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The Topology and Organization of Unstable Periodic Orbits in Hodgkin-Huxley Models of Receptors with Subthreshold Oscillations

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I. Introduction

If the behavior of a system is deterministic and nonperiodic, then it is chaotic. Chaos is generated by the interplay between two mechanisms that operate on a flow in phase space: stretching and squeezing. The first mechanism is responsible for 'sensitivity to initial conditions,' while the second is responsible for recurrently building up a self-similar (fractal) structure.

The purpose of the present article is to describe a set of equations that has been proposed to model neurons with subthreshold oscillations [1], to show that this model can generate chaotic behavior, and to describe how the stretching and squeezing mechanisms operate on the phase space for this model.

These stretching and squeezing mechanisms in phase space are described in terms of topology. They act concurrently to build up a strange attractor. They simultaneously organize all the unstable periodic orbits in the strange attractor *in a unique way*. This unique organization is a tool that has been used to classify strange attractors [2]. It is also the probe which is used to identify the mechanism which generates chaotic behavior in specific dynamical systems. We will apply this probe to understand how the flow in the phase space appropriate for neurons with subthreshold oscillations is deformed under the deterministic equations of the model. We will show that the mechanism involved is one which has previously been identified [3]. It is responsible for chaos in the Duffing oscillator and in the YAG laser. It has been affectionately called the 'jelly roll' or the 'gateau roulé' mechanism. The reason is simply that these delightful edibles are built up by exactly the same mechanism.

This contribution is organized as follows. In Sec. II we review briefly the basic Hodgkin-Huxley model of electrical activity in a neuron. The modified version of the Hodgkin-Huxley model is discussed in Sec. III. This model describes nerve cells which fire without external inputs. In Sec. IV we describe the behavior of the output of this model, while in Sec. V we discuss how this behavior is manifested both in the phase space of the model as well as in an appropriate, reduced phase space of smaller dimension.

In Sec. VI we describe the classification of low dimensional strange attractors by topological means, and outline the Topological Analysis Program in Sec. VII. We apply this program to the analysis of the strange attractors generated by the modified Hodgkin-Huxley equations in Sec. VIII. There we find that the strange attractor is of 'jelly roll' type. Strange attractors of this type have previously been analyzed. As a result, many of the properties exhibited by the modified Hodgkin-Huxley equations have already been well studied. Some of these results are summarized in Sec. IX.

Secs. X and XI are devoted to a description of how it is possible to go beyond the program of analyzing low dimensional chaotic dynamical systems which is described in Secs. VI and VII. In Sec. X we describe how to simulate dynamical systems without necessarily going through the intermediary of developing a system of equations to mimic the flow ('flows without equations'). In Sec. XI we present preliminary results on how the stretching and squeezing mechanisms can occur in higher (than 3) dimensional dynamical systems, and under what conditions a discrete classification theory, as exists for three dimensional strange attractors, can exist in higher dimensions. Our results are summarized in Sec. XII.

II. Hodgkin-Huxley Equations

Hodgkin and Huxley treated the axon as an electrical device [4]. This device carries a current, I, along the axon of the neuron. The membrane is permeable to ionic currents, I_{ions}, produced by important anions and cations. In addition, the membrane has a capacitance, C_M, per unit length. A potential difference, V, exists across the neuron membrane. By visualizing the axon as a series of Gaussian pillboxes whose walls consist of the cylindrical membrane bounded by a pair of circular sections perpendicular to the axis, they were able to construct a partial differential equation describing propagation of electrical pulses along the axis of the neuron. The current conservation equation for each pillbox has the form

$$I = C_M \frac{dV}{dt} + \sum I_{ions} \tag{1}$$

The ionic species which contributed most substantially to the current flow through the membrane are Na^+, K^+, Ca^{++}, and Cl^-.

Under rest conditions, the membrane is polarized so that the potential in the interior is about 65 mV less than the exterior potential ($V \simeq -65$ mV). This potential difference is maintained by ion pumps. At rest, the concentrations of Na^+ and Cl^- outside the neuron greatly exceed the concentrations inside: $[Na^+]_{outside}/[Na^+]_{inside} \sim 9$ and $[Cl^-]_{outside}/[Cl^-]_{inside} \sim 6$, while the reverse is true for the potassium ion: $[K^+]_{inside}/[K^+]_{outside} \sim 20$. These ratios depend strongly on the potential V and weakly on the ambient temperature, T.

As a depolarization wave moves down the axon, sodium channels open and Na^+ flows into the axon. The membrane becomes depolarized. The Na^+ influx stops after a short time (~ 1 ms), and the potassium channels open. A fast efflux of K^+ then takes place, acting to restore the polarization across the membrane.

Neural dynamics was modeled with the current conservation equation

$$C_M \frac{dV}{dt} = I - (I_{Na^+} + I_{K^+} + I_{Cl^-}) \tag{2}$$

The ionic currents are

$$I_{ion} = g_{ion}(V - \mu_{ion}) \tag{3}$$

Here μ_{ion} is a chemical potential for each ion. This is established by ion pumps which transport ions through the membrane. The ionic conductances, g_{ion}, depend sensitively on V. These conductances are modeled by the following phenomenological equations:

$$\begin{aligned} g_{Na^+} &= m^3 h \bar{g}_{Na^+} \\ g_{K^+} &= n^4 \bar{g}_{K^+} \\ g_{Cl^-} &= \bar{g}_{Cl^-} \end{aligned} \tag{4}$$

The factors m, h, n which appear in the equations for the ionic conductances were assumed to obey simple relaxation equations of the form $dc/dt = -(c - c_\infty)/\tau$:

$$\begin{aligned} \tfrac{dm}{dt} &= -(m - m_\infty)/\tau_1 \\ \tfrac{dh}{dt} &= -(h - h_\infty)/\tau_2 \\ \tfrac{dn}{dt} &= -(n - n_\infty)/\tau_3 \end{aligned} \tag{5}$$

These three functions were interpreted as probabilities. Their respective steady state values, m_∞, h_∞, and n_∞, depend strongly on V but weakly on T.

In the absence of current flows ($I = 0$), the Hodgkin-Huxley equations for an isolated segment of an axon reduce to a four dimensional dynamical system in the four variables (V, m, h, n). This system consists of the current conservation equation (2) and the three relaxation equations (5), together with the constitutive equations (3) and (4). This system has a stable fixed point whose equilibrium values are $(m, h, n) = (m_\infty, h_\infty, n_\infty)$, with V determined from the transcendental equation

$$I_{Na^+} + I_{K^+} + I_{Cl^-} = 0 \tag{6}$$

As a result, the Hodgkin-Huxley equations model passive ("Platonic") nerve cells. In the absence of external stimulations, including coupling to other nerve cells, this model does not generate time dependent membrane potentials.

III. Modified Hodgkin-Huxley Equations

A number of experimental findings have challegned the idea that neurons fire only in response to external stimuli. Experiments have been carried out on neurons isolated from the inputs of other neurons [5], thermosensitive neurons isolated from thermal inputs [6], electroreceptors isolated from electrical stimuli [7], and mechanoreceptors isolated from mechanical stimuli [8]. There is a growing body of evidence that neural oscillations are intrinsic [9].

In order to account for the possibility that neural spike train activity could be intrinsic, Braun *et al* [1] refined the basic Hodgkin-Huxley equations by modeling in greater detail the nature of the ion current flows. In this elaboration of the basic Hodgkin-Huxley model, the ion current flows are dominated by two physical processes:

1. Specific ion gates open at appropriate membrane potentials. This gate opening allows ions to flow into or out of the axon in a way which attempts to equilibrate the internal and external ion concentrations. This is a fast process. Gate time scales are short.

2. Ion pumps operate to transfer specific ions through the membrane and attempt to maintain an ion concentration gradient across the membrane. This is a slow process. Pump time scales are long.

To simplify the model of nerve cell dynamics. Braun *et al* begin with the basic Hodgkin-Huxley equation (2), neglect the Cl^- ion current, assume that the current flow along the axon is in the nature of a "leakage current," and include a noise term:

$$C_M \frac{dV}{dt} = I_l + noise - (I_{Na^+} + I_{K^+}) \tag{7}$$

Then both current flows are written explicitly in terms of gate (fast) and pump (slow) current terms

$$\begin{array}{ccccccccc} I_{Na^+} & = & I_{Na-g} & + & I_{Na-p} & = & I_d & + & I_{sd} \\ I_{K^+} & = & I_{K-g} & + & I_{K-p} & = & I_r & + & I_{sr} \end{array} \tag{8}$$

The current flows I_i $(i = d, r, sd, sr)$ are

$$I_i = \rho g_i a_i (V - V_i) \tag{9}$$

Here g_i is the maximum ion conductance, V_i is the reverse potential, and a_i is an activation variable. The activation variables obey relaxation equations

$$\frac{da_i}{dt} = -\frac{\phi(a_i - a_{i,\infty})}{\tau_i} \qquad i = d, r, sd \tag{10}$$

$$\frac{da_{sr}}{dt} = -\frac{\phi(\eta I_{sd} + k a_{sr})}{t_{sr}} = -\frac{\phi(a_{sr} + \eta' I_{sd})}{\tau_{sr}} = -\frac{\phi(a_{sr} - a_{sr,\infty})}{\tau_{sr}} \tag{11}$$

In the last expression $\tau_{sr} = t_{sr}/\eta$, $\eta' = k/\eta$, and $a_{sr,\infty} = -\eta' I_{sd}$. The weakly temperature dependent scale factors $\rho(T)$, $\phi(T)$ are

$$\rho = 1.3^{(T-T_0)/10} \qquad \phi = 3.0^{(T-T_0)/10} \qquad T_0 = 25^{\circ} \tag{12}$$

The asymptotic relaxation values are assumed to have a Fermi function form

$$a_{i,\infty} = \frac{1}{1 + \exp\left(-(V - V_{0,i})/\Delta_i\right)} \qquad i = d, r, sd \tag{13}$$

Here $V_{0,i}$ is the half-activation value of V ($a_{i,\infty} = \frac{1}{2}$ when $V = V_{0,i}$) and Δ_i is a 'wall thickness,' determining the range over which activation takes place. Specifically, the activation a_i changes through the middle half (46.22%) of its range as V changes from $V_i - \Delta_i$ to $V_i + \Delta_i$.

The Hodgkin-Huxley model, as modified by Braun *et al*, is a five dimensional dynamical system. The five ordinary differential equations for this model consist of the current conservation equation (7), the three relaxation equations (10) for the activation coefficients a_i, $(i = d, r, sd)$, and the equation (11) for the activation coefficient a_{sr}. It is this last equation which is responsible for subthreshold oscillatory activity in this modification of the Hodgkin-Huxley model.

IV. Model Behavior

The modified Hodgkin-Huxley equations (7), (10), and (11) describe neurons with subthreshold oscillations. This five dimensional dynamical system has been studied both with noise [1] and without noise [1,3]. We have studied this system by integrating the equations of motion using standard Runge-Kutta methods with a fixed time step $\Delta t = 0.05$ ms for the parameter values shown in Table 1. The system has been studied as a function of the ambient temperature, T, in the range $10^{\circ} \leq T \leq 35^{\circ}C$. In this study, temperature can be considered as a bifurcation parameter. We set the noise term to zero in this study. The effects of noise will be discussed below.

The bifurcation diagram resulting from this study is shown in Fig. 1. In the inset to this figure we show a typical voltage output ($T \sim 17^{\circ}C$). The voltage output consists of a series of (depolarization) spikes separated by a deep repolarization minimum at about -65 mV. Each

Table 1: Parameter values for use with the Hodgkin-Huxley equations. These include: maximum conductance g ($\mu A/cm^2$), decay time τ (ms), wall thickness Δ (mV), reverse potential V_i (mV), and half activation potential $V_{i,0}$ (mV). In addition, $C_M = 1\ \mu$, $t_{sr} = 20$, $k = 0.17$, $\eta = 0.012$, so that $\tau_{sr} = 20/0.012$, and $\eta' = 0.17/0.012$

			g conductance $\mu A/cm^2$	τ decay time ms	Δ_i width mV	V_i reverse mV	$V_{0,i}$ activation mV
d	Na^+	$fast$	1.5	?	-4	$+50$	-25
r	K^+	$fast$	2.0	2	-4	-90	-25
sd	Na^+	$slow$	0.25	10	11	$+50$	-40
sr	K^+	$slow$	0.40	1600??		-90	

group of spikes is called a burst. All the spikes are sharp and have a maximum at about the same value. The time interval between successive spikes in a burst increases monotonically and systematically. The minimum between spikes in a burst lies well above the repolarization minimum. In most cases, after the last spike in a burst, the voltage decreases rapidly to the repolarization minimum. This behavior is exhibited by the bursts labeled $4f$ in the inset to Fig. 1. However, in some cases the voltage slowly attempts to rise to another spike, but fails to reach a maximum and returns to the repolarization minimum. This behavior is exhibited by the bursts labeled $3r$ in the inset to Fig. 1.

In Fig. 1 we plot the time interval between successive spikes in the model output as a function of the temperature. At high temperatures ($T \sim 32^{\rm o}$, not shown) there is one spike per burst, and the model output is periodic. In other temperature ranges the model output is also periodic, with two spikes per burst ($22^{\rm o} \leq T \leq 25^{\rm o}$), three spikes per burst ($17^{\rm o} \leq T \leq 21.5^{\rm o}$), four spikes per burst ($15^{\rm o} \leq T \leq 16^{+\,\rm o}$), eight spikes per burst ($14^{\rm o} \leq T \leq 15^{-\,\rm o}$), five spikes per burst ($\leq T \simeq 12^{-\,\rm o}$). In other regions, the behavior appears to be chaotic, with an unpredictable mix of bursts containing n and $n+1$ spikes ($n = 2, 3, 4$).

The bifurcation diagram gives the impression that the output generated by the modified Hodgkin-Huxley equations is chaotic in certain ranges of temperature. The strongest signatures for chaos, from this diagram, are the initiation of what appears to be a period doubling cascade at $T \sim 15^{\rm o}$, and the scatter of interspike intervals between regions where there are n and $n+1$ well-defined interspike time intervals.

It is useful to label the bursts according to their spike morphology as follows:

nf: n sharp spikes, followed by a return to the deep repolarization minimum

nr: n sharp spikes, followed by an incomplete depolarization rise before returning to the deep repolarization minimum

Then we will see in the following sections that the order in which the bursts occur, as a function of decreasing temperature, is

$$2f \quad 2r \quad 3f \quad 3r \quad 4f \quad 4r \quad 5f \quad 5r \quad \cdots \tag{14}$$

Figure 1: Interspike time intervals plotted as a function of ambient temperature, T, for the modified Hodgkin-Huxley equations. This bifurcation diagram shows alternation between periodic and chaotic behavior. Inset: typical model output in a chaotic regime ($T \sim 17^oC$).

Figure 2: Projection of the phase space trajectory in a chaotic regime ($T = 12.6^oC$) into three two dimensional subspaces: (a) $(y_1, y_2) = (V, a_d)$; (b) $(y_1, y_3) = (V, a_r)$; (c) $(y_2, y_3) = (a_d, a_r)$. Since the projection is a closed curve in each case, the five dimensional system is effectively three dimensional.

Periodic behavior consists of bursts of one type, specifically nf. Chaotic behavior consists of unpredictable mixtures or two (or more) types of bursts that are adjacent in this sequence. In fact, with a little imagination, we can designate the bursts of type nr (n full spikes followed by a feeble failure to spike) by the fraction $n + \frac{1}{2}$, since these bursts are intermediate between bursts with n spikes and those with $n + 1$ spikes.

V. Phase Space

The state of a neuron modeled by the modified Hodgkin-Huxley equations is determined by the coordinates of a point $(V, a_d, a_r, a_{sd}, a_{sr}) = (y_1, y_2, y_3, y_4, y_5) \in R^5$. It is very difficult to visualize phase space trajectories in R^5 which are generated by these equations.

Projections of phase space trajectories onto the 10 two dimensional subspaces (y_i, y_j) $(1 \leq i < j \leq 5)$ show that the three variables $(V, a_d, a_r) = (y_1, y_2, y_3)$ evolve 'coherently.' In Fig. 2 we project the phase space trajectory in the chaotic regime ($T = 12.6^oC$) into the three subspaces (y_i, y_j) $(1 \leq i < j \leq 3)$ to show the high degree of correlation among these three variables. Since these three variables are so highly correlated, only one of them is independent. In other words, the system is effectively three dimensional, and its properties can be studied in the 'reduced' phase space $(V, a_{sd}, a_{sr}) = (y_1, y_4, y_5)$.

The projection of the attractor at $T = 12.6^oC$ into the reduced three dimensional phase space is shown in Fig. 3. In this figure the horizontal axis is y_4, the vertical axis is y_5, and y_1 comes out of the page. The projection strongly suggests the presence of a strange attractor.

The surest way to demonstrate the presence of chaotic motion in a dynamical system is to locate unstable periodic orbits. This can be done by constructing a Poincaré section and looking for fixed points in the return map.

The attractor shown in Fig 3 has a 'hole in the middle.' This means that we can construct a *global* Poincaré section by attaching a half plane to an axis which passes through this hole. A

Figure 3: Strange attractor at $T = 12.6^oC$ projected onto the $(y_4, y_5) = (a_{sd}, a_{sr})$ plane.

Figure 4: First return map on the Poincaré section. Intersections with the diagonal indicate unstable period one orbits. The branches which intersect the diagonal depend on the temperature. (a) $T = 12.6^oC$: $6f, 5r, 5f, 4r, 4f, 3r$; (b) $T = 13.5^oC$: $5f, 4r, 4f$; (c) $T = 16.5^oC$: $4f, (3r)$. As T increases, the first return map slides to the left and changes shape slightly.

very convenient Poincaré section is obtained by the condition $dy_4/dt = 0$, $y_4 <$ some threshold. The threshold is taken below the minimum value of y_4 which occurs between the spikes in one burst, and the maximum value which the minimum of y_4 assumes during the repolarization stage.

This Poincaré section is valid throughout the entire temperature range shown in Fig. 1. In particular, it shows that the periodic orbits with n spikes per burst ($n = 1, 2, 3, 4, 5$) are all period one orbits.

The value of y_4 is recorded each time the phase space trajectory intersects this Poincaré section. This information is used to construct a file of intersections $y_4(i)$, where $y_4(i)$ is the value of y_4 at the i^{th} intersection with the Poincaré section. The first return map, $y_4(i + 1)$ vs. $y_4(i)$, is shown in Fig. 4 for three values of the temperature. This figure provides two important pieces of information.

First, the return map is very 'thin' at all temperatures. This means that this dynamical system is very dissipative at all the temperatures studied. The dimension of the strange attractor shown in Fig. 3 is $2 + \epsilon$, where ϵ is close to zero. This is compatible with the reduction in dimension $5 \rightarrow 3$ discussed above.

Second, as the temperature changes, the return map changes systematically. This can be seen because we have labeled the branches of the return map by burst type. As the temperature increases, the return map 'moves to the left.'

At $T = 12.6^oC$ the return map shows six intersections with the diagonal. These are the branches which describe bursts with the morphology $6f, 5r, 5f, 4r, 4f, 3r$. The two least unstable branches are $5f$ and $4f$. The branches nr are extremely unstable, as can be seen from their almost vertical slopes. This means that such bursts are very rarely seen. Peaks with morphology of this type are destroyed by small amounts of noise. At this temperature, the model output consists of spike train bursts almost entirely of type $5f, 4r$, and $4f$.

As the temperature increases to 13.5^oC two things happen. First, the branches $6f, 5r$, which are very unstable at $T = 12.6^oC$, no longer intersect the diagonal at 13.5^oC. The disappearance

Figure 5: Period one orbits $5f, 4r, 4f$ for the strange attractor shown in Fig. 3.

of these intersections has no observational effect on the spike train output. Second, the branch $3r$, which nearly intersects the diagonal at $T = 12.6^{o}C$, drops further below the diagonal at $T = 13.5^{o}C$ and in fact no longer appears in the return map. At this temperature, the return map exhibits only the three branches $5f, 4r, 4f$.

As the temperature increases further, to $T = 16.5^{o}C$, the shape of the first return map, and its intersection with the diagonal, continue to change. The unstable branches $5f, 4r$ fail to intersect the diagonal, and drop from the return map. Then the intersection angle between the branch $4f$ and the diagonal approaches -45^{o}, and as it does, an inverse period doubling cascade occurs along this branch ($14^{o}C < T < 16^{o}C$). At $T = 16.0^{o}C$ the branch $4f$ is again slightly unstable, but the branches $(3r, 3f)$ almost intersect the diagonal. That this is the case can be seen by approaching $T = 16.5^{o}C$ from above. As the temperature descends towards $T = 17.0^{o}C$, the branch $3f$ is stable, but this period one orbit takes increasingly long times to complete its orbit as $T \rightarrow 17.0^{o}C$. This divergence of the period is a clear signature of an impending tangency between a peak of the return map and the first return diagonal. The reason is that the flow slows down in the neighborhood of the branch $3r$. This tangency occurs at $T = 17.0^{o}C$. Slightly below this temperature there is an intermittency between the 'virtual' period one branch with three spikes per burst $(3r, 3f)$ and the slightly unstable branch $4f$. As T decreases from $17.0^{o}C$, this intermittency decreases in importance as the peak in the branch $(3r, 3f)$ moves further away from the diagonal. The intermittency ends (at $T \simeq 16.3^{o}C$) when the branch $4f$ becomes stable at the intersection with the diagonal.

The return map has the structure of a series of inverted parabolas (logistic maps) lined up side by side. Each labels two branches (nr, nf). They are contiguous and lined up from left to right in order of descending n. As T decreases, the diagonal moves towards the left, so that period one orbits with increasing numbers of spikes per burst are encountered. The bifurcation diagram (Fig. 1) clearly shows periodic (period one) behavior, period doubling cascades, episodes of intermittency, and chaos.

We have used these return maps to locate unstable periodic orbits in this dynamical system. In particular, we have used the return map at $T = 12.6^{o}C$ to locate three distinct period one orbits of type $5f$, $4r$, and $4f$. These, and some other low period orbits, were subsequently used to determine the topological structure of the strange attractor generated by the modified Hodgkin-Huxley equations. These orbits are shown in Fig. 5, using the same projection as in Fig. 3.

The following remarks about the projection from a five dimensional phase space to a three dimensional reduced phase space are in order.

1. Reduction in dimension always simplifies computations. In the present case this reduces the number of two dimensional projections from 10 to 3.

2. It is the significant separation in time scales that allows the reduction in dimension. Since the relaxations of a_d and a_r to their (moving) asymptotic values is much faster than the other two relaxation time rates (of a_{sd} and a_{sr}), it is possible to 'adiabatically eliminate' these two variables. This leaves a reduced dynamical system depending on only the three variables (y_1, y_4, y_5).

3. Adiabatic elimination of variables is an effective but at best *ad hoc* procedure to reducing the dimensionality of a dynamical system. A more general and powerful result, involving projection to an *inertial manifold*, has yet to be developed for dynamical systems.

4. The classification theory for strange attractors is now in mature form for low (3) dimensional strange attractors [2]. It does not yet exist for higher dimensional ($d > 3$) strange attractors. This means that the reduction in dimension $5 \rightarrow 3$ described above is essential for the topological analysis which will be carried out in the following sections.

VI. Classification of Strange Attractors by Integers

A powerful theory has recently been developed to classify low dimensional strange attractors [2]. Strange attractors of three dimensional chaotic dynamical systems can be classified by their topological properties. These properties are summarized, in turn, by sets of integers. We will describe how to extract these integers from chaotic data.

This classification theory extends to N dimensional dynamical systems provided their s-trange attractors have Lyapunov exponents which obey

$$\lambda_1 > \lambda_2 = 0 > \lambda_3 > \cdots \qquad \text{and} \qquad -\lambda_3 > \lambda_1 \tag{15}$$

Such *strongly contracting* dynamical systems have a Lyapunov dimension, d_L, which is less than three by the Kaplan-Yorke conjecture [10,11]:

$$d_L = 2 + \frac{\lambda_1}{|\lambda_3|} < 3 \tag{16}$$

Another way of looking at this condition is that the dynamical system has an inertial manifold of dimension three [2].

With the development of the topological classification theory, there are now three approaches to the analysis of chaotic dynamical systems.

1. Metric methods are based on determining the local geometric (fractal) structure of a strange attractor. Calculations of fractal dimensions and scaling functions require very long, clean data sets. The amount of data required grows very quickly with the underlying dimension. The result of a dimension calculation is a real number which provides information about the minimum dimension of the dynamical system. Some dimension calculations resemble a black art. Calculations degrade rapidly with increasing noise. The dimension estimate comes with no reasonable error estimates, no independent way to verify the estimate, and no underlying statistical theory.

Metric calculations provide no information on the mechanism which builds up fractal structures through repeated self-similar actions. Nor do they provide any information about what happens when control parameters are varied.

2. Dynamical methods are based on determining how rapidly phase space is deformed *on average*. This information is contained in the spectrum of Lyapunov exponents. These exponents can be computed with shorter, noisier data sets than are required for metric calculations. The largest Lyapunov exponent is relatively easy to compute; smaller exponents can be computed with increasing difficulty. The spectrum of Lyapunov exponents, λ_i, and the information dimension, d_i $(0 \leq d_i \leq 1)$, associated with each, provide information about the dimension of the underlying dynamical system [11]. Specifically, we order the Lyapunov exponents in the usual descending order

$$\begin{array}{ccccccccc} \lambda_1 & \geq & \lambda_2 & \geq & \lambda_3 & \cdots & \geq & \lambda_N \\ d_1 & \geq & d_2 & \geq & d_3 & \cdots & \geq & d_N \end{array} \tag{17}$$

In general, the first p exponents are positive, the $p+1^{st}$ is zero (it corresponds to the flow direction), and the remaining $N-(p+1)$ are negative. The information dimension d_i is $+1$ for all the positive exponents and for the flow direction. In the contracting directions it measures the fractal nature of the attractor, so generally for $i > p+1$, $d_i < 1$. The partial sum

$$S_k = \sum_{i=1}^{i=k} d_i \lambda_i \tag{18}$$

increases as k increases from $k=1$ to $k=p$, $S_p = S_{p+1}$, and decreases for $k > p+1$ until it reaches 0 at $k=n$, and remains at 0 for $n \leq k \leq N$. The Lyapunov dimension is

$$d_L = \sum_{i=1}^{n} d_i = \sum_{i=1}^{N} d_i \tag{19}$$

If the smallest (in magnitude) negative exponent λ_{p+2} is larger than the sum of all the positive exponents, then $S_{p+2} = 0$, $d_{p+2} = \sum_{i=1}^{p} \lambda_i / |\lambda_{p+2}|$,

$$d_L = p + 1 + \frac{\sum_{i=1}^{p} \lambda_i}{|\lambda_{p+2}|} \tag{20}$$

and the Kaplan-Yorke expression results. In the more general case that the system is not *strongly* contracting (in the sense that two or more negative Lyapunov exponents contribute to the dimension formula), the Kaplan-Yorke estimate provides an upper bound on the dimension of the strange attractor [11].

Calculations based on dynamical methods provide more information than calculations based on metric methods. However, the drawbacks are similar: they depend on globally averaged

Figure 6: Evolution of a cube of initial conditions under a flow. A cube of initial conditions (a) is stretched (b), (c). If motion occurs in a compact domain, distant points must eventually be returned to closer proximity (c), (d). The deformed neighborhood then returns to the original neighborhood (a), and the process is repeated.

measures; they provide no information on the mechanisms which build up the strange attractor; and they provide no information on what might happen when control parameters are varied.

3. Topological methods are based on an idea due to Poincaré [12]. That is, we can understand dynamical systems if we understand how the flow affects various neighborhoods in the appropriate phase space. This method requires small data sets (much smaller than required for dimension calculations), degrades gracefully with noise, results in integer values, can be tested by internal consistency checks, and has predictive value in a number of different directions [2]. It predicts which new periodic orbits can be created or annihilated under both small and large parameter variations. Most important, it describes the stretching and squeezing mechanisms which operate together to build up a strange attractor and to organize all the unstable periodic orbits in the strange attractor in a unique way. At the present time the analysis tool based on topology can be applied only to low dimensional dynamical systems. This includes three dimensional dynamical systems, but also includes dynamical systems with only one positive Lyapunov exponent but which are strongly contracting, so that the Lyapunov dimension obeys $2 < d_L < 3$. This includes strange attractors which exist in 3-dimensional inertial manifolds, such as the one identified for the modified Hodgkin-Huxley equations.

The basic idea behind the topological analysis method is illustrated in Fig. 6. In this figure we begin with a blob of points (mathematicians call this a *neighborhood*) in phase space (Fig. 6a), and follow it as it is deformed under the flow. At first the blob is stretched (Fig. 6b). **Stretching** is responsible for 'sensitivity to initial conditions,' which is responsible for positive Lyapunov exponents. However, two points in phase space cannot continue to be stretched apart indefinitely if the dynamics occurs in a bounded region (mathematicians call this a *compact domain*) of phase space. Ultimately, distant points must be squeezed back together (Fig. 6c, 6d). **Squeezing** is the repetitive process that builds up the 'self-similar' fractal structure which exists in the contracting directions, and which is responsible for negative Lyapunov exponents.

Figure 6 is a cartoon of what occurs during one cycle of a process which builds up a strange attractor by the 'Smale horseshoe mechanism.' This derives its name in part from the horseshoe shape of the blob in phase space after it is deformed during one cycle, and in part from the fact that it was first described by Smale [13]. The mechanism itself is a simple 'stretch and fold' process which is repeated. It is essentially this process, a 'stretch and roll' mechanism, which generates strange attractors in the modified Hodgkin-Huxley dynamics.

We point out here what should be obvious, but which nevertheless should be stated. Topol-

Figure 7: One of the first branched manifolds studied by Birman and Williams [14]. This branched manifold describes the topological organization of all the closed magnetic lines of force established by a constant current flowing in a figure 8 knot.

ogy is *qualitative*, so it may not be clear how knowledge of the stretching and squeezing mechanisms which it provides is connected to the *quantitative* information resulting from metric and dynamical analysis methods. The qualitative becomes quantitative when we describe exactly how much stretching (the positive Lyapunov exponents) and how much squeezing (the negative exponents) goes on. Once these quantitative measures are introduced, the qualitative becomes quantitative. These exponents need not be constant: they can be position dependent. Using them as well as topological information, it is possible to compute fractal dimensions, scaling functions, and average Lyapunov exponents. However, from the metric and dynamical measures alone, it is not possible to recover topological information about stretching and squeezing mechanisms.

There is a very nice way to classify the stretching and squeezing mechanisms which generate a low dimensional strange attractor. It is based on a theorem by Birman and Williams [14]. This theorem was originally stated for three dimensional dissipative dynamical systems which possess a hyperbolic strange attractor, for which $\lambda_1 > \lambda_2 = 0 > \lambda_3$ and $\lambda_1 + \lambda_2 + \lambda_3 < 0$. Birman and Williams proved that it was possible to project the flow down along the stable direction onto a two-dimensional branched manifold. The branched manifold is essentially the unstable invariant manifold, with some singularities. In this process, the periodic orbits are projected onto the branched manifold also. Their topological organization is unchanged during the projection. The projection is similar to increasing the dissipation of the dynamical system ($\lambda_3 \to -\infty$), so that the dimension approaches 2 ($d_L = 2 + \lambda_1/|\lambda_3| \to 2$). Periodic orbits cannot change their topological organization during the projection because they would have to cross through each other, thus violating the uniqueness theorem of Ordinary Differential Equations.

One of the branched manifolds originally studied by Birman and Williams is shown in Fig. 7. This describes the organization of all the closed magnetic field lines (these are the analogs of periodic orbits for a dynamical system) produced by a constant current flowing through a wire tied into the shape of a figure 8 knot. It can be seen that the branched manifold is made up of two types of units, shown in Fig. 8.

Splitting Chart: This describes stretching. It contains a singularity: the splitting point. This represents initial conditions which propagate into a fixed point.

Joining Chart: This describes squeezing. It contains a different type of singularity: the branch line. This represents points at which information about the past is lost.

Figure 8: Building blocks for stretching and squeezing mechanisms. Left: A cube of initial conditions evolves (flow direction is down) by stretching in one direction, shrinking in the other. Both directions are transverse to the flow. In the limit of high dissipation the flow becomes two dimensional. The flows going to different parts of phase space are separated by a singular point ('splitting point'). This singular point describes initial conditions going to a fixed point. Right: Two cubes of initial conditions in different parts of phase space are squeezed together. In the high dissipation limit, the two branches are joined at a singular line ('branch line'). This singularity describes loss of information about the previous history of the flow.

These two types of two dimensional charts are limits of three dimensional neighborhoods in which stretching and squeezing take place. This relation is shown in Fig. 8. The two can be combined into a single type of chart ('joining and splitting') which includes both types of singularities and simultaneously describes stretching and squeezing.

Every branched manifold is made up of splitting charts and joining charts joined together in Lego© fashion, with no free ends. Alternatively, every branched manifold can be constructed from 'joining and splitting' charts, in which the output ends of charts are connected to the input ends of other (or the same) chart(s) by two dimensional bands which twist and writhe around in phase space in various ways.

The branches in a branched manifold are determined as follows. Extend each splitting point back against the flow direction to the nearest branch line. Then a branch is a component of the projected flow between two branch lines. For example, the branched manifold shown in Fig. 7 has eight branches.

It is possible to describe branched manifolds algebraically. The information which must be encoded includes:

Twisting: How the branches twist around their axes;

Crossing: How the branches cross over or under each other;

Joining: The order (from top to bottom) in which the branches are joined at a branch line, in the projection of the branched manifold which is adopted;

Connecting: Which branches are joined to which.

This information is encoded in two $N \times N$ matrices and an array with N components. Here N is the number of branches in the branched manifold.

Crossing Matrix T(i,j): This matrix encodes the topological information about twisting and crossing. The diagonal matrix element $T(i,i)$ describes the twist of branch i. This is the signed number of crossings of one edge of branch i over the other edge. The off-diagonal matrix element $T(i,j)$ is the signed number of crossings of the two branches i and j. The sign convention is the usual: take tangent vectors to the upper and lower components

Figure 9: Branched manifolds for four standard dynamical systems used to study chaotic dynamics: (a) periodically driven Duffing oscillator; (b) periodically driven van der Pol oscillator; (c) Lorenz equations; (d) Rössler equations.

(edge, branch) in the projection, and rotate the upper tangent vector into the lower tangent vector through the smaller angle. If the rotation is right handed, the sign is +1; if left handed, it is −1.

Joining Array J(i): This array encodes information about the order in which branches are joined at branch lines. One useful convention is: the smaller $J(i)$ is, the closer the branch is to the observer.

Markov Transition Matrix M(i,j): This matrix encodes information about which branches are connected to which. The convention adopted is: $M(i,j) = 1$ if branch i flows into branch j, zero otherwise.

The crossing matrix T, joining array J, and Markov transition matrix M for the branched manifold shown if Fig. 7 are also shown in that figure.

An algebraic description for a branched manifold is useful because it can be used to identify the periodic orbits which exist in a strange attractor, and to compute the topological organization of these orbits through their Linking Numbers.

The algebraic description of a branched manifold is not unique. For example, it changes if the branched manifold is viewed from a different perspective. Further, branched manifolds can be deformed in many ways without altering either the spectrum or the topological organization of the periodic orbits which they contain [14].

Four nonlinear dynamical systems which exhibit chaotic behavior have been extensively studied. These are, in historical order: the Duffing oscillator [15] which is periodically driven; the van der Pol oscillator [16] which is periodically driven; the Lorenz equations [17]; the Rössler equations [18]. The branched manifolds for the strange attractors which these four systems generate over a certain standard range of parameter values are shown in Fig. 9. It can be seen by visual inspection that these four branched manifolds are inequivalent. There is no deformation of one that converts it to any of the others. Alternatively: there is no similarity transformation that takes the matrix representation of one to the matrix representation of any of the others. This means that it is futile to search for a smooth change of variables which transforms any one system into any of the others.

Several remarks are in order:

1. A global Poincaré section for a dynamical system can be determined from its branched manifold. It is the union of the branch lines.

2. For simple systems (Duffing, van der Pol, Lorenz, Rössler), the period of a closed orbit is intuitively obvious. For more complicated systems the period is not so obvious. It is useful to define the period as the linking number (LN) of the orbit with the union of closed loops C_i [14]:

$$Period(orbit) = LN(\cup_i C_i, orbit) = \sum_i LN(C_i, orbit) \tag{21}$$

   Here C_i is a loop in R^3, the space which contains the branched manifold. Each loop encircles one or more branches of the branched manifold. The loops are chosen so that all periods computed in this way are positive integers, and as small as possible. For the branched manifold of the figure 8 knot (Fig. 7), one loop suffices, and it is the figure 8 knot.

3. The topological entropy of a chaotic dynamical system is bounded above by the maximum eigenvalue of the Markov transition matrix which describes the branched manifold for the strange attractor. If all periodic orbits allowed by the branched manifold actually exist in the strange attractor (*i.e.*, the attractor is hyperbolic), then equality occurs.

4. A strange attractor is classified by projecting it down to its branched manifold. Once it has been so projected, it can be recovered, to some extent, by the reverse process of 'expansion' or 'blow-up' [2] (*c.f.*, Fig. 8). In this process each two dimensional splitting and joining chart is replaced by its three dimensional counterpart, and branches are replaced by 'flow tubes' [2]. The exponents for these flow tubes can be adjusted to reflect the properties of the original attractor. In this blow-up process the global Poincaré section, the union of branch lines, blows up to a union of disks, each disk being the blow-up of a branch line. The definition of period remains unchanged.

5. There is a common perception that the topological program works only for highly dissipative dynamical systems. This is not so. The fact that one of the first branched manifolds discussed by Birman and Williams carried the organization for all closed field lines of a *conservative* system should be enough to dispell this misconception.

VII. Topological Analysis Program

It is possible to extract the information about the branched manifold which describes a low dimensional strange attractor directly from data. The procedure for doing this has come to be known as the Topological Analysis Program. It was first announced in a paper which analyzed data from the Belousov-Zhabotinskii reaction [19].

Perhaps the most surprising thing about this program is that it is possible to extract a set of integers from chaotic data, to test whether this set of integers is correct, and then to use this set of integers to make testable predictions.

The topological analysis program for low dimensional dynamical systems consists of several steps. These are summzrized in Fig. 10. We describe these steps below.

Figure 10: Topological Analysis Program consists of a number of steps. Unstable periodic orbits can be identified either before or after the embedding. The topological part of this program ends with Template Verification. Vertical arrows describe 'feedback loops' which are used to reject, or increase confidence in, the steps that are identified.

Locate Periodic Orbits. Periodic orbits are present in abundance in a strange attractor. As control parameters are changed, some may even be stable over intervals. In a hyperbolic strange attractor, all periodic orbits are unstable. They are dense in hyperbolic strange attractors. Their topological organization uniquely identifies the strange attractor, and is in fact the Achille's Heel by means of which the topological structure of the strange attractor may be identified. By topological structure, we mean the two dimensional branched manifold which describes the stretching and squeezing mechanisms which act together to build up the strange attractor.

It is often possible, especially in low $(2+\epsilon)$ dimensional strange attractors, to locate unstable periodic orbits. One powerful method is the 'method of close returns.' This method has been used in Sec. III to locate some of the period one orbits in a strange attractor generated by the modified Hodgkin-Huxley equations. These orbits were shown in Fig. 5.

Embed in a Phase Space. Since the topological structure is determined by the linking numbers of periodic orbits, and these are defined in three dimensional spaces, a means must be found to construct a three dimensional phase space. This problem has to be approached from different directions, depending on circumstances.

For three dimensional systems (Duffing, van der Pol, Lorenz, Rössler) it is sufficient to use the variables intrinsic to the model.

For higher dimensional systems (modified Hodgkin-Huxley equations), a means must somehow be found to project into a three dimensional space. The optimum would be to have a mathematical theorem that guarantees the existence of a 3-dimensional inertial manifold for the dynamics if the Lyapunov dimension of the strange attractor is less than 3. This should be accompanied by a prescription for the projection into the inertial manifold. Unfortunately, we haven't yet achieved this optimum situation. A fallback, which has been extremely useful in many fields, is the use of adiabatic elimination of fast ('slaved') variables. We have used this method in Sec. V to construct an effectively 3-dimensional dynamical system from the original 5-dimensional modified Hodgkin-Huxley equations. Another useful alternative is reduction of dimension using a Singular Value Decomposition [20].

In the real world, acquiring data is a difficult and expensive proposition. Usually one is happy with a scalar (one-dimensional) time series. This means we must somehow create 3-vectors from scalars. Several ways exist to do this. The default is the time delay embedding. Although this has been proposed independently by Packard *et al* [21], Mañé [22], and Takens [23], the original idea goes back to Whitney [24].

The basic idea is the idea of transversality. If two manifolds $M_1^{m_1}$ and $M_2^{m_2}$ of dimensions m_1 and m_2 are contained in a manifold of dimension N^n ($M_1^{m_1} \subset N^n$, $M_2^{m_2} \subset N^n$) then either they do not intersect ($M_1^{m_1} \cap M_2^{m_2} = \emptyset$), or they intersect in a manifold $\bar{M}^{\bar{m}} = (M_1^{m_1} \cap M_2^{m_2})$ of dimension $\bar{m} = (m_1 + m_2) - n$. If $\bar{m} \geq 0$, the manifold $\bar{M}^{\bar{m}}$ is stable under perturbations. If $\bar{m} < 0$, the intersection disappears under perturbation ($M_1^{m_1} \cap M_2^{m_2} \to \emptyset$). If a dynamical system of dimension m is to be embedded in R^n, then self-intersections of the embedded manifold M^m will generally occur unless $n - 2m < 0$ (*i.e.*, $n \geq 2m + 1$). At such self-intersections the uniqueness theorem of the theory of ODEs is generally violated. According to this theorem, to reconstruct the dynamics of a 3-dimensional system it is *sufficient* to embed it in a 7-dimensional space. However, it is not *necessary*, and our experience [2] has shown that it almost always suffices to embed data generated by a 3-dimensional dynamical system in a 3-dimensional space. We *always* attempt such an embedding first, and go to higher dimensional embeddings only when low dimensional embeddings fail.

A second embedding procedure is the differential embedding [2,19], where a vector time series $\mathbf{y}(t)$ is created from a scalar time series $x(t)$ by

$$x(t) \to (y_1(t), y_2(t) = \dot{y}_1(t), y_3(t) = \dot{y}_2(t)) \qquad y_1(t) = x(t) \tag{22}$$

Since the data are discretely sampled ($x(t) \to x(t_i) = x(i)$), the time derivatives are estimated by the usual difference formulas.

This embedding is useful for two reasons. First, it already has the desired dynamical system form. Since $dy_1/dt = y_2$ and $dy_2/dt = y_3$, it is sufficient to determine an equation of motion only for y_3. Second, in an embedding using three differentially related variables, it is a simple matter to compute linking numbers of periodic orbits. In Fig. 11 we show a projection of a phase space constructed with the differential embedding (22). The y_1 axis is horizontal, the y_2 axis is vertical, and the y_3 axis is out of the page. Now consider two segments which cross in the upper half plane $y_2 > 0$. The slope of either is given by

$$slope = \frac{dy_2}{dy_1} = \frac{dy_2/dt}{dy_1/dt} = \frac{y_3}{y_2} \tag{23}$$

It is then clear that $y_3 = (slope) \times y_2$. Thus, the larger the slope, the closer the observer. As a result, all crossings in the upper half plane are left handed with crossing number -1, and those in the lower half plane are right handed with crossing number $+1$. This makes computing linking numbers particularly convenient in this representation of the data (see below).

The differential-integral embedding is closely related to (22). The difference is that in this embedding $y_2(t) = x(t)$, so that $y_1(t) = \int^t (x(\tau) - \bar{x})d\tau$ and $y_3(t) = \dot{x}(t)$. This has the same two virtues as the differential embedding. It is different in the following two ways. As a general rule of thumb, each differential or integral operation on experimental data decreases the signal to noise ratio by an order of magnitude. Except for very clean data, in the differential embedding the coordinate $y_3 = d^2x/dt^2$ may have an unacceptable signal to noise ratio, since

Figure 11: Crossing information. In a differential embedding, all crossings in the upper half plane are negative, those in the lower half plane are positive.

S/N is reduced by two orders of magnitude. Unacceptable means, in this case, that we cannot compute linking numbers. For the differential-integral embedding, both y_1 (the integral of x) and y_3 (the differential of x) have S/N reduced by only one order of magnitude, which is often acceptable. However, since y_1 integrates the data (subtracting out the data average), it is susceptible to long term secular trends. These can produce nonstationarity in the embedded data which is harmless in all other types of embeddings. When this occurs, the nonstationarity must be addressed by appropriate filters [2].

Another method for constructing vector from scalar data involves the Singular Value Decomposition [2,20]. This use of the SVD has been discussed in the literature and used effectively in many applications.

Topological Organization of Periodic Orbits.

Once a selection of periodic orbits has been extracted from the data and an embedding in R^3 has been adopted, it becomes possible to compute the topological invariants of these orbits. The topological invariants which are always useful are the Linking Numbers of pairs of orbits and the local torsions of individual orbits. If the attractor is contained in a solid torus $D^2 \times T^1$ (D^2 is the two dimensional disk and T^1 is the circle) then the Relative Rotation Rates [25] are even more powerful topological invariants than Linking Numbers.

In a differential embedding, linking numbers of orbit pairs are easily computed by counting the number of crossings in the lower half and upper half planes, subtracting the second from the first, and dividing by 2.

Identify a Branched Manifold.

The next step is to use the topological information gained in the previous step to guess an appropriate branched manifold. For complicated branched manifolds, such as that for the figure 8 knot, this isn't easy. For branched manifolds which can be embedded in the solid disk $D^2 \times T^1$ the task is simpler. In this case, each branch carries a period one orbit. The topological structure of the branched manifold is determined by

- Computing the linking numbers of all the period one orbits with each other. The off-diagonal matrix element $T(i,j)$ is twice this integer.

- Computing the local torsion of each period one orbit. This gives the diagonal matrix elements $T(i,i)$.

- Computing the linking numbers of some of the period two orbits with the period one orbits. This gives the array information $J(i)$.

In case some of the period one and/or period two orbits are not available, higher period orbits can be used to fill in the missing information.

This procedure is not entirely straightforward. The reason is as follows. The periodic orbits in phase space are simple closed curves. The periodic orbits on branced manifolds are labeled by the branches which are traversed. Each periodic orbit is labeled by a sequence of symbols. The problem is to identify a symbol sequence (on the branched manifold) with a closed curve (in phase space). In other words, we need a 1-1 mapping between orbits and symbols. When the return map is very 'thin,' as is the case shown in Fig. 4 for the modified Hodgkin-Huxley equations, creating this 1-1 map (a symbolic dynamics) is straightforward. In fact, we did this without even mentioning any problems in Sec. V. However, for systems which are not strongly dissipative, creating consistent partitions on appropriate Poincaré sections in phase space is a longstanding problem [26]. Fortunately, Plumecoq and Lefranc have now proposed a useful solution to the partition problem [26].

Validate the Branched Manifold.

Once a branched manifold has been proposed (tentatively identified), it is possible to compute the Linking Numbers and Relative Rotation Rates of all the periodic orbits which the branched manifold supports. These must be compared with the corresponding topological invariants for all the remaining periodic orbits extracted from the data, which were not used in the first place to identify the branched manifold. If the two sets of topological invariants (one from the orbits extracted from data, one from the corresponding orbits on the branched manifold) agree, then we have added confidence that the initial identification of the branched manifold was correct. If there is not complete disagreement, then either the branched manifold was identified incorrectly, or the partition needs to be modified.

The problems of creating a symbolic dynamics (creating a partition and a 1-1 mapping between symbol sequences and periodic orbits in phase space) and identifying the correct branched manifold are *global* problems. They must be solved *simultaneously*. There must be complete agreement between the topological invariants of all orbits extracted from data and their corresponding symbol sequences on a branched manifold.

This internal self consistency check (rejection criterion) is absent from both the metric and dynamical approaches to the analysis of chaotic data.

Strictly speaking, the Topological Analysis Program stops here. However, there is always the desire to do better: to construct an appropriate model to describe data which has been analyzed. We describe here the next two steps which can be taken in this effort.

Construct a Flow Model.

A dynamical system model has the form $dy/dt = F(y)$, $y \in R^n$. To model data, the functions $F_i(y)$ are usually expanded as a linear superposition of some set of basis functions Φ_α

$$\frac{dy_i}{dt} = \sum_\alpha A_{i,\alpha}\Phi_\alpha(y) \tag{24}$$

This is a *General Linear Model*, so standard methods (least squares, maximum liklihood) can be used to estimate the expansion coefficients $A_{i,\alpha}$. Standard methods (χ^2 test) can also be used to test whether this model is any good.

For the present purposes, $y \in R^3$. For a differential embedding two of the functions F_i are already known: $F_1(y) = y_2$, $F_2(y) = y_3$. Only the third function must be modeled. Thus the differential embedding has the added utility that it reduces by a factor of three the effort which is required to develop a model of the dynamics [2].

Once a model has been created, the qualitative validity of the model can be tested. This is done by subjecting its output to a Topological Analysis. If the branched manifolds determined from the data and from the model are not equivalent, the model is not a good representation of the data, and must be rejected. On the other hand, if the branched manifolds are the same, the model cannot be rejected.

Validate the Model.

A model of a physical process may pass the qualitative test just described, and still not be a very good representation of the dynamics. It would be useful to have some goodness of fit criterion for nonlinear models, analogous to the χ^2 goodness of fit test for linear models.

At the present time there is a very useful goodness of fit criterion for nonlinear models. Unfortunately, it lacks a quantitative underpinning. It is hoped that this quantitative underpinning will be supplied during the next decade.

The idea behind this goodness of fit test was proposed by Fujisaka and Yamada [27] and independently by Brown, Rulkov, and Tracy [28]. It goes back to an observation by Huyghens made 300 years ago. Huyghens observed that two pendulum clocks on opposite walls gained/lost time at slightly different rates. When they were placed on the same wall close enough they would synchronize their timekeeping.

The synchronization effect provides the basis for a nonlinear goodness of fit test. The idea is as follows. Assume that a real physical system satisfies the dynamical system equation $\dot{x} = F(x)$, and a model for this process is $\dot{y} = G(y)$, $x \in R^n, y \in R^n$, where y is supposed to describe x. Then in general, no matter how good the model is, sensitivity to initial conditions and sensitivity to control parameter values will guarantee that the distance between $x(t)$ and $y(t)$ will eventually become large.

A perturbation term can be added to the model equation which reduces y_i when it gets larger than x_i and increases y_i when it gets too small. A *linear* perturbation with this property has the form $-\lambda_i(y_i - x_i)$. The appropriately modified dynamical system becomes

$$\frac{dy_i}{dt} = G_i(y) - \lambda_i(y_i - x_i) \tag{25}$$

If the model is 'good,' a small value of $\lambda = (\lambda_1, \lambda_2, \cdots, \lambda_n)$ will cause the model output to follow the data. We then say that the data *entrain* the model output. The better the model, the smaller the value of λ which causes entrainment. The entrainment test has been used effectively to test the validity of some models [2].

Unfortunately, the entrainment test for nonlinear systems has not yet been made quantitative, as has the χ^2 test for linear systems.

Figure 12: Strange attractor of Fig. 3 replotted: (a) in the differential embedding; (b) in the integral-differential embedding.

VIII. Topological Analysis of the Modified Hodgkin-Huxley Equations

The analysis of strange attractors generated by the modified Hodgkin-Huxley equations follows the procedure described in the previous section.

The first step is the determination of unstable periodic orbits. This has already been done. It is facilitated using an appropriate first return map. For temperature regions in which the output is periodic (*e.g.*, $T \sim 20^oC$), the first return map consists of a single point. For regions in which a strange attractor exists, the first return map has the form shown in Fig. 4. From this map it is possible to locate initial conditions for unstable period one orbits which exist in the strange attractor. The second iterate of the map has been used to locate period two orbits. The p^{th} return allows location of period p orbits.

The second step in the topological analysis program is the construction of a useful embedding. One already exists (*c.f.* Fig. 3): it is the projection into the three dimensional inertial manifold (y_1, y_4, y_5). However, we also constructed differential and integral embeddings based on single variables. The strange attractor shown in Fig. 3 in the (y_1, y_4, y_5) embedding is replotted in the differential embedding (Fig. 12a) and integral-differential embedding (Fig. 12b) obtained from the coordinate y_4. These embeddings are useful since they simplify the computation of linking numbers. We computed the branched manifold for this system in each of these embeddings, and found it to be embedding independent.

The third step is the computation of the topological invariants of the unstable periodic orbits extracted from the strange attractor. The local torsion of the period one orbits was computed by displacing the initial condition slightly from that for the closed orbit, and computing the number of crossings of the closed orbit with its perturbation (which wasn't closed). The local torsion of the orbit nr is $\pi \times 2n$ while that for the orbit nf is $\pi \times (2n-1)$. The relation between this sequence of orbits and local torsions is systematic:

$$\begin{array}{cccccccccc} 6f & 5r & 5f & 4r & 4f & 3r & 3f & 2r & 2f & 1r \\ 11 & 10 & 9 & 8 & 7 & 6 & 5 & 4 & 3 & 2 \end{array} \tag{26}$$

The local torsions are measured in units of π in the series above. The linking numbers of adjacent period one orbits with local torsions $n\pi$ and $(n+1)\pi$ is $n/2$ or $(n+1)/2$, whichever is integer.

Two branched manifolds are compatible with the information obtained from the period one orbits. We know this because an identical mechanism has already been studied in the driven

Figure 13: (a) Inwards and (b) Outward winding scroll templates.

Duffing equation [29] and in the YAG laser [30]. Both branched manifolds are simple extensions of the branched manifold which describes the Smale horseshoe mechanism, which is illustrated in Fig. 6. Both of these branched manifolds roll up: one from outside to inside; the other from inside to outside. These two scrolling mechanisms are shown in Fig. 13. These figures summarize how neighborhoods in phase space are deformed under the flow. The algebraic description for each of these two branched manifolds is presented below each of the branched manifolds.

It can be seen from these figures that the topological organization of adjacent branches is identical in both the inward winding scroll and the outward winding scroll. Therefore, it is impossible to distinguish between the two branched manifolds on the basis of orbits extracted from a strange attractor that contains only two distinct, adjacent, unstable period one orbits. In order to distinguish between the two, we must study a strange attractor that possesses at least three inequivalent unstable period one orbits. Such strange attractors exist only at lower temperators.

For this reason, we concentrated on the strange attractor which exists at 12.6° C. The return map shows intersections with six contiguous branches, but we were able to find only three unstable period one orbits in the strange attractor. These were $5f, 4r, 4f$. The other three branches $(6f, 5r, 3r)$ are extremely unstable. That the orbits located belonged to contiguous branches simplified the calculations somewhat.

The linking numbers for all three pairs of period one orbits in both branched manifolds are 8/2=4. This can be seen from the template matrices, since $T(4f, 4r) = T(4f, 5f) = T(4r, 5f) = 8$ in both matrices. The two branched manifolds could only be distinguished by locating unstable period two orbits and computing their linking numbers. In fact, the orbits AB and BC $(A = 4f, B = 4r, C = 5f)$ have identical linking numbers with the period one orbits in both branched manifolds. It is only the period two orbit AC which has different linking numbers with the period one orbits in the two branched manifolds. The linking numbers in the two cases are

	Outside to Inside	Inside to Outside
$LN(A, AC)$	7	8
$LN(B, AC)$	8	8
$LN(C, AC)$	8	9

(27)

These linking numbers were computed using a general purpose code designed to compute linking numbers and relative rotation rates for periodic orbits [31]. The inputs to the code consist of the algebraic description of a branched manifold and a list of orbits by their symbolic dynamics. The ouput consists of a table of their Linking Numbers or a table of their Relative Rotation

Figure 14: Distinguishing between (a) outside to inside and (b) inside to outside scroll templates. Three branches $(4f, 4r, 5f)$ of the two scroll templates are shown. The three period one orbits are shown as vertical lines through the middle of each branch. The period two orbit $(4f, 5f)$ is shown going through the outer edge of the two exterior branches. Linking Numbers of this period two orbit with the three period one orbits are half the sum of the signed crossings shown, plus half the sum of the additional 16 crossings in the return flow, which has 8 half twists.

Figure 15: Periodic orbits in the differential embedding. (a) $4f$; (b) $4r$; (c) $5f$; (d) $(4f, 5f)$.

Rates.

These linking numbers were also computed visually, as illustrated in Fig. 14. The stretching and squeezing sections of the two branched manifolds are shown, with the outside to inside scroll on the left. The three period one orbits are shown propagating through the middle of the three branches. The period 2 orbit AC is shown propagating through the two outside branches. The linking number of the period two orbit (half the signed number of crossings) with each of the period one orbits is shown beneath each of the branches. For the outside to inside scroll these three integers are $(-1, 0, 0)$, while for the inside to outside scroll the three integers are $(0, 0, +1)$. Each must be added to the linking number in the return part of the map. This consists of 8 half-twists. These entangle each period one orbit with the period two orbit with a linking number of 8. The results of this computation are summarized above in Equ. (27).

We therefore located the period 2 orbit $AC = (4f, 5f)$ in the second return map at $T = 12.6^oC$. This orbit is shown in two embeddings in Figs. 15 and 16. The Linking Numbers of this orbit with the three period one orbits were computed. This computation showed clearly that the branched manifold which describes the strange attractor generated by the modified Hodgkin-Huxley equations is the outside to inside scroll template.

Table 2 provides the Linking Numbers of all orbits up to period three which can be found in the three branches $4f, 4r, 5f$ of this branched manifold.

Figure 16: Periodic orbits in the integral-differential embedding. (a) $4f$; (b) $4r$; (c) $5f$; (d) $(4f, 5f)$.

Table 2: Linking numbers for all orbits up to period three that occur on the three-branch template: $A = 4f, B = 4r, C = 5f$.

	A	B	C	A	A	B	A	A	A	A	A	A	B	B
Orbits				B	C	C	A	A	B	B	C	C	B	C
							B	C	B	C	B	C	C	C
A		4	4	7	7	8	11	11	11	11	11	11	12	12
B	4		4	8	8	8	12	12	12	12	12	12	12	12
C	4	4		8	8	9	12	12	12	13	12	13	13	13
AB	7	8	8		15	16	22	22	22	23	22	23	24	24
AC	7	8	8	15		16	22	22	23	23	23	23	24	24
BC	8	8	9	16	16		24	24	24	25	24	25	26	26
AAB	11	12	12	22	22	24		33	33	34	33	34	36	36
AAC	11	12	12	22	22	24	33		34	35	34	35	36	36
ABB	11	12	12	22	23	24	33	34		35	34	35	36	36
ABC	11	12	13	23	23	25	34	35	35		35	36	37	38
ACB	11	12	12	22	23	24	33	34	34	35		35	36	36
ACC	11	12	13	23	23	25	34	35	35	36	35		37	38
BBC	12	12	13	24	24	26	36	36	36	37	36	37		39
BCC	12	12	13	24	24	26	36	36	36	38	36	38	39	

IX. Jelly Rolls

The branched manifold which describes the strange attractor generated by the modified Hodgkin-Huxley equations has been observed previously in both the periodically driven Duffing oscillator [29] and in experimental data generated by a YAG laser [30]. It has been affectionately named the 'jelly roll' (Duffing) and the 'gateau roulé' (YAG laser).

The three systems which exhibit this jelly roll behavior are all slightly different. The YAG laser is a nonautonomous dynamical system, driven by external forcing with fixed periodicity. The Duffing oscillator is also a nonautonomous dynamical system, driven by external forcing with fixed periodicity. However, this stretching and squeezing mechanism operates in an identical way over two half-cycles, so that the branched manifold for the Duffing oscillator is actually the second iterate of the jelly roll. In both systems, at any given forcing frequency, all coexisting unstable period one orbits have the same period. By contrast, the modified Hodgkin-Huxley equations form an autonomous dynamical system. Coexisting unstable period one orbits have somewhat different periods. This can be seen from the original bifurcation diagram (Fig. 1). The time duration of a period one orbit is the sum of its interspike time intervals. This sum increases nonmonotonically as T decreases, with peaks at intermittency, that is, when orbits of type nr are present.

The jelly roll template will be used to provide a very simple, intuitive, and appealing description of the dynamics of receptors with subthreshold oscillations. The description involves two useful ratios. We first provide this description for the YAG laser. We then describe the small modifications needed to carry over the description to receptors with subthreshold oscillations.

As a first step, we unroll the scroll shown in Fig. 13a. The result is the distorted rectangle shown in Fig. 17. The flow is from left to right. At the beginning of a period ($t = 0$) a set of

Figure 17: Intuitive description of scroll dynamics for the YAG laser. The scroll shown in Fig. 13 is unrolled. A set of initial conditions flows from the left edge to the right, drifting upward and expanding. The right end is then rolled back up and the flow is reinjected back into the left edge. For the strange attractor generated by the modified Hodgkin-Huxley equations, the dark line indicates the duration of a period one orbit.

initial conditions exists along the vertical edge at the left. The vertical edge at the right ($t = P$) marks the end of a period. Fiducial marks measure the right hand edge in units (*i.e.*, π) of the left hand edge. Each unit carries an integer which reflects the torsion when this structure is rolled back up to the original scrolled structure.

As time evolves, the set of initial conditions (left hand edge) moves to the right, stretches (sensitivity to initial conditions, positive Lyapunov exponent), and drifts upward (increasing torsion). When the set of initial conditions arrives at the right hand edge, it is spread over several contiguous segments. The ratio of its length at the right hand edge to its original length is $R = e^{\lambda_1}$, where λ_1 is the positive Lyapunov exponent ($R =$ stretch ratio). The rate of upward drift is the ratio of the two time scales of the laser. There is an intrinsic oscillation time τ, and the externally imposed drive period, P. The image of the left hand edge extends along the right hand edge from about (P/τ) to about $(P/\tau) + R$.

The two ratios which characterize the dynamics are the time scale ratio P/τ and the expansion ratio $R = e^{\lambda_1}$.

1. The longer the period, P, the more scrolling (torsion) occurs.

2. The larger the stretching, R, the more branches are involved in the strange attractor.

Only slight modifications are required to port this intuitive description from the nonautonomous YAG laser to the autonomous receptor with subthreshold oscillations. In the latter case the period depends on the orbit. We have indicated this by a wavy solid line in Fig. 17. The role of P, the period of the external drive in the YAG laser, is replaced by $1/T$ ($T =$ temperature) in the modified Hodgkin-Huxley equations.

We now cut away all the branches which are not visited in this deformed rectangle, and rescroll the remaining branches. The resulting structure has the form shown in Fig. 18a. What happens next can best be illustrated using a cut rubber band, half a pair of suspenders, or a stretchy belt (all of which are useless!). Imagine taking one of these deformable structures, stretching it by pulling it along its long axis, and then twisting it about its long axis several times. What results has the form shown in Fig. 18a. If the tension is now relaxed, the structure 'untwists,' as shown in Fig. 18b. Mathematicians would describe this deformation as the conversion of twist for writhe. Indeed, there is a well known conservation relation among

Figure 18: Illustration of Equ. (??). (a) A rubber band is twisted about its stretched length. (b) When the tension is relaxed, it deforms, exchanging twist for writhe. (c) When the two ends are reconnected, the shape of the flow generated by the modified Hodgkin-Huxley equations is apparent.

the three quantities Link, Twist, and Writhe:

$$\text{Link} = \text{Twist} + \text{Writhe} \tag{28}$$

Mathematically, this is a remarkable relation, since neither term on the right is a topological quantity. They are both geometric, and when computed, may be real- rather than integer-valued. However, their sum is a topological quantity and always an integer [32].

In fact, one does not even have to go so far as using rubber bands or belts to visualize the transformation of twist to writhe. Anyone who has used a telephone (not cordless) has experienced this. This also occurs in DNA.

We make a geometrical model of the flow in the reduced phase space of the modified Hodgkin-Huxley model as follows. We relax the twist out of the branched manifold almost entirely. This converts, for example, 4 full twists on the branch $4r$ into 4 loops (writhes) without twist. The resulting structure mimics very well the flow in the phase space. Passage through the maximum of each loop corresponds to a spike in a burst. This is indicated in Fig. 18c.

It is not difficult to make predictions about what happens when control parameters are changed. The flow is pushed to contiguous branches. In the algebraic description of the branched manifold, the topological matrix $T(i,j)$ remains unchanged, as does the joining information contained in the array $J(i)$. The only part of the algebraic description which changes with control parameters is the Markov transition matrix. For flows involving branches $4f, 4r, 5f$ this matrix is

Label	Torsion	2	3	4	5	6	7	8	9	10	11
$1r$	2	0	0	0	0	0	0	0	0	0	0
$2f$	3	0	0	0	0	0	0	0	0	0	0
$2r$	4	0	0	0	0	0	0	0	0	0	0
$3f$	5	0	0	0	0	0	0	0	0	0	0
$3r$	6	0	0	0	0	0	0	0	0	0	0
$4f$	7	0	0	0	0	0	1	1	1	0	0
$4r$	8	0	0	0	0	0	1	1	1	0	0
$5f$	9	0	0	0	0	0	1	1	1	0	0
$5r$	10	0	0	0	0	0	0	0	0	0	0
$6f$	11	0	0	0	0	0	0	0	0	0	0

(29)

As control parameters are changed (*e.g.*, the ambient temperature), the block of 1's on the diagonal moves up or down the diagonal, possibly contracting to a 2×2 submatrix, perhaps

Figure 19: Two projections of a 'writhing torus' with writhe = 2 [33]. This figure was kindly supplied by J. Palencia.

expanding to a 4×4 matrix. The direction in which the allowed transition block moves depends on the ratio P/τ in the YAG laser, or its analog in the nerve cell. The size of the block depends on the stretching factor or Lyapunov exponent, and is $n\times n$, where $n=[R]+1$ or $[R]+2$, $[R]$ is the integer part of R, and $R=e^{\lambda_1}$.

X. Flows Without Equations

Branched manifolds provide more than a means of classifying strange attractors. They even provide more than a very good representation of the flow in strongly dissipative strange attractors of dimension $2+\epsilon$, $\epsilon\sim0$. They provide a means for accurately representing the flow in strange attractors which are far from the dissipative limit (ϵ not small).

The basic idea is that the branched manifold provides a 'backbone' or 'skeleton' for the flow. If one 'blows up' by expanding in the transverse direction, this is the same as expanding against the contracting direction. This replaces two dimensional splitting and joining charts by their three dimensional counterparts (*c.f.*, Fig. 8), and replaces two dimensional branches by three dimensional 'flow tubes' [2]. The result is a flow in R^3 which has the topological organization of the initial strange attractor, but for which the flow is now generated without the benefit of dynamical system equations of motion.

How does this work for the modified Hodgkin-Huxley equations? Flow modeling of this type has already been done for the Duffing oscillator [29]. We simply take the results of that study and apply them to the current problem, with appropriate modifications.

The flow takes place in a topological disk $D^2\times T^1$, which has been deformed by the conversion of twist to writhe. Two views of a structure of this type ('writhing torus'), with a writhe of 2, are shown in Fig. 19 [33]. We first imagine the flow to take place within a solid cylinder. Then we map the cylinder into the writhing torus, identifying the two ends of the cylinder. This produces a strange attractor with the correct topological structure, provided suitable care is taken. We will describe the necessary 'suitable care' below.

The flow in the cylinder is modeled in two phases. The two processes described in Fig. 17 provide the skeleton for this model. However, those described in Fig. 17 are noninvertible, while the model we provide below is for an invertible map, and subsequently, for a flow.

The first phase, which models stretching, occurs from $s=0$ to $s=1$ (s measures distance along the axis of the cylinder of length 2). In this phase, a set of initial conditions in a strip at $s=0$ is stretched out and rotated around the axis of the cylinder. The second phase, which models squeezing, occurs from $s=1$ to $s=2$. In this phase, a set of initial conditions, the circle at $s = 1$, is deformed into the interior of an open strip in the interval $0 \leq \theta \leq \pi$ at $s = 2$. The cylinder is wrapped around, with the end at $s = 2$ identified with the end at $s = 0$.

First, we describe the mappings which take initial conditions to final states in the two processes.

In the first (stretching) process, a set of initial conditions at $s = 0$ in a thin strip extending from $\theta = 0$ to $\theta = \pi$ is deformed into a thin strip at $s = 1$ extending from $\theta = \phi$ to $\theta = \phi + \lambda\pi$ (*c.f*, Fig. 20a). The outer and inner edges of the strip are defined by $ae^{-\gamma\theta}$ and $be^{-\gamma\theta}$. For a point with coordinates (r_0, θ_0) in the first strip, the map, $M_{1\leftarrow 0}(r_0, \theta_0)$, from $s = 0$ to $s = 1$ is

$$\begin{array}{ccccc} \theta_0 & \rightarrow & \theta_1 & = & \phi + \lambda\theta_0 \\ r_0 & \rightarrow & r_1 & = & r_0 e^{-\gamma(\theta_1 - \theta_0)} \end{array} \tag{30}$$

In this map the 'drift' is measured by the angle ϕ, and the increase in torsion is measured by the ratio ϕ/π. The parameter λ is the stretch factor R. The parameter γ describes the dissipation: how quickly the flow spirals down to the axis of the cylinder. At $\theta = 0$ the strip has outer and inner radii a and b. In order to guarantee invertibility of this map, we require $ae^{-2\pi\gamma} < b$.

In the second (squeezing) process, a set of initial conditions at $s = 1$ in the interior of a circle of radius a is mapped into the interior of the strip at $s = 2$ extending from $\theta = 0$ to $\theta = \pi$ (*c.f.*, Fig. 20b). This is conveniently done in two stages. First, the circle is transformed into a long, thin ellipse by squeezing along one diameter. Then this ellipse is mapped into the interior of the strip described above. For a point in the circle with coordinates $(r_1, \theta_1) \rightarrow (x_1, y_1) = (r_1 \cos\theta_1, r_1 \sin\theta_1)$, the map $M_{2\leftarrow 1}(r_1, \theta_1)$ from $s = 1$ to $s = 2$ is

$$\begin{array}{ccccccc} \text{Circle} & \rightarrow & \text{Ellipse} & & x' & = & \frac{1}{2}(a-b)(x_1/a) \\ (x_1, y_1) & \rightarrow & (x', y') & & y' & = & y_1 \\ & & & & & & \\ \text{Ellipse} & \rightarrow & \text{Strip} & & \theta_2 & = & \frac{1}{2}(\xi_1 + \xi_2) + \frac{1}{2}(\xi_1 - \xi_2)(y'/a) \\ (x', y') & \rightarrow & (r_2, \theta_2) & & r_2 & = & \left[\frac{1}{2}(a+b) + x'\right] e^{-\gamma\theta} \end{array} \tag{31}$$

In this map the two angles $0 \leq \xi_2 < \xi_1 \leq \pi$ describe how extended the mapping of the ellipse into the strip is.

The map from one end of the cylinder to the other is the composition of the two maps above

$$(r_2, \theta_2) = M_{2\leftarrow 0}(r_0, \theta_0) = M_{2\leftarrow 1}(r_1, \theta_1) \cdot M_{1\leftarrow 0}(r_0, \theta_0) \tag{32}$$

Iteration of this composition map can then reproduce the dynamics which is observed on a plane, for example, a Poincaré section of the flow.

This map is fairly complicated. It depends on the seven unfolding parameters $(a, b, \phi, \lambda, \gamma, \xi_1, \xi_2)$. It has been studied over a limited range of these parameters [29]. In this range of control parameter values, it describes the alternation between periodic and chaotic behavior in periodically driven dynamical systems, with sequential increase of torsion (number of spikes/burst) as the ratio of P/τ increases (modeled by ϕ/π above). This model also describes the bifurcation sequences that can occur when branches with higher torsion are created and those with lower torsion are annihilated. It clearly shows a 'snake' of period one orbits as a function of the

Figure 20: Mappings $D^2(s=0) \rightarrow D^2(s=1) \rightarrow D^2(s=2)$. Top: The cylinder has circular cross sections at $s=0$, $s=1$, and $s=2$. (a) The cross section at $s=0$ is mapped to the cross section at $s=1$ according to Equ. (30). The shaded region in the strip on the left spirals around and down toward the axis of the cylinder. (b) The cross section at $s=1$ is mapped to the cross section at $s=2$ in two steps according to Equ. (31). First, the disk is compressed to thickness $a-b$ along one axis. Second, this long thin ellipse is mapped to the strip extending from $\theta=0$ to $\theta=\pi$ in the disk at $s=2$. Top right: The sigmoidal function $f(s)$ which interpolates a flow from a map has derivative(s) equal to zero at both ends.

Figure 21: Period one snake. For any value of ϕ, one or more period one orbits exist in the map (32). As ϕ increases, these orbits are created and annihilated in a systematic way. In the modified Hodgkin-Huxley flow, period one behavior nf and nr occurs along the branches $2n-1$ and $2n$, respectively.

parameter ϕ/π (*c.f.*, Fig. 21). As ϕ increases, branches with torsion $2n$ and $2n+1$ (*e.g.*, 4 and 5) come into existence via saddle node bifurcations, and then branches with torsion $2n-1$ and $2n$ (*e.g.*, 3 and 4) go out of existence via inverse saddle node bifurcations. This is the sequence of events that occurs in the bifurcation diagram of the modifed Hodgkin-Huxley equations as the temperature is lowered. The even (orientation preserving) branches are unstable when born, and remain unstable throughout their lives. The unstable period one orbit nr occurs on the branch with torsion $2n$. Orbit nf occurs on the branch with torsion $2n-1$. Bifurcation sequences can occur along the odd branches. However, these bifurcation sequences must reverse themselves before the odd branches are annihilated, for example, as the temperature is lowered.

Equation (32) above defines a *map* from one face of a cylinder at $s=0$ to another face at $s=2$. The modified Hodgkin-Huxley equations define a *flow*. It is possible to construct a flow from a map by simple interpolation schemes. For example, if $x \in R^n$ ($n=2$ in our case) has values x_0 at $s=0$ and x_1 at $s=1$, then it is a simple matter to interpolate at intermediate positions $0 \leq s \leq 1$ by means of a weighted average:

$$x(s) = x_0 \times (1 - f(s)) + x_1 \times f(s), \qquad 0 \leq s \leq 1, \qquad f(0)=0, f(1)=1 \tag{33}$$

The simplest interpolation is linear, with $f(s)=s$. This interpolation has the disadvantage of having discontinuous first derivatives at the endpoints of the interval. To remove this disadvantage, it is useful to use a sigmoidal shaped function $f(s)$ with the properties

$$\begin{array}{llll} f(0)=0 & f^{(1)}(0)=0 & \cdots & f^{(k)}(0)=0 \\ f(1)=1 & f^{(1)}(1)=0 & \cdots & f^{(k)}(1)=0 \end{array} \tag{34}$$

This guarantees that the flow and its first k derivatives ($f^{(k)}(1)$ is the k^{th} derivative of f, evaluated at $s = 1$) are continuous everywhere. A similar interpolation can be used to create a smooth flow between the faces of the cylinder at $s = 1$ and $s = 2$.

Once a smooth flow has been constructed in the cylinder, it is possible, by 'wrap-around,' to generate a smooth flow in the torus $D^2 \times T^1$ by identifying the end at $s = 2$ with the end at $s = 0$.

In order to generate a flow of the type shown in Fig. 3, the cylinder should be mapped into a writhing torus of the type shown in Fig. 19. There are two subtleties about this map (*i.e.*, the 'suitable care' which must be taken):

1. All radii of curvature of the writhing torus must be sufficiently large. Otherwise, singularities of the involution map will lie inside the image of the cylinder, and the uniqueness theorem of the theory of Ordinary Differential Equations will be violated.
2. The writhe of the torus and the twist of the flow must add to the proper linking number (*c.f.*, Equ (28)). The writhe of the torus is its number of loops (*c.f.*, Fig. 19), while the twist of the flow is determined by the angle ϕ.

The Lyapunov exponents and Lyapunov dimensions for any of the flows defined in this way can be estimated as follows. The Jacobian for the map $M_{1\leftarrow 0}$ is the ratio of two areas, the area $A(0)$ of the strip in the disk at $s = 0$, and the area $A(1)$ of the elongated strip in the disk at $s = 1$. The area of the original strip is $A(0) \sim \pi(a-b)e^{-\gamma\pi/2}$, while its image has area $A(1) \sim \lambda\pi(a-b)e^{-\gamma[\phi+\lambda\pi/2]}$. As a result,

$$J_0 \sim \frac{A(1)}{A(0)} \sim \frac{\lambda\pi(a-b)e^{-\gamma[\phi+\lambda\pi/2]}}{\pi(a-b)e^{-\gamma\pi/2}}$$

In a similar way, the Jacobian of the second map is the ratio of areas. The ratio of the ellipse to the circle is $\sim (a-b)/(2a)$. The ellipse is stretched by a factor $(\xi_1 - \xi_2)/2$ and squeezed by a factor of $e^{-\gamma(\xi_1+\xi_2)/2}$ on being mapped into the strip in the disk at $s = 2$, so that

$$J_1 \sim \frac{A(2)}{A'(1)} \sim \frac{a-b}{2a}\frac{\xi_1-\xi_2}{2}e^{-\gamma(\xi_1+\xi_2)/2}$$

The product of these two Jacobians is equal to $e^{\lambda_1+\lambda_2+\lambda_3}$, where λ_i are the Lyapunov exponents for the flow. In regions where chaotic behavior is observed, $\lambda_1 > 0$ and $\lambda_3 < 0$. The exponent along the flow direction (λ_2) is zero. Taking logarithms, we find

$$\lambda_1 + \lambda_3 \sim \ln(\lambda) - \left\{\gamma(\phi + \lambda\frac{\pi}{2}) + \gamma\left(\frac{\xi_1+\xi_2}{2} - \frac{\pi}{2}\right) + \ln(\frac{a}{a-b}) + \ln(\frac{\pi}{\xi_1-\xi_2}) + \ln(\frac{4}{\pi})\right\} \quad (35)$$

If it is a good approximation to identify the factor λ with the stretch factor $R = e^{\lambda_1}$, then $\lambda_1 \sim \ln(\lambda)$. The negative Lyapunov exponent, λ_3, is then what is left over in the expression above. This has larger magnitude than $\lambda_1 = \ln(\lambda)$, since the map $M_{2\leftarrow 0}$ contracts areas. ¿From these expressions, we derive an estimate for the Lyapunov dimension of the strange attractor generated by the interpolated flow

$$d_L \simeq 2 + \frac{\ln(\lambda)}{\left\{\gamma(\phi + \lambda\frac{\pi}{2}) + \gamma\left(\frac{\xi_1+\xi_2}{2} - \frac{\pi}{2}\right) + \ln(\frac{a}{a-b}) + \ln(\frac{\pi}{\xi_1-\xi_2}) + \ln(\frac{4}{\pi})\right\}} \tag{36}$$

This estimate holds independent of the interpolating functions $f(s)$ used to create smoothe flows from the maps.

Although the process of creating flows without dynamical equations of motion involves a fair amount of bookkeeping, it has the virtue that it is relatively straightforward and the topological structure of the strange attractor can easily be controlled: it is an input. In addition, it is likely to be easier to create models of interacting neurons through coupled geometric models of the type just described, than by proliferating sets of dynamical equations of motion, and then searching through a very large control parameter space for the subset of values which reproduces the observed properties.

XI. Chaos in Higher Dimensions

Before discussing chaos in higher dimensions (than 3), we first address two questions:

1. Why should we bother?

2. How is it done?

We address the first question first, since it is simpler. If a single receptor with subthreshold oscillations exhibits chaotic (deterministic nonperiodic) behavior, then two such cells (the flow is now in R^{5+5}) can also exhibit this kind of behavior. If we would like to be able to understand realistic neural networks, we must be able to understand chaos in higher dimensions.

The second question has a simple answer: 'We don't know.' However, there are some hints as to what a theory of deterministic nonperiodic behavior in higher dimensions might look like.

In some sense, we have already addressed the question of chaos in higher dimensions. The modified Hodgkin-Huxley equations are definitely not a three dimensional dynamical system: the phase space is R^5. However, there is only one unstable Lyapunov exponent, and the system is strongly contracting. This means that it is possible to project this system into a three dimensional inertial manifold (in our case, $D^2 \times T^1 subset R^3$) in which Linking Numbers *can* be computed.

If the phase space cannot be reduced to three dimensions, by projection, adiabatic elimination of slaved variables, or otherwise, then we cannot use the Birman-Williams theorem to provide information about the topological organization of unstable periodic orbits, since they don't link in spaces of dimension greater than 3.

However, the most important part of the Birman-Williams theorem may not be about the organization of unstable periodic orbits at all, but simply the fact that it is possible to project down along part of the stable invariant manifold to get something closely related to the initial dynamical system, but possessing important singularities. It is, after all, the singularities (splitting points, branch lines) which identify the stretching and squeezing mechanisms in R^3.

It is likely that a theorem of the following form might be valid. Arrange the Lyapunov exponents of a strange attractor as described in Equ. (17). Then

1. The flow can be projected along the most strongly contracting directions corresponding to the most negative exponents $\lambda_{n+1}, \cdots, \lambda_N$. This projects the flow into an n-dimensional inertial manifold.

2. Within the inertial manifold, the flow can be projected along the remaining more weakly contracting directions, corresponding to the remaining negative exponents $\lambda_{p+2}, \cdots, \lambda_n$. This projects the flow onto a $p+1$-dimensional branched manifold.

In a theorem of this type it will be necessary to replace 'Lyapunov exponent' by 'local Lyapunov exponent.' That is, the Lyapunov exponents are functions of position, $\lambda_i \rightarrow \lambda_i(x)$, where x is in the basin of the strange attactor $\mathcal{SA}$. The integer, n (*c.f.*, Equ (19)) is a function of position, $n(x)$. The dimension, n_M, of the inertial manifold containing the strange attractor is then

$$n_M \quad = \quad \underset{x \in \mathcal{SA}}{Max} \quad n(x)$$

Within this inertial manifold the n_M remaining Lyapunov exponents will vary in value, some even changing signs. Therefore the number of positive Lyapunov exponents, p, is also a function of position. We define the maximum number of positive Lyapunov exponents, p_M, as we defined n_M above. Then we project along a minimum number $n_M - (p_M + 2)$ of stable directions onto a branched manifold of dimension $p_M + 1$.

We should remark here that Lyapunov exponents are averages over local Lyapunov exponents:

$$\{\lambda_1, \lambda_2, \cdots, \lambda_N\} = \langle\{\lambda_1(x), \lambda_2(x), \cdots, \lambda_N(x)\}\rangle \tag{37}$$

It is possible that none of 'the' Lyapunov exponents (the *averaged* quantities) is positive, while one or more of the *local* Lyapunov exponents is positive in regions of phase space where stretching and squeezing take place. Strange attractors with no positive (averaged) Lyapunov exponents can be created in this way. Such attractors have been called 'strange nonchaotic attractors.'

To understand why such a theorem could be useful, we consider first a simple case: the receptor with subthreshold oscillations. The phase space is 5-dimensional, and the flow takes place in the disk $D^4 \times T^1 \subset R^5$. There is a global Poincaré section for this flow, corresponding to a fixed phase in T^1. This Poincaré section is 4-dimensional. The first part of the hypothetical theorem guarantees a projection into an inertial manifold $D^2 \times T^1 \subset D^4 \times T^1$. The global Poincaré section in this inertial manifold is now 2-dimensional. The second part of the hypothetical theorem guarantees a further projection of the flow down to a 2-dimensional branched manifold.

Figure 22: Folds and strange attractors. (a) A line segment R^1 is deformed by stretching in the plane, then compressed by projecting it down to another line segment. The second line segment is mapped back to the first by an affine transformation. The result is a logistic map. (b) A long thin rectangle is deformed by stretching into a parabolic shape, then squeezed. The resulting horseshoe shape is mapped back to the original rectangle by an affine transformation. An orientation preserving map of Henon type results.

The intersection of the two dimensional branched manifold with the Poincaré section is typically (mathematics: generically) a one dimensional manifold, M^1. Under the flow, M^1 is mapped back onto itself (first return map). This first return map must possess a singularity, otherwise it would be invertible, information about the past would not be lost, and entropy would not be generated by the flow.

The theory of singularities of mappings is well known, at least in low dimensions. If we ask: what singularities can occur (generically) in mappings of M^1 to itself, the answer was given by Whitney [34]: the only *local* singularity is the fold map, A_2. The stretching and squeezing involved in the fold return map are shown in Fig. 22a. The canonical mechanism displayed leads directly to the logistic map. Blowing this back up, as described above, leads to an orientation preserving Henon map, described in Fig. 22b.

The one dimensional intersection M^1 can look like a piece of R^1. It can also have nontrivial boundary conditions, and be topologically equivalent to the circle T^1. In this case, the first return map is equivalent to the standard circle map. Blowing this up produces the annulus map. The T^1 singularity describes systems with Hopf bifurcations in general, and the periodically driven van der Pol oscillator in particular.

In this way, the simplest singularity in the reduced phase space $D^2 \times T^1$ describes the following often studied maps:

M^1	Noninvertible	Invertible
R^1	Logistic	Henon
T^1	Circle	Annulus

(38)

By adding additional fold singularities, we are able to describe more extended *nonlocal* singularities, such as the scrolling which gives rise to the branched manifolds for the receptor with subthreshold oscillations. All branched manifolds in R^3 can be classified according to their singularity structure [2].

A similar treatment can be carried out in higher dimensions [35]. We give just one example to give a flavor of the riches that await our fuller understanding. We assume a flow has constant Lyapunov exponents $\lambda_1 > \lambda_2 > \lambda_3 = 0 > \lambda_4 \cdots > \lambda_{N+1}$ and is contained in a disk $D^N \times T^1$. We also assume $\lambda_1 + \lambda_2 + \lambda_3 + \lambda_4 < 0$. Then this flow can be projected into a 4-dimensional inertial manifold $D^3 \times T^1$. There is once again a global Poincaré section. There is a further

Figure 23: Cusps and strange attractors. A segment of a plane R^2 is deformed by stretching in R^3, then compressed by projecting it down into a plane, producing a cusp singularity. The second plane section is mapped back to the first by an affine transformation. The plane section can be thickened, analogous to the construction shown in Fig. 22(b). The resulting stretched and squeezed shape is mapped back to the original thickened plane by an affine transformation.

projection of the flow down to a 3-dimensional branched manifold. Typically, the intersection of this 3-dimensional branched manifold with the global 3-dimensional Poincaré section is a 2-dimensional manifold M^2 (by transversality and $3+3-4=2$). The return map induced by the flow must be singular, for the reasons expressed above. This raises a well posed question: What are the singularities of mappings $M^2 \rightarrow M^2$? Again, the answer has been given by Whitney [34]. The only local singularities are the fold A_2 and the cusp A_3. Fig. 23 illustrates the stretching and squeezing generated by the cusp singularity. As with the fold, nonlocal singularities are also possible. Again, as with the fold, M^2 may have the topology of a neighborhood of R^2, or it may have more interesting boundary conditions. In fact, rather than there being only two topologically inequivalent manifolds as in one dimension, with $M^1 = R^1$ or $M^1 = T^1$, there is now a countable set including R^2, S^2 (sphere), $T^1 \times T^1$ (torus), $R^1 \times T^1$ (cylinder), as well as some nonorientable manifolds like the Möbius strip, the Klein bottle, and the real projective plane.

Topological inequivalence has important consequences for the study of chaos. For example, in the one dimensional cases described above, generic noninvertible maps $R^1 \rightarrow R^1$ can have any number of nonlocal folds, but generic noninvertible maps $T^1 \rightarrow T^1$ can only have an even number of folds, and they must be related to each other in very specific ways. Further, in a family of mappings $F(a) : T^1 \rightarrow T^1$, important precursor phenomona (*e.g.*, mode locking) occur even before the noninvertible limit is reached. In the case of two dimensions ($M^2 \rightarrow M^2$), in which a much larger variety of inequivalent global boundary conditions exist, the spectrum of behavior is much richer.

More generally, it appears that there is a class of discretely classifiable branched manifolds for higher dimensional dynamical systems. We use the ideas outlined in Sec. X and in Figs. 22 and 23 to outline the theory. Imagine a strange attractor which has (for simplicity) constant Lyapunov exponents and for which the inertial manifold is $D^N \times T^1$. We assume that there are N_u positive and N_s negative Lyapunov exponents, so that $N_u + N_s = N$. Then we project the flow onto a branched manifold of dimension $N_u + 1$ (+1 for the flow direction). The intersection of the branched manifold with a Poincaré section defined by constant phase in T^1 is an N_u dimensional manifold, M^{N_u}. The flow around T^1 induces a first return map: $M^{N_u} \rightarrow M^{N_u}$. This map must possess singularities, otherwise we would not lose information about the past (this is the 'branch line argument'). This means that we can determine the backbone of the strange attractor by determining what singularities exist in mappings $M^{N_u} \to M^{N_u}$.

This is a well defined question. Without going into generalities, we state here that among all singularities there are two infinite series of simple singularities which are already encountered in Catastrophe Theory [36]: the cuspoids ($A_k, k \geq 2$) and the umbilics ($D_k, k \geq 4$). These singularities are defined by their germs, which are mappings $R^K \to R^K$ for which the Jacobian vanishes identically at the singular point. For A_k and D_k, $K = 1$ and 2. These germs have perturbations, as follows

Singularity	Germ	Perturbation
A_k	$x_1 \to f_1 = x_1^k$	$\sum_{j=1}^{k-2} a_j x_1^j$
D_k	$x_1 \to f_1 = x_1^{k-2} + x_2^2$ $x_2 \to f_2 = x_1 x_2$	$\sum_{j=1}^{k-3} a_j x_1^j + a_{k-2} x_2$

If we regard the control parameters a_j as coordinates z_j, then the cuspoid singularity can be encountered stably in a space with dimension 1 (for x_1) + $k-2$ (for $z_1, z_2, \cdots, z_{k-2}$) = $k-1$. The fold singularity A_2 can therefore first be encountered in one dimension, and in fact occurs generically as a local singularity in mappings $R^1 \to R^1$. Similarly, the cusp singularity A_3 first occurs in mappings $R^2 \to R^2$. The umbilic D_k first occurs in mappings $R^k \to R^k$ ($k \geq 4$), by similar arguments.

Since the flow produces a singular map of an N_u dimensional space onto itself, we can make the identification:

$$\#\text{germ variables}(x) + \#\text{unfolding coordinates}(z) = \#\text{unstable directions}(N_u)$$

We now observe (*c.f.*, Fig. 22) that the fold singularity $x \to x^2$ cannot continuously deform the line R^1 into the folded line x^2 unless there is additional room for the deformation to take place continuously. This is generally true for all singular *maps*. In order for the singularity of the map $M^{N_u} \to M^{N_u}$ to be created *continuously*, the manifold M^{N_u} must be smoothly deformed in a space of higher dimension (recall that M^{N_u} occurs in D^N, $N = N_u + N_s$). The minimal number of dimensions that is required for this deformation is the dimension of the germ of the singularity: 1 for A_k and 2 for D_k.

The deformation in the phase space $D^N \times T^1$ can be treated as described in Sec. X for flows in $D^2 \times T^1$. We first imagine that the flow takes place in a solid cylinder $D^N \times R^1$ of length 2. Then we group the variables into three types

$$\begin{array}{lll} x & \text{germ variables} & \multirow{2}{*}{\Big\}\ \text{unstable manifold}} \\ z & \text{unfolding variables} & \\ y & \text{deforming directions} & \}\ \text{stable manifold} \end{array}$$

During the first phase of the flow, from $s = 0$ to $s = 1$, stretching takes place. During the second phase, from $s = 1$ to $s = 2$, squeezing takes place. These processes take place as follows

$$\begin{array}{ccccc} \left[\begin{array}{c} x \\ z \\ y \end{array}\right] & \xrightarrow{r} & \left[\begin{array}{c} x \\ z \\ y + rf(x;z) \end{array}\right] & \xrightarrow{\epsilon} & \left[\begin{array}{c} \epsilon x \\ z \\ y + f(x;z) \end{array}\right] \\ & & & & \\ s = 0 & & s = 1 & & s = 2 \\ & \text{stretching} & & \text{squeezing} & \end{array} \tag{39}$$

Here $f(x; z)$ represents the perturbed singularity (= germ + perturbation). During the stretching phase, r increases from 0 to 1. During the squeezing phase, ϵ decreases from 1 to a sufficiently small value. For $\epsilon \neq 0$, this map is invertible. For noninvertible maps (*i.e.*, of the branched manifold to itself) we begin with all coordinates $y = 0$, and go all the way to the limit $\epsilon = 0$.

The final step is to wrap the solid cylinder around, and identify the output at $s = 2$ with the input at $s = 0$. The most general way this can be done, without altering distances (*i.e.*, leaving the Lyapunov exponents unchanged), is through an affine transformation (orthogonal rotation + translation).

The result is: A discrete classification of dynamical systems in higher dimensions, analogous to that described in [2] for three dimensional systems, is possible when

$$\begin{array}{rcl} N_u & \geq & \dim(\text{germ}) + \dim(\text{unfolding}) \\ N_s & = & \dim(\text{germ}) \end{array} \tag{40}$$

In particular, stretching and squeezing mechanisms more complicated than of cuspoid type can first be encountered in 7 dimensional dynamical systems. The mechanism is the $D_{\pm 4}$ singularity, the dynamical system must have four unstable directions and two stable directions, in addition to the flow direction. The dimension of the strange attractor obeys $5 < d_L < 7$, the branched manifold is 5 dimensional, and its intersection with a Poincaré section is four dimensional.

The hypothetical theorem described at the beginning of this Section has another application. If in fact it is possible to carry out the double projection as hypothesized, then the resulting branched manifold serves again as a skeleton for the flow in the inertial manifold. The branched manifold can be 'blown up' to construct a series of flow tubes in the reduced phase space. These tubes split and recombine (stretch and squeeze) to generate flows in spaces often more complicated than the cyclic spaces $D^N \times T^1$. Further, these flow tubes have full dimension in the reduced phase space. This means they cannot cross through each other. So although linking numbers for periodic orbits fail to exist for reduced phase spaces of dimension greater than three, linking numbers of flow tubes in inertial manifolds are well defined, no matter what the dimension. This means that the topological organization of the flow is rigidly determined.

If the organization of these tubes in the reduced phase space is known, then it is possible to create higher dimensional strange attractors without dynamical system equations of motion. The method is as described in Sec. X.

There is a great deal to be said for modeling dynamics geometrically, without equations. First, equations (such as the modified Hodgkin-Huxley equations) are opaque to our understanding. It is usually hard work to squeeze meaning out of a set of equations. Specifically, the topological and geometric description of the flow in phase space generated by these equations provides more information and understanding than the equations themselves. This was the message contained in Secs. VIII and IX. Further, it is often difficult to find parameter values for which a set of equations exhibits chaotic behavior, and the difficulty appears to increase with dimension (this is Arnol'd's Principle of 'the fragility of fine things'). Finally, the effects of noise, both large and small control parameter variations, and other perturbations, can be visualized more easily in a geometric setting than in the traditional setting of coupled ordinary nonlinear differential equations.

XII. Discussion and Conclusions

Several different types of neuron receptors fire even in the absence of sensory inputs (subthreshold oscillations). It seems that these nerve cells are probing their surroundings (other nerve cells), and in turn are being probed, even in the absence of external stimulation.

The equations originally designed to describe the electrical activity of the neuron [1] do not exhibit this phenomenon (Sec. II). These equations describe 'Platonic' nerve cells: no input, no output. In order to account for subthreshold activity in many sensor neurons, the Hodgkin-Huxley equations have been modified by Braun and his colleagues [3]. The modified equations specifically take into account the differences in time scales between ion pump (slow) and ion gate (fast) processes (Sec. III). By including the transfer of only two ion types, Na^+ and K^+, across the neuron membrane, Braun *et al* were able to construct a five dimensional model of neurons which exhibit subthreshold oscillations. This model shows a complicated mixture of periodic and nonperiodic behavior as a function of ambient temperature.

The bifurcation diagrams (interspike intervals vs. T), both with and without noise, strongly suggest that these equations generate chaotic behavior over some temperature ranges (Sec. IV). If in fact neurons do probe each other even in the absence of external inputs, then it seems that they would want to respond very quickly to any changes in ambient conditions. It is a well-known principle of engineering design [36] that if a system is to respond very quickly to changes, it must be intrinsically unstable. A system operating in a chaotic regime satisfies this condition exquisitely. Indeed, if a nerve cell produces no output, or a periodic output, over a wide range of operating conditions (*i.e.*, it is stable), then it is not responsive to inputs, and might as well be dead. If not, it soon will be, according to Darwinian laws.

By integrating the 5-dimensional dynamical system [3], we have shown that it is effectively three dimensional (Sec. V). In retrospect, we should be able to predict this because of the wide separation in time scales in the relaxation equations (*c.f.*, Table 1). However, multitime scaling methods are not yet sufficiently powerful to allow us to do this. Nor is there yet a useful theorem for projecting a dynamical system into a suitable lower dimensional inertial manifold.

It has recently become possible to test unequivocally for the presence of chaos in dynamical systems [2] (Sec. VI). This topological test probes for the stretching and squeezing mechanisms which generate chaotic behavior. It has built in self consistency checks and degrades gracefully with noise, as opposed to the other two (metric, dynamical) methods of analyzing data.

However, at present, the topological test requires the dynamics to be 'low dimensional' (Sec. VII).

We have confirmed that the modified Hodgkin-Huxley equations generate a chaotic voltage output in certain temperature ranges [3]. We have done this by identifying the stretching and squeezing mechanisms which operate on the (reduced) phase space of this dynamical system (Sec. VIII). It is the 'jelly role' or 'gateau roulé' mechanism. This mechanism has previously been identified for the periodically driven Duffing oscillator [29] and the YAG [30] laser. As a result, it is possible to port many of the observations and predictions about behavior from these two systems to the behavior of neurons with subthreshold oscillations (Sec. IX). We have been able to construct a model of the flow in phase space which is appealing at an intuitive level, since it relates the spikes in an output burst to the conversion of twist to writhe in the phase space flow. Further, this model has a number of predictive capabilities, many of which have been verified.

The effects of noise are twofold. One effect is intrinsic to the system under study; the other applies to all systems for which a topological analysis is applicable. In the first case, orbits of type nr are exceptionally unstable against perturbations. What makes them so unstable is the last incomplete rise before the voltage returns to its repolarization minimum. The duration of this half peak is particularly long compared to the duration of the preceeding spikes. This means that noise has an enhanced effect on this feature because of its length. In particular, noise will either enhance or destroy the partial depolarization rise. That is, in the presence of noise, we have the stochastic destruction

$$nr \longrightarrow \begin{matrix} (n+1)f \\ nf \end{matrix}$$

This means, for example, that noise will destroy all orbits in Table 2 containing the symbol B $(A = 4f, B = 4r, C = 5f)$. To period three, the only periodic orbits we would expect to find in the presence of significant noise are the five orbits $(A, C; AC; AAC, ACC)$. However, their Linking Numbers remain as described in Table 2.

The second effect of noise is more general. The higher the noise level, the more difficult it is to identify orbits of higher period. For once Murphy (author of the famous law) is on vacation: the most important orbits in this analysis methodology are the lowest period orbits. Orbits of higher period are principally used for confirmation purposes. Until the noise level reaches the stage that orbits of period one and two can no longer be located in the data, this analysis method will succeed.

We have also seen that it is possible to model chaotic dynamics geometrically, without aid of dynamical system equations of motion (Sec. X). Although this may not be an important point for a single isolated neuron with subthreshold oscillations, this ability can play a powerful role in studying interacting neurons. If the (full) phase space for the single neuron is $D^4 \times T^1$, then for two neurons it is $(D^4 \times T^1)^{\otimes 2} = D^8 \times T^2$. At this stage it would be really useful to have an inertial manifold theorem to reduce dimension (of D^8 to D^4, for example). If the two neurons do not interact, there is not necessarily any relation between their time evolution. But if there is an interaction, their time evolution might easily become synchronized. In this case there is a further reduction $T^2 \rightarrow T^1$. One possible mechanism for this reduction is very beautiful, and intrinsic to this model. At any temperature, the time duration of each unstable period one orbit is different. A small coupling will then act to encourage *synchronization* of the outputs by causing them to phase lock. This is easy because of the temporal diference of the period one orbits. The bifurcation $T^2 \leftrightarrow T^1$ ($T^n \leftrightarrow T^1$ for n neurons) which describes phase locking synchronization is likely to play a very important role in learning and behavior modification.

We close this discussion by listing the areas in which new contributions would be very useful.

- Multitime scale analysis should be developed to the point where it is possible to determine the effective dimensionality of a system involving a number of equations of relaxation type, with different time scales.
- A theorem of the type discussed in Sec. XI would be useful in several ways. First, it would relate the dimension of an inertial manifold to the spectrum of local Lyapunov exponents. Second, it would relate the local Lyapunov dimension of a strange attractor to the local Lyapunov exponents.
- Such a theorem would be even more useful if it included a prescription for the projection into an inertial manifold.
- Generalization of the Birman-Williams theorem to higher dimensions would allow projection of a strange attractor to a suitable branched manifold. These are the objects for which a classification theory exists in low dimensions. By analogy, they should be classifiable in higher dimensions, and provide caricatures for the flows generating the strange attractors, as well.
- A classification theory for higher dimensional dynamical systems is badly needed. Otherwise, how is it possible to analyze data without knowing what we are looking for? Such a classification theory should include a description of squeezing mechanisms (such as singularity theory provides). It should also include a rich spectrum of results, depending on global boundary conditions.
- A good model for coupling between interacting neurons with subthreshold oscillations is required. Only then will it be possible to study the phenomena involved in the interactions between such neurons.

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