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Head-on Collisions of Waves in an Excitable FitzHugh–Nagumo System: a Transition from Wave Annihilation to Classical Wave Behavior

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For the particular case of an excitable FitzHugh–Nagumo system with diffusion, we investigate the transition from annihilation to crossing of the waves in the head-on collision. The analysis exploits the similarity between the local and the global phase portraits of the system. We find that the transition has features typical of the nucleation theory of first-order phase transitions, and may be understood through purely geometrical arguments. In the case of periodic boundary conditions, the transition is an infinite-dimensional analog of the creation and the vanishing of limit cycles via a homoclinic Andronov bifurcation. Both before and after the transition, the behavior of a single cell continues to be typical for excitable systems: a stable equilibrium state, and a threshold above which an excitation pulse can be induced. The generality and qualitative character of our argument shows that the phenomenon described can be observed in excitable systems well beyond the particular case presented here.

1. Introduction

When nonlinear waves in the nerve or muscle fibers or in the heart collide with each other, they mutually annihilate (Tasaki, 1949; Wiener & Rosenblueth, 1946; Krinsky, 1984; Krinsky *et al*., 1991; Keener & Sneyd, 1998). There are, however, cases where the experiment and theory have shown that the inelasticity of the collisions is not that drastic. Both in reaction–diffusion systems (Rotermund *et al*., 1991) and in hydrodynamics (Santiago *et al*., 1997), there is now evidence of a variable degree of inelasticity in collisions as well as in reflections. For example, when two such non-linear dissipative waves collide obliquely in bi-dimensional medium, one or two waves may re-emerge with trajectories altered or phase-shifted, relative to the pre-collision paths (Santiago *et al*., 1997). In head-on collisions, equivalent to one-dimensional collisions, evidence also exists that the waves may cross each other (Legrand, 1987; Meinhardt, 1995; Aslandi & Mornev, 1996, 1997, 1999; Mornev *et al*., 1996; Santiago *et al*., 1997; Argentina *et al*., 1997).

These kinematic features are similar to characteristic properties of solitons in conservative media (Zabusky & Kruskal, 1965). In the present paper, we consider the collision properties of nonlinear waves in an excitable medium of FitzHugh–Nagumo type, which is paradigmatic to account for quite a variety of biological, biochemical and neurobiological phenomena. In particular, we discuss one-dimensional collisions and show under which circumstances when waves or pulses collide, they may cross each other and hence do not annihilate. Note that the space–time plot of a head-on collision mimics an oblique collision in real space or a reflection of a wave with a wall.

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In Section 2, we pose the model problem to be studied and we show the properties of its underlying dynamical system and the influence of diffusion. Section 3 is devoted to a geometric description of the phenomena related to non-annihilating head-on collisions. Finally in Section 4, we summarize the essence of our results and argue about its universality.

2. Collision of Excitable Waves in the FHN Model

We use the one-dimensional FitzHugh–Nagumo model (FHN) with non-zero diffusion coefficients for both species (FitzHugh, 1961; Nagumo *et al.*, 1962):

$$u_t = -v - u(u-1)(u-a) + u_{xx}, \qquad v_t = \varepsilon(u - bv) + \delta v_{xx}. \tag{1}$$

The variables u and v represent the activator and inhibitor, respectively. The parameter ε measures the ratio of the time-scales associated to each of the variables, and is usually a smallness parameter.

The excitable behavior is controlled by the parameter a, and the ratio of the diffusivities is given by δ. For instance, for the Belousov–Zhabotinsky chemical reaction (Zhabotinskyii, 1974), $\delta \sim 1$ whereas for problems with biological membranes, δ is practically vanishing.

3. Diffusionless Problem and its Underlying Dynamical System

For the homogeneous system obtained by neglecting diffusion in eqn (1), we have

$$u_t = -v - u(u-1)(u-a), \qquad v_t = \varepsilon(u - bv). \tag{2}$$

The origin is steady solution, or fixed point, that becomes unstable (Andronov–Hopf bifurcation) when $a + \varepsilon b = 0$.

When $b > 4/(a-1)^2$, the saddle-node bifurcation yields two new fixed points: $p = (u_+, u_+/b)$, $q = (u_-; u_-/b)$ where $u_\pm = 1 + a/2 \pm ((1-a)^2 - 4/b)^{1/2}$.

Following (Argentina *et al.*, 1997), we will investigate the phase portrait of system 2 when

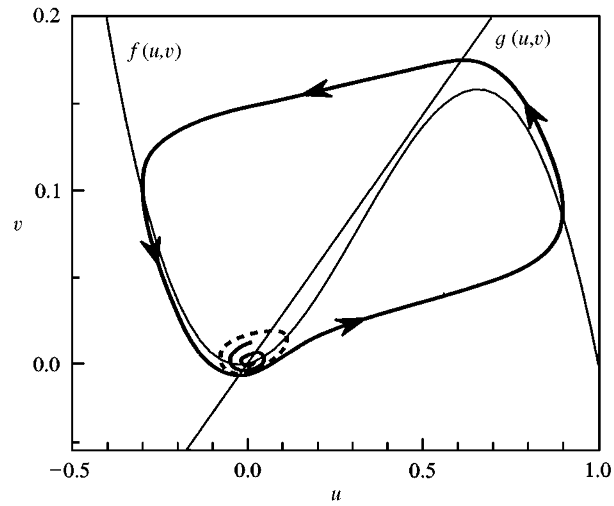

FIG. 1. Phase portrait of FitzHugh–Nagumo model (2). There is bistability between the limit cycle ▬, and stable fixed point whose basin of attraction is plotted in - - -. The nullclines $f(u,v) = -v - u(u-1)(u-a)$ and $g(u,v) = u - bv$ are shown in —. Parameters are: $\varepsilon = 0.015$, $b = 3.5$ and $a - 0.045$.

a limit cycle and a stable fixed point coexist (Fig. 1).

Let us assume that the origin is the only stable fixed point. When we vary the parameter a, an Andronov–Hopf bifurcation occurs (Andronov *et al.*, 1971).

The birth of the limit cycle may be either super- or sub-critical. For the latter case, this provides a range of parameter values leading to the sought bistability.

4. The Role of Diffusion

We numerically calculated solutions of the full eqn (1) with the Runge–Kutta method, approximating spatial derivatives by centered finite differences. Six hundred points were used for spatial discretization. Typical time step was 0.1, and size of the spatial domain was 300.

For the usual parameter regime where excitability is expected (i.e. when the homogeneous dynamical system possesses at least one stable attractor, the trivial fixed point) the parameter a must be small and positive to insure propagation of pulses (Rinzel & Keller, 1973; Zykov, 1987). As bistability requires negative values of a that may prevent the existence of solitary waves, we first verify that excitable waves do propagate in this bistable medium. If $\delta = 0$, localized perturbations create localized oscillatory solutions (and not a solitary wave) spreading over the whole domain. If $\delta \neq 0$, competition between the diffusion, and the amplification due to the local dynamics of eqn (2) towards the stable limit cycle, enables propagation of pulses for a finite range of values of δ. This is the essence of an argument developed long ago by Taylor and Burgers to justify the stable propagation of nonlinear dissipative localized disturbances like shocks (Whitham, 1974). On the one hand, for $\delta \leqslant 0.85$, the pulses are metastable and more than two waves may emerge after a head-on collision. After many collisions, a train of waves spreading over the spatial domain becomes unstable and generates synchronized oscillations in space. On the other hand, for δ sufficiently large $\delta \geqslant 1.30$, diffusion tends to suppress the waves.

To study numerically the collisions of excitable waves, we take a large enough spatial domain such that we could assume it unbounded.

We first investigate a localized perturbation of the trivial state placed in the center of the domain. Depending on the size and the amplitude of the perturbation, the excitation may disappear or be amplified to create a pair of excitable pulses.

If the perturbation is big enough, after a transient regime, two waves emerge and propagate towards the boundaries. There is a barrier that must be overcome in order to produce localized propagating solutions. This is a nucleation manifold (or ignition manifold) that acts as a separatrix. From the dynamical systems point of view, such barrier is just a manifold that divides the functional phase portrait into two regions.

For fixed values of ε, b, and δ, and for various values of a, the predicted outcome of the head-on collision of waves or pulses is the following. If $|a|$ is small enough, the two waves disappear after a head-on collision as in most excitable media.

If $|a|$ becomes big enough, the two waves cross each other. If one approaches the critical value of a when the transition occurs, the two waves coalesce during the collision into a nearly stationary solution.

Then, depending on the value of a, after a finite time, the two waves may be re-emitted. In the functional phase portrait, this suggests that the flow passes very near a fixed point.

5. Steady States, Nucleation Solution and the Geometrical Picture

Stationary solutions of eqn (1) obey the following equations:

$$\begin{aligned} u_{xx} &= v + u(u-a)(a-1), \\ v_{xx} &= \frac{\varepsilon}{\delta}(bv-u). \end{aligned} \tag{3}$$

Let us call $\Gamma(x)$ a solution that at infinity tends towards the motionless or the trivial state.

Using a variant of a shooting method, $\Gamma(x)$ is computed (Press *et al.*, 1992). This solution is compared in Fig. 2 with the profile of the variable u (the collision solution) during the collision process followed by a direct simulation of eqn (1).

The two solutions are nearly the same, thus the collision solution is a fixed point in the functional phase portrait.

Let us investigate its stability.

The computation of the spectrum has been performed using a finite-difference scheme to approximate the spatial derivatives.

The spectrum should have a zero eigenvalue that corresponds to the eigenfunction $(\Gamma_u x, \Gamma_v x)$, since the problem is invariant under translation.

Note that this eigenvalue shows the existence of a continuous family of nucleation solutions parametrized by its position in the domain. This eigenvalue found numerically is 3×10^{-3} rather than zero, which provides an estimate of the accuracy of the numerical scheme.

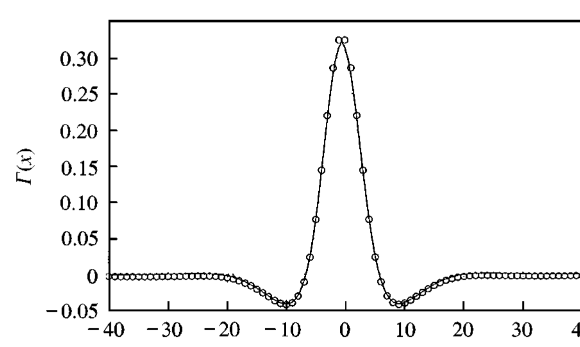

FIG. 2. Comparison between the stationary solution $\Gamma(x)$ computed with a variant of a shooting method (—) and the quasi-stationary solution (○) obtained while two pulses were colliding.

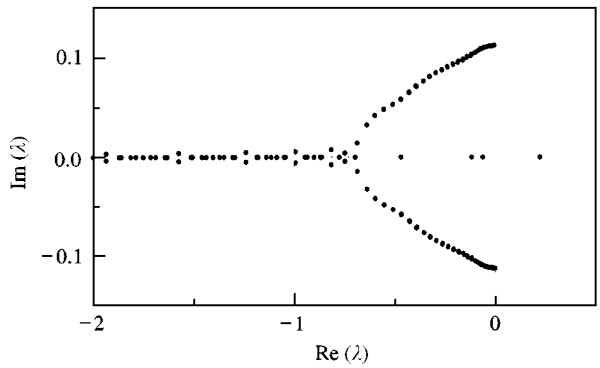

FIG. 3. Linear stability analysis of the stationary solution that connects the rest state. It is seen that this solution is unstable but possesses just one eigenvalue that is positive. The complex eigenvalues near the imaginary axis belongs to the continuous spectrum and plays no role for the stability here.

The spectrum is presented in Fig. 3. It appears that the stationary solution is unstable and possesses just one eigenvalue with positive real part.

Thus, the codimension-one center stable manifold of the stationary solution acts as a separatrix, and $\Gamma(x)$ can be considered as a nucleation solution, i.e. the critical drop permitting the creation of pulses.

An analytical computation shows that the complex eigenvalues near the imaginary axis belong to the continuous spectrum whose eigenvectors oscillate periodically at infinity with a low wave number.

These eigenvalues play no role for this transition if one is considering localized perturbations, hence the negative eigenvalue, whose eigenvector is localized, and closest to the imaginary axis ($\lambda_- \simeq -0.063$) governs the stable dynamics. The phase portrait is therefore split into two regions corresponding to two different evolutions for a given initial condition of system 1.

If the homogeneous trivial state is perturbed, depending on the position of the flow in the phase portrait, two pulses may emerge or not. When pulses are created, the corresponding flow is nearly defined by the unstable manifold $W_u(x)$ of the nucleation solution, and pulses propagate towards the boundaries.

Take now two pulses propagating in our infinite domain and colliding. There is crossing and hence non-annihilation if the collision solution is able to re-emit the pulses. We do not consider the case when only one pulse is re-emitted, following a collision (Santiago *et al.*, 1997).

Geometrically, the transition appears associated with the relative position of the one-dimensional collision manifold defined by the two colliding waves, relative to the stable manifold of the nucleation solution. The threshold of the transition is associated with the fusion of these two manifolds.

When the spatial domain is periodic, and two pulses initiated in the center of the domain arrive at the boundaries, then they collide.

Once again, depending on the position of the collision solution in the functional phase portrait, the two pulses may be re-emitted after the collision. This solution is a perturbation of $\Gamma(x')$, where $x' = x - L/2$ and L is the size of the domain. Let us denote by $W_u(x)$ the unstable manifold of the nucleation solution $\Gamma(x)$. The transition is related to the connection of the unstable manifold $W_u(x)$ with the center stable manifold $W_s(x')$. The evolution depends on the location of $W_u(x)$ on either of the two sides of the separatrix provided by the center stable manifold $W_s(x')$ of $\Gamma(x')$. Accordingly,

- If the unstable manifold $W_u(x)$ goes between the fixed point O and the center stable manifold $W_s(x')$ as shown in Fig. 4(a), the system decays to the stable stationary state.

  This is the standard phase portrait for dynamics of solitary waves in excitable media. The product of a collision is not big enough to recreate the two pulses.
- If $W_u(x)$ becomes $W_s(x')$ as shown in Fig. 4(b), the motion is a heteroclinic orbit connecting the two nucleation solutions $\Gamma(x)$ and $\Gamma(x')$. In this case, the product of a collision corresponds exactly to the nucleation solution.
- If $W_u(x)$ goes behind $W_s(x')$ as shown in Fig. 4(c), the motion becomes periodic like the resulting flow of an Andronov homoclinic bifurcations (Andronov *et al.*, 1971). This solution is highly anharmonic, since the flow passes close to the two saddle points $\Gamma(x)$ and $\Gamma(x')$. Consequently, the collision can last a long time [as seen in Fig. 4(b)]. Here, the product of a collision is big enough to re-excite the system and hence the re-emission of the two waves.

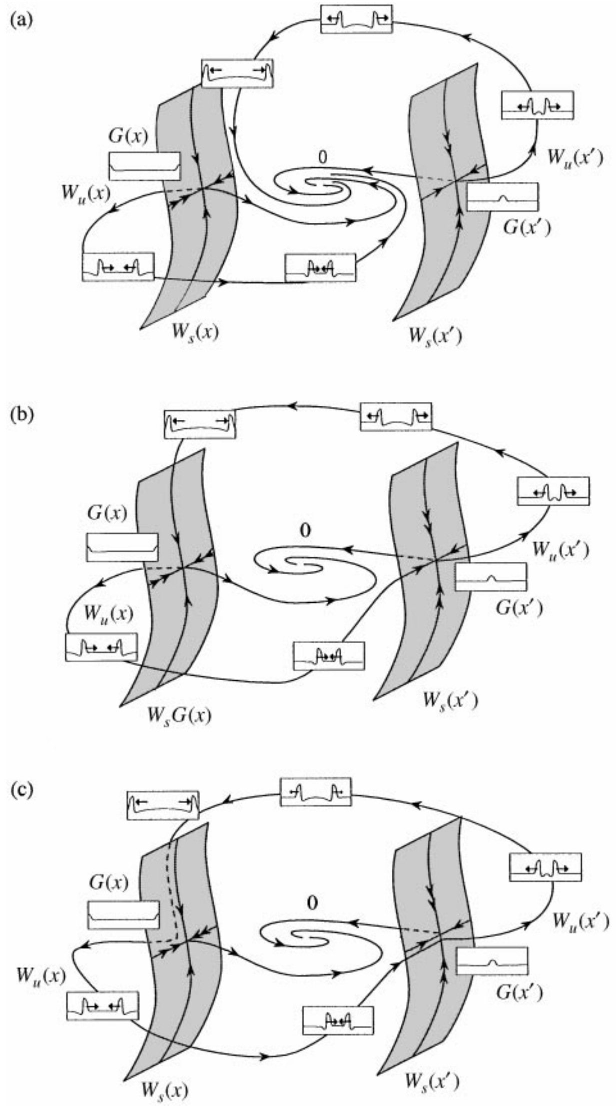

FIG. 4. Qualitative phase portrait of the partial differential equation (1). The right column shows colliding pulses in the middle of the domain, so all the functions depend on $x' = x - L/2$. The left column shows the same event at the boundaries. (a) When the unstable manifold $W_u(x)$ of the nucleation solution is not able to enter tangently to the center stable one $W_s(x')$, the pulses do not cross each other. Such phase portrait is the classic phase portrait for excitable systems. (b) At the bifurcation point, the unstable manifold of the nucleation solution $W_u(x)$ goes into the center stable one $W_s(x')$, and a heteroclinic loop appears. (c) Once the Andronov homoclinic bifurcation has been obtained, the pulses collide periodically in the spatial domain, and the attractor is a stable limit cycle. The gray surfaces are the nucleation manifolds. The point 0 is the rest state.

6. Conclusion and Outlook

The main result of this work can be formulated in a clearly intuitive way. It is associated to a "nucleation drop" well known in first-order phase transitions. The result of the collision depends upon whether the nucleation drop is created. If the nucleation drop is not created, then the waves annihilate themselves after the collision. If the nucleation drop is created, two new waves are generated. They propagate away from the collision place, and the final result is that the waves crossed each other and did not mutually annihilate. The geometrical arguments show that the transition from wave preservation to wave annihilation is associated to a Andronov homoclinic bifurcation. The main feature of this transition is that the time of collision of excitable waves diverges logarithmically when approaching the threshold. This can be easily checked in experiments. Another important feature of Andronov homoclinic bifurcation is that it needs just one parameter. This means that the transition described here is robust enough to be observed in biological systems.

A more qualitative formulation is presented below. The bifurcation is characterized by a logarithmic divergence of the period near the threshold. Since in a homoclinic bifurcation, for most of the time T, the system is near the saddle point. A linear computation gives the following result: $T \simeq -(1/\lambda_+)$ In $|\mu|$, where μ is the controlling parameter measuring the distance (here $\mu = a - a^*$) and λ_+ is the positive eigenvalue of the saddle point of the partial differential equation.

This is confirmed numerically as illustrated in Fig. 5. Moreover, fitting the curve $T = f(a)$ gives the unstable eigenvalue $\lambda_+ \simeq 0.217 \pm 0.005$, while the direct computation of the eigenvalues of the stationary solution presented in Fig. 3 yields $\lambda_+ \simeq 0.221 \pm 0.003$. This nice agreement found supports the validity of the geometrical approach describing the transition in terms of a global bifurcation.

The transition occurs near the onset of the limit cycle for the local dynamics. This oscillating behavior seems to be responsible for the non-annihilation following a head-on collision, since it gives the waves a kind of inertia. When two pulses collide, the limit cycle helps to reconstruct the nucleation solution.

As a general conclusion, we can say that transition from waves annihilation, typical for biological systems, to classical wave behavior can be understood in terms of the Andronov

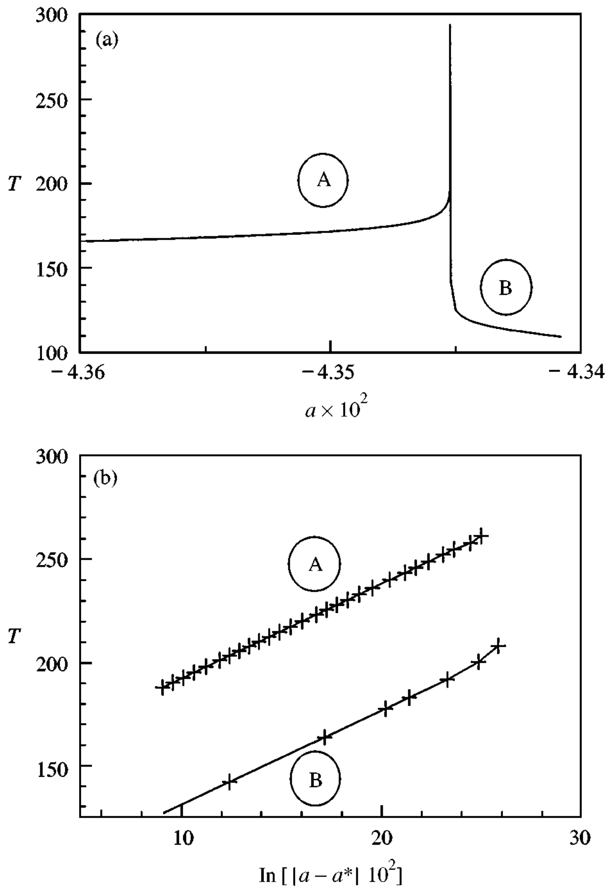

FIG. 5. Numerical proof of the Andronov bifurcation: estimation of the time T the flow uses near the nucleation solution vs. the parameter a. The part of the curve named A (resp. B) corresponds to the estimated time of the period when waves are crossing (resp. not crossing) (a) T vs. a. It is seen that a divergence occurs for $a^* \simeq -4.3452 \times 10^{-2}$. (b) A semilogarithmic plot T vs. $-\ln|a - a^*|$ shows that the type of divergence is logarithmic. Other parameters are $b = 3.5$, $\varepsilon = 0.015$ and $\delta.1.25$.

homoclinic bifurcation (Andronov *et al*., 1971). It is of codimension one, the transition is robust and has been already observed in some physical, chemical, and biological models (Argentina, 1999).

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