Mathematical Medicine and Biology (2011) **28**, 217–226
doi:10.1093/imammb/dqq012
Advance Access publication on August 4, 2010

Oscillatory pulses in FitzHugh–Nagumo type systems with cross-diffusion

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[Received on 17 November 2009; revised on 19 May 2010; accepted on 28 May 2010]

We study FitzHugh–Nagumo type reaction–diffusion systems with linear cross-diffusion terms. Based on an analytical description using piecewise linear approximations of the reaction functions, we completely describe the occurrence and properties of wavy pulses, patterns of relevance in several biological contexts, in two prototypical systems. The pulse wave profiles arising in this treatment contain oscillatory tails similar to those in travelling fronts. We find a fundamental, intrinsic feature of pulse dynamics in cross-diffusive systems—the appearance of pulses in the bistable regime when two fixed points exist.

Keywords: cross-diffusion; reaction–diffusion systems; pulse solutions; pattern formation.

1. FitzHugh–Nagumo systems with cross-diffusion

The well-known FitzHugh–Nagumo (FHN) system (FitzHugh, 1961; Nagumo, 1962) has been studied as a model for nerve conduction to understand the dynamics of the interaction between the membrane potential and the restoring force and to capture the basic properties of excitable membranes. Extension of the FHN model to systems where cross-diffusive effects play a role is a topic that is receiving increasing attention in the pattern formation community; see, for instance, the recent review by Vanag & Epstein (2009). Ecology provides many examples of vegetative pattern formation arising from the motion of one species in response to gradients in the abundance of other species. Cross-diffusion-induced patterns arise not only in living systems (e.g. the classical chemotactic motion of the bacterium *Escherichia coli*) but also in some social systems (ordinary citizens versus drug dealers, 'crimo-taxis', Epstein, 1997). Furthermore, in the chemistry of catalysis, competition of adsorbed species for surface sites can also give rise to cross-diffusion effects. Our approach is very much in the spirit of Berezovskaya *et al.* (2008) and focuses on developing a semi-analytic working tool aimed at understanding one basic pattern produced by cross-diffusion effects combined with chemical reactions of the FHN type—wavy pulses.

In 2008, Berezovskaya *et al.* (2008) modified the FHN system to model the spatial propagation of neuron firing. Certain drugs or external chemicals affect the rates at which sodium channels close and potassium channels open, thus altering the normal firing dynamics of a neural membrane (Berezovskaya *et al.*, 2008). This generic effect of a drug can be modelled by incorporating a cross-diffusion term in the original FHN model, i.e.

$$\frac{\partial u}{\partial t} = u - u^3 - v + D\frac{\partial^2 u}{\partial x^2} + h\frac{\partial^2 v}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = \varepsilon(u - v), \qquad (1)$$

where t is time, x is a 1D spatial variable and the non-negative constants D and h are the self- and cross-diffusion coefficients, respectively; the positive constant ε is the ratio of two characteristic time scales.

A similar kind of reaction–diffusion model is a pursuit and evasion predator–prey system (Tsyganov *et al.*, 2007) in which the prey seek to evade the predators and the predators pursue the prey. Thus, the prey move away from higher concentrations of predators, and the predators move in the direction of increasing prey levels, so that the additional 'cross-diffusive' contributions to the rate equations, proportional to the species gradients, have a positive sign for the prey and a negative one for the predator. When diffusion plays a negligible role in the dispersal of the populations and the cross-diffusion terms are linear, the spatial evolution of the populations can be described by the system (Biktashev & Tsyganov, 2005)

$$\frac{\partial u}{\partial t} = u(1-u)(u-a) - v + h_v\frac{\partial^2 v}{\partial x^2}, \quad 0 < a < 1,$$
$$\frac{\partial v}{\partial t} = \varepsilon(u - v) - h_u\frac{\partial^2 u}{\partial x^2}, \qquad (2)$$

where a denotes the excitation threshold. Analytical insight into this model was obtained from Biktashev & Tsyganov (2005) using a piecewise linear approximation, with the Heaviside step function $\theta(u-a)$ replacing the cubic reaction term in the first equation, similar to one used in the Rinzel–Keller (Rinzel & Keller, 1973; Rinzel & Terman, 1982) caricature

$$\frac{\partial u}{\partial t} = -u + \theta(u-a) - v + \frac{\partial^2 u}{\partial x^2},$$
$$\frac{\partial v}{\partial t} = \varepsilon u \qquad (3)$$

of the classical FHN model with self-diffusion. This approach allows one to obtain the wave solutions and determine their speed.

Wave solutions of the front type have recently been studied for the bistable regime of the cross-diffusive FHN system (Zemskov & Loskutov, 2008). The aim of this study is to extend these approaches beyond fronts to the travelling solitary pulses that typically appear in a large class of excitable systems. We describe here the corresponding dynamical behaviour, obtain the pulse profiles, and, finally, determine the wave speed.

2. Travelling pulse solutions in FHN type systems

We focus here on the construction of travelling wave solutions, i.e. waves that propagate with unchanging profiles and constant speed. Travelling waves result from the interplay of two effects, namely, interaction between the species and the spatial dispersal. If one or both effects are missing, travelling waves cannot occur. By a pulse, we mean a wave that encompasses an excursion from a steady state and a return back to it, i.e. a type of solitary wave. In the FHN model, such travelling pulses can propagate if a threshold perturbation is exceeded.

To obtain closed-form solutions, we use a piecewise linear approximation for the non-linear reaction term and examine two basic dynamical regimes: excitable and bistable. The excitable regime is realized when there is only one fixed point in the phase plane, whereas the bistable regime is related to the existence of two fixed points. These regimes may be generated by appropriate choice of the model parameters in the reaction functions. A double cross-diffusive FHN type system that exhibits both regimes is described by the following equations:

$$\frac{\partial u}{\partial t} = -\alpha u - v + \theta(u-a) + h_v \frac{\partial^2 v}{\partial x^2},$$

$$\frac{\partial v}{\partial t} = \varepsilon u - \beta v - h_u \frac{\partial^2 u}{\partial x^2}. \tag{4}$$

In (4), we have modified the classical Rinzel–Keller kinetics (Rinzel & Keller, 1973; Rinzel & Terman, 1982) by changing the coefficient of u in the first equation from 1 to α and inserting the v term with coefficient β into the second. The motivation for this extension is to analyse the general conditions for excitable or bistable behaviour in terms of the parameters α and β. The parameter $\alpha \in (0, 1)$ determines the slopes of the u-null-cline and can be chosen as zero for the excitable regime to allow analytic treatment. When $\beta = 0$ (the classical Rinzel–Keller kinetics) and $a > 0$, we have the excitable regime with one fixed point, while $\beta = \varepsilon$ and $0 < a < 1/2$ gives two intersections of the null-clines, i.e. bistable kinetics. More generally, excitability is found when the right-hand branch of the u-null-cline, $v = 1 - \alpha u$, lies below the v-null-cline for $u > a$, while bistability occurs when these two null-clines intersect in that region. The condition for bistability is thus

$$\alpha + \frac{\varepsilon}{\beta} > \frac{1}{a}. \tag{5}$$

The boundary conditions $u, v(x \to \pm\infty) = 0$ define the pulse solution, while $u, v(x \to -\infty) = 0$ and $u, v(x \to +\infty) = \text{const.}$ correspond to a front. We will study here only travelling pulses. Thus, we start from the Rinzel–Keller form (Rinzel & Keller, 1973; Rinzel & Terman, 1982) of the FHN system modified to include cross-diffusion; this type of model was explored by Biktashev & Tsyganov (2005). Introducing the travelling wave coordinate $\xi = x - ct$, where c is the wave speed, we write the travelling wave equations in the form

$$h_v \frac{\mathrm{d}^2 v}{\mathrm{d}\xi^2} + c\frac{\mathrm{d}u}{\mathrm{d}\xi} - \alpha u - v + \theta(u-a) = 0, \quad -h_u \frac{\mathrm{d}^2 u}{\mathrm{d}\xi^2} + c\frac{\mathrm{d}v}{\mathrm{d}\xi} + \varepsilon u - \beta v = 0. \tag{6}$$

The general solutions $u(\xi)$ and $v(\xi)$ can be found as

$$u(\xi) = \sum_{n=1}^{4} A_n \,\mathrm{e}^{\lambda_n \xi} + u^*,$$

$$v(\xi) = \sum_{n=1}^{4} B_n \,\mathrm{e}^{\lambda_n \xi} + v^*, \tag{7}$$

where A_n, B_n, u^* and υ^* are constants to be determined in each of the regions $u < a$ and $u > a$. The constants a and α and the ratio β/ε determine the number of intersection points for the null-clines $-\alpha u^* - \upsilon^* + \theta(u-a) = 0$ and $u^* - (\beta/\varepsilon)\upsilon^* = 0$ and the corresponding dynamical regime, excitable or bistable, according to (5). Therefore, for simplicity, we set $\varepsilon = 1$ in what follows.

We construct the pulse solution from three pieces: a central spike and two tails that decay to zero at $\xi \to \pm\infty$. These analytic solutions are found by invoking matching conditions on the continuity of the functions, $u(\xi)$ and $\upsilon(\xi)$, and their derivatives, $\mathrm{d}u(\xi)/\mathrm{d}\xi$ and $\mathrm{d}\upsilon(\xi)/\mathrm{d}\xi$, at the two matching points, ξ_1 and ξ_2, which separate the first from the second and the second from the third pieces of the solution, respectively. An additional condition, $u(\xi) = a$, fixes the wave at the matching point. Thus, the full set of matching conditions reads

$$\begin{aligned}
&u_1(\xi_1) = u_2(\xi_1), \quad u_2(\xi_2) = u_3(\xi_2),\\
&\frac{\mathrm{d}u_1(\xi_1)}{\mathrm{d}\xi} = \frac{\mathrm{d}u_2(\xi_1)}{\mathrm{d}\xi}, \quad \frac{\mathrm{d}u_2(\xi_2)}{\mathrm{d}\xi} = \frac{\mathrm{d}u_3(\xi_2)}{\mathrm{d}\xi},\\
&\upsilon_1(\xi_1) = \upsilon_2(\xi_1), \quad \upsilon_2(\xi_2) = \upsilon_3(\xi_2),\\
&\frac{\mathrm{d}\upsilon_1(\xi_1)}{\mathrm{d}\xi} = \frac{\mathrm{d}\upsilon_2(\xi_1)}{\mathrm{d}\xi}, \quad \frac{\mathrm{d}\upsilon_2(\xi_2)}{\mathrm{d}\xi} = \frac{\mathrm{d}\upsilon_3(\xi_2)}{\mathrm{d}\xi},\\
&u_1(\xi_1) = a, \quad u_2(\xi_2) = a.
\end{aligned} \tag{8}$$

The same matching conditions hold for the pulse solutions in both the excitable and the bistable regimes.

2.1 *Excitable regime*

To obtain an exactly soluble model, we consider the special excitable case when $\alpha = \beta = 0$. Inserting the general solutions (7) into the model equations, we obtain the following matrix equation:

$$\begin{pmatrix} c\lambda_n & h_\upsilon \lambda_n^2 - 1 \\ 1 - h_u\lambda_n^2 & c\lambda_n \end{pmatrix} \begin{pmatrix} A \\ B \end{pmatrix} = 0. \tag{9}$$

The characteristic equation $(h_u\lambda_n^2 - 1)(h_\upsilon\lambda_n^2 - 1) + c^2\lambda_n^2 = 0$ yields four eigenvalues

$$\lambda_{1-4} = \pm\frac{1}{\sqrt{2h_u h_\upsilon}}\sqrt{h_u + h_\upsilon - c^2 \pm \sqrt{\varGamma}} \tag{10}$$

with $\varGamma = (c^2 - h_u - h_\upsilon)^2 - 4h_u h_\upsilon$. When $\varGamma$ is positive, the eigenvalues are real and the waves consist of exponential functions, whereas when $\varGamma$ is negative, we obtain complex eigenvalues and oscillatory waves. We concentrate on the situation with complex eigenvalues. Then, we can write ($\mathrm{i}^2 = -1$)

$$\begin{aligned}
\lambda_{1,2} &= \pm\frac{1}{\sqrt{2h_u h_\upsilon}}\sqrt{h_u + h_\upsilon - c^2 + \mathrm{i}\gamma} = \pm(y + \mathrm{i}z),\\
\lambda_{3,4} &= \pm\frac{1}{\sqrt{2h_u h_\upsilon}}\sqrt{h_u + h_\upsilon - c^2 - \mathrm{i}\gamma} = \pm(y - \mathrm{i}z),
\end{aligned} \tag{11}$$

where

$$y = \frac{1}{\sqrt{2h_u h_v}}\sqrt{\sqrt{h_u h_v} + \frac{h_u + h_v - c^2}{2}},$$

$$z = \frac{1}{\sqrt{2h_u h_v}}\sqrt{\sqrt{h_u h_v} - \frac{h_u + h_v - c^2}{2}} \tag{12}$$

and $\mathrm{i}\gamma = \sqrt{\Gamma}$.

In Fig. 1, we plot the $\Gamma = \Gamma(c, h_u, h_v)$ dependence for three values of the activator and inhibitor cross-diffusion constants, h_u and h_v. We fix h_v and vary h_u because $\Gamma(c, h_u, h_v)$ is symmetric in h_u and h_v, i.e. Γ is invariant to the replacement $h_u \to h_v$ and $h_v \to h_u$. Since wave solutions with oscillatory tails exist only for negative values of Γ, the figure demonstrates that oscillatory waves occur in a restricted interval of the wave speed.

The three-piece pulse solutions take the form

$$\begin{aligned}
u_1(\xi) &= \mathrm{e}^{y\xi}[A_1\cos(z\xi) + A_3\sin(z\xi)], \quad \xi \leqslant \xi_1,\\
u_2(\xi) &= \mathrm{e}^{y\xi}[\bar{A}_1\cos(z\xi) + \bar{A}_3\sin(z\xi)]\\
&\quad + \mathrm{e}^{-y\xi}[\bar{A}_2\cos(z\xi) + \bar{A}_4\sin(z\xi)], \quad \xi_1 \leqslant \xi \leqslant \xi_2,\\
u_3(\xi) &= \mathrm{e}^{-y\xi}[A_2\cos(z\xi) + A_4\sin(z\xi)], \quad \xi \geqslant \xi_2,\\
v_1(\xi) &= \mathrm{e}^{y\xi}[B_1\cos(z\xi) + B_3\sin(z\xi)], \quad \xi \leqslant \xi_1,\\
v_2(\xi) &= \mathrm{e}^{y\xi}[\bar{B}_1\cos(z\xi) + \bar{B}_3\sin(z\xi)]\\
&\quad + \mathrm{e}^{-y\xi}[\bar{B}_2\cos(z\xi) + \bar{B}_4\sin(z\xi)] + 1, \quad \xi_1 \leqslant \xi \leqslant \xi_2,\\
v_3(\xi) &= \mathrm{e}^{-y\xi}[B_2\cos(z\xi) + B_4\sin(z\xi)], \quad \xi \geqslant \xi_2.
\end{aligned} \tag{13}$$

Inserting these solutions into the matching conditions yields algebraic equations. We solve these numerically to obtain the wave speed c, the eight amplitudes A_n and $\bar{A}_n$ and the distance between the two interfaces, $\xi_2 - \xi_1$. The B_n and $\bar{B}_n$ may be determined from the corresponding A amplitudes, and we

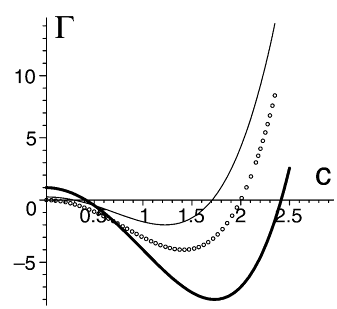

FIG. 1. Excitable regime. Dependence of $\Gamma = \Gamma(c, h_u, h_v)$ on wave speed c with $h_u = h_v = 1$ (circles), $h_u = 1/2, h_v = 1$ (thin line) and $h_u = 2, h_v = 1$ (thick line). Waves with oscillatory tails may only exist for negative values of Γ.

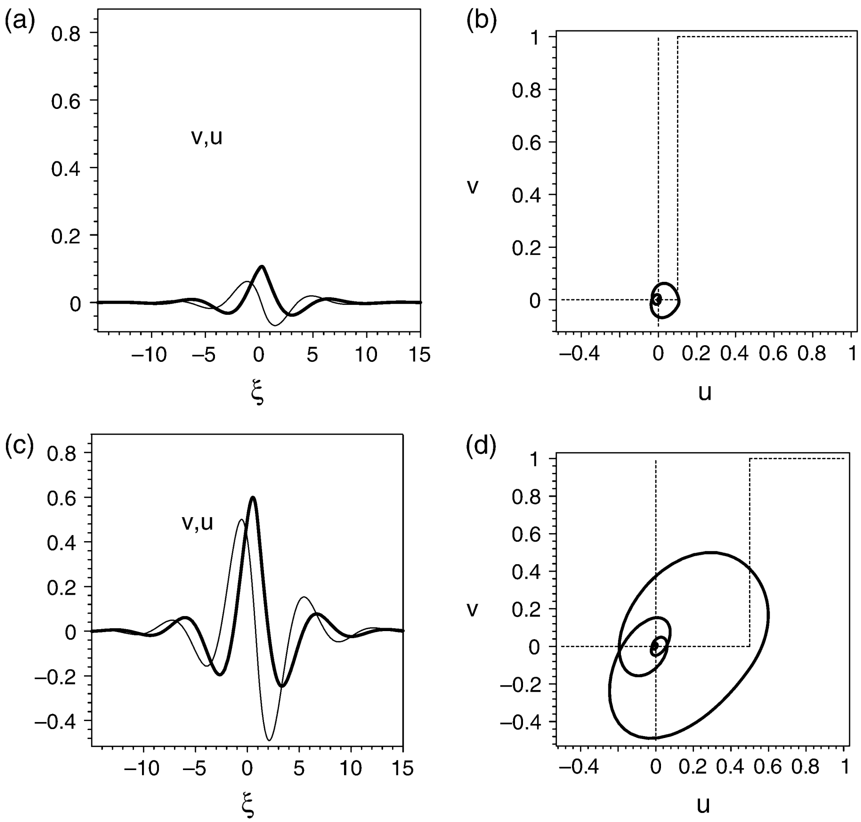

FIG. 2. Waves in the excitable regime for (a, b) small pulse and (c, d) large pulse solutions: (a, c) activator $u(\xi)$ (bold lines) and inhibitor $v(\xi)$ (thin lines) profiles; (b, d) $u - v$ trajectories. The excitation threshold is chosen as (a, b) $a = 0.1$ and (c, d) $a = 0.5$, and the wave speed is found as (a, b) $c \approx 1.857$ and (c, d) $c \approx 1.876$. The null-clines are shown in (b, d) by dashed lines.

may arbitrarily set $\xi_1 = 0$ for convenience. Pulse solutions for the case with cross-diffusion coefficients with equal magnitude are shown in Fig. 2 for two values of the excitation threshold a. We see that this threshold determines the wave amplitude: a low excitation threshold generates a small wave (Fig. 2 (a and b)) and a high value of a produces a large wave (Fig. 2(c and d)). The oscillations in the pulse profile occur both in front and in back of the wave, but the spike is so narrow that there are no oscillations in that region. In the phase plane (Fig. 2(b and d)), the oscillations form a closed trajectory with 'right- and left-rotated' spirals. Following Carpio & Bonilla (2003), we refer to these pulses as 'wavy' pulses. This form of travelling wave appears in two-variable systems of parabolic equations with at least one diffusive component. Carpio & Bonilla (2003) have studied a one-component system in which travelling fronts with oscillatory tails were found in a model of a chain of diffusively coupled non-linear oscillators.

2.2 *Bistable regime*

Next, we turn our attention to the bistable case when $\alpha = \beta = 1$, and the excitation threshold lies in the range $0 < a < 1/2$. For the sake of analytic solvability, we also restrict our consideration to the situation when $h_u = h_v = 1$. Then, from the matrix equation

$$\begin{pmatrix} c\lambda_n - 1 & \lambda_n^2 - 1 \\ 1 - \lambda_n^2 & c\lambda_n - 1 \end{pmatrix} \begin{pmatrix} A \\ B \end{pmatrix} = 0, \tag{14}$$

we find the characteristic equation, which yields the following eigenvalues (Zemskov & Loskutov, 2008):

$$\lambda_{1,2} = -\frac{\mathrm{i}c}{2} \pm \sqrt{1 - \frac{c^2}{4} + \mathrm{i}} = \pm(y + \mathrm{i}z) - \frac{\mathrm{i}c}{2},$$

$$\lambda_{3,4} = \frac{\mathrm{i}c}{2} \pm \sqrt{1 - \frac{c^2}{4} - \mathrm{i}} = \pm(y - \mathrm{i}z) + \frac{\mathrm{i}c}{2}, \tag{15}$$

where

$$y = \sqrt{\left[\sqrt{(1 - c^2/4)^2 + 1} + 1 - c^2/4\right] \Big/ 2},$$

$$z = \sqrt{\left[\sqrt{(1 - c^2/4)^2 + 1} - (1 - c^2/4)\right] \Big/ 2}. \tag{16}$$

Hence, the pulse solution is

$$\begin{aligned}
u_1(\xi) &= \mathrm{e}^{y\xi}[A_1 \cos(p_-\xi) + A_3 \sin(p_-\xi)], \quad \xi \leqslant \xi_1, \\
u_2(\xi) &= \mathrm{e}^{y\xi}[\bar{A}_1 \cos(p_-\xi) + \bar{A}_3 \sin(p_-\xi)] \\
&\quad + \mathrm{e}^{-y\xi}[\bar{A}_2 \cos(p_+\xi) + \bar{A}_4 \sin(p_+\xi)] + 1/2, \quad \xi_1 \leqslant \xi \leqslant \xi_2, \\
u_3(\xi) &= \mathrm{e}^{-y\xi}[A_2 \cos(p_+\xi) + A_4 \sin(p_+\xi)], \quad \xi \geqslant \xi_2, \\
v_1(\xi) &= \mathrm{e}^{y\xi}[B_1 \cos(p_-\xi) + B_3 \sin(p_-\xi)], \quad \xi \leqslant \xi_1, \\
v_2(\xi) &= \mathrm{e}^{y\xi}[\bar{B}_1 \cos(p_-\xi) + \bar{B}_3 \sin(p_-\xi)] \\
&\quad + \mathrm{e}^{-y\xi}[\bar{B}_2 \cos(p_+\xi) + \bar{B}_4 \sin(p_+\xi)] + 1/2, \quad \xi_1 \leqslant \xi \leqslant \xi_2, \\
v_3(\xi) &= \mathrm{e}^{-y\xi}[B_2 \cos(p_+\xi) + B_4 \sin(p_+\xi)], \quad \xi \geqslant \xi_2.
\end{aligned} \tag{17}$$

Here, we have introduced the additional notation $p_\pm = z \pm c/2$.

The pulse speed, c, versus excitation threshold, a, diagram for the bistable regime is shown in Fig. 3. For simplicity, we plot here only the situation when the speed is positive. We see that when the speed is high enough there is only a single pulse solution, whereas for slower waves, the curve becomes multivalued—pulses can occur with the same speed but different width as shown in Fig. 4. Since the speed is positive, and therefore the pulses propagate from left to right, the activator $u = u(\xi)$ and inhibitor $v = v(\xi)$ profiles (Fig. 4(a and c)) make clear that, in contrast to the excitable case where oscillations occur on both sides of the spike, the pronounced oscillations here arrive only before the

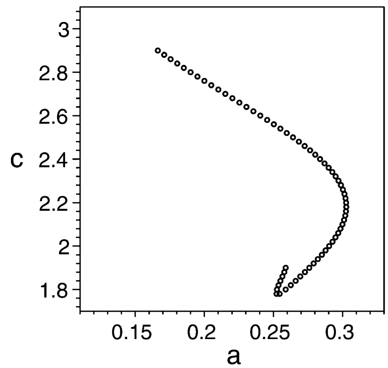

FIG. 3. Bistable regime. Pulse speed c versus excitation threshold a for the case with equal cross diffusion constant $h_u = h_v = 1$.

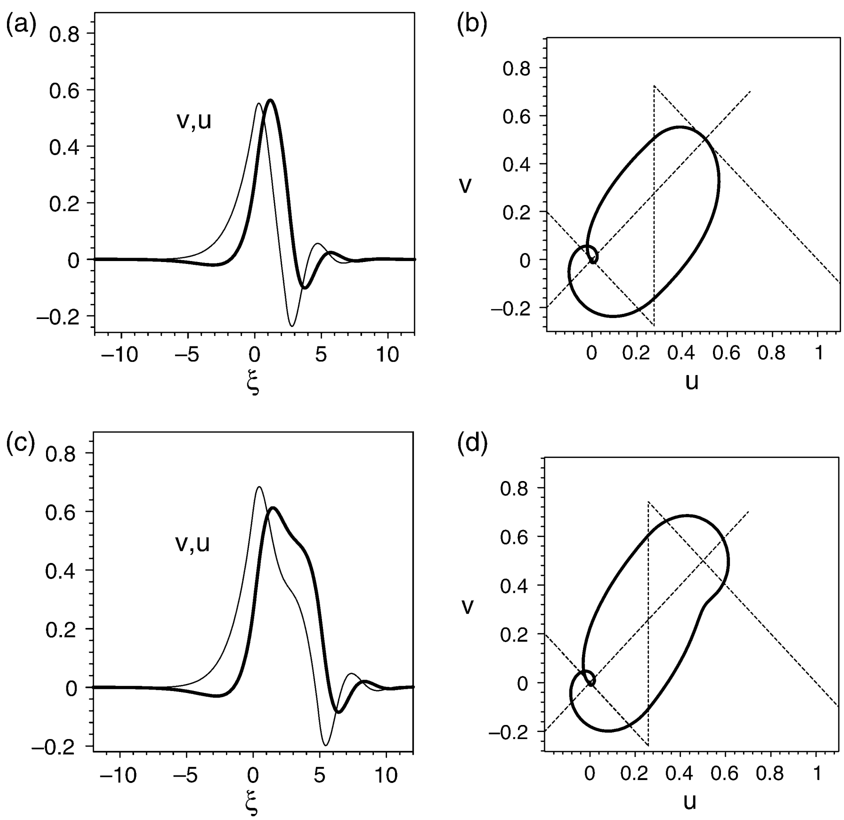

FIG. 4. Wave profiles in the bistable regime for (a, b) a narrow pulse and (c, d) a wide pulse: (a, c) activator $u(\xi)$ (bold lines) and inhibitor $v(\xi)$ (thin lines) profiles and (b, d) $u - v$ trajectories. The value of the speed is chosen as $c = 1.9$ and the excitation threshold is found as (a, b) $a \approx 0.28$ and (c, d) $a \approx 0.26$. The null-clines are shown in (b, d) by dashed lines.

spike. On the $u - v$ phase plane the solutions form a closed curve with one spiral, which corresponds to the pronounced oscillation, around the fixed point. However, in the case of the broad pulse, the spike in the $u - v$ phase plane includes the region with the second fixed point (see Fig. 4d), and the proximity to this point causes the wave form of the spike to deform.

3. Discussion

Modified versions of the FitzHugh–Nagumo model with cross-diffusive interactions between the potential and recovery variables may be useful in exploring the effects of certain drugs on the neuron firing process (Berezovskaya *et al.*, 2008). The model parameters, i.e. the cross-diffusion coefficients and the wave speed, characterize the axon's ability to propagate action potentials (Berezovskaya *et al.*, 2008). Travelling pulses with large values of the speed correspond to the ordinary propagation of nerve impulses. Smaller speeds of impulse propagation or a large cross-diffusion coefficient may make the ordinary propagation of nerve impulses impossible, causing them to propagate with decreasing amplitude or as damped oscillations. Variation of the cross-diffusion coefficients constrains the velocities of waves. Thus, the speed of transmission of a signal along the axon may be reduced as a result of the effect of a drug (Berezovskaya *et al.*, 2008).

We have considered here the behaviour of a single travelling pulse. In addition to fronts, the model should also exhibit periodic pulse trains as well as finite trains of several pulses for appropriate choices of parameters. Such patterns may be of relevance in neural systems and merit further exploration in future studies of this rich family of models.

3.1 *Summary*

We have analytically described one basic type of travelling wave—a single pulse—in reaction–diffusion systems of the FHN type with linear cross diffusion. A characteristic feature of the dynamics is the appearance of pulses in the bistable regime, when two fixed points exist and fronts can also arise. Another distinguishing feature of this type of solution is that the travelling pulses have oscillatory tails. Travelling waves that can display oscillatory behaviour have also been found in prey–predator systems with logistic prey growth and with both predator and prey dispersing by self-diffusion (Murray, 2003). The bistable dynamical regime in this model also gives rise to front solutions that approach one of the steady states monotonically or in an oscillatory fashion. The piecewise linear methodology allows us to solve the model equations exactly, build travelling wave profiles and determine their wave speed. The strategy employed here can be applied to a large class of 1D, two-variable reaction–diffusion systems.

Acknowledgment

We thank F. Sagués and V. A. Volpert for reading and commenting on the manuscript.

Funding

Russian Foundation for Basic Research (07-01-00295 to E.P.Z.); US National Science Foundation (CHE-0526866 to I.R.E. and E.P.Z.).

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