Meandering Transition in Two-Dimensional Excitable Media

Alain Karma
Physics Department, Northeastern University, Boston, Massachusetts 02115
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The transition from periodic to quasiperiodic spiral-wave rotation is studied numerically by the pseudospectral method in a two-variable model of excitable kinetics. Quasiperiodic behavior originates from a supercritical Hopf bifurcation of one branch of circularly rotating spiral-wave solution. The secondary frequency is strongly determined by the presence of a second nearby branch of solution rotating about a larger hole radius. Scaling laws consistent with numerical results are proposed for the spiral-tip orbits in the critical region.

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Rotating spiral waves have long been observed in extremely diverse systems. The best known examples include the blue waves of oxidation propagating in the Belousov-Zhabotinskii (BZ) reaction,[1] the waves of neuromuscular activity in the myocardial tissue,[2] and waves of cyclic-AMP (adenosine monophosphate) in social amoeba colonies of *Dictyostlelium discoideum.*[3] Over the years, major theoretical[4-7] and experimental[8-10] progress has been made in understanding the shape and dynamics of these waves.

In the BZ reaction, conditions are found under which the tip of the spiral rotates in a perfectly *periodic* circular motion about a fixed center. In other conditions, the spiral tip is found to deviate significantly from circular trajectories, following epicyclelike orbits.[8-10] The term *meander* was first introduced by Winfree to describe this type of anomalous motion.[8] Although observed essentially in chemical systems, this phenomenon is also of interest in cardiology since it may be the cause of cardiac arrythmias which can lead to fibrillation of the heart muscle.[1,11] Very recently, a sharp transition between periodic (circular) and quasiperiodic (compound) spiral rotation was found in a BZ experiment especially designed to characterize the long-time asymptotic dynamics of the waves.[10] A secondary frequency, incommensurate with the primary rotation frequency, was found to appear in the reagent signaling the above transition, the tip trajectories being well approximated by retrograde epicycles constructed from these two frequencies. Numerical simulations of various two-variable models of excitable kinetics have also revealed the occurrence of noncircular spiral-tip trajectories which seem well fitted by epicycles.[11-13] Although it now seems clear from these studies that the phenomenon of *meander* originates from some type of transition to quasiperiodic behavior a fundamental understanding of the nature of this transition is still lacking.

In this Letter, we report the results of a numerical study of a two-variable model of excitable kinetics which determines for the first time in a quantitative way the exact nature of the meandering transition, and brings new insights on the origin of the secondary frequency at the transition. Meander is found to occur via a Hopf bifurcation of one of two branches of circularly rotating spiral-wave solutions when the excitability parameter of the model δ exceeds a threshold value δ_c. Perturbations decay exponentially below the transition, the decay rate vanishing linearly with $\varepsilon \equiv \delta - \delta_c$ at the transition. The saturation amplitude of the unstable mode obeys the $\varepsilon^{1/2}$ behavior characteristic of supercritical bifurcations. The Hopf frequency is found to be strongly determined by the existence of a second branch of solution which remains stable at the transition. Scaling laws for the tip orbits follow from the analytical structure of the variables in the critical region.

The two-variable model was chosen to be of the simple FitzHugh-Nagumo form:[14]

$$\frac{\partial u}{\partial t} = \nabla^2 u - v + 3u - u^3 , \tag{1a}$$

$$\frac{\partial v}{\partial t} = \alpha(u - \delta) , \tag{1b}$$

where the medium becomes more susceptible to perturbations as δ increases and α controls the ratio between the fast excitory period τ and the total transit time T of the signal. Model equations of the type of Eq. (1) retain some important qualitative features of spiral-wave dynamics while remaining amenable to analytical and numerical treatment.

Equation (1) was solved using a conventional pseudospectral scheme with a basis of Fourier modes and periodic boundary conditions. This method (used extensively to simulate hydrodynamic systems) is superior to finite-difference methods in spatial accuracy. It also has the advantage that the time stepping of the Laplacian operator in Eq. 1(a) is easily performed implicitly in Fourier space, thereby allowing a larger time step to be taken while maintaining numerical stability. Identical runs on 128×128 and 256×256 lattices yielded identical spiral-tip dynamics, thereby demonstrating the insensitivity of the results to boundary effects. Lattice units (time steps) ranging between 0.3 and 0.5 (0.05 and 0.1) were found to provide sufficient resolution. The model was studied over a range of values of α and δ. The meandering transition was found to occur by increasing δ at fixed α or decreasing α at fixed δ. We only report here the results of a detailed study of the transition as a function of δ for $\alpha=0.665$. Similar results were obtained for other values of α. In this parameter range the ratio between the fast and slow time scales is already small in the present model ($\tau/T\sim 1/10$ for an isolated pulse).

The dynamics of spiral rotation was explored by two different methods: (a) by the conventional method of studying the trajectories of the spiral tip,[11-13] defined here to be the point of vanishing normal velocity on the spiral contour $u=0$ which lies inside the narrow excitory region; (b) by studying the spatiotemporal behavior of the variables near the spiral center (one variable suffices and u was selected here). This method provides an independent source of information which helps characterize the unstable mode of the system and allows a more precise quantitative characterization of the transition.

Two separate branches of circularly rotating spiral-wave solutions were found in the neighborhood of the meandering transition. The hole radius determined from the circular trajectory of the spiral tip and the rotational frequency are denoted by $R^{(n)}$ and $f^{(n)}$, respectively. The index $n=0,1$ numbers the two branches of solutions. First, consider the $n=0$ branch. $R^{(0)}$ ($f^{(0)}$) decreases (increases) monotonously with increasing δ until the onset of compound rotation at $\delta=\delta_c$ (the exact value $\delta_c=-1.09886$ is determined below from the zero crossing of the decay rate of perturbations as a function of δ). Deviations from circular rotation increase continuously for $\delta>\delta_c$ and the transition is completely reversible. The quantitative nature of this transition was obtained by means of method (b) above. For steady-state rotation, the value of $(u^{(n)},v^{(n)})$ at the center of rotation is given by the fixed point $(\delta,3\delta-\delta^3)$ of Eq. (1). It can easily be shown that the analytic behavior of the fields in the neighborhood of the fixed point must be of the form of the lowest nondiverging eigenfunction of the Laplacian operator.[15] In a fixed (nonrotating) frame defined by the standard polar coordinates (r,θ) we must have

$$u^{(n)}(r,\theta,t)=\delta+C^{(n)}re^{i(\theta-2\pi f^{(n)}t)}+O(r^3)+\text{c.c.}, \quad (2)$$

where $v^{(n)}$ is trivially related to $u^{(n)}$ by Eq. (1b). The position (x_c,y_c) of the center corresponding to $r=0$ in Eq. (2) (which generically does not coincide with a lattice point), and $C^{(n)}$ can be determined accurately from the amplitude of the periodic time signals $u_{i,j}(t)$ of three lattice points on a square enclosing the center. Once the center is determined, time signals from other nearby lattice points provide a measure of $u^{(n)}(r,\theta,t)$ at a discrete set of values of $r=r_{ij}=[(x_i-x_c)^2+(y_j-y_c)^2]^{1/2}$.

The transition was studied from the time signals $u_{i,j}(t)$ on a 3×3 sublattice enclosing the spiral center in the long-time asymptotic state of the system. Above the transition, time signals of $u_{i,j}(t)$ away from the spiral center generally contain two frequencies (f_{1q},f_{2q}) with a higher harmonic structure. Increasingly near the center, however, higher harmonics become small and the time signals can be simply characterized in terms of two oscillating modes with complex amplitudes $(A^{(0)},B)$: $u_{i,j}(t)=A^{(0)}(r_{ij})e^{i2\pi f_{1q}t}+B(r_{ij})e^{i2\pi f_{2q}t}+\text{c.c.}$ Below the transition ($\delta<\delta_c$) we recover $|A^{(0)}(r)|=C^{(0)}r$ and $B(r)=0$. The characteristic variations of the amplitudes with r above the transition are shown in Fig. 1 for $\delta=-1.09865$. The form $|A^{(0)}(r)|=C^{(0)}r$ persists at the transition and the amplitude $B(r)$ of the secondary frequency is found to be nearly independent of r. Since $B(r)$ approaches a constant at the origin, analytic consistency of the solution implies that the corresponding mode be independent of θ, with the first corrections of order r^2. The numerical findings therefore imply that the asymptotic form of u at small r in the quasiperiodic regime can be written as follows (this behavior is also consistent with the requirement that linearly unstable modes of the system be orthogonal to the null space of the linearized operator around steady-state solutions[15]):

$$u(r,\theta,t)=\delta+C^{(0)}re^{i(\theta-2\pi f_{1q}t)}+Be^{i2\pi f_{2q}t}+O(r^2)+\text{c.c.} \quad (3)$$

Next, the quantitative nature of the transition to quasiperiodic behavior was determined by studying the variations with δ of the decay rate of perturbations slightly below the transition, and of the amplitude $|B|$ in the long-time asymptotic state slightly above the transition. The relaxation dynamics of perturbations generated by suddenly increasing δ to a new value was studied from the time signals of the $u_{i,j}(t)$ on the 3×3 center sublattice. Simulations as long as a 100 rotation periods

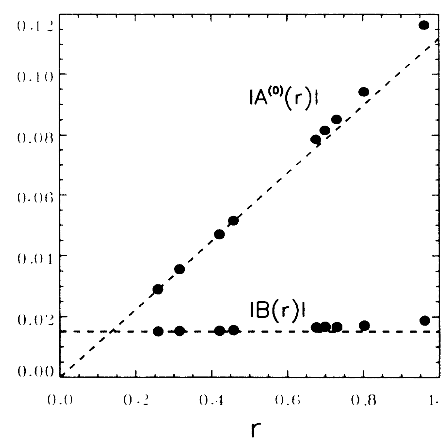

FIG. 1. Radial dependence of the amplitudes characterizing the two frequencies of the quasiperiodic time signals near the spiral center for $\delta=-1.09865$. Each solid circle corresponds to one lattice point on the 3×3 sublattice enclosing the spiral center. Consistent behavior is found with the small-r analytical forms $|A^{(0)}(r)|=C^{(0)}r$ and $|B(r)|=\text{const}$. For comparison the primary radius of tip orbits $R_1\simeq 2.2$ at the same value of δ.

were necessary to extract accurately the decay rate and the asymptotic value of $|B|$ close to the transition. $|B(t)|$ was found to obey an exponential decay form $|B(t)| \sim \exp(\sigma t)$ (over two decades of amplitude). The decay rate was found to vanish linearly with ε (at $\delta = \delta_c = -1.09886$), and the saturation amplitude $|B|$ above the transition was found to obey the square-root behavior characteristic of supercritical bifurcations:

$$\sigma \cong 340 \varepsilon f^{(0)}, \tag{4a}$$

$$|B| \cong 0.86 \varepsilon^{0.5 \pm 0.01}. \tag{4b}$$

An important consequence of the large numerical prefactor in Eq. (4a) is that the transition region to quasiperiodic behavior is extremely narrow as a function δ (α as well). For $\varepsilon \cong 10^{-3}$ the growth rate of perturbations is already of the same order as the primary rotational frequency. Consequently, the *critical region* [the range of value of ε where the scaling form of Eq. (4b) holds accurately] is very small here. Significant deviations arise for $\varepsilon \sim 5 \times 10^{-4}$.

Since the transition occurs continuously from the $n=0$ branch the primary frequency $f_{1q} = [f^{(0)}]_{\delta=\delta_c} \simeq 5 \times 10^{-2} + O(\varepsilon)$ in the critical region. The Hopf frequency f_{2q}, however, is not *a priori* determined. Numerically, we find interestingly that $[f_{2q}]_{\delta=\delta_c}$ is only a few percent smaller than the primary frequency $[f^{(1)}]_{\delta=\delta_c}$ of a second branch ($n=1$) of circularly rotating spiral-wave solution which remains stable at $\delta=\delta_c$. The possibility for the existence of two distinct spiral waves at small hole radius was discussed previously in the context of a modified FitzHugh-Nagumo model[16] and hysteretic effects were found numerically in this model, with the imposition of an artificial no-flux boundary condition at the hole radius.[17] Spirals on the $n=0$ and 1 branches and their respective hole radii below the transition are shown in Fig. 2. The $n=1$ branch is reached discontinuously from the $n=0$ branch when δ is decreased below some value $\delta^{(0)}_{\min} < \delta_c$. The $n=1$ branch terminates with a discontinuous transition to the quasiperiodic state reached continuously from the $n=0$ branch if δ is increased beyond some value $\delta^{(1)}_{\max} > \delta_c$ (here $\delta^{(0)}_{\min} = -1.103$ and $\delta^{(1)}_{\max} = -1.097$). The prolonged stability of the $n=1$ branch with increasing δ (i.e., decreasing $R^{(0)}$ and $R^{(1)}$) is consistent with the fact that $R^{(1)} > R^{(0)}$. Since the two branches are clearly distinct and do not intersect at δ_c, the closeness of $f^{(1)}$ and f_{2q} suggest that the linearly unstable mode of the $n=0$ branch is strongly related to the $n=1$ branch. During compound rotation, the spiral arm is seen to oscillate between two structures which approximate in turn the steady-state arms of the $n=0$ and 1 branches as shown in Fig. 3.

Spiral-tip orbits in previous numerical and experimental studies were found to be well approximated by epicycles.[10,12,13] The frequency spectrum of one of the coordinates [$x(t)$ here] of the spiral tip was used here to investigate the nature of the orbits. Typical spectra of $x(t)$ at two values of δ above the transition are shown in Fig. 4. More generally, the tip orbits can be characterized in terms of multiple epicycles of the form

$$x(t) + iy(t) = \sum_j R_j e^{i2\pi F_j t}. \tag{5}$$

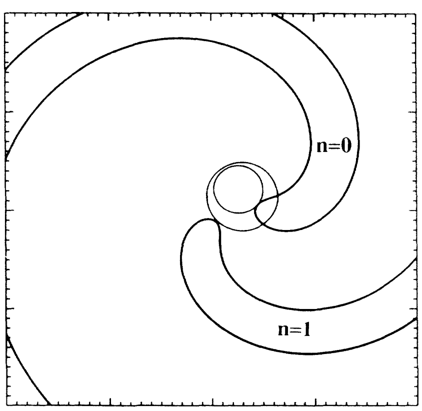

FIG. 2. Spirals from two separate branches ($n=0,1$) of circularly rotating solutions for $\delta = -1.102 < \delta_c$. $R^{(1)}=3.3$, $f^{(1)}=3.8\times10^{-2}$, $R^{(0)}=2.4$, and $f^{(0)}=4.7\times10^{-2}$. Compound rotation originates continuously from the small-hole-radius branch ($n=0$).

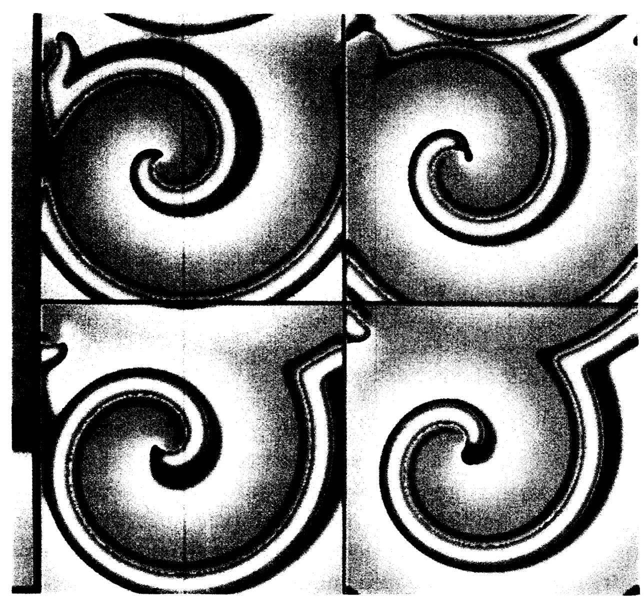

FIG. 3. Time sequence of the fast variable u for $\delta = -1.090$ with 256×256 Fourier modes [time increases clockwise from upper-left with $\frac{1}{4}$ of the primary rotation period ($\frac{1}{4} f_{1q}$) between each frame]. The color coding of u is indicated in the left-hand column where u varies linearly from -2 to 1.8. A narrow red coding around $u=\delta$ was chosen to bring out the dynamics of the core region.

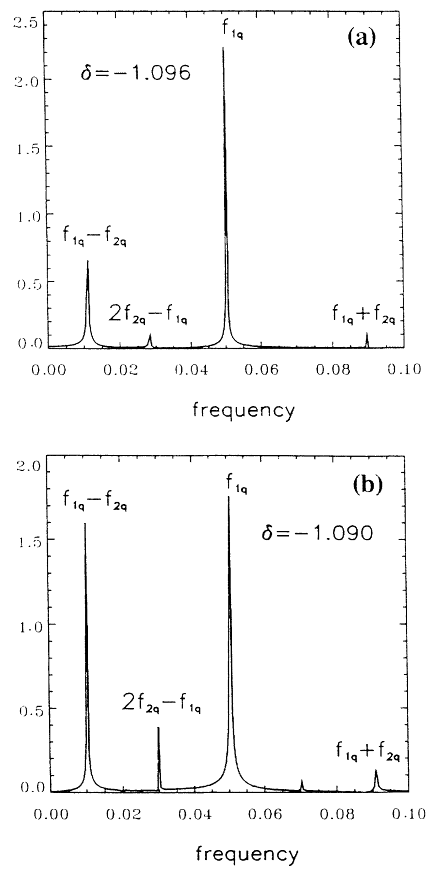

FIG. 4. Frequency spectrum of $x(t)$ for (a) $\delta=-1.096$ ($\varepsilon=0.003$) and (b) $\delta=-1.090$ ($\varepsilon=0.009$). The magnitudes of the peaks determine the radii of the spiral-tip orbits.

The radii (R_j) in Eq. (5) are given by the magnitudes of the peaks in the spectra at the corresponding frequencies (F_j). It is apparent from Fig. 4(a) that, even outside the critical region, the orbits are well approximated by a simple epicycle with $F_1=f_{1q}$ $[f_{1q}=f^{(0)}+O(\varepsilon)]$ and $F_2=f_{1q}-f_{2q}$ ($F_1/F_2\cong 4.6$). However, other peaks are present in the spectrum of $x(t)$ and the question arises as to how the radii of the different peaks scale with ε in the critical region. To answer this question, consider the weakly nonlinear analysis of the $n=0$ branch of circularly rotating waves, in a rotating frame of reference $(r,\phi)\equiv(r,\theta-2\pi f^{(0)}t)$. If the transition occurs via a standard supercritical Hopf bifurcation, as strongly implied by the forms of Eqs. (3), (4a), and (4b), then the variable u in the critical region should have the general scaling form

$$u(r,\phi,t)=u^{(0)}(r,\phi)+\varepsilon^{1/2}U(r,\phi)e^{i2\pi f_{2q}t}+\text{c.c.}+O(\varepsilon)\,,$$

where $U(r,\phi)$ is parallel to the u component of the unstable eigenvector with eigenvalue $\sigma+i2\pi f_{2q}$ and could, in principle, be determined by a linear stability analysis of the $n=0$ branch. It follows from this general form that the tip trajectories [defined implicitly here by $u(r,\phi,t)=0$ and $\partial u/\partial t-2\pi f^{(0)}\partial u/\partial\phi=0$] must be to lowest order in $\varepsilon^{1/2}$ *epi-epicycles* with F_1 and F_2 as defined above, $F_3=f_{1q}+f_{2q}$, $R_1=R^{(0)}+O(\varepsilon)$, $R_2\sim\varepsilon^{1/2}$, and $R_3\sim\varepsilon^{1/2}$. Numerically we found consistent scaling behavior with $R_2\cong 12\varepsilon^{0.5\pm 0.08}$ but R_3 was too small to be determined accurately in the critical region. The additional peaks in the spectrum at $2f_{2q}-f_{1q}$ and $3f_{2q}-f_{1q}$ correspond to higher harmonics of the unstable mode whose magnitudes should scale respectively as $|B|^2\sim\varepsilon$ and $|B|^3\sim\varepsilon^{3/2}$ in the critical region. As seen in Fig. 4, outside the critical region R_3 saturates to a small value while R_2 and the first harmonic peak at $2f_{2q}-f_{1q}$ continue to grow with increasing ε. Further away from the transition the spectra of $x(t)$ become increasingly richer in harmonic content but compound rotation maintains a high degree of regularity. It would be valuable to extend the present study to other models of excitable media in order to determine the degree of universality of the meandering transition.

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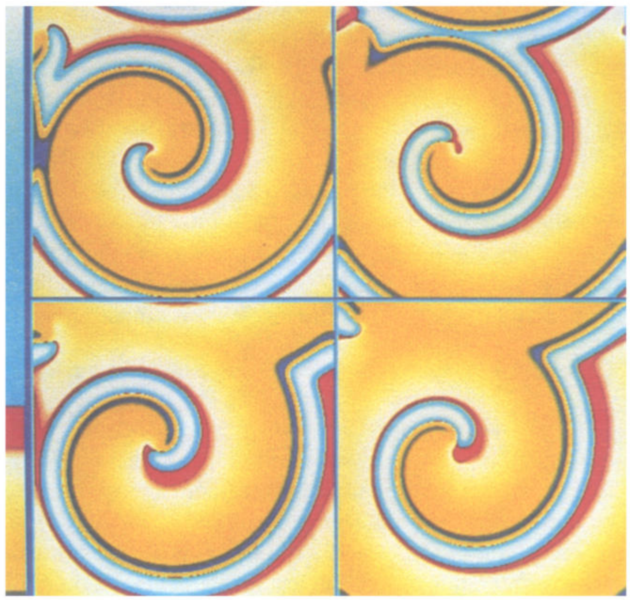

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