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SECONDARY BIFURCATION IN NEURONAL NETS*

G. B. ERMENTROUT† AND J. D. COWAN‡

Abstract. The possibility of multiple complex eigenvalues in a neural net is demonstrated. Group theoretic techniques are used to derive the bifurcation equations near multiple complex eigenvalues. A selection mechanism between standing and traveling waves is shown that depends only on internal parameters. Quasi-periodic solutions and hysteresis between different oscillations are obtained. The application of this model to the study of epileptic behavior is discussed.

Introduction. One of the most remarkable properties of the electrical activity of the central nervous system is that it is both ubiquitous and incessant. Anyone who has ever looked at an electroencephalographic (EEG) record will confirm this observation. There are many questions to be posed and answered concerning this activity. Which neuronal structures generate this activity? How is it generated? What is its function? In what fashion is it related to the firing patterns of individual neurons in the brain? In this and related papers [Ermentrout and Cowan (1979), Ermentrout and Cowan (1979a)], we seek to answer some of these questions by showing how organized spatio-temporal neuronal activity patterns can arise in a net of coupled neurons by a process of symmetry breaking from an initially uniform resting state. We use bifurcation theoretic techniques to study the evolution and stability of small amplitude solutions branching from the unstable uniform state. In two earlier papers, we showed the existence of spatially periodic stationary patterns when bifurcation occurred at a simple zero eigenvalue and a variety of spatio-temporal patterns when bifurcation occurred at a pair of imaginary eigenvalues [Ermentrout and Cowan (1979), Ermentrout and Cowan (1979a)]. In the latter paper it was conjectured that stable, quasiperiodic patterns could occur in certain cases.

In this paper we shall demonstrate secondary bifurcation when two pairs of complex conjugate eigenvalues cross the imaginary axis simultaneously. Bauer et al. (1975) made use of a perturbation method to study secondary bifurcation for a model of spherical shells. Using multiple timing methods, Cohen (1977) showed secondary bifurcation for a system of differential equations when there were multiple complex eigenvalues. Keener (1976) used a similar technique to determine the bifurcation structure of a system of reaction-diffusion equations when there were multiple eigenvalues. Here, we utilize the recently developed group-theoretic methods of Sattinger (1977) to describe the bifurcation structure at multiple complex eigenvalues. We show that there is a distinct pattern selection mechanism for stable activity patterns which depends solely on the "internal" parameters of the set.

1. Neuronal net equations. Definitions and preliminaries. In the appendix, we introduce the following system of nonlinear integral equations which describe the activity of a ring of excitatory and inhibitory neurons:

$$(1.1) \quad \begin{aligned} (a) \quad & E(x, t) = S_1\{h(t) \otimes [\alpha_{11}w_{11}(x) * E(x, t) - \alpha_{21}w_{21}(x) * I(x, t)]\}, \\ (b) \quad & I(x, t) = S_2\{h(t) \otimes [\alpha_{12}w_{12}(x) * E(x, t) - \alpha_{22}w_{22}(x) * I(x, t)]\}, \\ (c) \quad & E(x + 2\pi, t) = E(x, t); \quad I(x + 2\pi, t) = I(x, t). \end{aligned}$$

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Here $E(x, t)$ and $I(x, t)$ denote the activities of excitatory and inhibitory neurons and

$$(1.2) \quad \begin{aligned} (a) \quad h(t) \otimes u(t) &= \int_0^\infty h(\tau) y(t-\tau) d\tau, \\ (b) \quad w(x) * v(x) &= \int_{-\infty}^\infty w(x-x') v(x') dx'. \end{aligned}$$

The periodic boundary conditions imply that the net is in a ring. In previous papers, we have assumed unnecessary artificial symmetries which can eliminate whole classes of otherwise stable solutions. Here, we drop these assumptions, but still assume that the tissue is topologically a ring, a condition which is common both anatomically and physiologically [P. Rinaldi, G. Jukasy, and M. Verzeano (1977)].

The only assumptions we make on the nonlinear functions are:

$$(1.3) \quad \begin{aligned} (a) \quad S(0) &= 0; \\ (b) \quad S(u) &\text{ is monotone nondecreasing;} \\ (c) \quad S(u) &\text{ is Lipschitz continuous;} \\ (d) \quad S(u) &\text{ is sufficiently differentiable.} \end{aligned}$$

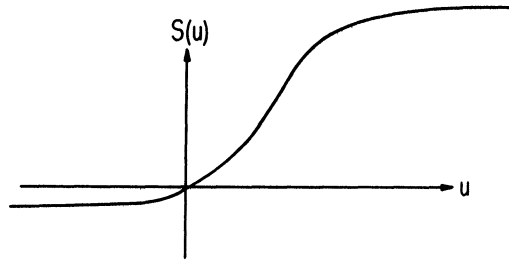


FIG. 1. Nonlinear firing rate-potential curve.

Figure 1 depicts a typical nonlinear function satisfying (1.3). The temporal weighting function, $h(t)$, is assumed for simplicity to be of the form:

$$(1.4) \quad h(t) = \exp(-t), \quad t \geq 0.$$

The spatial weights satisfy:

$$(1.5) \quad \begin{aligned} (a) \quad w_{ij}(x) &= w(x/\sigma_{ij})/\sigma_{ij}; \\ (b) \quad \int_{-\infty}^\infty w(x) dx &= 1; \\ (c) \quad w(-x) &= w(x); \\ (d) \quad w(x) &\text{ decreases with increasing } |x|. \end{aligned}$$

From (1.5b, c), the Fourier transform of w exists and it is even. We denote this transform by $W(k^2)$. Then from (1.5a), $W_{ij}(k^2) = W(\sigma_{ij}^2 k^2)$. There is histological evidence supporting these assumptions [Sholl (1956)]; in particular, it has been found that the connectivity falls off exponentially with distance between cells. Here σ_{ij} are space constants determining the rate of falloff between populations i and j .

Let B denote the Banach space of bounded R^2 -valued functions periodic in the first argument with the sup norm:

$$\|\mathbf{u}(x, t)\|_0 = \left\{ \sup_{0 \leq x \leq 2\pi} \sup_{0 \leq t < \infty} |u_1(x, t)| + \sup_{0 \leq x \leq 2\pi} \sup_{0 \leq t < \infty} |u_2(x, t)| \right\}$$

where $u_j(x, t)$ are the components of $\mathbf{u}(x, t)$. Let $\mathbf{G}(E, I)$ denote the operator

$$(1.6) \quad \mathbf{G}(E, I) \equiv \begin{bmatrix} E(x, t) - S_1\{h(t) \otimes (\alpha_{11}w_{11}(x) * E(x, t) - \alpha_{21}(x) * I(x, t))\} \\ I(x, t) - S_2\{h(t) \otimes (\alpha_{12}w_{12}(x) * E(x, t) - \alpha_{22}w_{22}(x) * I(x, t))\} \end{bmatrix}.$$

Then, it is readily shown that \mathbf{G} maps B into itself. We define the following linear transformation on B :

$$(1.7) \quad \begin{aligned} T_r \mathbf{u}(x, t) &= \mathbf{u}(-x, t), \\ T_\alpha \mathbf{u}(x, t) &= \mathbf{u}(x + \alpha, t), \quad \alpha \in R, \\ T_\beta \mathbf{u}(x, t) &= \mathbf{u}(x, t + \beta), \quad \beta \in R. \end{aligned}$$

Each map, T , takes B into itself and commutes with the nonlinear operator, G :

$$T_r \mathbf{G} = \mathbf{G} T_r, \quad T_\alpha \mathbf{G} = \mathbf{G} T_\alpha, \quad T_\beta \mathbf{G} = \mathbf{G} T_\beta.$$

The operator T_r reflects the x -axis about the origin. The assumption that the cortical net is isotropic is necessary and sufficient in order that T_r commute with G . T_α and T_β represent translations in space and time respectively. That G commutes with T_α is embodied in the assumption of cortical spatial homogeneity. Since the physical properties of the net do not change with time, all temporal interactions are ‘‘homogeneous’’ and thus G commutes with T_β .

We say a solution to (1.1) is *linearized stable* if there are no solutions to the linearized problem which grow exponentially for positive time. The linearized equation about the rest state $(E, I) = (0, 0)$ is:

$$(1.8) \quad \mathcal{L}_0 \begin{bmatrix} u \\ v \end{bmatrix} \equiv \begin{bmatrix} -u - h(t) \otimes [\alpha_{11}S'_1(0)w_{11} * u - \alpha_{21}S'_1(0)w_{21} * v] \\ -v - h(t) \otimes [\alpha_{12}S'_1(0)w_{12} * u - \alpha_{22}S'_2(0)w_{22} * v] \end{bmatrix} = 0.$$

Solutions to this are of the form:

$$(1.9) \quad \begin{pmatrix} u \\ v \end{pmatrix} = \Phi^n \exp(\nu_n t \pm inx)$$

where n is a nonnegative integer and Φ^n and ν_n are eigenfunctions and eigenvalues of the following matrix:

$$(1.10) \quad H(n^2) = \begin{bmatrix} -1 + \alpha_{11}S'_1(0)W_{11}(n^2) & -\alpha_{21}S'_1(0)W_{21}(n^2) \\ \alpha_{12}S'_2(0)W_{12}(n^2) & -1 - \alpha_{22}S'_2(0)W_{22}(n^2) \end{bmatrix}.$$

Solutions grow exponentially if for some n , $\text{Re } \nu_n > 0$. This can happen in two ways: a pair of complex conjugate eigenvalues crosses the imaginary axis for some n or a simple eigenvalue becomes positive. The first case occurs when the trace of $H(n^2)$ changes from negative to positive, while the determinant remains positive. The second case occurs when the determinant of $H(n^2)$ changes from positive to negative, while the trace remains negative. In previous work, we discussed these two cases when they occurred at a unique value of n^2 . There are at least four other possibilities:

- (1) the determinant vanishes simultaneously for two differing values of n ,
- (2) the determinant vanishes for n_1 and the trace for $n_2 \neq n_1$,
- (3) the trace vanishes simultaneously for two differing values of n ,
- (4) combinations of the above three cases leading to as many as 6 eigenvalues with zero real parts.

Keener studied (1) and (2) for a system of reaction-diffusion equations and we expect similar behavior to occur for (1.1). The paper is concerned with an analysis of case (3) because of its complexity and its novelty. The fourth case is certain to generate a wide variety of complex patterns, but it is beyond the scope of this brief paper to discuss them.

We now introduce two bifurcation parameters, μ and λ , defining them by $\alpha_{11} = \tilde{\alpha}_{11} + \mu$; $\alpha_{22} = \tilde{\alpha}_{22} + \lambda$. We assume that for $\lambda = \mu = 0$ the trace vanishes for two differing wave numbers, n_1 and n_2 . In fact for stability, n_1 and n_2 must be consecutive. To see this we plot the real part of $\nu_n(\lambda, \mu)$ (the eigenvalue of H with maximal real part) in Fig. 2.

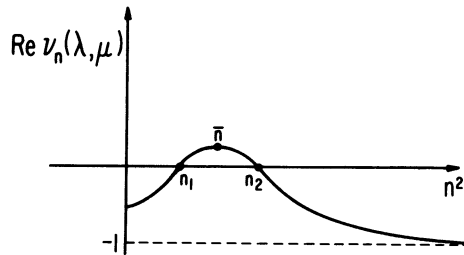


FIG. 2. Real part of the maximal eigenvalue, $\nu_n(\lambda, \mu)$.

As n^2 increases, $\text{Re } \nu_n(\lambda, \mu)$ becomes negative for all values of μ and λ . In order for two different wave numbers to have a zero real part it is necessary that the curve $\text{Re } \nu_n(\lambda, \mu)$ be convex upward for some range of n as in the figure. If n_1 and n_2 are not consecutive then there is at least one other value of n , \bar{n} , such that $\text{Re } \nu_{\bar{n}}(\mu, \lambda) > 0$. Thus the initial instability occurs, not at the pair of wave numbers, (n_1, n_2) , but rather at \bar{n} . Based on other results in which there is a discrete spectrum, all solutions bifurcating at n_1 and n_2 will be unstable since the first bifurcating wave number is \bar{n} . Thus we require n_1 and n_2 to be consecutive; i.e., $n_2 = n_1 + 1$. For all other values of n , it is assumed that at $\mu = \lambda = 0$, $\text{Re } \nu_n(0, 0) < 0$. In order for the trace to vanish for two consecutive integers, we require

$$\tilde{\alpha}_{11} = [2 + \tilde{\alpha}_{22} W_{22}(n_1^2)] / W_{11}(n_1^2) S'_1(0),$$

$$\tilde{\alpha}_{22} = \frac{2}{S'_2(0)} \frac{W_{11}(n_1^2) - W_{11}((n_1 + 1)^2)}{[W_{22}(n_1^2) W_{11}((n_1 + 1)^2) - W_{22}((n_1 + 1)^2) W_{11}(n_1^2)]}.$$

Both $\tilde{\alpha}_{22}$ and $\tilde{\alpha}_{11}$ must be positive in order for this to make physical sense. $\tilde{\alpha}_{11}$ is positive if $\tilde{\alpha}_{22}$ is positive, thus we must determine when $\tilde{\alpha}_{22}$ is positive. Because $w(x)$ decreases as $|x|$ increases, $W_{11}(n_1^2) - W_{11}((n_1 + 1)^2) > 0$. $W_{22}(n_1^2) W_{11}((n_1 + 1)^2) - W_{22}((n_1 + 1)^2) W_{11}(n_1^2) > 0$ implies

$$\frac{W(\sigma_{22}^2 n_1^2)}{W(\sigma_{22}^2 (n_1 + 1)^2)} > \frac{W(\sigma_{11}^2 n_1^2)}{W(\sigma_{11}^2 (n_1 + 1)^2)}.$$

This occurs only if $\sigma_{22}^2 > \sigma_{11}^2$ since $W(k^2)$ is strictly increasing as a function of k^2 . The interpretation of this is that there must be long-range lateral disinhibition, i.e., the spread of the inhibitory-inhibitory interactions must exceed that of the excitatory-excitatory interactions. Furthermore, in order that $\det H(n^2)$ remain positive for all n , α_{21} and α_{12} must be large and σ_{12} and σ_{21} must be small compared with σ_{11} and σ_{12} . This implies strong short-range coupling between the two populations. The lack of "lateral inhibition" (σ_{12}, σ_{21} small) characterizes both isolated [Krnjevic, Reiffenstein and Silver (1970)] and epileptic cortex [Matsumoto and Ajmone-Marsan (1964) and Petsche and Sterc (1968)], wherein rhythmic neuronal activity is often observed. Thus our results and assumptions agree qualitatively with experimental observations: short-range lateral inhibition is associated with cortical synchronous rhythmic activity.

Let $\omega_1 = \sqrt{\det H(n_1^2)}$, $\omega_2 = \sqrt{\det H(n_1 + 1)^2}$. Let us denote Φ^{n_1} by Φ_1 and Φ^{n_2} by Φ_2 . Then we have:

$$(1.11) \quad \begin{aligned} H(n_1^2)\Phi_1 &= i\omega_1; & H(n_2^2)\Phi_2 &= i\omega_2, \\ H(n_1^2)\bar{\Phi}_1 &= -i\omega_1; & H(n_2^2)\bar{\Phi}_2 &= -i\omega_2. \end{aligned}$$

Here \bar{a} is the complex conjugate of a . With these definitions, it follows that for $\mu = \lambda = 0$, the linear operator \mathcal{L}_0 , defined in (1.8) with $\alpha_{11} = \bar{\alpha}_{11}$, $\alpha_{22} = \bar{\alpha}_{22}$ has either a six or eight dimensional kernel generated by six or eight complex eigenfunctions. If $n_1 = 0$ and $n_2 = 1$, then the kernel is six dimensional and is generated by:

$$(1.12) \quad \begin{aligned} \phi_1(x, t) &= \Phi_1 e^{i\omega_1 t}; & \phi_2(x, t) &= \bar{\Phi}_1 e^{-i\omega_1 t}; \\ \phi_3(x, t) &= \Phi_2 e^{ix+i\omega_2 t}; & \phi_4(x, t) &= \bar{\Phi}_2 e^{-ix+i\omega_2 t}; \\ \phi_5(x, t) &= \bar{\phi}_4(x, t); & \phi_6(x, t) &= \bar{\phi}_3(x, t). \end{aligned}$$

If, instead, $n_1 \neq 0$, then the kernel is eight dimensional and is generated by the eight complex eigenfunctions:

$$(1.13) \quad \begin{aligned} \phi_1(x, t) &= \Phi_1 e^{in_1 x+i\omega_1 t}; & \phi_2(x, t) &= \bar{\Phi}_1 e^{-in_1 x+i\omega_1 t}; \\ \phi_3(x, t) &= \bar{\phi}_2(x, t); & \phi_4(x, t) &= \bar{\phi}_1(x, t); \\ \phi_5(x, t) &= \Phi_2 e^{in_2 x+i\omega_2 t}; & \phi_6(x, t) &= \bar{\Phi}_2 e^{-in_2 x+i\omega_2 t}; \\ \phi_7(x, t) &= \bar{\phi}_6(x, t); & \phi_8(x, t) &= \bar{\phi}_5(x, t). \end{aligned}$$

We make one final assumption: ω_1 and ω_2 are not rationally related, in particular, we except the cases, $\omega_1 = 2\omega_2$, $\omega_2 = 2\omega_1$, $\omega_2 = 3\omega_1$, and $\omega_1 = 3\omega_2$. These can be dealt with using the techniques of this paper, but complicate matters, while contributing little to the understanding of the secondary bifurcation.

Remarks. If ω_1 and ω_2 are not rationally related, then the sums of the $\phi_j(x, t)$ may give quasiperiodic behavior. This leads to the problem of small divisors in the higher order expansion for the solution. Thus we presume that this analysis is only formally valid. By requiring only that the spatial variable be periodic, we have increased the size of the null-space by a factor of two. If we restrict the symmetry of the spatial pattern (e.g., by requiring solutions to be waves), we can reduce the dimensionality of the kernel at the expense of losing a whole class of stable solutions (see § 3).

In *two* component reaction diffusion systems, this situation can never occur because the trace of the linearized system is always given by $-(D_1 + D_2)n^2 + \alpha_{11} + \alpha_{22}$. There can never be two values of n for which the trace has the same value unless D_1 and D_2 vanish identically. In this case there is no diffusion at the lowest order. Hershkwitz-

Kauffman and Nicolis (1979) have studied systems with small diffusion and in fact showed secondary bifurcation to various wave forms.

2. Bifurcation equations. In this section, we exploit the symmetry of (1.1) to derive the bifurcation equations. Let $G(\lambda, \mu)$ be our mapping from B into B . At $(\lambda, \mu) = (0, 0)$ and $\mathbf{u} = 0$, $G_{\mathbf{u}}(0, 0)$ has an m -dimensional kernel generated by ϕ_i , $i = 1, \dots, m$. If we suppose that it has an m -dimensional cokernel as well, then using the Lyapunov-Schmidt technique, we can reduce the problem to that of solving an m th order system of algebraic equations:

$$(2.1) \quad F_i(\lambda, \mu, z_1, z_2, \dots, z_m) = 0, \quad i = 1, \dots, m.$$

By the appropriate scaling of λ, μ and z_i , it suffices to study only the lowest order terms of F_i . Then to lowest order the solution to (1.1) is given by:

$$(2.2) \quad u(x, t) = \sum_{i=1}^m z_i \phi_i(x, t)$$

where the z_i satisfy (2.1). Thus, solving (2.1) gives us a good picture of the nature of the solutions to (1.1). In general, the form of the lowest order solutions of (2.1) is nontrivial to calculate, involving extensive computation.

For problems similar to (1.1), many authors have used multiple time scales and a variety of similar perturbation procedures. The point we wish to make here is that the basic structure of the bifurcation equations can be readily obtained by exploiting the symmetries of the problem. Actual coefficients for the bifurcation equations can only be calculated by brute force techniques and thus present a tedious algebraic problem. Because our problem itself is a qualitative abstraction of a real neural net, we believe that the most important point is the structure of the solutions and not their precise numerical values.

Sattinger (1977) proved that if a nonlinear operator is covariant with respect to symmetry transformations (i.e., the operator commutes with them), then so are the bifurcation equations. Let $\mathbf{F} = (F_1, F_2, \dots, F_m)$ be the set of bifurcation equations where m is either six or eight depending on whether or not n_1 is zero. The coordinates in η , the null space of \mathcal{L}_0 , are (z_1, \dots, z_m) . Thus any element $\phi \in \eta$, may be written:

$$\phi = \sum_{i=1}^m z_i \phi_i.$$

It follows from the above result of Sattinger that $T_r F = F T_r$, $T_\beta F = F T_\beta$ and $T_\alpha F = F T_\alpha$. The effect on the kernel of each of these linear maps for $n_1 = 0$ is:

$$(2.3) \quad \begin{aligned} (a) \quad T_\alpha(z_1, z_2, z_3, z_4, z_5, z_6) &= (z_1, z_2, e^{i\alpha} z_3, e^{-i\alpha} z_4, e^{i\alpha} z_5, e^{-i\alpha} z_6), \\ (b) \quad T_\beta(z_1, z_2, z_3, z_4, z_5, z_6) &= (e^{i\beta\omega_1} z_1, e^{-i\beta\omega_1} z_2, e^{i\beta\omega_2} z_3, \\ &\quad e^{i\beta\omega_2} z_4, e^{-i\beta\omega_2} z_5, e^{-i\beta\omega_2} z_6), \\ (c) \quad T_r(z_1, z_2, \dots, z_6) &= (z_1, z_2, z_4, z_3, z_6, z_5). \end{aligned}$$

We introduce the map J , which takes the complex conjugate. Since we seek real solutions, $\bar{z}_i = z_j$ when $\bar{\phi}_i = \phi_j$. Thus $JF = \bar{F}J$ and J acts on η as

$$(2.3d) \quad J(z_1, z_2, \dots, z_6) = (z_2, z_1, z_6, z_5, z_4, z_3).$$

For the case $n_1 > 0$, we find:

$$\begin{aligned}
 (a) \quad T_\alpha(z_1, \dots, z_8) &= (e^{in_1\alpha} z_1, e^{-in_1\alpha} z_2, e^{in_1\alpha} z_3, e^{-in_1\alpha} z_4, \\
 &\quad e^{in_2\alpha} z_5, e^{-in_2\alpha} z_6, e^{in_2\alpha} z_7, e^{-in_2\alpha} z_8), \\
 (b) \quad T_\beta(z_1, \dots, z_8) &= (e^{i\omega_1\beta} z_1, e^{i\omega_1\beta} z_2, e^{-i\omega_1\beta} z_3, e^{-i\omega_1\beta} z_4, \\
 &\quad e^{i\omega_2\beta} z_5, e^{i\omega_2\beta} z_6, e^{-i\omega_2\beta} z_7, e^{-i\omega_2\beta} z_8), \\
 (2.4) \quad (c) \quad T_r(z_1, \dots, z_8) &= (z_2, z_1, z_4, z_3, z_6, z_5, z_8, z_7), \\
 (d) \quad J(z_1, \dots, z_8) &= (z_4, z_3, z_2, z_1, z_8, z_7, z_6, z_5).
 \end{aligned}$$

We now derive the bifurcation equations for $n_1 > 0$. The case $n_1 = 0$ follows similar considerations.

Consider $T_r F = FT_r$. This implies that:

$$\begin{aligned}
 (2.5) \quad F_2(z_1, \dots, z_8) &= F_1(z_2, z_1, z_4, z_3, z_6, z_5, z_8, z_7), \\
 F_3(z_1, \dots, z_8) &= F_4(z_2, z_1, z_4, z_3, z_6, z_5, z_8, z_7), \\
 F_6(z_1, \dots, z_8) &= F_5(z_2, z_1, z_4, z_3, z_6, z_5, z_8, z_7), \\
 F_7(z_1, \dots, z_8) &= F_8(z_2, z_1, z_4, z_3, z_6, z_5, z_8, z_7).
 \end{aligned}$$

From (2.4d) it follows that

$$\begin{aligned}
 (2.6) \quad F_4(z_1, \dots, z_8) &= \bar{F}_1(z_4, z_3, z_2, z_1, z_8, z_7, z_6, z_5), \\
 F_8(z_1, \dots, z_8) &= \bar{F}_5(z_4, z_3, z_2, z_1, z_8, z_7, z_6, z_5).
 \end{aligned}$$

We have reduced the computation from eight nonlinear equations to two, F_1 and F_5 . For the case $n_1 = 0$, we have the relations:

$$\begin{aligned}
 (2.7) \quad F_2(z_1, \dots, z_6) &= \bar{F}_1(z_2, z_1, z_6, z_5, z_4, z_3), \\
 F_4(z_1, \dots, z_6) &= F_3(z_1, z_2, z_4, z_3, z_6, z_5), \\
 F_5(z_1, \dots, z_6) &= F_3(z_2, z_1, z_5, z_6, z_3, z_4), \\
 F_6(z_1, \dots, z_6) &= \bar{F}_3(z_2, z_1, z_6, z_5, z_4, z_3),
 \end{aligned}$$

thus only F_1 and F_3 must be computed.

Generally, each F_i ($i = 1, \dots, 8$) is a sum of homogeneous multinomials in the elements z_j :

$$F_i = B_i^1(z_j) + B_i^2(z_j, z_k) + B_i^3(z_j, z_k, z_p) + \dots$$

where $B_i^q(z_{j_1}, \dots, z_{j_q})$ is a homogeneous multinomial of degree q . Since each of the transformations T and J are linear, we only have to examine each B_i^q separately. Consider the linear term for F_i :

$$\sum a_j z_j.$$

Since $T_\alpha F = FT_\alpha$ and $T_\beta F = FT_\beta$, we must have

$$T_\alpha T_\beta F_1 = e^{i(\alpha n_1 + \beta \omega_1)} \sum a_j z_j = \sum a_j e^{i(\pm \alpha n_s \pm \beta \omega_s)}$$

where $s = 1$ or 2 and we take \pm depending on j . This must hold for all α and β , thus $a_j = 0$ except for $j = 1$. Thus the linear term for F_1 is $a_1 z_1$. Similarly, we find the linear term of

F_5 is $b_1 z_5$. We remark that both a_1 and b_1 depend only on the internal parameters of the system and on n_1 and n_2 and could be computed if necessary.

We now consider the quadratic terms $\sum a_{jk} z_j z_k$. It is clear that the sum is covariant if and only if each of the terms is, thus we look at $z_j z_k$. From $T_\alpha T_\beta F = F T_\alpha T_\beta$, we find

$$e^{in_1\alpha + i\omega_1\beta} a_{jk} z_j z_k = e^{\pm in_s\alpha \pm i\omega_s\beta} e^{\pm in_r\alpha \pm i\omega_r\beta} a_{jk} z_j z_k$$

where we take \pm , and s, r depending on the values of j and k . Since we have assumed that ω_1 and ω_2 are not rationally related and the above expression must hold for all α, β , it is clear that $a_{jk} = 0$ for all j and k and there are no quadratic terms. This applies to F_5 as well.

Because there are no quadratic terms, to determine the bifurcation equations, we must examine the cubic terms. For F_1 , we must have:

$$e^{in_1\alpha + i\omega_1\beta} a_{jkl} z_j z_k z_l = e^{\pm in_p\alpha \pm i\omega_p\beta \pm in_s\alpha \pm i\omega_s\beta \pm in_r\alpha \pm i\omega_r\beta} a_{jkl} z_j z_k z_l,$$

where, again, we take \pm , and $p, s, r = 1, 2$, depending on j, k and l . There are four cubic terms which contribute if ω_1 and ω_2 are not rationally related:

$$(2.8) \quad \begin{aligned} & -a_3 z_1^2 z_4, \\ & -a_4 z_1 z_2 z_3, \\ & -a_5 z_1 z_5 z_8, \\ & -a_6 z_1 z_6 z_7. \end{aligned}$$

The negative sign has been chosen for convenience. For F_5 , the cubic terms are:

$$(2.9) \quad \begin{aligned} & -b_3 z_5^2 z_8, \\ & -b_4 z_5^2 z_6 z_7, \\ & -b_5 z_5 z_1 z_4, \\ & -b_6 z_5 z_2 z_3. \end{aligned}$$

To lowest order, we have determined the bifurcation equations for $n_1 > 0$. For $n_1 = 0$, we have

$$(2.10) \quad \begin{aligned} F_1(z_1, z_2, \dots, z_6) &= a_1 z_1 - z_1(a_3 z_1 z_2 + a_5 z_3 z_6 + a_6 z_4 z_5), \\ F_3(z_1, z_2, \dots, z_6) &= b_1 z_3 - z_3(b_3 z_3 z_6 + b_4 z_4 z_5 + b_5 z_1 z_2). \end{aligned}$$

This still represents a formidable system of six or eight algebraic equations in six or eight unknowns. For $n_2 > 0$, we introduce the following transformation, using the reality condition:

$$(2.11) \quad \begin{aligned} z_1 &= r_1 e^{i\theta_1}, & z_2 &= r_2 e^{i\theta_2}, & z_3 &= r_2 e^{-i\theta_2}, & z_4 &= r_1 e^{-i\theta_1}, \\ z_5 &= r_3 e^{i\theta_3}, & z_6 &= r_4 e^{i\theta_4}, & z_7 &= r_4 e^{-i\theta_4}, & z_8 &= r_3 e^{-i\theta_3}. \end{aligned}$$

For $n_1 = 0$, we introduce a similar change of variables:

$$(2.12) \quad \begin{aligned} z_1 &= r_1 e^{i\theta_1}, & z_2 &= r_1 e^{-i\theta_1}, & z_3 &= r_2 e^{i\theta_2}, \\ z_4 &= r_3 e^{i\theta_3}, & z_5 &= r_3 e^{-i\theta_3}, & z_6 &= r_2 e^{-i\theta_2}. \end{aligned}$$

Using these transformations, the bifurcation equations become:

$$(2.13) \quad \left. \begin{aligned} a_1 r_1 - r_1 [a_3 r_1^2 + a_4 r_2^2 + a_5 r_3^2 + a_6 r_4^2] &= 0 \\ a_1 r_2 - r_2 [a_3 r_2^2 + a_4 r_1^2 + a_5 r_4^2 + a_6 r_3^2] &= 0 \\ b_1 r_3 - r_3 [b_3 r_3^2 + b_4 r_4^2 + b_5 r_1^2 + b_6 r_2^2] &= 0 \\ b_1 r_4 - r_4 [b_3 r_4^2 + b_4 r_3^2 + b_5 r_2^2 + b_6 r_1^2] &= 0 \end{aligned} \right\} (n_1 > 0),$$

$$\left. \begin{aligned} a_1 r_1 - r_1 [a_3 r_1^2 + a_5 r_2^2 + a_6 r_3^2] &= 0 \\ b_1 r_2 - r_2 [b_3 r_2^2 + b_4 r_3^2 + b_5 r_1^2] &= 0 \\ b_1 r_3 - r_3 [b_3 r_3^2 + b_4 r_2^2 + b_5 r_1^2] &= 0 \end{aligned} \right\} (n_1 = 0).$$

3. Analysis of the bifurcation equations. To lowest order in (μ, λ) we have solutions (E, I) :

$$(3.1) \quad \begin{pmatrix} E(x, t) \\ I(x, t) \end{pmatrix} = \bar{r}_1 \operatorname{Re} \Phi_1 e^{i(\omega_1 t + \theta_1)} + \bar{r}_2 \operatorname{Re} \Phi_2 e^{i(\omega_2 t + x + \theta_2)} + \bar{r}_3 \operatorname{Re} \Phi_2 e^{i(\omega_2 t - x + \theta_3)} \quad (n_1 = 0)$$

where \bar{r}_k solves (2.14) and θ_k are arbitrary phase factors. For $(n_1 > 0)$ we have:

$$(3.2) \quad \begin{pmatrix} E(x, t) \\ I(x, t) \end{pmatrix} = \bar{r}_1 \operatorname{Re} \Phi_1 e^{i(\omega_1 t + n_1 x + \theta_1)} + \bar{r}_2 \operatorname{Re} \Phi_1 e^{i(\omega_1 t - n_1 x + \theta_2)} + \bar{r}_3 \operatorname{Re} \Phi_2 e^{i(\omega_2 t + n_2 x + \theta_3)} + \bar{r}_4 \operatorname{Re} \Phi_2 e^{i(\omega_2 t - n_2 x + \theta_4)} \quad (n_1 > 0)$$

where \bar{r}_k solves (2.13) and θ_k are arbitrary phase factors. Solving (2.13) or (2.14) is a difficult problem and stability of the resultant solutions is even more difficult to prove. Here, we make the following basic assumption: stable solutions of the algebraic problem (those in which the eigenvalues of the Jacobian matrix about that particular solution have negative real parts) generate stable solutions to the full operator equation. While this is not generally true, it has been shown to hold in a wide variety of similar problems (see Sattinger (1977a)).

We note in (3.1) and (3.2) several interesting cases. In (3.1) if either $\bar{r}_2 = 0$ or $\bar{r}_3 = 0$, then the “2-mode” is a traveling wave (by “2-mode” we mean the solutions with $n = n_2$). On the other hand if $\bar{r}_2 = \bar{r}_3$, then the “2-mode” is a standing spatially periodic oscillation. Similarly, if $\bar{r}_1 \neq 0$, $\bar{r}_2 = \bar{r}_4 = 0$, and $\bar{r}_3 \neq 0$, then both modes are traveling waves in (3.2). If $\bar{r}_1 = \bar{r}_2$, $\bar{r}_3 = \bar{r}_4$, both modes are standing waves. If we make any of these four assumptions, the problems (2.13) and (2.14) reduce to a simpler form:

$$(3.3) \quad \begin{aligned} A_1 r - r [A_3 r^2 + A_5 s^2] &= 0, \\ B_1 s - s [B_3 s^2 + B_5 r^2] &= 0 \end{aligned}$$

where A_k, B_k, r, s depend on which particular assumptions we make: In Table 1, we have listed the forms of A_k, B_k, r, s for each of the four cases. Our major result is that these solutions are *stable* solutions of the complete systems (2.13) or (2.14) if and only if they are stable solutions to the *reduced* problem (3.3) and satisfy additional assumptions. We note that there are other similar choices such as $\bar{r}_2 = 0, r_3 \neq 0$ in the case $n_1 = 0$. These are treated in the same manner as below and the stability results are basically the same.

THEOREM 3.1. $(n_1 = 0)$. *The reduced solutions*

- (a) $\bar{r}_3 = 0$ or
- (b) $\bar{r}_2 = \bar{r}_3$

TABLE 1
Values of parameters for reduced systems.

	$n_1 = 0$ $\bar{r}_3 = 0$	$n_1 = 0$ $\bar{r}_2 = \bar{r}_3$	$n_1 > 0$ $\bar{r}_2 = \bar{r}_4 = 0$	$n_1 > 0$ $\bar{r}_2 = \bar{r}_1, \bar{r}_4 = \bar{r}_3$
A_1	a_1	a_1	a_1	a_1
A_3	a_3	a_3	a_3	$a_3 + a_4$
A_5	a_5	$a_5 + a_6$	a_5	$a_5 + a_6$
B_1	b_1	b_1	b_1	b_1
B_3	b_3	$b_3 + b_4$	b_3	$b_3 + b_4$
B_5	b_5	b_5	b_5	$b_5 + b_6$
r	\bar{r}_1	\bar{r}_1	\bar{r}_1	\bar{r}_1
s	\bar{r}_2	\bar{r}_2	\bar{r}_3	\bar{r}_3

are stable solutions of (2.14) if and only if they are stable solutions of (3.3) and satisfy

(a) $\operatorname{Re} b_3 < \operatorname{Re} b_4$ or

(b) $\operatorname{Re} b_4 < \operatorname{Re} b_3$

respectively.

Proof. We shall only do case (a) as case (b) follows from a similar proof. We first remark that:

$$a_1 = a_3\bar{r}_1^2 + a_5\bar{r}_2^2; \quad b_1 = b_3\bar{r}_2^2 + b_5\bar{r}_1^2.$$

Linearizing about \bar{r}_1 , \bar{r}_2 , and $\bar{r}_3 = 0$, we obtain:

$$\begin{bmatrix} -2a_3\bar{r}_1^2 & 2a_5\bar{r}_2\bar{r}_1 & 0 \\ -2\bar{r}_2\bar{r}_1b_5 & -2b_3\bar{r}_2^2 & 0 \\ 0 & 0 & (b_3 - b_4)\bar{r}_2^2 \end{bmatrix}.$$

The eigenvalues of this matrix are $(b_3 - b_4)\bar{r}_2^2$ and the eigenvalues of the 2×2 matrix in the upper left-hand corner. This is identically the matrix obtained by linearizing the reduced system (3.3) about $r = \bar{r}_1$ and $s = \bar{r}_2$, with A_k, B_k as in Table 1. Thus the result is proven.

THEOREM 3.2. ($n_1 \neq 0$). *The reduced solutions*

(a) $\bar{r}_2 = \bar{r}_4 = 0$ or

(b) $\bar{r}_2 = \bar{r}_1, \bar{r}_4 = \bar{r}_3$

are stable solutions of (2.13) if and only if they are stable solutions of (3.3) and satisfy

(a) $\operatorname{Re} \{(a_3 - a_4)\bar{r}_1^2 + (a_5 - a_6)\bar{r}_3^2\} < 0$ and

$$\operatorname{Re} \{(b_3 - b_4)\bar{r}_1^2 + (b_5 - b_6)\bar{r}_3^2\} < 0,$$

or

(b) the eigenvalues of

$$M_D \equiv \begin{bmatrix} -2\bar{r}_1^2(a_3 - a_4) & -2\bar{r}_1\bar{r}_3(a_5 - a_6) \\ -2\bar{r}_1\bar{r}_3(b_5 - b_6) & -2\bar{r}_3^2(b_3 - b_4) \end{bmatrix}$$

are in the left half plane, respectively.

Proof. Case (a) can be handled in a manner similar to the method used in Theorem 3.1. While the same method works for case (b), the computation of the eigenvalues is complicated, thus we will use a slightly different proof. The linearization matrix for

$\bar{r}_2 = \bar{r}_1, \bar{r}_4 = \bar{r}_3$ is:

$$\begin{bmatrix} -2a_3\bar{r}_1^2 & -2a_4\bar{r}_1^2 & -2a_5\bar{r}_1\bar{r}_3 & -2a_6\bar{r}_1\bar{r}_3 \\ -2a_4\bar{r}_1^2 & -2a_3\bar{r}_1^2 & -2a_6\bar{r}_1\bar{r}_3 & -2a_5\bar{r}_1\bar{r}_3 \\ -2b_5\bar{r}_1\bar{r}_3 & -2b_6\bar{r}_1\bar{r}_3 & -2b_3\bar{r}_3^2 & -2b_4\bar{r}_3^2 \\ -2b_6\bar{r}_1\bar{r}_3 & -2b_5\bar{r}_1\bar{r}_3 & -2b_4\bar{r}_3^2 & -2b_3\bar{r}_3^2 \end{bmatrix} \equiv M_F$$

and that of the reduced problem, (3.3), is:

$$\begin{bmatrix} -2\bar{r}_1^2(a_3 + a_4) & -2\bar{r}_1\bar{r}_3(a_5 + a_6) \\ -2\bar{r}_1\bar{r}_3(b_5 + b_6) & -2\bar{r}_3^2(o_3 + b_4) \end{bmatrix} \equiv M_R.$$

Let

$$P = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}, \quad P^{-1} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & -1 & 1 \end{bmatrix}.$$

This transformation has the effect of breaking ‘‘perturbations’’ of the solution $\bar{r}_2 = \bar{r}_1, \bar{r}_4 = \bar{r}_3$ into symmetric and nonsymmetric parts. Since P is nonsingular, the eigenvalues of M_F are the same as those of:

$$PM_F P^{-1} = \begin{bmatrix} -2\bar{r}_1^2(a_3 - a_4) & -2a_4\bar{r}_1^2 & -2\bar{r}_1\bar{r}_3(a_5 - a_6) & -2a_6\bar{r}_1\bar{r}_3 \\ 0 & -2\bar{r}_1^2(a_3 + a_4) & 0 & -2\bar{r}_1\bar{r}_3(a_5 + a_6) \\ -2\bar{r}_1\bar{r}_3(b_5 - b_6) & -2\bar{r}_1\bar{r}_3 b_6 & -2\bar{r}_3(b_3 - b_4) & -2\bar{r}_3^2 b_4 \\ 0 & -2\bar{r}_1\bar{r}_3(b_5 + b_6) & 0 & -2\bar{r}_3^2(b_3 + b_4) \end{bmatrix}.$$

Unlike M_F , the eigenvalue equation of this matrix is readily obtained:

$$\det (PM_F P^{-1} - eI) = \{[-2\bar{r}_1^2(a_3 + a_4) - e][-2\bar{r}_3^2(b_3 + b_4) - e] - 4\bar{r}_1^2\bar{r}_3^2(a_5 + a_6)(b_5 + b_6)\} \\ \cdot \{[-2\bar{r}_1^2(a_3 - a_4) - e][-2\bar{r}_3(b_3 - b_4) - e] - 4\bar{r}_1^2\bar{r}_3^2(a_5 - a_6)(b_5 - b_6)\}.$$

(Here I is the 4×4 identity matrix. The first factor is the eigenvalue equation for M_R , the reduced matrix. The second factor is the eigenvalue equation for

$$M_D \equiv \begin{bmatrix} -2\bar{r}_1^2(a_3 - a_4) & -2\bar{r}_1\bar{r}_3(a_5 - a_6) \\ -2\bar{r}_1\bar{r}_3(b_5 - b_6) & -2\bar{r}_3^2(b_3 - b_4) \end{bmatrix}.$$

A necessary and sufficient condition for stability of the solution $\bar{r}_1 = \bar{r}_2$ and $\bar{r}_3 = \bar{r}_4$ is that the eigenvalues of both M_R and M_D lie in the left half complex plane. These conditions imply (b).

These two theorems considered with a stability analysis of the reduced system completely characterize the stability of traveling and standing waves for the full problem. There are undoubtedly other solutions to (2.13) and (2.14), but as we remarked at the beginning of this section, the wave solutions are the most interesting physically.

We now analyze the reduced equations (3.3). Since these are complex, we cannot expect to find solutions in general when λ and μ vary. This problem can be solved by introducing the additional parameters, σ_1, σ_2 which serve to change the critical frequencies, ω_1, ω_2 as λ, μ vary. That is, $\omega_1 \sim \omega_1^0 + \sigma_1, \omega_2 \sim \omega_2^0 + \sigma_2$ where ω_1^0, ω_2^0 are defined in (1.11) and σ_1, σ_2 are small variations of the same order as λ, μ . This is typical of Hopf bifurcation problems—the frequency does not remain fixed. These new

parameters only appear (to lowest order) in the imaginary parts of A_1, B_1 . We introduce the parameters as:

$$(3.4) \quad A_1 = a_{11}\mu - a_{12}\lambda + i\sigma_1, \quad B_1 = b_{11}\mu - b_{12}\lambda + i\sigma_2.$$

It suffices to consider linear dependence on the bifurcation parameters since higher order terms can be scaled out. $a_{11}, a_{12}, b_{11}, b_{12}$ are all real and for convenience, positive. We write:

$$\begin{aligned} A_3 &= \underline{A}_3 + iA'_3, \\ B_3 &= \underline{B}_3 + iB'_3, \\ A_5 &= \underline{A}_5 + iA'_5, \\ B_5 &= \underline{B}_5 + iB'_5, \end{aligned}$$

and assume $\underline{A}_3, \underline{B}_3, \underline{A}_5, \underline{B}_5$ are positive so that bifurcation is supercritical. A solution to the bifurcation equations is a (μ, λ) -parametrization of r, s, σ_1, σ_2 :

$$(3.5) \quad \begin{aligned} a_{11}\mu - a_{12}\lambda - (\underline{A}_3 r^2 + \underline{A}_5 s^2) &= 0, \\ \sigma_1 - (A'_3 r^2 + A'_5 s^2) &= 0, \\ b_{11}\mu - b_{12}\lambda - (\underline{B}_3 s^2 + \underline{B}_5 r^2) &= 0, \\ \sigma_2 - (B'_3 s^2 + B'_5 r^2) &= 0. \end{aligned}$$

Thus, fixing μ, λ determines r, s and consequently, σ_1, σ_2 .

We finally assume that if λ is fixed, then the "2-mode" bifurcates initially as μ is increased, thus, $b_{12}/a_{12} < b_{11}/a_{11}$. We consider the four most interesting cases.

Case (i): $\underline{A}_5/\underline{B}_5 > a_{11}/b_{11} > \underline{A}_3/\underline{B}_3$. Then Fig. 3 obtains and a secondary branch with components in both frequencies bifurcates from the "2-mode." The pure "2-mode" which is either a standing or a traveling wave loses stability and the new quasi-periodic solutions obtain. While this behavior may appear "chaotic" or random, the frequency spectrum would show two distinct peaks at the corresponding frequencies, not unlike the spectrum of actual brainwaves.

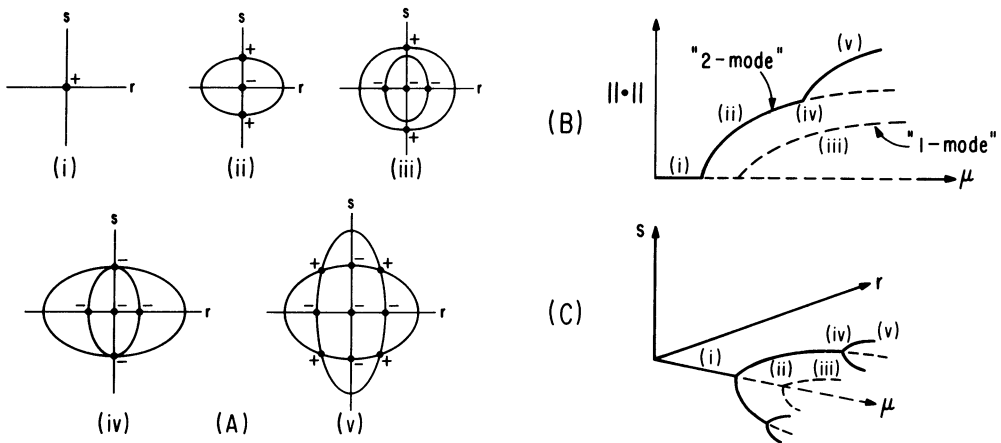


FIG. 3. Case (i): $\underline{A}_5/\underline{B}_5 > a_{11}/b_{11} > \underline{A}_3/\underline{B}_3$;

(3a) Evolution of the phase plane of (3.3) as μ increases and μ is fixed (+ denotes a stable equilibrium and - an unstable equilibrium).

(3b) Corresponding bifurcation diagram. (Dotted lines are unstable solutions and solid lines are stable solutions.)

(3c) Bifurcation diagrams in (r, s, μ) -space.

Case (ii): $\underline{A}_5/\underline{B}_5 < a_{11}/b_{11} < \underline{A}_3/\underline{B}_3$. This case is shown in Fig. 4 and its main point of interest is the appearance of a stable branch corresponding to the pure "1-mode." The existence of multiple oscillations is of physical interest since by perturbing either of the two stable branches, one can switch between the two frequencies. There are cases in which such switching occurs in the nervous system and consequently this multistability may be relevant.

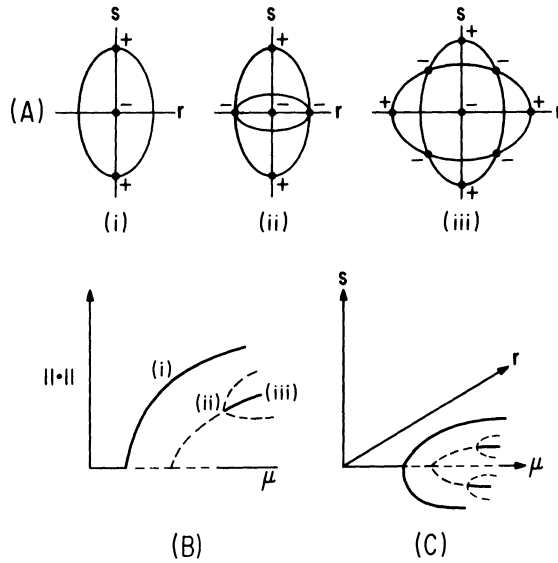


FIG. 4. Case (ii): $A_5/B_5 < a_{11}/b_{11} < A_3/B_3$; (4a, b, c): same as in Fig. 3.

Case (iii): $a_{11}/b_{11} > \underline{A}_3/\underline{B}_3 > \underline{A}_5/\underline{B}_5$. Figure 5 shows the diagrams for this case. Here, unlike case (ii), there is only a finite interval of values for μ in which both frequencies can coexist. As a result, hysteresis between the two oscillations is possible.

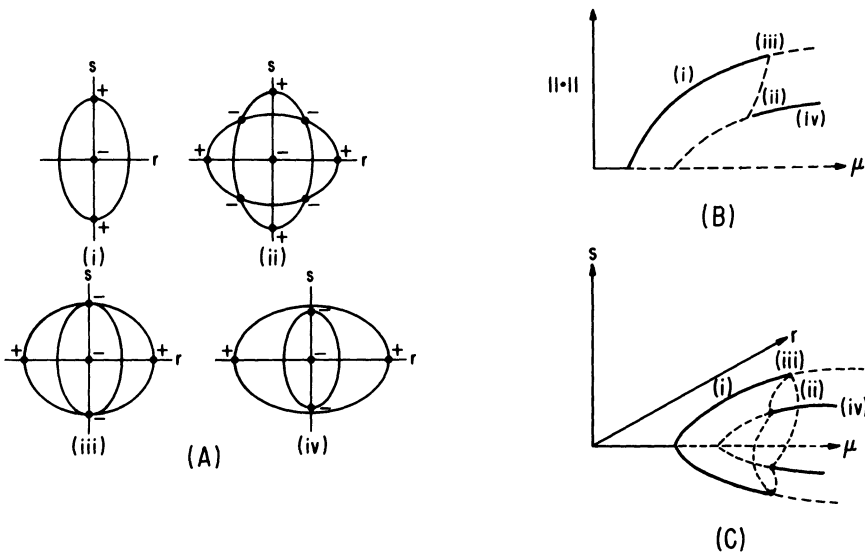


FIG. 5. Case (iii): $a_{11}/b_{11} > \underline{A}_3/\underline{B}_3 > \underline{A}_5/\underline{B}_5$; (5a, b, c) same as in Fig. 3.

Case (iv): $a_{11}/b_{11} > A_5/B_5 > A_3/B_3$. The most relevant case from a biological viewpoint and the one which motivated this paper is illustrated in Fig. 6. For small

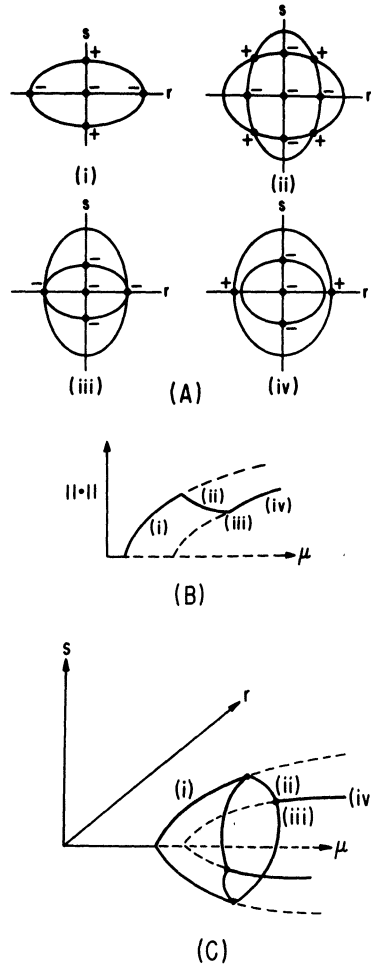


FIG. 6. Case (iv): $a_{11}/b_{11} > A_5/B_5 > A_3/B_3$; (6a, b, c) same as in Fig. 3.

values of the "2-mode" is stable and as μ increases the amplitude gradually increases. Eventually, this mode loses stability and a stable branch consisting of a mixture of both "1-" and "2-modes" bifurcates. Further increases in μ result in a loss of stability of the mixed mode and a smooth transition to the pure "1-mode." If we assume that the parameters are such that in each of the modes, the traveling waves are selected, then in this case there is a smooth switch from one frequency to a differing one. Such events are seen in the gradual transition from tonic to clonic seizures in ictal epilepsy. There is considerable evidence that epileptic oscillations are in fact traveling waves [Petsche and Sterc (1968)]. Furthermore it has been proposed that this transition occurs because of an increase in extracellular potassium as the seizure progresses [Krnjevic, Reiffenstein, and Silver (1970), Matsumoto and Ajmone-Marsan (1964)]. The effect of potassium

ions is to increase the “excitability” of the network. Since μ is related to the degree of excitation of the net, it is of interest to compare this particular case with the above transition in epilepsy. In Fig. 7 we have redrawn a recording of the slow transition

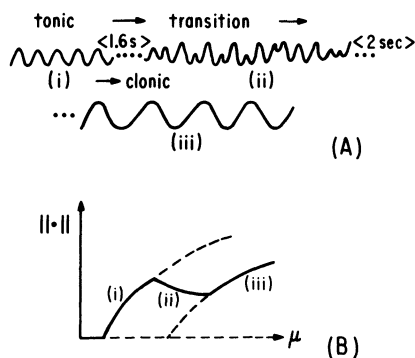


FIG. 7. (7a) Evolution of an ictal seizure through tonic and clonic stages (from Matsumoto and Ajmone-Marsan (1964)); (7b) Plausible bifurcation diagram associated with (7a).

between the tonic and clonic seizures. There is initially a small amplitude oscillation (probably a traveling wave) representing the tonic stage. As the seizure progresses, there is a mixture of several frequencies (region ii in Fig. 7). This resembles qualitatively the intermediate region in the bifurcation diagram (labeled ii in 7b). Finally in the later stages of the seizure, a new large amplitude “pure” frequency dominates (the clonic stage, (iii) in the figure). Thus in an epileptic episode, the possibility of new oscillatory structures “branching” from an unstable mode is clearly possible.

Conclusions. There is no doubt that such complex behavior can and does occur in a neuronal net comprising several cell types. Here, we have considered one of the simpler possible nets comprising excitatory and inhibitory cells. In the absence of spatial interactions these two-component systems can admit limit cycles, but for topological reasons, quasi-periodic behavior is impossible. As soon as we allow aggregates of cells to interact spatially, there is a jump in the complexity of behavior, to traveling waves, spatially inhomogeneous oscillations, or quasi-periodic solutions.

While the main point of this paper was to demonstrate that secondary bifurcations may occur in a neural net, we have also shown the importance of maintaining the innate symmetries of the problem. Indeed, we have demonstrated a selection mechanism for either standing or traveling waves, which depends only on the internal parameters of the system. For example, the sign of $\text{Re}(b_3 - b_4)$ determines whether there will be stable standing waves or traveling waves for the $n_1 = 0$ case. Had we restricted our solutions to be traveling phenomena (as is often done in such bifurcation problems) we would have neglected an entire class of *stable* solutions. Thus despite the added complexity of the full bifurcation problem, such symmetry restrictions should not be made, in general.

Acknowledgments. We would like to thank Professor D. H. Sattinger for suggesting the application of group theoretic techniques to the problem. We also express gratitude to the referees for helpful criticism and to Ms. A. Pasley, for her services in the preparation of the manuscript.

Appendix. We consider a net of excitatory and inhibitory neurons distributed in a line along the x -axis. Let $E(x, t)$ and $I(x, t)$ denote their respective firing rates. A neuron at x is influenced by a neuron at x' and this influence depends only on the distance between the two cells, $|x - x'|$. Thus the effect of $E(x', t)$ on the excitatory cell at w is $w_{11}(|x - x'|)E(x', t)$. Similarly, we tabulate the spatial effects of the remaining interactions:

$$(A.1) \quad \begin{array}{ll} \text{excitatory } (x')\text{---inhibitory } (x); & w_{12}(|x - x'|)E(x', t) \\ \text{inhibitory } (x')\text{---excitatory } (x); & w_{21}(|x - x'|)I(x', t) \\ \text{inhibitory } (x')\text{---inhibitory } (x); & w_{22}(|x - x'|)I(x', t). \end{array}$$

Here we have implicitly assumed that the net is both *homogeneous* and *isotropic* in that the influences are independent of position and direction. Histological data indicate that this is a reasonable simplification and furthermore that the $w_{ij}(x)$ are exponentially decreasing functions of their argument [Sholl (1956)]. We assume that $w_{ij}(x)$ integrate to 1 over R since they are in some sense probabilities of connection.

The impulses at the presynaptic axonal terminal effect a release of transmitter which either depolarizes or hyperpolarizes the postsynaptic membrane. This results, respectively, in an excitatory postsynaptic potential (EPSP) or an inhibitory postsynaptic potential (IPSP). If $f(t)$ is the presynaptic firing rate of some neuron, then we find that the resultant postsynaptic potential is:

$$(A.2) \quad V(t) = \alpha \int_0^t h(\tau) f(t - \tau) d\tau.$$

$h(t)$ generally incorporates delays (due to transmitter diffusion), rise times and exponential decays of the potential. The decay rate is the most relevant facet for the model, thus we assume for simplicity that $h(t) = \exp(-t)$. α is positive or negative according as the presynaptic neuron is excitatory or inhibitory. Therefore, the postsynaptic potential of an excitatory neuron at x due to cells at x' is:

$$(A.3a) \quad \begin{aligned} PSP_E(x, x', t) = & \alpha_{11} \int_0^t h(\tau) w_{11}(|x - x'|) E(x', t - \tau) d\tau \\ & - \alpha_{21} \int_0^t h(\tau) w_{21}(|x - x'|) I(x', t - \tau) d\tau. \end{aligned}$$

Similarly, the postsynaptic potential of an inhibitory neuron at x due to cells at x' is:

$$(A.3b) \quad \begin{aligned} PSP_I(x, x', t) = & \alpha_{12} \int_0^t h(\tau) w_{12}(|x - x'|) E(x', t - \tau) d\tau \\ & - \alpha_{22} \int_0^t h(\tau) w_{22}(|x - x'|) I(x', t - \tau) d\tau. \end{aligned}$$

Since a neuron receives inputs from many spatial regions, the total membrane potential of the neuron is the sum over space of all of the postsynaptic potentials. Thus,

if we let $\Phi_E(x, t)$ and $\Phi_I(x, t)$ denote the respective membrane potentials of the excitatory and inhibitory neurons, we have:

$$(A.4) \quad \begin{aligned} \Phi_E(x, t) &= \int_{-\infty}^{\infty} dx' PSP_E(x, x', t), \\ \Phi_I(x, t) &= \int_{-\infty}^{\infty} dx' PSP_I(x, x', t). \end{aligned}$$

Finally, to close the system, we note that the firing rate of a cell is a nonlinear function of the membrane potential. Careful physiological measurements of the responses of cortical neurons have established that the following relationships hold [Creutzfeldt, Lux and Watanabe (1966)]:

$$(A.5) \quad \begin{aligned} E(x, t) &= S_1(\Phi_E(x, t)), \\ I(x, t) &= S_2(\Phi_I(x, t)). \end{aligned}$$

Here, S_1 and S_2 are monotone, nondecreasing, bounded, continuous functions such as illustrated in Fig. 1.

We are interested in the asymptotic behavior ($t \rightarrow \infty$) of a net that is topologically a ring of size 2π . Thus we impose periodic boundary conditions:

$$(A.6) \quad \begin{aligned} E(x + 2\pi, t) &= E(x, t), \\ I(x + 2\pi, t) &= I(x, t), \end{aligned}$$

and let $t \rightarrow \infty$ in the temporal convolutions. Combining (A.3)–(A.6) we find that $E(x, t)$ and $I(x, t)$ satisfy:

$$(A.7) \quad \begin{aligned} E(x, t) &= S_1 \left[\int_0^{\infty} h(\tau) d\tau \int_{-\infty}^{\infty} dx' \{ \alpha_{11} w_{11} (|x - x'|) E(x', t - \tau) \right. \\ &\quad \left. - \alpha_{21} w_{21} (|x - x'|) I(x', t - \tau) \} \right], \\ I(x, t) &= S_2 \left[\int_0^{\infty} h(\tau) d\tau \int_{-\infty}^{\infty} dx' \{ \alpha_{12} w_{12} (|x - x'|) E(x', t - \tau) \right. \\ &\quad \left. - \alpha_{22} w_{22} (|x - x'|) I(x', t - \tau) \} \right]. \end{aligned}$$

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