Wave Pattern Selection in an Excitable System

Kyoung J. Lee*
Department of Physics, Korea University, Seoul, Korea
(Received 4 April 1997)

Wave pattern selection between periodic spirals and periodic circular pacemaker waves in excitable media is investigated with numerical simulations in a FitzHugh-Nagumo reaction-diffusion model. When spirals have oscillatory tails circular waves are more likely dominant over spirals, whereas it is opposite when spirals have monotonic tails. In both cases a coherent state is achieved in an asymptotic limit with a single period and a velocity. The observed wave pattern selection mechanism seems to underlie the competition between spirals and circular waves observed in signaling activity of *Dictyostelium discoideum* amoebae population. [S0031-9007(97)04280-4]

PACS numbers: 87.10.+e, 05.70.Ln, 82.20.Wt, 82.40.Ck

In a variety of chemical, biological, and physical media, we find coherent spatiotemporal patterns of chemical waves referred as "excitable waves" [1,2]. Two topologically different wave structures are known to exist in excitable media identified so far—circular waves and rotating spirals. These waves have been a subject of numerous studies during the last two decades because of their interesting nonlinear dynamics and more recently because of their various biological or physiological implications in a variety of living systems [3–5]. Many different aspects of excitable waves have been addressed before but the dynamical process of entrainment between different types of waves and the resulting wave pattern selection are poorly understood. Understanding such phenomena would be quite important in explaining many biological phenomena including morphogenic development of amoeba population [3], heart dynamics and associated diseases [4], and signal processing in neurons such as in the visual cortex [6].

The origins of circular waves and spirals in excitable media are very different. A concentric circular wave train arises from a "pacemaker" that periodically initiates a wave, whereas a rotating spiral forms from a broken wave end that is not associated with any pacemakers. Pacemakers are known to be spatial inhomogeneities randomly distributed in the medium. In a given excitable medium, a spiral selects a unique period [7] for a given initial condition, whereas circular wave trains (or targets) generated from pacemakers can have different values of period. In both cases, waves travel away from the sources and upon collision they annihilate. In the presence of stochastic noise and random distribution of inhomogeneities, spirals and various pacemaker wave trains can coexist simultaneously, but compete and ultimately entrain each other to a coherent state with a single period and a velocity. The final asymptotic states are in some cases governed by spirals and in other cases governed by pacemakers. An example of such competing dynamics resulting in two different coherent wave patterns was reported recently in quantitative laboratory experiments on a signaling activity in populations of amoeba *Dictyostelium discoideum* (Fig. 1).

It is our interest to know in general context of excitable media, what the underlying mechanism behind the wave pattern selection is and how the asymptotic state varies with a systematic change in a control parameter. These questions are investigated numerically with a FitzHugh-Nagumo reaction-diffusion model that has been used as a generic excitable system faithfully capturing the behavior of many excitable waves [8]. Our FitzHugh-Nagumo model is a two-species reaction-diffusion model:

$$\frac{\partial U}{\partial t} = \nabla^2 U - V + U - U^3,$$

$$\frac{\partial V}{\partial t} = \delta \nabla^2 V + \epsilon (U - \alpha V - \beta).$$

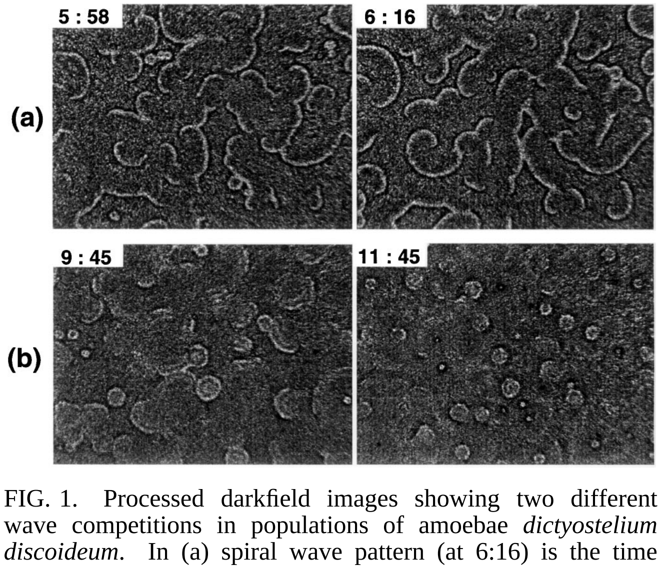

FIG. 1. Processed darkfield images showing two different wave competitions in populations of amoebae *dictyostelium discoideum*. In (a) spiral wave pattern (at 6:16) is the time asymptotic state selected from an initial mixed state of spirals and circular pacemaker waves (5:58) [at a cell population density of 21.8×10^5 cells/cm^2], whereas in (b) circular waves are selected (11:45) from an initial mixed state (9:45) [at cell population density of 7.3×10^5 cell/cm^2]. All frames show a 24×18 (mm^2) domain. The details on this experiment can be found in Ref. [3].

The variables U and V represent the concentrations of the activator and the inhibitor species, respectively. ϵ, α, and β are parameters of the reaction kinetics, and δ is the ratio of diffusion coefficients of two species.

Numerical simulations of the model are performed to investigate competitions between a spiral and a pacemaker wave in an excitable regime (Fig. 2). The spiral at $t = 0$ originates from a straight wave segment that is initially placed on the upper right-hand corner. A pacemaker is also initially seeded at the lower left-hand corner. The sequence of frames in Fig. 2(a) shows a spiral wave gradually invading a slower pacemaker, inhibiting the nucleation of circular wave, and eventually setting the period of the entire system in a coherent one of its own. By choosing different values of ϵ and β for the pacemaking region, however, it is also possible to have a pacemaker with a smaller period than the rotation period of the spiral in otherwise the same medium. Figure 2(b) shows such a case. This time, the pacemaker wave train gradually takes over the spiral territory and sets the period of the whole system to the one of the pacemaker. The broken wave end at $t = 140$ is no longer able to generate waves of its own.

The two asymptotic states shown in Figs. 2(a) and 2(b) are significantly different. First, one has spiral and the other has circular waves. Second, they have different periods and wavelengths. These differences originate simply from the fact that the pacemaker in Fig. 2(a) [Fig. 2(b)] has a period longer [shorter] than the rotation period of the spiral. We find that the competition between two different wave trains is based solely on their periods, regardless of the nature of the wave-generating source. Two different wave trains upon head-on collision annihilate each other. Therefore, if one wave train has a smaller period than that of the second wave train, the spatial location where the collision occurs would gradually shift toward the source with a longer period and eventually the slower source would be entrained. The slower one loses its role as a source for waves. A similar phenomenon was discussed earlier by V. I. Krinsky and K. I. Agladze in the context of induced spiral drift [9].

It has been known that for any excitable media there is a lower limit on the period of wave train below which the structure is unstable [10]. An excitable medium can support various periodic wave trains as long as their periods are greater than the lower limit. A spiral is then a particular wave state among the many allowed states by the medium [11]. This is also true in the FitzHugh-Nagumo model, and it can be best illustrated on a dispersion curve shown in Fig. 3(a) [12]. First, there exists a minimum period ($\tau_{\min}$). When a pacemaker has a τ smaller than $\tau_{\min}$, no wave can be initiated at all or the wave initiation skips at every two or three periods, or becomes intermittent [13]. For these cases, the average period of the wave train is longer than $\tau_{\min}$. For the given parameter values spiral selects a unique period (τ_s) and velocity (v_s) as marked with a square [Fig. 3(a)]. Hence, if there is a pacemaker in the medium that happens to have a period between $\tau_{\min}$ and τ_s, it will eventually entrain spirals. In the opposite case, spirals will entrain slower pacemakers.

If we assume that pacemakers with different periods to appear are equal in a medium with random inhomogeneities, the size of the gap, $\tau_{\min} < \tau < \tau_s$, then should

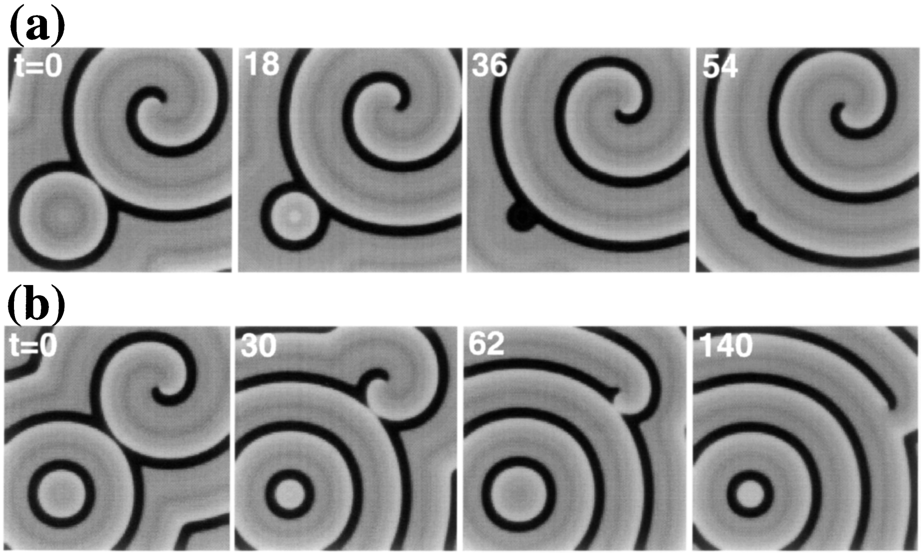

FIG. 2. Two different competitions between a spiral and a periodic pacemaker. In (a) the spiral entrains the pacemaker, whereas in (b) the pacemaker entrains the spiral. The spirals have a rotation period of 55.4. The pacemaker (a small region with a radius of 4 grids) in (a) and (b) produces waves at a period of 66.4 and 44.3, respectively. For the bulk medium, $\epsilon = 0.12$, $\alpha = 1.0$, $\beta = -0.2$, and $\delta = 0.1$. The pacemaking region in (a) and (b) has ($\epsilon = 0.06$, $\beta = 0$) and ($\epsilon = 0.04$, $\beta = -0.12$), respectively. The equations are computed using a fourth-order Runge-Kutta method with adjustable time step. Each image of 128 × 128 grids shows the U field in 256 grey scale.

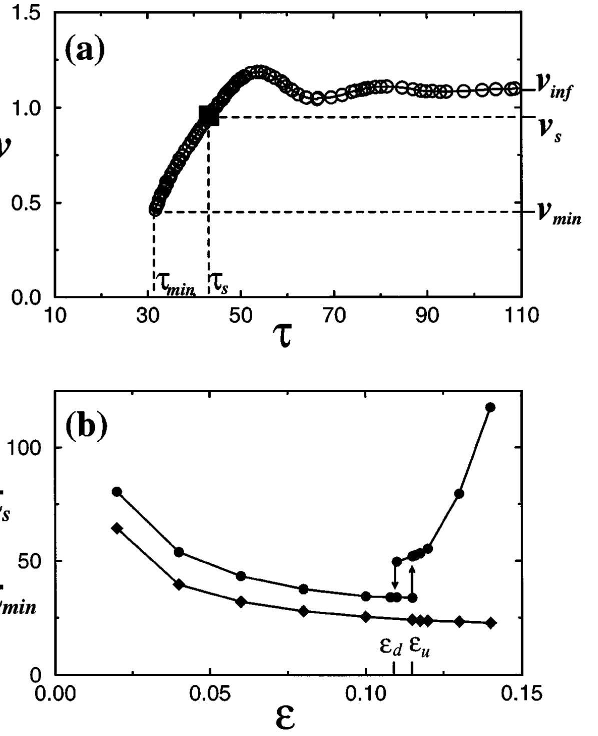

FIG. 3. (a) A typical dispersion curve [velocity v vs period τ] numerically computed for the FitzHugh-Nagumo model. $\tau_{\min}$ and $v_{\min}$ are the minimum period and the minimum velocity of a periodic wave train that can be supported by the medium. τ_s and v_s are the rotation period and the velocity of a spiral determined by the medium. The parameter values used are the same as in the caption for Fig. 2, except $\epsilon = 0.06$. (b) τ_s (dot) and $\tau_{\min}$ (diamond) plotted as functions of ϵ.

reflect the probability of having a pacemaker wave state as the asymptotic pattern. We thus investigate how τ_s and $\tau_{\min}$ vary with a systematic change in a control parameter [Fig. 3(b)] [14]. It is found that $\tau_{\min}$ slowly decreases monotonically with increasing ϵ. On the other hand, τ_s initially decreases very much like $\tau_{\min}$ with increasing ϵ but starts to increase abruptly and sharply beyond $\epsilon_u = 0.1175$. With the decreasing sequence of ϵ, a similar discontinuous transition occurs at $\epsilon_d = 0.1085$, slightly smaller than ϵ_u. The two abrupt transitions are hysteric, forming a narrow bistable window [12]. Consequently, the gap between τ_s and $\tau_{\min}$ stays very small and hardly changes before the bistable window, but sharply increases thereafter. Accordingly, the probability that the circular wave state would become a final state from an initial mixed state is much higher in the region to the right of the bistable window. This becomes more pronounced as ϵ increases beyond ϵ_u.

The abrupt increase in τ_s at ϵ_u is directly related with the qualitative shape change in the refractory tail of spiral. For $\epsilon < \epsilon_u$ (for example, $\epsilon = 0.06$) each wave monotonically decays to the next wave, but for $\epsilon > \epsilon_d$ (for example, $\epsilon = 0.12$ and 0.14) each wave has an oscillatory tail showing a few small amplitude humps [Fig. 4(a)]. The origin of these extra humps can be understood by examining the delicate structure of the flow generated by the local dynamics of spiral around the fixed point of the associated homogeneous system as shown in Figs. 4(b) and 4(c). While the trajectory generated by the local dynamics approaches the fixed point from the left and escapes to the right immediately when $\epsilon = 0.06$, it approaches and makes a few small loops before being reinjected to the right when $\epsilon = 0.12$ and 0.14. During the extra loopings, the variations in U and V are very small but the dynamics are quite slow.

A simple linear stability analysis on the homogeneous system shows that the associated fixed point is a stable focus except for small values of ϵ ($0 < \epsilon < 1.66 \times 10^{-4}$) for which it is a node. Hence, the flow generated by the homogeneous system spirals into the fixed point for most parameter regime that is being considered. The local dynamics of the spiral in a diffusively coupled system is, however, not the same as the dynamics generated by the homogeneous system, since it is strongly influenced by the neighbors. For $\epsilon < \epsilon_u$, the perturbation from attached neighbors is strong enough to completely bypass the spiraling loop, whereas for $\epsilon > \epsilon_d$ the perturbation is not strong enough to avoid the extra loop. The abrupt

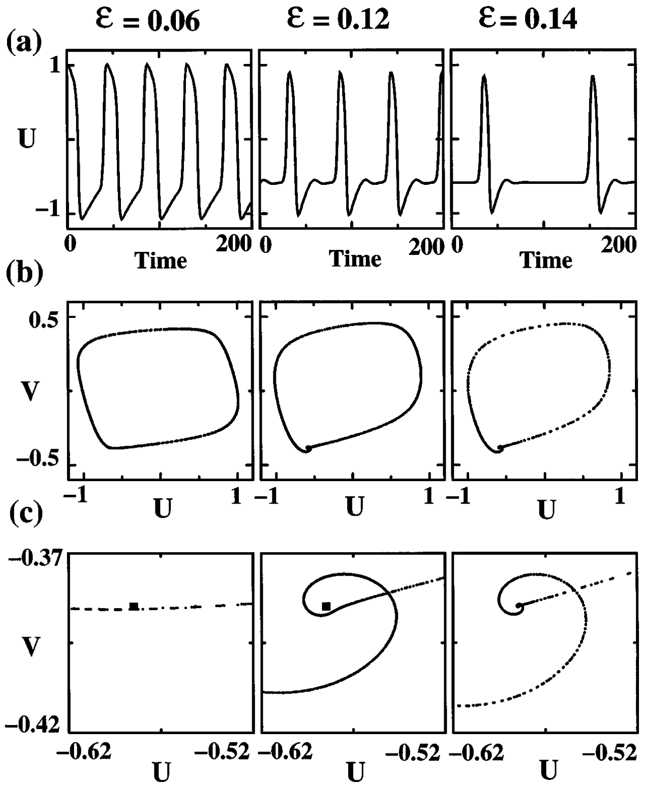

FIG. 4. (a) Time series of U field obtained at a fixed location away from the spiral's core in simulations of spiral, (b) time series of the U and V fields plotted in U-V phase plane, (c) blown-up pictures of (b) near the fixed point (marked with a square) of the homogeneous system. Plots in each column are obtained with the values of ϵ given on the top.

transitions of the bistability are due to the underlying threshold dynamics and the hysteresis is due to the differing perturbation strengths that are set by the wavelength of the associated wave train.

The qualitative shape change in the refractory tails with a change in control parameter can be also noticed in the signaling patterns of amoeba. In Fig. 1(b) at 9:45 most waves have a noticeable secondary hump shadowing the primary wave peaks, while in Fig. 1(a) no such secondary hump is visible. According to our model analysis, the probability of having pacemaker waves as the asymptotic state is great when spirals have an oscillatory tail, whereas it is low when spirals have a simply decaying tail. The experimental results shown in Fig. 1 seem to be consistent with the model analysis.

Our analysis, of course, is based on the assumption that different pacemakers with differing periods appear with equal probability. However, there could be some active factors which would influence the probability distribution function of the pacemaker period. We identify such a factor—the size of the pacemaker. It is found that there is a critical pacemaking domain size below which no wave will be created at all. Furthermore, the minimum size varies depending on the value of ϵ and β, and thus determined period of the pacemaker. For a small value of ϵ ($< \epsilon_u$), a pacemaker with $\tau < \tau_s$ requires a minimum domain size that is several times larger than that of a pacemaker with $\tau > \tau_s$. For a large value of ϵ ($> \epsilon_d$), the trend is the opposite. Since in a controlled system a physically large inhomogeneity is less likely to be retained, we infer that the slower (faster) pacemaker is more likely to form when ϵ is smaller (larger) than ϵ_u—an additional factor supporting our analysis that spiral (pacemaker waves) would be favored for small (large) ϵ.

In summary, the wave pattern selection between spiral and circular pacemaker waves is studied in a FitzHugh-Nagumo reaction-diffusion model. By investigating the nature of the steady state of the associated homogeneous system, the local dynamics generated by spirals, and the required minimum pacemaking domain size together, we suggest that circular pacemaker waves are much more likely to dominate over spirals when spirals have oscillatory tails and the opposite when spirals have monotonic tails. The observed wave pattern selection mechanism seems to underlie the similar experimental observations in the signaling activity of amoeba [3]. Future work will include similar analysis on the Matial-Goldbeter model [15], which is a more realistic model describing the signaling waves in amoeba. Also, more work needs to be done in experiment for statistical analysis of the pacemaker periods and quantitative investigation of the wave profiles. Since the FitzHugh-Nagumo model has been used successfully as a generic excitable system for investigating various phenomena in diverse excitable systems, the observed phenomena would likely occur in a broad range of excitable systems.

We acknowledge many helpful discussions with E. Cox, R. Goldstein, and A. Winfree. The work was supported in part by the Ministry of Education of Korea (DSRI-96-2444), the Ministry of Science and Technology (HPC-COSE) of Korea, and Korea University.

---

*Electronic address: kyoung@nld.korea.ac.kr

[1] *Waves and Patterns in Chemical and Biological Media*, edited by H. L. Swinney and V. I. Krinsky (MIT/North-Holland, Cambridge, MA, 1992).

[2] G. Ertl, Science **254**, 1750 (1991).

[3] K. J. Lee, E. C. Cox, and R. E. Goldstein, Phys. Rev. Lett. **76**, 1174 (1996).

[4] L. Glass, Phys. Today **45**, No. 8, 40 (1996).

[5] J. Lechleiter, S. Girard, D. Clapham, and E. Peralta, Nature (London) **350**, 505 (1991).

[6] C. M. Gray, P. König, A. K. Engel, and W. Singer, Nature (London) **338**, 334 (1996).

[7] In some excitable media the tip of a spiral can have a nonperiodic motion [see D. Barkley, Phys. Rev. Lett. **72**, 164 (1994), and references therein]. In this paper we deal only with periodic spirals.

[8] A. Hagberg and E. Meron, Phys. Rev. Lett. **72**, 1120 (1994); D. M. Petrich and R. E. Goldstein, Phys. Rev. Lett. **72**, 1120 (1994); A. Karma, Phys. Rev. Lett. **65**, 2824 (1990).

[9] V. I. Krinsky and K. I. Agladze, Physica (Amsterdam) **8D**, 50 (1983).

[10] J. D. Dockery, J. P. Keener, and J. J. Tyson, Physica (Amsterdam) **30D**, 177 (1988).

[11] M. Gerhardt, H. Schuster, and J. J. Tyson, Science **247**, 1563 (1990).

[12] A similar dispersion curve was numerically computed earlier by A. T. Winfree, Phys. Lett. A **149**, 203 (1990); Physica (Amsterdam) **49D**, 125 (1991).

[13] The stability of periodic and nonperiodic wave trains is discussed in C. Elphick, E. Meron, and E. A. Spiegel, Phys. Rev. Lett. **61**, 496 (1988); SIAM J. Appl. Math. **50**, 490 (1990).

[14] ϵ is chosen for a control parameter with no particular reason. α or β could have been used as well.

[15] A. Goldbeter, Nature (London) **253**, 540 (1975); J. Martiel and A. Goldbeter, Biophys. J. **52**, 807 (1987).