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Where do dispersion curves end? A basic question in theory of excitable media

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We use our recent exactly solvable model of excitable media with nondiffusive control kinetics to study periodic wave trains in an excitable medium. We explicitly find restitution and dispersion curves for such a medium that are protocol independent. We also introduce an approximate stability criterion for periodic waves, which is based on the solitary pulse stability. Using our analytical periodic solutions as the initial conditions in our numerical experiments we demonstrate that this criterion indeed determines the minimal wavelength and propagation velocity below which both a solitary pulse and a periodic wave train quickly die.
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Different processes in a distributed nonlinear system generally occur on different space and time scales. Determining such scales is a fundamental step in understanding key phenomena in any nonlinear medium. In hydrodynamics and traditional nonlinear wave theory this fact has long been a matter of full consensus. Spatiotemporal scales always emerge in analysis of pattern formation, stability, and evolution of reaction diffusion (RD) systems [1–7]. Spatial and temporal scales (L,τ) of a wave process in one dimension are incorporated in the dispersion curve $c=c(k)$, where c is the wave velocity and k is the wave number. Each point (c,k) of such a curve and its slope dc/dk determine a (L,τ) pair [for example as $L=2\pi/k$, or $L=(1/c)(dc/dk)$, and $\tau=L/c$]. Of particular interest are such characteristic points of the dispersion curve as its extrema, inflection and end points, since they can often be thought of as representative scales for some particular processes. Unfortunately, classical methods of singular perturbation theory [1,2] for RD systems do not allow uniform estimates that are valid in the most interesting region of small velocities. In this Rapid Communication we use our exactly solvable model [8] of excitable media to introduce a general ''recipe'' for finding the ''slow'' end point on the dispersion curve, which is key for determining the fate of the RD waves. The end point of the dispersion curve determines the fundamental length and time scales introduced in Refs. [6], which are crucial for our understanding of various phenomena in excitable media.

We will consider a set of RDEs of the form [8]

$$\frac{\partial u}{\partial t}-\frac{\partial^2 u}{\partial x^2}=-i(u,v)\equiv-\begin{cases}\lambda u, & \text{if } u<v\\ u-1, & \text{if } u\geqslant v,\end{cases} \quad (1)$$

$$\frac{\partial v}{\partial t}=\varepsilon[\zeta u+v_r-v], \quad (\varepsilon>0), \quad (2)$$

where $\varepsilon>0$ is the dimensionless relaxation rate for the slow variable v which has a meaning of an excitation threshold potential, $\zeta>0$ is the u-v coupling constant, the constant $v_r>0$ is the ground (resting) state v value that determines the depth of the minima of $v(\xi)$, and $\lambda>0$ is the resting state conductivity (see Ref. [8]). We will seek a steadily propagating periodic wave train with velocity c, so u and v depend only on the variable $\xi=x-ct$, and so Eqs. (1) and (2), respectively, become

$$u''(\xi)+cu'(\xi)=i(u,v), \quad (3)$$

$$v'(\xi)-\delta v=-\delta[\zeta u+v_r] \quad (\delta\equiv\varepsilon/c). \quad (4)$$

On one period from $\xi=-L_h$ to $\xi=L_f$ (see Fig. 1) the piecewise equation (3) has a solution of the form

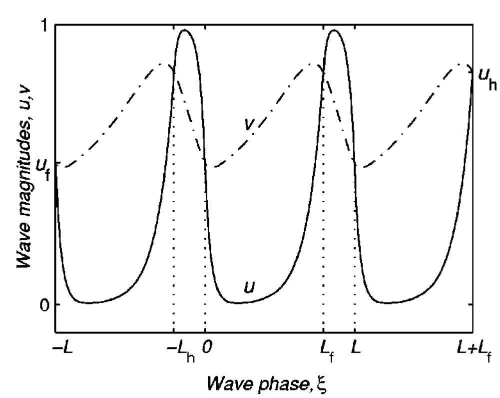

FIG. 1. Snapshot of a periodic traveling wave train $u=u(\xi)$ and $v=v(\xi)$ for $c=0.5$ at $\lambda=0.2$, $\zeta=1.25$, $\varepsilon=0.03$, $v_r=0.3$. The values of L_f, L_h, and $L=L_f+L_h$ and $u_f\equiv u(0)=v_f\equiv v(0)$, and $u_h\equiv u(-L_h)=v_h\equiv v(-L_h)$ are marked.

$$u=\begin{cases}1-Me^{k_2\xi}-Ne^{k_2'(\xi+L_h)}, & -L_h\le\xi\le 0\\ Ae^{k_1\xi}+Be^{k_1'(\xi-L_f)}, & 0\le\xi\le L_f,\end{cases}\tag{5}$$

where the lengths L_h, L_f are introduced in Fig. 1 and $k_1<0$ and $k_1'>0$ are solutions of the characteristic equation $k^2+ck-\lambda=0$, while $k_2>0$ and $k_2'<0$ are the roots of the characteristic equation $k^2+ck-1=0$. The first line in Eq. (5) represents the wave's head (top), the second its front and back. Using Eq. (5) one can find $v(\xi)$ from Eq. (4) as

$$v=v_r+\begin{cases}\zeta+M'e^{k_2\xi}+N'e^{k_2'(\xi+L_h)}-Pe^{\delta\xi}, & -L_h\le\xi\le 0\\ -A'e^{k_1\xi}-B'e^{k_1'(\xi-L_f)}+Qe^{\delta\xi}, & 0\le\xi\le L_f,\end{cases}\tag{6}$$

where P,Q are integration constants and M',N',A',B' are expressed through M,N,A,B as follows: $M'=M\zeta\delta/(k_2-\delta)$, $N'=N\zeta\delta/(k_2'-\delta)$, $A'=A\zeta\delta/(k_1-\delta)$, $B'=B\zeta\delta/(k_1'-\delta)$. Given the propagation speed c, the entire solution $(u(\xi),v(\xi))$ incorporates eight unknown parameters, the six integration constants A,B,M,N,P,Q, and two lengths L_f and L_h. The functions u and v must satisfy six continuity and periodicity conditions $u(+0)=u(-0)$, $u'(+0)=u'(-0)$ and $v(+0)=v(-0)$, and $u(-L_h)=u(L_f)$, $u'(-L_h)=u'(L_f)$ and $v(-L_h)=v(L_f)$. Two more equations are the excitation and deexcitation conditions $u(0)=v(0)$ and $u(-L_h)=v(-L_h)$, respectively, which immediately follow from our definition of $i(u,v)$ in Eq. (1). These eight equations determine two dispersionlike dependences $L_f=L_f(c)$ and $L_h=L_h(c)$. Since the spatial period L is the wavelength, these dependences determine the dispersion relation for the medium

$$L=L_f(c)+L_h(c).\tag{7}$$

In fact, the dependence of the head width $L_h=L_h(c)$ represented via the time period L/c describes restitution properties of the medium, which can be more conventionally represented by plotting L_h versus L_f (using c as a parameter). Both the dispersion and restitution curves are *protocol independent* and thus characteristic properties of the medium.

The dispersion and restitution curves can be found analytically with the exponentially small errors (ESE) when ε is sufficiently small, $\varepsilon\ll\lambda\le 1$ (the requirement $\lambda\le 1$ is nonrestrictive). In the ESE approximation, the coefficients M,N,A,B in Eq. (5) are simply related to the transition amplitudes u_f and u_h (Fig. 1) as $A=u_f$, $B=u_h$, $M=1-u_f$, $N=1-u_h$. Other constants are also readily found and we obtain

$$L_h(c)=\frac{1}{\delta}\ln\frac{\zeta[R_f(c)-\delta S_f(c)]+v_r-u_f(c)}{\zeta[R_h(c)-\delta S_h(c)]+v_r-u_h(c)},\tag{8}$$

$$L_f(c)=\frac{1}{\delta}\ln\frac{u_h(c)-v_r+\zeta S_h(c)\delta}{u_f(c)-v_r+\zeta S_f(c)\delta},\tag{9}$$

where $\delta=\varepsilon/c$, the transitional amplitudes u_f and u_h (see Fig. 1) are simple explicit functions of c given in Ref. [8], $S_f=u_f(c)/[k_1(c)-\delta]$, $S_h=u_h(c)/[k_1'(c)-\delta]$ and

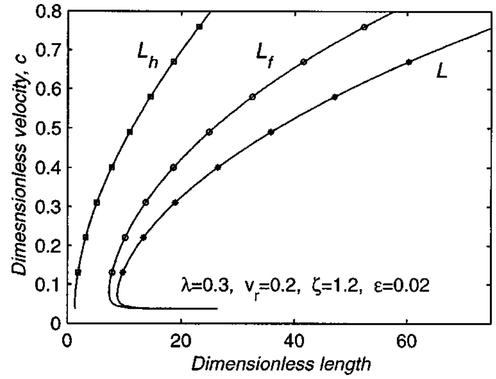

FIG. 2. Theoretical and numerical dispersion and restitution curves, $L=L(c)$, $L_h=L_h(c)$, and $L_f=L_f(c)$.

$$R_f=1+\delta\left(\frac{1-u_f(c)}{k_2(c)-\delta}+\frac{u_f(c)}{k_1(c)-\delta}\right),\tag{10}$$

$$R_h=1+\delta\left(\frac{1-u_h(c)}{k_2'(c)-\delta}+\frac{u_h(c)}{k_1'(c)-\delta}\right).\tag{11}$$

One can readily check that errors in Eqs. (8) and (9) are indeed on the order of $\exp(-aL_f)$ and $\exp(-bL_h)$, where a and b are positive constants of the order of unity. Because the widths L_h and L_f are of the order of $1/\varepsilon$, the errors are $o(\varepsilon^n)$ for any $n>0$ and the above equations are accurate within any power of ε. The ESE approximation is thus exact in terms of the parameter ε and is the zero approximation in terms of powers of the parameter $\varepsilon_1\equiv\exp(-1/\varepsilon)=o(\varepsilon^n)$. It is important that the ESE approximation holds even for very degenerate waves with near minimum velocity.

The expressions (8)–(11) are explicit and analytical and cannot be obtained in any other existing model. Solutions of different models with a piecewise linear source look similar, but the joining equations (smoothness, etc.) are extremely complex in other models and have to be solved numerically, which renders such models actually numerical. For example, in the model introduced by McKean [9] and studied in detail by Rinzel and Keller [10] the coefficients analogous to ours are found by (numerically) solving a set of very sophisticated transcendental equations involving powers to the ratios of roots of a cubic equation, which makes analytical analysis virtually impossible.

Figure 2 depicts the dispersion and restitution properties of the medium and illustrates the accuracy of Eqs. (8) and (9). Our explicit equations (8)–(11) also indicate that there can exist additional (topologically disconnected) low velocity branches of such curves, which is an unexpected feature. For the parameter values used for the plots in Fig. 2 this corresponds to the velocities well below $c<0.037$ (not shown). Despite multiple attempts neither these nor any other points of the dispersion curve in the lower left corner of the graph could be reached in our numerical simulations. Solving numerically their linear stability equations Rinzel and Keller (Ref. [10]) found that the minimum speed never reaches the merging point of the upper and lower branches of the dispersion curve, the stably propagating waves cease to exist at a higher speed: only a portion of the upper branch of the dispersion curve represents linearly stable solutions. The marginal (critical) velocity c_{cr} can in principle be found via

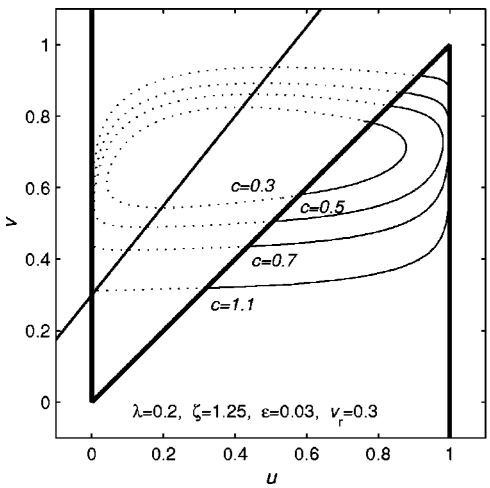

FIG. 3. Phase portraits of the periodic wave trains on the (u,v) plane for different c. The portions corresponding to heads of the u waves are shown by solid lines, dashed lines corresponding to the region where $u<v$. The N-shaped bold line is the nullcline $i(u,v)=0$, and the straight solid line $v=\zeta u+v_r$ is the nullcline for Eq. (2).

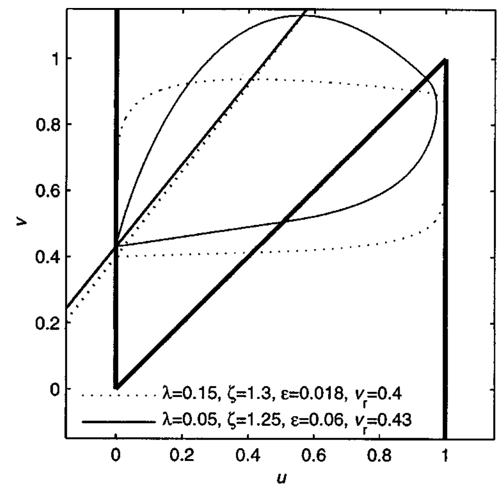

FIG. 4. Phase portraits of two solitary waves and the nullclines on the (u,v) plane (the corresponding wave configurations are shown in Fig. 1 of Ref. [8]).

the linear stability analysis, which is fairly difficult in the periodic case [10] particularly because the linearized problem for perturbations is not self-adjoint and the corresponding eigenvalues are complex.

The existence of explicit analytical solutions for our model allows us to suggest a simplified approach and formulate approximate stability conditions by extending those for a solitary pulse to the periodic case. Each single wave of the infinite train actually propagates in incompletely recovered medium with the slow control variable v always staying far away from its equilibrium value v_r. Our idea is to approximate a single pulse of the infinite wave train in such an incompletely recovered nonuniform medium by a solitary pulse in a uniform medium with appropriately redefined threshold value. Then the known existence (stability) conditions for the solitary pulse will produce the existence conditions for the periodic wave train. It appears intuitively evident that the periodic solutions do exist on the upper branch at large wavelengths. We therefore only need to find the marginal case corresponding to the minimum velocity of stable propagation. With this aim in view let us compare phase portraits of a periodic wave train and a solitary pulse.

Figure 3 displays phase portraits on the (u,v) plane for periodic waves (5) and (6) at four different points of the dispersion curve $L=L(c)$. The curve corresponding to $c=1.1$ describes a wave with very long recovery (interpulse) time and is very close to a solitary pulse. Such curves start off the nullcline $u=0$ at $v\approx v_r$. Notice that the phase trajectories for lower propagation velocities never follow the nullcline $i(u,v)=0$ and therefore cannot be well approximated using singular perturbation theory. Figure 4 displays phase portraits of two solitary waves. The lower portions of the loops situated to the left of the bold diagonal are straight lines and correspond to the foot region. Since in the solitary pulse case [8] $v(\xi)=v_r+[\zeta\delta/(\delta-k_1)]u_f\exp(k_1\xi)$ and $u(\xi)=u_f\exp(k_1\xi)$ the equation of such a straight line is $v=v_r+u\zeta\delta/(\delta-k_1)$ with the intercept being v_r. The maximum value of the threshold v_r for which a solitary pulse solution still exists determines the critical pulse velocity c_{cr} [$\max v_r^{sp}(c)\equiv v_r^{sp}(c_{cr})$, $c_{cr}=c_{cr}(\varepsilon,\zeta,\lambda)$, where $v_r^{sp}(c)$ is given by Eq. (17) and shown in Fig. 2 in Ref. [8]]. In the periodic case the u wave in the region $\xi>0$ near $\xi=0$ can be approximated by the same expression and v waves can be written as $v(\xi)\approx Q+v_r+[\zeta\delta/(\delta-k_1)]u_f\exp(k_1\xi)$, because the second term in the second line in Eq. (6) is exponentially small while the last term changes slowly and can be "fro-

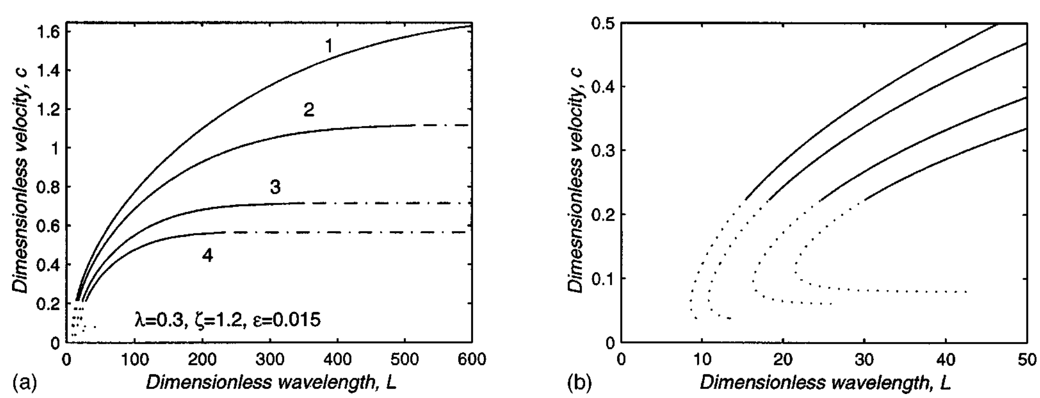

FIG. 5. Dispersion curves for different values of the threshold v_r and fixed values of other parameters. Panel (b) is a blow up of the lower left corner region in panel (a). The quickly decaying, (subcritical) solutions are shown by dotted lines. Dash-dotted lines in panel (a) indicate the solitary pulse limit. Curves 1 through 4 correspond to $v_r=0.2$, 0.3, 0.4, and 0.44, respectively.

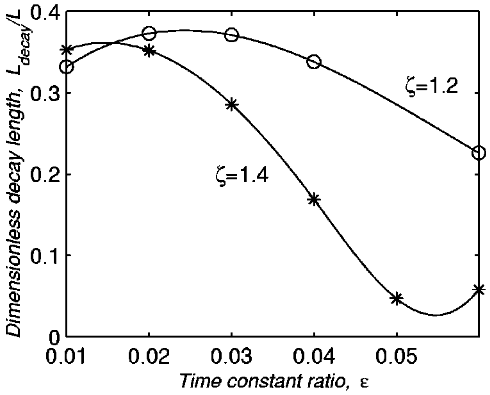

FIG. 6. Decay length L_{decay} as a function of ε for two values of the u-v coupling constant ζ. The value of L_{decay} is the distance that the wave passes by the instant when the points of intersection between $u(\xi)$ and $v(\xi)$ merge and the excited region in which $u(\xi)>v(\xi)$ vanishes.

zen'' at its value Q corresponding to $\xi=0$. This approximation is good because the ''recovery'' equation is of the first order and hence only the v value at $\xi=0$ matters while $v'(0)$ is irrelevant. In the ESE approximation the constant Q can be expressed as $Q=v_r^{sp}(c)-v_r$, which yields $v(\xi)=v_r^{sp}(c)+[\zeta\delta/(\delta-k_1)]u_f\exp(k_1\xi)$, and on the (u,v) phase plane describes the straight line,

$$v=v_r^{sp}(c)+u\zeta\delta/(\delta-k_1), \tag{12}$$

with intercept $v_r^{sp}(c)$. This straight line is the extrapolation of the solid lines in Fig. 3 into the region left of the diagonal using a solitary pulse solution with the same initial conditions at $\xi=0$. As we showed in Ref. [8] the function $v_r^{sp}(c)$ has a maximum at a critical velocity c_{cr} $[\max\{v_r^{sp}(c)\}\equiv v_r^{sp}(c_{cr})]$ and therefore determines the marginally stable propagation velocity $c_{cr}=c_{cr}(\varepsilon,\zeta,\lambda)$ for the periodic wave train in the medium under consideration. Our result appears to be quite intuitive and general since propagation over incompletely recovered medium is always slower [the upper branch of the dispersion curve $c=c(L)$ is monotonically growing]. Thus the periodic wave train cannot exist in the medium in which even a solitary pulse cannot propagate. It is worth emphasizing again that Eq. (12) and the entire conclusion could be reached only due to the unique opportunity presented by the explicit expressions for all the constants in Eqs. (5) and (6).

Figure 5 displays a family of dispersion curves at fixed $\lambda,\varepsilon,\zeta$ and four different values of v_r. The solid and dotted lines represent actual calculations (using the above theory) for the velocities above c_{cr}. The (horizontal) dash-dotted line in panel (a) corresponds to the solitary pulse limit. The dotted-line portions of the dispersion curves correspond to unobservable wave trains with velocities below critical. In order to test our conclusion that the periodic waves corresponding to the portions of the dispersion curve below c_{cr} do not propagate, we have performed a series of numerical experiments to measure the decay length L_{decay} in the subcritical velocity region. We computed periodic solutions of our RD system (1) and (2) in an excitable ring with circumference L with the initial conditions given by our analytical expressions (5) and (6) for $c=c_{cr}$. This wave configuration evolves and propagates along the ring in a nonstationary manner: the excited region in which u is suprathreshold ($u>v$) becomes smaller and smaller and finally disappears at the instant when the wave has passed a distance L_{decay}. Figure 6 displays L_{decay}/L versus ε for two values of ζ. One can see that the excitation corresponding to $c=c_{cr}$ indeed disappears very quickly, before it passes 2/5 of the wavelength. All our numerical experiments using the above model support the conclusion that the critical velocity c_{cr} (the solitary pulse marginal stability hypersurface) indeed accurately defines the end point of the theoretical dispersion curve. It reveals that the conditions for an excitation to decay are practically identical for both a solitary pulse and a periodic wave-train solution (Fig. 5). In other words, the minimal solitary pulse velocity c_{cr} determines an absolute lower boundary for the velocity of a periodic excitation wave with any period, finite or infinite.

In summary, the steadily propagating wave train in our model can be explicitly written on the entire period in a broad parameter range. The integration constants can be found from a set of transcendental equations, which can be compactly solved within any power of the smallness parameter ε. The method allows us to define the restitution curve in a protocol independent way. We have found a simple ''rule of thumb'' for the critical propagation velocity c_{cr} for periodic excitation waves, which determines the left boundary of the existence-stability region on the dispersion and restitution curves. This is important since all nontrivial nonstationary scenarios must evolve exclusively near this boundary.

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