

Chaotic oscillations and the genesis of meaning in cerebral cortex

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Abstract

Single neurons generate action potentials that express their output in pulse frequencies, so that sensory stimuli can be microscopically expressed as spatial patterns of phase-locked firing of "feature detector" neurons. The visual, auditory, somatic, and olfactory cortices generate dendritic potentials that oscillate at frequencies from 1-100 Hz. These waves reveal macroscopic activity arising from synaptic interactions of millions of neurons. They share a spatially coherent oscillation as a "carrier", by which spatial patterns of amplitude modulation (AM) are transmitted in distinctive configurations, when subjects receive sensory stimuli they have learned to discriminate. These spatial AM patterns are unique to each subject, are not invariant with respect to stimuli, and cannot be derived from the stimuli by logical operations. The "carrier" is aperiodic, usually dispersed over a wide spectral range. Our simulations of the "carrier" indicate that its dynamics is chaotic, and that sequential patterns are freshly constructed during perception, because chaotic systems can create as well as destroy information. The entire experience of a subject, which is embedded in synaptic connections in cortex that were modified during learning, can be brought instantly to bear at each state transition by which a new construction is initiated. It is suggested that "feature binding" revealed by microscopic recording is related to the formation of a "chaotic construct" early in the process of perception.

Peripheral versus Central "Neural Coding"

At the outset of this Symposium, we should ask: why is it that a "neural code" is "temporal", and in what sense? The answer is that neurons are built to communicate over distances ranging from fractions of a millimeter to several meters. One part of a neuron (a synapse on a dendrite) communicates to another part (the axon at the cell body) by generating electric current (Figure 1). The dendrites form a tree made of an electrically conducting interior surrounded by an insulating membrane with thousands of synapses on it. Each synapse acts as a small battery to drive current, always in a closed loop. Excitatory current flows inwardly at the synapse and outwardly at the trigger zone. Inhibitory loop current flows in the opposite direction. The sum at the trigger zone

determines the output firing rate, which is a microscopic state variable. The same current flowing across the external resistance of the cortex sums with the loop currents of neighboring neurons to constitute a local mean field. This macroscopic state variable is recorded with electrodes as local field potentials (LFPs or electroencephalograms, EEGs) and with SQUIDS as magnetoencephalograms (MEGs).

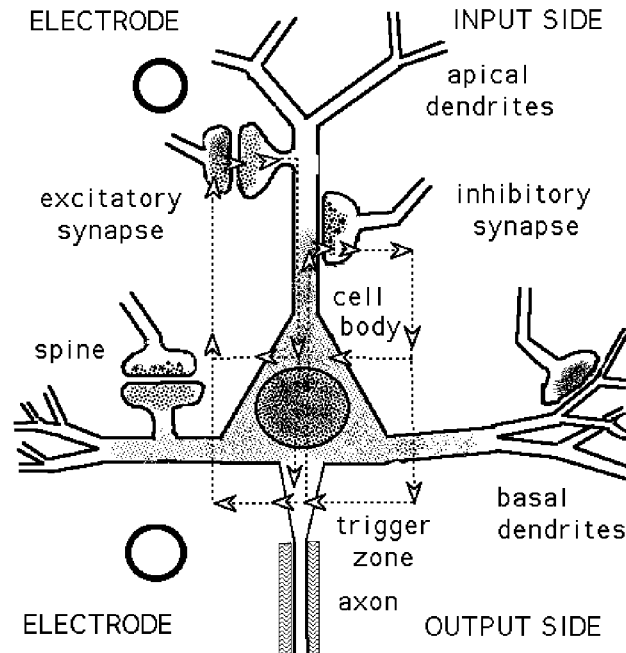


Figure 1 The sum of dendritic loop current (dashed lines) at the trigger zone determines neural firing rate. The extracellular sum with many neurons determines the EEG. From Freeman (1992a).

Over short distances less than half a millimeter, which is typical of dendritic trees, the synapse serving as chemically activated batteries can effectively alter the membrane voltage at the axon by its current, but for longer distances this mechanism is not effective, owing to the leakage of the neuronal membrane. The dendrites provide an immense surface area onto which thousands of axons from other neurons form synapses. The currents that flow preferentially to the cell body through the enlarging dendritic trunks are summed as they flow across the axon membrane, but they cannot proceed far down the axon. Instead, the trigger zone at the start of the axon transforms the sum into a train of impulses, each of which is a traveling wave of loop current that goes reliably to the end of the axon and all its branches without loss. The amplitude of the dendritic current is expressed as the frequency of the pulse train. At the synapses, it is re-expressed in the amplitude of the dendritic current that is released by the chemical neurotransmitter of the axon terminals. Hence the "code" of axons is a temporal pulse frequency, whereas the "code" of dendrites is a continuously varying amplitude of current.

Sensory neurons exist in large arrays found in the skin, inner ear, nose and retina, so that a stimulus is expressed as a spatial pattern of action potentials carried in parallel along sensory nerves. Typically only a small fraction of the axons in a nerve is activated by a stimulus, the others remaining silent or at their level of background activity, so that the "signal" of the stimulus is said to be "encoded" in the frequencies of firing of that subset of

axons subserving the specific energies of the activated stimulus receptors. Thus the "code" of the sensory, motor, and autonomic parts of the peripheral nervous system is the spatial pattern of temporal pulse rates. The same "code" appears to hold also for the ascending and descending pathways and relays in the brainstem and spinal cord. Serious efforts have been made over the past four decades to extend this model to the cerebral cortex as well, with considerable success in characterizing the receptive fields and "feature detector" properties of cortical neurons in primary sensory areas. However, there is reason to question whether this model is appropriate for understanding perception as distinct from sensation. Sensation is computable; perception is not.

The "feature detector" interpretation, deriving from the experimental work of Mountcastle (1957), Lettvin et al. (1959), Hubel and Wiesel (1962) and others, holds that when a complex sensory stimulus arrives in sensory cortex, a small subset of neurons is vigorously excited or inhibited. Milner (1974) and von der Malsburg (1983) have investigated systematically some of the ambiguities that arise when diverse stimuli can activate the same spatial pattern of neural pulse rates. To solve the "binding problem" they have proposed a mechanism of phase-locked periodic oscillations in mean pulse rates. In this view the pulse trains should be periodic and share the same frequency in order that the phase of oscillation be defined. The findings of Gray et al. (1991) and Eckhorn et al. (1988) appear to bear out this proposed solution at a low modulation frequency near "40 Hz" (Bressler, 1990). Hence, visual cortical function might be explained by a model based on periodic orbits with phase-locked pulses at some common rate in a network of neurons.

Periodic versus Aperiodic Oscillations

It is the aspect of periodicity wherein the model falls short of the biological data. If cortical neurons were routinely observed to fire periodically at a designated network frequency, then the Milner-von der Malsburg model would be justified. Periodically firing neurons are indeed found on occasion, but these neurons lie in a small tail in a wide distribution of firing rates, and this statistical property is predicted for a collection of random pulse generators each with a refractory period. The great majority of central neurons yield pulse interval histograms that conform to a Poisson distribution rather than to periodicity. The time-lagged correlations between the pulse trains of pairs of neurons tend to be vanishingly small (Abeles, 1991), which could not be so if the neurons usually had the same pulse rate, whether or not they fired in phase. Tovée & Rolls (1992) have also noted some of the experimental problems encountered in using oscillations to solve the "binding problem", including the relative sparseness of periodically oscillatory cells, the variable frequencies and amplitudes of oscillations, and the incompatibility of the slow onset and long duration of bursts of synchrony in comparison to the rapidity of object recognition.

A further problem is that the mean firing rates of most cortical neurons are much less than the prevailing peak frequencies of cortical dendritic potentials (EEGs) in the gamma band, 20 - 90 Hz including the nominal "40 Hz" (Bressler & Freeman, 1980). In a typical perceptual event lasting on the order of a tenth of a second a participating neuron firing at a mean rate of 10 pulses/second has time to fire only once or twice, if at all. This fact is obscured by commonly used techniques of spike-triggered averaging of EEGs, multiple unit extracellular recording, and correlation analysis of spike trains. These methods enhance the illusion of narrow band oscillation by expressing the variation of the frequency in the decaying envelope of the correlation function at the center frequency. Unaveraged records from the rabbit (Freeman & Viana Di Prisco, 1986) and monkey (Freeman & van Dijk, 1987) cortex reveal broad spectrum EEG activity relating to goal-directed behavior on single trials, which is oscillatory but not periodic. The definitions of "phase locking" and "phase coherence" (as distinct from spatial coherence of broad spectrum activity) can only be derived for discrete frequencies. The phase of a continuous frequency distribution

cannot be defined, although the time lags between simultaneously recorded traces of an aperiodic "carrier" waves can be extracted and re-expressed as a phase at a center frequency.

In brief, cortical pulse trains and EEG waves are mostly aperiodic, so that the central code cannot be the same as the peripheral code. This should be expected, because peripheral neurons seldom interact with other neurons but offer each a private path from the receptor to the central nervous system. In contrast, each cortical neuron is embedded in a milieu of millions of neurons, and it continually transmits to a subset of several thousand other neurons sparsely distributed among those millions and receives from several thousand others in a different subset. Unlike the peripheral neuron the central neuron has continual background activity owing to its synaptic interactions with its neighbors. Each pulse exerts an excitatory action that is returned in a randomized distribution over time by innumerable other neurons at differing distances and conduction delays, which can be modeled as a diffusion process (Freeman, 1975). This background firing is self-regulated and self-stabilized. It is a characteristic property of cortical neural populations not shared by peripheral neuron arrays (Freeman, 1974). Therefore the preferred definition of intensity of central neural activity is not pulse frequency but pulse density. Owing to the large numbers of neurons in each local neighborhood, the density is continuous and not discrete. It is a macroscopic variable like the local temperature of a gas as distinct from the kinetic energy of the gas molecules.

Thus single cortical neurons normally are not periodic oscillators that can be entrained, but they are members of large populations that oscillate aperiodically by distributed synaptic interactions between excitatory and inhibitory neurons. The neurons sharing the macroscopic, aperiodic oscillations comprise a local neighborhood that can be viewed as an equivalence class, in which the burden of firing is rotated at random among the members in a form of time multiplexing. Sparse firing in this condition is desynchronized necessarily at the microscopic neural level, but appropriate averages such as correlation of EEGs with multineuronal recordings can reveal coupled, near-periodic oscillations in firing probability reflecting the macroscopic pulse density (Freeman, 1975). The local neighborhoods corresponding to cortical columns and hypercolumns seldom have anatomical boundaries of their internal synaptic connections, so that an area of cortex composed of hundreds and even thousands of neighborhoods can act as a coherent element of function in generating a spatially coherent "carrier" wave. These distributed neural populations are dynamically unstable and are capable of very rapid global state transitions, by which the amplitude modulation of the common oscillation, the "carrier" wave, switches abruptly from one spatial pattern to another, and thereby it can easily fulfill the most stringent timing requirements encountered in object recognition.

Resonance versus Self-organization

The hypothesis underlying the Milner-von der Malsburg formulation of the "binding problem" is that cortex operates by establishing strong correlations ("phase locking") among a small subset of neurons having high pulse rates in a given time window. That subset is determined by the stimulus. An alternative hypothesis holds that the cortex operates by extracting weak covariances among across a very large population of neurons having low firing rates (Freeman, 1991a, 1992b). This hypothesis is based on a striking difference between two types of central path, one that provides topographic mapping from an array of transmitting neurons to an array of receiving neurons, the other having divergence of axons that provides for spatial integration of the transmitted activity. An example of the difference between topographic mapping and spatial divergence is seen in the first and second paths of the olfactory system (Figure 2). If the oscillations in transmitted pulse density are spatially coherent by having a common instantaneous "carrier"

frequency, then spatial patterns of amplitude modulation are selectively read out by spatial integration over pathways with strong axonal divergence. This coherence can be achieved by the cooperativity inherent in sparse synaptic interactions in cortical populations, and the transform effected by the output path defines the self-organized macroscopic activity as the cortical "signal".

A test between these two hypotheses cannot be based solely on pulse recording, because both "feature binding" and global coherence are expected to appear as "phase locking". On the one hand, coherence by the "feature binding" hypothesis can be demonstrated among a small number of neurons by time ensemble averaging of their activity with respect to the time of onset of a repeated stimulus, which emphasizes the center frequency of a distribution of frequencies. On the other hand, coherence by the "chaotic construct" hypothesis can be demonstrated among all of the neurons in an area of cortex by spatial ensemble averaging (Freeman, 1991b), because they participate in every perceptual response to a stimulus, but in varying degrees after they have performed their individual duties in sensory "feature extraction".

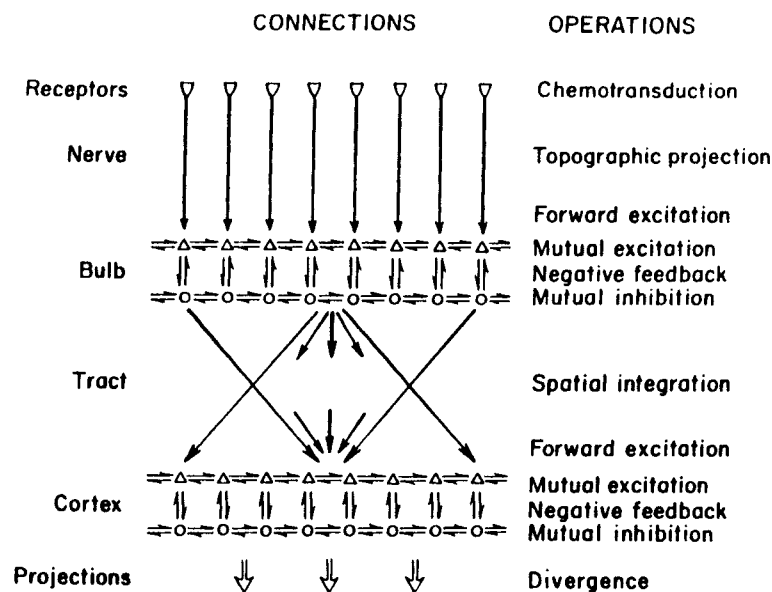


Figure 2. The input path from receptors to the bulb has some topographic specificity. The output path to the prepyriform has broad axonal divergence, which provides a basis for spatial integration of bulbar output and extraction of the "carrier" wave. From Freeman (1983).

A definitive test between these hypotheses is to determine whether the output of sensory cortex is determined by the properties of a stimulus or by the context (the meaning of a stimulus for the subject). In operational terms, the question is answered by measuring cortical responses to discriminative conditioned stimuli during learning. If the cortical patterns are stimulus-dependent, they will remain invariant under changes in association. If the patterns depend on the internal connectivity of the cortex as the basis for their self-organization, they will vary with changes in context including accumulated experience. This is because the microscopic peripheral "code" is forced into the cortex by the injection of stimulus-related activity, whereas the coexisting macroscopic central "code" is self-organized by the spatially patterned synaptic connections and excitability states of trigger zones in each functional area of cortex (Freeman, 1975, 1992a,b).

The macroscopic pulse densities are entirely compatible with the microscopic pulse frequencies of individual neurons, because only a very small fraction of the variance of the pulse trains of single neurons is co-variant with the local mean field of a neighborhood, on the order of 1 part in 1,000 (Freeman, 1975). This low fraction means that macroscopic patterns cannot be reliably observed with microelectrode recording of action potentials. They must be observed by recording the extracellular potentials of summed dendritic loop currents (Figure 1), because, as noted, the same current that controls the axonal pulse frequencies crosses the extracellular resistance, where it sums with the currents from all other neurons in the local neighborhood that have the appropriate dendritic geometry. That the extracellular current sum is the main contributor to the EEG is shown by the experimental finding that the probabilities of firing of neurons observed singly and in small groups simultaneously are in close statistical relationship to the EEG recorded in the near vicinity (Freeman, 1975; Eeckman and Freeman, 1990, 1991). Therefore the EEG can provide an experimental basis for estimating the local mean field of contributory neurons.

The sum is also an instantaneous spatial ensemble average, as distinct from a temporal ensemble average that requires storage of sequential traces over time. There is no evidence that cortical populations have the ability to store, retrieve, and average the kind of detail that goes into an averaged evoked potential, but because the axonally transmitted cortical output typically undergoes spatial divergence and dendritic integration (Figure 2), it is obvious that the typical transmission pathway from cortex performs spatial ensemble averaging. From this interpretation it follows that the EEG, when properly recorded and analyzed, provides the best experimental access we have to the spatial patterns that constitute cortical output (Freeman, 1991b).

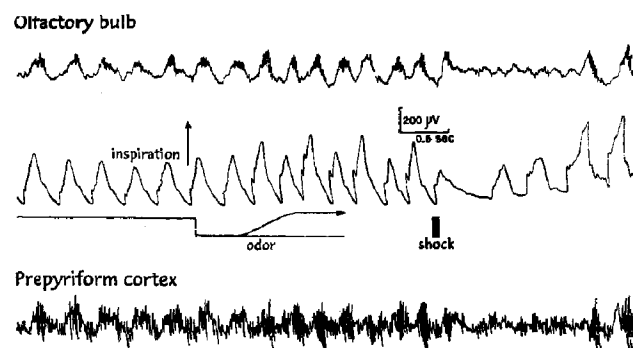


Figure 3. A conditioned response (middle trace, sniffing) is induced by pairing a CS+ (amyl acetate) with an aversive shock, while the EEG is recorded from the bulb and cortex. The CS concentration is from a calibration trial. From Freeman & Schneider (1982).

Experimental observations of macroscopic cortical activity

The method of choice for observing the spatial patterns of cortical activity is to record EEGs from arrays of electrodes placed surgically onto the surface of an area of cortex, at spacings sufficiently close together (half to one millimeter apart in an 8x8 rectangular pattern) to provide a window 25 to 50 square millimeters onto a coherent domain of cortical activity. The procedure has been applied most extensively to the olfactory bulb of rabbits (Figure 2). Time series are recorded over the full extent of a 6 second trial, in which a rabbit is asked to discriminate from the control air (C) one of two odorant conditioned stimuli (CSs) that arrives 0.5 second after the midpoint of the trial (Figure 3). The rabbits are trained by pairing one of the stimuli (the CS+) and not the other (the CS-) with a

reinforcing unconditioned stimulus (the US). The conditioned response (CR) is a change in respiration (sniffing). Each EEG record is edited by locating a burst with each inhalation, extracting its common wave form (its "carrier") on the 64 channels, and relating its spatial pattern of amplitude (Figure 4) to the odorants (C, CS+, or CS-). Repetition of trials and sessions with different CSs and reinforcement combinations yield sets of burst patterns that fall into distinct classes. Analysis with multivariate statistics shows that the classes conform to the odorants far better than would be expected by chance (Grajski et al., 1986; Freeman & Grajski, 1987).

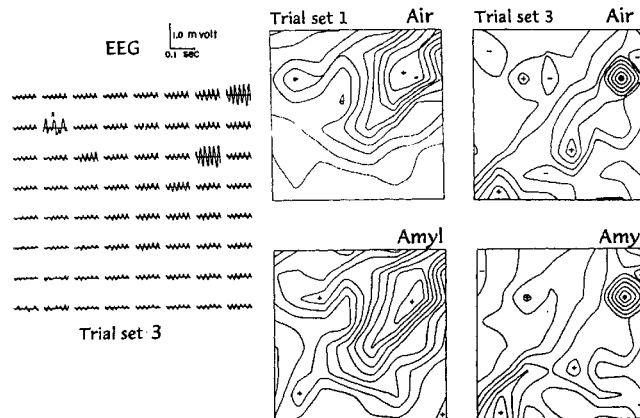


Figure 4. The 64 traces from one burst are high pass filtered to remove the respiratory wave. The root mean square (RMS) amplitudes averaged over sets of 10 trials from control and test periods with amyl acetate as the CS+ give contour plots. From Freeman & Schneider (1982).

The key finding is exemplified in Figure 4 by the changes in the C and CS+ spatial patterns from the first session to the third session. The stimuli are the same, but the patterns differ. What has changed is the context in which the discrimination is being performed, owing to the introduction for the first time of an aversive US, which changes for the rabbit the meaning of the background odor. The lack of invariance of the EEG patterns with respect to the stimuli has also been demonstrated by generalization, overtraining, serial conditioning, discriminative conditioning with both appetitive and aversive USs, and reversal of the US between CS+ and CS-, by which the stimuli are the same but the meanings are changed (Freeman & Viana Di Prisco, 1986). Each change of adding a new stimulus or changing a reinforcement appears to change all of the patterns by a small amount, on the average about 7% of the intrinsic variation of each pattern (Freeman & Grajski, 1987), including the control pattern for C. The fact that the EEG manifests the output of the bulb to the prepyriform cortex is demonstrated by the strong correlation of the EEG of the bulb with that of the cortex (Bressler, 1987a,b), showing that the bulbar oscillation forces the patterned oscillations in the cortex.

These data support the "chaotic construct" hypothesis for the olfactory system. The modifications of pre-existing patterns that accompany the formation of new patterns for newly learned classes of stimuli can be viewed as an essential property of an associative memory system, because the formation of new connections between new and old stored elements requires that all items be altered when new ones are entered. To the extent that these findings can be extended to other sensory systems they will have profound implications for science and human understanding, because they imply that our knowledge of the outside world is constructed by neurodynamics, not derived by logical operations on

sensory data in the manner of the machines that we presently use for information processing (Freeman, 1991a).

Extension of the observations to vision, audition, and touch

Neocortical EEGs are far more complex than those from paleocortex. Bursts are less prominent, the temporal spectra tend to the "1/f" type, and spatial spectra fall more rapidly with increasing spatial frequency, possibly because of the greater thickness of neocortex. There is no obvious forcing function comparable to the respiratory wave with inhalation by which to segment the records; the alpha and theta waves are too ephemeral to serve as markers for perceptual events. There are no clear edges of domains comparable to those of paleocortex. The olfactory bulb, cortex, and hippocampus have been extensively modeled (e.g. Rall & Shepherd, 1968; Wilson & Bower, 1992; Li & Hopfield, 1989; Granger, Ambros-Ingerson & Lynch, 1989; Kammen et al., 1989; Liljenstrom, 1989), but no comparable body of experience exists for neocortex. The four classes of model for oscillation, exemplified by Andersen & Andersson's (1968) thalamocortical pacemaker, Elul's (1972) statistical model, Llinás' (1988, Llinás & Ribary, 1993) cellular model, and Konig & Schillen's (1991) negative feedback model with excitatory and inhibitory cells, fail to include the deeper three layers, and are inadequately developed for EEG simulation with aperiodic solutions (Freeman, 1987a).

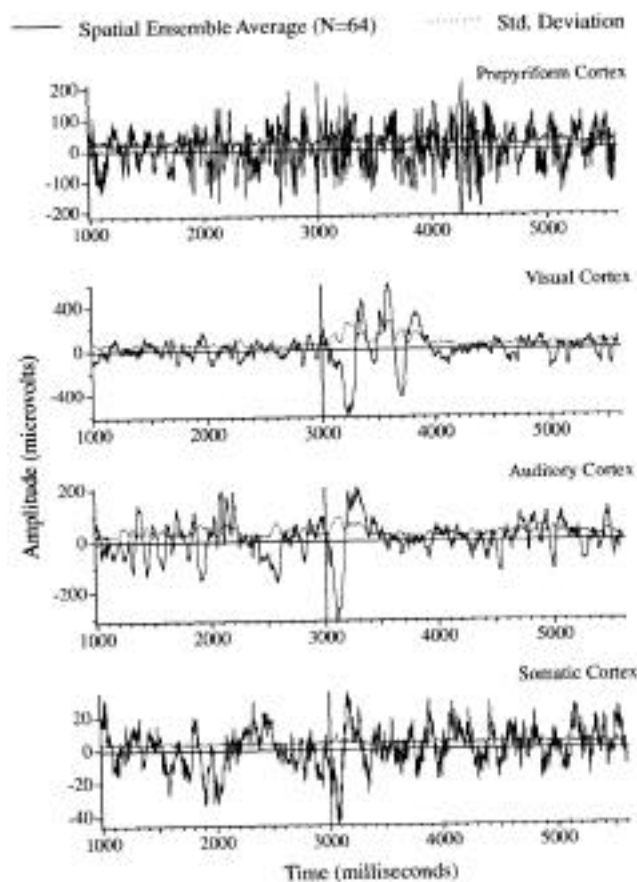


Figure 5. Each spatial ensemble average (heavy curve) and standard deviation (SD, light curve) were computed by averaging the 64 EEG traces recorded on the same trial to give the "carrier".

Preliminary studies with new techniques for EEG analysis have yielded new data, which show that the neocortical dynamics of the visual, auditory, and somatic cortices conforms in main outline to that of the paleocortex, but with some interesting differences. Examples in Figure 5 show spatial ensemble averages of 64 EEG traces (single trials) from the visual, auditory, somatic, and prepyriform (olfactory) cortices of rabbits that were trained to discriminate between a CS+ and a CS- in the appropriate modality on randomly interspersed trials. The 64 unaveraged records reveal the shared aperiodic oscillations that are typical of cortical EEGs. In contrast, after time ensemble averaging over 40 trials in a training session, the stimulus-evoked response at midpoint becomes easily visible as the classical Event Related Potential (ERP, Figure 6). The neocortical temporal spectra (Figure 7, top) conform in the main to the "1/f" pattern of linear decrease in log power with increasing log frequency from 3-100 Hz, with little of the excess power in the gamma range that characterizes the olfactory system. The spatial spectra (Figure 7, bottom) reveal in common a concave-downward fall in power to a "noise" plateau with increasing spatial frequency, which is more rapid for the neocortex than for the paleocortex. For both paleocortex and neocortex the bulk of power is in the range of 0.1 to 0.5 cycles/millimeter.

On the basis of these graphical and spectral analyses two methods of decomposition were employed: a modified Fourier decomposition (FFT, Freeman & Viana Di Prisco, 1987) and principle component analysis (PCA, , Freeman & Van Dijk, 1987; Meyer-Kress, Barczys & Freeman, 1991). An example is shown in Figure 8 (left) for a window 120 msec in duration, in which the 64 unaveraged traces from the visual cortex have been band pass filtered between 10 - 80 Hz (see Figure 4). The spatial ensemble average (upper frame) has been fitted with the sum of 5 cosines that are linearly modulated in amplitude and frequency with time and optimized in frequency and phase by nonlinear regression. The same curve (lower frame) has been fitted with the largest 5 components. The 2 sets of 5 basis functions are shown in Figure 9.

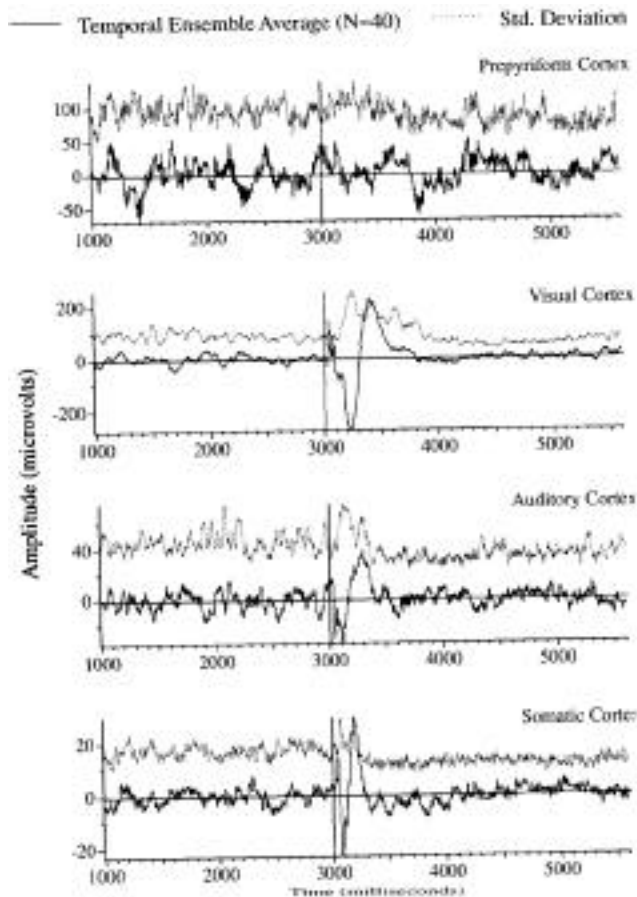


Figure 6. Each **time ensemble average** and SD were from the 40 spatial ensemble averages in a session, yielding the Event Related Potential (ERP).

The 64 amplitudes of the dominant component from each method give a 64x1 column vector to represent the pattern in an EEG segment, which determines a point in 64-space. The difference between two individual patterns is measured by the Euclidean distance between the points. In the absence of reliable features by which to segment the EEGs in time, spatial pattern classification of CS+ vs. CS- segments is repeated across the entire length of each 6-second EEG, using a moving window stepped every 20 msec across 20 CS- records and 20 CS+ records. The window has been varied from 60 to 200 msec in increments of 20 msec, to find an optimal value of 120 msec. Spatial pattern classification is computed on a binomial probability scale, based on the number of CS- and CS+ spatial patterns which lie closest to their respective centroid, as measured by the Euclidean distance. Each centroid is formed using half of the data set; the other half of the data set is classified by that centroid. This is repeated by using the second half of the data set to compute its centroid and then classifying the first half of the set. The trial-specific separation is expressed as a probability that the observed amount of correct classification is due to chance.

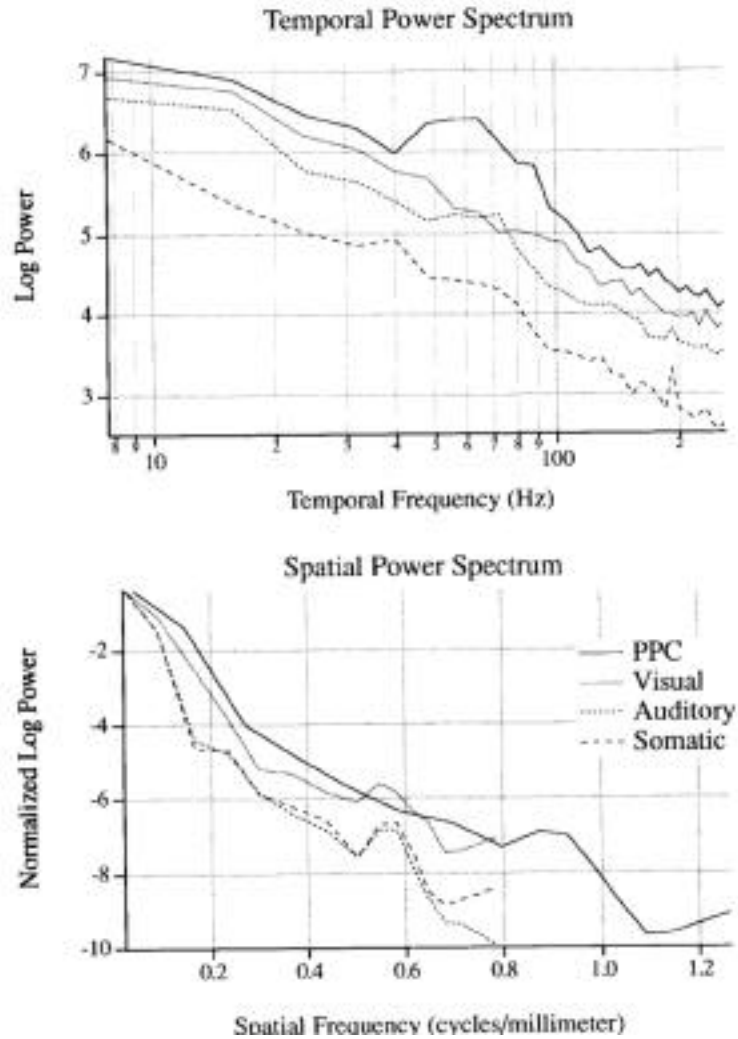


Figure 7. (top) The temporal spectra are averages from 24 time windows of EEGs each 128 msec in length. (bottom) The spatial power spectra are from 120 msec windows of each cortical EEG.

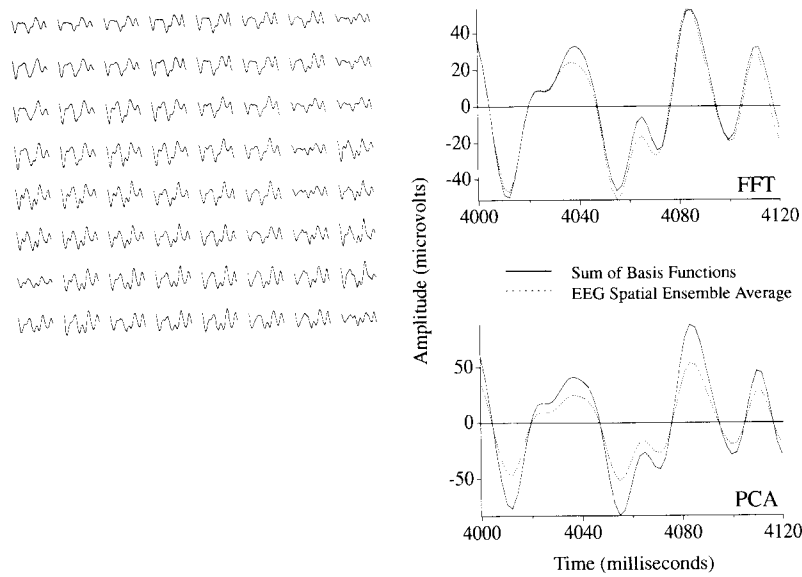


Figure 8. A visual cortical EEG segment has been filtered at 10 - 80 Hz (left). The spatial ensemble average (right) is fitted with the sum of 5 basis functions by FFT and PCA.

Three distinct time periods are seen in which the spatial patterns for CS+ and CS- are significantly separated (Figure 10). Period 1 occurs when the sensory stimulus arrives and establishes a reaction in the cortex. Period 2 lies in the vicinity of the P300 component of the ERP, when it appears. Period 3 takes place in the vicinity of the CR. A late Period 4 is marked by a substantial decrease in the variance of the EEGs (Figure 6), indicating spatial pattern stabilization, but there is no separation of spatial patterns relating to the CSs. The prepyriform cortex showed a segment of significant separation about 0.5 sec after the odorant arrival (0.5 sec after the opening of the solenoid controlling odorant delivery, Figure 3). No effort was made to synchronize the samples to respiration across the 20 trials, so that it is a measure of the increased likelihood of a sniff occurring at 0.5 sec that any separation at all occurs with the lagged window method. The use of clicks, shocks and light flashes enhances the likelihood of perceptual sampling close to the moment of impulse stimulus delivery to the neocortex.

Examples of the spatial patterns of the EEGs in the control period and the 4 post-stimulus time periods are shown by columns in Figure 11 (a) as time ensemble averages over the 20 trials with each CS- in rows 1 and 3 and CS+ in rows 2 and 4. The results of the two methods for the decomposition are also compared. In Figure 11 (b) rows 1 and 2 show the same patterns constructed from RMS amplitudes of the 64 channels, which provide quick though less precise access to the patterns obtained by decomposition. Rows 3 and 4 show the spatial patterns from a reversal of the reinforcement several weeks later. The pattern differences are statistically significant for all 5 Periods between the sessions, as in Figure 4 for the olfactory bulb data.

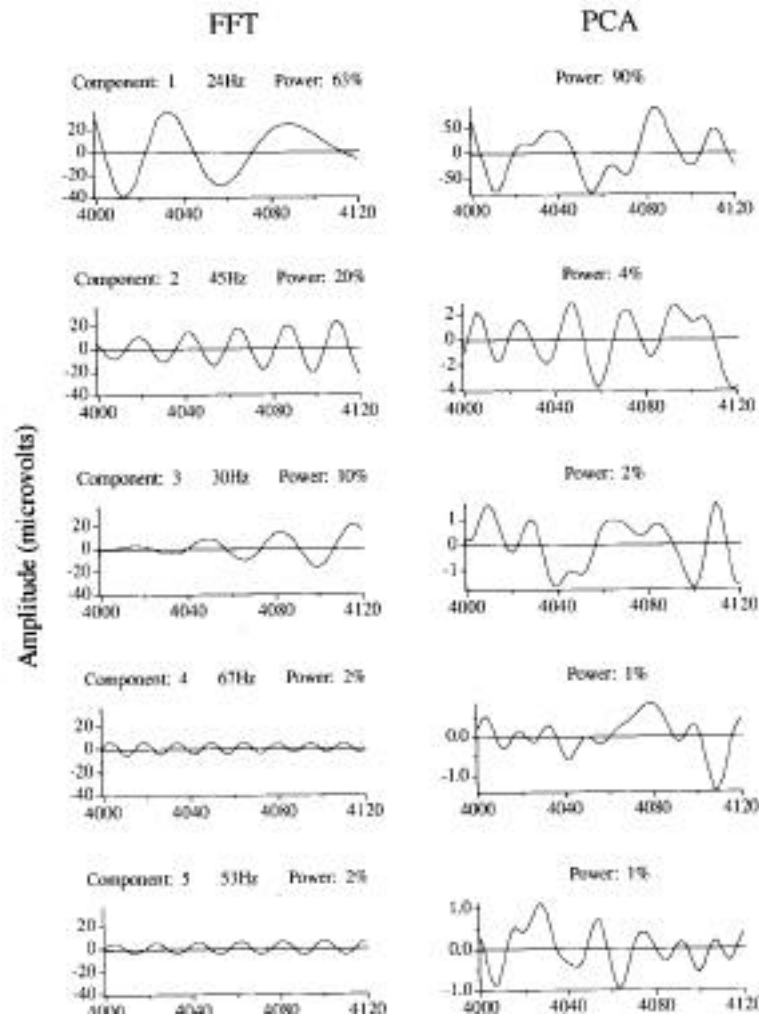


Figure 9. The basis functions are shown for the EEG segment in Figure 8.

These results show that the three main sensory neocortices have functional properties similar to those of the olfactory system in several respects. (a) Multichannel EEG recordings yield an aperiodic "carrier" wave form common to the whole array. (b) The spatial patterns of amplitude modulation of the "carrier" across the array suffice to classify recorded events with respect to CSs; (c) this happens only in time segments when cortical operations underlying discrimination of the stimuli appear to be in progress; and (d) comparison of patterns across trials with replication with or without reversal of the reinforcement contingency again manifests a lack of invariance of the spatial patterns with respect to unchanging stimuli. Preliminary assays have shown that the information that supports the pattern classification in neocortex is more broadly distributed across the temporal and spatial spectra than was the case for the olfactory bulb (Freeman & Viana Di Prisco, 1986; Freeman & Baird, 1987), and is also uniformly distributed across channels. The conclusion that the central patterns are not invariant with respect to stimuli is consistent with that of Bartlett (1932), whose detailed studies of the process of remembering by humans revealed both the lack of invariance and the cultural dependence of the recollections produced by the subjects. They reinforce his view that the process of remembering is not "

... the re-excitement in some way of fixed and changeless 'traces' ... " (op. cit., p. vi). It is instead a process by which an organism has " ... the capacity to turn round upon its own 'schemata' and to construct them afresh. This is a crucial step in organic development. It is where and why consciousness comes in; it is what gives consciousness its most prominent function. ... " (op. cit., p. 206). The key word is "construct". The finding that the same stimulus can presage the formation of differing patterns contingent on intervening experience implies that no analytic algorithm or computational procedure can derive the brain activity patterns from the stimulus. The trajectory for construction in dynamical phase space is unique for each brain, owing to the unique history of each brain. We therefore look to nonlinear dynamical systems for an explanation of the mechanisms of the construction.

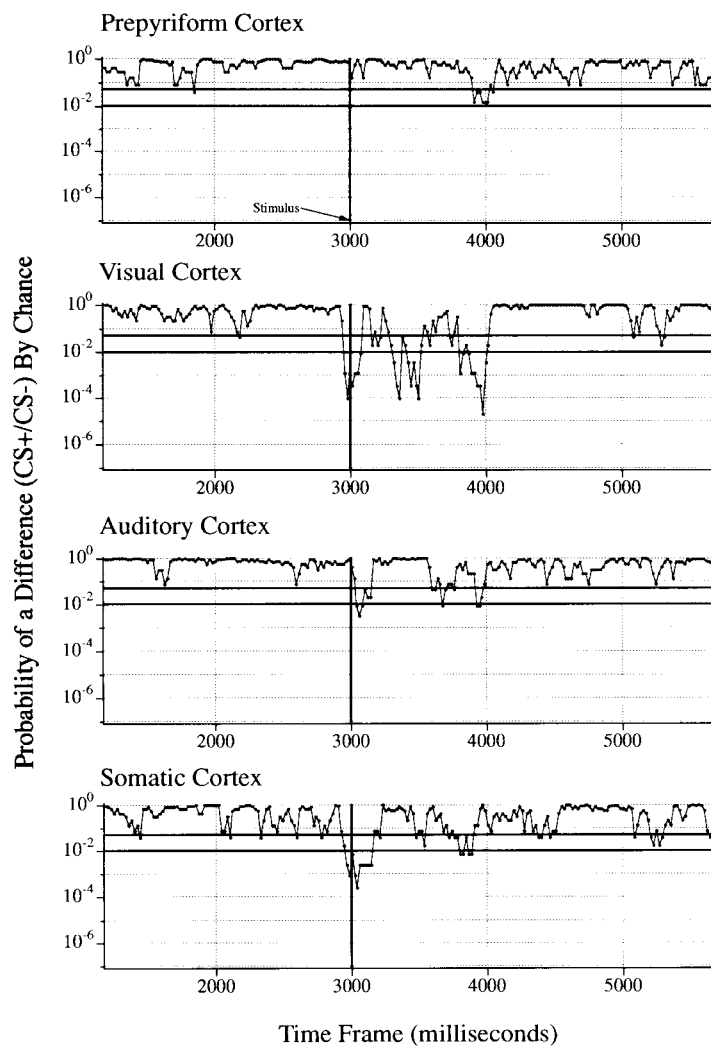


Figure 10. The probability that a spatial AM pattern difference (CS+/CS-) was due to chance was calculated for each cortex (see Figures 5 and 6). Comparable results were found with FFT and PCA.

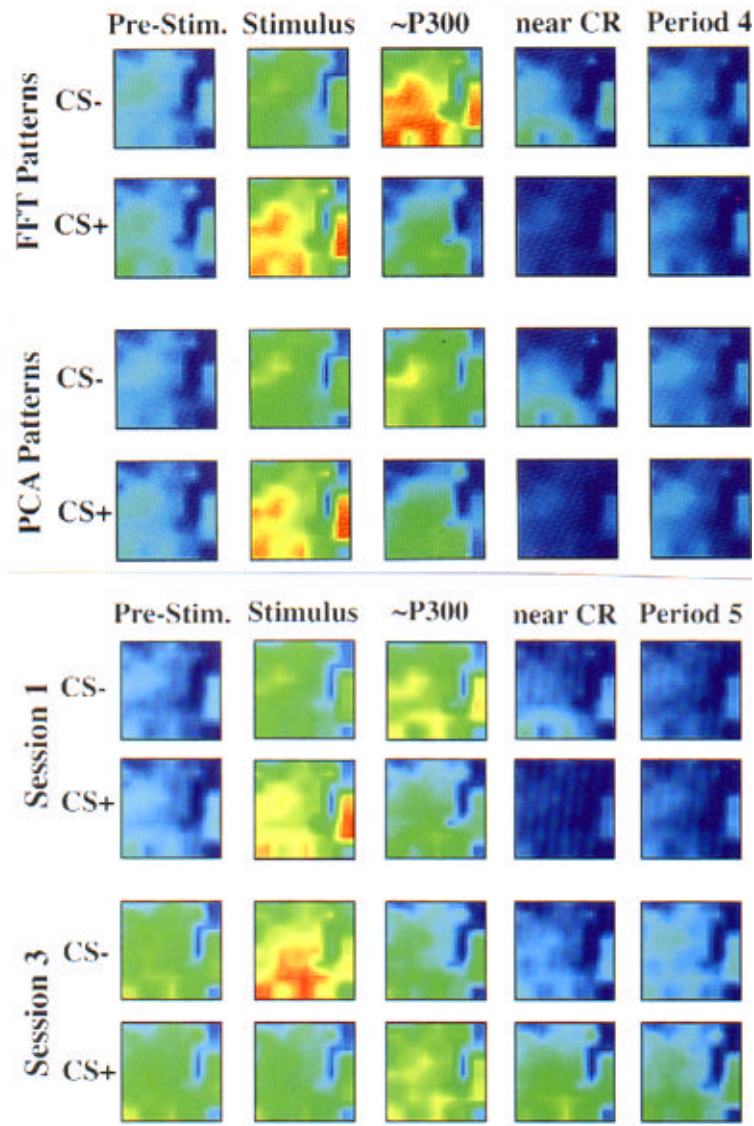


Figure 11. (a) The differences in centroids of spatial patterns for CS+ and CS- in visual cortex by PCA and FFT in Periods 1-3 are contrasted with a lack of differences in the prestimulus control Period 0 and Period 4. (b) Upon reversal of the reinforcement the spatial patterns revealed lack of invariance for the same stimuli (see Figure 4).

Roles for chaotic dynamics in the construction of patterns

Dynamical systems such as the brain have their preferred modes of operation. Given a set of initial conditions corresponding to sensory input and the existing state of the brain, a recognizable and reproducible spatiotemporal pattern of function will reliably though not inevitably follow. Examples are to sleep, wake, stand, walk, run, etc. The observed pattern is described as an "attractor", simply because the brain or brain system is seen to converge to the pattern from a variety of starting points, as though it were "attracted". The range of initial conditions that allow convergence to a pattern is called the "basin of

attraction", in analogy to a ball rolling into a cup to its base (a "point" attractor) under the influence of gravity. The brain has many states, each with its attractor and basin of attraction. Typically the effect of a stimulus is to change the brain or one of its parts from one basin to another. The change is called a state transition, which is said to follow destabilization of the brain from a prior basin of attraction. There are two kinds of state transition of interest for sensory cortex. One is a system change, such as from sleep to waking, from rest to arousal by fear, hunger, etc., or from naivete to knowledge of a new stimulus (learning), which is enacted by chemical neuromodulators acting on the cortical neurons and changing their properties. This is described as a "bifurcation", and the factor that induces the change is called a bifurcation parameter (Thompson & Stewart, 1988). The other is a change that is induced and maintained by sensory input, which is described as "itinerancy" (Tsuda, 1991), and which does not involve a structural modification or parameter change in the system.

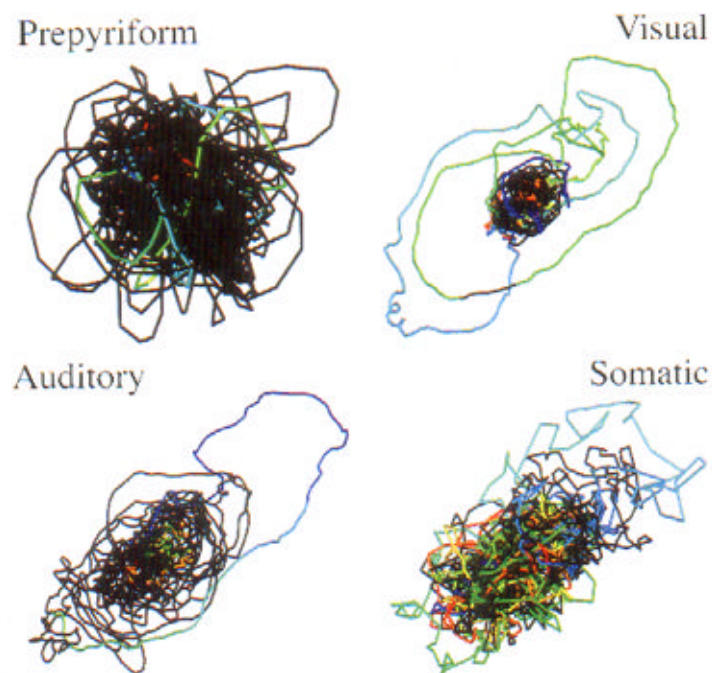


Figure 12. Phase portraits are shown for the EEG spatial ensemble averages in Figure 5, color coded with the three periods of pattern difference shown in Figures 10 and 11 (a).

Our data show that an act of perception that is accompanied by a change in cortical activity pattern reflects an itinerant state transition, and that learning to identify a new stimulus is a bifurcation (Freeman, 1992a). We conceive each sensory cortex as maintaining a global attractor, which is like a hotel with many rooms or "wings". When the subject is at rest the wings are shut, and the system remains in a central "lobby", which is manifested by spatially and temporally aperiodic activity having the disorder of chaos. Upon arousal the level of activity increases and the doors to the wings are opened. This is a bifurcation. When a known stimulus arrives, the system moves through a door to an appropriate wing and is confined there for the duration of the stimulus. The itinerant entry into a wing and its confinement are revealed by a baseline shift in potential and a burst of oscillation that is amplitude modulated spatially and temporally. A phase portrait consisting of an EEG trace

plotted on one axis against itself lagged in time on another axis (Figure 12) show a central tangle during the pre-stimulus Period 0 (the "lobby") and a complex set of loops for Periods 1 to 3, color coded to distinguish them. These phase portraits are 2-dimensional projections from a higher dimensional space of the chaotic attractors that govern the cortical dynamics. The prepyriform and neocortical attractors resemble those already reported for the bulb and other parts of the olfactory system (Freeman, 1992a). The basin of attraction for a wing corresponds to the generalization gradient for the correct response to a sensory stimulus, which is never twice identical owing to random variation in its impingement on the array of equivalent sensory receptors and the resulting microscopic pattern of input to the cortex. We postulate that there are as many wings for each global attractor as there are classes of stimuli that are discriminable at the level of a primary sensory cortex.

The construction of a new wing and its paths of access requires modification of synapses during learning. Our experiments and modeling (Freeman, 1975; Yao et al., 1991) indicate that the pre-existing modifiable synapses are those that interconnect the excitatory neurons in cortex. During the presentation of a stimulus under reinforcement the subset of the neurons that are co-activated by the stimulus has its set of mutually excitatory connections strengthened, so as to form a nerve cell assembly in the sense described by Hebb (Viana Di Prisco, 1984). Thereafter the assembly responds in a stereotypic way when any of its members is excited, providing the basis for generalization from examples to significant classes of input. This operation lies close to the heart of the process of perception (Lashley, 1948). Owing to the strengthened mutual excitation, a weak stimulus is amplified strongly (Freeman, 1979a,b,c) and selectively (Edelman & Freeman, 1990). We conceive that it is the activity of the assembly that guides the entire system across a separatrix into the appropriate wing at the instant of the state transition forced by the input.

Chaotic dynamics may play a critical role in the Hebbian learning process, particularly in the construction of a new wing that differs from any that have come before. If the inhaled air does not contain a known odorant but a novel chemical, then an existing wing is not accessed, and a recognizable spatial pattern of the aperiodic "carrier" fails to form (Freeman & Schneider, 1982; Skarda & Freeman, 1987; Gray & Skinner, 1988; Grajski & Freeman, 1989). Activity does not conform to any pre-existing spatial pattern. Strengthening of a Hebbian synapse requires concomitant activity in pre- and postsynaptic neurons. If this activity were organized by an existing wing, then the synaptic change might reinforce an existing spatial pattern for output. If a new pattern is to be created, then the activity that drives the synapses must be new. A chaotic generator appears to be an optimal way that cortex can do this.

Only one wing at a time can be accessed, but it may occupy the entire extent of an area of cortex and the complement of neurons within it. This factor plays a critical role in the process by which a spatial amplitude pattern is read out by the targets to which a sensory cortex transmits. As already noted for the olfactory system (Figure 2) the axons comprising the bulbar output pathway branch repeatedly and spread widely to their targets. Corresponding to this spatial divergence of output is the convergence from widely dispersed transmitting bulbar neurons to each receiving prepyriform neuron that performs the integration. Anatomical divergence is far more common in the brain than is the topographic, point-to-point mapping, best known for the input pathways to primary sensory cortex. The effect of the spatial integration is to minimize activity in the transmitter that does not have the same instantaneous frequency and phase, and to enhance the reception of the "carrier" irrespective of its local variations in amplitude. In effect the integral transform serves to define the "signal" of the transmitter as that part of the transmitted activity that is due to the global cooperative interactions and to remove the uncorrelated activity as "noise".

The spatial integration of transmitted output imposes another constraint on the transmitter. The phase dispersion of the coupled oscillatory neighborhoods cannot exceed a range on the order of a quarter cycle of the center frequency in the distribution, or cancellation of some parts of the output by other parts must occur. Measurement of phase gradients in the olfactory bulb show that the constraint is met for the bursts, and the mechanism by which it is achieved has been described as "anomalous dispersion" (Freeman, 1990). Measurements of phase in visual cortical recordings (Gray et al., 1989; Eckhorn et al., 1988) indicate that neocortical activity also adheres to this criterion.

Herein can be seen two compelling reasons for the existence of oscillations as the basis for central coding. First, during Hebbian learning the likelihood of coincident firing of pairs of neurons is enhanced by their shared fluctuations imposed by the macroscopic state as an "order parameter" (Haken & Stadler, 1990). Second, the signal to noise ratio of the output of the integral transform is enhanced by an oscillatory input. Neither of these enhancements could occur for steady state ("D.C.") inputs. Neither requires that the oscillations be aperiodic, but our simulations suggest that transitions from one wing to another are facilitated by the broad spectrum of the "carrier", so that the system is less likely to get stuck in a wing than if the "carrier" were periodic (a limit cycle).

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