Arch. Mech., **62**, 2, pp. 121–133, Warszawa 2010

Mechanical effects coupled with calcium waves

B. KAŹMIERCZAK, M. DYZMA

Institute of Fundamental Technological Research
Polish Academy of Sciences
Pawińskiego 5b
02-106 Warsaw, Poland
e-mail: bkazmier@ippt.gov.pl

In the paper we find explicit formulae for heteroclinic travelling wave solutions in the system of equations describing the dynamics of cytosolic calcium concentration and the accompanying mechanical phenomena.

Key words: calcium waves, reaction-diffusion systems, mechanochemical coupling.

1. Introduction

This paper presents explicit travelling wave solutions to a system of equations, describing the evolution of the calcium propagation and the associated mechanical phenomena in biological media (cells and tissues). This system of equations has the following form:

$$\frac{\partial c}{\partial t} = D\nabla^2 c + f(c) + \gamma\theta, \tag{1.1}$$

$$\nabla \cdot \boldsymbol{\sigma} = 0, \tag{1.2}$$

where $\theta = \nabla \cdot \mathbf{u}$ is the dilation and $\mathbf{u}$ is the displacement. The stress tensor $\boldsymbol{\sigma} \equiv \sigma_{ij}$, where

$$\sigma_{ij} = \theta\lambda\delta_{ij} + 2G\epsilon_{ij} + \nu_1\theta_{,t}\delta_{ij} + \nu_2\epsilon_{ij,t} + \tau_{ij}. \tag{1.3}$$

In Eq. (1.1), c denotes the free cytosolic calcium concentration, D is its effective diffusion coefficient, $f(c)$ is the function describing calcium transport into and out of the cytosol. In Eq. (1.3), ϵ_{ij} are the components of the deformation tensor $\boldsymbol{\epsilon} = 1/2(\nabla\mathbf{u} + \nabla\mathbf{u}^T)$, λ and G are the Lamé coefficients, whereas ν_1 and ν_2 are the viscosity coefficients. τ_{ij} are the components of the so-called active traction tensor $\boldsymbol{\tau}$ (resulting from the actin-myosin interaction). Below, we assume that τ is a diagonal tensor of the form

$$\tau = \mathrm{diag}(\tau_{11}, \tau_{22}, \tau_{33}).$$

In Eq. (1.2), the inertial terms have been neglected, due to the fact that the considered mechanical phenomena (connected with the wave of calcium concen-

tration) induce relatively slow motion of the medium. Also, the divergence of the stress tensor is assumed to be equal to zero. This means that there are no external constraints for the expansion or contraction of different parts of the medium. This assumption will be changed in the last section of the paper. For the review of various aspects of calcium dynamics, see e.g. [2]. The linear form of the mechanical term $\gamma\theta$ in Eq. (1.1) is postulated in [7].

The dynamics of the local calcium concentration inside a cell or tissue coordinates many physiological processes. It plays a key role in transferring signals from the surrounding medium into the interior of the cell. It governs also the process of bridging between actin and myosin fiber proteins. This process is especially important in myocyte long cells and leads to their contraction. On the other hand, the local mechanical deformations of the medium influence the dynamics of calcium through the term $\gamma\theta$ in Eq. (1.1). The explicit form for purely chemical travelling waves, i.e. for $\gamma = 0$, are well-known (see e.g. [7]); however, up to our knowledge, the explicit travelling wave solutions to system (1.1)–(1.2) have not been studied.

In this paper we will find some explicit solutions of travelling wave type for system (1.1)–(1.2). This provides some insight into the phenomenon of the mechano-chemical coupling described by this system of equations. We confine ourselves to three geometrical cases. These cases have been considered in [8] and are depicted in Fig. 1. Thus in the paper we consider the calcium waves in an unbounded bulk medium, in thin infinite layers which in their undeformed state are planes [1], and infinitely long cylinders of sufficiently small radius. The last situation can be physically realized e.g. in the case of long myocyte cells [6].

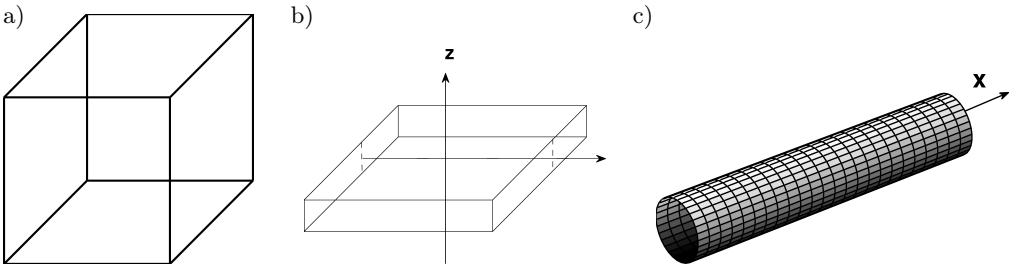

FIG. 1. The geometrical cases considered in the paper. a) Bulk medium (large in every direction), b) Infinite plane layer of sufficiently small width $2d$, c) Long cylinder of sufficiently small radius.

REMARK 1. Calcium dynamics is a complex phenomenon, consisting of numerous intracellular pathways and the exchange of calcium ions between extracellular matrix (ECM) and cell interior. However, in this paper we confine

ourselves only to the processes related to the activated calcium, calcium release from endoplasmic reticulum vesicles into the cytoplasm. This simplifying assumption allows us to use a description based on the reaction-diffusion equation. □

2. Analysis of the mechanical equation

For the Reader's convenience we repeat here the analysis of the mechanical equation, which can be found in [8] or [5]. As we have mentioned, we are interested in plane travelling waves solutions to the system (1.1)–(1.2), propagating along the x-axis. *As a result we may assume here that* $c = c(x,t)$.

REMARK 2. The last assumption is in fact a kind of homogenization assumption, by which we neglect the boundary effects or non-homogeneity of the internal endoplasmic calcium vessels distribution. □

Bulk medium

In the case of bulk medium it is natural to assume that all the components of the deformation tensor ϵ depend only on x and t and that $\epsilon_{ij} \equiv 0$ except for ϵ_{11} (consequently, $u_2 \equiv 0$ and $u_3 \equiv 0$). We thus have $\theta = \epsilon_{11}$ and the x-component of Eq. (1.2) gives

$$(\lambda\theta + 2G\theta + (\nu_1 + \nu_2)\theta_{,t} + \tau_{11})_{,x} = 0,$$

which, after integrating and putting the integration constant to zero (assuming that there are no external forces), leads to the equation

$$\lambda\theta + 2G\theta + (\nu_1 + \nu_2)\theta_{,t} + \tau = 0,$$

with $\tau = \tau(c) = \tau_{11}(c)$.

Infinite layer

Now, let us consider the case of an infinite thin layer. We fix the system of coordinates in such a way that the x-axis is parallel to the layer and the z-axis is perpendicular to it (as shown in Fig. 1). As before, *we assume that all the components of the tensors* σ *and* ϵ *depend only on* x *and* t*, but do not depend on* y *and* z. According to the translational symmetry with respect to y, we can suppose that $u_2 \equiv 0$, hence $\epsilon_{22} \equiv 0$. We also demand the plane stress conditions on the boundary planes $\{(x,y,z) : z = \pm d\}$ (see [3]). That is to say, we suppose that for $z = \pm d$

$$\sigma_{i3} = 0, \qquad i = 1,2,3. \tag{2.1}$$

Thus, in this case we obtain:

1. From the balance of mechanical forces:

$$(\lambda\theta + 2G\epsilon_{11} + \nu_1\theta_{,t} + \nu_2\epsilon_{11,t} + \tau_{11})_{,x} = 0. \tag{2.2}$$

2. From the boundary conditions on the boundary planes (by taking $i = 3$):

$$\lambda\theta + 2G\epsilon_{33} + \nu_1\theta_{,t} + \nu_2\epsilon_{33,t} + \tau_{33} = 0. \tag{2.3}$$

Though referring only to the boundary conditions at $z = \pm d$, Eq. (2.3) is valid in the whole thin layer, as we assume that the components of the tensor $\boldsymbol{\sigma}$ do not depend on the variable z. Integrating Eq. (2.2) and assuming the integration constant to be zero, we obtain

$$\sigma_{11} = \theta\lambda + 2G\epsilon_{11} + \nu_1\theta_{,t} + \nu_2\epsilon_{11,t} + \tau_{11} = 0, \tag{2.4}$$

hence by adding it to Eq. (2.3), we obtain the first-order differential equation for the dilation θ

$$2(\lambda + G)\theta + (2\nu_1 + \nu_2)\theta_{,t} + \tau_{11} + \tau_{33} = 0. \tag{2.5}$$

Fibers

In the case of waves propagating in fibers (e.g. long cells as myocytes) we assume cylindrical symmetry of the problem and that $\tau_{22} = \tau_{33}$. In this case we have $\epsilon_{22} = \epsilon_{33}$, so $\theta = \epsilon_{11} + 2\epsilon_{33}$. Formally, the boundary conditions and the balance of forces have the same form as in the case of thin layers, then

$$(\lambda\theta + 2G\epsilon_{11} + \nu_1\theta_{,t} + \nu_2\epsilon_{11,t} + \tau_{11})_{,x} = 0,$$

$$\lambda\theta + 2G\epsilon_{22} + \nu_1\theta_{,t} + \nu_2\epsilon_{22,t} + \tau_{22} = 0,$$

$$\lambda\theta + 2G\epsilon_{33} + \nu_1\theta_{,t} + \nu_2\epsilon_{33,t} + \tau_{33} = 0,$$

(we use the Cartesian system of coordinates, keeping in mind however the radial symmetry). Summing up these equations, after the integration of the first one we obtain again a first-order equation for the dilation θ:

$$(3\lambda + 2G)\theta + (3\nu_1 + \nu_2)\theta_{,t} + \tau_{11} + 2\tau_{33} = 0.$$

Thus in all three cases we arrive at the same type of first-order ODE. This equation has the form:

$$K\theta + \mu\theta_{,t} + \tau = 0. \tag{2.6}$$

The coefficients K, μ and τ depend on the case considered and τ is an appropriate function of the components of the tensor $\boldsymbol{\tau}$ and they are *given explicitly in* Table 1.

Table 1. The coefficients K, μ and τ in Eq. (2.6).

	$K(\lambda, G)$	$K(E, \nu)$	μ	τ
bulk medium	$\lambda + 2G$	$\frac{E(1-\nu)}{(1+\nu)(1-2\nu)}$	$\nu_1 + \nu_2$	τ_{11}
thin layer	$2\lambda + 2G$	$\frac{E}{(1+\nu)(1-2\nu)}$	$2\nu_1 + \nu_2$	$\tau_{11} + \tau_{33}$
fiber	$3\lambda + 2G$	$\frac{E}{1-2\nu}$	$3\nu_1 + \nu_2$	$\tau_{11} + 2\tau_{33}$

Finally, let us recall that the Young modulus E and Poisson's ratio ν are related to the Lamé coefficients by the relations:

$$\lambda = \frac{E\nu}{(1+\nu)(1-2\nu)}, \qquad G = \frac{E}{2(1+\nu)}$$

and

$$E = \frac{G(2G+3\lambda)}{\lambda+G}, \qquad \nu = \frac{\lambda}{2(\lambda+G)}.$$

3. Travelling wave solutions

Solutions of travelling wave type describe many important phenomena in biology [7], chemistry [10] and physics (e.g. different models of phase transitions [9]). Looking for travelling wave solutions we assume that

$$c(x,y,z,t) = c(x-vt), \qquad \theta(x,y,z,t) = \theta(x-vt), \tag{3.1}$$

where v is the speed of the wave. Moreover, we assume that the displacement have also the form of a travelling wave in the x-direction, i.e.

$$\mathbf{u}(x,y,z,t) = \mathbf{u}(x-vt,y,z). \tag{3.2}$$

System (1.1)–(2.6) changes then to a system of ordinary diffrential equations of the form:

$$Dc'' + vc' + f(c) + \gamma\theta = 0, \tag{3.3}$$

$$-v\mu\theta' + K\theta + \tau = 0. \tag{3.4}$$

Here $'$ denotes the derivative with respect to $\xi = x - vt$. Thus, we are looking for heteroclinic solutions to system (3.3)–(3.4), that is to say the $C^2(\mathbb{R}^1)$ functions c and θ such that $\lim_{\xi\to-\infty} c(\xi) = c_1$, $\lim_{\xi\to\infty} c(\xi) = c_3$ and $\lim_{|\xi|\to\infty} \theta(\xi) = 0$.

Here c_1 and $c_3 > c_1$ denote the two stable equilibrium concentrations of the cytosolic calcium. When considering the system (1.1)–(1.2), we also assume that

$$\tau(c_1) = \tau(c_3) = 0, \quad \text{and} \quad \tau(c) \geq 0. \tag{3.5}$$

The function $f(\cdot)$ is often modelled in the form $f(c) = A(c-c_1)(c-a)(c_3-c)$ with appropriately chosen constants A, c_1, c_3 and a. For considerations concerning the physical values of A and the effective diffusion coefficient D, see e.g. [5] or [6]. Obviously, due the possibility of appropriate scaling, we can assume without losing generality that $c_1 = 0$ and $c_3 = 1$.

In the whole paper we will take the following assumptions:

ASSUMPTION 1. $f(c) = Ac(c-a)(1-c)$ and $(1-2a) > 0$. □

ASSUMPTION 2. The coefficients γ, λ, G, ν_1, ν_2 are constants, whereas $\tau = \tau(c)$. □

REMARK 3. The condition demanding that λ, G, ν_1, ν_2 are constants can be relaxed to the condition that λ, G, ν_1, ν_2 are appropriate functions of c. However, for clarity of exposition, we will not consider this generalization here. □

REMARK CONCERNING THE FORM OF $\tau(c)$. As we are not able to find explicit solutions in general, the form of $\tau = \tau(c)$ will be somehow adjusted to the form of the function θ. The precise form of $\tau = \tau(c)$ can depend on the kind of the tissue. It should be however positive for all c and must vanish for large c. In the paper, for sufficiently small relative values of the viscosity coefficient μ, $\tau = \tau(c)$ behaves approximately as $c(1-c)$, so it vanishes for $c = 0$ (as shown in Fig. 2a). Only in the last section $\tau(0) > 0$ (as in Fig. 2b). This agrees with the qualitative characterization of the traction terms, e.g. in [7]. □

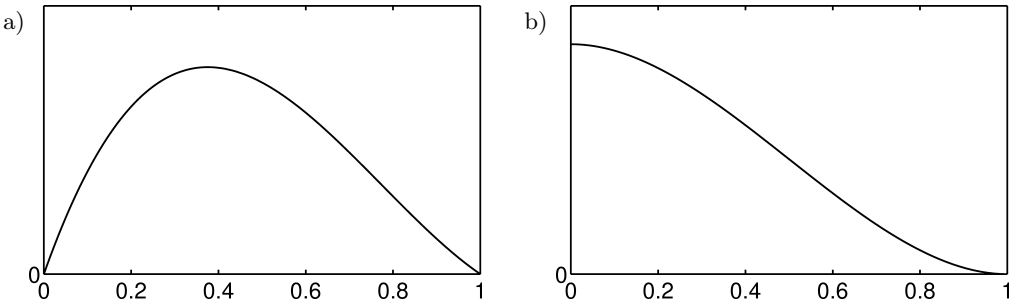

FIG. 2. a) The qualitative shape of τ as a function of $c \in [0,1]$ considered in Sec. 3; b) The shape of the function τ considered in Sec. 4.

It is known that for $\theta = 0$, Eq. (3.3) has a heteroclinic solution connecting its constant steady states $c = 0$ and $c = 1$ for one and only one value of the parameter v equal to

$$v = -(AD/2)^{1/2}(1-2a).$$

The solution is of the form:

$$c(\xi) = \frac{1}{1+\exp(-(A/2D)^{1/2}\xi)}.$$

We prove that under some assumption concerning the form of τ, a similar function satisfies the considered system. Let us make an assumption:

$$c = \frac{1}{1+\exp(-s\xi)}, \tag{3.6}$$

with $s \geq 0$. This function satisfies the identity:

$$c' = sc(1-c) \tag{3.7}$$

and $c(0) = 1/2$. Next, let us suppose that

$$\theta(\xi) = -qc(\xi)(1-c(\xi)) \tag{3.8}$$

for some positive $q \in \mathbb{R}^1$. Then

$$\theta' = -sqc(1-c)(1-2c). \tag{3.9}$$

Putting (3.8) into Eq. (3.3) and determining the profile of the wave, we obtain

$$Dc'' + vc' + Ac(c-a)(1-c) - \gamma qc(1-c) = 0$$

or equivalently:

$$Dc'' + vc' + Ac(c-a+\gamma qA^{-1})(1-c) = 0.$$

This equation has a heteroclinic solution

$$c(\xi) = \frac{1}{1+\exp(-(A/2D)^{1/2}\xi)} \tag{3.10}$$

satisfying the condition $c(0) = 1/2$ **iff**

$$v = -(AD/2)^{1/2}\left(1-2(a+\gamma qA^{-1})\right). \tag{3.11}$$

This means in particular that $s = \sqrt{A/2D}$. According to (3.6), (3.10) and (3.11),

$$vs = -\frac{A}{2}\left(1-2(a+\gamma qA^{-1})\right). \tag{3.12}$$

ASSUMPTION 3. Let for τ defined in Table 1, $\tau = \tau(c)$ be such that the identity

$$qc(1-c)\left[K + \frac{A}{2}\left(1-2(a+\gamma qA^{-1})\right)\mu(1-2c)\right] = \tau(c) \tag{3.13}$$

is satisfied (with μ given in Table 1). □

According to (3.12), the left-hand side of (3.13) can be written as $qc(1-c)\left[K - vs\mu(1-2c)\right]$, so Eq. (3.4) is fulfilled.

Displacements

Bulk medium. In this case we have $\mathbf{u} \equiv (u_1, 0, 0)$ and $u_1(x, y, z, t) = \int_{-\infty}^{\xi} \theta(h)dh$, so demanding that $u_1 \to 0$ for $x - vt \to -\infty$, we have according to (3.9):

$$u_1 = -qc(x, y, z, t)\sqrt{\frac{2D}{A}}.$$

Infinite layer. This case is described by Eq. (2.5). For simplicity, we also assume that

$$\tau_{11} = \tau_{33}.$$

Then by (2.5)

$$(\lambda + G)\theta + (\nu_1 + \nu_2/2)\theta_{,t} + \tau_{11} = 0, \tag{3.14}$$

whereas from (2.4)

$$\sigma_{11} = \theta\lambda + 2G\epsilon_{11} + \nu_1\theta_{,t} + \nu_2\epsilon_{11,t} + \tau_{11} = 0. \tag{3.15}$$

From (3.15) we obtain:

$$\sigma_{11} = \theta(\lambda + G) + 2G\epsilon_{11} + \left(\nu_1 + \frac{\nu_2}{2}\right)\theta_{,t} + \left[-G\theta - \frac{\nu_2}{2}\theta_{,t}\right] + \nu_2\epsilon_{11,t} + \tau_{11} = 0$$

and finally, by subtracting (3.14) we get

$$2G\epsilon_{11} + \left[-G\theta - \frac{\nu_2}{2}\theta_{,t}\right] + \nu_2\epsilon_{11,t} = 0. \tag{3.16}$$

Similarly, using (2.5) and (2.3) one obtains

$$2G\epsilon_{33} + \left[-G\theta - \frac{\nu_2}{2}\theta_{,t}\right] + \nu_2\epsilon_{33,t} = 0. \tag{3.17}$$

Neglecting the viscosity coefficient at the time derivative of ϵ_{11} in Eq. (3.16), we obtain:

$$2G\epsilon_{11} = G\theta + \frac{\nu_2}{2}\theta_{,t}.$$

By assumption,

$$G\theta + \frac{\nu_2}{2}\theta_{,t} = -Gqc(1 - c) - v\frac{\nu_2}{2}\theta' = \left(-G\frac{q}{s}c - v\frac{\nu_2}{2}\theta\right)'.$$

Using (3.2), we thus have

$$2Gu_1(x, y, z, t) = \int_{-\infty}^{\xi} \epsilon_{11}(h)dh = -G\frac{q}{s}c(\xi) - v\frac{\nu_2}{2}\theta(\xi)$$

$$= -G\frac{q}{s}c(\xi) - vq\frac{\nu_2}{2}c(\xi)(1 - c(\xi)),$$

hence

$$u_1(x,y,z,t) = -qc(\xi)\sqrt{\frac{D}{2A}}\left[1 - A\frac{\nu_2}{2G}(1-2(a+\gamma qA^{-1}))(1-c(\xi))\right].$$

The integration constant has been assumed to be equal to zero to assure that $u_1(-\infty) = 0$.

Now, let us analyze Eq. (3.17). By means of (3.9) we have

$$\begin{aligned} G\theta + \frac{\nu_2}{2}\theta_{,t} &= -Gqc(1-c) - v\frac{\nu_2}{2}\theta' \\ &= -Gqc(1-c) + vs\frac{\nu_2}{2}qc(1-c)(1-2c), \end{aligned}$$

so neglecting the viscosity coefficient by the time derivative of ϵ_{33} and using the fact that, by assumption, ϵ_{33} does not depend on z, we obtain by means of (3.12)

$$\begin{aligned} (3.18) \qquad & u_3(x,y,z,t) \\ & = -qc(\xi)(1-c(\xi))\left[\frac{1}{2} + \frac{A}{2G}(1-2(a+\gamma q))\frac{\nu_2}{2}(1-2c(\xi))\right] z. \end{aligned}$$

Similar calculations can be made for fibers and the bulk medium (with respect to the displacements in the x-direction). In the case of fibers (infinite cylinders) we use the fact of the radial symmetry, from which it follows that the dependence of the radial displacement on the radius r is the same as the dependence of u_3 on z at the z-axis. That is why the displacement along the radius is equal to $\epsilon_{33}\boldsymbol{r}$. The qualitative behaviour of the displacements u_1 and u_3 (in the case of thin layers and fibers) is shown in Fig. 3 and Fig. 4, respectively.

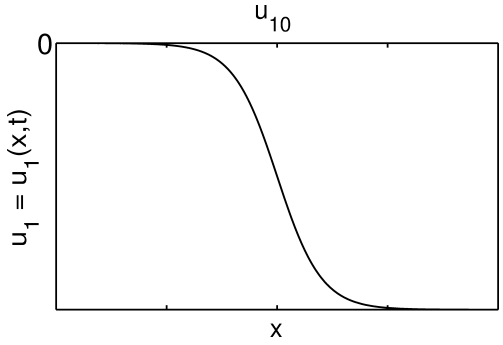

FIG. 3. Displacements in the x-directions. The displacement vectors $u_1(x,t)$ are directed to the left. $u_1(x,t) \to 0$ as $x \to -\infty$ and $u_1(x,t) \to u_{10} < 0$ as $x \to \infty$.

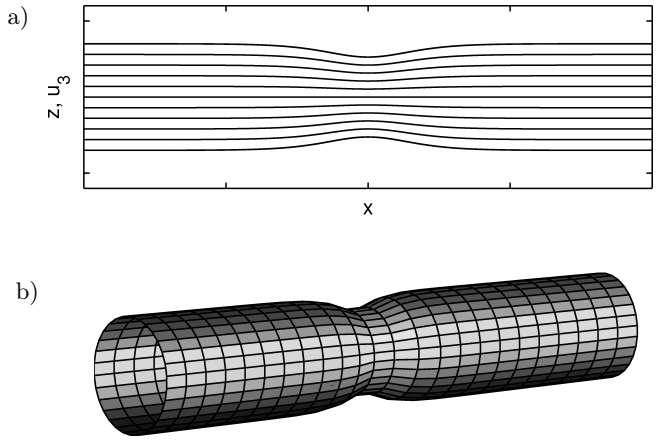

FIG. 4. Displacements in the z-direction; a) thin layer; b) long cylinder.

Remarks

1. Eq. (3.16) can be solved explicitly also with $\nu_2 \neq 0$. However, the solution obtained would have a much more complicated form. It is proved in [5] that for $\nu_2 \to 0$, this solution tends in $C^1(\mathbb{R})$-norm to the solution of Eq. (3.16) with $\nu_2 = 0$. This reasoning is justified by the fact that in most of the biological tissues, the viscosity effects for displacements propagating with the speeds characteristic for cytosolic calcium waves (10–100 μm/s) are small with respect to the elastic effects [4, 7].

2. As it follows from (3.18), $\epsilon_{13} \neq 0$ with $\epsilon_{13} = O(d)$. However, since the displacement vector is expressed up to linear terms in z, it is reasonable to take into account the strain tensor up to the zero-order terms in z since differentiation lowers the order of approximation by 1 (see [5]). In this sense, the assumed condition that the components of σ and ϵ depend only on x is satisfied. Thus asymptotically as $d \to 0$, we have $u_3 \equiv 0$, whereas the expression (3.18) can be viewed as a first-order perturbation. □

We have thus shown the validity of the following theorem.

THEOREM 1. *Let Assumptions* 1, 2 *and* 3 *be satisfied. Then for all* $q > 0$, *system* (3.3), (3.4) *has a heteroclinic solution* (v, c, θ) *with* v *given by* (3.11), $c(\xi)$ *by* (3.10) *and* $\theta(\xi)$ *by* (3.8). *The solution is unique up to a translation in* ξ. □

The functions $c(x - vt)$ and $\theta(x - vt)$, together with the corresponding displacement functions **u** (which were found above), satisfy the initial PDE system (1.1)–(1.3) exactly in the case of bulk unbounded medium. In the case of thin infinite layer and fibers, under the assumption of plane stress conditions on the boundary, system (1.1)–(1.3) is satisfied up to the terms of order $O(d)$ as $d \to 0$.

4. Mechanochemical travelling waves with mechanical constraints

In this section we consider the travelling wave solutions of the system

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c + f(c) + \gamma\theta, \tag{4.1}$$

$$\nabla \cdot \boldsymbol{\sigma} = k\mathbf{u}, \tag{4.2}$$

where $k = \text{const} > 0$. That is to say, we take into account the possibility of mechanical constraints which can counteract the displacements of the medium. The specific form of this constraint given by the right-hand side of Eq. (4.2) is called the Winkler model. We use the same methodology as in the previous sections. To be more precise, we exploit the explicit solution of the form (3.6) by appropriate choice of the function $\tau(c)$. For definiteness, we confine ourselves to the case of *bulk medium*. By the considerations of Sec. 2, in the case a plane travelling wave propagating along the x-axis in the bulk medium, we can assume that $\theta = \epsilon_{11}$ and $\mathbf{u} = (u_1, 0, 0) =: (u, 0, 0)$. It follows that

$$\theta = u_{,x} = u',$$

where $'$ denotes the differentiation with respect to $\xi = x - vt$. Unlike the previous section, we demand that $u(\xi) \to 0$ for $\xi \to \pm\infty$ by assuming

$$u(\xi) = -\zeta c'(\xi).$$

It follows that $\theta(\xi) = u'(\xi) = -\zeta c''(\xi)$. If we suppose that $c(\xi)$ is given by (3.6), then

$$\theta = -s\zeta c(1-c)(1-2c) \tag{4.3}$$

and θ' is a fourth-order polynomial in c, vanishing for $c = 0$ and $c = 1$. Eq. (4.2) can thus be written as

$$v\mu\theta' + Ks\zeta c(1-c)(1-2c) - k\zeta c + \eta = \tau(c), \tag{4.4}$$

where η is an integration constant. Obviously, for $\eta > 0$ sufficiently large, $\tau(c) \geq 0$ for $c \in [0,1]$ and $\tau(1) = 0$. Moreover, it follows from the implicit function theorem that for k sufficiently large with respect to K and μ sufficiently small, we can choose the constant $\eta > 0$ so large that $\tau(c) \geq 0$ for $c \in [0,1]$ and $\tau(1) = 0$. An example of such a graph is depicted in Fig. 2b). Putting the form of θ into Eq. (3.14) we arrive, by using (4.3), at the equation

$$Dc'' + vc' + Ac(c-a)(1-c) - \gamma s\zeta c(1-c)(1-2c) = 0.$$

Hence, for $\widetilde{\zeta} = \zeta/A$,

$$Dc'' + vc' + A(1 + 2\gamma\zeta s)c(1-c)(c - (a + \gamma\widetilde{\zeta}s)(1 + 2\gamma\widetilde{\zeta}s)^{-1}) = 0.$$

To calculate s we have to solve the equation

$$s = \left(\frac{A(1 + 2\gamma\widetilde{\zeta}s)}{2D}\right)^{1/2}$$

which implies

$$s = \frac{A\gamma\widetilde{\zeta} + \sqrt{A(2D + A\gamma^2\widetilde{\zeta}^2)}}{2D} = \frac{\gamma\zeta}{2D} + \sqrt{\frac{A}{2D} + \frac{\gamma^2\zeta^2}{4D^2}}.$$

Having the parameter s, we can calculate the speed of the wave. Thus

$$v = -\sqrt{\frac{(A + 2\gamma\zeta s)D}{2}}\left(1 - (a + \gamma\widetilde{\zeta}s)(1 + 2\gamma\widetilde{\zeta}s)^{-1}\right),$$

which can be written as

$$v = -Ds\left(1 - \frac{2a + 2\gamma\zeta s/A}{1 + 2\gamma\zeta s/A}\right).$$

This expression in its unfolded form is rather complicated. Asymptotically, for very large k, we have $\eta \cong \tau(0)$ and $\zeta \cong \tau(0)/k$, and the influence of mechanics on the speed of the wave is very small.

The graphs of displacement (u_1 – smooth line) and the dilation (θ – circled line) versus the coordinate x are given in Fig. 5.

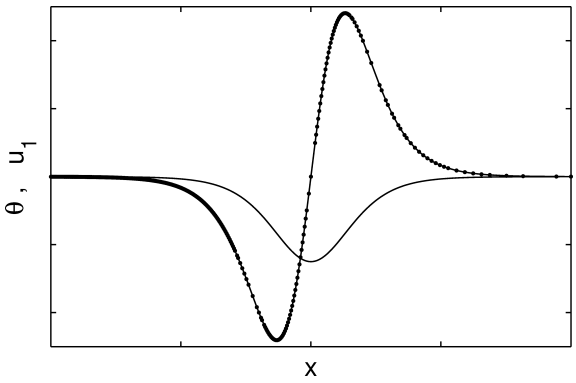

FIG. 5. Displacement u_1 (smooth line) and the dilation θ (circled line) for system (4.1)–(4.2).

5. Conclusions

In the paper we have presented explicit formulae for the travelling wave profiles as well as their speeds in a model describing the dynamics of cytosolic calcium and the accompanying mechanical effects, under some simplifying assumptions concerning the form of the traction $\tau(c)$ and the cubic-like source term $f(c)$. The meaning of this result is twofold: firstly, the explicit solution can provide us with some insight into the phenomena of mechano-chemical coupling; secondly, they can serve as a starting point for the analysis of more general problems.

Acknowledgements

This paper has been partially supported by the MNiSW grant N N501 132936 and by the FNP TEAM project "Mechanistic aspects and spatial organization of cell signalling". The authors are grateful to Kazimierz Piechór for helpful remarks and to Mikołaj Karpiński for help in preparing the manuscript.

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Received June 2, 2009; revised version December 28, 2009.