

## NONLINEAR DYNAMICS OF PATTERN FORMATION AND PATTERN RECOGNITION IN THE RABBIT OLFATORY BULB\*

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A mathematical model of the process of pattern recognition in the first olfactory sensory cortex of the rabbit is presented. It explains the formation and alteration of spatial patterns in neural activity observed experimentally during classical Pavlovian conditioning. On each inspiration of the animal, a surge of receptor input enters the olfactory bulb. EEG activity recorded at the surface of the bulb undergoes a transition from a low amplitude background state of temporal disorder to coherent oscillation. There is a distinctive spatial pattern of rms amplitude in this oscillation which changes reliably to a second pattern during each successful recognition by the animal of a conditioned stimulus odor. When a new odor is paired as conditioned stimulus, these patterns are replaced by new patterns that stabilize as the animal adapts to the new environment.

I will argue that a unification of the theories of pattern formation and associative memory is required to account for these observations. This is achieved in a model of the bulb as a discrete excitable medium with spatially inhomogeneous coupling expressed by a connection matrix. The theory of multiple Hopf bifurcations is employed to find coupled equations for the amplitudes of competing unstable oscillatory modes. These may be created in the system by proper coupling and selectively evoked by specific classes of inputs. This allows a view of limit cycle attractors as “stored” fixed points of a gradient vector field and thereby recovers the more familiar dynamical systems picture of associative memory.

### 1. Introduction

In this paper I will describe the experimental and theoretical investigation of a neural system in rabbits that is involved in olfactory pattern recognition. The olfactory bulb is the first sensory cortex for the processing of odor information from the nose. I will present a model that accounts for its observed behavior and exhibits novel principles of pattern recognition. The mathematical analysis explains how an oscillating system may pattern recognize and is expected to be of use for other oscillating neural structures suspected of similar function, such as the next stage of olfactory processing—the prepyriform cortex.

For our experiments, an  $8 \times 8$  array of 64 electrodes, about a half centimeter wide, is perma-

nently implanted on the surface of the olfactory bulb of adult rabbits. Through this array we observe the spatial and temporal patterns of electrical voltage generated by neural activity in the bulb which is known as the electroencephalogram or “EEG”. The experiment involves placing an animal in a light and sound proof box and digitally recording this EEG activity by computer during the presentation of odors paired with water according to a classical Pavlovian conditioning schedule.

At the peak of each inspiration, the EEG shows a brief transition from a state of low level irregular activity to a high amplitude coherent oscillation with a distinctive spatial pattern of rms amplitude. This creation of order from disorder or pattern from homogeneity is called “pattern formation”. It can occur in an open system when an influx of energy (sensory input in this case) causes the homogeneous state to lose stability or “bifurcate”, and an ordered state (“dissipative structure”) becomes the new stable state.

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The above experiments combining behavioral and physiological observations have established that specific patterns are correlated with specific odor recognition responses and that these change with learning. This demands a theory of olfactory pattern recognition that combines the mathematical description of the emergence of order by instability with the mathematics of associative memory used to model learning and pattern recognition in neural networks. Neither theory by itself is sufficient to account for both pattern formation and learning. Each must be generalized to accomplish the fusion\*.

I will outline and justify a program to model the rabbit olfactory bulb as a discrete excitable neural medium whose spatial inhomogeneity arises from the modification of its internal coupling with learning. A multiple Hopf bifurcation analysis of the model will indicate that the system may then exhibit a set of distinct spatial patterns or "modes" of oscillatory instability. When these are in close competition for the resources of the system, the initial condition or "input" to the system may give a lead to one particular mode or another that allows it to win the growth competition. I will argue that this mechanism of competing instabilities, known as "nonlinear mode selection", is implicit in dynamical associative memories and provides the key to how a pattern forming system can pattern recognize.

This is the central notion of the paper. Within the range of internal coupling that leads to properly balanced competition, a pattern forming sys-

tem can pattern recognize because its modes of pattern forming instability are selectively evoked by different classes of inputs. A given mode then denotes a category of input. "Recognition" occurs in the olfactory bulb when input with an odor-specific spatial structure drives the system state beyond the threshold of homogeneous stability through a multiple Hopf bifurcation. The spatial structure of the input breaks the symmetry of the bifurcation and sends the system into the basin of a particular spatially inhomogeneous limit cycle attractor which now "represents" that input as its "associated" output.

We show that the bifurcation from the resting state into oscillation and back can supply an important signal amplification and memory reset operation for the animal. Dynamical systems theory is central to this theoretical approach. It is employed to produce a mathematical picture of the process of competition among modes that effects pattern recognition. The experimentally observed behavior of the bulb is easily visualized in this portrait, including the impact of chaotic attractors on the function of pattern recognition. Two sections of the paper describe experimental and theoretical background and provide a verbal overview of the mathematical model. This is then presented in the last section.

*Motivation.* Biological systems are capable of feats of pattern recognition and more obviously of pattern formation (evolution, morphogenesis) which are far beyond the capability of any man-made systems. As emerged in several talks of this conference, human superiority in game playing may almost entirely be due to this pattern recognition ability. Clearly there are principles of natural design that surpass the present concepts behind our efforts in engineering and artificial intelligence. It is the prospect of extracting such principles that motivates this work. The same frontier is addressed by many of the papers presented here. The experimental system to be discussed in this paper will illustrate some of the theoretical notions that

\*Stephen Grossberg has extended his theory of pattern recognition by "adaptive resonance" to the specific case of standing waves of oscillation in the olfactory bulb and cortex (see refs. 16a-d). Grossberg and Amari [1] and others have considered multilevel systems where learning occurs in a cross-correlating network of inputs from one level to another and pattern formation and selection and contrast enhancement by lateral inhibition occurs in the second level. The analysis here is restricted to the bulb alone and explains how a single layer of tissue with its own crosscorrelating feedback might accomplish classification of inputs. This is the "fusion" of pattern formation and pattern recognition in a single neural medium that is suggested by the anatomy and physiology of both the bulb and pyriform cortex.

have been advanced and provoke new ones as well.

## 2. Biological and experimental background

### 2.1. Function of the olfactory bulb

The anatomy and physiology of the olfactory bulb are well studied. The physical accessibility of the bulb and the relative simplicity of its anatomical structure (paleocortex) combined with the sophistication of its sensory performance make it an ideal system for the study of biological pattern recognition. The olfactory system is capable of reliable detection and identification of minute concentrations of odor that can stimulate in a single inspiration only a tiny fraction of the nasal receptors that might be sensitive to it (as few as 10 out of  $10^6$ ) [9].

The pattern recognition problem faced in part by the bulb, then, is the extraction of an invariant odor class from any particular random spatial distribution of odor molecules appearing on the nasal receptor surface by convection during a given inspiration. This lack of intrinsic spatial structure in the objects of olfactory perception requires the olfactory system to perform classification in an abstract manner without benefit of the feature preprocessing found in the visual system. It is perhaps therefore a more general example of associative memory and may exhibit the principles of higher level processing.

### 2.2. Anatomy of the olfactory bulb

The cortical tissue of the bulb may roughly be viewed (see fig. 1) as a two-dimensional sheet of interacting excitatory and inhibitory neural populations. These are the mitral cells (excitatory) and granule cells (inhibitory). Receptor input is in parallel from the nasal mucosa surface to the bulb surface. Output is also in parallel from the opposite side of the bulb to the pyriform cortex. Receptor fibres map the surface of the mucosa

topographically onto the surface of the bulb. It is generally thought that the spatial pattern of input to the bulb produced by the stimulation of a subset of receptors sensitive to an odor is the "code" that carries information about odor type.

### 2.3. Physiology of the bulb and its sigmoid gain function

Freeman [9–15] has done extensive measurement, experiment, and modeling of the olfactory bulb on anatomical, physiological, and behavioral levels. It is known that the major generators of the surface EEG potential of the tissue are the inhibitory granule cells. These produce a verticle dipole field of ionic current in the surrounding tissue as their internal voltage varies. Thus the EEG supplies a readout of the activity of one element of the medium from which the activity of the rest may be inferred. Since the granule cells receive synaptic input mostly from mitral cell basal dendrites (see fig. 1), the EEG can be considered to be an observable for the local variation in average mitral cell voltage. Average granule cell voltage can be said to "follow" the mean mitral cell voltage with some synaptic delay time required for chemical transmission. Freeman was therefore able to measure the sigmoid nonlinearity of voltage to pulse conversion in the mitral population by the construction of histograms of single mitral cell pulse output at various levels of EEG amplitude and for different time lags [9, 10]. From this, the probability of pulse output conditional on mean cell voltage amplitude was derived by normalization. As Grossberg has pointed out, a sigmoid function can easily arise in a population as the integral of a gaussian distribution of the individual neuron thresholds [16a–d].

The slope and height of this sigmoid function was found to vary with the state of arousal of an animal. It was low and flat for anesthetized animals, but high and steep for awake thirsty animals. Freeman derived a model of this unusual function which I will use [10]. It has a parameter  $Q_m$  which increases the slope and height of the

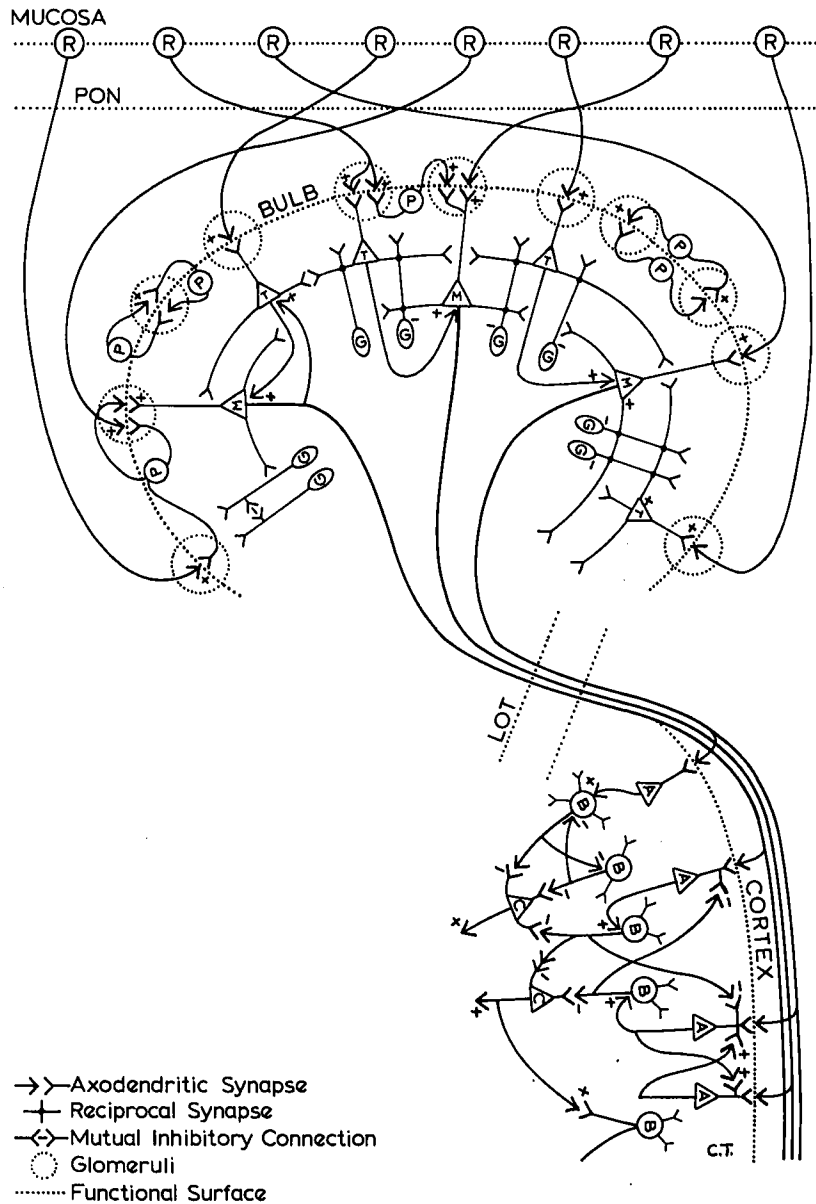


Fig. 1. Anatomical architecture of major features of olfactory system indicating cell types, their connections and their synaptic action. (+) = excitatory; (-) = inhibitory; R = receptor cell; G = granule cell; T = tufted cell which is roughly equivalent to M = mitral cell; P = periglomerular cell. The nasal mucosa is the receptor surface in the nose. Dotted circles indicate glomeruli which delineate cortical "columns" where parallel receptor input is bunched onto apical dendrites of a set of mitral cells below. Output is in parallel from mitral cells to the prepyriform cortex which has a similar architecture and oscillates in phase with the olfactory bulb. Mitral cell outputs also loop back ("recurrent collaterals") and are thought to cross couple with many other mitral cells by axosomatic (to the cell body) synapses which modify during learning (from ref. 9).

sigmoid and is related to the maximum pulse density measured in the neural mass. It may reflect the operation of an as yet unknown mechanism of arousal controlled by central brain pathways.

He has also studied evoked potentials to characterize the spatial properties of the bulb, measuring the spatial divergence of connection density from one cell population type to another as the standard deviation of a Gaussian [9]. He found short range lateral inhibition and long range excitation—quite different properties from the usual neural field, but just the property which we will see is required for associative memory.

#### 2.4. Pattern formation in the olfactory bulb

Purely physiological observation of the EEG reveals a remarkable dynamical transition (bifurcation) at the peak of a 3–8 Hz “respiratory slow wave” which arises from the surge of receptor input that accompanies inspiration. In awake and motivated animals, a high amplitude coherent

oscillation or “burst” with a dominant spectral peak in the range of 40–80 Hz emerges from the low level spatially phase locked but temporally irregular background activity that rides on the respiration wave (see fig. 2). As the respiratory wave falls during expiration, the oscillation subsides. During the burst, the EEG over the whole surface of the bulb oscillates at a common frequency, but, like a standing wave, it exhibits a specific spatial pattern of variation in relative amplitude that remains constant in time (see fig. 3).

This is rather startling since it constitutes the creation of order from disorder or structure from homogeneity which I refer to as “pattern formation”. One might expect to see only slightly fluctuating uniformity in the recorded EEG since it is a macroscopic voltage averaged over a large number of seemingly stochastic microscopic neural events in a “soup” of densely interconnected and intermixed neurons. There are many fascinating parallels here to the appearance of ordered macroscopic patterns of concentration in chemical reactions, convection in hydrodynamics, or populations in ecology [18].

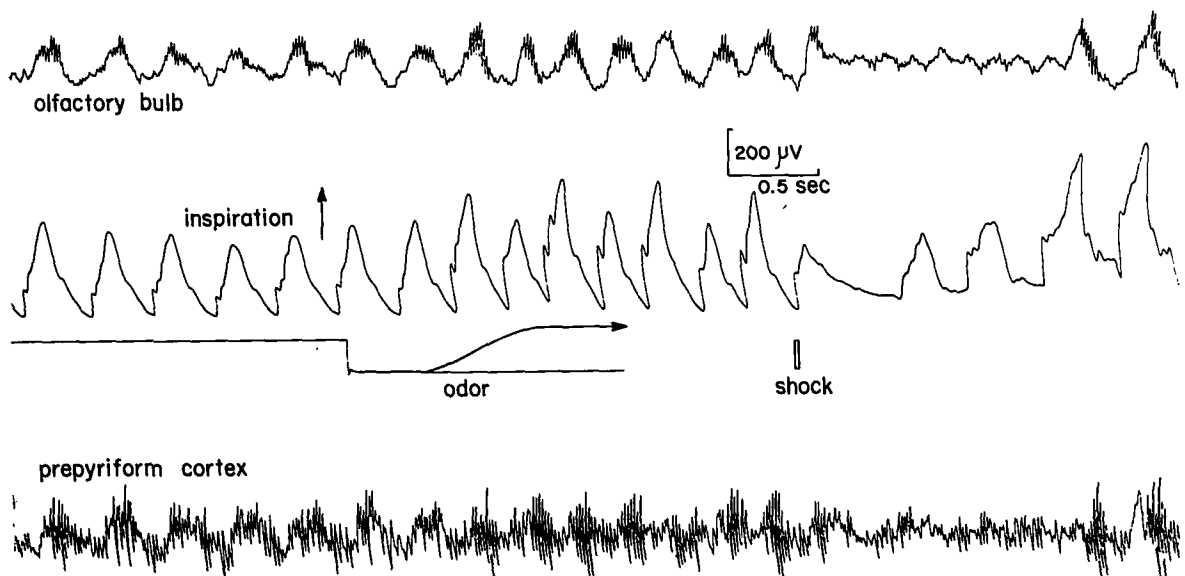


Fig. 2. Upper trace—unfiltered EEG for a single channel in olfactory bulb shows respiratory slow wave (4 Hz) with “burst” (50 Hz) at the peak. Middle traces—pneumograph output showing actual lung movement and trace below showing timing of conditioned stimulus odor release and shock for aversive conditioning. Lower trace—unfiltered EEG of prepyriform cortex, (from ref. 13).

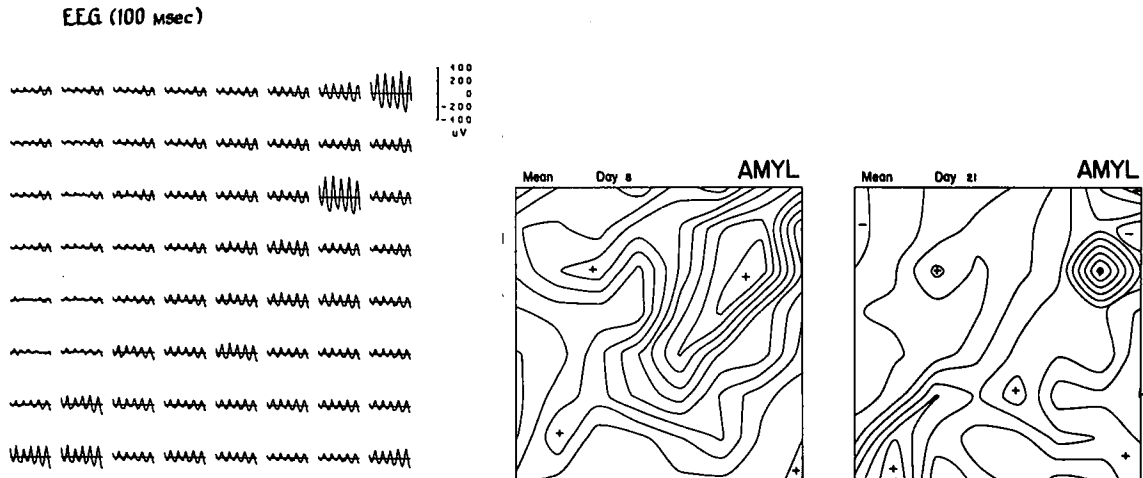


Fig. 3. Left – EEG traces of all 64 channels of  $8 \times 8$  electrode array (size =  $4 \times 4$  mm) on the surface of the olfactory bulb for one burst. The same temporal waveform is found on every channel but with variations in amplitude and phase ( $60^\circ$  max) across the array. Right – Contour plots of root mean squared spatial amplitude patterns for amyl acetate (CS+) in conditioning session 1 (left) becoming more differentiated and stable by session 3 (right) (from ref. 12).

### 2.5. Pattern recognition in the olfactory bulb

Pioneering studies of Freeman's laboratory [9–15], linking behavior and olfactory neurophysiology, show statistically robust correlations of changes in the spatial structure of the rms amplitude of EEG burst activity with behavior during classical conditioning of rabbits to olfactory stimuli. Digital image processing techniques [13, 14] are employed. EEG variation not corresponding to granule cell activity is reduced by temporal and spatial filtering. Spatial deconvolution is used to remove distortion from volume conduction in the tissue and improve spatial resolution. Factor and discriminant analysis and tree structured classification methods are then applied to the resulting data [15].

There is a distinctive spatial pattern of oscillation (the “control” pattern) exhibited by a thirsty animal waiting for an odor which is conditioned stimulus (CS+) that heralds the arrival of water (see fig. 3). When this odor actually appears, the control pattern is temporarily replaced by another pattern specific to the “recognition” of that odor (the “CS+” pattern). This occurs most often on those trials when the animal indicates this recogni-

tion in its behavior by giving the conditioned licking response in advance of water delivery. There is also a shift from the control pattern to the “CS–” pattern when a randomly presented odor (CS–) is released. The animal may indicate recognition of this odor by sniffing but gives no licking response.

When a new odor is paired as CS+, a new pattern emerges during its presentation and stabilizes in the first conditioning session (see fig. 3). Before any conditioning is done there is no change of pattern when different odors are released. There appears to be some reorganization of all patterns when any aspect of the conditioning situation is changed and the relative magnitudes of these changes are currently under investigation. What we define as a “pattern” here is in fact a cluster of patterns that is statistically distinguishable from other clusters. Evoked potential studies in connection with conditioning experiments [9] indicate that the coupling strengths of excitatory axosomatic synapses of mitral cells to other mitral cells (see fig. 1) are altered during learning. Thus behavioral and physiological evidence suggests that the bulb is a pattern forming system that can

“learn” to form different patterns in response to different inputs.

## 2.6. Macroscopic information processing in the bulb

The EEG itself is only an epiphenomenon or “indicator” of underlying neural activity. It can be argued, however, that the macroscopic patterns it reveals in the densities of that underlying activity are in fact the information bearing degrees of freedom in the system and the full details of microscopic events are of lesser significance.

Neural spikes of CNS neurons are generally Poisson distributed in time like radioactive decay events—even in response to deterministic input [22]. A certain seemingly irreducible stochasticity appears to be introduced in the triggering of synaptic transmission and activation of postsynaptic channels [19]. This implies that there is reduced information in a single pulse interval or a particular microstate of the system—defined as the instantaneous voltage and firing state of every neuron. Experimentally observed firing rates for individual mitral cells in the bulb are about one pulse for every fifth cycle of a 50 Hz EEG burst [10]. In this case there is no way for the mean pulse rate of a single cell to smoothly track its input as is suggested in many models of neurons [24, 28]. It would seem that reliable computation on the time scale of a perceptual event in this system (the animal can respond to a single sniff) must be done by ensembles of cells or space averages at a more macroscopic level [19].

Less than 1% of the activity of any single neuron in the bulb is observed to contribute to the EEG [9]. Mitral cells are known to give pulse output to other mitral cells and the rest of the brain, but granule cells are thought by many to transmit only graded analog synaptic voltages locally without pulses. At the population level, both analog cell voltage and digital spike activities are indistinguishable “densities”. The EEG is like an intensive thermodynamic state variable reflecting the voltage “pressure” produced by the mass ac-

tion of microscopic neural wave and pulse events which constitute what Harth has called a “neuron gas” [19].

Freeman [9] hypothesizes that inhomogeneous macroscopic spatial and temporal patterns of this microscopic activity are true macrostates resulting from a nonequilibrium order/disorder transition like that observed in the formation of Bénard cells of convection in fluid dynamics [5] or scroll waves of concentration in the Zhabotinski reaction [37]. These events of the neural mass transpire over distance and time scales of millimeters and seconds, which are several orders of magnitude larger than the scales of individual neural events. If microscopic processing were completely reliable, it could well occur without forming any structure at all on the macroscopic level. The system seems designed to form these macroscopic patterns since the range of inbuilt lateral inhibition is a determinant of the observed maximum spatial frequency of one half cycle per millimeter [14]. The state space of information processing in the bulb may thus conceivably be of the dimensionality of this “thermodynamic” configuration space which we can observe through the EEG as opposed to the dimensionality of its microscopic phase space. This is one argument behind our hypothesis that we are observing activity which is relevant to biological computation and that the infeasible parallel microelectrode investigation of all single cell microstates is not required.

The main argument of course is that the EEG patterns we observe are sufficient for us to predict the animal’s response during an experiment with statistically significant reliability and must therefore contain relevant information however crude it might be [13, 15]. While the complete picture of the microscopic generation of neural macrostates may await the application of new experimental techniques and a rigorous irreversible statistical mechanics of neural activity, it is clear that the more thermodynamic pattern formation perspective which deals with this pattern space of averaged variables is an important part of the description of bulbar processing.

### 3. Theoretical background

#### 3.1. Pattern formation versus learning

By “pattern formation” I have referred somewhat loosely to this emergence of macroscopic order on top of microscopic disorder. More specifically I am speaking of a particular mathematical approach developed since Turing [34] which is often applied to “excitable media” with internal sources of energy such as reaction–diffusion systems, nerve membrane, heart muscle, or neural tissue. One might say “self-excitable” medium to get the idea. These systems are “triggered”, not “forced” by external energy sources as the hydrodynamical systems are, and therefore can act as amplifiers, as we hypothesize for the bulb. The work of Meinhardt [29] or Murray [30] on reaction–diffusion patterns of activator–inhibitor chemical concentrations exemplifies the approach as does the work of Wilson and Cowan [35, 36], Ermentrout and Cowan [4–7], or Amari [1] on “neural field theory”. By itself, however, this mathematical perspective is unable to account for the swift modification of EEG burst patterns in the bulb during pattern recognition and with learning. The standard pattern formation approach is designed to explain the spontaneous selection of a single dominant pattern instability by a fixed intrinsic diffusion constant or neural connectivity function and given extrinsic boundary conditions.

#### 3.2. Associative memory

There is of course a considerable body of theory detailing the principles and capabilities of systems that learn and do pattern recognition. Of particular interest for the olfactory bulb is the work of Kohonen [28], Anderson [2], Palm [31], Amari [1], and more recently Hopfield [23–25] and Sejnowski [20] which I will lump together under the heading of “associative memory”. An associative or “content addressable” memory is usually a network of coupled elements which receive input in parallel as

in the bulb and whose parallel output is then a pattern which is the mode of the network previously “associated” with that input (see fig. 4). The key to the memory capability of the elements lies in the coupling matrix which specifies a distinct modifiable connectivity or “synaptic weight” from each element to every other. Many different output patterns may be stored simultaneously in the same network and evoked separately by the “associated” inputs when the coupling matrix is built up by a suitable synapse modification rule. The principle is roughly that an “input” vector (pattern) which is similar to an eigenvector (stored pattern) of the coupling matrix will most prominently “evoke” a multiple of that eigenvector (stored pattern) as a result of the matrix multiplication. Again, this approach by itself is insufficient to describe the olfactory bulb since there is no place for oscillation in these models, no bifurcation, and no explanation of the emergence of macroscopic order from microscopic disorder. The modifiable cross coupling used here, however, is conceivably found in the olfactory bulb and is the natural feature to incorporate in a pattern formation model to get it to simulate the pattern recognition performance of the bulb.

Freeman [12] hypothesizes that learning and memory formation occur when feedback to the bulb from reward/punishment centers during a motivationally important sensory event initiates a process of chemical modification. This effects a

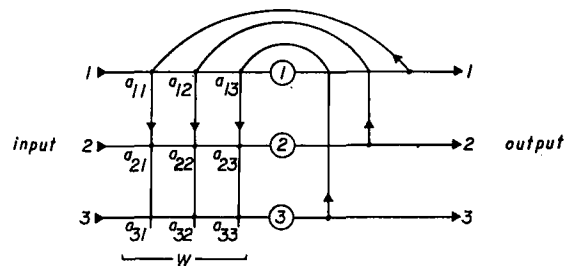


Fig. 4. Parallel “vector” input and output of an associative network with coupling matrix  $W$ . Circled numbers represent neural subpopulations. Each connects to every other with modifiable density or “effectiveness”  $a_{ij}$ . Such connectivity may be achieved in the olfactory bulb by axon collaterals of excitatory mitral cells (see fig. 1).



"print" command by the Hebb synapse rule whereby synaptic connectivity between simultaneously active neurons is increased. His simulations [12] showed that this new pattern of spatial connectivity can cause a new spatial pattern of EEG activity.

### 3.3. Unified approach

It seems appropriate then to seek a fusion of the mathematical approach to pattern formation in continuum neural field theories with the mathematics of associative memory used to model learning and pattern recognition in discrete neural networks. Common ground between approaches is to be found in the general language of dynamical systems theory as is the case for much of the work that inspired this conference. The critical departure from standard pattern formation theory and the bridge to associative memory is provided here by the use of discrete excitable neural medium with a full coupling matrix that specifies a unique and modifiable coupling from each compartment of the medium to each other compartment as in associative memory networks.

This violates the usual pattern formation assumption that the medium is homogeneous. Homogeneity implies that exactly the same spatial coupling function (usually local and symmetric) is found at all points of the medium. The spatial convolutions of neural field theory are ruled out and the beautiful continuum approach of Ermentrout and Cowan [4–7] is lost. However, as we shall see, learning is now possible since sets of input selected instabilities of arbitrary spatial structure may be determined by the coupling matrix in the manner of an associative memory. We seek adaptive as opposed to "spontaneous" symmetry breaking.

### 3.4. Mathematics of associative memory

In the olfactory bulb, the cross coupling axon collaterals of the populations of output mitral cells (see fig. 1) are hypothesized by Freeman to

form a matrix  $W$  of synaptic connectivity (see fig. 4). An input vector produces a pattern in the feedback matrix which is the correlation of that input with itself. The process is called autoassociation and this network model is called a correlation matrix memory [28, 31]. Learning and memory storage occur when a Hebb synapse modification increases the synaptic coupling  $a_{ij}$  between elements  $i$  and  $j$  according to the product of their activities. A synapse can compute this locally by increasing in strength if the cell it contacts fires when the synapse is active. A global or "collective" effect, however, is obtained from these local computations. Since  $a_{ij} = a_{ji}$ ,  $W$  is a symmetric matrix with orthogonal eigenvectors. If successive orthogonal input vectors  $x_i$  are stored by this Hebb synapse rule, then the matrix  $W$  is built up as

$$W = \sum_{i=1}^N \mu_i x_i x_i^T,$$

and for input  $x_j$ , output

$$Wx_j = \mu_j x_j,$$

where the  $\mu_i$  are the eigenvalues of the stored eigenvectors or modes of the network. The eigenvalues represent the frequency of learning or strength of memory storage of that input event and give the magnitude of its output on recall.

The distinction between learning and pattern recognition which is made through the paper is evident here. "Learning" involves this modification of the coupling matrix ( $W$ ) which results in the storage of an input pattern. Once the system is thus "programmed" with a set of patterns (the typewritten alphabet for example) it is ready to do "recognition" of any given input (such as the letter A with one leg cut short by a fading typewriter ribbon) by determining which stored pattern it most resembles. This can also be thought of as memory recall or an act of perception.

Input (like this letter A) which is not exactly an eigenvector (stored pattern) elicits output in these linear memories which is a linear combination of

the presently stored eigenvectors. This can be shown to be the least squares best fit or unbiased estimator of that input [28]. The largest eigenvector can be selected by a threshold operation if stereotyped or "categorical" recognition is desired [2]. The storage capacity of this associative memory is defined by Kohonen [28] as the number of patterns that can be stored without crosstalk on recall. At best it is the number of eigenvectors, which equals the number of elements. Achieving this is dependent on the orthogonality or statistical separability of the patterns to be stored.

### 3.5. Associative memories as dynamical systems

A useful generalization of the notion of associative memory was given by Hopfield. He stated that a dynamical system which has multiple stable fixed point equilibria can be viewed as a content addressable memory [25]. The fixed point attractors in the state space are the stored memories. All initial conditions or "inputs" are classified by the basins of attraction to give the "associated" attractor as an output pattern. From this vantage practically any physical system that can be described by a set of differential equations can be examined to determine its associative memory and pattern recognition capabilities.

In particular, a pattern formation model of the olfactory bulb with modifiable coupling may be so examined. The memory capacity is clearly related to the number of attractors in the system. The size and shape of the basins or "classes" and the actual pattern "similarity" of the inputs within are the critical issues for pattern recognition. All of this information about recognition behavior is contained in the phase portrait or vector field of the system. To be capable of learning, however, the system must also be programmable. There must be some process of parameter change (like synapse modification) whereby the vector field can be altered to arrive at categories that are of service to a larger system.

The initial conditions within a basin can be considered to be deformed or incomplete or noisy

versions of the attractor and we say that the dissipative dynamics "reconstructs" the proper output and is "noise tolerant" or "error correcting". This principle is everywhere in use since the digital elements (bits) of any computer are in fact two-attractor dynamical systems with this property. In much of dynamical systems theory, attention is focused on the detailed structure of attractors. Here emphasis is on the location of separatrices between basins that indicate the classification being accomplished by the system dynamics\*.

### 3.6. Dynamical interpretation of experimental observations

From the experimental standpoint, observations can be mapped directly into this conceptually simple framework without resort to the usual perceptual or computer metaphors requiring figure and background or addresses or template matches. We hypothesize, for example, that the statistically distinct and stable EEG patterns we observe indicate attractors in the state space of bulbar dynamics established by learning. The set of initial conditions produced by background odors of the experiment box on various sniffs fall within the basin of the attractor we see as the control pattern. The electrochemical output activity from this tissue dynamic now "represents" this class of environmental states to the rest of the brain. It doesn't really matter what the attractor is like or how much it is altered by later learning, provided it can be distinguished by succeeding associative memories from different attractors evoked by other environmental states.

We might imagine the entire cortex to be a set of associative memories interconnected in parallel

\*Separatrices correspond to the hypersurfaces set by a statistical clustering algorithm during its "learning" phase. Indeed such an algorithm itself may be viewed as a dynamical system when it is in operation as a recognizer. It "evolves" physically on some machine from an initial state that includes input data to a final "attracting" state which announces the category it has found for that input.

by the well known cortical–cortical fibres. Some receive input in parallel from sensory surfaces, others from inner motivational states, and others give output in parallel to motor systems. When the CS + odor appears, the new input pattern shifts the system state so that it goes through the bifurcation to oscillation and into the basin of a different attractor which we observe as the CS + activity pattern. This new output now falls within the basin of different attractors in other brain structures. Subsequent internal dynamical events lead ultimately to an activity pattern impinging on motor cortex that lies within the basin of the particular attractor in motor cortex which generates the appropriate licking response. For the CS – we see a sniff, which is the manifestation of a different motor cortex attractor. The learning “experience” is envisioned to involve alteration of attractor interrelations throughout the brain with the final result of “associating” external stimuli and inner states with effective responses. This “gestalt” is the invariant that the animal learns.

In the sensory cortex which we observe, the control, CS +, and CS – attractors serve to classify and discriminate motivationally relevant environmental states. Our experiments are designed to limit the specific attractors evoked to control, CS +, and CS –. Other attractors have been observed during continuous 4 min recordings, however, which indicates that many modes may be stored in the bulb. The variance that we observe in the patterns here classed as a single attractor may well result from fluctuations in the many internal parameters of the system which we do not control or because several similar attractors here may be classed together by succeeding brain structures.

The fact that all the previously observed attractors in the bulb appear to change with later learning is not surprising from a dynamical systems perspective. The entire vector field of such a highly coupled nonlinear dynamical system will generally be perturbed by any parameter change – much less the global alteration of an extensive set of parameters like the coupling matrix. How a working biological memory, which involves a dynamical

system as complicated as the olfactory bulb, surmounts or makes use of this is a fascinating issue. If further data analysis and experiment cannot demonstrate the existence of patterns in the bulb which are largely invariant during other unrelated conditioning, then this is evidence against the simple idea that the bulb is a completely autonomous associative memory. It may then be a scratchpad memory or coarse associative pre-processor or a subsystem partially slaved to higher levels. Given the famous plasticity of the nervous system and the primacy of the sensory-motor-motivation gestalt, it is not impossible that vector fields of neural subsystems throughout the brain are modified in concert during learning to retain the stimulus-response relationship which is the invariant that the animal clearly exhibits in our experiments.

It may be unrealistic to extrapolate from engineering designs and expect to see absolutely unchanging neural activity in a single subsystem denoting the permanent storage of an invariant category of sensory input. In general, artificial associative memories are given a fixed environment to be learned and the problems of long term plasticity or open ended relearning in a changing environment are not addressed. From the outset Stephen Grossberg [16a–d] has taken this issue of the long term stability of neural codes to be a central concern of his work. He proposes a specific solution to the problem for the olfactory bulb and pyriform cortex as a unit, which is possibly compatible with our theory and observations of the bulb, but beyond the scope our present data to confirm.

### 3.7. *Mathematics of dynamical associative memory*

The transition from the previous linear analysis of associative memory to the nonlinear dynamical perspective is illustrated by a model from Anderson [2]. Here an input vector excites associated combinations of eigenvectors in the feedback matrix of the neural circuit, as before, but now dynamics are considered so that  $x_i(t+1) = x_i(t)$

$+Wx_i(t) = (1 + \mu_i)x_i(t)$ . This system exhibits positive feedback and is inherently unstable for those evoked eigenvectors with positive eigenvalues. These grow at different rates until components of the total state vector begin to saturate at positive or negative limits. When the saturation function is a discrete step, the state vector is forced to an attractor in the corner of a hypercube in the direction of the eigenvector which wins the growth competition with the largest cumulative coefficient.

The saturation nonlinearity has therefore a selective effect like the thresholding operation which could be applied in the previous linear model. This is essentially nonlinear mode selection of instabilities as found in pattern formation, but here with emphasis on many simultaneous instabilities and their selection by "input" or initial condition. A particular input will excite instabilities (eigenvectors) of greatest similarity to it in the feedback matrix. These are given a lead in the growth race that overrides the intrinsic growth rates (eigenvalues) which would spontaneously select a single dominant pattern in the usual pattern formation situation. Thus nonlinear mode competition allows separate attractors with separate basins or classes of inputs attracted to each. Within each basin the inputs are similar enough to "select" that particular attractor which thus "represents" them. By nonlinear mode selection, then, the system goes to saturation at the attractor whose basin contained the input. This situation of competition among instabilities leading to multiple basins of attraction in the state space is the key to how a pattern forming system can pattern recognize. It is the central notion of this paper and we must show that it is possible in the olfactory bulb for physiologically reasonable ranges of synaptic coupling. We will investigate the mechanism in mathematical detail later for the case of oscillatory instabilities\*.

\*It is clear that massively parallel hardware of this sort will be required to implement large expert systems that can respond in real time. Hinton [6] has demonstrated that semantic networks may be embedded in the pattern vectors of an

Hopfield [25], exploiting the physical imagery and mathematics of Ising spin glass models, has shown that a symmetric coupling matrix with zero diagonal provides a Liapunov function or "energy landscape" for the system dynamics. This implies that the vector field of the system is a "gradient vector field" – the gradient of some similar potential function which establishes its fixed point attractors. We have seen above that use of the Hebb synapse rule (in a network without self-connections) naturally forms such a matrix. From the engineering standpoint we have here a method of "soft programming" the system to establish its attractors by design.

Physically, the total energy in the activity of the self-exciting system is increasing as it goes unstable and "votes itself energy" from internal sources. The negative of this gives a monotone "objective function" which system dynamics can be said to "minimize". An optimization "landscape" is provided by the bounds on energy expansion set by the saturation process. The gradient flow is non-mixing, as required for associative memory, so that nearby points in the state space (similar input patterns) stay nearby and evolve to or are "reconstructed" to the same stereotyped attractor pattern.

### 3.8. Dynamical computation and the sigmoid function

A bridge to computation theory is provided by this expression of perception or pattern recognition as an optimization problem [20]. When the saturation function is sigmoidal, as it is in the olfactory bulb, Hopfield [24] shows that the process of simulated annealing in the Boltzmann architecture [20] can be emulated by the variation of a parameter like  $Q_m$  which increases the sigmoid slope (or "nonlinear gain" in Freeman's language [10]). The sigmoid slope has the effect of "temper-

associative memory, and Anderson (this conference) has since constructed an expert system using the model above and shown remarkable similarities to human performance in ease and relative reaction time of recall.

ature" in the Metropolis algorithm which alters the smoothness of the optimization landscape.

The annealing algorithm is well known to effectively optimize  $N_p$  complete problems in polynomial time [26]. The analog networks of Hopfield and Tank [23] can relax to such solutions (at a fixed sigmoid slope) in several time constants – microseconds in VLSI designs, or milliseconds if made of elements with the decay times of neurons. This relaxation could easily occur in the beginning of the 200 millisecond olfactory burst. The key to the computational power of either the Boltzmann or Hopfield architectures seems to be the ability to vary temperature or sigmoid slope and control the scale of features in the dynamic landscape along a range from the coarsest and most global to the most detailed. Variation of this simple hardware parameter accomplishes computational feats one expects to require "intelligent" appraisal as Kirkpatrick noted [26].

Here then is a major computational principle hypothesized for biological processing. It is intimately connected with a network architecture like that found in the olfactory bulb and a sigmoid like that which Freeman has measured and found to vary in slope with arousal. Investigation of the possibility of this type of processing in the olfactory bulb is therefore an important objective of our work\*.

### 3.9. Complications of olfactory bulb dynamics

In order to handle the observed dynamics of the bulb, the notion of associative memory must be generalized beyond the Hopfield definition. It must allow arbitrary attractors such as the obvious limit cycle oscillations and perhaps even chaotic attractors of low dimension. Oscillation is ubiquitous in biological systems [38]. There may well be principles of natural design inherent in periodic dynamics as yet undiscovered by human designers

\* Grossberg [16a–d] gives an elegant and detailed analysis of the principles behind the power of the sigmoid function in pattern recognition and an alternative perspective on the role of arousal.

who understandably avoid the mathematical uncertainties currently involved.

Because our system oscillates, it cannot have a gradient vector field. This eliminates the spin glass view of the coupling matrix as directly providing a Liapunov function to determine stable fixed points. Our attractors are limit cycles. Although the system can still be thought of as expanding into a saturation landscape that selects modes, its coupling matrix is necessarily nonsymmetric and the relation between stored periodic attractors and the matrix elements that modify with learning is complicated. A promising approach to the determination of this relationship is being pursued by Alan Lapedes and coworkers at Los Alamos. He uses the computational power of a Hopfield network with symmetric coupling as a master system to establish coupling coefficients in a nonsymmetric "slave" net which oscillates like the olfactory bulb. Preliminary simulations indicate that there indeed exist couplings by which multiple oscillatory modes may be stored simultaneously and separately retrieved (Alan Lapedes – personal communication). This might be taken as a "proof" that an oscillating system may be programmed to function as an associative memory in the manner we are suggesting. It fundamentally validates the theoretical approach of this paper.

### 3.10. Signal detection by bifurcation

In the analysis of the preceding models, there is normally no parallel at all to the respiration driven bifurcation to instability found in the olfactory bulb. Hopfield's analog model [24], however, could be gated in and out of stability by an average input bias that shifts the sigmoid just as in the bulb. The need for such a memory reset mechanism is apparent in an animal which needs to continually resample its environment and repeat its perceptual computation of environmental states. Since the detectable concentration of odor can be very small, it is highly unlikely that the spatial structure (information content) of input is by itself a powerful enough perturbation of the

bulbar state to effect transitions between basins. Therefore the system must inverse bifurcate during expiration to allow escape from the last basin of attraction.

Respiration naturally supplies the rhythmic sampling operation for olfaction. The huge surge of average input level during inspiration occurs in the absence of any specific odorant and is due possibly to respiratory stimulation of some other kind of receptor (say an inspiration sensitive mechanoreceptor) in order to effect the bifurcation. Spatial variations constitute in fact a small fraction of the total input variation revealed by the respiratory slow wave. The slow wave itself dwarfs even the full burst amplitude (see fig. 2). In the forward direction during inspiration, the bifurcation may allow transition from a weakly attracting background state which is easily perturbed by the informational structure of input to a strongly attracting limit cycle that "detects" or categorizes it. The power of an excitable medium to amplify is evident in this mechanism. It may help explain the famous sensitivity of the olfactory system to infinitesimal concentrations of odor.

### 3.11. Multiple Hopf bifurcations

To visualize a multiple bifurcation, a simple mechanical analogy may be of assistance. Consider a thin symmetric column subject to a compression load that represents our spatially uniform respiratory input bias level. At some pressure corresponding to a bifurcation point, the column will buckle to the side. It can do so in any direction in  $360^\circ$  around the original vertical axis. Some slight asymmetry in the load, representing the spatial pattern of input above, will determine this direction. Thus the column bifurcation can be viewed as an input asymmetry detector that amplifies small deviations into large macroscopic ones as we have discussed. Learning might be represented as a serrated collar around the column which quantizes the possible buckling directions and acts as the saturation landscape that guides the buckling to some final position or "attractor". All input

asymmetries in a range of directions are now classified to the same final state.

The symmetry of an originally circular collar is broken arbitrarily by successive dents of learning experiences that form the serrations. The collar is only a visual aid for what could be broken symmetries in the equations for the structure of the column itself. In either the structure of the column or the coupling matrix of our network, learning gives the predetermined modes in which the symmetry of the system can be broken by input perturbations. It may be that most neural network models may usefully be viewed as operating at a bias level beyond an implicit bifurcation point where multiple basins of attraction are already established.

It is specifically the spatial pattern of amplitude and not the phase of EEG oscillation that Freeman has found to be correlated with pattern recognition in the bulb [14]. It may be that amplitude is the only degree of freedom that an oscillating system can use for pattern recognition. Necessarily or fortuitously, the theory of multiple Hopf bifurcations may be employed to find equations for the amplitudes of oscillatory modes independent of their phase. This allows us to recover a view of the stored limit cycle attractors as fixed points of these new equations in a new vector field. This is the vector field in our system that must be examined for its pattern recognition character.

A gradient vector field with multiple stable fixed points is only one possibility here. It is necessary to determine the range of parameters required in the original system to realize irrotational flow and achieve the associative memory function. We can then assess the physiological plausibility of the model in quantitative detail. Most of the experimentally observed behaviors of our system can be very concretely visualized in this mathematical picture for various values of parameters. It is possible as well to investigate the impact on the function of pattern recognition of parameter perturbations leading to more exotic dynamical flows like chaos which may underlie unique principles of

neural computation beyond those already discovered for networks with fixed point attractors [23]. Investigation of the annealing effect of sigmoid slope on the vector field of amplitudes in our system must be done by consideration of  $Q_m$  as an additional bifurcation parameter. Analytic results may be obtained for two simultaneous instabilities, while large scale systems of high codimension (number of simultaneous instabilities) will require symbolic and numerical computation.

An important way that our bifurcation analysis of instabilities differs from the preceding portrait of saturating instabilities in associative nets is that our analysis is "local". In other words the mode selecting nonlinearity giving rise to the saturation landscape is restricted to low order terms of the Taylor expansion about the bifurcation point. Nothing so strong as the complete saturation of components implied by the hypercube is required. The selection of modes necessary for associative memory is therefore consistent with the near sinusoidal oscillations we observe in the bulb.

### 3.12. *Freeman's model*

Freeman [6] has produced a detailed model of the olfactory bulb from lumped network analysis of the excitatory and inhibitory anatomical subpopulations. He considers their connection densities and the neural operations performed at synapses, in dendrites, and at axon trigger zones. Linearizing the sigmoidal pulse output function at an operating point allowed him to write linear transfer functions for the network which, in his analysis, imply second order differential equations and their solutions. Gains in the network at various operating points were evaluated by fitting experimental with theoretical root loci, and constants in the solutions were then determined by fitting theoretical curves to measured evoked potentials (impulse responses).

In this linear analysis, the surge of input with respiration biases network elements upward on their sigmoid curves to regions of steeper slope. In the complex plane this appears as an ad hoc gain

increase which moves a pair of complex poles along their root locus through the imaginary axis into oscillation. This now unstable oscillation increases until regions of decreasing sigmoid gain are reached and the poles return to the imaginary axis for a stable limit cycle. Freeman also simulated the full spatially distributed nonlinear model and was able to replicate the behavior of the EEG in great detail [11]. This included being able to alter its spatial patterns by changing the coupling between mitral cells according to the Hebb synapse rule [12]. This is a pattern formation model with discrete associative connectivity, but its ability to learn different patterns and separately retrieve them has not yet been thoroughly investigated.

### 3.13. *Present approach*

The complexity of Freeman's model, owing to the fidelity with which it represents real anatomy and physiology, is such that analytical decomposition to reveal the principles of its operation is difficult. Because I seek basic principles, I choose to neglect the synaptic delay that contributes the second time constant in Freeman's equations and simplify to a first order equation for a single neural population. At the bifurcation point, the second order poles contribute "fast variables" that do not strongly affect local dynamics. As in the activator and inhibitor chemical approach to pattern formation [29], I use two competitive autocatalytic subpopulations as the elementary "kinetic" cell. This constitutes the space independent or homogeneous part of the distributed system to be constructed later. One of these units may be thought of as roughly equivalent to a cortical column. While the full fidelity of olfactory simulation is lost, a considerable gain in simplicity and universality is achieved. Any "exitable medium" can be built of these compartments. This could be thought of, for example, as a predator-prey system with the inhibitory cells as cannibalistic predators.

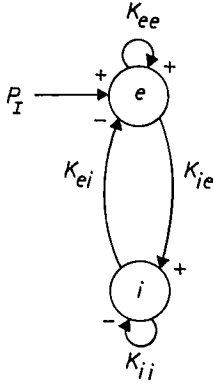


Fig. 5. Schematic diagram of coupling within a single compartment of the excitable medium. Circles *e* and *i* are excitatory and inhibitory neural subpopulations corresponding to mitral and granule cells in the bulb (see fig. 3). They are densely interconnected and intermixed in the "neuropil" or "neural mass." The similarity to a "soup" of chemical reagents suggests the use of this type of diagram which is used for chemical reaction kinetics.  $P_I$  is the external receptor input to mitral cells (see fig. 3) and the  $K_{ij}$  are coupling densities or "rate constants" with the sign of synaptic action indicated.

#### 4. Mathematical model

##### 4.1. Phase plane portrait of a single compartment

Following Wilson and Cowan [35], but retaining Freeman's notation and neglecting refractory periods (which are insignificant at the spike rates observed in the bulb), the basic equations for coupled subpopulations appear as follows (fig. 5):

$$\dot{p}_e = -ap_e + aG[k_{ee}p_e - k_{ei}p_i + p_I], \quad (1)$$

$$\dot{p}_i = -ap_i + aG[k_{ie}p_e - k_{ii}p_i], \quad (2)$$

where  $p_e$ ,  $p_i$  are pulse densities in the excitatory and inhibitory cell populations,  $a$  is the membrane time constant including synaptic delay,  $p_I$  is pulse input, and  $k_{ij}$  the density of synaptic coupling from population  $j$  to  $i$ .  $G(v)$  is the sigmoid mean cell voltage to pulse density conversion in a population.

Nullclines may be found since the sigmoid  $G$  has a unique inverse  $G^{-1}$ . For  $\dot{p}_e = \dot{p}_i = 0$  we get

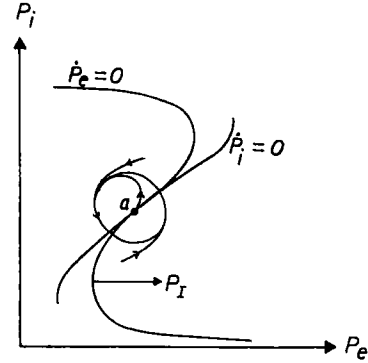


Fig. 6. Nullclines in the vector field for a single compartment of the excitable medium. The locus  $\dot{p}_e = 0$  has negative slope and is shifted by the input level  $P_I$ . The intersection point (a) where both derivatives are zero is a singular or equilibrium point of the vector field. Here we show it after the Hopf bifurcation when it is unstable and leads to the limit cycle flow indicated with arrows.

(fig. 6):

$$\dot{p}_e = 0: \quad k_{ei}p_i = k_{ee}p_e - G^{-1}(ap_e) + p_I,$$

$$\dot{p}_i = 0: \quad k_{ie}p_e = k_{ii}p_i + G^{-1}(ap_i).$$

The negative slope of the  $\dot{p}_e = 0$  nullcline is due to the  $-G^{-1}$  term in that equation, since the difference of the sigmoid and the constant curve  $k_{ei}p_i = k_{ee}p_e$  gives this shape. The input term  $p_I$  will shift the  $\dot{p}_e = 0$  curve, which provides all the classic ingredients for excitable, oscillatory, and bistable behavior as the intersection of nullclines is varied. This kind of phase portrait (see fig. 6) is the defining characteristic of an element of an "excitable medium". As we have already suggested, the bulb seems designed to "burst" or be "gated" in and out of the oscillatory state by the mechanism outlined above. Uninterrupted limit cycle activity is seen only in drug-induced states. The smooth rise and fall in burst amplitude with input (fig. 1) is indicative of the supercritical Hopf bifurcation we will analyse.

There is evidence from small concentric phase gradients found in the bulb that the burst nucleates and spreads from a randomly varying point in space on each inspiration much like a wave of heart contraction from the pacemaker region. In



our system it might be expected that the highest point of the spatial input pattern would be first to induce the Hopf bifurcation to oscillation and therefore phase lead the remainder of the surface\*. These leads are on the order of the axonal transmission delays from one point of the tissue to another ( $< 6^\circ/\text{mm}$ ). The spatial patterns of oscillation amplitude are insensitive to these shifting phase patterns. This to be expected if the pattern recognition function of the amplitude activity is to extract an invariant odor class from the spatially varying input generated by the random impact of odor molecules on the receptor surface during inspiration.

#### 4.2. Hopf bifurcation of a single compartment

Following the approach to pattern formation used for reaction-diffusion or neural field equations, these space independent equations can be linearized about a point  $\bar{p}_e$  and  $\bar{p}_i$  where the nullclines of the kinetics cross in a configuration just at the onset of the limit cycle instability (i.e. the point of Hopf bifurcation). In spatial terms this is equivalent to assuming a mean level of input  $p_1$  from which the pattern of spatial perturbation about  $p_1$  will excite a particular mode of instability as input does in Anderson or Hopfields' model. Substituting the expression for  $p_e$  from the nonlinear nullcline equations into that for  $p_i$  gives

$$\bar{p}_i = \frac{p_1}{k_{ei}} + \frac{k_{ee}k_{ii}}{k_{ei}k_{ie}}\bar{p}_i + \frac{k_{ee}}{k_{ei}k_{ie}}G^{-1}(\bar{p}_i) - \frac{G^{-1}\left[\frac{G^{-1}(\bar{p}_i)}{k_{ie}} + \frac{k_{ii}}{k_{ie}}\bar{p}_i\right]}{k_{ei}}$$

which can be solved numerically for  $\bar{p}_i$  as a function of input  $p_1$ , sigmoid parameter  $Q_m$ , and the coupling coefficients  $k_{ee}$ ,  $k_{ei}$ ,  $k_{ie}$ ,  $k_{ii}$ . From equilibrium point values  $\bar{p}_e(\bar{p}_i)$  and  $\bar{p}_i(p_1)$ , the value

of the Jacobian may be calculated. The equations for perturbation  $p'_e$  and  $p'_i$  about  $\bar{p}_e$  and  $\bar{p}_i$  are

$$\begin{bmatrix} p_e - \bar{p}_e \\ p_i - \bar{p}_i \end{bmatrix} = \begin{bmatrix} p'_e \\ p'_i \end{bmatrix} = \begin{bmatrix} -1 + k_{ee}f(v_e) & -k_{ei}f(v_e) \\ k_{ie}f(v_i) & -1 - k_{ii}f(v_i) \end{bmatrix} \begin{bmatrix} p'_e \\ p'_i \end{bmatrix},$$

where

$$v_e = k_{ee}\bar{p}_e - k_{ei}\bar{p}_i, \quad v_i = k_{ie}\bar{p}_e - k_{ii}\bar{p}_i$$

and

$$f(v) = \exp\left[v - \frac{e^v - 1}{Q_m}\right] = G'(v).$$

Since  $f(v)$  is always positive, the Jacobian is  $\begin{bmatrix} \pm a & -b \\ c & -d \end{bmatrix}$  giving characteristic equation

$$\mu^2 + [\text{Tr}]\mu + \text{Det} = 0$$

implying

$$\mu_{1,2} = -\frac{1}{2}\text{Tr} \pm \frac{1}{2}\sqrt{\text{Tr}^2 - 4\text{Det}}.$$

Now the Hopf bifurcation occurs when the trace  $\text{Tr} = 0 = \pm a - d$  which requires  $a > 0$  and physiologically means that autocatalytic positive feedback  $k_{ee}f(v_e) > 1$ . This yields purely imaginary eigenvalues  $\mu_{1,2} = \pm iw$ ,  $w = \sqrt{\text{Det}} = \sqrt{cb - ad}$  for positive determinant ( $cb > ad$ ). Thus we can find the bifurcation point  $(p_e^0, p_i^0)$  as a function of input  $p_1$  by iterating through values of  $p_1$ , for given choices of  $Q_m$ ,  $k_{ee}$ ,  $k_{ie}$ ,  $k_{ei}$ ,  $k_{ii}$  and graphing the resultant trace and determinant in the coefficient plane (see fig. 7) to find the point at which the above conditions are satisfied. More precisely we can insert the trace  $J = 0$  condition and add  $p_1$  as a variable in Newton's method to solve directly for the bifurcation point.

\*These gradients may be similar to the "target patterns" Winfree sees in the Belusov-Zhabotinsky system after initial nucleation of the reaction [37].

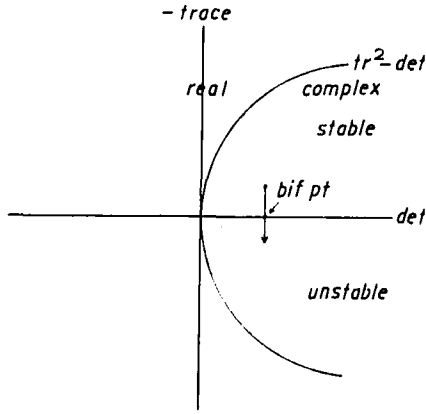


Fig. 7. Stability of the equilibrium point seen in fig. 6 can be determined in the coefficient plane above. This shows the trace and determinant of the Jacobian matrix of the equations for a single compartment of the medium linearized at the equilibrium point. Eigenvalues of this matrix are complex to the right of the curved line showing the locus  $\text{Tr}^2 - \text{Det}$  and real to the left. They are negative above the horizontal axis and positive below implying stability and instability respectively of the equilibrium point. The bifurcation point for a Hopf bifurcation is shown where the real part of a complex eigenvalue passes thru zero to positive and the system goes unstable.

#### 4.3. Compartmentalized spatial model

All of the above has dealt with a single element of our excitable medium. Now we must expand to include spatial terms and consider how associative recall might occur. I have chosen a spatially discrete “compartmental” approximation to the excitable surface in order to employ a connection matrix for long range coupling in the medium. Redundant regions of the bulb are lumped into a minimal space element over which the average density of neural activity is constant and between which the amplitude is seen to vary. Such elements are on the order of the size of the columns which lie below the glomeruli in the olfactory bulb (see fig. 1). There are about 2000 of these in the bulb and they may roughly be identified with the oscillating local “kinetic” elements we have just modeled which are to be coupled by the connection matrix. This is the crucial point of fusion of neural field theory and associative memory, as discussed earlier. The usual neural field assumption of homogeneous connectivity [4–7]

does not hold here, since each compartment has its own distinct set of coefficients coupling it to the others.

To consider this multi-oscillator system extended in space, we add coupling terms to  $N$  of the preceding pairs of kinetic equations, where all possible interconnections are allowed and the range of later ( $w_{ei}$  or  $w_{ie}$ ) negative feedback coupling of a given population element to its neighbors is given by the limits of the corresponding summation terms (fig. 8). The experimentally determined spatial divergences of connection for the olfactory bulb may be used, expressed as multiples of the step size of discretization of space.

$$\dot{p}_e^i = -ap_e^i + aG \left[ k_{ee} p_e^i - k_{ei} p_i^i \right] + \sum_{j=1}^N w_{ee}^{ij} p_e^j - \sum_{j=-\sigma}^{+\sigma} w_{ei}^{ij} p_i^j + p_i^i, \quad (3)$$

$$\dot{p}_i^i = -ap_i^i + aG \left[ k_{ie} p_e^i - k_{ii} p_i^i \right] + \sum_{j=-\sigma}^{+\sigma} w_{ie}^{ij} p_e^j - \sum_{j=1}^N w_{ii}^{ij} p_i^j. \quad (4)$$

Excitatory–excitatory and inhibitory–inhibitory coupling is assumed to be full range. This was also found by Ermentrout and Cowan [4], in a neural field analysis, to be necessary for the spatially

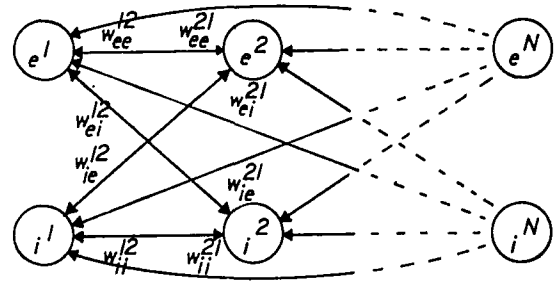


Fig. 8. Spatial coupling (only) between compartments of the medium. Coupling within the compartments which was shown in fig. 5 is here suppressed. All possible spatial couplings are considered with the densities expressed by the coefficients  $w_{ij}^{kl}$ . In particular full cross coupling is required for  $w_{ee}^{ij}$  excitatory–excitatory mitral cell collaterals which modify with learning and for disinhibition  $w_{ii}^{ij}$ .

inhomogeneous bulk oscillations we observe. Full cross coupling (or a fast traveling wave) is necessary in an associative memory, since missing parts of an incomplete input must be made active by the network, and that requires lateral coupling to those elements. The nondecrementing neural impulse seems ideally designed to mediate this fast nonlocal influence. This associative or “reconstructive” action of the bulb is strongly to be distinguished

from the divisive and contrast enhancing effect of lateral inhibition that is the focus of attention in most neural, mechanical, or reaction–diffusion pattern forming systems. The short range lateral inhibition found in the bulb and other neural systems can still normalize and orthogonalize input [16a], which can serve as preprocessing for an associative memory to optimize its storage capacity [28].

#### 4.4. Jacobian matrix of spatial model

In vector notation, the set of equations of  $N$  space independent units appears as  $\mathbf{P}' = \mathbf{M}\mathbf{P}'$ , where  $\mathbf{P}'$  is a vector of  $N$  pairs of  $p'_e$  and  $p'_i$ , perturbation variables, and  $\mathbf{M}$  is a matrix of  $N$  of the previous two dimensional “kinetic” matrices in a diagonal band that gives the constant local internal coupling of the excitatory and inhibitory populations. For a high dimensional system, the coupling densities in space, as Freeman measured them, would appear in the matrix as lateral sections of the band. Short range net excitation would be followed by longer range net lateral inhibition, followed by long range net excitation. Again, following the reasoning of a pattern formation approach, the explicitly “spatial” terms of eq. (3) and (4) that couple these  $N$  oscillators at their bifurcation points are added as a perturbation of this linearized system. This is done in a matrix  $\mathbf{W}$  containing only the off diagonal entries missing from  $\mathbf{M}$ . This gives  $\mathbf{P}' = \mathbf{M}\mathbf{P}' + \mathbf{W}\mathbf{P}'$ , which is a discrete form of a linearized activator–inhibitor type reaction–diffusion equation,

$$\mathbf{X}_t = \mathbf{M}\mathbf{X} + \mathbf{D}\nabla^2\mathbf{X} \text{ or neural field equation}$$

$$E_t(x) = \alpha E(x) + \int W(x - x') E(x) dx'.$$

Having thus used this decomposition to see the connection, we can collapse  $\mathbf{M}$  and  $\mathbf{W}$  because we have discrete space and obtain  $\dot{\mathbf{P}}' = \mathbf{A}\mathbf{P}'$  where  $\mathbf{A} = [\mathbf{M} + \mathbf{W}]$ , and  $\mathbf{A}$  comes from the Jacobian of the coupled eqs. (3) and (4). Explicitly in two dimensions,

$$\mathbf{A} = \begin{bmatrix} a & -b & & \\ c & -d & & \\ & & a & -b \\ & & c & -d \end{bmatrix} + \begin{bmatrix} & e & -f & \\ & g & -h & \\ e & -g & & \\ f & -h & & \end{bmatrix} = \begin{bmatrix} a & -b & e & -f \\ c & -d & g & -h \\ e & -g & a & -b \\ f & -h & c & -d \end{bmatrix},$$

$$\begin{bmatrix} p_e^1 \\ p_i^1 \\ p_e^2 \\ p_i^2 \end{bmatrix} = \begin{bmatrix} -1 + k_{ee}f(v_e^1) & -k_{ei}f(v_e^1) & w_{ee}^{12}f(v_e^1) & -w_{ei}^{12}f(v_e^1) \\ k_{ie}f(v_i^1) & -1 - k_{ii}f(v_i^1) & w_{ie}^{12}f(v_i^1) & -w_{ii}^{12}f(v_i^1) \\ w_{ee}^{21}f(v_e^2) & -w_{ei}^{21}f(v_e^2) & -1 + k_{ee}f(v_e^2) & -k_{ei}f(v_e^2) \\ w_{ie}^{21}f(v_i^2) & -w_{ii}^{21}f(v_i^2) & k_{ie}f(v_i^2) & -1 - k_{ii}f(v_i^2) \end{bmatrix} \begin{bmatrix} p_e^1 \\ p_i^1 \\ p_e^2 \\ p_i^2 \end{bmatrix},$$

where

$$v_e^1 = k_{ee}p_e^1 - k_{ei}p_i^1 + w_{ee}^{12}p_e^2 - w_{ei}^{12}p_i^2 \quad \text{and} \quad v_i^1 = k_{ie}p_e^1 - k_{ii}p_i^1 + w_{ie}^{12}p_e^2 - w_{ii}^{12}p_i^2,$$

and similarly for  $v_e^2$  and  $v_i^2$ . Here  $f(v)$  is as before, and  $p_e$  and  $p_i$  inside  $v$  are evaluated at the bifurcation point found before for a single oscillator,  $\bar{p}_e^1 = \bar{p}_e^2$ ,  $\bar{p}_i^1 = \bar{p}_i^2$ . This assumption that the effect of the coupling is small and does not disturb the original equilibrium point saves us in this preliminary argument from numerical solution of simultaneous nonlinear equations.

#### 4.5. Multiple Hopf bifurcation – Linear part

Now it is necessary to check the plausibility of obtaining the multiple Hopf bifurcation we need for pattern recognition in this coupled two oscillator system. Having added off diagonal terms, are there values of this coupling such that we can still get two purely imaginary eigenvalues when we rediagonalize? Simplifying matrix  $A$  by inserting the uncoupled bifurcation point condition  $a = d$  and assuming a physiologically possible symmetry in reciprocal coupling densities, we have that  $k_{ei} = k_{ie}$ , which implies that  $c = b$ , and since  $w_{ei}^{ij} = w_{ie}^{ij}$ , which (very roughly) allows  $f = g$ , we see that  $A$  is of the form

$$\begin{bmatrix} a & -b & e & -f \\ b & -a & f & -h \\ e & -f & a & -b \\ f & -h & b & -a \end{bmatrix},$$

where all coefficients are positive and the signs are given by the excitatory or inhibitory nature of the coupling\*. The question is whether there exists a range of values of  $(a, b, e, f, h)$  in the matrix  $A$  such that this coupled system contains two pairs of complex eigenvalues with zero or near zero real parts. This corresponds now to two possible modes or relative amplitudes of coupled oscillation going unstable simultaneously. It is similar to multiple

bifurcations in hydrodynamics where convective roll instabilities occur at several different orientations at the same time to form a hexagonal Bénard cell [27, 32].

The determinant of  $[A - I]$  was calculated and the resulting quartic equation solved using Macsyma (symbolic algebra program) to give eigenvalues

$$\mu_{1,2} = \pm [h^2 + (2e + 4a)h + 4a^2 + e^2 + 4ae$$

$$- 8bf - 4b^2 - 4f^2]^{1/2} \pm h \pm (-e),$$

$$\mu_{3,4} = \pm [h^2 + (2e - 4a)h + 4a^2 + e^2 - 4ae$$

$$+ 8bf - 4b^2 - 4f^2]^{1/2} \pm h \pm (-e),$$

which are purely imaginary for  $a > b$  as before and for  $h = e$  small relative to  $b, f$  large. Physiologically this corresponds to large reciprocal excitatory–inhibitory negative feedback. There is a still greater range of matrix values that can lead to simultaneous instabilities if we drop the constraints given by this pattern formation approach, where we have begun the analysis with uncoupled oscillators exactly at their bifurcation points. In that case, however, we must employ numerical methods to find the bifurcation point directly for the full coupled system.

We know that, for any set of matrix values in the range which gives purely imaginary eigenvalues, there exists an invertible matrix  $U$  such that

$$U^{-1}\dot{P} = [U^{-1}AU]U^{-1}P,$$

\* The alternating signs of the columns are due to the distinct excitatory and inhibitory neural populations. Each has output of only one sign as real neurons do. Such a matrix of real neurons is clearly nonsymmetric.

where

$$U^{-1}AU = \begin{bmatrix} 0 & -w^1 & & \\ w^1 & 0 & & \\ & & 0 & -w^2 \\ & & w^2 & 0 \end{bmatrix}.$$

This coordinate transformation  $U$  establishes the center manifold on which the real parts of the linear terms are zero and do not contribute to the dynamics of the system.

#### 4.6. Multiple Hopf bifurcation – Nonlinear terms

On this surface we must look to the nonlinear terms to assess dynamical tendencies. Expanding the sigmoid to third order about the equilibrium point, which is zero for the perturbation variables, gives

$$G(v) = v + \alpha v^2 + \beta v^3,$$

where

$$\alpha = \frac{1}{2} - \frac{1}{Q_m^2}$$

and

$$\beta = \frac{1}{6} - \frac{1}{2Q_m^2} + \frac{1}{6Q_m^3}.$$

This gives nonlinear terms  $N(v) = \alpha v^2 + \beta v^3$  in one dimension where  $v$  is a function of the perturbation variables  $p'_e$  and  $p'_i$ . A much more complicated expression is obtained from the multivariable Taylor expansion in four dimensions, which we will simply indicate as  $N(P)$ .

At this point we have a decomposition of the original coupled equations into linear and nonlinear terms in the perturbation variables  $P' = P - P^0$  at the bifurcation point  $P^0$ ,

$$\dot{P}' = AP' + N(P'),$$

where  $P'$  at time zero is the spatial pattern of in-

put to the system. Applying the transformation  $U$  gives us the form of the full nonlinear equations on the center manifold,  $U^{-1}\dot{P} = [U^{-1}AU]U^{-1}P + U^{-1}N(P)$ . The normal form theorem allows us to remove the nonresonant terms in the Taylor expansion  $U^{-1}N(P)$  without altering the topological form of the implied vector field.

#### 4.7. Amplitude equations

Guckenheimer and Holmes have analysed the unfolding of this codimension two bifurcation in great detail [17]. The normal form of coupled amplitude equations to which most all nonresonant systems with this degenerate linear part reduce is

$$\dot{r}_1 = \mu_1 r_1 + a_{11} r_1^3 + a_{12} r_1 r_2^2, \quad \dot{\theta}_1 = w_1 + \mathcal{O}(r_1), \quad (5)$$

$$\dot{r}_2 = \mu_2 r_2 + a_{22} r_2^3 + a_{21} r_2 r_1^2, \quad \dot{\theta}_2 = w_2 + \mathcal{O}(r_2), \quad (6)$$

plus terms of fifth order and up in the amplitudes, providing the nonresonant condition holds that  $m w_1$  differs from  $n w_2$  for  $|m| + |n| \leq 4$ . Here  $_1$  and  $_2$  are unfolding parameters representing the relative motion of the real parts of the complex eigenvalues of the Jacobian of the system through zero under the influence of the bifurcation parameter. They are dummy variables that allow us to perturb the vector field to either side of the bifurcation point and examine the families of possible vector fields which occur for various values of  $\mu_1/\mu_2$ . Now  $r_1$  and  $r_2$  are modes or linear combinations of the original space coordinates  $p^1$  produced by the diagonalizing coordinate transformation  $U^{-1}AU$ , and so correspond to the spatial patterns of amplitude that we record in the bulb. Since the amplitudes are decoupled from the azimuthal components, they may be considered separately.

Looking first at the linear part of the amplitude equations, we see that the eigenvalues  $\mu_i$  give the exponential growth rates of the amplitudes of the unstable modes of oscillation. In a purely linear analysis these are independent, and the spatial

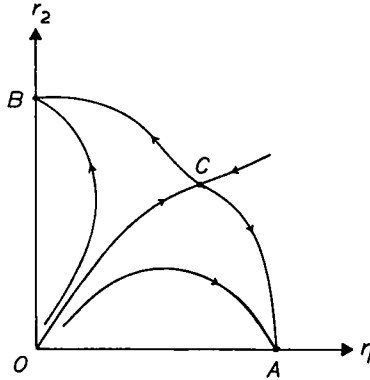


Fig. 9. Gradient vector field of amplitudes of oscillating modes  $r_1, r_2$  required for pattern recognition function. There are always up to four equilibria. Point 0 is unstable and point C is a saddle point. The orbit from 0 to point C is a separatrix separating the basins of attraction for fixed point attractors A and B. Since the amplitude of the other mode is zero at each attractor, only one frequency of oscillation with a distinct spatial structure of amplitude will be observed as in the olfactory bulb.

pattern eigenvector with the largest eigenvalue dominates the instability. The nonlinear terms of the amplitude equations show how this picture is modified in real physical systems. For various combinations of the signs of coefficients  $a_{ij}$ , different classes of vector fields of oscillation amplitudes  $r_1$  and  $r_2$  are generated [11]. The particular type of flow that describes our experimental results and satisfies the function of pattern recognition occurs for  $a_{ij} < 0$ , and is analyzed in detail by Segel under the name of nonlinear stability theory [32, 33]. Now  $(r_1, r_2) = (0, 0)$  is always an equilibrium and up to three other equilibria A, B, C are possible as shown in fig. 9, one on each axis and one in the interior.

#### 4.8. Gradient vector field of the amplitude equations

The  $a_{ij}$  negative is descriptive of a great many physical systems, since exponential growth is most often halted by some limit to give a sigmoid growth and saturation curve, as we have in the present case of neural activity. This "self-damping" appears in the amplitude equations in the  $a_{ij}r_i^3$  terms. The second effect, evident in the

$a_{ij}r_i r_j^2$  crossterms is "intermode suppression". This expresses the fact that the same circumstance which limits one mode amplitude will generally place many growing amplitudes in competition such that the increase of one suppresses the growth of others. The situation of "natural selection" of modes in competition for scarce resources is ubiquitous, and, as we have seen, constitutes the basis of operation (the "saturation landscape") of other dynamical associative memories.

The vector field of fig. 9 is evident for

$$a_{11}/a_{21} < \mu_1/\mu_2 < a_{12}/a_{22},$$

which implies

$$a_{12}a_{21} > a_{11}a_{22}.$$

When intermode suppression is sufficiently strong relative to self-damping, either mode 1 or mode 2 wins the competition, depending on initial conditions, and fixed points A and B are stable attractors, with interior point C being a saddle. An initial advantage conferred by the input pattern on one mode amplitude can overcome an intrinsically smaller growth rate at the bifurcation point. The orbit from  $(0, 0)$  to C forms a separatrix and we see that all initial conditions  $R(0) = U^{-1}P'(0)$  are partitioned into basins of attraction for A and B.

This accomplishes classification of spatial patterns or input perturbations  $P'(0)$  as in the Hopfield or Anderson models, and again we have a gradient vector field corresponding physically to a saturation landscape for the growing mode. Conceivably a Liapunov function can be found for this form of the amplitude equations. Results of Grossberg [16c] on these "competitive" dynamical systems where the  $a_{ij}$  are negative show that in certain cases the flow can be "monotone". This implies, even in high dimensional systems, that almost all trajectories converge to fixed point attractors, as we would like, and limit cycles and chaos are ruled out.

The basins of attractions may vary in size with learning until point C collides with A or B, leaving only one stable attractor and no separatrix. This implies that only one attractor is learned. This occurs for  $\mu_1/\mu_2 > a_{12}/a_{22}$ , when the growth rate of mode  $r_1$  so exceeds that of  $r_2$  that it always dominates regardless of initial conditions. Thus, optimal memory storage and pattern recognition require a flat eigenvalue spectrum and strong intermode suppression.

The number of stable attractors with separate basins (the memory capacity) in this ideal case is equal to the number of bifurcating eigenvalues (instabilities), or in other words, the codimension of the bifurcation. The high codimension bifurcation needed to get high memory capacity is one property that makes useful associative memories of this type unusual as dynamical systems to study. Real physical systems with the kind of symmetry that our homogeneous background state exhibits do demonstrate bifurcations with potentially infinite degeneracy, as in the case of the selection by fluctuation of one of  $2\pi$  possible orientations for a convective roll instability [32]. The picture of a great many memory modes simultaneously near critical is quite physically conceivable.

#### 4.9. Dynamical portrait of experimental observations

Experimental results described earlier confirm that the animals' recognition of the odor to which he is conditioned is accompanied by a statistically significant shift in the recorded EEG amplitude pattern. This is illustrated here by the convergence of the system to attractor B (CS+) instead of A (control) because of the new initial input condition. The basin of attractor B represents all input spatial patterns due to variations in receptor stimulation by odor B. Since the amplitude of all other modes at attractor B is zero, only one pattern is observed at one frequency. Because of the nonresonance condition, different attractors observed at different times will differ in frequency – as is seen experimentally.

For  $a_{11}a_{22} > a_{12}a_{21}$ , where self-damping exceeds intermode suppression, only the interior attractor is stable, representing a mixed mode case where both modes always coexist at some relative amplitude. This implies a quasiperiodic oscillation (an attracting torus in the four dimensional state space), since  $w_1$  and  $w_2$  are essentially irrationally related by the assumption of the nonresonance condition. Most attractors observed experimentally show oscillation in the range of 60–80 Hz, with a well defined peak containing over 60% of the spectral energy. About 20–40% of the time, however, we observe bursts which contain significant secondary peaks occurring in the range of 40–80 Hz while the dominant peak is less well defined and has generally shifted below 60 Hz. The spatial patterns of these bursts with broader spectral content are not similar enough to form a statistical cluster distinct from those of the patterns for waiting and for recognition. This is not surprising, if these are quasiperiodic attractors, since two mode patterns with different frequencies are superimposed. Freeman [15] hypothesizes that these “disorderly” attractors signal indecision or “failure of convergence” of the system to a learned mode. This is indeed a conceivable interpretation of this mixed mode vector field. Since the prepyriform cortex generally phase locks to the frequency of the bulb, it appears that intercortical communication must be by a single mode which Freeman [9] calls a “wave packet”\*.

Another mechanism for these bursts is exhibited in the possible vector fields of the model when perturbations from the  $a_{ij}$  negative are considered. Here the interior contains a limit cycle attractor. In this case a third frequency (perhaps of low amplitude) appears as a modulation of the amplitudes of patterns  $r_1$  and  $r_2$ , and again the system is quasiperiodic (a 3-torus) with no exclusive choice of either mode. Empirical measurement of the dimensionality of these attractors and

\*This is perhaps because Grossberg's “adaptive resonance” must occur between bulb and cortex for accurate recognition [16d].

reconstruction of their geometries from time series is in progress. This will help us to decide these issues and judge the accuracy of the model.

#### 4.10. *Chaos and pattern recognition*

A further possibility, as we deviate from “competitive” amplitude equations, is that these unclassifiable bursts may be chaotic. This could be true in spite of the peaked spectrum, since it is a characteristic of “phase coherent” chaotic attractors whose orbits are close to but not actually periodic [8]. The occurrence of chaos is quite common in physical systems as a secondary global bifurcation from the toroidal or the modulating limit cycle flows described above [17]. The question of whether these experimentally observed bursts are in fact due to deterministic chaos in the intrinsic dynamics of the system or to quasiperiodic dynamics plus noise may be difficult to answer empirically. However, it may be possible theoretically to prove the existence of chaos in certain parameter ranges by global bifurcation theory using Melnikov’s method [11].

The pattern recognition implications of a vector field with a chaotic flow in the interior of the quadrant between attractors A and B are particularly interesting. A fractal separatrix could appear, as discussed by Grebogi and Ott [16], where a chaotic flow in the neighbourhood of C so convolutes the boundary separating attractors A and B that it is impossible to say which will capture a particular initial condition in this region. The fractal dimension of the boundary determines the degree of uncertainty that an input goes to A or B. By this mechanism the system could make probabilistic classification decisions in some areas of its state space.

#### 4.11. *Future directions*

In the codimension two case, the most immediate objective will be to establish a computer program that determines the relative eigenvalue magnitudes  $\mu_i$  and the nonlinear normal form

coefficients  $a_{ij}$  as a function of the original system parameters ( $Q_m, k_{ee}, k_{ei}, k_{ie}, k_{ii}$ ) and spatial coupling parameters ( $w_{ee}, w_{ei}, w_{ie}, w_{ii}$ ). Ranges of these leading to observed or interesting possible behavior as anticipated above may then be ascertained and checked for physiological plausibility. The major mathematical difficulties in extending this analysis to large scale systems, whether discrete or continuous space is employed, are those introduced by the high codimension of the bifurcation envisioned here. Coulet and Spiegel [3] have developed techniques for calculating amplitude equations for an arbitrary number of modes in a “polycritical space” near a high dimensional center manifold.

Utilizing Macsyma with only the competitive form of amplitude equations to consider, it is expected that we will be able to analyse a number of modes sufficient to assess quantitatively the associative memory capabilities of this system. We will test its experimental validity in detail and investigate the relation between the vector field of the amplitude equations and modifications in the coupling matrix of the underlying equations of the full system. Analog electronic models are under construction and we are investigating the design of an optical simulator for the exploration of the vector field of high dimensional models.

#### 4.12. *Summary and conclusions*

Led by the demands of the experimentally observed behavior of the EEG in the rabbit olfactory bulb, I have expounded a conception of its operation sufficiently detailed for mathematical treatment. The principle features of neural activity required in a model of the bulb are 1) that it bifurcate to form ordered macrostates on top of microscopic disorder, 2) that these states are oscillatory, 3) that the oscillation is spatially phase locked at a single frequency, and 4) that changes in the spatial amplitude pattern and not the spatial phase structure or frequency of the oscillation are correlated with learning and recognition behavior during classical Pavlovian conditioning. I



have formulated a model with these features that extends the theories of pattern formation and associative memory beyond the usual restricting assumptions of each—homogeneity of the neural medium and lack of oscillation—to create a synthesis which is capable of describing the observed behavior of the olfactory bulb and elucidating the principles of its operation as a pattern recognition system.

The basic hypothesis is that during conditioning the connectivity of the bulb is inhomogeneously modified to form specific input-sensitive modes of oscillatory instability distinguishable by their spatial amplitude structure. Analysis has shown how certain classes of coupling in the model can lead to these simultaneous instabilities. The simulations of Lapedes have established further that couplings exist for which these oscillatory modes may indeed be selectively evoked by different inputs. I have argued that the mechanism of competing instabilities, oscillatory or not, is central to the operation of dynamical associative memories and explains how a pattern forming system can pattern recognize. We have indicated how the respiration driven bifurcation of the equilibrium state in and out of stability may accomplish signal detection and memory reset for the animal.

The potential of the dynamical systems approach has been demonstrated in the power of multiple bifurcation theory to determine amplitude equations for oscillatory modes and illuminate the conditions of competition among these modes which leads to their input selectibility. When the eigenvalue spectrum is flat and the amplitude equations are "competitive" (negative coefficients in the nonlinear terms), the vector field of the amplitude equations can be a gradient vector field with multiple fixed point attractors. This has been shown to provide a convenient theoretical visualization of the changes in EEG attractors observed in an animal during pattern recognition. Perturbations of this flow leading to quasiperiodic and chaotic attractors may be descriptive of other EEG patterns seen experimentally. The negative impact of these patterns on the

animal's recognition performance observed experimentally is also clearly predicted in this picture.

This approach establishes avenues of theoretical exploration which have the potential of revealing new principles as well as inspiring new experimental tests and measurements of neural pattern recognition systems. These include the determination of statistically distinct attractors in neural activity correlated with different sensory inputs and behavioral responses, the mapping of basins of attraction for inputs, the determination of attractor dimension, and the reconstruction of attractor geometry from time series.

## References

- [1] S. Amari, "Competitive and Cooperative Aspects in Dynamics of Neural Excitation and Self-Organization", in *Competitive and Cooperative Networks*, S. Amari and M.A. Arbib, eds., Lecture Notes in Biomath. 45 (Springer, Berlin, New York, 1982).
- [2] Anderson and Hinton, eds., *Parallel Models of Associative Memory* (LEA, New Jersey, 1981).
- [3] P.H. Coullet and E.A. Spiegel, "Amplitude Equations for Systems with Competing Instabilities", *SIAM J. Appl. Math.* 43, No. 4 (1983).
- [4] G.B. Ermentrout and J.D. Cowan, "Temporal Oscillations in Neuronal Nets", *J. Math. Biol.* 7 (1979) 265.
- [5] G.B. Ermentrout and J.D. Cowan, "A Mathematical Theory for Visual Hallucination Patterns", *Biol. Cyber.* 34 (1979) 137.
- [6] G.B. Ermentrout and J.D. Cowan, "Secondary Bifurcation in Neuronal Nets", *Siam J. Appl. Math.* 39, No. 2 (1980).
- [7] G.B. Ermentrout, "Asymptotic Behavior of Stationary Homogeneous Neuronal Nets", in *Competitive and Cooperative Networks*, S. Amari and M.A. Arbib, eds., Lecture Notes in Biomath. 45 (Springer, Berlin, New York, 1982).
- [8] D. Farmer, J. Crutchfield, H. Froehling, N. Packard and R. Shaw, "Power Spectra and Mixing Properties of Strange Attractors", in *Nonlinear Dynamics*, Helleman, ed., *Annals of the New York Academy of Science*, vol. 357 (1980).
- [9] W.J. Freeman, *Mass Action in the Nervous System*, New York: Academic Press, (1975).
- [10] W.J. Freeman, "Nonlinear Gain Mediating Cortical Stimulus-response Relations", *Biol. Cybernetics* 33 (1979) 237.
- [11] W.J. Freeman, "Nonlinear Dynamics of Paleocortex Manifested in the Olfactory EEG", *Biol. Cybernetics* 35 (1979) 21.

- [12] W.J. Freeman, "EEG Analysis gives Model of Neuronal Template Matching Mechanism for Sensory Search with Olfactory Bulb", *Biol Cybernetics* 35 (1979c) 221.
- [13] W.J. Freeman and K.A. Grajski, "Relation of Olfactory EEG to Behavior: Time Series Analysis", *Behavioral Neuroscience*, submitted (1985).
- [14] W.J. Freeman and B. Baird, "Relation of Olfactory EEG to Behavior: Spatial Analysis", to be published (1985).
- [15] W.J. Freeman and K.A. Grajski, "Correlation of EEG with Behavior: Factor Analysis", to be published (1985).
- [16] C. Grebogi, S. McDonald, E. Ott, J. Yorke, "Final State Sensitivity: an Obstruction to Predictability", *Physics Letters* 99A (1983) 415.
- [16a] S. Grossberg and S. Elias, "Pattern Formation, Contrast Control, and Oscillations in the Short Term Memory of Shunting On-Center Off Surround Networks", *Biol Cybernetics* 20 (1975) 69.
- [16b] S. Grossberg, "Adaptive Classification and Universal Recoding: II. Feedback, Expectation, Olfaction, Illusions", *Biol Cybernetics* 23 (1976) 187.
- [16c] S. Grossberg, "Decisions, Patterns, and Oscillations in Nonlinear Competitive Systems with Applications to Volterra-Lotka Systems", *J. Theor. Biol.* 73 (1978) 101.
- [16d] S. Grossberg, "Adaptive Resonance in Development, Perception and Cognition", *SIAM-AMS proc.* 13 (1981) 106.
- [17] J. Guckenheimer and D. Holmes, *Nonlinear Oscillations Dynamical Systems, and Bifurcations of Vector Fields* (Springer, New York, 1983).
- [18] H.G.D. Haken, *Pattern Formation and Pattern Recognition* (Springer, New York, 1979).
- [19] E. Harth and R. Wong, "Stationary States and Transients in Neural Populations", *J. Theor. Biol.* 40 (1973) 77.
- [20] G. Hinton, T. Sejnowski and D. Ackley, "Boltzman Machines: Constraint Satisfaction Networks that Learn", Tech. Report SMU-CS-84119 (1984).
- [21] M.W. Hirsch, "Systems of Differential Equations that are Competitive or Cooperative II: Convergence Almost Everywhere", *Siam J. Math. Anal.* 16, No. 3 (1985).
- [22] A.V. Holden, *Models of the Stochastic Activity of Neurons*, Lecture Notes in Biomath. 12 (Springer, New York, 1976).
- [23] J. Hopfield and D.W. Tank, "Neural Computation of Decisions in Optimization Problems", *Biol. Cybern.* 52 (1985) 141.
- [24] J.J. Hopfield, "Neurons with Graded Response have Collective Computational Properties like those of Two State Neurons", *Proc. Natl. Acad. Sci. USA* 81 (1984) 3088.
- [25] J.J. Hopfield, "Neural Networks and Physical Systems with Emergent Collective Computational Abilities", *Proc. Natl. Acad. Sci. USA* 79 (1982) 2554.
- [26] S. Kirkpatrick, C.D. Gelatt and M.P. Vecchi, "Optimization by Simulated Annealing", *Science* 220 (1983) 671.
- [27] E. Knobloch, M. Golubitsky and J.W. Swift, "Symmetries and Pattern Selection in Rayleigh-Bénard Convection", *Physica* 10D (1984) 249.
- [28] T. Kohonen, *Self-Organization and Associative Memory* (Springer, Berlin, 1984).
- [29] H. Meinhardt, *Models of Biological Pattern Formation* (Academic Press, New York, 1982).
- [30] Murray, *Nonlinear Diffusion Models in Biology*, (Oxford Univ. Press, Oxford, 1976).
- [31] G. Palm, *Neural Assemblies - An Alternative Approach to Artificial Intelligence* (Springer, Berlin, New York, 1983).
- [32] L.A. Segel, "The Nonlinear Interaction of a Finite Number of Disturbances to a Layer of Fluid Heated from Below", *J. Fluid Mech.* 21 (1965) 359.
- [33] L.A. Segel, *Modeling Dynamic Phenomena in Molecular and Cellular Biology* (Cambridge Univ. Press, Cambridge, 1984).
- [34] A.M. Turing, "The Chemical Basis of Morphogenesis", *Phil.-Trans. R. Soc. Lond. B* 237 (1952) 5.
- [35] H.R. Wilson and J.D. Cowan, "Excitatory and Inhibitory Interactions in Localized Populations of Model Neurons", *Biophysical Journal* 12 (1972) 1.
- [36] H.R. Wilson and J.D. Cowan, "A Mathematical Theory of the Functional Dynamics of Cortical and Thalamic Nervous Tissue", *Biol. Cyber.* 34 (1979) 137.
- [37] A.T. Winfree and S.H. Strogatz, "Singular Filaments Organize Chemical Waves in Three Dimensions", *Physica* 8D (1983) 35.
- [38] A.T. Winfree, *The Geometry of Biological Time* (Springer, New York, 1980).