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LARGE SCALE SPATIALLY ORGANIZED ACTIVITY IN NEURAL NETS*

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Abstract. A model for the spatiotemporal activity of neuronal nets is proposed. Stationary periodic spatial patterns are discussed from the point of view of bifurcation theory. Existence of spatial patterns on the whole line is established by the implicit function theorem. Singularity theory is used to study the local structure of the bifurcation equations. A Poincaré–Lindstedt series is developed to establish the form of the periodic stationary states and their stability. The biological relevance of these patterns is briefly discussed.

1. Introduction. In the past few years, numerous models of large scale neuronal interactions have been proposed [2]–[4]. These models all share several common mechanisms which we now describe. Suppose we consider a set of interconnected neurons distributed over the line with the following simple properties:

(1) Each neuron has a membrane potential, V_k, associated with it.

(2) The output firing frequency (impulses per second) or current, I_k, is a function of the membrane potential, $I_k = S(V_k)$.

(3) The net current ψ_{kj}, contributed by the neuron at k to another neuron at j is weighted by some constant, α_{kj}; $\psi_{kj} = \alpha_{kj} I_k$.

(4) The total postsynaptic potential, ϕ_{kj}, contributed by this current depends on the temporal characteristics of the dendrites:

$$\phi_{kj} = \int_{-\infty}^{t} h(t-\tau)\psi_{kj}(\tau)\,d\tau.$$

Here, $h(t)$ is characteristic of the dendrite cable properties and may contain delays, etc. For our purposes, we take $h(t) = \exp(-t/\mu)/\mu$; which represents a simple RC-network, with μ the time constant of the membrane.

(5) Finally these postsynaptic potentials are summed to yield the total membrane potential of the neuron:

$$V_j(t) = \sum_k \phi_{kj} = \int_{-\infty}^{t} h(t-\tau)\sum_k \alpha_{kj} S(V_k(\tau))\,d\tau + \int_{-\infty}^{t} h(t-\tau)P_j(\tau)\,d\tau, \tag{1.1}$$

where we have also included external stimulating currents, $P_j(t)$. Taking $h(t)$ as above

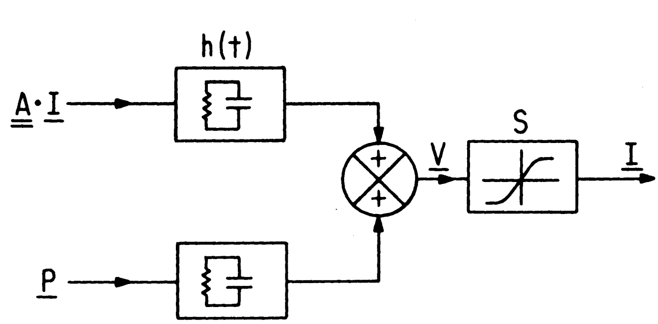

FIG. 1. *Neural net described in text.*

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leads to the system of ordinary differential equations:

$$\mu \frac{dV_j}{dt} = -V_j + \sum_k \alpha_{kj} S(V_k(t)) + P_j(t), \qquad j = 0, 1, 2, \cdots. \tag{1.2}$$

We assume that the weights may be written

$$\alpha_{kj} = \alpha w(|j-k|); \qquad \sum_k w(|k|) = 1,$$

that is an absolute number, α, times a "probability" of connection, $w(|j|)$. Since w depends only on the distance between connections, we are additionally assuming that the tissue is isotropic. Under these conditions, we may take the continuum limit of (1.2), assuming there are infinitely many neurons distributed along the x-axis:

$$\mu \frac{\partial V}{\partial t}(x, t) = -V(x, t) + \alpha \int_{-\infty}^{\infty} w(|x-y|) S(V(y, t))\, dy + P(x, t). \tag{1.3}$$

In general, $S(z)$ is a bounded monotone increasing function with an inflection point occurring at the "threshold." Examples include the logistic function and the Heaviside step function. Data indicate that the $i-v$ characteristic of cortical neurons has this form, shown in Fig. 2 [10]. For this paper and numerical simulations, we shall take

$$S(z) = \left(\frac{q_0}{r+1}\right)[1/(1+\exp(-\nu(z-\theta))) - 1/(1+\exp(\nu\theta))], \tag{1.4}$$

where q_0 is the charge delivered per impulse, r the refractory period; ν determines how rapidly S increases, and θ determines the inflection point in the $i-v$ characteristic. We have subtracted an additional term from $S(z)$ so that $S(0) = 0$. This is a mathematical simplification and does not alter the qualitative results significantly.

So far we have assumed α is positive and in so doing considered a population of excitatory neurons (if $\alpha < 0$, then they would be inhibitory). A more realistic model incorporates various other cell types, so we generalize (1.3) to a multipopulation model. Let $V_n(x, t)$ denote the membrane potential of the nth cell type at point x and time t.

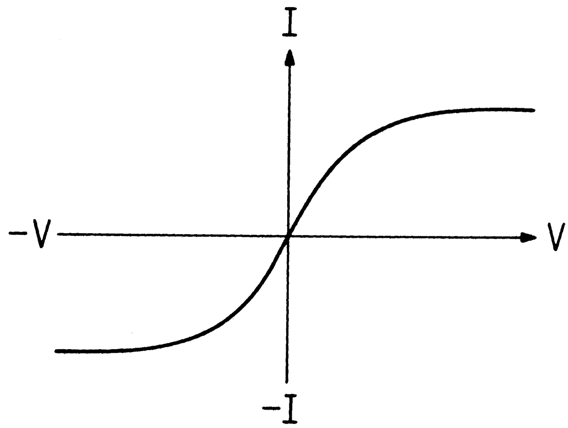

FIG. 2. *Nonlinear "$i-v$" characteristic for a single neuron.*

Then (1.3) generalizes to:

$$\mu_n \frac{\partial V_n}{\partial t}(x, t) = -V_n(x, t) + \sum_{m=1}^{M} \alpha_{mn} \int_{-\infty}^{\infty} W_{mn}(|x-x'|) S_m(V_m(x', t))\, dx' + P_n(x, t), \qquad n = 1, \cdots, M. \tag{1.5}$$

$S_m(V_m)$ is of the same form as (1.4) with different thresholds, θ_m, and "excitabilities," ν_m. μ_n is the time constant of the nth population, α_{mn} determines the absolute synaptic strength between populations m and n, and $w_{mn}(x)$ determines the rate of falloff of these connections. For notational convenience we write $W * U$ to mean the spatial convolution,

$$\int_{-\infty}^{\infty} W(x-x')U(x')\, dx'.$$

Let $\underset{\sim}{S}(\underset{\sim}{V}) = (S_1(V_1), \cdots, S_M(V_M))$, $\underset{\sim}{V} = (V_1, \cdots, V_M)$, $\underset{\sim}{P} = (P_1, \cdots, P_M)$, and $\mathbf{K}(y) = (\alpha_{mn} W_{mn})$. Assume $\mu_n = \mu$, $n = 1, \cdots, M$. Then (1.5) may be written as:

$$\mu \frac{\partial \underset{\sim}{V}}{\partial t} = -\underset{\sim}{V} + \mathbf{K} * \underset{\sim}{S}(\underset{\sim}{V}) + \underset{\sim}{P}. \tag{1.6}$$

Define $\underset{\sim}{Y}(x, t)$ by

$$\underset{\sim}{V} = \mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P}. \tag{1.7}$$

Then (1.6) may be written as

$$\mu \frac{\partial \underset{\sim}{Y}}{\partial t} = -\underset{\sim}{Y} + \underset{\sim}{S}(\mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P}), \tag{1.8}$$

where we now assume the inputs, $P_n(x)$, are independent of time. Since S_n is bounded above and below, so are the solutions $\underset{\sim}{Y}(x, t)$. This work is concerned with the stationary solutions of (1.8) bifurcating from the zero solution for the cases $M = 1, 2$, thus we study the stationary equations:

$$-\underset{\sim}{Y} + \underset{\sim}{S}(\mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P}) = 0. \tag{1.9}$$

2. Mathematical preliminaries. In order to rigorously apply bifurcation methods to (1.9), we must make some additional assumptions on $\underset{\sim}{S}$ and $\mathbf{K}$, as well as the topology of the network. Except in § 3, we assume that the system or tissue is connected in a ring of length, Λ, i.e., we impose periodic boundaries. Because of the symmetry of $\mathbf{K}(x)$, i.e., $\mathbf{K}(x) = \mathbf{K}(-x)$, we observe that $\mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P}$ is even in x as long as $\underset{\sim}{P}$ and $\underset{\sim}{Y}$ are even, thus we may restrict the solution space to even, continuous, bounded, periodic functions. Let Z denote the Banach space of even, periodic functions with the C_0 norm. For a large class of weighting functions, $w_{nm}(x)$, the operator, $O: Z \to Z$, defined by $O(\underset{\sim}{Y}) = \mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P}$ is compact and thus the nonlinear operator,

$$\eta(\underset{\sim}{Y}) = S(\mathbf{K} * \underset{\sim}{Y} + \underset{\sim}{P})$$

is also compact. We assume that $\underset{\sim}{S}(\underset{\sim}{V})$ is smooth so that the Fréchet derivatives of $\eta(\underset{\sim}{Y})$ exist to sufficiently high order. It is readily verifiable that $\eta: Z \to Z$.

We now review the Lyapunov–Schmidt method and an application of the Malgrange preparation theorem to bifurcation problems (see [1] for a complete discussion with applications). Let $A(\lambda, \cdots, \lambda_n): Z \to Z$ be a nonlinear map, Fréchet differentiable with respect to $z \in Z$, and to each of the real parameters, $\lambda_1, \cdots, \lambda_n$. Consider the equation:

$$A(\lambda_1, \cdots, \lambda_n)Z = 0 \tag{2.1}$$

and suppose that there is always a trivial solution, $z = \tilde{z}(\lambda_1, \cdots, \lambda_n)$, which we take to be zero. Let $T \equiv A(0, 0, \cdots, 0)$. Assume that $DT(0)$ is singular with a one-dimensional kernel generated by w_0, and a one-dimensional co-kernel generated by v_0. We wish to investigate the bifurcation of solutions of (2.1) as the parameters vary. Let $E: Z \to$ range $(DT(0))$ and $Q: Z \to \text{Ker}\,(DT(0))$ be the standard projections to the range of $DT(0)$ and the kernel of $DT(0)$. Because $DT(0)$ is one to one as a map from $(I-Q)Z$ to EZ, there is an inverse map, $M: EZ \to (-Q)Z$. Write $z = y + w$, where $z \in Z$, $w = Qz$, $y = (I-Q)z$. Then (2.1) may be written as

$$DT(0)z = -Az + DT(0)z. \tag{2.2}$$

Applying the operators, ME and $(I-E)$, we obtain:

$$y = ME[-A(w+y) + DT(0)y], \tag{2.3a}$$

$$(I-E)A(w+y) = 0. \tag{2.3b}$$

Using the implicit function theorem applied to (2.3a), we solve uniquely for $y = y*(A, w)$, with $y*(T, 0) = 0$. Substituting into (2.3b), we obtain

$$(I-E)A(w + y*(A, w)) \equiv F(w, A) = 0. \tag{2.4}$$

The operator $F(\cdot, A)$ defines a map from ker $(DT(0))$ to co-ker $(DT(0))$, so that for $w = uw_0$, there is some real number, $f(u, A)$, such that $F(uw_0, A) = f(u, A)v_0$, since the co-kernel is one-dimensional. If we now assume that A depends on the λ_i in some nice fashion, then solutions to (2.1) correspond to solutions to

$$f(u; \lambda_1, \lambda_2, \cdots, \lambda_n) = 0. \tag{2.5}$$

We have reduced the infinite dimensional bifurcation problem to one of finding the zeros of a real valued function depending on parameters. Since this is only a map from the reals to the reals, we can use some very powerful geometric theorems developed in the last 25 years.

THEOREM 2.1 ([12]). *Let $f: R \times R^n \to R$ and suppose that $f(u; 0, 0, \cdots, 0) = Cu^k + O(u^{k+1})$, $C \neq 0$. Suppose that*

$$\frac{\partial f}{\partial \lambda_i}(u; 0, 0, \cdots, 0) = \sum_{j=0}^{k-2} a_{ij}\frac{u^j}{j!} + O(u^{k-1}), \qquad i = 1, 2, \cdots, n,$$

and that the rank of (a_{ij}) is $k-1$. Then there is a coordinate system near the origin:

$$\bar{\lambda}_i = \xi_i(\lambda_1, \lambda_2, \cdots, \lambda_n), \qquad i = 1, 2, \cdots, n,$$

$$\bar{u} = \eta(u; \lambda_1, \lambda_2, \cdots, \lambda_u)$$

such that f has the following normal form:

$$\bar{f}(\bar{u};\ \bar{\lambda}_1, \bar{\lambda}_2, \cdots, \bar{\lambda}_n) = \bar{u}^k + \sum_{j=1}^{k-1} \bar{\lambda}_i \bar{u}^{j-1}.$$

For $k \leqq 5$ this is simply elementary co-rank one catastrophe theory. The result we obtain in § 4 is that for certain parameters, the bifurcation set associated with the solutions of (1.9) is equivalent to that of the butterfly catastrophe.

3. Bifurcation to spatially periodic solutions on the whole line. In contrast to § 2 and the rest of this paper, we shall consider a model which is distributed over the whole line. We demonstrate the existence of a two-parameter family of periodic solutions bifurcating from the trivial solutions in the case $M=2$. We shall also show that only spatially homogeneous solutions bifurcate from the rest state when $M=1$. The model we use is due to Feldman and Cowan (1975), but the method can easily be generalized to other models with more than two populations of neurons. Before proceeding, we remark that it will be demonstrated that strong inhibitory influences are necessary ("lateral inhibition") in order for bifurcation to occur at a nonzero wave number. Thus this is in some sense a minimal model for generating stable periodic structures. We consider the following equations:

$$\text{(3.1)} \qquad \begin{aligned} \frac{\partial Y_e}{\partial t} &= -Y_e + S_e(\alpha_{ee}(\lambda) w_{ee} * Y_e - \alpha_{ie}(\lambda) w_{ie} * Y_i), \\ \frac{\partial Y_i}{\partial t} &= -Y_i + S_i(\alpha_{ei}(\lambda) w_{ei} * Y_e - \alpha_{ii}(\lambda) w_{ii} * Y_i), \end{aligned}$$

where we have scaled out the time constant, μ, $\alpha_{mn}(\lambda)$ are the weights which we assume depend on λ analytically when λ is near zero. Assume that the $w_{mn}(x)$ satisfy:

(i) $w_{mn}(x) = w(x/\sigma_{mn})/\sigma_{mn}$,
(ii) $\int_{-\infty}^{\infty} e^{ikx} w(x)\, dx \equiv \hat{w}(k^2)$ exists and is analytic in k^2,
(iii) $\lim_{k\to\pm\infty} \hat{w}(k^2) = 0$; $\hat{w}(0) = 1$,
(iv) $\hat{w}(k^2)$ decreases as k^2 increases.

We remark that $w_{mn}(k^2) = w(k^2\sigma_{mn}^2)$ and that σ_{mn} are space constants determining how rapidly $w_{mn}(x)$ fall off as x increases.

Since $S_j(0) = 0$, it follows that $Y_e = Y_i = 0$ is a solution to (3.1) for all values of λ. This solution corresponds to the cells firing at resting level. We wish to examine the stability of the rest state with respect to small perturbations of various wave numbers. This requires looking at the solutions to the linearized problem:

$$\text{(3.2)} \qquad \frac{\partial}{\partial t}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -u + S_e'(0)[\alpha_{ee}(\lambda) w_{ee} * u - \alpha_{ie}(\lambda) w_{ie} * v] \\ -v + S_i'(0)[\alpha_{ei}(\lambda) w_{ei} * u - \alpha_{ii}(\lambda) w_{ii} * v] \end{pmatrix} \equiv L(\lambda)\begin{pmatrix} u \\ v \end{pmatrix}.$$

From the above assumptions, (3.2) has solutions:

$$\text{(3.3)} \qquad \begin{pmatrix} u(x,t) \\ v(x,t) \end{pmatrix} = \underline{\Phi}(\lambda, k^2) \exp(\xi(\lambda, k^2)t + ikx);$$

where $\underline{\Phi}(\lambda, k^2)$ is an eigenvector with eigenvalue $\xi(\lambda, k^2)$ of the matrix, $H(\lambda, k^2)$:

$$\text{(3.4)} \qquad H(\lambda, k^2) = \begin{vmatrix} -1 + S_e'(0)\alpha_{ee}(\lambda)\hat{w}(k^2\sigma_{ee}^2) & -S_e'(0)\alpha_{ie}(\lambda)\hat{w}(k^2\sigma_{ie}^2) \\ S_i'(0)\alpha_{ei}(\lambda)\hat{w}(k^2\sigma_{ei}^2) & -1 - S_i'(0)\alpha_{ii}(\lambda)\hat{w}(k^2\sigma_{ii}^2) \end{vmatrix}.$$

The following assumptions must be made on the eigenvalues, $\xi(\lambda, k^2)$:

ASSUMPTION 1. *There is a* $\lambda = \lambda_0$, *which we take to be zero for convenience, and a* $k_0^2 > 0$ *such that for all* $|k^2 - k_0^2| < \delta_1 |\lambda - \lambda_0| < \delta_2$, $H(\lambda, k^2)$ *has a unique eigenvalue with maximum real part and it is real and simple. Denote it by* $\xi_1(\lambda, k^2)$. *Let* $I_\lambda = \{k^2 | \xi_1(\lambda, k^2) \geqq 0\}$. *Then we assume that*:

$$I_\lambda = \begin{cases} \varnothing & \text{for } \lambda_0 - \delta_2 < \lambda < \lambda_0, \\ k_0^2 & \text{for } \lambda = \lambda_0;\ k_0^2 > 0, \\ \text{bounded interval of positive length} & \text{for } \lambda_0 < \lambda < \lambda_0 + \delta_2. \end{cases}$$

In Fig. 3, we illustrate this assumption. The requirement that $k_0^2 \neq 0$ implies that the instability occurs at a nonzero frequency. We shall show that strong lateral interactions are necessary for $k_0^2 \neq 0$. From Assumption 1 it follows that $\det(H(0, k_0^2)) = 0$, $H(0, k_0^2)$ has a simple zero eigenvalue, with eigenfunction:

$$\underset{\sim}{\Phi}(0, k_0^2) = \begin{pmatrix} 1 \\ \rho \end{pmatrix}, \tag{3.5}$$

where $\rho = [-1 + S'_e(0)\alpha_{ee}(0)\hat{w}(k_0^2\sigma_{ee}^2)]/[S'_e(0)\alpha_{ie}(0)\hat{w}(k_0^2\sigma_{ie}^2)]$.

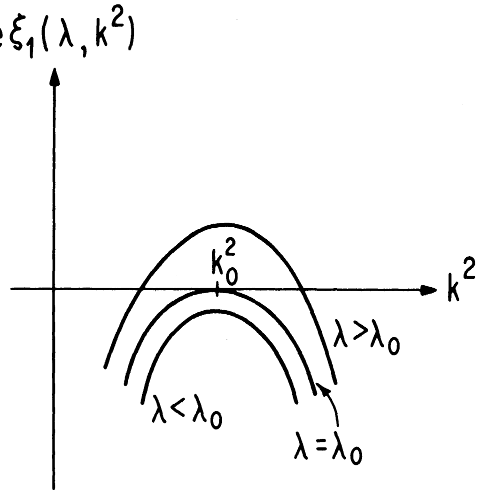

FIG. 3. *Assumption* 1 (*see text for details*).

Similarly the adjoint or transpose matrix, $H^t(0, k_0^2)$ has an eigenspace spanned by

$$\underset{\sim}{\Psi}(0, k_0^2) = \begin{pmatrix} 1 \\ \rho^* \end{pmatrix}, \tag{3.6}$$

where $\rho^*[1 - S'_e(0)\alpha_{ee}(0)\hat{w}(k_0^2\sigma_{ee}^2)]/[S'_i(0)\alpha_{ei}(0)\hat{w}(k_0^2\sigma_{ei}^2)]$.

Since $S'_e(0)$, $S'_i(0)$ are both positive, as are the $\alpha_{mn}(0)$ and $w(k_0^2\sigma_{mn}^2)$, then in order for $\det(H(0, k_0^2))$ to vanish, we must have $S'_e(0)\sigma_{ee}(0)\hat{w}(k_0^2\sigma_{ee}^2) > 1$ for otherwise the determinant would always be positive. Thus $\rho^* < 0$ and $\rho > 0$. Biologically this implies that for some range of λ and k_0^2 the excitatory cells exhibit local recurrent excitation (excitatory-excitatory interactions) greater than the decay rate due to membrane leakage. (This is very similar to the situation in activator-inhibitor models studied by Fife and others). We further remark that for $M = 1$, a zero eigenvalue occurs only if

$$-1 + S'_e(0)\alpha_{ee}(0)\hat{w}(k^2\sigma_{ee}^2) = 0.$$

Since $\hat{w}(k^2\sigma_{ee}^2)$ decreases as k^2 increases, the maximum for this expression always occurs at $k = 0$, so that only spatially homogeneous solutions initially bifurcate from zero.

Before turning to Assumption 2, which is a kind of transversality condition, we show that lateral inhibition is a necessary condition for $k_0^2 > 0$.

LEMMA. *A necessary condition for* $k_0^2>0$ *is that*

$$\alpha_{ei}(0)\alpha_{ie}(0)[\sigma_{ei}^2+\sigma_{ie}^2]>\alpha_{ee}(0)\alpha_{ii}(0)[\sigma_{ii}^2+\sigma_{ee}^2]+\frac{\sigma_{ee}^2\alpha_{ee}(0)}{S_i'(0)}-\frac{\sigma_{ii}^2\alpha_{ii}(0)}{S_e'(0)}.$$

The proof of this lemma is in the appendix.

We thus see that if the lateral interactions, $\alpha_{ei}(0)$, $\alpha_{ie}(0)$, σ_{ie}, σ_{ie}, are large compared to the "self" interactions, $\alpha_{ii}(0)$, $\alpha_{ee}(0)$, σ_{ee}, σ_{ii}, that $k_0^2\neq 0$. Thus in order for such spatial patterns to occur in the absence of boundary conditions, we require inhibition.

ASSUMPTION 2.

$$\begin{pmatrix}1\\ \rho^*\end{pmatrix}\begin{pmatrix}S_e'(0)\alpha_{ee}'(0)\hat{w}(k_0^2\sigma_{ee}^2) & -S_e'(0)\alpha_{ie}'(0)\hat{w}(k_0^2\sigma_{ie}^2)\\ S_i'(0)\alpha_{ei}'(0)\hat{w}(k_0^2\sigma_{ei}^2) & -S_i'(0)\alpha_{ii}'(0)\hat{w}(k_0^2\sigma_{ii}^2)\end{pmatrix}\begin{pmatrix}1\\ \rho\end{pmatrix}\neq 0,$$

where

$$\alpha_{nm}'(0)=\frac{\partial}{\partial\lambda}\alpha_{nm}(\lambda)|_{\lambda=0}.$$

If we expand $H(\lambda, k_0^2)$ as $H(0, k_0^2)+\lambda H_1(0, k_0^2)$ then Assumption 2 implies that the inner product, $(\underline{\Psi}(0, k_0^2), H_1(0, k_0^2)\underline{\Phi}(0, k_0^2))\neq 0$ or that

$$\frac{\partial}{\partial\lambda}\operatorname{Re}(\xi(\lambda, k_0^2))|_{\lambda=0}\neq 0.$$

THEOREM 3.1. *Given Assumptions* 1 *and* 2 *and that the nonlinear function is* $C^r(r\geqq 2)$, *then the stationary equation may be written as*

$$L(\lambda)\underline{u}+G(\lambda,\underline{u})=0, \tag{3.7}$$

where

$$\underline{u}=\begin{pmatrix}Y_e(x)\\ Y_i(x)\end{pmatrix}.$$

$L(\lambda)$ *is as in* (3.2) *and* $G(\lambda,\underline{u})$ *comprises the remaining terms of higher order in* Y_e, Y_i, *and* λ. *It is easily shown that* G *is* C^{r-1}, *and for* $\underline{u}$ *and* λ *near zero*, $G(\lambda,\underline{u})\leqq C\|\underline{u}\|^2$. *Under such conditions there is a two-parameter family of periodic functions*, $(Y_e(x;\varepsilon,q), Y_i(x;\varepsilon,q))$ *and a real number*, $\lambda(\varepsilon,q)$, *continuous in* ε *and* q, *and defined for* $|\varepsilon|$, $|q|$ *small, such that*

(1) Y_e, Y_i *satisfy* (3.7) *for each fixed* ε *and* q,

(2) Y_e, *and* Y_i *are periodic in* x *with period* $2\pi/\sqrt{k_0^2+q}=p$,

(3) $\int_0^p[Y_e(x;\varepsilon,q)+\rho^*Y_i(x;\varepsilon,q)]\cos x\,dx=\varepsilon$,

(4) $\lambda(0,0)=0$ *and* $Y_e(x;0,0)=Y_i(x;0,0)=0$.

In the appendix, we sketch the proof of this theorem, which in a somewhat similar situation has been demonstrated by Fife (1977). He studied a system of partial differential equations occurring in reaction and diffusion, rather than integral equations as in (3.1). Under the above conditions, the bifurcation diagram shown in Fig. 4 arises. Case (a) corresponds to supercritical bifurcation, case (b) to subcritical bifurcation. We conjecture that all solutions bifurcating subcritically are unstable, while there exist infinitely many stable supercritical solutions (see Fife for a more complete discussion of stability).

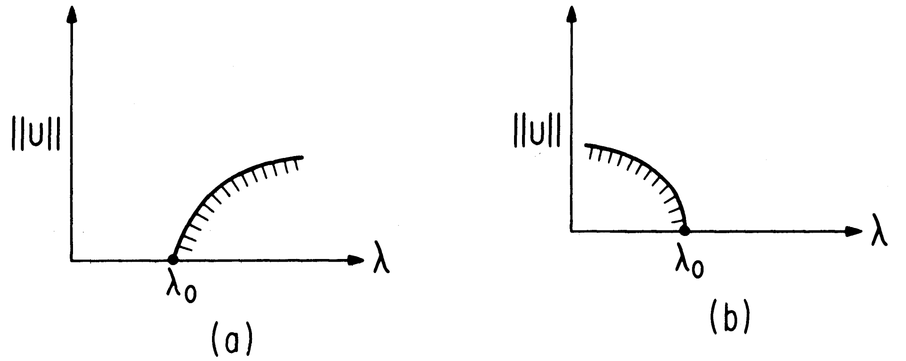

FIG. 4. *Two parameter bifurcation*; (a) *supercritical*, (b) *subcritical.*

Summarizing, we have shown the existence of spatially periodic solutions even on the entire real line. The reason one does this is to examine the systems of type (3.1) in absence of any boundary effects. Hence all behavior found in these systems is due solely to interactions between populations of cells and not to anisotropies at boundaries.

4. Multiparameter generic bifurcations. We show that under certain generic conditions on a set of parameters, $(\lambda_1, \lambda_2, \lambda_3, \lambda_4)$ the number of stationary solutions to the model system (4.1):

$$\begin{aligned}\frac{\partial}{\partial t}\begin{pmatrix} Y_e \\ Y_i \end{pmatrix} &= -\begin{pmatrix} Y_e \\ Y_i \end{pmatrix} + \begin{bmatrix} S_e((\alpha_{ee}+\lambda_1)w_{ee} * Y_e - \alpha_{ie}w_{ie} * Y_i + \lambda_3 P_e) \\ S_i((\alpha_{ei}+\lambda_2)w_{ei} * Y_e - \alpha_{ii}w_{ii} * Y_i + \lambda_4 P_i) \end{bmatrix} \\ &\equiv A(\lambda_1, \lambda_2, \lambda_3, \lambda_4)\underline{w}; \qquad \underline{w} = \begin{pmatrix} Y_e(x,t) \\ Y_i(x,t) \end{pmatrix}\end{aligned} \tag{4.1}$$

is the same as the number of solutions of a certain fifth order polynomial with coefficients depending on $\lambda_1, \lambda_2, \lambda_3, \lambda_4$. In fact, the bifurcation set of (4.1) is shown to be equivalent to that of the butterfly catastrophe or in a somewhat less restricted case that of the cusp catastrophe. As in § 2, we restrict our results to a ring of tissue in which solutions even in space are sought, i.e., $\underline{w}(x+\Lambda) = \underline{w}(x)$ and $\underline{w}(-x) = \underline{w}(x)$, where Λ is the length of the ring. Changing the length of Λ is equivalent to changing the critical frequency at which bifurcation occurs, thus we can assume without loss in generality that $\Lambda = 2\pi$.

If bifurcation occurs at the zero wave number (i.e., spatially homogeneous solutions), we can study the phase plane as the parameters change from their critical values. Thus we can see directly the evolution of the new solutions as $\lambda_1, \lambda_2, \lambda_3, \lambda_4$ are altered. Before continuing it is worth mentioning that the restriction to even functions is not necessary to apply the Lyapunov–Schmidt method, but only to use Theorem 2.1. Indeed, without this restriction and appropriate scaling of the parameters, the system (4.1) can be reduced to finding solutions to a pair of third order polynomials in two variables.

We can immensely simplify the necessary calculations by assuming that $S_e(z)$ and $S_i(z)$ are symmetric functions in z, i.e., $S_j(-z) = -S_j(z)$. If we put S as in (1.4), this is the same as setting $\theta_e = \theta_i = 0$. This is not unreasonable since the thresholds may be absorbed into the external inputs, P_e, P_i; thus the system (4.1) is still quite general.

Following the method outlined in § 2, we examine the linearized operator, $DT(0)$, obtained by setting $\lambda_i = 0$ and taking the Fréchet derivatives with respect to Y_e and Y_i

evaluated at zero:

$$DT(0)\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -u + S_e'(0)[\alpha_{ee}w_{ee} * u - \alpha_{ie}w_{ie} * v] \\ -v + S_i'(0)[\alpha_{ei}w_{ei} * u - \alpha_{ii}w_{ii} * v] \end{pmatrix}.$$

With the assumptions of periodicity and evenness in x, $DT(0)$ is Fredholm with zero index and one-dimensional kernel generated by $\begin{pmatrix} 1 \\ \rho \end{pmatrix} \cos k_0 x$ where where ρ is as in (3.5). We note that λ_1, λ_2 modify the "weight" of excitatory coupling within the net of cells and λ_3, λ_4 modify the stimulus intensity. Given (4.1) and parameters λ_i we show that there are conditions under which the assumptions of Theorem 2.1 are satisfied. Appendix C outlines the procedure and technical results necessary to verify that Theorem 2.1 with $k = 5$ holds. We can summarize the results by stating that certain computable qualities must not vanish. In particular, if we expand the stimuli, $P_e(x)$ and $P_i(x)$ in terms of their Fourier components:

$$\begin{pmatrix} P_e(x) \\ P_i(x) \end{pmatrix} = \sum_{j=0}^{\infty} \begin{pmatrix} a_j^e \\ a_j^i \end{pmatrix} \cos jx,$$

then $a_{k_0}^e$, $a_{k_0}^i$ must be nonzero. This is to be expected since only the components of the critical frequency can "excite" the unstable mode and contribute to the bifurcating solution.

To help visualize the effects of the parameters on the small amplitude solutions, we consider the simplest case when the critical frequency is zero. In this case, the isoclines give a complete picture of the effects of $\lambda_1, \lambda_2, \lambda_3, \lambda_4$. In Fig. 5a, the case when $\lambda_1 = \lambda_2 = \lambda_3 = \lambda_4 = 0$ is shown corresponding to a fifth order degeneracy of the zero state. As λ_1 or λ_2 increase two new solutions appear, Fig. 5b which depending on the balance between λ_1 and λ_2 are either stable or unstable. We note that there is a symmetry of the solutions when $\lambda_3 = \lambda_4 = 0$ but that as these parameters change the symmetry is broken, Fig. 5d. In Fig. 6a we show the bifurcation diagram associated with the transition from Fig. 5a to Fig. 5b, while in Fig. 6b, the transition from Fig. 5a to Fig. 5d is shown. Another possibility is shown in Fig. 5c, where for certain changes in λ_1, λ_2 there are five solutions. This may be regarded in some sense as a secondary bifurcation. Again as long as $\lambda_3 = \lambda_4 = 0$, there is symmetry of the five solutions but introduction of λ_3 or λ_4 destroys this symmetry, Fig. 5e.

By the results in the Appendix, the same situation occurs for $k_0 \neq 0$, the only difference being that the theorem can be conveniently displayed for $k_0 = 0$ using the phase plane. In Fig. 7a we show the bifurcation set of the polynomial:

$$u^5 + \tilde{\lambda}_1 u^4 + \tilde{\lambda}_e u^2 + \tilde{\lambda}_2 u + \tilde{\lambda}_4 = 0.$$

Here, u is roughly equivalent to the size of the component in the kernel of $DT(0)$ of the solution, $\begin{pmatrix} Y_e(x) \\ Y_i(x) \end{pmatrix}$, and because of symmetry, we suggest that $\tilde{\lambda}_3, \tilde{\lambda}_4$ depend only on λ_3, λ_4 and $\tilde{\lambda}_1, \tilde{\lambda}_2$ on λ_1, λ_2. When $\lambda_3 = \lambda_4$, $\lambda_1 = \lambda_2$ and equality A.8 of the Appendix does not hold, then the bifurcation set (Fig. 7b) is that of the cusp catastrophe:

$$u^3 + \tilde{\lambda}_1 u + \tilde{\lambda}_3 = 0.$$

As a final remark, we suggest that experimentally one will never see the sharp transitions as in Fig. 6a, but rather the imperfect bifurcation shown in Fig. 6b. Constant inputs and noise levels of the brain have the effect of adding symmetry breaking parameters to the system.

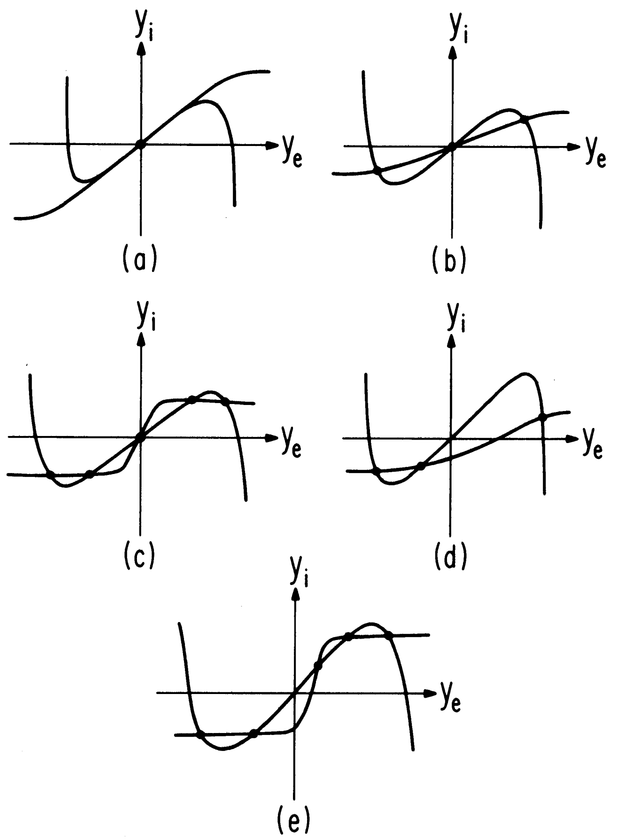

FIG. 5. *Isoclines with fifth order degeneracy*: (a) *one degenerate solution*, (b) 3 *solutions*, $\pm u$, 0, (c) 5 *solutions* $\pm u$, $\pm u_2$, 0, (d) 3 *solutions*, u_1, u_2, u_3, (e) 5 *solutions*, u_1, u_2, u_3, u_4, u_5.

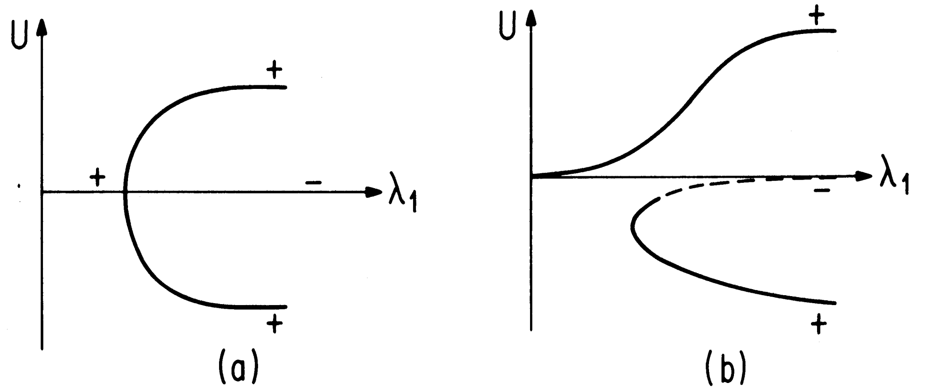

FIG. 6. *Bifurcation diagrams*: (a) *symmetric solutions*, (b) "*imperfect*" *bifurcation*.

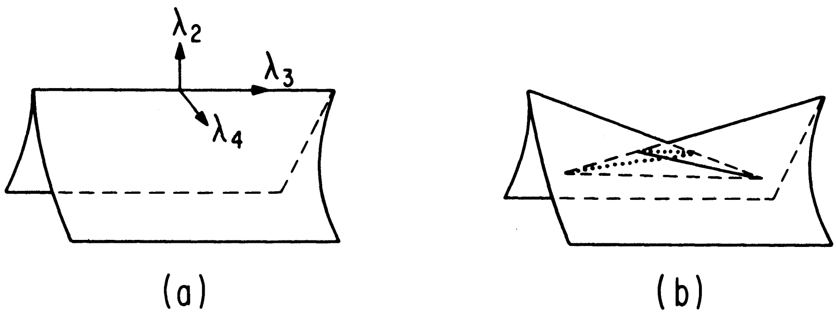

FIG. 7. "*Butterfly*" *catastrophe*: (a) $\lambda_1>0$, (b) $\lambda_1<0$.

5. Asymptotic expansions for two-dimensional nets. In this section a Poincaré–Lindstedt series is developed for the bifurcating steady states. With the same conditions on the boundaries, the one-dimensional system becomes:

$$(5.1)\qquad \begin{aligned} &Y_e(x)=S_e\left(\lambda\int_{-\infty}^{\infty} w(|x-x'|)Y_e(x')\,dx'\right),\\ &Y_e(x+\Lambda)=Y_e(x);\qquad Y_e(-x)=Y_e(x),\end{aligned}$$

where we put Λ as the length of the ring of tissue. Linearizing about $Y_e=0$, leads to the problem:

$$(5.2)\qquad -u(x)+S_e'(0)\lambda\int_{-\infty}^{\infty} w(|x-x'|)u(x')\,dx'\equiv L_0u=0.$$

This has solutions $u(x)=A\cos 2k\pi x/\Lambda$, where k is a nonnegative integer, if and only if λ satisfies

$$(5.3)\qquad \lambda=\lambda_k=1/[S_e'(0)\hat{w}(4k^2\pi^2)\Lambda^2)],$$

where

$$\hat{w}(\omega^2)=\int_{-\infty}^{\infty} w(x)\,e^{i\omega x}\,dx.$$

The points of bifurcation are at λ_k and these can be ordered $\lambda_{k_1}<\lambda_{k_2}<\cdots$. By well-known bifurcation results [9], only the first bifurcating branch is stable, thus $\lambda_{\min}=\min_k\lambda_k$ must be determined. Since $\hat{w}(\omega^2)$ is strictly decreasing, $1/\hat{w}(\omega^2)$ is strictly increasing so that the minimum must occur at $\omega^2=0$, whence, $\lambda_{\min}=\lambda_0=1/S_e'(0)$. This is the trivial wave number and the solutions bifurcating from λ_0 are constant, indeed they are solutions to $Y=S_e(\lambda Y)$. We can solve this graphically and similarly determine that all bifurcations are supercritical and thus stable (see Fig. 8).

The more interesting case arises when inhibition is introduced into the network, thus we consider the case of two populations, excitatory and inhibitory. As was shown in § 3 this is necessary for the appearance of spatial structure without introducing inhomogeneities in the system of the boundaries. The steady state equations for a

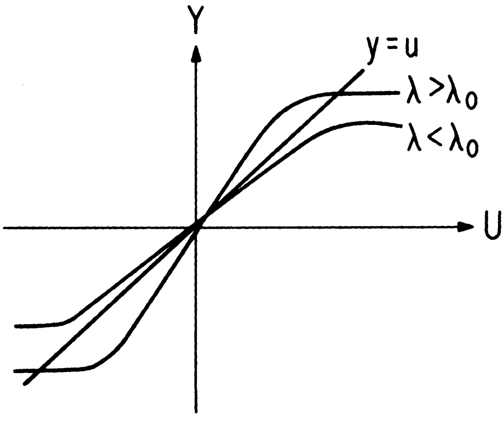

FIG. 8. *Graphical solution of the one-dimensional neural model.*

typical two-population net are:

$$(5.4)\qquad \begin{aligned} &Y_e = S_e(\alpha_{ee}\lambda w_{ee} * Y_e - \alpha_{ie}w_{ie} * Y_i),\\ &Y_i = S_i(\alpha_{ei}\lambda w_{ei} * Y_e - \alpha_{ii}w_{ii} * Y_i),\\ &Y_e(x+\Lambda) = Y_e(x), \qquad Y_i(x+\Lambda) = Y_i(x),\\ &Y_e(-x) = Y_e(x), \qquad Y_i(-x) = Y_i(x). \end{aligned}$$

Linearizing about the trivial solution, $Y_e = Y_i = 0$ leads to:

$$(5.5)\qquad L(\lambda)\binom{u}{v} \equiv -\binom{u}{v} + \begin{pmatrix} S_e'(0)[\alpha_{ee}\lambda w_{ee} * u - \alpha_{ie}w_{ie} * v] \\ S_i'(0)[\alpha_{ei}\lambda w_{ei} * u - \alpha_{ii}w_{ii} * v] \end{pmatrix} = 0.$$

This has solutions

$$\binom{u(x)}{v(x)} = \Phi(k, \lambda)\cos\frac{2k\pi x}{\Lambda}, \qquad k = 0, 1, 2, 3, \cdots,$$

where $\Phi(k, \lambda)$ satisfies $\mathbf{H}(\lambda, 4k^2\pi^2/\Lambda^2)\Phi(k, \lambda) = 0$ and $\mathbf{H}(\lambda, \omega^2)$ is as in (3.4). Here, $\alpha_{ee}(\lambda) = \lambda\alpha_{ee}$, $\alpha_{ie}(\lambda) = \alpha_{ie}$, $\alpha_{ei}(\lambda) = \alpha_{ei}\lambda$, $\alpha_{ii}(\lambda) = \alpha_{ii}$. This has a nontrivial solution if and only if $\det H(\lambda, 4k^2\pi^2/\Lambda^2) = 0$. This yields an equation for the discrete λ_k, $k = 0, 1, 2, \cdots$. As above, we may order these

$$0 < \lambda_{k_1} < \lambda_{k_2} < \cdots$$

and similarly, only the branch bifurcating from the smallest will be stable. By the result in § 3, we know that sufficient "lateral inhibition" often implies that

$$\lambda_{\min} = \min_k \lambda_k$$

is not λ_0, the bifurcation point at the zero wave number. Hence, we may assume $\lambda_{\min} = \lambda_{k_0}$ with $k_0 \neq 0$, so that the bifurcating solutions will be nonconstant over space. As in § 4, we may also assume that S_e and S_i are symmetric so that their even derivatives vanish. Thus we assume that at $\lambda = \lambda_{k_0}$, an eigenvalue of the full linearized evolution system becomes zero, and at all other wave numbers, the eigenvalues have negative real parts. The eigenfunction associated with λ_{k_0} is

(5.6)
$$\begin{pmatrix}\phi_e(x)\\ \phi_i(x)\end{pmatrix}=\begin{pmatrix}1\\ \rho\end{pmatrix}\cos\frac{2k_0\pi x}{\Lambda},$$

where

$$\rho=\frac{-1+S_e'(0)\alpha_{ee}\lambda_{k_0}\hat{w}_{ee}(4k_0^2\pi^2/\Lambda^2)}{S_e'(0)\alpha_{ie}\hat{w}_{ie}(4k_0^2\pi^2/\Lambda^2)}.$$

As in § 3, $\rho>0$, and $\hat{w}_{jl}(\omega^2)$ is the Fourier transform of $w_{jl}(x)$. We expand $Y_e(x)$, $Y_i(x)$ and $\lambda-\lambda_{k_0}$ in terms of small parameter, ε, which is essentially the amplitude (see below) of the bifurcating solution:

(5.7)
$$\begin{pmatrix}Y_e(x;\varepsilon)\\ Y_i(x;\varepsilon)\end{pmatrix}=\varepsilon\begin{bmatrix}Y_{e0}(x)\\ Y_{i0}(x)\end{bmatrix}+\varepsilon^2\begin{bmatrix}Y_{e1}(x)\\ Y_{i1}(x)\end{bmatrix}+\varepsilon^3\begin{bmatrix}Y_{e2}(x)\\ Y_{i2}(x)\end{bmatrix},\qquad \lambda-\lambda_{k_0}=\varepsilon\gamma_1+\varepsilon^2\gamma_2+-.$$

Substituting (5.7) into (5.4) and collecting equal powers of ε leads to a sequence of linear inhomogeneous equations:

(5.8)
$$L_0\begin{bmatrix}Y_{en}(x)\\ Y_{in}(x)\end{bmatrix}=\begin{bmatrix}a_n(x)\\ b_n(x)\end{bmatrix},\qquad n=0,1,2,\cdots,$$

with $L_0=L(\lambda_{k_0})$. The first few $a_n(x)$, $b_n(x)$ are

$$a_0(x)=b_0(x)=0,\qquad a_1(x)=\gamma_1S_e'(0)\alpha_{ee}w_{ee}*Y_{e0},$$

$$b_1(x)=\gamma_1S_i'(0)\alpha_{ei}w_{ei}*Y_{eo},$$

$$a_2(x)=-S_e'(0)\alpha_{ee}w_{ee}*(\gamma_2Y_{eo}+\gamma_1Y_{e1})-\frac{S_e'''}{6}(0)(\lambda_{k_0}\alpha_{ee}w_{ee}*Y_{e0}-\alpha_{ie}w_{ie}*Y_{i0})^3,$$

$$b_2(x)=-S_i'(0)\alpha_{ei}w_{ei}*[\gamma_2Y_{e0}+\gamma_1Y_{e1}]-\frac{S_i'''}{6}(0)[\lambda_{k_0}\alpha_{ei}w_{ei}*Y_{eo}-\alpha_{ii}w_{ii}*Y_{i0}]^3.$$

Since L_0 is Fredholm and has a nontrivial kernel, the equation, $L_0\underline{W}=\underline{f}$ is solvable if and only if $\underline{f}$ is orthogonal to the eigenfunction of the adjoint L_0^*:

(5.9)
$$L_0^*\begin{bmatrix}\phi_e^*\\ \phi_i^*\end{bmatrix}=\begin{bmatrix}-\phi_e^*+S_e'(0)\lambda_{k_0}\alpha_{ee}w_{ee}^*\phi_e^*+S_i'(0)\alpha_{ei}\lambda_{k_0}w_{ei}^*\phi_i^*\\ -\phi_i^*-S_e'(0)\alpha_{ie}w_{ie}^*\phi_e^*-S_i'(0)\alpha_{ii}w_{ii}^*\phi_i^*\end{bmatrix},$$

(5.9) has a solution:

$$\begin{pmatrix}\phi_e^*(x)\\ \phi_i^*(x)\end{pmatrix}=\zeta^*\begin{pmatrix}1\\ \rho^*\end{pmatrix}\cos\frac{2k_0\pi x}{\Lambda};\qquad \rho^*=\frac{1-S_e'(0)\lambda_{k_0}\alpha_{ee}\hat{w}_{ee}(4k_0^2\pi^2/\Lambda^2)}{S_i'(0)\lambda_{k_0}\alpha_{ei}w_{ei}(4k_0^2\pi^2/\Lambda^2)},$$

$$\zeta^*=1/(1+\rho\rho^*).$$

As before $\rho^*<0$. Note that we have multiplied the vector $\begin{pmatrix}1\\ \rho^*\end{pmatrix}$ by a constant ζ^*. In Appendix D it is shown that this factor is not infinite ($\rho\rho^*\neq-1$). Our purpose is to normalize the solutions in some sense, for now the inner product

$$\left\langle\begin{pmatrix}\phi_e^*(x)\\ \phi_i^*(x)\end{pmatrix}\begin{pmatrix}\phi_e(x)\\ \phi_i(x)\end{pmatrix}\right\rangle=\frac{1}{\pi}\int_0^{2\pi}\{\phi_e^*(x)\phi_e(x)+\phi_i^*(x)\phi_1^*(x)\}\,dx=1.$$

Thus we assume that the solutions we obtain using the perturbation scheme satisfy:

$$\left\langle \begin{pmatrix} \phi_e^*(x) \\ \phi_i^*(x) \end{pmatrix} \begin{pmatrix} Y_e(x;\varepsilon) \\ Y_i(x;\varepsilon) \end{pmatrix} \right\rangle = \varepsilon. \tag{5.10}$$

This determines the solutions uniquely, as well as the amplitude, ε.

Solving (5.8) for $n = 0, 1$, we obtain:

$$\begin{pmatrix} Y_{e0}(x) \\ Y_{i0}(x) \end{pmatrix} = \begin{pmatrix} 1 \\ \rho \end{pmatrix} \cos 2k_0\pi x/\Lambda; \qquad \begin{pmatrix} Y_{e1}(x) \\ Y_{i1}(x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}; \qquad \gamma_1 = 0.$$

The solution for $Y_{e1}(x)$, and $Y_{i1}(x)$ obtains from the normalization condition, (5.10). Finally to $O(\varepsilon^3)$ we find:

$$\begin{pmatrix} Y_e(x;\varepsilon) \\ Y_i(x;\varepsilon) \end{pmatrix} = \begin{pmatrix} 1 \\ \rho \end{pmatrix} \cos 2k_0\pi x/\Lambda + O(\varepsilon^3),$$

$$\lambda - \lambda_{k_0} = \gamma_2\varepsilon^2 + O(\varepsilon^3); \qquad \gamma_2 = \left[\frac{S_e'''(0)}{S_e'(0)^3} + \frac{S_i'''(0)}{S_i'(0)^3}\rho^3\rho^*\right].$$

The direction of bifurcation dermines the stability of the solutions, thus if γ_2 is positive, bifurcation is supercritical and the small amplitude solutions are stable. On the other hand if γ_2 is negative, bifurcation is subcritical and the small amplitude solutions are unstable. Since $\rho^3\rho^* < 0$ and $S_e'''(0); S_i'''(0) < 0$ if $S_e'''(0)/S_i'(0)\rho^3\rho^* > -S_e'''(0)/S_e'(0)^3$, i.e.,

$$\frac{S_i'''(0)}{S_i'(0)^3}\left[\frac{[-1+\alpha_{ee}S_e'(0)\lambda_{k_0}\hat{w}_{ee}(4\pi^2k_0^2/\Lambda^2)]^4}{[\alpha_{ie}w_{ie}(4\pi^2k_0^2/\Lambda^2)]^3[S_i'(0)\alpha_{ei}\hat{w}_{ei}(4k_0^2\pi^2/\Lambda^2)]}\right] < -S_e'''(0).$$

Thus for strongly recurrent excitatory nets (α_{ee} large) we have unstable solutions while for strong lateral inhibition, there is stability. In Figs. 9a and 9b we draw the bifurcation diagrams for the stable and unstable cases respectively.

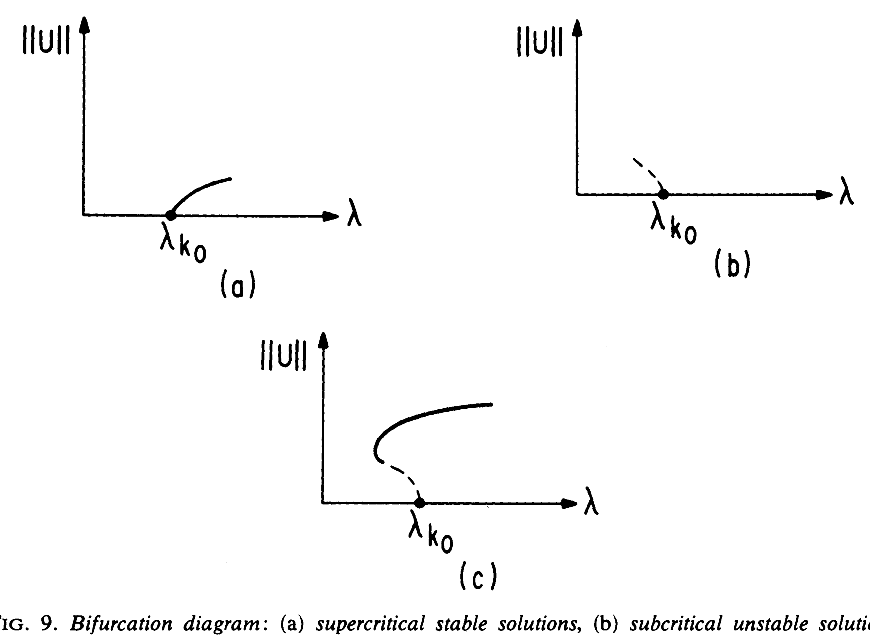

FIG. 9. *Bifurcation diagram*: (a) *supercritical stable solutions,* (b) *subcritical unstable solutions,* (c) *conjectured "full" picture showing "large amplitude" stable solutions.*

Remarks. It is assumed that $|\rho^*\rho^3| \neq 1$ for otherwise we would have to continue the calculations to the next two highest orders. This is the situation we had in section four where there was a fourth order degeneracy of the rest state.

Numerical calculations of the above system indicate that for subcritical bifurcation, stable large amplitude solutions exist both super- and subcritically. This leads us to the conjectured bifurcation diagram 9c. In this particular network, subcritical bifurcation leads to hysteresis with respect to changes in the parameter λ. As λ is increased beyond λ_{k_0} the net must switch to the new large amplitude solution. As λ decreases below λ_{k_0}, there is a value, at which the system must switch back to the zero state. Because of this multistability, the subcritical case may in fact be the more biologically relevant: multistability and hysteresis are quite common in the nervous system.

6. Conclusions. Evidently, the one- and two-dimensional nets considered here exhibit a startling range of stationary behavior. However, in order to make the analysis more tenable we had to make some simplifications at the boundaries. The true system should be considered over a finite domain rather than the circle of tissue considered here. Following the technique of Pazy and Rabinowitz, we have demonstrated bifurcations in the single population mode; in nonperiodic domains which are not spatially homogeneous. Thus there are some major differences between our simplified system and the actual system for the single excitatory model. On the other hand, numerical simulation of the two-population model in a finite nonperiodic domain yields solutions qualitatively very similar to the ones obtained in § 5. As we mentioned previously, the boundary conditions seem to exhibit little qualitative effect in the two-population system.

Most applications of bifurcation theory and nonlinear analysis in the biological sciences have been concerned with the study of systems of reacting and diffusing chemicals. In these applications, the nontrivial solutions have been supposed to represent the mechanism of pattern formation in developing embryos. We believe such pattern formation arising from instability commonly occurs in the vertebrate nervous system.

The biological significance of these spatially periodic solutions is not completely clear although we believe they may be related to certain simple visual hallucinations. Indeed, in his book, Klüver discusses the ubiquity of periodic phenomena in mescaline induced hallucinations [6]. Furthermore, many simple visual hallucinations exhibit startling periodicity of a few very simple patterns (see for example [11]). We hope to extend this work to two spatial dimensions in an attempt to further elucidate the spatial structure of cortical networks at an instability.

Appendix A. Proof of Lemma 3.1. In order that $k_0^2 > 0$, we want the determinant $\Delta(0, k^2) \equiv \det H(0, k^2)$ to obtain a minimal value at $k^2 = k_0^2 \neq 0$. Since $\lim_{k^2 \to \infty} \Delta(0, k^2) = 1$ and for k large $\Delta(0, k^2)$ increases, we require $\Delta(0, k^2)$ to be decreasing at $k^2 = 0$; i.e.,

$$\text{(A.1)} \qquad \frac{\partial}{\partial k^2} \Delta(0, k^2)\bigg|_{k^2=0} < 0.$$

Let

$$w_0 = \frac{\partial \hat{w}}{\partial k^2}\bigg|_{k^2=0}.$$

Then

$$\begin{aligned}\frac{\partial\Delta}{\partial h^2}(0,k^2)\bigg|_{k^2=0} &= -w_0[(1+S_i'(0)\alpha_{ii}(0))\sigma_{ee}^2\alpha_{ee}(0)S_e'(0)\\ &\quad +(-1+S_e'(0)\alpha_{ee}(0))\sigma_{ii}^2\alpha_{ii}(0)S_i'(0)]\\ &\quad + w_0S_i'(0)S_e'(0)\alpha_{ie}(0)(\sigma_{ie}^2+\sigma_{ei}^2).\end{aligned} \tag{A.2}$$

Since $w_0 < 0$ by assumption (iv), the inequality (A.1) becomes

$$\alpha_{ei}(0)\alpha_{ie}(0)(\sigma_{ei}^2+\sigma_{ie}^2) > (\sigma_{ii}^2+\sigma_{ee}^2)\alpha_{ee}(0)\alpha_{ii}(0)+\frac{\sigma_{ee}^2\alpha_{ee}(0)}{S_i'(0)}-\frac{\sigma_{ii}^2\alpha_{ii}(0)}{S_e'(0)},$$

as is required.

Appendix B. Proof of Theorem 3.1. Because Fife's result [5] is for a set of second-order differential equations, we shall show how to set up our system of integral equations as a map between Banach spaces and thus apply his proof. We seek solutions which are small with an amplitude, ε, and a spatial frequency, k near k_0. Since all spatial interactions are even, we let $q = k^2 - k_0^2$ denote the deviation from the critical wave number. This is the second parameter of the two-parameter family of Theorem 3.1. To simplify analysis we scale the space variable x by setting $y = kx$. Thus we seek solutions which are 2π-periodic in y. With this assumption, the convolutions $w_{jl}(x) * u(x)$ become, in the new variable, $(1/k)w_{jl}(y/k) * u(y)$. We wish to expand this convolution in terms of q as is done in Fife for the operator

$$k^2Dd^2/dx^2 = (k_0^2+q)Dd^2/dx^2.$$

In general, this is not easy, but we present a technique which works for a large class of connecting functions. Let

$$\hat{w}_{jl}(\omega^2) = \int_{-\infty}^{\infty} \exp(i\omega x)w_{jl}(x)\,dx$$

be the Fourier transform of $w_{jl}(y)$, then the transform of $(1/k)w_{jl}(y/k)$ is

$$\hat{w}_{jl}(k^2\omega^2) = \hat{w}_{jl}((k_0^2+q)\omega^2).$$

Since we have assumed that the Fourier transforms of the $w_{jl}(x)$ are analytic, we may expand $\hat{w}_{jl}((k_0^2+q)\omega^2)$ as:

$$\hat{w}_{jl}((k_0^2+q)\omega^2) = \hat{w}_{jl}(k_0^2\omega^2)+q\hat{w}_{jl}^1(k_0^2\omega^2)+q^2\hat{w}_{jl}^2(k_0^2\omega^2)+\cdots.$$

We next invert this to obtain a sequence of connection functions:

$$w_{jl}(y/k)/k = w_{jl}(y/k_0)/k_0+qw_{jl}^1(y)+q^2w_{jl}^2(y)+\cdots.$$

As an example, we take $w(x) = \exp(-|x|)/2$; then

$$\hat{w}((k_0^2+\omega)q^2) = \frac{1}{1+\omega^2k_0^2}\left[1-q\frac{\omega^2}{1+\omega^2k_0^2}+\frac{q^2\omega^4}{(1+\omega^2k_0^2)^2}-\cdots\right]$$

and upon inverting, we obtain the sequence:

$$w(y/k)/k = \frac{1}{2k_0}\exp(-|x|/k_0)+\sum_{n\geqq 1} w^n(y),$$

$$w^n(y) = \frac{(-1)^n\pi}{k_0^{2+2n}n!}\frac{d^n}{dz^n}[z^{n-1/2}\,e^{-|x|\sqrt{z}}]_{z=1/k_0^2}.$$

The original problem may be written as

$$L(\lambda, q)\underline{u} + G(\lambda, q, \underline{u}) = 0, \tag{B.1}$$

with $L(\lambda, q)\underline{u} = L_0\underline{u} + \lambda L_{10}\underline{u} + qL_{01}\underline{u} + \lambda q L_{11}\underline{u} + \cdots$. $L_0\underline{u} = 0$ has solutions

$$\underline{u} = \alpha\begin{pmatrix}1\\ \rho\end{pmatrix}\cos y = \underline{\phi}, \qquad -\alpha\begin{pmatrix}1\\ \rho\end{pmatrix}\sin y = \underline{\phi}', \qquad ' = \frac{d}{dy},$$

where $\alpha \in R$ is picked so that

$$\langle \underline{\phi}, \underline{\phi}\rangle = \frac{1}{\pi}\int_0^{2\pi} |\phi|^2\, dy = 1.$$

The linear adjoint problem has two linearly independent solutions

$$\psi = \begin{pmatrix}1\\ \rho^*\end{pmatrix}\cos y; \qquad \psi' = -\begin{pmatrix}1\\ \rho^*\end{pmatrix}\sin y.$$

Define P_1, P_2 to be the projections onto span $\{\psi, \psi'\}$, e.g., $P_1\underline{f} = \langle \underline{f}, \psi\rangle\psi$; $P_2\underline{f} = \langle \underline{f}, \psi'\rangle\psi'$. Let $E = I - P_1 - P_2$ be the projection onto the range of L_0. Let X be the Banach space of continuous, bounded 2π-periodic functions with values in R^2. Write $X = \{\phi, \phi'\}\oplus Z$ so that $z \in Z \to L_0\underline{z} \neq 0$. $L_0 : Z \to EX$ is one to one so that $M = L_0^{-1}$ exists as a bounded operator from EX to Z. Since $X = \{\phi, \phi'\}\oplus Z$ all solutions in X may be decomposed to

$$\underline{u} = \beta_1\underline{\phi} + \beta_2\underline{\phi}' + \underline{v} = \alpha\begin{pmatrix}1\\ \rho\end{pmatrix}(\beta_1\cos y + \beta_2 \sin y) + \underline{v}, \qquad \underline{v} \in Z.$$

We may translate the y coordinate at will since the connection functions, $w_{jl}(y - y')$ are invariant under translations, thus we may assume that $\beta_2 = 0$. We seek solutions which have small "amplitudes," letting $\beta_1 = \varepsilon$ be the amplitude, we see

$$\frac{1}{\pi}\int_0^{2\pi} \underline{u}(x)\underline{\phi}(x)\, dx = \varepsilon.$$

Thus solutions of the form

$$\underline{u}(y) = \varepsilon(\underline{\phi}(y) + \underline{w}(y)), \qquad \underline{w} \in Z,$$

are sought. Finally, let $F(\underline{u}, \varepsilon, \lambda, q) = (1/\varepsilon)G(\varepsilon\underline{u}, \lambda, q)$. Our problem (B.1) may be written:

$$L_0 w + \lambda L_1(\underline{\phi} + \underline{w}) + qL_{01}(\underline{\phi} + \underline{w}) + \cdots + \varepsilon F(\underline{\phi} + \underline{w}, \lambda, v) = 0 \tag{B.2}$$

or $L_0\underline{w} + R(\underline{w} + \underline{\phi}; \varepsilon, \lambda, q) = 0$. For each $(\varepsilon, \lambda, q)$, $R : Z \to X$. Applying E, P_1, P_2, we observe (B.2) is equivalent to

$$\begin{aligned} &L_0\underline{w} + \varepsilon R(\underline{w} + \underline{\phi}; \lambda, \varepsilon, q) = 0,\\ &P_1 R(\underline{w} + \underline{\phi}; \lambda, \varepsilon, q) = 0,\\ &P_2 R(\underline{w} + \underline{\phi}; \lambda, \varepsilon, q) = 0. \end{aligned} \tag{B.3}$$

The remaining results derived by Fife hold now and the theorem is verified. Clearly, Q, M, L_0, R preserve even functions so we may pick $\underline{w}$ to be even so that $P_2R(\underline{w} + \underline{\phi}; \varepsilon, \lambda, q)$ vanishes.

Appendix C. Generic bifurcation structure of the network. We derive the necessary expressions for application of the Malgrange preparation theorem. Recall that X is the Banach space of even continuous, bounded 2π-periodic functions and $A(\lambda_1, \lambda_2, \lambda_3, \lambda_4)$ is a four-parameter operator mapping X to itself. Let $T = A(0, 0, 0, 0)$ and assume that $DT(0)$ is Fredholm with a one-dimensional kernel and co-kernel. We showed in § 4 that the kernel is generated by

$$\underset{\sim}{\phi} = \alpha \begin{pmatrix} 1 \\ \rho \end{pmatrix} \cos k_0 x$$

and the co-kernel by $\underset{\sim}{\psi} = \alpha^* \begin{pmatrix} 1 \\ \rho^* \end{pmatrix} \cos k_0 x$. The inner product on X is $\langle f, g \rangle = (1/\pi) \int_0^{2\pi} f_1 g_1 + f_2 g_2 \, dx$ and we put $\alpha = (1+\rho^2)^{-1}$, $\alpha^* = (1+\rho^{*2})^{-1}$ so that $\langle \underset{\sim}{\psi}, \underset{\sim}{\psi} \rangle = \langle \underset{\sim}{\phi}, \underset{\sim}{\phi} \rangle = 1$. In this case, $X = Z$. The projection E is given by $I - P$ where

$$P\underset{\sim}{f} = \langle \underset{\sim}{f}(x), \underset{\sim}{\psi}(x) \rangle \underset{\sim}{\psi}(x).$$

We also need the operator, ME. E is obtained by applying $I - P$. To get M we write

$$DT(0)\underset{\sim}{r} = \underset{\sim}{v},$$

where $\underset{\sim}{v} = E\underset{\sim}{z}$, $\underset{\sim}{z} \in X$, and solve for $\underset{\sim}{r}$. This always has a solution since $\underset{\sim}{v} \in \operatorname{ran}(DT(0))$ by definition. In terms of actual computation we start with some function $\underset{\sim}{f} = \begin{vmatrix} f_1(x) \\ f_2(x) \end{vmatrix}$ and obtain $E\underset{\sim}{f}$:

$$\begin{pmatrix} v_1(x) \\ v_2(x) \end{pmatrix} = E \begin{pmatrix} f_1(x) \\ f_2(x) \end{pmatrix} = \begin{pmatrix} f_1(x) \\ f_2(x) \end{pmatrix} - \left\{ \frac{\alpha^*}{\pi} \int_0^{2\pi} f_1(x) \cos x + \rho^* f_2(x) \cos x \, dx \right\} \alpha^* \begin{pmatrix} 1 \\ \rho^* \end{pmatrix} \cos x.$$

Next the linear inhomogeneous system of equations:

$$\text{(C.1)} \qquad \begin{pmatrix} -g_1(x) + S_e'(0)[\alpha_{ee} w_{ee} * g_1 - \alpha_{ie} w_{ie} * g_2] \\ -g_2(x) + S_i'(0)[\alpha_{ei} w_{ei} * g_1 - \alpha_{ij} w_{ii} * g_2] \end{pmatrix} = \begin{pmatrix} v_1(x) \\ v_2(x) \end{pmatrix}$$

is solved. since $v_1(x)$, $v_2(x)$ can be expanded in a Fourier series, (C.1) is reduced to solving systems of algebraic equations for the components of $(g_1(x), g_2(x))$. Thus $ME\underset{\sim}{f} = \underset{\sim}{g}$.

Our principal task is to obtain the various derivatives of the function $f(u, \lambda_1, \lambda_2, \lambda_3, \lambda_4)$ evaluated at $u = 0$, $\lambda_i = 0$. We know that $\underset{\sim}{y}$ satisfies

$$\underset{\sim}{y}(u, \lambda_1, \lambda_2, \lambda_3, \lambda_4) = ME[-A(\lambda_1, \lambda_2, \lambda_3, \lambda_4)(u\underset{\sim}{\phi} + Y) + DT(0)(u\underset{\sim}{\phi} + y)].$$

To simplify calculations we expand $A(\lambda_1, \lambda_2, \lambda_3, \lambda_4)$:

$$\begin{aligned} A(\lambda_1, \lambda_2, \lambda_3, \lambda_4) \begin{pmatrix} Y_3 \\ Y_i \end{pmatrix} &= \begin{bmatrix} -Y_e + S_e'(0)(\alpha_{ee} w_{ee} * y_e - \alpha_{ie} w_{ie} * y_i) \\ -Y_i + S_i(0)(\alpha_{ei} w_{ei} * y_e - \alpha_{ii} w_{ii} * y_i) \end{bmatrix} \\ &\quad + \frac{1}{6} \begin{bmatrix} S_e'''(0)[\alpha_{ee} w_{ee} * Y_e - \alpha_{ie} w_{ie} * Y_i]^3 \\ S_i'''(0)[\alpha_{ei} w_{ei} * Y_e - \alpha_{ii} w_{ii} * Y_i]^3 \end{bmatrix} \\ &\quad + \frac{1}{120} \begin{bmatrix} S_e^{(v)}(0)[\alpha_{ee} w_{ee} * Y_e - \alpha_{ie} w_{ie} * Y_i]^5 \\ S_i^{(v)}(0)[\alpha_{ei} w_{ei} * Y_e - \alpha_{ii} w_{ii} * Y_i]^5 \end{bmatrix} \\ \text{(C.2)} \qquad &\quad + \lambda_1 \begin{bmatrix} w_{ee} * Y_e(S_e'(0)) + \dfrac{S_e'''(0)}{2}(\alpha_{ee} w_{ee} * Y_e - \alpha_{ii} w_{ii} * Y_i)^2 \\ 0 \end{bmatrix} \end{aligned}$$

$$+\lambda_2\begin{bmatrix} 0 \\ w_{ei} * Y_e(S_i'(0)) + \dfrac{S_i'''(0)}{2}(\alpha_{ei}w_{ei} * Y_e - \alpha_{ii}w_{ii} * Y_i)^2 \end{bmatrix}$$

$$+\lambda_3 P_e\begin{bmatrix} S_e'(0) + \dfrac{S_e'''(0)}{2}(\alpha_{ee}w_{ee} * Y_e - \alpha_{ii}w_{ii} * Y_i)^2 \\ 0 \end{bmatrix}$$

$$+\lambda_4 P_i\begin{bmatrix} 0 \\ S_i'(0)\dfrac{S_i'''(0)}{2}(\alpha_{ei}w_{ei} * Y_e - \alpha_{ii}w_{ii} * Y_i)^2 \end{bmatrix} + \text{higher order terms},$$

where the higher order terms are in $\lambda_i\lambda_j$, Y_e^6, Y_i^6, etc. Using implicit differentiation of the functions $F(u, T)$ and $y(u)$, we find:

$$\frac{\partial F}{\partial u}(0, T) = 0; \qquad \frac{\partial^2 F}{\partial u^2}(0, T) = 0; \qquad \frac{\partial^3 F}{\partial u^3}(0, T) = (I - E)D^3T(0)[\underline{\phi}, \underline{\phi}, \underline{\phi}],$$

$$\frac{\partial^4 F}{\partial u^4}(0, \phi) = 0, \qquad \frac{\partial^5 F}{\partial u^5}(0, T) = (I - E)[D^5T(0)[\underline{\phi}, \underline{\phi}, \underline{\phi}, \underline{\phi}, \underline{\phi}] + 10D^3T(0)[\underline{\phi}, \underline{\phi}]Y'''(0)]$$

$$y'(0)T) = y''(0, T) = 0, \qquad y'''(0, T) = -ME[D^3T(\underline{\phi}, \underline{\phi}, \underline{\phi})].$$

Here, $D^nT(0)$ is the nth Fréchet derivative of the operator T, $y'(0)$, $y''(0)$, etc., represents the various derivatives of y with respect to the scalar, u, evaluated at $u = 0$. We use the definition of ME to find:

$$y'''(0, T) = \begin{bmatrix} A_{11}\cos k_0 v + A_{13}\cos k_0 x \\ A_{21}\cos k_0 v + A_{23}\cos k_0 x \end{bmatrix},$$

where the coefficients $A_{11}, A_{13}, A_{21}, A_{23}$ depend on the various parameters and $S_0'''(0)$, $S_i'''(0)$ and are quite complicated. Note that $A_{11} + A_{21}\rho^* = 0$. In order for fourth order degeneracy to occur, we require $\partial^3 F/\partial u^3(0, T) = 0$ that is:

$$\text{(C.3)} \qquad \begin{aligned} \frac{\partial^3 f}{\partial u^3} &= \frac{\alpha^3}{6\pi\alpha^*}\int_0^{2\pi} \frac{S_e'''(0)}{S_i'(0)^3}\cos^4 k_0 x + \frac{S_i'''(0)}{S_i'(0)^3}\rho^3\rho^*\cos^4 k_0 x\,dx \\ &= \frac{\alpha^3}{4\alpha^*}\left[\frac{S_e'''(0)}{S_e'(0)^3} + \frac{S_i'''(0)}{S_i'(0)^3}\rho^3\rho^*\right] = 0. \end{aligned}$$

If as in § 5, if we assume that S_e and S_i are the same, then the expression, (C.3), is the same as that obtained in § 5. Evaluation of $\partial^5 F/\partial u^5$ determines whether we must continue to higher orders;

$$\frac{\partial^5 F}{\partial u^5}(0, 1) = (I - E)[D^5T(0)[\phi, \phi, \phi, \phi, \phi) + D^3T(0)[\underline{\phi}, \underline{\phi}, \underline{y}'''(0)]].$$

From the argument at the end of four based on phase plane techniques, we know that there can at most be five steady states, thus for $k_0 = 0$, this expression does not vanish. We believe that in general for nonzero k_0, it does not vanish.

To determine the derivatives of f with respect to λ_i and hence verify the transversality condition, we consider the operator $T + \lambda_i R_i$. Here R_i is any one of the four operators multiplied by λ_i in (C.2). Evaluating these various derivatives at $u = 0$, $\lambda_i = 0$, and again using implicit differentiation, we obtain

$$\frac{\partial F}{\partial \lambda_j}(0, T) = (I-E)R_j(0), \qquad \frac{\partial^2 F}{\partial \lambda_j\,\partial u}(0, T) = (I-E)DR_j(0)\underline{\phi},$$

$$\frac{\partial^3 F}{\partial \lambda_j\,\partial u^2}(0, T) = (I-E)[D^3T(0)[\underline{\phi}, \underline{\phi}, y_{\lambda_j}(0)] + D^2R_j(0)[\underline{\phi}, \underline{\phi}]),$$

$$\frac{\partial^4 F}{\partial \lambda_j\,\partial u^3}(0, T) = (I-E)[D^3T(0)[\underline{\phi}, \underline{\phi}, y_{u\lambda_j}(0)] + D^3R_j(0)[\underline{\phi}, \underline{\phi}, \underline{\phi}] + DR_j(0)y'''(0)].$$

For $j = 1, 2$,

$$R_j(0) = D^2R_j(0) = 0, \quad DR_1(0)\underline{\phi} = \begin{bmatrix} S_e'(0)w_{ee} * \phi_1 \\ 0 \end{bmatrix}, \quad DR_2(0) = \begin{bmatrix} 0 \\ S_i'(0)w_{ei} * \phi_1 \end{bmatrix},$$

and finally,

$$D^3R_j(0)[\underline{\phi}, \underline{\phi}, \underline{\phi}] = \frac{1}{2}\begin{cases} \begin{bmatrix} w_{ee} * \phi_1 S_e'''(0)(\alpha_{ee}w_{ee} * \phi_1 - \alpha_{ie}w_{ie} * \phi_2)^2 \\ 0 \end{bmatrix}, & j = 1, \\ \begin{bmatrix} 0 \\ w_{ei} * \phi_1 S_i'''(0)(\alpha_{ei}w_{ei} * \phi_1 - \alpha_{ii}w_{ii} * \phi_2)^2 \end{bmatrix}, & j = 2, \end{cases}$$

where

$$\underline{\phi} = \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \alpha \begin{pmatrix} 1 \\ \rho \end{pmatrix} \cos k_0 x.$$

For $j = 3, 4$,

$$DR_j(0) = D^3R_j(0) = 0, \quad R_1(0) = \begin{bmatrix} S_e'(0)P_e(x) \\ 0 \end{bmatrix}, \quad R_2(0) = \begin{bmatrix} 0 \\ S_i(0)P_i(x) \end{bmatrix}$$

and

$$D^2R_j(0) = \begin{cases} \begin{bmatrix} \dfrac{P_e(x)}{2} S_e'''(0)(\alpha_{ee}w_{ee} * \phi_1 - \alpha_{ie}w_{ie} * \phi_2)^2 \\ 0 \end{bmatrix}, & j = 3, \\ \begin{bmatrix} 0 \\ \dfrac{P_i(x)}{2} S_i'''(0)(\alpha_{ei}w_{ei} * \phi_1 - \alpha_{ii}w_{ii} * \phi_2)^2 \end{bmatrix}, & j = 4. \end{cases}$$

From these expressions, the importance of the inputs is now evident, for we can now show that the matrix, (a_{ij}) of Theorem 2.1 is not of rank four if either of the inputs has no component in the critical frequency. The derivatives of y with respect to the parameters are:

$$y_{\lambda_3} = -ME\begin{bmatrix} S_e'(0)P_e(x) \\ 0 \end{bmatrix}, \qquad y_{\lambda_4} = -ME\begin{bmatrix} 0 \\ S_i'(0)P_i(x) \end{bmatrix}, \qquad y_{\lambda_2} = y_{\lambda_1} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

$$y_{\lambda_3 u} = y_{\lambda_4 u} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \qquad y_{\lambda_1 u} = -ME\begin{bmatrix} S_e'(0)w_{ee}(k_0^2)\cos k_0 x \\ 0 \end{bmatrix},$$

$$y_{\lambda_2 u} = -ME\begin{bmatrix} 0 \\ S_i'(0)w_{ei}(k_0^2)\cos k_0 x \end{bmatrix}.$$

Suppose that P_e for example has no components in $\cos k_0 x$, then clearly since ME "preserves" frequency, neither do $y_{\lambda_3}(0)$. $\partial F/\partial\lambda_3(0,0)$ is zero since there are also no components in $\underline{\phi}$. Computation of $\partial^3 F/\partial\lambda\ \partial u^3(0,0)$ also shows that this is zero, since y_{λ_3} has no components in k_0. Thus the third row of the matrix, (a_{ij}) consists of zeros and consequently is not of rank 4. Other conditions which are computable must also hold, but this particular example is the most intuitive.

Appendix D. Proof of the statement in § 5 ($1+\rho\rho^*>0$). We show that $1+\rho\rho^*>0$. Suppose instead that $1+\rho\rho^*\leqq 0$. Put

$$\beta_{ee}=\alpha_{ee}\hat{w}_{ee}(4\pi^2k_0^2/\Lambda^2)S_e'(0)\lambda_{k_0},\qquad \beta_{ei}=\alpha_{ei}\hat{w}_{ei}(4\pi k_0^2/\Lambda^2)S_i'(0)\lambda_{k_0}),$$

$$\beta_{ie}=\alpha_{ie}\hat{w}_{ie}(4\pi^2k_0^2/\Lambda^2)S_e'(0),\qquad \beta_{ii}=\alpha_{ii}\hat{w}_{ii}(4\pi k_0^2/\Lambda^2)S_i'(0).$$

Then, if $1+\rho\rho^*\leqq 0$, we find:

(D.1) $$-\frac{(-1+\beta_{ee})^2}{\beta_{ei}\beta_{ie}}\leqq -1.$$

Since $\det H(\lambda_{k_0}, 4\pi^2k_0^2/\Lambda^2)=(-1+\beta_{ee})(1+\beta_{ii})+\beta_{ei}\beta_{ie}=0$, (D.1) becomes

(D.2) $$-\frac{(-1+\beta_{ee})}{(1+\beta_{ii})}\leqq -1,\qquad (-1+\beta_{ee})-(1+\beta_{ii})\geqq 0.$$

But the expression on the left hand side of (D.2) is the trace of $H(\lambda_{k_0}, 4\pi^2k_0^2/\Lambda^2)$ which is strictly negative, so we have a contradiction and $1+\rho\rho^*>0$.

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