

Spiral Competition in Three-Component Excitable Media

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(Received 21 September 1995)

Excitable wave patterns consisting of large coherent spirals are observed during the aggregation of *Dictyostelium amoebae*. These emerge from an initially disordered state which arises via random cell firing. In this work, we show that this phenomenon can be understood as being due to a specific spiral competition instability which occurs in certain three-component excitable medium models. This instability can be understood as symmetry breaking of a spiral pair leading to one spiral suppressing and expelling another.

PACS numbers: 87.22.-q, 05.45.+b

The study of spiral waves in excitable media has been a focus of significant attention in recent years. Spirals have been found to be a relevant wave pattern in a variety of chemical systems such as celebrated Belousov-Zhabotinsky (BZ) reactions [1], in the electrophysiological activity of heart tissue [2], oxidation of CO on a platinum surface [3], aggregation of *Dictyostelium* [4], etc. Significant progress has been achieved in this area through detailed numerical and analytical investigations of generic reaction-diffusion models [5–7]. For example, it was found both theoretically and experimentally that the spirals can exhibit rich dynamic behavior ranging from periodic and quasiperiodic meandering to chaotic hypermeandering and spiral turbulence.

To date, the emphasis in these studies has been on simplest two-component reaction-diffusion systems which exhibit excitable behavior. These models consist of coupled equations for a fast field u and a slow field v . A typical example is the FitzHugh-Nagumo model which takes the form [9]

$$\partial_t u = \nabla^2 u + \frac{1}{\epsilon} u(1-u)[u - u_{\text{thr}}(v)], \quad (1)$$

$$\partial_t v = \delta \nabla^2 v + u - v, \quad (2)$$

where $\epsilon \ll 1$ is a small positive parameter, δ is the ratio of diffusion coefficients of two variables, $u_{\text{thr}} = (b+v)/a$ is the v -dependent threshold defining the excitability of the medium, and a, b are the parameters of the model. Equations (1) and (2) describe many experimentally determined features of spiral waves, for example, frequency selection, meandering instabilities, interaction with boundaries, defects, etc. [5,10].

However, this model as well as other two-component systems fails to reproduce a number of other important phenomena seen in experiments. In particular, small-scale disordered initial conditions never evolve toward formation of large coherent spirals, as is often observed in the early stage of amoebae aggregation [11] (see Fig. 1). On the contrary, after a short transient a number of spiral-like defects remain unchanged and the coherence length of the system never becomes significantly larger than the

characteristic size of a spiral core. It is thus of interest to understand what mechanism might be operative so as to accomplish pattern coarsening.

In this Letter we show that the formation of large coherent spirals can be caused by coupling the usual excitable dynamics to an additional slow field w . This additional degree of freedom responds positively to excitation of the fast u field and modifies the excitability of the medium. All this takes place with a characteristic time scale which is slower than the v field response. We will show on the basis of numerical simulations of this three-component model that a small spiral pair (a large number of which are nucleated from typical random initial conditions) undergoes a symmetry-breaking instability (compare [12]), where one member of the spiral pair overwhelms its neighbor and pushes it to the periphery. This instability leads to coarse graining of the wave pattern leaving only few “large”

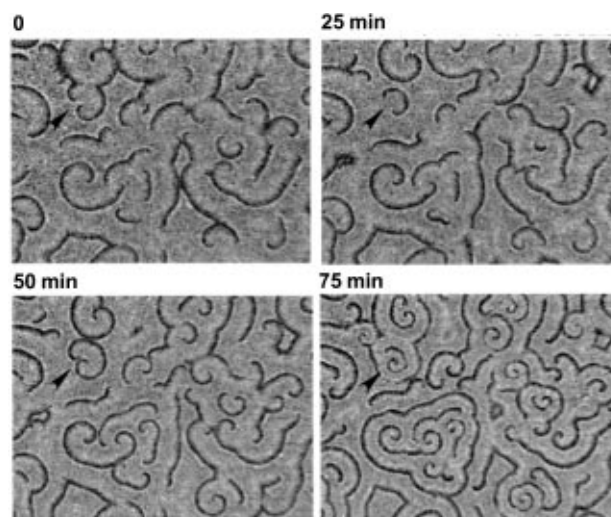


FIG. 1. A sequence of dark-field photographs of an aggregating *Dictyostelium* colony with density 2.2×10^6 cells/cm² beginning several hours after starvation. Each panel is 24×18 mm². The arrows indicate a specific example of spiral pair symmetry breaking. Courtesy of K. J. Lee, E. C. Cox, and R. E. Goldstein. (See Lee *et al.* [11].)

spirals. This instability does not occur in any two-component model of excitable media studied to date.

To be specific, let us assume that the ultraslow field w has the same type of coupling to the fast field as does the v field. This yields an equation similar to Eq. (2)

$$\partial_t w = \sigma \nabla^2 w + \beta u - \alpha w, \quad (3)$$

where constants $\alpha, \beta \ll 1$ characterize the relaxation of w and the rate of coupling with u , respectively, and σ is the diffusivity of w . Also, we assume that the growth of w increases spiral frequency. This can be achieved by changing the excitability threshold to be

$$u_{\text{thr}} = \frac{v + b}{a} + w. \quad (4)$$

Although the remainder of this paper will focus on this specific model choice, we have checked that other models of this class with positive feedback between excitation and excitability exhibit the same phenomenon. In particular, one can explain the aforementioned experimental results in *Dictyostelium* aggregation by taking into account the feedback from the cAMP waves to the expression of the genes coding for the signaling system in the individual cells [8].

We performed numerical simulations with Eqs. (1)–(3), using a modified version of the EZspiral code written by Barkley [9]. A typical time evolution of the system started from random initial conditions is shown in Fig. 2. After a short initial transient many spiral defects appear [Fig. 2(a)]. This picture is similar to a generic behavior of two-component systems evolving from random initial con-

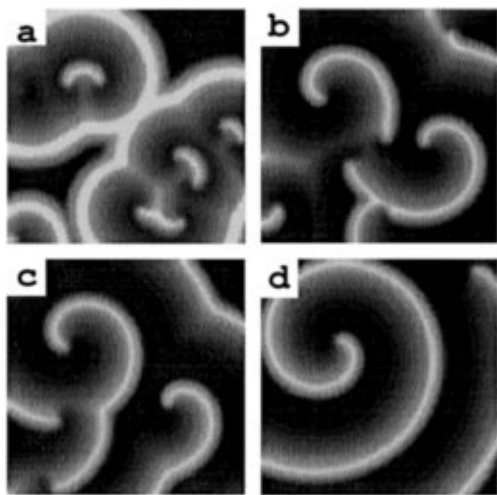


FIG. 2. Dynamics of the spiral competition. The parameters of Eqs. (1)–(3) are $a = 0.75, b = 0.01, \epsilon = 0.025, \alpha = 0.05, \beta = 0.03, \delta = 0.05$, and $\sigma = 0.2$. The number of grid points was 121×121 , the size of the integration domain 50×50 . Gray-coded images show the primary slow field v (black corresponds to $v = 0$ and white is $v \geq 0.6$) at the moments of time (a) $t = 7.8$; (b) $t = 39$; (c) $t = 86$; and (d) $t = 177$.

ditions. In two-component systems this disordered pattern of spiral-like defects is persistent, as the (superexponentially weak [13]) spiral interaction does not destroy spiral pairs. However, in contrast to two-component systems, the model (1)–(3) proceeds to exhibit nontrivial spiral competition [Figs. 2(b)–2(d)]. As a result, a number of spiral defects monotonically decrease leaving finally a large single spiral in the whole integration domain [Fig. 2(d)]. For small values of diffusivities in slow variables δ, σ , meandering of spiral cores is observed. For larger values of the diffusivities the meandering is absent, but the symmetry breaking instability persists. We conclude that the spiral meandering is not necessary for symmetry breaking.

A number of the defects N as a function of time are shown in Fig. 3. During the integration time the total number N drops from 11 to 1. The number of defects decays approximately exponentially in time. This indicates that the time it takes for the symmetry-breaking instability to halve the number of spirals is to some extent independent of the size scale of the competing spirals. In the absence of a theory of this instability, it is hard to say at present if this surprising scale independence would persist to larger length scales than can be seen in our simulations.

It is worth pointing out that a spiral pair instability is known to occur for spirals in the complex Ginzburg-Landau (GL) model [12]; there, the instability is caused by the response of the spiral frequency to the motion of the shock (a sink which absorbs waves emitted by the spirals). As was shown in Ref. [12] the advance of the shock towards the spiral core leads to a frequency decrease and, consequently, accelerates the shock motion.

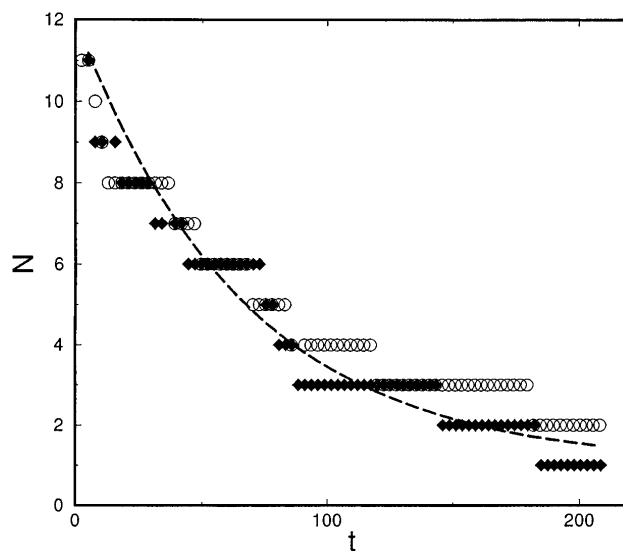


FIG. 3. The number of defects N as a function of time. The parameters of model as in Fig. 2. The symbols (open circles and diamonds) correspond to different random initial conditions. Dashed line shows exponential fit $N = 11 \exp[-0.015t] + 1$.

However, in two-component excitable systems, at least in the limit of small ϵ , this mechanism is absent. In Ref. [13] it was shown that in contrast to the GL model, a symmetric configuration of spirals in the two-component model is stable. Also, in two-component excitable media, in general, the spiral interaction is extremely weak and negligible on any realistic time scale. Therefore, we believe that this type of symmetry breaking requires the existence of the third field, and it is specifically the feedback through this third field which is responsible for the strong interaction of spiral cores.

A more detailed look at the decay of an almost symmetric spiral pair is shown in Fig. 4. The ultraslow field w has a circular depression near the spiral cores [see Fig. 4(b)]. This feature is clearly due to the fact that at the core of the spiral u is always in a refractory state corresponding to u close to zero (in excited zone $u \rightarrow 1$). As a result, w assumes some nonzero value only due to diffusion effects, which are relatively weak. This depression then causes a reduction of the excitability for the fast variable and thereby impedes the spiral rotation. As one sees in the figure, the “losing” spiral has a smaller value of w at the core, and, therefore, smaller frequency

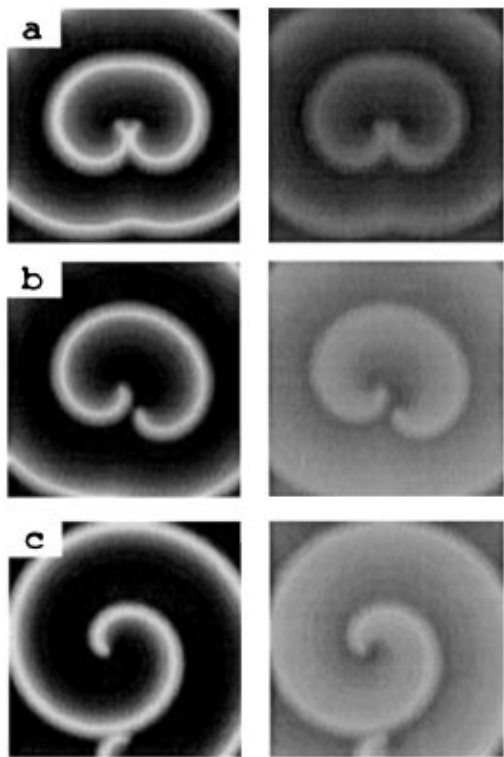


FIG. 4. The breakdown of the spiral pair. Gray-coded images show both the primary slow field v (right) and the ultraslow field w (left) for the moments of time (a) $t = 10.4$; (b) $t = 41.6$; and (c) $t = 79.3$. (The “color” table for v is the same as in Fig. 2, the color table for w spans from black at $w = 0.05$ to white at $w = 0.1$). The parameters of the simulations are the same as in Fig. 2, except for $\alpha = 0.06$, $\beta = 0.025$, $\delta = 0.2$, and $\sigma = 0.3$.

of rotation. As a result, a phase lag is introduced between the tips of the two spirals. As we will now argue, this lag is the basic process driving the spiral pair symmetry breaking.

Finally, we would like to suggest a plausible scenario underlying the symmetry breaking. Let us consider two almost symmetric spirals. The positions of spiral tips are characterized by the angles $\phi_{1,2}$ with respect to the straight line connecting the cores, and the instantaneous spiral frequencies are given by $\partial_t \phi_{1,2}$. For the ideally symmetric spiral pair, $\phi_1 = \phi_2$. The phase dynamics can be written in the form

$$\partial_t \phi_{1,2} = \omega_0(\bar{w}) + \gamma w_{1,2}. \quad (5)$$

Here we denoted by \bar{w} a value of w typical of the entire medium, and by $w_{1,2}$ the values of w at the spiral cores. In fact, $w_{1,2}$ controls the dynamics of spirals, whereas \bar{w} remains almost constant throughout the process of spiral competition. The constant γ should be strictly positive because larger w corresponds to higher excitability and therefore higher frequency of spiral rotation. For $w_{1,2}$ we have an equation following from Eq. (3)

$$\partial_t w_{1,2} = -\alpha w_{1,2} + \beta \bar{u}_{1,2}, \quad (6)$$

where $\bar{u}_{1,2}$ are averaged (over a spiral period) values of u at the spiral cores. The key assumption we make is that $\bar{u}_{1,2}$ depend on the phase difference $\phi = \phi_1 - \phi_2$. Indeed, the phase ϕ controls the distribution of the u field, and, as a result, a different amount of u will diffuse towards the core if ϕ changes. For almost symmetric configuration the dependence should be linear

$$\bar{u}_{1,2} = u_0 \pm \nu \phi. \quad (7)$$

After simple transformations we obtain the following equation for ϕ :

$$\partial_t^2 \phi = -\gamma \alpha \partial_t \phi + 2\nu \gamma \phi. \quad (8)$$

If $\nu > 0$, we will obtain a growth of the phase ϕ and, consequently, the breaking of the symmetric pair. There is no obvious way to determine the constant ν characterizing the response of the core to the phase shift. However, we have implicit evidence that supports our construction. In Fig. 5, the phase difference ϕ is shown for the run presented in Fig. 4. Indeed, one sees that ϕ grows monotonically until the second spiral gets destroyed at $T \approx 20.0$ when $\phi = -0.2$ (note that the frequency difference is still small at this stage).

In summary, we have shown how a simple three-component extension of the usual class of excitable media models exhibits a new symmetry-breaking phenomena. Our results to date are mostly computational, but we have presented a simple scenario in which the most relevant

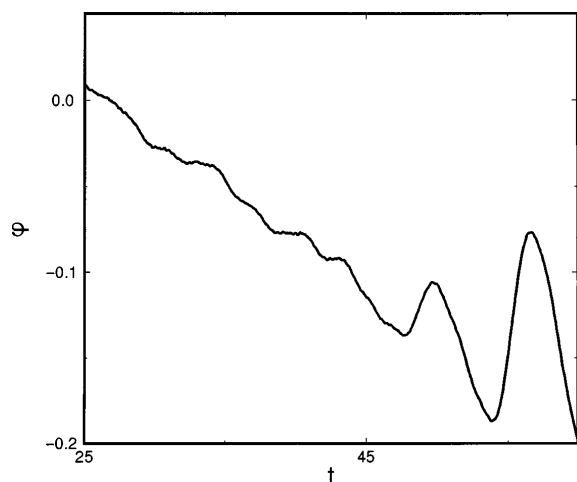


FIG. 5. The angle difference $\phi = \phi_1 - \phi_2$ between the tips of two spirals for the simulation of Fig. 4.

dynamical variable is the phase difference between the two spiral tips. The coarsening of the wave pattern that results from this instability is known to occur in at least one excitable system (amoebae aggregation) where the ultraslow field can be associated with genetic expression encoding the signal transduction and response machinery. It would be predicted to occur whenever there is a positive feedback from signal to excitability.

We would like to acknowledge useful conversations with R. Goldstein, D. Kessler, W. Loomis, and G. Shaulsky. This work was supported in part by NSF Grant DMR94-15460 (H.L.) and the U.S. Department of Energy (L.T.). The work of I.A. was partially sup-

ported by the Raschi Foundation. I. A. acknowledges the hospitality of the Institute for Nonlinear Science, UCSD.

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