. & Bishop, C.M. (eds.) [1999] *Pulsed Neural Networks*. (MIT Press, Cambridge MA).
- Maclean, P.D. [1969] *The Triune Brain*. (Plenum Press, New York).
- ΜαχΧυλλοχη, Ω.Σ. & Πιττσ, Ω. [1943] Α λογικαλ χαλχυλυσ οφ τηε ιδεασ ιμμαανεντ ιν νερωπουσ αχιπιτιψ. *Βυλλ. Ματη. Βιοπηψσ.* **5**: 115-133.
- Μεολεαυ-Ποντψ Μ. [1945/1962] *Πηενομενολογη οφ Πεορχεπιιον.* (Χ Σμητη, Τρανσ.). (Ηυμανιτιεσ Πρεεσσ, Νεω Ψοοκ).
- Μιψασηιτα Ψ [1995] Ηοω τηε βοαιν χρεατεσ μαγεορψ: προφεχτιον το προμαορψ πισυαλ χοορτεξ. *Σχηενχε* **268**: 1719-1720.
- Nicolelis, M.A.L., Ghazanfar, A.A.A., Stambaugh, C.R., Oliveira, L.M.O., Laubach, M., Chapin, J.K., Nelson, R.J. & Kaas, J.H. [1998] Simultaneous encoding of tactile information by three primate cortical areas. *Nature Neurosci.* **1**: 621-630.
- Νυνεξ, Π. Α. [1981] *Ελεχτριχ Φιελδσ οφ τηε Βοαιν: Τηε Νευροπηψσιχο οφ ΕΕΓ.* (Οξφοορδ Υ. Π., Νεω Ψοοκ).
- Ohl, F.W., Scheich, H. & Freeman, W.J. [2001] Change in pattern of ongoing cortical activity with auditory category learning. *Nature* **412**: 733-736.
- O'Keefe, J. & Nadel, L. [1978] *The hippocampus as a cognitive map*. (Clarendon Press, Oxford UK).
- Panksepp, J. [1998] *Affective Neuroscience: The Foundations of Human and Animal Emotions*. (Oxford U.P., Oxford UK).
- Parkinson, G. H. R. (ed.) [1968] *The Theory of Meaning*. (Oxford U.P., London).
- Piaget, J. [1930] *The Child's Conception of Physical Causality*. (Harcourt, Brace, New York).

- Pribram, K. H. [1971] *Languages of the Brain; Experimental Paradoxes and Principles in Neuropsychology*. (Prentice-Hall, Englewood Cliffs, N.J.).
- Prigogine, I. [1980] *From Being to Becoming: Time and Complexity in the Physical Sciences*. (W. H. Freeman, San Francisco).
- Principe, J.C., Tavares, V.G., Harris, J.G. and Freeman, W.J. [2001] Design and implementation of a biologically realistic olfactory cortex in analog VLSI. *Proc. IEEE* **89**: 1030-1051.
- Quiroga, R.Q., Kraskov, A., Kreuz, T. & Grassberger, P. [2002] Performance of different synchronization measures in real data: A case study on electroencephalographic signals. *Physical Rev. E* **65**: 041903.
- Quiroga, R.Q., Kreuz, T. & Grassberger, P. [2002] Event synchronization: A simple and fast method to measure synchronicity and time delay patterns. *Physical Rev. E*: **66**: 041904.
- Robinson, P.A., Wright, J.J. & Rennie, C.J. [1998] Synchronous oscillations in the cerebral cortex. *Phys. Rev. E* **57**: 4578-4588.
- Robinson, P.A., Loxley, P.N., O'Connor, S.C. & Rennie, C.J. [2001] Modal analysis of corticothalamic dynamics, electroencephalographic spectra, and evoked potentials. #041909. *Physical Rev. E* **6304**: N4 PT1:1909,U515-U526.
- Roelfsema, P.R., Engel, A.K., König, P. & Singer, W. [1997] Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature* **385**: 157-161.
- Roland, P.E. [1993] *Brain Activation*. (Wiley-Liss, New York).
- Rosenblatt, F. [1962] *Principles of Neurodynamics: Perceptrons and the Theory of Brain Mechanisms*. (Spartan Books, Washington DC).
- Schillen, T.B. & König, P. [1994] Binding by temporal structure in multiple feature domains on an oscillatory neuronal network. *Biol. Cybern.* **70**: 397-405.
- Searle, J.R. [1992] *The Rediscovery of Mind*. (MIT Press, Cambridge MA).
- Shannon, C.E. [1948] A mathematical theory of communication, Bell Telephone System Tech. Publ. Monograph B-1598, 1-80.
- Sherrington, C.S. [1940] *Man on his Nature*. (Cambridge U.P., Cambridge UK).
- Sholl, D.A. [1956] *The Organization of the Cerebral Cortex*. (Methuen, London).
- Singer, W., Engel, A.K., Kreiter, A.K., Munk, M.H.J., Neuenschwander, S. & Roelfsema, P.R. [1997] Neuronal assemblies: Necessity, significance, and detectability. *Trends Cog. Sci.* **1**: 252-161.
- Singer, W. & Gray, C.M. [1995] Visual feature integration and the temporal correlation hypothesis. *Ann. Rev. Neurosci.* **18**: 555-586.
- Skarda, C.A. & Freeman, W.J. [1987] How brains make chaos in order to make sense of the world. *Behav. & Brain Sci.* **10**: 161-195.
- Srinivasan, R., Nunez, P. L. & Silberstein, R. B. [1998] Spatial filtering and neocortical dynamics: estimates of EEG coherence. *IEEE Trans. Biomed Engin.* **45**: 814-826.
- Steels, L & Brooks, R. (eds.) [1995] *The Artificial Life Route to Artificial Intelligence: Building Embodied, Situated Agents*. (L. Erlbaum Assoc., Hillsdale, N.J).
- Steriade, M. [2000] Corticothalamic resonance, states of vigilance and mentation. *Neurosci.* **101**: 243-276.
- Steriade, M. [2001] Impact of network activities on neuronal properties in corticothalamic systems. *J. Neurophysiol.* **86**: 1-39.
- Stonier, T. [1997] *Information and Meaning: An Evolutionary Perspective*. (Springer-Verlag, New York).

- Tallon-Baudry, C., Bertrand, O., Perronet, F. & Pernier, J. [1998] Induced β -band activity during the delay of a visual short-term memory task in humans. *J. Neurosci.* **18**: 4144-4154.
- Taylor J.G. [1997] Neural networks for consciousness. *Neural Networks* **10**: 1207-1225.
- Tovée, M.J. & Rolls, E.J. [1992] The functional nature of neuronal oscillations. *Trends Neurosci.* **15**: 387.
- Traub, R.D., Whittington, M.A., Stanford, I.M. & Jefferys, J.G.R. [1996] A mechanism for generation of long-range synchronous fast oscillations in the cortex. *Nature* **383**: 421-424.
- Tsitolovsky, L.E. & Babkina, N.V. [2002] Neurons evaluate both the amplitude and the meaning of signals. *Brain Res.* **946**: 104-118.
- Tsuda, I. [2001] Toward an interpretation of dynamics neural activity in terms of chaotic dynamical systems. *Behav. & Brain Sci.* **24**: 793-847.
- Vaadia, E. [2000] Cognitive neuroscience - Learning how the brain learns. *Nature* **405**: 523-525.
- Valéry, P. [1957] *Oeuvres. (Ed. établie et annotée par Jean Hytier)* (Gallimard, Paris).
- von der Malsburg, C. [1983] How are nervous structures organized? pp. 238-249 in: *Synergetics of the Brain*, Basar, E., Flohr, H., Haken, H. & Mandell, A.J. (eds.) (Springer-Verlag, Berlin).
- Watts, D.J. & Strogatz, S.H. [1998] Collective dynamics of 'small world' networks. *Nature* **394**: 440-442.
- Whittington, M.A., Faulkner, H.J., Doheny, H.C. & Traub, R.D. [2000] Neuronal fast oscillations as a target site for psychoactive drugs. *Pharmacol. & Therap.* **86**: 171-190.
- Wilson, H.R. & Cowan, J.D. [1973] Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysics J.* **12**: 1-24.
- Wright, J.J. & Liley, D.T.J. [1996] Dynamics of the brain at global and microscopic scales: Neural networks and the EEG. *Behav. & Brain Sci.* **19**: 285-302.
- Young, R. M. [1970] *Mind, Brain and Adaptation in the Nineteenth Century: Cerebral Localization and its Biological Context from Gall to Ferrier.* (Clarendon Press, Oxford UK).