Propagation failure in discrete bistable reaction-diffusion systems: Theory and experiments

J. C. Comte, S. Morfu, and P. Marquié*
Laboratoire LE2I, FRE CNRS 2309, Université de Bourgogne, Aile de l'Ingénieur, Boîte Postale 47870, 21078 Dijon cedex, France
(Received 21 February 2001; published 17 July 2001)

Wave front propagation failure is investigated in discrete bistable reaction-diffusion systems. We present a theoretical approach including dissipative effects and leading to an analytical expression of the critical coupling beyond which front propagation can occur as a function of the nonlinearity threshold parameter. Our theoretical predictions are confirmed by numerical simulations and experimental results on an equivalent electrical diffusive lattice.

DOI: 10.1103/PhysRevE.64.027102 PACS number(s): 82.40.Ck, 47.35.+i, 47.54.+r

I. INTRODUCTION

In recent decades, nonlinear wave propagation in strongly dissipative or reaction-diffusion systems has attracted considerable attention. Indeed, reaction-diffusion equations arise in many areas of physics, biology, chemistry, and ecology [1,2]. The flame of a candle, a nerve impulse, spiral waves in excitable chemical reagents, as well as cell or animal population dynamics, to cite but a few, are examples of nonlinear diffusion. Furthermore, as many reaction-diffusion systems of biological origin, for example, in neuro- [3,4] and cardiophysiology [5,6], are intrinsically discrete, it has become clear that continuous reaction-diffusion equations provide an inadequate description of the behavior of these systems, where the interplay between nonlinearity and spatial discreteness can lead to effects not present in continuum models. Among these effects is the important phenomenon of *wave propagation failure*, shared by most diffusively coupled systems of excitable cells (there exist also particular cases of nonlinear diffusive lattices that do not exhibit this phenomenon [7,8]). As propagation failure may lead, in the context of neuro- and cardiophysiology, to the breakdown of the systems with potentially fatal consequences, it has been the subject of numerous studies [5,6,9–14]. In particular, it has been observed that there exists a nonzero critical value of the intercellular coupling strength under which wave fronts fail to propagate. In order to gain understanding of this crucial phenomenon, it is necessary to determine this critical coupling strength analytically.

As a model, we consider the usual dimensionless discrete version of the Nagumo equation [15]

$$\frac{du_n}{dt}=D[u_{n+1}+u_{n-1}-2u_n]+f(u_n), \tag{1}$$

where u_n is the state of the nth lattice site, D the coupling strength, and $f(u_n)$ a bistable nonlinear function of the form $f(u_n)=-u_n(u_n-a)(u_n-1)$.

The main goal of this paper is to present a theoretical approach leading to an analytical expression of the critical coupling $D_c(a)$ beyond which front propagation can occur. Contrary to previous theoretical studies [16–19] in which the stationary case of Eq. (1) $(du_n/dt=0)$ was considered, our method, presented in Sec. II, includes dissipative effects, expressed by the term du_n/dt. Our theoretical predictions are confirmed by numerical simulations (Sec. III) and experimental results on an equivalent electrical diffusive lattice (Sec. IV). Finally, Sec. V concludes the paper.

II. THEORETICAL STUDY

From a physical point of view, Eq. (1) can also model an *overdamped* chain of harmonically coupled particles lying in a double well on site potential $U(u_n)$, with $f(u_n)=-dU(u_n)/du_n$. We propose to determine the minimum coupling strength $D_c(a)$ over which the boundary and initial conditions

$$u_1=1 \quad (t\geqslant 0),$$

$$u_2<a \quad (t=0), \tag{2}$$

$$u_n=0 \quad (3\leqslant n\leqslant N \text{ and } t=0)$$

will give rise to a traveling kinklike wave joining the two states $u=0$ and 1, corresponding to the minima of the potential $U(u_n)$. Here, as in [19], we consider that only the front site $n=2$ experiences nonlinearity, while the other sites $(n>2)$ are close enough to $u=0$ to be in the linear regime (Fig. 1). For a traveling wave to be initiated, let us point out that it is necessary for the front site $n=2$ to pass the energy barrier (with maximum height ΔV) in $u=a$ separating the two potential minima, in spite of the loss mechanism. Indeed, as is well known, climbing a hill against the wind requires more effort and more time than without any wind, although the distance to be covered remains constant. Thus, and it is of crucial importance in our investigation, as we consider an overdamped system, the dissipation effects expressed by the term du_n/dt have to be taken into account in the determination of the critical coupling.

One might wonder then how to include these dissipative effects in the problem. The answer ensues from the following remarks. Using boundary and initial conditions (2) in Eq. (1) and setting $u_2=v$ leads to the evolution equation of the site $n=2$,

*Electronic address: marquie@u-bourgogne.fr

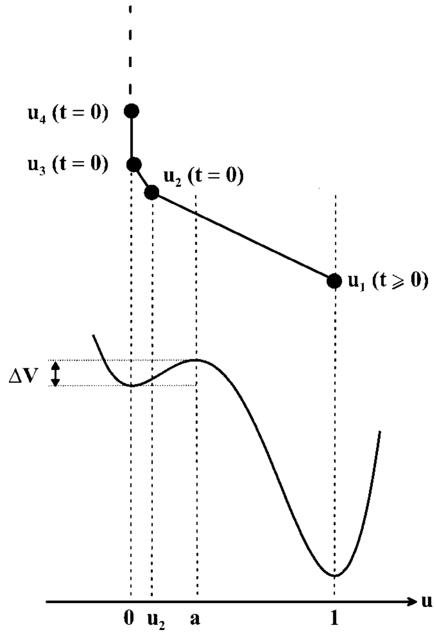

FIG. 1. Schematic representation of the boundary and initial conditions loaded in the chain, with the corresponding bistable potential. To initiate front propagation, lattice site $n=2$ (u_2) has to pass the energy barrier at $u=a$ (with maximum height ΔV) separating the two potential minima at $u=0$ and 1.

$$\frac{dv}{dt}=D[1-2v]-v(v-a)(v-1). \tag{3}$$

In the particular case where all the cells are uncoupled ($D=0$), Eq. (3) reduces to

$$\frac{dv}{dt}=-v^3+v^2(1+a)-av. \tag{4}$$

This equation means that in the no coupling limit the dissipative effects (dv/dt) are exactly balanced by the nonlinear cubic function $f(u=v)=-v^3+v^2(1+a)-av$. Now, if we introduce a progressively increasing coupling D (with $D \ll 1$), the friction force will be only slightly modified, compared to the no coupling case. This leads us to suppose, first, that the friction force can still be expressed by a cubic polynomial of the form $P(u)=\alpha u^3+\beta u^2+\gamma u$. Furthermore, as we consider in this study small values of the coupling (the propagation failure occurring for a small but nonzero value of the coupling, $D_c \ll 1$) the structure of the friction force will be conserved for $u\in[0;1]$ by choosing $\alpha=-1$ in $P(u)$. Under these conditions, Eq. (3) becomes

$$D[1-2v]=-Av^2+Bv, \tag{5}$$

with $A=1+a-\beta$ and $B=a+\gamma$. The right-hand side of Eq. (5) can be viewed as a force including both the initial cubic function $f(u)$ and the friction force, and deriving from a new potential $G(u)$. This potential must present for $u\in[0;1]$ the same minimum at $u=0$, maximum at $u=a$, and maximum barrier height ΔV as the initial potential U (as represented in Fig. 2). Indeed, as stated before, the influence of dissipative

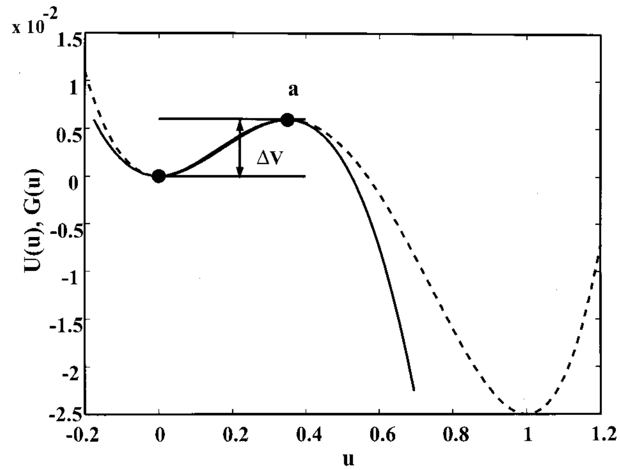

FIG. 2. Initial bistable potential $U(u)$ (dashed line) and new potential $G(u)$ including dissipative effects (continuous line). The two potentials share the same maximum barrier height ΔV between $u=0$ and a.

effects does not change the fact that, starting from any initial condition $u=v\in[0;a]$, the front site $n=2$ has to pass the energy barrier (with maximum height ΔV) at $u=a$ to initiate front propagation. Then the parameters A and B in Eq. (5) can be obtained easily, which leads to

$$D[1-2v]=-(1-a/2)(v-a)v. \tag{6}$$

This second degree equation expresses the exact balance between the force resulting from the coupling (left-hand side term) and the force resulting from the new on-site potential including dissipative effects (right-hand side), which corresponds to the propagation failure limit. In fact, the front site $n=2$ would pass the barrier if the coupling strength was greater than the on-site nonlinearity. Thus Eq. (6) admits a unique solution if its discriminant $\Delta(D)=0$, which leads to the analytical expression of the critical coupling

$$D_c(a)=(a-2)[a-1+\sqrt{1-2a}]/4. \tag{7}$$

III. NUMERICAL RESULTS

The theoretical expression (7) has been compared with the results of numerical simulations on a 200 cell lattice, using a fourth order Runge-Kutta method with a time step $dt=0.01$. As presented in Fig. 3, our results (dashed line a) are in perfect agreement with numerical results ($\Diamond$). Let us emphasize that our analytical expression $D_c(a)$ is valid in the whole range $a\in[0;0.5]$, contrary to previous estimations of this critical coupling strength. In particular, Keener [16] and Erneux and Nicolis [17] showed, respectively, that the critical value of D below which propagation failure occurs is related to the nonlinearity parameter a by $D_c=a^2/4$, but only in the case $a\ll 1$ (curve c in Fig. 3). On the other hand, Keener [16] also proposed an estimate of D_c above which propagation was assured $D_c=[2a^2-a+2-2(a+1)\sqrt{a^2-3a+1}]/25$, but restricted to $a\leqslant 0.382$ (curve b in Fig. 3). Nevertheless, if we consider

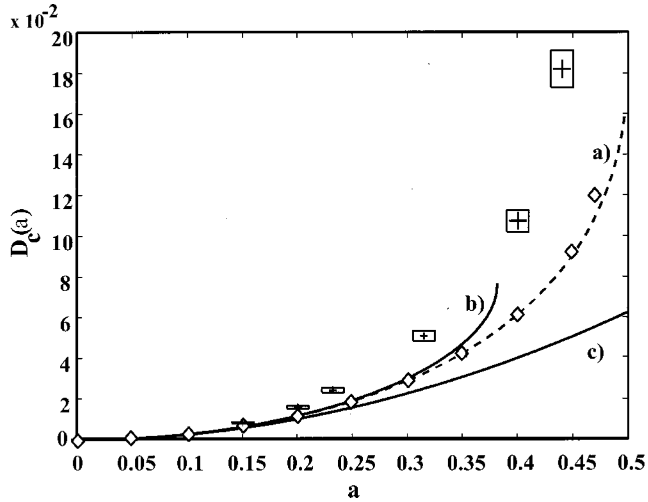

FIG. 3. Curves of the critical coupling inducing propagation failure. Our theoretical predictions (dashed line a) are compared with numerical simulations results ($\diamond$) and experimental measures (+). Previous analytical results [16,17] are also presented (continuous lines b and c).

$a \ll 1$ in Eq. (7), our results agree with previous ones, since we also obtain $D_c(a) \simeq a^2/4$.

IV. EXPERIMENTAL RESULTS

Let us finally present an experimental determination of the critical coupling $D_{c,\mathrm{expt}}(a)$ inducing propagation failure, using a nonlinear diffusive electrical lattice [20]. The lattice consists of $N = 48$ elementary cells, resistively coupled by linear adjustable resistors r and containing a nonlinear resistor R_{NL} in parallel with a linear capacitor C (see Fig. 4). The nonlinear resistor R_{NL} presents a cubic type current-voltage characteristic of the form

$$I(U) = U(U-\alpha)(U-\beta)/\lambda, \tag{8}$$

with $\lambda = R_0\alpha\beta, R_0$ being a weighting resistor. From the Kirchhoff laws, and setting $d = R_0/r$ and $\tau = t/C$, we derive, for $2 \leqslant n \leqslant N-1$, the set of discrete equations of Fisher [21] or Nagumo without a recovery term, introduced for simulating genetic diffusion and information propagation along nerve axons,

$$\frac{dU_n}{d\tau} = d[U_{n+1} + U_{n-1} - 2U_n] - \frac{U_n}{\alpha\beta}(U_n-\alpha)(U_n-\beta). \tag{9}$$

The description of the system is completed by assuming zero-flux or Neumann boundary conditions (for $n=1$ and N).

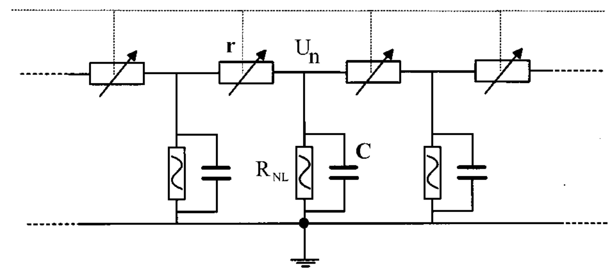

FIG. 4. Schematic representation of the nonlinear diffusive electrical lattice. All the $N = 48$ elementary cells are resistively coupled by linear adjustable resistors r and contain a nonlinear resistor R_{NL} in parallel with a linear capacitor C.

For each value of the parameter $a = \alpha/\beta$, all the coupling resistors r are adjusted to their maximum value $r_{\max}$ (the very small coupling case) in order to be in the propagation failure regime. Then these resistors are decreased simultaneously (the coupling is then increased) until the critical value r_c is reached that induces a propagative front from the Heaviside-type initial condition loaded in the lattice. After normalization, our experimental results, presented in Fig. 3 with their uncertainty domains (+ signs), are qualitatively in good agreement with both our theoretical predictions and numerical simulation results even if there exists a slight discrepancy. This is probably due to the fact that the current-voltage characteristic of the nonlinear resistors does not have exactly a cubic shape, as the parameter $\alpha/\beta = a$ is modified.

V. CONCLUSION

In summary, we have presented a method allowing characterization of the propagation failure phenomenon in discrete bistable reaction-diffusion systems. This approach including dissipative effects leads to a general analytical relation between the critical coupling strength beyond which front propagation can occur and the barrier parameter or threshold of the bistable potential. Considering the example of the discrete Nagumo equation, our predictions were confirmed by numerical simulations and experimental results on a nonlinear diffusive electrical lattice. Let us point out finally that our method is of general interest since it could be applied to discrete systems with bistable behavior including both inertia and dissipation. We believe then that our method can allow a better understanding of physical, biophysical, or chemical real phenomena, in particular, in the contexts of neuro- and cardiophysiology. Indeed, since realistic models are rather complicated, it is important, using simple lattice models, to describe the real phenomena involved with fairly good accuracy.

[1] J. D. Murray, *Mathematical Biology* (Springer-Verlag, Berlin, 1989).
[2] A. C. Scott, *Nonlinear Science—Emergence and Dynamics of Coherent Structures* (Oxford University Press, Oxford, 1999).
[3] A. C. Scott, Rev. Mod. Phys. **47**, 487 (1975).
[4] J. Bell, in *Reaction-Diffusion Equations*, edited by K. J. Brown and A. A. Lacey (Clarendon Press, Oxford, 1990), pp. 95–116.
[5] J. P. Keener, J. Theor. Biol. **148**, 49 (1991).

[6] M. deCastro, E. Hofer, M. Muñuzuri, M. Gómez-Gesteira, G. Plank, I. Schafferhofer, V. Pérez-Muñuzuri, and V. Pérez-Villar, Phys. Rev. E **59**, 5962 (1999).
[7] P. C. Bressloff and G. Rowlands, Physica D **106**, 255 (1997).
[8] J. C. Comte, P. Marquié, and M. Remoissenet, Phys. Rev. E **60**, 7484 (1999).
[9] R. S. MacKay and J.-A. Sepulchre, SIAM (Soc. Ind. Appl. Math.) J. Appl. Math. **47**, 556 (1987).
[10] W. C. Cole, J. B. Picone, and N. Sperelakis, Biophys. J. **53**, 809 (1988).
[11] V. Booth and T. Erneux, Physica D **188**, 206 (1992); V. Booth, T. Erneux, and J. P. Laplante, J. Phys. Chem. **98**, 6537 (1994).
[12] J. P. Laplante and T. Erneux, Physica A **188**, 89 (1992); J. Phys. Chem. **96**, 4931 (1992).
[13] V. Pérez-Muñuzuri, V. Pérez-Villar, and L. O. Chua, J. Circuits Syst. Comp. **3**, 215 (1993).
[14] A. R. Anderson and B. D. Sleeman, Int. J. Bifurcation Chaos Appl. Sci. Eng. **5**, 63 (1995).
[15] J. Nagumo, S. Arimoto, and S. Yoshisawa, Proc. IRE **50**, 2061 (1962).
[16] J. P. Keener, SIAM (Soc. Ind. Appl. Math.) J. Appl. Math. **47**, 556 (1987).
[17] T. Erneux and G. Nicolis, Physica D **67**, 237 (1993).
[18] I. Mitkov, K. Kladko, and J. E. Pearson, Phys. Rev. Lett. **81**, 5453 (1998).
[19] K. Kladko, I. Mitkov, and A. R. Bishop, Phys. Rev. Lett. **84**, 4505 (2000).
[20] S. Binczak, J. C. Comte, B. Michaux, P. Marquié, and J. M. Bilbault, Electron. Lett. **34**, 1061 (1998).
[21] R. A. Fisher, Ann. Eugen. **7**, 335 (1937).