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PERIOD DOUBLINGS AND POSSIBLE CHAOS IN NEURAL MODELS*

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Abstract. A formal perturbation method is derived for the study of bifurcation near a degenerate zero eigenvalue. This results in a third order differential equation with a single quadratic nonlinearity. Numerical solutions of this show successive period doubling bifurcations and eventual "chaos." The problem arises in the study of neural equations when an additional excitatory channel or cell is added to standard two-component models which oscillate. It also applies to a Van der Pol oscillator coupled to a simple RC circuit. Numerical simulations of a modified FitzHugh–Nagumo system agree qualitatively with the behavior of the bifurcation equations.

1. Introduction. Chaos is a loosely defined term for deterministic nonperiodic behavior of a dynamical system. Examples of this phenomenon exist in both nature and mathematical models of natural phenomena [9], [16], [18]. The best understood chaos is that which appears via successive period doublings in certain discrete systems [4], [15]. For differential equations, the best known examples of chaos are in periodically forced systems such as the Van der Pol oscillator [7] and systems with a homoclinic orbit [1], [6], [8], [11]. Little is known of the transition to chaos in autonomous systems; most work involves numerical computation of solutions [16], [18].

In this paper, we introduce a class of general systems which numerically appear to admit autonomous chaos. This nonperiodic behavior seems to rise from a succession of period doubling bifurcations in a certain reduced equation. Included in this general class of systems are certain neuronal oscillators with an additional positive feed back term. This has a curious effect of restabilizing the oscillating neural net in some instances. On the other hand, under certain easily computable conditions, there is a loss of stability of the rest state at a zero eigenvalue with algebraic multiplicity *three*. We describe a formal bifurcation method for analyzing this degeneracy which is in many ways similar to the one rigorously described by Kopell and Howard [13].

In the next section we describe the neural models which are extensions of the familiar FitzHugh–Nagumo equation [21] and the Wilson–Cowan equation [22] for excitatory and inhibitory neural populations. Section 3 describes our bifurcation method and § 4 presents a numerical and analytical description of the bifurcation equations. In the final subsection of § 4, we compare numerical solutions of the reduced model to those of the full modified FitzHugh–Nagumo model.

2. Some neural models. Many neural models of diverse phenomena are qualitatively similar in that they consist of two distinct components. One of these activates or excites the "tissue" and the other inhibits activity. Coupled together, these two component systems admit a wide variety of different behaviors including excitability, multiple states and oscillations. Among the best known examples of two-component neural models are the FitzHugh–Nagumo equation (FHN) and the Wilson–Cowan equations (WC). The FHN system consists of a voltage variable v and a recovery variable w and has the form

$$\frac{dv}{dt} = f(v) - w - v + J_0, \qquad \frac{dw}{dt} = a_2 v - \kappa w, \tag{2.1}$$

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where $f(v)-v$ is a cubic shaped function which is negative for $v>0$ and large and positive for $v<0$ and large. κ and a_2 are positive constants; κ is proportional to the time constant of recovery. J_0 is an applied current. This model was devised as a simplification of the Hodgkin–Huxley model of the squid axon. w can be viewed as a "potassium"-like variable and f takes into account rapid sodium influx.

The Wilson–Cowan system is a model for corticothalamic interactions and comprises a population of excitatory pyramidal cells, P, and a population of inhibitory interneurons, I [22]. This system can be written as:

$$\frac{dP}{dt}=-P+a_{11}S_1(P)-a_{21}S_2(I), \qquad \frac{dI}{dt}=-\kappa I+a_{12}S_1(P). \tag{2.2}$$

S_1, S_2 are sigmoidal or linear functions which represent the firing rates of a cell given the membrane potentials, P and I. a_{ij} are synaptic strengths which are positive and correspond to the amplitude of post synaptic potentials. We notice that $-P+a_{11}S_1(P)$ and $-v+f(v)$ are qualitatively similar in shape. Both (2.1) and (2.2) admit small amplitude stable oscillations [21] which arise from a Hopf bifurcation. In [3] it is shown that (2.2) admits a small amplitude homoclinic orbit. Thus, if a small periodic forcing is applied, the results of Keener [11] could presumably be used to prove the existence of chaos. Such solutions are reminiscent of the small amplitude "noisy" behavior of the resting EEG under rhythmic thalamic modulation [2].

In spite of the complexity of behavior associated with these systems, they cannot produce autonomous aperiodic solutions. We therefore ask what effect an additional "excitatory" variable has on the system. This could take the form of an excitatory interneuron in (2.2) or an additional inward conductance in (2.1). There are many situations which seem to dictate this addition: Rall and Shepherd [17] pose a 3-variable system for olfactory potentials; Shepherd [20] suggests that many cortical networks can be modeled by a large excitatory pyramidal cell and excitatory and inhibitory interneurons. In Fig. 1, we depict such an arrangement abstracted from Shepherd [20, p. 354]. If E represents the firing rate of the excitatory interneuron, then the mathematical model of Fig. 1 corresponding to (2.2) has the form:

$$\begin{aligned}&\frac{dP}{dt}=-P+a_{11}S_1(P)-a_{21}S_2(I)+a_{31}S_3(E),\\ &\frac{dI}{dt}=-\kappa I+a_{12}S_1(P), \qquad \frac{dE}{dt}=-\rho E+a_{13}S_1(P).\end{aligned} \tag{2.3}$$

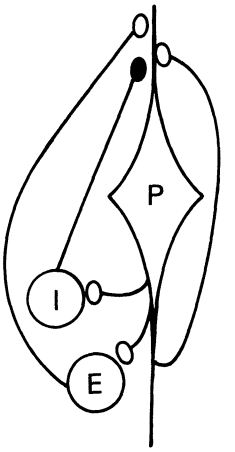

FIG. 1. *General schematic diagram for the neocortical network (adapted from Shepherd).*

If $a_{13}=a_{31}=0$, then (2.3) is identical to (2.2).

Suppose we allow the existence of an additional linear inward conductance in the FHN model, u. Then (2.1) can be rewritten as:

$$\frac{dv}{dt}=f(v)-v-w+u+J_0,\quad \frac{dw}{dt}=a_2v-\kappa w,\quad \frac{du}{dt}=a_3v-\rho u. \tag{2.4}$$

Conceivably, u could represent an additional sodium channel. The two-conductance model proposed by Goldstein and Rall is an analogous example:

$$\begin{aligned}\frac{dV}{dt}&=-V+\mathscr{E}(1-V)-\mathscr{I}(V+.01),\\ \frac{d\mathscr{E}}{dt}&=k_1V^2+k_2V^4-k_3\mathscr{E}-k_4\mathscr{I},\qquad \frac{d\mathscr{I}}{dt}=k_5\mathscr{E}+k_6\mathscr{E}I-k_7\mathscr{I}.\end{aligned} \tag{2.5}$$

Here $\mathscr{I}$ is analogous to w in (2.4) and I in (2.3) while $\mathscr{E}$ is like u or E. As a final remark, models of this type turn up when a Van der Pol oscillator is resistively coupled to a simple RC circuit such as shown in Fig. 2 with equations:

$$C\frac{dv}{dt}=f(v)-y+\frac{z-v}{R_c},\quad L\frac{dy}{dt}=v,\quad C'\frac{dz}{dt}=-\frac{z}{R'}+\frac{v-z}{R_c}. \tag{2.6}$$

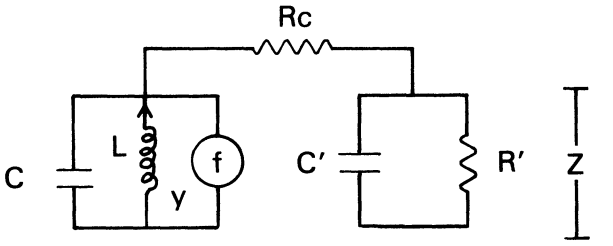

FIG. 2. *A Van der Pol oscillator resistively coupled to a simple* RC *circuit.*

We ask first, what is the effect on this additional component on the stability of the rest state, and second, whether these systems can become chaotic. Rössler has shown conceptually that positive feedback to oscillatory systems can sometimes result in chaotic behavior [18]. To begin to answer this question of chaos, we review the results of Keener [11]. Suppose that a system of differential equations, linearized about an equilibrium point, has a zero eigenvalue of algebraic multiplicity *two*. Then under fairly general circumstances, this degeneracy can be unfolded to yield a one-parameter family of homoclinic orbits [13]. Keener applies a weak "slow" periodic modulation to this system and uses the results of Chow et al. to obtain chaos in general equations [1]. Thus, periodic forcing of an arbitrary system near a degeneracy can develop aperiodic solutions. Obviously by "coupling" two such second order systems together to form a fourth order system, one could obtain autonomous chaos. But we wish to find such solutions with only third order systems. Langford [14] studies bifurcation to tori in third and higher dimensional systems near a critical point. In their case, the linear system simultaneously admits a zero eigenvalue and a pair of imaginary eigenvalues. More recently Holmes has shown "chaotic" behavior for this singularity [8]. If we let

$$p(\lambda)=\lambda^3+a_2\lambda^2+a_1\lambda+a_0$$

denote the characteristic polynomial of the third order linearized system, then both of the above results correspond to the vanishing of two of the three coefficients. If $a_1 = a_0 = 0$, then zero is an algebraically double eigenvalue. If $a_2 = a_0 = 0$, $a_1 > 0$, then $0, \pm i\sqrt{a_1}$ are eigenvalues. The next level of complexity occurs when $a_1 = a_2 = a_0 = 0$; that is, zero is an eigenvalue with multiplicity *three* and geometric multiplicity one. This is the case which we study in this paper. The analysis is given in the next section for the general n-dimensional case.

Before continuing with the formal analysis, we return to the neural equations. When can this type of degeneracy occur? In all cases; we will suppose that the phase plane for the two-variable model has the form depicted in Fig. 3. With no loss in

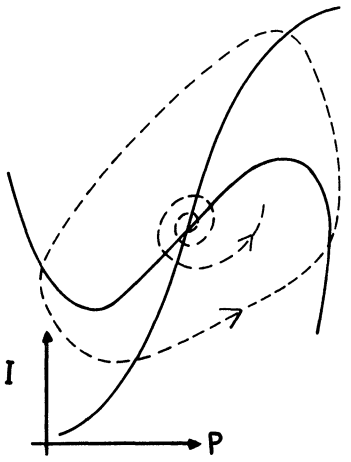

FIG. 3. *Phase plane configuration for the neural models. The x axis is the inhibitory variable and the y axis is the excitatory variable.*

generality we assume the unique equilibrium point is (0, 0). Both (2.1) and (2.2) can be arranged into this configuration. If we let S_2, S_3 be linear, $a_1 = f'(0)$ or $S_1'(0)a_{11}$, $a_2 = a_{12}S_1'(0)$, $a_3 = a_{13}S_1'(0)$, and $a_{21} = a_{31} = 1$ (with appropriate scaling), then the linearization about (0, 0, 0) of third order systems has the form:

$$\frac{d}{dt}\begin{pmatrix} Z_1 \\ Z_2 \\ Z_3 \end{pmatrix} = \begin{pmatrix} -1+a_1 & -1 & 1 \\ a_2 & -\kappa & 0 \\ a_3 & 0 & -\rho \end{pmatrix}\begin{pmatrix} Z_1 \\ Z_2 \\ Z_3 \end{pmatrix}. \tag{2.7}$$

Note that the configuration of Fig. 3 implies $a_1 > 0$. Our parameters are the excitatory terms a_1, a_2, a_3, which correspond to the effects of V or P on w, u, v or I, E, P. The eigenvalues of this matrix satisfy:

$$\begin{aligned} &\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0, \\ &A_2 = 1 + \kappa + \rho - a_1, \\ &A_1 = a_2 - a_3 - (a_1 - 1)(\kappa + \rho) + \kappa\rho, \\ &A_0 = a_1\rho - a_3\kappa - \kappa\rho(a_1 - 1). \end{aligned} \tag{2.8}$$

The equilibrium point (0, 0, 0) is stable if and only if

$$\text{(2.9)}\quad \begin{aligned} &\text{(a)} && A_1>0,\quad A_2>0,\quad A_0>0,\\ &\text{(b)} && A_2A_1-A_0>0. \end{aligned}$$

Condition (a) requires that the activator or excitatory influences, a_3, a_1, are not too large. Condition (b) which is the Routh–Hurwitz criterion takes the form

$$\text{(2.10)}\quad (a_2\kappa-a_3\rho)-(a_1-1)(a_2-a_3)-(a_1-1)(\kappa+\rho)^2+(a_1-1)^2(\kappa+\rho)+(\kappa+\rho)\kappa\rho>0.$$

The first three terms can contribute to instability. If the inhibition is strong enough and a_1 is large, (2.10) will be violated and will result in a Hopf bifurcation. It is clear that parameters can be arranged so that $A_0=A_1=0$ or $A_2=A_0=0$. Hence bifurcation to tori and homoclinic orbits can probably occur in this system. We now establish conditions on (κ,ρ) so that a triple zero eigenvalue occurs. This requires $A_2=A_1=A_0=0$ or:

$$\text{(2.11)}\quad a_1=1+\kappa+\rho,\quad a_2=\kappa^3/(\kappa-\rho),\quad a_3=\rho^3/(\kappa-\rho).$$

Since a_j must be positive, we find $\kappa>\rho$ is a necessary and sufficient condition; the inhibitory interneuron or outward current acts more quickly than the excitatory interneuron or secondary inward current. Self activation, a_1, must be large enough to overcome the decay effects due to the time constants. Finally, we note that (κ,ρ) can be chosen less than or greater than 1, hence, these two terms can respond slower or quicker than the principle activation, V or P.

As a final comment suppose we set $a_3=0$. Then the two-variable system when linearized has the form:

$$\begin{pmatrix} \kappa+\rho & -1 \\ \dfrac{\kappa^3}{\kappa-\rho} & -\kappa \end{pmatrix}.$$

The eigenvalues of this are complex and have positive real parts so that, in most cases, the two-variable model admits an oscillating solution. Tuning a_3 corresponds to injecting a positive feedback term back into the oscillation; thus the situation resembles that discussed by Rössler.

The remainder of this paper concerns the behavior of these third order nonlinear systems when a_1, a_2, a_3 depart from criticality. Since the method is completely general, we treat an n-dimensional system in the next section.

3. Canonical reduction. We consider the equation:

$$\text{(3.1)}\quad \frac{du}{dt}=A(\bar\mu,\bar\nu,\bar\gamma)u+Q(u,u)+\text{h.o.t.}$$

where $(\bar\mu,\bar\nu,\bar\gamma)$ are parameters, A is an $n\times n$ matrix $(n>2)$, and Q is an n-vector of quadratic forms. "h.o.t." means terms in higher order in the parameters and in u. We suppose that $A(0,0,0)=A_0$ has a zero eigenvalue with geometric multiplicity one and algebraic multiplicity three. Therefore, there are 3 unique real vectors (e_1,e_2,e_3) which satisfy:

$$\text{(3.2)}\quad A_0e_1=0,\quad A_0e_2=e_1,\quad A_0e_3=e_2,\quad e_j\cdot e_k=\delta_{jk}.$$

There are also 3 unique real vectors (f_1,f_2,f_3) which satisfy:

$$\text{(3.3)}\quad A_0^Tf_3=0,\quad A_0^Tf_2=f_3,\quad A_0^Tf_1=f_2,\quad f_j\cdot e_k=\delta_{jk},$$

where "T" denotes the transpose. The characteristic polynomial of A is a function of the three parameters and can be written:

$$P(\lambda) \equiv \det(A-\lambda) = \lambda^n + \sum_{j=0}^{n-1} c_j(\bar{\mu}, \bar{\nu}, \bar{\gamma})\lambda^j. \tag{3.4}$$

Since zero is a triple eigenvalue of A_0, we have:

$$c_0(0,0,0) = c_1(0,0,0) = c_2(0,0,0) = 0, \qquad c_3(0,0,0) \neq 0. \tag{3.5}$$

We demand that the remaining eigenvalues of A_0 lie in the left half complex plane so that our constructed solutions can be linearly stable. A "transversality" condition on the independence of the three parameters must be assumed. We let:

$$c_{j1} = \frac{\partial c_j}{\partial \bar{\mu}}\bigg|_{(0,0,0)}, \quad c_{j2} = \frac{\partial c_j}{\partial \bar{\nu}}\bigg|_{(0,0,0)}, \quad c_{j3} = \frac{\partial c_j}{\partial \bar{\gamma}}\bigg|_{(0,0,0)}, \quad j = 0, 1, 2. \tag{3.6}$$

We suppose that:

$$\det(c_{jk}) \neq 0. \tag{3.7}$$

(3.7) allows us to introduce a nonsingular change of parameter coordinates which satisfy:

$$\mu \sim c_2(\bar{\mu}, \bar{\nu}, \bar{\gamma}), \quad \nu \sim c_1(\bar{\mu}, \bar{\nu}, \bar{\gamma}), \quad \gamma \sim c_0(\bar{\mu}, \bar{\nu}, \bar{\gamma}). \tag{3.8}$$

In general the computations required to verify (3.7) are tedious since (3.4) must be calculated. The following lemma provides a straightforward means of calculating the coefficients, c_{jk} without the use of the characteristic polynomial.

PROPOSITION 1. *Let c_3, c_4, c_5 be the coefficients of $P(\lambda)$ when $\bar{\mu} = \bar{\nu} = \bar{\gamma} = 0$ (note $c_3 > 0$, $c_4 \geqq 0$, $c_5 \geqq 0$, for stability). Then*:

$$\begin{pmatrix} c_3 & 0 & 0 \\ c_4 & c_3 & 0 \\ c_5 & c_4 & c_3 \end{pmatrix} \begin{pmatrix} \kappa_j \\ \beta_j \\ \alpha_j \end{pmatrix} = -\begin{pmatrix} c_{2j} \\ c_{1j} \\ c_{0j} \end{pmatrix}, \qquad j = 1, 2, 3, \tag{3.9}$$

where

$$\begin{aligned} &\alpha_j = f_3 A_j e_1, \qquad \beta_j = f_2 A_j e_1 + f_3 A_j e_2, \\ &\kappa_j = f_1 A_j e_1 + f_2 A_j e_2 + f_3 A_j e_3, \\ &A_1 = \frac{\partial A}{\partial \bar{\mu}}\bigg|_{(0,0,0)}, \quad A_2 = \frac{\partial A}{\partial \bar{\nu}}\bigg|_{(0,0,0)}, \quad A_3 = \frac{\partial A}{\partial \bar{\gamma}}\bigg|_{(0,0,0)}. \end{aligned} \tag{3.10}$$

Proof. A satisfies its own characteristic polynomial:

$$A^n + \cdots + c_5 A^5 + c_4 A^4 + c_3 A^3 + c_2 A^2 + c_1 A + c_0 = 0. \tag{3.11}$$

Pick a parameter, differentiate (3.11) with respect to it, and set $(\bar{\mu}, \bar{\nu}, \bar{\gamma}) = 0 \cdots$

$$\begin{aligned} &\cdots + c_5(A_0^2 A_j A_0^2) + c_4(A_0^2 A_j A_0 + A_0 A_j A_0^2) \\ &\quad + c_3(A_0^2 A_j + A_0 A_j A_0 + A_j A_0^2) \\ &\quad + c_{2j} A_0^2 + c_{1j} A_0 + c_{0j} \equiv L_j = 0. \end{aligned} \tag{3.12}$$

L_j is a linear operator on R^n. We apply L_j to e_k and take the inner product of the result with f_1. This leads to the expressions for α_j, β_j, and κ_j. This completes the proof of the proposition.

Let

$$m_{jk} = f_j A_1 e_k,\ n_{jk} = f_j A_2 e_k \quad \text{and} \quad g_{jk} = f_j A_3 e_k. \tag{3.13}$$

Proposition 1 implies:

$$\begin{aligned}\tilde{C}M &\equiv \begin{pmatrix} c_3 & 0 & 0 \\ c_4 & c_3 & 0 \\ c_5 & c_4 & c_3 \end{pmatrix} \begin{pmatrix} m_{11}+m_{22}+m_{33} & n_{11}+n_{22}+n_{33} & g_{11}+g_{22}+g_{33} \\ m_{21}+m_{32} & n_{21}+n_{32} & g_{21}+g_{32} \\ m_{31} & n_{31} & g_{31} \end{pmatrix} \\ &= -\begin{pmatrix} c_{21} & c_{22} & c_{23} \\ c_{11} & c_{12} & c_{13} \\ c_{01} & c_{02} & c_{03} \end{pmatrix} \equiv \hat{C}.\end{aligned} \tag{3.14}$$

Det $(\tilde{C}) = c_3^3 \neq 0$, so to verify (3.7), we need only evaluate det M. Since each component of M is easily computed through (3.10), the verification of the "transversality" condition is trivial. We assume that det $(\hat{C}) \neq 0$, so that M is invertible.

To obtain the canonical equation, we take as our ansatz:

$$u(t) = \varepsilon^3 e_1 x + \varepsilon^4 e_2 y + \varepsilon^5 e_3 z + w, \qquad \tau = \varepsilon t, \tag{3.15}$$

where $w \cdot e_j = 0$, ε is a small number, and (x, y, z) are functions of τ. We substitute (3.15) into (3.1) and apply the adjoint vectors f_1, f_2, f_3 to the resultant equation. This leads to:

$$\begin{aligned}
&\text{(a)} \quad \frac{dx}{d\tau} = y + \frac{x}{\varepsilon}(\bar{\mu}m_{11} + \bar{\nu}n_{11} + \bar{\gamma}g_{11}) + y(\bar{\mu}m_{12} + \bar{\nu}n_{12} + \bar{\gamma}g_{12}) + \varepsilon R_1, \\
&\text{(b)} \quad \frac{dy}{d\tau} = z + \frac{x}{\varepsilon^2}(\bar{\mu}m_{21} + \bar{\nu}n_{21} + \bar{\gamma}g_{21}) + \frac{y}{\varepsilon}(\bar{\mu}m_{22} + \bar{\nu}n_{22} + \bar{\gamma}g_{22}) \\
&\qquad\qquad + z(\bar{\mu}m_{23} + \bar{\nu}n_{23} + \bar{\gamma}g_{23}) + \varepsilon R_2, \\
&\text{(c)} \quad \frac{dz}{d\tau} = qx^2 + \frac{x}{\varepsilon^3}(\bar{\mu}m_{31} + \bar{\nu}n_{31} + \bar{\gamma}g_{31}) + \frac{y}{\varepsilon^2}(\bar{\mu}m_{32} + \bar{\nu}n_{32} + \bar{\gamma}g_{32}) \\
&\qquad\qquad + \frac{z}{\varepsilon}(\bar{\mu}m_{33} + \bar{\nu}n_{33} + \bar{\gamma}g_{33}) + \varepsilon R_3
\end{aligned} \tag{3.16}$$

where R_1, R_2, R_3 depend on the parameters in higher orders and $q = f_3 \cdot Q(e_1, e_1)$. We must assume that q is nonzero, which is in general true. We differentiate (3.16a) twice, (3.16b) once, and combine with (3.16c) to obtain the third order equation:

$$\begin{aligned}
\frac{d^3x}{d\tau^3} &= \frac{1}{\varepsilon}[\bar{\mu}(m_{11}+m_{22}+m_{33}) + \bar{\nu}(n_{11}+n_{22}+n_{33}) + \bar{\gamma}(g_{11}+g_{22}+g_{33})]\frac{d^2x}{d\tau^2} \\
&+ \frac{1}{\varepsilon^2}[\bar{\mu}(m_{32}+m_{21}) + \bar{\nu}(n_{32}+n_{21}) + \bar{\gamma}(g_{32}+g_{21})]\frac{dx}{d\tau} \\
&+ \frac{1}{\varepsilon^3}[\bar{\mu}m_{31} + \bar{\nu}n_{31} + \bar{\gamma}g_{31}]x + qx^2 + \text{terms in } (\bar{\mu}, \bar{\nu}, \bar{\gamma}, \varepsilon).
\end{aligned} \tag{3.17}$$

We use the fact that M is invertible to introduce new parameters:

$$M\begin{pmatrix} \bar{\mu} \\ \bar{\nu} \\ \bar{\gamma} \end{pmatrix} = -\begin{pmatrix} \varepsilon\mu \\ \varepsilon^2\nu \\ \varepsilon^3\gamma \end{pmatrix}. \tag{3.18}$$

This leads to the equation:

$$\frac{d^3x}{d\tau^3}+\mu\frac{d^2x}{d\tau^2}+\nu\frac{dx}{d\tau}+\gamma x-qx^2=O(\varepsilon). \tag{3.19}$$

(3.19) is our canonical three-parameter unfolding of the singular vector field $d^3x/d\tau^3 = qx^2$. The remainder of this paper is devoted to an analysis of (3.19) for various parameter values.

Before analyzing (3.19), we must show that the three parameters a_1, a_2, a_3 in the neural models are sufficient. That is, we must show that the matrix M defined by (3.13) is invertible. At criticality,

$$A_0=\begin{pmatrix} \kappa+\rho & -1 & 1 \\ \dfrac{\kappa^3}{\kappa-\rho} & -\kappa & 0 \\ \dfrac{\rho^3}{\kappa+\rho} & 0 & -\rho \end{pmatrix}.$$

A_1 is the zero matrix with a 1 in the top left corner, A_2 is zero with a 1 in the second row, first column, and A_3 is zero with a 1 in the lower left corner. The eigenvectors and adjoint eigenvectors are easily computed:

$$\begin{aligned} e_1&=\left(1,\frac{\kappa^2}{\kappa-\rho},\frac{\tau^2}{\kappa-\rho}\right), & f_1&=(1,0,0), \\ e_2&=\left(0,\frac{-\kappa}{\kappa-\rho},\frac{-\tau}{\kappa-\rho}\right), & f_2&=(\kappa+\rho,-1,1), \\ e_3&=\left(0,\frac{1}{\kappa-\rho},\frac{1}{\kappa-\rho}\right), & f_3&=(\kappa\rho,-\tau,\mu). \end{aligned} \tag{3.20}$$

Finally, the matrix M is given by:

$$M=\begin{pmatrix} 1 & 0 & 0 \\ \kappa+\rho & -1 & 1 \\ \kappa\rho & -\rho & \kappa \end{pmatrix} \tag{3.21}$$

and its determinant is $\rho-\kappa\neq 0$. Thus transversality holds and the parameters a_1, a_2, a_3 are sufficient to unfold the degeneracy. We now compute q, the nonlinear term,

$$q=f_3\cdot Q(e_1,e_1).$$

For the FHN system:

$$Q(x,y,z)=\begin{pmatrix} \dfrac{f''(0)}{2x^2} \\ 0 \\ 0 \end{pmatrix},$$

and for the Wilson–Cowan system

$$Q(x,y,z)=\frac{1}{2}\begin{pmatrix}(1+\kappa+\rho)S_1''(0)x^2-S_2''(0)y^2+S_3''(0)z^2\\ \frac{\kappa^3}{\kappa-\rho}S_1''(0)x^2\\ \frac{\rho^3}{\kappa-\rho}S_1''(0)x^2\end{pmatrix}.$$

Thus, we find

$$q=\frac{\kappa\rho f''(0)}{2} \qquad \text{(FHN)},$$

(3.22)

$$q=\frac{S_1''(0)}{2}+\frac{\frac{S_3''(0)\kappa^2}{2}-\frac{S_2''(0)\rho^2}{2}}{\kappa-\rho} \qquad \text{(WC)}.$$

In particular if S_3 and S_2 are linear, q is nonzero if $S_1''(0)\neq 0$. Similarly, we demand $f''(0)\neq 0$ as well. Finally, if $S_3=S_2$, q for the WC equations is:

$$\frac{[S_1''(0)+(\kappa+\rho)S_2''(0)]}{2}.$$

Generally $q\neq 0$, so that all of the conditions required in this section are satisfied for the neural models and we can expect them to behave as does equation (3.19).

4. Analysis of the canonical system. (3.19) is the simplest general third order nonlinear system; there is but one quadratic nonlinearity. Yet it seems that this system is capable of generating a wide variety of interesting behavior. We will only concern ourselves with periodic solutions and the numerical transition to chaos. We fix μ, ν and increase γ. Initially the rest state is stable. For increasing γ there is a stable limit cycle which arises through a supercritical Hopf bifurcation. This bifurcation loses stability and a new $2T$-periodic solution arises. Continued increase of γ results in a succession of period doubling bifurcations ultimately ending in what appear to be chaotic solutions.

4.1. Periodic solution. We rewrite (3.19) when $\varepsilon=0$ as the third order system:

$$\frac{dx}{d\tau}=y-\mu x,\quad \frac{dy}{d\tau}=z-\nu x,\quad \frac{dz}{d\tau}=qx^2-\gamma x. \tag{4.1}$$

There is a pair of equilibria, $\mathbf{x}_0=(x_0,y_0,z_0)=(0,0,0)$ and $\mathbf{x}_1=(x_1,y_1,z_1)=(q/\gamma,\mu q/\gamma,\nu q/\gamma)$. Both equilibria cannot be simultaneously stable; we therefore restrict our attention to $\mathbf{x}_0=(0,0,0)$. Stability of $\mathbf{x}_0$ is determined by the roots of

$$\lambda^3+\mu\lambda^2+\nu\lambda+\gamma=0, \tag{4.2}$$

that is, we require

(4.3)

(a) $\mu>0,\quad \nu>0,\quad \gamma>0,$

(b) $\mu\nu-\gamma>0$ (Routh criterion).

If (4.3b) is violated, a pair of complex eigenvalues crosses the imaginary axis and may result in an Hopf bifurcation. Suppose $\gamma=\mu\nu$. Then (4.2) has roots $-\mu$ and $\pm i\sqrt{\nu}$ and if (4.3) is satisfied these are imaginary roots. For $|\gamma-\mu\nu|$ small there may be a

limit cycle. Existence and stability of this cycle are determined by the direction of birfurcation. q can be scaled out of the problem so we take $q=1$. Through by-now-standard techniques, we obtain the bifurcation direction:

$$\begin{aligned}
&\gamma \sim \mu\nu + \delta^2\gamma_2 + O(\delta^3),\\
&\omega = \sqrt{\nu} + \delta^2\omega_2 + O(\delta^3),\\
&\gamma_2 = \frac{2\mu^2+\delta\nu}{[\mu\nu(\mu^2+4\nu)]}, \qquad \delta \ll 1,\\
&\omega_2 = \frac{-2}{[3\nu\sqrt{\mu}(\mu^2+4\nu)]}.
\end{aligned} \tag{4.4}$$

Here ω is the frequency of the oscillator and δ is the amplitude. Since $\gamma_2 > 0$, the bifurcation is supercritical and a stable small amplitude limit cycle exists. We remark that Keener [10] studies the appearance of small amplitude oscillations when there is a zero eigenvalue of multiplicity *two*. In his problem, terms of order ε are necessary to obtain the bifurcation direction. The higher order calculation is unnecessary for our system. The remainder of this section is a numerical study of (3.19) when $\varepsilon = 0$ and $\gamma > \mu\nu$. We also show that the chaos persists for $\varepsilon \neq 0$ in the FHN example.

4.2. Cascading bifurcations and chaos. Before resuming our analysis, we show that (3.19) is identical to one of Rössler's prototypes for chaos in third order systems. In [18], Rössler studies the following system:

$$\dot{x} = -y - z, \quad \dot{y} = x, \quad \dot{z} = a(y - y^2) - bz. \tag{4.5}$$

If we differentiate the second equation twice and the first equation once, we obtain:

$$\frac{d^3\gamma}{dt^3} + b\frac{d^2y}{dt^2} + \frac{dy}{dt} + (a+b)y - ay^2 = 0. \tag{4.6}$$

With $\mu = b$, $\nu = 1$, $\gamma = a+b$, $q = a$, we see that (4.6) is identical to (3.19) so that Rössler's prototype is within the class of our canonical unfolding.

We return to (4.1) and study the effect of increasing γ. In our simulations of (4.1), $q=2$, $\nu=2$, $\mu=1$, so $\gamma_c = 2$. Solutions to (3.1) were found by integrating the differential equations until a periodic solution was reached. Numerical integration was performed using a package Gear–Adams technique contained in MLAB [12]. In Fig. 4, we depict the limit cycle for $\gamma = 3$. This and subsequent figures are all drawn as stereo pairs. As γ increases a critical value $\gamma_1 \approx 3.089$ is reached at which the limit cycle loses stability. A new periodic solution with twice the period bifurcates from the unstable cycle. This "$2T$-periodic" cycle is depicted in Fig. 5 for $\gamma = 3.25$. This oscillation remains stable until $\gamma = \gamma_2 \sim 3.351$. A new periodic solution with period approximately four times that of the original cycle appears when the $2T$-periodic solution loses stability. In Fig. 6, we depict this "$4T$-periodic" cycle for $\gamma = 3.38$. Again, this solution remains stable until a value $\gamma = \gamma_2 \sim 3.410$ is reached. An "$8T$-periodic" solution bifurcates and is shown in Fig. 7 for $\gamma = 3.42$. In Fig. 8, we depict the "$16T$-periodic" solution which bifurcates from the $8T$-periodic solution at $\gamma = \gamma_4 \sim 3.423$. Beyond this point it becomes very difficult to calculate higher harmonic solutions although we believe that they exist. For γ above about 3.45 chaos-like solutions appear, that is, there are bounded aperiodic solutions to the equation. A typical chaotic solution is shown in Fig. 9 for $\gamma = 3.5$. This behavior persists for γ up to about 3.75. We remark that the chaotic attractor appears to be a twisted two-dimensional

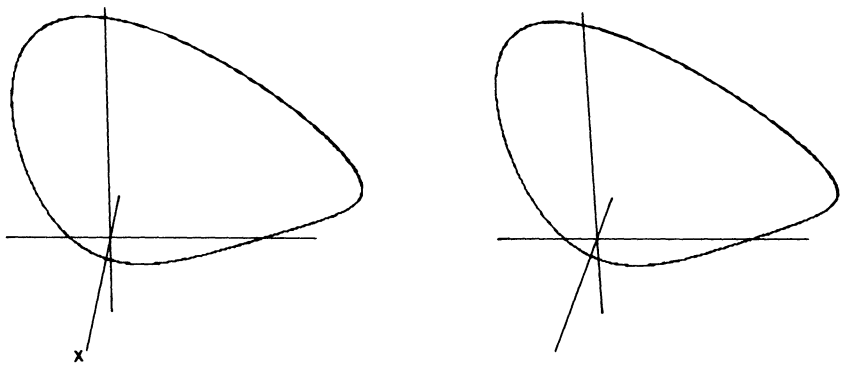

FIG. 4. *Periodic solution to* (4.1). $\mu = 1$, $\nu = 2$, $q = 2$, $\gamma = 3$. *Initial conditions*: $(x(0), y(0), z(0)) = (.8528, -.8309, -.6271)$ *Axes are x, y, z starting at bottom and going counterclockwise. Axes*: $-.35 < x < .7$, $-.4 < y < .61$, $-.28 < z < .75$; *left image is for right eye and vice versa. (To view hold* 40 *cm from eyes. Cross eyes so that there are* 4 *images. If the two center images are fused and brought into focus,* 3*-dimensional shape appears.)*

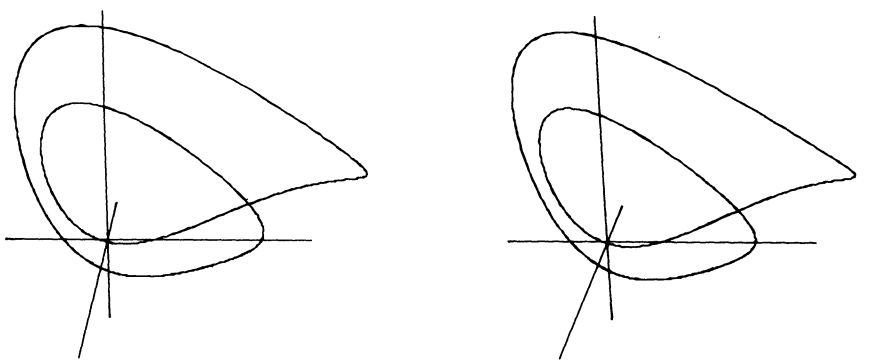

FIG. 5. *Same as Fig.* 1. *Initial conditions*: $(-.6372, -.1615, 1.433)$ *Axes*: $-.35 < x < .7$, $-.38 < y < .65$, $-.3 < z < .75$; $\gamma = 3.25$.

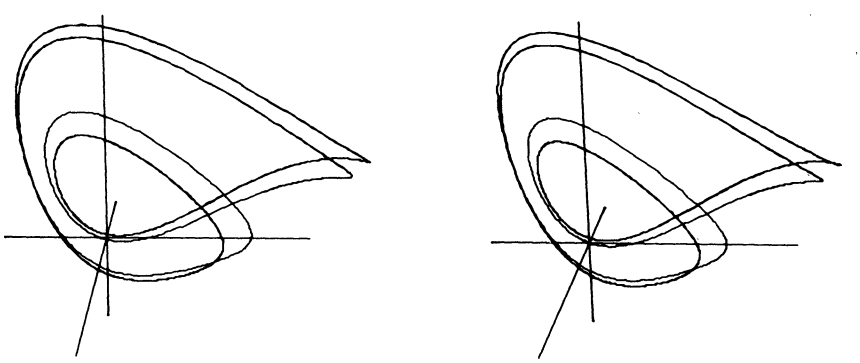

FIG. 6. *Same as Fig.* 1. *Initial conditions*: (1.199, .3470, .7449) *Axes*: $-.35 < x < .7$, $-.37 < y < .65$, $-.3 < z < .73$; $\gamma = 3.38$.

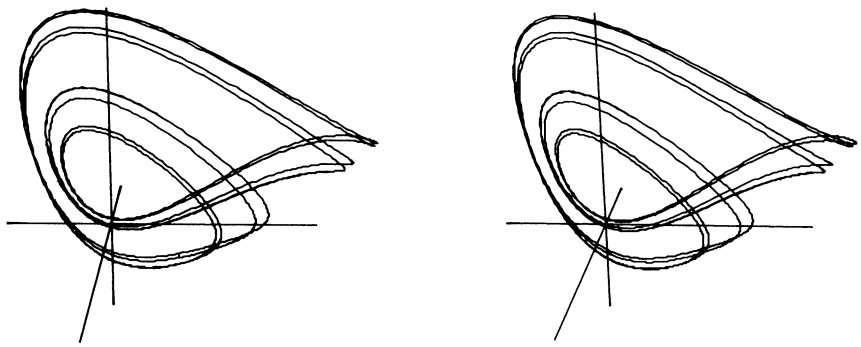

FIG. 7. *Same as Fig.* 1. *Initial conditions*: (.3945, 1.699, 1.799) *Axes*: $-.35 < x < .7$, $-.37 < y < .65$, $-.31 < z < .71$; $\gamma = 3.42$.

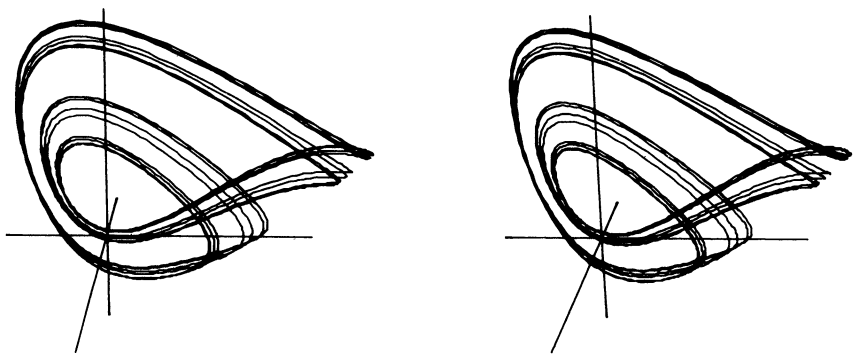

FIG. 8. *Same as Fig.* 1. *Initial conditions*: (1.0428, 1.681, 1.000) *Axes*: $-.34 < x < .7$, $-.37 < y < .65$, $-.31 < z < .74$; $\gamma = 3.428$.

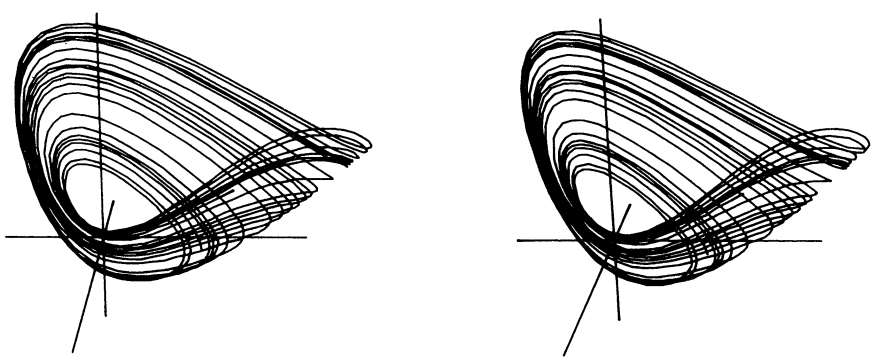

FIG. 9. *Aperiodic solution, same as Fig.* 1. *Initial conditions*: (1.115, .1238, .7274). *Axes*: *same as Fig.* 5; $\gamma = 3.5$.

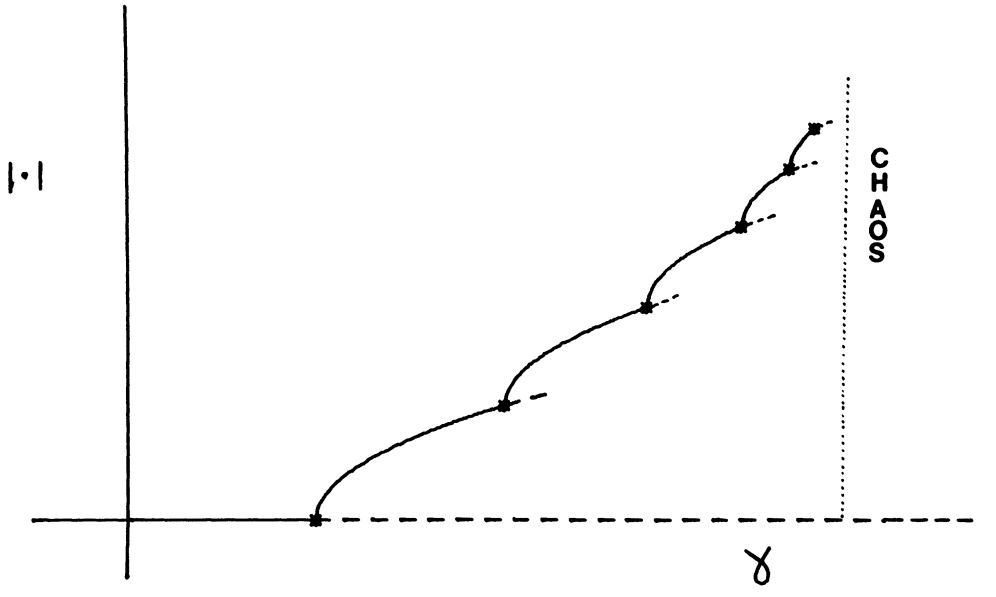

FIG. 10. *Conjectured bifurcation diagram showing successive period doubling bifurcations preceding chaotic behavior.*

band. The divergence of (3.1) is $-\mu < 0$ so that the dimension of the attractor cannot exceed 2. This succession of bifurcations is similar to the analogous sequence for a large class of discrete models. One is tempted to suggest the bifurcation diagram shown in Fig. 10. Feigenbaum [4] has recently shown for a large class of mappings that if b_n is the value of a parameter b at which a 2^n-point cycle occurs, then

$$\lim_{n\to\infty} \delta_n = \frac{b_{n+1}-b_n}{b_{n+2}-b_{n+1}} = 4.669\cdots \tag{4.7}$$

is a universal constant. We have tabulated the analogous ratio for the 4 bifurcations that we have computed. The results, shown in Table 1, indicate that the ratio will eventually be Feigenbaum's universal constant. This is not surprising since the existence of these period doubling bifurcations can be ascertained by looking at the Poincaré map as a function of γ. Feigenbaum's result holds for such maps.

Based on the numerical results of this section, we conjecture that for certain ranges of μ, $\nu > 0$, as γ is increased there will always be a sequence of period doubling bifurcations ultimately ending in chaos. More exact numerical techniques must be

TABLE 1
Bifurcation to $2^n T$-periodic solutions.

n	γ_n	$(\gamma_{n+1}-\gamma_n)/(\gamma_{n+2}-\gamma_{n+1}) \equiv \delta_n$
0	2.000	4.1565
1	3.089	4.4407
2	3.351	4.5384
3	3.410	-
4	3.423	-

used in order to find exact values of the bifurcation points and perhaps the existence of period-3 oscillations. This could be done by following the Floquet exponents of the basic periodic solution.

4.3. Full problem. We have demonstrated numerically that (3.19) admits chaotic solutions when $\varepsilon = 0$. We turn now to the FHN equations for $\varepsilon \neq 0$ and show that chaos persists in this system. The FHN equations can be written as a simple third order system. We substitute the critical values of the parameters $(ab, a_2, a_3) \equiv (\kappa+\rho, \kappa^3/(\kappa-\rho), \rho^3/(\kappa-\rho))$ into this system. When $\kappa = 2$, $\rho = 1$, we find the scaled full system can be written as:

$$
\begin{aligned}
&y''' + \mu y'' + \nu y' + \gamma y + 2y^2 = \varepsilon H(y, y', y'', \varepsilon), \\
&H(y, y', y'', \varepsilon) = 2\varepsilon^2 y^3 + 9y'(2y - 3\varepsilon^3 y^2) + 2\varepsilon y'^2(1 - 3\varepsilon^3 y).
\end{aligned} \tag{4.8}
$$

When $\varepsilon = 0$, we have (4.1). Although an exhaustive check of parameter ranges has not been done, we find that the limit cycle persists even for ε as high as 0.5.

Henceforth, γ will vary while (μ, ν) remain fixed at (1, 2). In Fig. 11, the solution to (4.8) is shown in the (y', y'')-plane with ε fixed at $\varepsilon = 0.1$. Initially, there is an Hopf bifurcation which leads to a stable limit cycle as γ increases. This is shown in

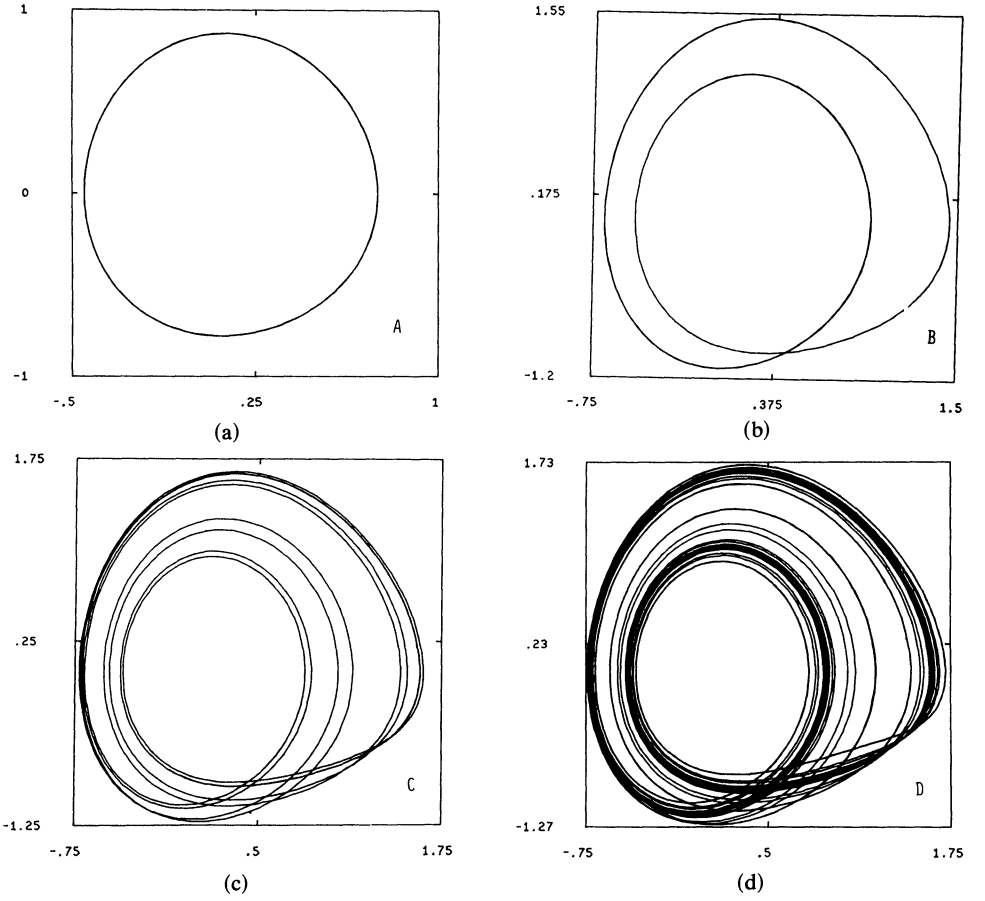

FIG. 11. *Integration of the full* FHN *equation with* $\varepsilon = .1$ *for* γ *increasing*; (a) $\gamma = 2.5$, *a stable limit cycle*; (b) $\gamma = 3.1$, *a doubled loop oscillation*; (c) $\gamma = 3.2$, *the eight-looped solution*; (d) $\gamma = 3.25$, "*chaos.*" *Plot is V vs* $\dot{V}$.

Fig. 11a for $\gamma = 2.5$. In Fig. 11b we depict the double looped oscillation at $\gamma = 3.1$. The 8-looped cycle is shown in Fig. 11c for $\gamma = 3.2$. When $\gamma \approx 3.25$, the solution is as in Fig. 11d, which bears a qualitative resemblance to the "chaotic" solution shown in Fig. 9.

This example shows that the numerical chaos is robust and does not disappear when high order terms are added. We are led to conclude that (1) a triply degenerate zero eigenvalue can be unfolded to a system which admits chaos-like solutions and (2) that various neuronal oscillators with excitatory feedback can behave chaotically. The chaos we have investigated seems to arise from a succession of period doubling bifurcations; this sequence follows Feigenbaum's general rule.

The technique described here can be applied to arbitrary systems of order 3 or higher. The resultant canonical equation is simpler in form than most other systems which have been shown to behave chaotically. Because of this simplicity it may be easier to show how the chaotic behavior arises as γ is increased. Recently Marzec and Spiegel [23] have studied a class of third order systems which lead to chaotic behavior via period doubling bifurcations. We can write these as:

$$\dot{x} = y, \quad \dot{y} = -\nu y - \left[x^n - \sum_{k=0}^{n-2} \alpha_k(\lambda) x^k \right], \quad \dot{\lambda} = -\varepsilon[\lambda + g(x)] \tag{4.9}$$

where $g(x)$ is a polynomial in x and ε is small. (4.9) was suggested as a generic recipe for producing chaos in third order systems. One can derive (4.9) by slowly changing the bifurcation parameters in one of Thom's catastrophes. If $\alpha_0(\lambda) = \hat{\alpha}\lambda + O(\lambda^2)$ and $g(x) = \bar{g}x + O(x^2)$, then $(\lambda, y, x) = (0, 0, 0)$ is an equilibrium point and the eigenvalues for the linearized system satisfy:

$$\rho^3 + (\nu + \varepsilon)\rho^2 + \nu\varepsilon\rho - \hat{\alpha}\varepsilon\bar{g} = 0. \tag{4.10}$$

If, as suggested in [23], $\nu = \varepsilon\delta$ and additionally we set $\hat{\alpha} = \varepsilon^2\alpha$, (4.10) becomes

$$\rho^3 + \varepsilon(\delta + 1)\rho^2 + \varepsilon^2\delta\rho + \varepsilon^3\alpha\bar{g} = 0. \tag{4.11}$$

When $n = 2$, under suitable scaling of (x, y, λ), we see that (4.9) can be reduced to the form (4.1) with the following identifications: $\mu = \delta + 1 = \nu + 1$, $\gamma = \alpha\bar{g}$. So (4.9) with $n = 2$ is a restriction of (4.1) to $\mu = \nu + 1$. Since Marzec and Spiegel are primarily concerned with the cases where n is odd, our results for $n = 2$ complement their observations as well as producing a derivation of the equations from a general nth order system. In the event that the quadratic nonlinearity in (4.1) vanishes, similar techniques might be used to derive the more general system (4.9).

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