ISSN 1063-7761, Journal of Experimental and Theoretical Physics, 2008, Vol. 107, No. 2, pp. 344–349. © Pleiades Publishing, Inc., 2008.
Original Russian Text © E.P. Zemskov, A.Yu. Loskutov, 2008, published in Zhurnal Éksperimental'noĭ i Teoreticheskoĭ Fiziki, 2008, Vol. 134, No. 2, pp. 406–412.

STATISTICAL, NONLINEAR, AND SOFT MATTER PHYSICS

Oscillatory Traveling Waves in Excitable Media

E. P. Zemskov[a] and A. Yu. Loskutov[b]
[a] Dorodnitsyn Computing Center, Russian Academy of Sciences, Moscow, 119333 Russia
[b] Moscow State University, Moscow, 119992 Russia
e-mail: e-zemskov@yandex.ru
e-mail: loskutov@chaos.phys.msu.ru
Received November 27, 2007

Abstract—A new type of waves in an excitable medium, characterized by oscillatory profile, is described. The excitable medium is modeled by a two-component activator–inhibitor system. Reaction–diffusion systems with diagonal and cross diffusion are examined. As an example, a front (kink) represented by a heteroclinic orbit in the phase space is considered. The wave shape and velocity are analyzed with the use of exact analytical solutions for wave profiles.

PACS numbers: 82.40.Bj, 82.40.Ck
DOI: 10.1134/S1063776108080189

1. INTRODUCTION

Distributed active (excitable) media [1], unlike passive media, can transmit signals over large distances without attenuation or distortion. Wave formation and propagation in such media are described by reaction–diffusion equations where kinetics and transport are represented by nonlinear reaction terms and diffusion, respectively [1–3]. The simplest one-dimensional reaction–diffusion equation was originally analyzed in [4] as applied to biological problems.

In this paper, we analyze one-dimensional two-component activator–inhibitor systems of the form

$$\begin{aligned}\frac{\partial u}{\partial t} &= f(u, v) + D_u\frac{\partial^2 u}{\partial x^2} + h_v\frac{\partial}{\partial x}\left[Q_v(u, v)\frac{\partial v}{\partial x}\right],\\ \frac{\partial v}{\partial t} &= g(u, v) + D_v\frac{\partial^2 v}{\partial x^2} + h_u\frac{\partial}{\partial x}\left[Q_u(u, v)\frac{\partial u}{\partial x}\right],\end{aligned} \quad (1)$$

where $f(u, v)$ and $g(u, v)$ are reaction terms and D_u and D_v are diffusion coefficients. When $h_u = h_v = 0$, the model reduces to a reaction–diffusion system with self-diffusion. When $h_{u,v} \neq 0$, we have a cross-diffusion system. The present analysis is restricted to systems with linear cross diffusion ($Q_{u,v}(u, v) = \text{const}$).

Waves of various kinds can be observed in reaction–diffusion systems: stationary spatial patterns, spatiotemporal chaos, etc. In this paper, we describe one-dimensional traveling waves with oscillatory profiles. The one-component equation

$$\frac{\partial u}{\partial t} = f(u) + D_u\frac{\partial^2 u}{\partial x^2}$$

has oscillatory solutions if at least one of its singular points is a focus. In this case, a nonmonotonic self-similar solution is represented by an orbit emanating from the focus. It may describe a rightward- or leftward-propagating wave, and the oscillatory profile may be localized near its leading or trailing front, accordingly [5].

In this paper, we use the FitzHugh–Nagumo model of an excitable medium [6] in a form amenable to exact analytical treatment [7] to show that oscillatory traveling waves can develop in a two-component system, with front corresponding to an orbit joining two saddle points. In the model considered here, wave solutions with oscillatory profiles describe traveling waves (i.e., waves described by functions of a single variable $\xi = x - ct$, where c is wave velocity). Since the oscillatory profile is stationary in the frame moving with the wave, profile oscillation can be treated as a particular case of spatiotemporal oscillation. Spatiotemporal oscillatory solutions of general form were obtained numerically in [14].

Traveling waves with nonoscillatory profiles have been known and studied for a long time. For the piecewise linear FitzHugh–Nagumo model considered here, nonoscillatory traveling-wave solutions were obtained in [7] and oscillatory ones were found in [12]. This paper continues this line of research and presents new results obtained for a piecewise linear reaction–diffusion system by taking into account cross diffusion.

2. TRAVELING WAVES WITH OSCILLATORY PROFILE

In this section, we consider one-dimensional two-component reaction–diffusion systems described by extended FitzHugh–Nagumo models with diffusing activator and inhibitor.

2.1. Model without Cross Diffusion

When both components diffuse, an extended FitzHugh–Nagumo model can be written as

$$\frac{\partial u}{\partial t} = u(u-a)(1-u) - v + D_u\Delta u,$$
$$\frac{\partial v}{\partial t} = \varepsilon(u - bv) + D_v\Delta v, \tag{2}$$

where a, b, and ε are constant parameters. The first two parameters determine the wave pattern: a front (heteroclinic orbit), a pulse (homoclinic orbit), or a periodic pulse train. The parameter ε relates the time scales of variation of the dependent variables.

Model (2) is extensively used as a basic one in modern chemical physics. Originally, it was proposed to describe excitation and propagation in nerve. As applied to chemical reaction dynamics, the variables u and v represent activator and inhibitor concentrations, respectively.

To obtain analytical solutions [8–10] to system (2), the reaction term in the activator equation is generally represented by the piecewise linear function

$$f(u, v) = -u - v + \theta(u - u_0),$$

where u_0 is a constant parameter and $\theta(u)$ is the Heaviside step function [11]. We consider this model in the one-dimensional case:

$$\frac{\partial u}{\partial t} = -\alpha u - v - 1 + 2\theta(u-u_0) + D_u\frac{\partial^2 u}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = \varepsilon(u - v) + D_v\frac{\partial^2 v}{\partial x^2}. \tag{3}$$

For $D_u = D_v = 1$, exact traveling-wave solutions to this system were found analytically in [12]. By changing to the variable $\xi = x - ct$, Eqs. (3) are rewritten as ordinary differential equations. Since the reaction term in the activator equation is a piecewise linear function, the solutions to the system are the sums of exponential terms matched at points of discontinuity. For certain combinations of model parameters, these terms are replaced by sines and cosines corresponding to oscillatory profiles. Details can be found in [12].

As an example of traveling wave with oscillatory profile, Fig. 1 shows the solution describing an activator front with negative velocity. Here, the profile oscillation decays with increasing coordinate while the wave shape itself remains invariant in time, in contrast to the waves with profiles oscillating in space and time obtained in [14].

We consider in some detail the equation for the front velocity (in the case of $\alpha = 1$) obtained by reducing the number of equations used in the matching procedure. Using the expression for the excitation threshold,

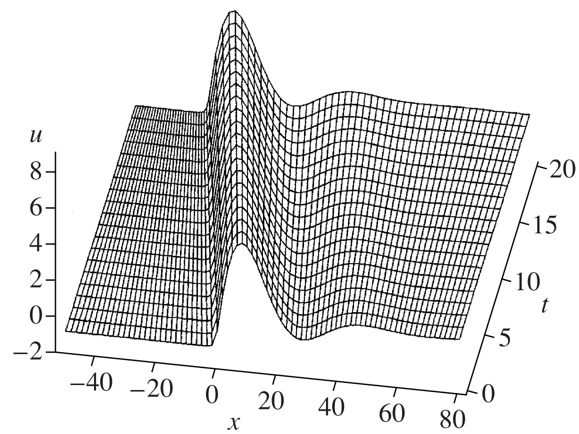

Fig. 1. Diagonal diffusion. Space-time diagram of evolution of the activator front for $\varepsilon = 0.05$, $\alpha = 0.1$, and $u_0 = 0$.

$$u_0 = \frac{c}{4}\frac{1}{1-\gamma^2/\varepsilon}\frac{1}{\sigma\rho}\left[\sigma - \frac{\gamma^2}{\varepsilon}\rho - \frac{\gamma}{\varepsilon}(\sigma - \rho)\right], \tag{4}$$

where

$$\rho = \sqrt{c^2/4 + (\varepsilon+1)/2 + \sqrt{(\varepsilon-1)^2/4 - \varepsilon}},$$
$$\sigma = \sqrt{c^2/4 + (\varepsilon+1)/2 - \sqrt{(\varepsilon-1)^2/4 - \varepsilon}}, \tag{5}$$
$$\gamma = (\varepsilon-1)/2 + \sqrt{(\varepsilon-1)^2/4 - \varepsilon},$$

we find that there exists a stationary pattern in a symmetric system (when $u_0 = 0$).

The diagram relating the front velocity to the time-scale ratio ε exhibits a pitchfork bifurcation known as *nonequilibrium Ising–Bloch bifurcation* [13, 14]. The curves of front velocity versus excitation threshold in Fig. 2, predicted by (4) and (5), demonstrate that the nonequilibrium Ising–Bloch bifurcation is between one-to-one (Fig. 2c) and many-to-one (Fig. 2a) correspondence between c and u_0. In Fig. 2a, the upper and lower branches of the many-valued curve, which correspond to stable solutions (two Bloch fronts propagating in opposite directions), meet the middle branch, which corresponds to an unstable solution (Ising front), at certain critical values of the excitation threshold. The two fronts with positive velocities described in [15] correspond to the upper branch and part of the middle one in the diagrams shown here. A complete scenario of the nonequilibrium Ising–Bloch bifurcation was presented in [14] for a cubic FitzHugh–Nagumo model.

As the time-scale ratio ε increases, the curve of a many-valued function degenerates into the curve representing a one-valued one (Fig. 2c): the Bloch fronts disappear, and the Ising front becomes stable. The profiles of the Ising and Bloch fronts may oscillate or not, depending on the value of ε. Oscillatory profiles corre-

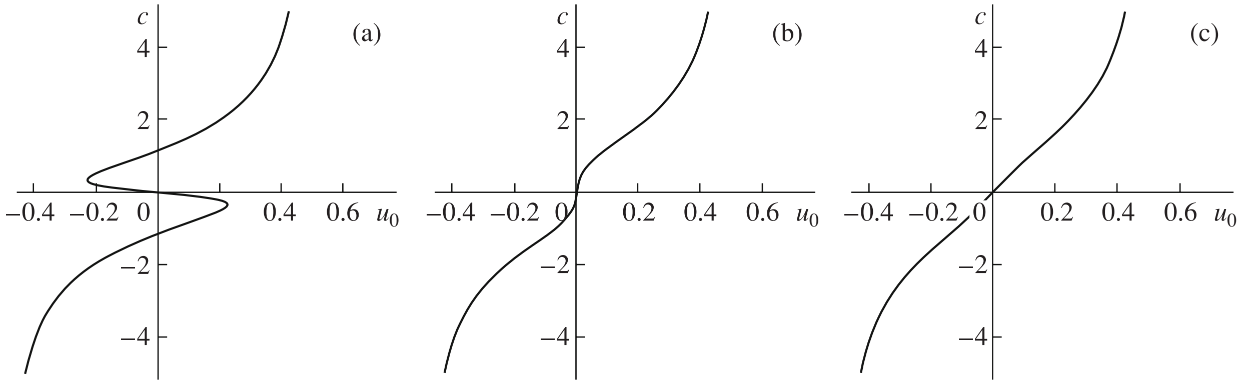

Fig. 2. Diagonal diffusion. Wave velocity vs. excitation threshold for ε = 0.01 (a), 0.3 (b), and 1.0 (c).

spond to $\varepsilon_{im}^- < \varepsilon < \varepsilon_{im}^+$, where $\varepsilon_{im}^{\pm} = 3 \pm 2\sqrt{2}$ [12]. These oscillations are pronounced in the profiles of traveling fronts and discernible in the tail of a traveling wave. In the present model, similar behavior is exhibited by pulse solutions. In the case of a periodic pulse train, an oscillatory profile corresponds to an anomalous dispersion relation between pulse velocity and period.

2.2. Model with Cross Diffusion

Taking into account cross diffusion, we can construct a variety of wave patterns. For example, given the reaction scheme

$$A + Y \longrightarrow X, \quad B + X \longrightarrow Y + D,$$
$$X + X \longrightarrow C, \quad Y + P \longrightarrow E$$

(see [2] for details), we have the distributed model

$$\frac{\partial x}{\partial t} = Ay - Bx - x^2 + \frac{\partial}{\partial r}\left(D_{xx}\frac{\partial x}{\partial r} + D_{xy}\frac{\partial y}{\partial r}\right),$$

$$\frac{\partial y}{\partial t} = Bx - Py + \frac{\partial}{\partial r}\left(D_{yy}\frac{\partial y}{\partial r} + D_{yx}\frac{\partial x}{\partial r}\right).$$

Models of this kind can be used to describe various wave patterns under minimal constraints on lumped kinetics, the key requirement being that influx from outside the system (here, supply of species A [2]) is sufficiently large.

Cross diffusion is used in ecology to describe predator–prey systems with positive taxis[1] of predators up the gradient of the prey concentration (pursuit) and negative taxis of prey down the gradient of the predator concentration (evasion) [3].

[1] In biology, taxis is a directional response of an organism to a stimulus [5], such as anemotaxis or rheotaxis stimulated by currents of air or water, respectively.

Reaction–diffusion systems with linear cross diffusion have the form

$$\frac{\partial u}{\partial t} = f(u, v) + D_u\frac{\partial^2 u}{\partial x^2} + h_v\frac{\partial^2 v}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = g(u, v) + D_v\frac{\partial^2 v}{\partial x^2} - h_u\frac{\partial^2 u}{\partial x^2}, \tag{6}$$

where the signs of $h_{u,\,v}$ are chosen to describe a pursuit–evasion game in a predator–prey system. When taxis is taken into account by introducing $\partial_x(u\partial_x v)$ and $\partial_x(v\partial_x u)$ terms, the reaction-diffusion system has soliton-like solutions that pass through each other and reflect from impermeable boundaries [20]. Following [21], we retain only the cross-diffusion terms here.

Cross diffusion in the absence of self-diffusion implies that the transport of one species is determined by the diffusive flux of the other species. For example, in the host–parasite model of population dynamics, changes in the parasite population are caused by diffusion of the host population [16]. Cross-diffusion systems have been analyzed in numerous studies [17–19].

The modified FitzHugh–Nagumo model with cross diffusion examined here is

$$\frac{\partial u}{\partial t} = -u - v - 1 + 2\theta(u - u_0) + \frac{\partial^2 v}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = \varepsilon(u - v) - \frac{\partial^2 u}{\partial x^2}. \tag{7}$$

Exact analytical solutions to this system are easily found when ε = 1. The general solution is written as

$$u(\xi) = \sum_n A_n e^{\lambda_n \xi} + u^*,$$
$$v(\xi) = \sum_n B_n e^{\lambda_n \xi} + v^*, \tag{8}$$

where A_n, B_n, u^*, and v^* are constants determined separately for $u < u_0$ and $u > u_0$. The constants B_n can be expressed in terms of A_n (see below).

Substituting (8) into (7), we obtain the matrix equation

$$\begin{pmatrix} c\lambda - 1 & \lambda^2 - 1 \\ -(\lambda^2 - 1) & c\lambda - 1 \end{pmatrix}\begin{pmatrix} A \\ B \end{pmatrix} = 0. \qquad (9)$$

The corresponding characteristic equation,

$$(\lambda^2 - 1)^2 - i^2(c\lambda - 1)^2 = 0$$

($i^2 = -1$), has four roots:

$$\begin{aligned} \lambda_\pm &= -\frac{ic}{2} \pm \sqrt{1 - \frac{c^2}{4} + i} = \pm y \pm iz - \frac{ic}{2}, \\ \lambda_\pm^* &= \frac{ic}{2} \pm \sqrt{1 - \frac{c^2}{4} - i} = \pm y \mp iz + \frac{ic}{2}, \end{aligned} \qquad (10)$$

where

$$\begin{aligned} y &= \sqrt{\frac{\sqrt{(1 - c^2/4)^2 + 1} + 1 - c^2/4}{2}}, \\ z &= \sqrt{\frac{\sqrt{(1 - c^2/4)^2 + 1} - (1 - c^2/4)}{2}} \end{aligned} \qquad (11)$$

are positive quantities. The front profile is described by the solutions

$$\begin{aligned} u_1(\xi) &= e^{y\xi}[A_+\cos(p_-\xi) + A_+^*\sin(p_-\xi)] - 1/2, \\ u_2(\xi) &= e^{-y\xi}[A_-\cos(p_+\xi) + A_-^*\sin(p_+\xi)] + 1/2, \\ v_1(\xi) &= e^{y\xi}[B_+\cos(p_-\xi) + B_+^*\sin(p_-\xi)] - 1/2, \\ v_2(\xi) &= e^{-y\xi}[B_-\cos(p_+\xi) + B_-^*\sin(p_+\xi)] + 1/2, \end{aligned} \qquad (12)$$

where $p_\pm = z \pm c/2$ and the constants B are expressed as

$$\begin{aligned} B_\pm &= \pm\frac{c(2y - q_\mp)A_\pm - (c^2 + 2yq_\mp)A_\pm^*}{c^2 + q_\mp^2}, \\ B_\pm^* &= \pm\frac{c(2y - q_\mp)A_\pm^* + (c^2 + 2yq_\mp)A_\pm}{c^2 + q_\mp^2}, \end{aligned} \qquad (13)$$

with

$$q_\pm = \frac{1 \pm cy}{p_\pm}.$$

The matching procedure involves five equations: two equations for u and v, two for their derivatives, and an equation stating that the value of u at the matching point is u_0. Since these five equations contain five unknowns ($A_\pm$, $A_\pm^*$, and c), the front velocity c can be determined. Its dependence on the excitation threshold u_0 is illustrated by Fig. 3. It is clear from the figure that the velocity curve is qualitatively similar to that obtained for the system with self-diffusion, but the bifurcation point is different. Indeed, when $\varepsilon = 1$, we have a many-valued curve for the cross-diffusion system and a single-valued one in the case of self-diffusion (cf. Fig. 2c). By analogy, we refer to the corresponding fronts described by the cross-diffusion model as Ising and Bloch ones.

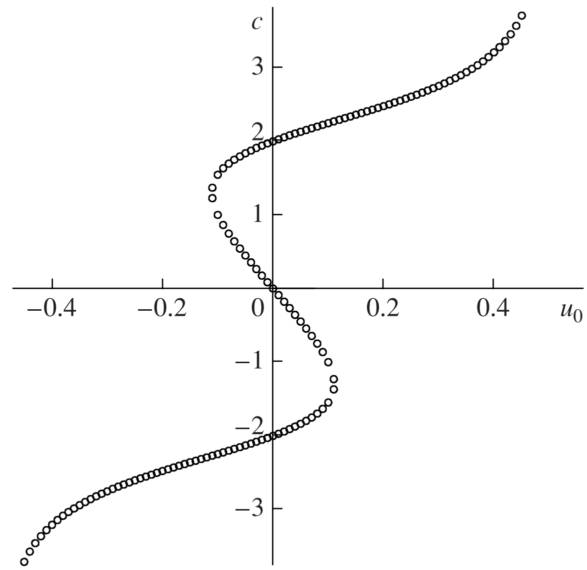

Fig. 3. Cross diffusion. Wave velocity vs. excitation threshold for $\varepsilon = 1$.

Examples of fronts are depicted in Fig. 4. The Bloch front has a nonzero velocity, and its profile exhibits pronounced oscillations. The Ising front is stationary, and its form is characteristic of fronts in inhibitor–activator systems, except that the u and v profiles are reversed. The traveling (Bloch) fronts depicted here have positive velocities: the fronts shown in Fig. 4a move rightwards and the pronounced oscillations are ahead of the wave, as distinct from those in the system with diagonal diffusion considered above.

Traveling waves of the types described here are possible in systems with more equations. For example, oscillatory fronts in a three-component reaction–diffusion system with one activator and two inhibitors (with diagonal diffusion) were examined in a recent study [22].

3. CONCLUSIONS

We have shown that traveling waves developing in the two-component system can have profile oscillations, in contrast to those in the one-component system.

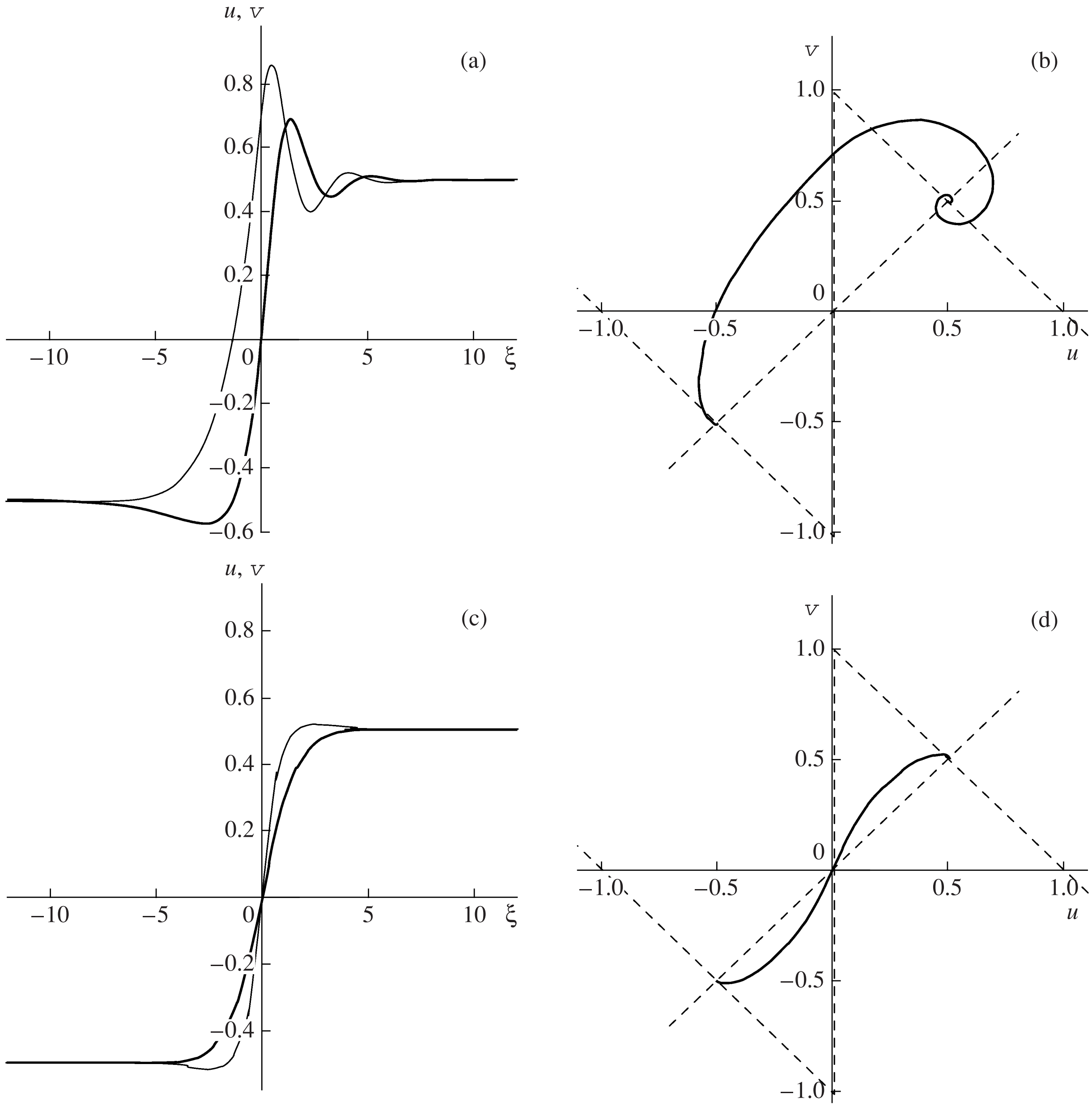

Fig. 4. Cross diffusion. (a, c) Activator $u(\xi)$ and inhibitor $v(\xi)$ front profiles (solid and thin curves, respectively) and (b, d) corresponding phase portraits; (a, b) traveling front with $c = 2$; (c, d) stationary front. The excitation threshold is held constant at $u_0 = 0$. Nullclines $f(u, v) = 0$ and $g(u, v) = 0$ are represented by dashed lines (b, d).

This wave pattern can be interpreted as a quasi-oscillatory one, since decay of the oscillations makes it radically different from the oscillatory one (periodic pulse train). Nondecaying waves of the latter type in two-dimensional systems are spiral or circular excitation waves emitted by a point source.

When multiple patterns of this kind are generated, spatiotemporal chaos develops in an excitable medium [14]. This spiral-wave turbulence is known not to be transient; i.e., it persists for an arbitrarily long time in the absence of external disturbance [1]. The study of such regimes is of great current interest because of applications in arrhythmology. In particular, it was recently found that chaos in most models of excitable media can be suppressed by weak parametric or direct forcing (see [1] and references therein). For more realistic systems, as those describing an excitable (e.g., cardiac) tissue, it has been shown that spiral-wave turbulence can be suppressed by applying a weak force to a small region of the medium [23].

The onset of spatiotemporal chaos in FitzHugh–Nagumo-type models is due to the front bifurcation described in this paper: a change in a parameter of the medium causes the front to change direction, and the spiral wave or circular excitation waves emitted by a point source break up. Therefore, it is interesting to examine the effect of profile oscillations on the behavior of spiral or circular excitation waves involving changes in front velocity.

ACKNOWLEDGMENTS

We thank M.A. Tsyganov for advice on cross-diffusion systems. The work of E.P.Z. was supported by the Russian Foundation for Basic Research, project no. 07-01-00295.

REFERENCES

1. A. Yu. Loskutov and A. S. Mikhaĭlov, *Principles of the Theory of Complex Systems* (Regulyarnaya i Khaoticheskaya Dinamiki, Moscow, 2008) [in Russian].
2. V. A. Vasil'ev, Yu. M. Romanovskiĭ, and V. G. Yakhno, *Autowave Processes* (Nauka, Moscow, 1987) [in Russian].
3. J. D. Murray, *Mathematical Biology* (Springer, Berlin, 2003).
4. A. N. Kolmogorov, I. G. Petrovskiĭ, and N. S. Piskunov, Byull. Mosk. Gos. Univ., Ser. A: Mat. Mekh. **1**, 1 (1937); R. A. Fisher, Annu. Eugen. **7**, 355 (1937).
5. Yu. M. Svirezhev, *Nonlinear Waves, Dissipative Structures, and Catastrophes in Ecology* (Nauka, Moscow, 1987) [in Russian].
6. R. FitzHugh, Biophys. J. **1**, 445 (1961); J. Nagumo, S. Arimoto, and Y. Yoshizawa, Proc. IRE **50**, 2061 (1962).
7. J. Rinzel and J. B. Keller, Biophys. J. **13**, 1313 (1973).
8. A. Ito and T. Ohta, Phys. Rev. A: At., Mol., Opt. Phys. **45**, 8374 (1992).
9. S. Koga, Physica D (Amsterdam) **84**, 148 (1995).
10. E. M. Kuznetsova and V. V. Osipov, Phys. Rev. E: Stat. Phys., Plasmas, Fluids, Relat. Interdiscip. Top. **51**, 148 (1995).
11. H. P. McKean, Adv. Math. **4**, 209 (1970).
12. E. P. Zemskov, V. S. Zykov, K. Kassner, and S. C. Müller, Nonlinearity **13**, 2063 (2000).
13. P. Coullet, J. Lega, B. Houchmanzadeh, and J. Lajzerowicz, Phys. Rev. Lett. **65**, 1352 (1990).
14. A. Hagberg and E. Meron, Chaos 4, 477 (1994); A. Hagberg and E. Meron, Nonlinearity **7**, 805 (1994).
15. J. Rinzel and D. Terman, SIAM J. Appl. Math. **42**, 1111 (1982).
16. M. A. Tsyganov, V. N. Biktashev, J. Brindley, et al., Usp. Fiz. Nauk **177**, 275 (2007) [Phys.—Usp. **50** (3), 263 (2007)].
17. R. Burridge and L. Knopoff, Bull. Seismol. Soc. Am. **57**, 341 (1967).
18. J. H. E. Cartwright, E. Hernandez-Garcia, and O. Piro, Phys. Rev. Lett. **79**, 527 (1997).
19. Y. A. Kuznetsov, Y. Antonovsky, V. N. Biktashev, and E. A. Aponina, J. Math. Biol. **32**, 219 (1994).
20. M. A. Tsyganov, J. Brindley, A. V. Holden, and V. N. Biktashev, Phys. Rev. Lett. **91**, 218102 (2003); M. A. Tsyganov and V. N. Biktashev, Phys. Rev. E: Stat., Nonlinear, Soft Matter Phys. **70**, 031901 (2004).
21. V. N. Biktashev and M. A. Tsyganov, Proc. R. Soc. London, Ser. A **461**, 3711 (2005).
22. E. P. Zemskov, Phys. Rev. E: Stat., Nonlinear, Soft Matter Phys. **73**, 046127 (2006).
23. A. Yu. Loskutov and S. A. Vysotskiĭ, Pis'ma Zh. Éksp. Teor. Fiz. **84** (9), 616 (2006) [JETP Lett. **84** (9), 524 (2006)].

Translated by A. Betev