

Mechano-chemical calcium waves in systems with immobile buffers

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WE STUDY THE EXISTENCE of travelling waves of the free cytosolic calcium concentration in the presence of immobile buffers. We also take into account the mechano-chemical interaction. In the proof we use the *a priori* estimates for solutions of systems with diffusing buffers and pass to zero with their diffusion coefficients.

1. Setting of the problem

IN THE PAPER we analyze the problem of existence and properties of travelling wave solutions to a system of equations describing the evolution of the concentration of the cytosolic calcium inside the cells in the presence of immobile buffers. The model analyzed in this paper includes also the mechanical effects which accompany the non uniform distribution of calcium concentration under the assumption of the smallness of terms containing viscosity coefficients. The travelling waves are obtained in a limiting procedure from the waves for systems with non-zero diffusing coefficients of the buffers. To carry out this procedure, we apply the theory of travelling waves for the non-degenerate systems contained in [13] and pass to the limit with the diffusion coefficients of the buffers. The existence of chemical travelling waves together with their stability for the degenerate system (with non-diffusing buffers) was proved in a straightforward way in the paper [12]. It seems however, that the method used in our paper sheds an additional light on the properties of travelling waves in buffered systems. It considers the system with non diffusing buffers as a limit of equations with small diffusing coefficients and provides some additional information about the behaviour of solutions for the whole family of systems (parametrized by the values of the diffusion coefficients). In a sense it is more realistic, because in many situations we should take into account small but non vanishing diffusivities of the buffers. It should be emphasized that the above method of the existence proof exploits essentially the special structure

of the source terms of the considered equations, namely their monotonicity property.

Some results on the stability of equilibrium states and a threshold phenomenon for diffusing and non diffusing buffers are contained in [11]. However, the problem of relation between the travelling wave solutions for systems with diffusing and non diffusing buffers was not undertaken there.

Moreover, the considerations contained in the present paper may be treated as a preparatory step towards a more profound analysis (at the level of travelling waves) of coupling between the chemical and mechanical effects in systems with immobile buffers. To be more precise, in this paper we consider only elastic mechanical effects, whereas the viscous phenomena are neglected. These phenomena may be taken into account by using perturbation methods. Such an analysis, in the case of systems without buffers, has been carried out in [5].

The majority of papers (see, e.g. [10, 12] and the references therein) takes only chemical effects into account. However, the experimental evidence shows that waves of calcium concentration can be activated by a mechanical stimulus (see Fig. 12.8 in [6]). Similarly, the variation of calcium concentration causes also some mechanical effects in the tissue, like, e.g. the phenomenon of motility of some microorganisms [7–9].

The cell cytoplasm consists mostly of a viscoelastic gel with macromolecular fibres, composed of actin linked by myosin bridges. When these fibers are strongly linked, the cytoplasm tends to the gel-state and it solates otherwise. In this way the cell may contract and change its shape. *The sol-gel transition and thus the cell's contractility is controlled chemically by the calcium concentration in the cytogel* [8, 9]. Thus the mathematical description of the above mentioned processes should take into account both the variations in the calcium concentration as well as the accompanying mechanical stresses. Such a model can be found for example in [9, 8] and it constitutes the basis of our considerations here.

The evolution of free calcium and buffers concentrations is often described ([2, 6, 10]) by the following system of equations:

$$(1.1) \quad \begin{aligned} \frac{\partial u}{\partial t} &= D\Delta u + g(u) + \sum_{i=1}^n [k_-^i v_i - k_+^i u(b_0^i - v_i)] + \gamma\theta, \\ \frac{\partial v_i}{\partial t} &= D_i\Delta v_i - [k_-^i v_i - k_+^i u(b_0^i - v_i)], \quad i = 1, \dots, n. \end{aligned}$$

Here Δ denotes the Laplace operator in the space \mathbb{R}^s , $s \geq 1$, u denotes the free cytosolic calcium concentration, whereas v_i denotes the concentration of these particles of the i -th buffer, which have attached the calcium ions. Thus $v_i = [Ca^{2+} B_i]$ and $b_0^i = [B_i] + [Ca^{2+} B_i]$; $k_-^i > 0, k_+^i > 0$ are kinetic constants. $D > 0$ and $D_i > 0$ denote the diffusion coefficients of calcium and the i -th buffer

respectively. The influence of mechanics on chemistry follows from the presence of the term $\gamma\theta$, where γ is a constant and $\theta = \nabla \cdot \mathbf{d}$ denotes the mechanical dilation, i.e. the divergence of the displacement field \mathbf{d} . The above system is to be supplemented by the equation describing the balance of mechanical forces. It has the form (see [8] p. 591):

$$(1.2) \quad \nabla \cdot \left\{ \frac{E}{1+\nu} \left[\boldsymbol{\varepsilon} + \frac{\nu}{1-2\nu} \theta \mathbf{I} \right] + \mu_1 \frac{\partial \boldsymbol{\varepsilon}}{\partial t} + \mu_2 \frac{\partial \theta}{\partial t} \mathbf{I} + \tau(c) \mathbf{I} \right\} = 0.$$

The first term under the divergence symbol is the elastic part of the stress tensor (corresponding to elastic forces), the second term is the viscous part (corresponding to viscous forces) and the third term is the so-called traction tensor (corresponding to the traction forces). The expression on the right-hand side denotes the volume forces. As we have mentioned above $\mathbf{d} = \mathbf{d}(\mathbf{x}, t)$ denotes the displacement, $\boldsymbol{\varepsilon}$ is the strain tensor, i.e. $\boldsymbol{\varepsilon} = 1/2(\nabla \mathbf{d} + \nabla \mathbf{d}^T)$, E – Young modulus, ν – Poisson ratio, μ_1, μ_2 – shear and bulk viscosities, \mathbf{I} – unit matrix, $\tau(u) \mathbf{I}$ – active concentration stress resulting from the actin-myosin traction $\tau(u)$. Let us note that the inertial forces have been neglected. Also the external forces $\rho \mathbf{d}$ measuring the strength of the cells attachment to the surrounding medium, have not been taken into account.

In this paper we confine ourselves to a spatially one-dimensional case. Then Eq. (1.2) changes to a simpler form:

$$(1.3) \quad \frac{\partial}{\partial x} \left[\mu \frac{\partial \theta}{\partial t} + K\theta + \tau(u) \right] = 0,$$

where

$$\mu = \mu_1 + \mu_2$$

and

$$K = E(1-\nu)/[(1+\nu)(1-2\nu)].$$

We are interested in solutions to system (1.1)–(1.3) which tend to finite well defined limits for $|x| \rightarrow \infty$. A special class of such functions are the so-called travelling wave solutions. Thus we are looking for solutions having the following form:

$$(1.4) \quad u(x, t) = u(\xi), \quad v_i(x, t) = v_i(\xi), \quad \theta(x, t) = \theta(\xi), \quad i = 1, \dots, n,$$

where $\xi := x - qt$; $q \in \mathbb{R}^1$ is the speed of the wave. The above ansatz changes the system (1.1)–(1.2) into a system of ordinary differential equations of the form:

$$(1.5) \quad Du'' + qu' + g(u) + \sum_{i=1}^n G_i(u, v_i) = 0,$$

$$(1.6) \quad D_i v_i'' + qv_i' - G_i(u, v_i) = 0, \quad i = 1, \dots, n,$$

$$(1.7) \quad -q\mu\theta' + K(\theta, u)\theta + \tau(u) = \sigma,$$

where symbol $'$ denotes differentiation with respect to the variable ξ , σ is an integration constant and

$$(1.8) \quad G_i(u, v_i) = k_-^i v_i - k_+^i u (b_0^i - v_i).$$

As we have mentioned above, we neglect the term $q\mu\theta'$ treating it as not essential in comparison with the elastic term $K(\theta, u)\theta$ for typical values of μ , K (see, e.g. [1]) q and the width of the wave. The considered waves are very slow, with the speed q of the order of several μm per second ([6, 2]). For example, for striated muscle we have: $\mu = 2 \text{ kPa}\cdot\text{s}$, $E = 10^3 \text{ kPa}$ and the mean ratio of the viscous to elastic forces $(q\mu|\theta'|)/(K|\theta|)$ is of the order of $5 \cdot 10^{-3}$. As we noted, the viscosity phenomena may be taken into account by using the perturbation methods [5].

ASSUMPTION 1. Let $\mu = 0$. Let us assume that for all $u \geq 0$ and all $\sigma \in \mathbb{R}^1$, the equation $K(\theta, u)\theta + \tau(u) = \sigma$ has a unique solution $\theta_0(u, \sigma)$ of C^1 class. \square

In view of the Assumption 1, the analysis of system (1.5)–(1.7) is equivalent to the analysis of the system

$$(1.9) \quad Du'' + qu' + f(u) + \sum_{i=1}^n G_i(u, v_i) = 0,$$

$$(1.10) \quad D_i v_i'' + qv_i' - G_i(u, v_i) = 0, \quad i = 1, \dots, n,$$

where

$$(1.11) \quad f(u) = g(u) + \gamma\theta_0(u, \sigma).$$

ASSUMPTION 2. Assume that $\sigma \in \mathbb{R}^1$ is such that the function $f(\cdot)$ is of bistable type, i.e. that the equation $f(u) = 0$ has exactly three solutions: $u_1 > 0$, $u_3 > u_1$ and $u_2 \in (u_1, u_3)$. The zeros u_1 and u_3 are stable, i.e. $f'(u_1) < 0$, $f'(u_3) < 0$, whereas u_2 is unstable, i.e. $f'(u_2) > 0$. \square

A standard example of a function satisfying the above assumption is a cubic polynomial $f(u) = (u - w)(1 - u)(u - u_0)$, $w \geq 0$, with $u_0 \in (w, 1)$.

It is easy to note that there are exactly three constant steady states of the system (1.9)–(1.10), corresponding to the three solutions of the equation $f(u) = 0$, namely:

$$(1.12) \quad P_k = (u_k, v_1^k, \dots, v_n^k), \quad k = 1, 2, 3,$$

where

$$(1.13) \quad v_j^k = u_k \frac{k_+^j b_0^j}{(k_-^j + k_+^j u_k)}.$$

It is easy to note that

$$(1.14) \quad v_j^1 < v_j^2 < v_j^3, \quad j = 1, \dots, n,$$

thus component-wise

$$(1.15) \quad P_1 < P_2 < P_3.$$

In this paper we are interested in the travelling wave solutions to system (1.9)–(1.10) in the limit $D_i \rightarrow 0$, $i = 1, \dots, n$, joining the constant steady states P_1 and P_3 . We thus assume that the functions $u(\xi)$ and $v_i(\xi)$, $i = 1, \dots, n$, satisfy the following boundary conditions at infinities:

$$(1.16) \quad \begin{aligned} \lim_{\xi \rightarrow -\infty} (u(\xi), v_1(\xi), \dots, v_n(\xi)) &= (u_1, v_1^1, \dots, v_n^1) = P_1, \\ \lim_{\xi \rightarrow \infty} (u(\xi), v_1(\xi), \dots, v_n(\xi)) &= (u_3, v_1^3, \dots, v_n^3) = P_3, \\ \lim_{|\xi| \rightarrow \infty} (u'(\xi), v_1'(\xi), \dots, v_n'(\xi)) &= (0, 0, \dots, 0). \end{aligned}$$

Let us note that the functions G_i given by (1.8) are of C^∞ class of their arguments. Let us denote:

$$(1.17) \quad U := (U_1, U_2, \dots, U_{n+1}) := (u, v_1, \dots, v_n)$$

and

$$(1.18) \quad \begin{aligned} F_1(U) &:= f(u) + \sum_{i=1}^n G_i(u, v_i), \\ F_i(U) &:= -G_{i-1}(u, v_{i-1}), \quad i = 2, \dots, n+1. \end{aligned}$$

According to the Assumption 2 and the form of the functions G_i , one can easily note that for all $U \in [P_1, P_3]$ the following conditions hold

$$(1.19) \quad F_{i,j}(U) \geq 0, \quad i \neq j,$$

where $F_{i,j} = F_{i,U_j}$.

Conditions (1.19) are the so-called monotonicity conditions (see [13]). Moreover,

$$(1.20) \quad F_{1,j}(U) > 0, \quad F_{j,1}(U) > 0, \quad j > 1.$$

As we have mentioned above, our main aim is to prove the existence of heteroclinic solutions for a partially degenerated version of the system (1.9)–(1.10), i.e. the system

$$(1.21) \quad Du'' + qu' + f(u) + \sum_{i=1}^n G_i(u, v_i) = 0,$$

$$(1.22) \quad qv'_i - G_i(u, v_i) = 0, \quad i = 1, \dots, n.$$

In a spatially one-dimensional case, this is equivalent to the existence of heteroclinic travelling waves for the system:

$$(1.23) \quad \begin{aligned} \frac{\partial u}{\partial t} &= D \frac{\partial^2 u}{\partial x^2} + f(u) + \sum_{i=1}^n G_i(u, v_i), \\ \frac{\partial v_i}{\partial t} &= -G_i(u, v_i), \quad i = 1, \dots, n. \end{aligned}$$

In the existence proof we will refer to the properties of a single scalar equation of the form:

$$(1.24) \quad Du'' + qu' + f(u) = 0.$$

This equation has a unique (up to a translation in ξ), heteroclinic solution u_r (such that $u(-\infty) = u_1$ and $u(\infty) = u_3$), corresponding to the speed q_r .

Summarizing, in the paper we prove that monotone travelling waves for systems with vanishing diffusion for all of the buffers, i.e. for systems (1.23), are a limit of travelling waves with monotone profiles in the systems with non-zero diffusion coefficients D_i , $i = 1, \dots, n$. Monotonicity is an important property here since it is known (see Theorem 6.1 p. 245 in [13]) that non monotone travelling waves are unstable, whereas the monotone ones are stable. As we have said above, the information about the influence of elastic mechanical effects on the chemical travelling wave is stored in the source term $f(u)$. By means of the results of Sec. 2 we are able to prove, for all arbitrarily small but non-zero diffusion coefficients of the buffers, the existence of the desired heteroclinic travelling waves, using the theory contained in [13] (see Theorem 1 on page 13). The existence result for the travelling wave solutions to system (1.21)–(1.22) is formulated in Theorem 3 on page 20.

2. Linearization matrices

In this section we will present the properties of the matrices obtained by linearization of the source terms at the right-hand sides of the system (1.9)–(1.10), at the points P_k , $k = 1, 2, 3$. The objective of this section is to characterize the eigenvalues and eigenvectors of the above mentioned matrices.

One can easily check that for $u = u_k + \delta u$, $v_j = v_j^k + \delta v_j$, the first-order Taylor expansion of the vector function corresponding to the source terms of

system (1.9)–(1.10) has the following form:

$$(2.1) \quad \begin{bmatrix} f(u) + \sum_{i=1}^n G_i(u, v_i) \\ -G_1(u, v_1) \\ \dots \\ -G_n(u, v_n) \end{bmatrix} \cong \mathcal{M} \begin{bmatrix} \delta u \\ \delta v_1 \\ \dots \\ \delta v_n \end{bmatrix},$$

where $(n+1) \times (n+1)$ matrix \mathcal{M} is defined as

$$(2.2) \quad \mathcal{M} = \begin{bmatrix} a - \sum_{i=1}^n a_i & b_1 & \dots & b_n \\ a_1 & -b_1 & \dots & 0 \\ \dots & \dots & \dots & \dots \\ a_n & 0 & \dots & -b_n \end{bmatrix},$$

with

$$(2.3) \quad a = f_{,u}(u_k), \quad a_i = -G_{i,u}(u_k, v_i^k), \quad b_i = G_{i,v_i}(u_k, v_i^k).$$

According to (1.8) and (1.13), the following inequalities are satisfied:

$$(2.4) \quad a_i > 0, \quad b_i > 0, \quad i = 1, \dots, n.$$

In Section 4 we will need the following lemma characterizing the properties of the matrix \mathcal{M} .

LEMMA 1. *The matrix \mathcal{M} is irreducible. For $a < 0$, the eigenvalues μ of the matrix \mathcal{M} are contained in the left half-plane $\text{Re}(\mu) < 0$, for $a > 0$ the eigenvalues μ of the matrix \mathcal{M} are contained in the right half-plane $\text{Re}(\mu) > 0$.*

□

In Section 3 we will also need the lemma concerning the positivity of the eigenvector corresponding to the principal (Perron–Frobenius) eigenvalue of the matrix \mathcal{M} . The notion of the principal eigenvalue is given in

LEMMA 2. *Let C be an $N \times N$ matrix with non-negative off-diagonal entries. Then C has a real eigenvalue $\mu_{PF}(C)$ such that an associated eigenvector has non-negative components and every other eigenvalue of C has its real part less than $\mu_{PF}(C)$.*

□

The following lemma holds.

LEMMA 3. *Let \mathcal{M} be defined by conditions (2.1)–(2.2). Then its principal eigenvector (corresponding to the principal eigenvalue) may be chosen positive independently of the value of a .*

□

The proof of Lemmas 1 and 3 is straightforward and is based on Theorems 5 and 6, p. 350, Theorems 1, 2, p. 334 and Theorem 3, p. 344 in [3]. (The details are left to the reader.)

3. Estimations of the derivatives and the speed for heteroclinic solutions to system (1.9)–(1.10)

In this section using the special structure of the considered system, we estimate the derivatives of the monotone heteroclinic solutions to system (1.9)–(1.10) together with the values of the speed q . (We assume that such solutions exist. The existence theorem for the non-degenerate system, i.e. with all the diffusion coefficients positive, is given in Sec. 4.) Our aim is mainly to examine the properties of the heteroclinic solutions as the coefficients D_i , $i = 1, \dots, n$ tend to zero. The estimations derived in this section will be a basis for obtaining a solution to the system with $D_i = 0$.

LEMMA 4. *For any C^2 monotone heteroclinic solution $(u, v_1, \dots, v_n)(\cdot)$ of system (1.9)–(1.10) we have the estimations*

$$(3.1) \quad \|u\|_{C^3(\mathbb{R}^1)} < S_1, \quad \|v_i\|_{C^2(\mathbb{R}^1)} < S_2, \quad i = 1, \dots, n.$$

The constants S_1 and S_2 are independent of $D_i > 0$, $i = 1, \dots, n$. □

P r o o f. First, we will estimate the first derivative of the function $u(\cdot)$. Let us suppose that the supremum of u' is attained for some $\xi_0 \in \mathbb{R}^1$. As $\lim_{\xi \rightarrow \pm\infty} u'(\xi) = 0$, hence we must have $u''(\xi_0) = 0$ and $q = -G(u(\xi_0), v_1(\xi_0), \dots, v_n(\xi_0))(u'(\xi_0)^{-1})$, where we have denoted

$$(3.2) \quad G(u, v_1, \dots, v_n) = f(u) + \sum_{i=1}^n G_i(u, v_i).$$

Multiplying Eq.(1.9) by $u'(\xi)$ and integrating over $(-\infty, \xi_0)$, we arrive at the equality

$$\begin{aligned} \frac{1}{2} D u'^2(\xi_0) &= G(u(\xi_0), v_1(\xi_0), \dots, v_n(\xi_0)) \int_{-\infty}^{\xi_0} \frac{u'(\xi)}{u'(\xi_0)} u'(\xi) d\xi \\ &\quad - \int_{-\infty}^{\xi_0} G(u(\xi), v_1(\xi), \dots, v_n(\xi)) u'(\xi) d\xi. \end{aligned}$$

Hence, due to the monotonicity of the functions u, v_1, \dots, v_n , and the continuity of the function G , the right-hand side of this equation can be estimated from

above by the expression

$$C \int_{-\infty}^{\xi_0} u'(\xi) d\xi \leq Cu(\xi_0),$$

where C is a constant independent of the value of ξ_0 . As $D > 0$ we obtain from here the global boundedness of the C^1 norm of the function $u(\cdot)$ independently of the value of q . Next, note that for all $\xi \in \mathbb{R}^1$ we have $|qu'(\xi)| \leq |qu'(\xi_0)|$ (where ξ_0 is the point of supremum of u'). Thus using the equation for u , we can estimate also the second derivatives of this function. As a result, we have proved that

$$(3.3) \quad \|u\|_{C^2(\mathbb{R}^1)} < C_{2u}.$$

Now, we prove that also the C^1 norms of the functions v_k , $k = 1, \dots, n$, are bounded, without imposing any lower bounds for the coefficients $D_k > 0$. Suppose that $v'_k(\cdot)$ attains its global maximum at $\xi = \xi_0$. (Then ξ_0 must be finite as $v'_k(\xi) \rightarrow 0$ for $\xi \rightarrow \pm\infty$.) Differentiation of the k -th equation of system (1.10) with respect to ξ gives:

$$0 = D_k v_k'''(\xi_0) - G_{k,v_k}(u(\xi_0), v_k(\xi_0))v'_k(\xi_0) - G_{k,u}(u(\xi_0), v_k(\xi_0))u'(\xi_0).$$

As ξ_0 is the point of maximum of v'_k we must have $v_k'''(\xi_0) \leq 0$. Now, independently of ξ_0 ,

$$(3.4) \quad G_{k,v_k}(u(\xi_0), v_k(\xi_0)) \geq B_k > 0,$$

(see point 2 of the Assumption 2), so the sum of the first two terms at the right-hand side can be annihilated only by the third term as $-G_{k,u}(u(\xi_0), v_k(\xi_0)) > 0$. However, the last quantity is bounded for any $P_1 \leq (u, v_1, \dots, v_n) \leq P_3$. Thus $v_k(\cdot)$ must be bounded in its C^1 norm for all $k \in \{1, \dots, n\}$.

Finally, let us estimate the behaviour of the second derivatives of the functions v_k , $k = 1, \dots, n$ independently of the values of $D_k > 0$. These estimations are also based on inequalities (3.4). Namely, differentiating twice the equation for v_k , $k = 1, \dots, n$ (see the remark after Eq. (1.8)), we obtain

$$0 = D_k v_k''''(\xi) + qv_k'''(\xi) - G_{k,v_k}(u(\xi), v_k(\xi))v_k''(\xi) \\ - G_{k,u}(u(\xi), v_k(\xi))u''(\xi) - 2G_{k,uv_k}(u(\xi), v_k(\xi))u'(\xi)v_k'(\xi).$$

(Let us note that $G_{k,uu}(u, v_k) \equiv 0$ and $G_{k,v_k v_k}(u, v_k) \equiv 0$ due to the specific form of the function G_k given by (1.8).) Suppose that v_k'' attains its global maximum (minimum) at $\xi = \xi_0$. Then $v_k'''(\xi_0) = 0$, $v_k''''(\xi_0) \leq 0$ ($v_k''''(\xi_0) \geq 0$). Thus using

the inequality (3.4) we infer that $|v_k''(\xi_0)|$ can be estimated by $|u|_{C^2(\mathbb{R}^1)}$ and $|v|_{C^1(\mathbb{R}^1)}$.

Now, differentiating the equation for u and using the arguments leading to the estimations of the second derivatives of this function (as before (3.3)), we obtain the estimate of the third derivative of u . (The details are left to the reader.) We have thus completed the estimations (3.1). The lemma is proved. \square

LEMMA 5. *Let F be given by (1.18). Let $N(P_1)$ and $N(P_3)$ denote the eigenvector corresponding to the Perron–Frobenius eigenvalue of $DF(P_1)$ and $DF(P_3)$ respectively. Then there exist $r > 0$ and $\vartheta > 0$ such that for each $i \in \{1, \dots, n+1\}$,*

$$\text{dist}(U, W_{0i}) < \vartheta \implies F_i(U) < 0,$$

$$\text{dist}(U, W_{1i}) < \vartheta \implies F_i(U) > 0,$$

where

$$W_{0i} = \{U : P_1 \leq U \leq P_1 + rN(P_1), U_i = P_{1i} + rN_i(P_1)\},$$

$$W_{1i} = \{U : P_3 \geq U \geq P_3 - rN(P_3), U_i = P_{3i} - rN_i(P_3)\}.$$

\square

P r o o f. Let μ_{PF} denote the Perron–Frobenius eigenvalue of $DF(P_1)$. Then r may be taken so small that $F(P_1 + rN(P_1)) = rDFN(P_1) + o(r) < \frac{1}{2}r\mu_{PF}N(P_1)$. By means of conditions (2.1), (2.2) we conclude that $F_i(U) < 0$ for $U \in W_{0i}$. In consequence there exists $\vartheta = \vartheta(r) > 0$ such that the first of the above relations is satisfied. In the same way we prove the second relation. \square

LEMMA 6. *Let F and r be the same as in Lemma 5. Then for any point $U \in W_0 = \{U : P_1 \leq U \leq P_1 + rN(P_1), U \neq P_1\}$ there exists $i \in \{1, \dots, n+1\}$ such that $F_i(U) < 0$. Likewise, for any point $U \in W_1 = \{U : P_3 \geq U \geq P_3 - rN(P_3), U \neq P_3\}$ there exists $i \in \{1, \dots, n+1\}$ such that $F_i(U) > 0$. \square*

P r o o f. Let us take an arbitrary point $U = (U_1, \dots, U_{n+1}) \in W_0$. Let

$$\tilde{r} = \max_j (U_j - P_{1j})(rN_j(P_1))^{-1} = (U_k - P_{1k})(rN_k(P_1))^{-1}$$

for some $k \in \{1, \dots, n+1\}$. (Let us remind that the components of the Perron–Frobenius eigenvectors are strictly positive according to Lemma 3.) As $\tilde{r} \leq r$ then it follows from the proof of Lemma 5 that it holds with r replaced by \tilde{r} and $\vartheta(r)$ replaced by $\vartheta(\tilde{r})$. In consequence, $F_k(U) < 0$ for $u \in \widetilde{W}_{0k} = \{U : P_1 \leq U \leq P_1 + \tilde{r}N(P_1), U_k = \tilde{r}N_k(P_1)\}$. In the same way we consider the parallelepiped W_1 . The lemma is proved. \square

As a corollary to Lemma 6 we have the following lemma.

LEMMA 7. *Let F be the same as in Lemma 5. Then, there does not exist a point U , $0 < |U - P_1| < \tilde{\delta}$, $\tilde{\delta}$ sufficiently small, such that $F_i(U) \geq 0$ for all $i \in \{1, \dots, n+1\}$. Likewise there does not exist a point U , $0 < |P_3 - U| < \tilde{\delta}$, $\tilde{\delta}$ sufficiently small, such that $F_i(U) \leq 0$ for all $i \in \{1, \dots, n+1\}$. \square*

P r o o f. It suffices to take $\tilde{\delta} < r$ and apply Lemma 6. \square

Now, we are able to prove *a priori* estimates for q .

LEMMA 8. *If $(q, U(\cdot))$ is a strictly monotone heteroclinic solution for system (1.9)–(1.10), then $|q| < Q$, where Q is independent of U . \square*

P r o o f. As $U(\xi) \rightarrow P_1$ monotonically as $\xi \rightarrow -\infty$, then there must exist an index i and $\xi = \xi_0$ such that $U(\xi)$ enters the region $P_1 \leq U \leq P_1 + rN(P_1)$ through the (closed) set W_{0i} , i.e. $U(\xi_0) \in W_{0i}$ (see Lemma 5). Let us take $\xi_1 < \xi_0$ such that $U_i(\xi_0) - U_i(\xi_1) = \frac{\vartheta}{2}$. Integrating the i -th equation of system (1.9)–(1.10) we obtain

$$(3.5) \quad R_1 + q \frac{\vartheta}{2} + \int_{\xi_1}^{\xi_0} F_i(U(s)) ds = 0,$$

where $|R_1| \in (0, \max\{S_1, S_2\})$ according to Lemma 4, and $F_i(U(s)) < 0$ for $s \in (\xi_1, \xi_0)$ according to Lemma 7. If $q \leq 0$ then $q \geq -2R_1\vartheta^{-1}$. If $q > 0$ then by analyzing the behaviour of a heteroclinic trajectory near the P_3 , we can prove the upper bound for q . \square

4. Travelling waves for the non-degenerate system

By means of the results of Sec. 2 one can check the validity of the existence theorem for the heteroclinic solutions to system (1.9)–(1.10) for $D > 0$, $D_i > 0$, $i = 1, \dots, n$.

THEOREM 1. *Let the Assumption 2 be satisfied. Let D, D_1, \dots, D_n be positive. Then there exists a unique (up to a translation in ξ) heteroclinic strictly increasing solution to system (1.9)–(1.10) satisfying conditions (1.16). \square*

The proof follows from the results of Sec. 2 and Theorem 2.1, p. 15 in [13], which is cited below.

THEOREM 2. (Theorem 2.1, p.15 in [13])

Let us consider the system

$$(4.1) \quad \frac{\partial U}{\partial t} = A\Delta U + F(U),$$

where $\Delta = \partial^2/\partial x_1^2 + \dots + \partial^2/\partial x_s^2$, $s \geq 1$, $U = (U_1, \dots, U_N)$ is a vector-valued function, A is a diagonal positive-definite matrix and $C^1 \ni F(\cdot) : \mathbb{R}^N \rightarrow \mathbb{R}^N$. Let system (4.1) be monotone, i.e.

$$\frac{\partial F_i}{\partial U_j} \geq 0, \quad i, j = 1, \dots, N, \quad i \neq j.$$

Further, let the function $F(U)$ vanish in a finite number of points w_-, w_+ and \mathbf{U}_k , ($k = 1, \dots, m$) with $w_- < \mathbf{U}_k < w_+$. Let us assume that all the eigenvalues of the matrices $\partial F(w_-)$ and $\partial F(w_+)$ lie in the left half-plane, and that the matrices $\partial F(\mathbf{U}_k)$, ($k = 1, \dots, m$) are irreducible and have at least one eigenvalue in the right half-plane. Then there exists a unique monotone travelling wave, i.e. a constant q and a twice continuously differentiable monotone vector-valued function $U(\xi)$, $\xi = x_1 - qt$, satisfying the system

$$(4.2) \quad AU'' + qU' + F(U) = 0,$$

such that $U'_j(\xi) > 0$ for all $j = 1, \dots, N$, $\xi \in \mathbb{R}$, and

$$\lim_{\xi \rightarrow \pm\infty} U(\xi) = w_{\pm}, \quad \lim_{\xi \rightarrow \pm\infty} U'(\xi) = 0.$$

□

5. Existence of heteroclinic solutions to system (1.21)–(1.22)

In this section we will prove the existence of the heteroclinic solutions to system (1.21)–(1.22). Let us note that for $D_i = 0$, $i = 1, \dots, n$, and for $q \neq 0$, system (1.9)–(1.10) can be written as the first order system of ODEs of the form

$$(5.1) \quad \begin{aligned} u' &= z, \\ z' &= \frac{1}{D} \left[-qz - f(u) - \sum_{k=1}^n G_k(u, v_k) \right], \\ v'_i &= \frac{1}{q} G_i(u, v_i), \quad i = 1, \dots, n, \end{aligned}$$

with the following linearization around the point $(u_2, 0, v_1^2, \dots, v_n^2)$ (corresponding to P_2):

$$(5.2) \quad \begin{pmatrix} h_u \\ h_z \\ h_1 \\ \dots \\ h_n \end{pmatrix}' = L \begin{pmatrix} h_u \\ h_z \\ h_1 \\ \dots \\ h_n \end{pmatrix}$$

where

$$(5.3) \quad L = \begin{pmatrix} 0 & 1 & 0 & \dots & 0 \\ \frac{1}{D} \left[-a + \sum_{i=1}^n a_i \right] & -\frac{q}{D} & -\frac{1}{D} b_1 & \dots & -\frac{1}{D} b_n \\ -\frac{1}{q} a_1 & 0 & \frac{1}{q} b_1 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ -\frac{1}{q} a_n & 0 & 0 & \dots & \frac{1}{q} b_n \end{pmatrix},$$

with a , a_i and b_i satisfying Eqs. (2.2) and (2.5) with $k = 2$.

It may happen that while decreasing the coefficients D_i to zero the heteroclinic solution connecting P_1 with P_3 cannot split into two waves joining in turn the points P_1 with P_2 and P_2 with P_3 . We will prove that such a situation is impossible. Suppose to the contrary that the above splitting into the two heteroclinics is possible. These waves would be a limit (as $D_1, \dots, D_n \rightarrow 0$) of heteroclinics with positive first derivatives. Then, for a fixed $q \neq 0$ there would exist simultaneously:

- 1) non-negative eigenvalue λ_+ of the matrix (5.3) with $a > 0$ and a corresponding eigenvector $N_{2+} = (h_u, h_z, h_1, \dots, h_n)^T$ with non-negative components.
- 2) non-positive eigenvalue λ_- of the matrix (5.3) with $a > 0$ and a corresponding eigenvector $N_{2-} = (h_u, h_z, h_1, \dots, h_n)$ with $h_n \geq 0$, $h_k \geq 0$ and $h_z \leq 0$.

These conditions follow from the fact the second heteroclinic must start from P_2 into the set $\{(U : U - P_2 \geq 0 \text{ component-wise})\}$ as ξ increases from $(-\infty)$ whereas the first heteroclinic must achieve P_2 from the set $\{(U : U - P_2 \leq 0 \text{ component-wise})\}$ as ξ tends to (∞) .

LEMMA 9. *For a fixed $q \neq 0$ the Conditions 1 and 2 cannot be fulfilled simultaneously.* \square

P r o o f. First suppose that $q > 0$. Let us assume that there exists a non-negative eigenvalue $\lambda_+ \geq 0$ and a non-zero associated eigenvector is non-negative

and has the form $N_{2+} = (h_u, h_z, h_1, \dots, h_n)^T$. We have

$$(5.4) \quad LN_{2+} = \begin{pmatrix} h_z \\ \frac{1}{D} \left[-a + \sum_{i=1}^n a_i \right] h_u - \frac{q}{D} h_z - \frac{1}{D} \sum_{k=1}^n b_k h_k \\ -\frac{1}{q} a_1 h_u + \frac{1}{q} b_1 h_1 \\ \dots\dots\dots \\ -\frac{1}{q} a_n h_u + \frac{1}{q} b_n h_n \end{pmatrix}.$$

The non-negativity of the last n components of LN_{2+} implies that

$$-h_u a_k + h_k b_k \geq 0, \quad k = 1, \dots, n.$$

Simultaneously, the non-negativity of the second component implies

$$\sum_{k=1}^n (h_u a_k - h_k b_k) - q h_z - h_u a \geq 0, \quad k = 1, \dots, n.$$

For $q > 0$ and $a > 0$ the last two inequalities cannot be satisfied simultaneously.

So, let $q < 0$. Suppose that there exist a non-positive eigenvalue λ_- and the associated eigenvector $N_{2-} = (h_u, h_z, h_1, \dots, h_n)$ with $h_z \leq 0$, $h_u \geq 0$ and $h_k \geq 0$. Then $(LN_{2-})_{l+2} = \lambda_- h_l \leq 0$, $l = 1, \dots, n$, hence $\sum_{k=1}^n (h_u a_k - h_k b_k) \leq 0$.

Thus, as $(LN_{2-})_2 = \lambda_- h_z \geq 0$, we must have $-\frac{1}{D} a h_u - \frac{q}{D} h_z + \frac{1}{D} \sum_{k=1}^n (h_u a_k - h_k b_k) \geq 0$. As $a > 0$, this inequality may be fulfilled only for $h_u = h_z = 0$ and $\sum_{k=1}^n (h_u a_k - h_k b_k) = 0$. Consequently, each h_k must be equal to zero and $N_{2-} \equiv 0$.

This finishes the proof of the lemma. \square

When $D_i > 0$, the heteroclinic solutions $U(\xi)$ are monotonically increasing. Consequently, the solutions to system (5.1), if they exist, obtained by passing to the limit $D_i \rightarrow 0$ are nondecreasing. As $\xi \rightarrow \pm\infty$, the trajectories of these solutions in the $(n+1)$ -dimensional phase-space are tangent to the eigenvectors of the linearization matrices for system (5.1) at the points $(u, z, v_1, \dots, v_n) = (u_1, 0, v_1^1, \dots, v_n^1) := P_1^{n+1}$ and $(u, z, v_1, \dots, v_n) = (u_1, 0, v_1^3, \dots, v_n^3) := P_3^{n+1}$.

The following lemma can be proved:

LEMMA 10. *Assume that $a \neq 0$ and $a_k, b_k \neq 0$. Then $\lambda = 0$ cannot be an eigenvalue of the matrix (5.3). Let $N = (h_u, h_z, h_1, \dots, h_n)^T$ be an eigenvector of the linearization matrix (5.3) corresponding to an eigenvalue λ , such that:*

1. *If $\lambda \geq 0$, then N has non-negative components.*
2. *If $\lambda \leq 0$, then $h_u, h_1, \dots, h_n \geq 0$ and $h_z \leq 0$.*

Then the inequalities concerning the components of the vector N are strict. \square

P r o o f. First we will prove that the eigenvalue cannot be equal to 0. Suppose the contrary. Let $N = (h_u, h_z, h_1, \dots, h_n)$ be the vector associated with the eigenvalue $\lambda = 0$. From (5.4) we note that $h_z = 0$. Next $\sum_{k=1}^n (h_u a_k - h_k b_k) = 0$.

So, equating the second component to zero we obtain the equality $h_u a = 0$, which implies $h_u = 0$. Consequently, by equating the last k components of LN to zero we note that $h_k = 0$ for all k . Thus all the components of the associated eigenvector are equal to zero. So, we must have $\mathbb{R}^1 \ni \lambda \neq 0$. Suppose that $\lambda > 0$ and that the associated eigenvector N is non-negative (in particular $h_z \geq 0$). Then either $h_u = 0$ or $h_u, h_z > 0$. Suppose that $h_u = 0$. Then also $h_z = 0$. Consider the $(k + 2)$ th component of the vector LN (see Eq. (5.4)) equal to

$\lambda h_k \geq 0$. We thus obtain $\frac{1}{q} \sum_{k=1}^n h_k b_k \neq 0$, because at least one h_k must be non-

zero for N to be non-zero. Hence the second component of the vector LN cannot be equal to zero as it should be (due to fact that $h_z = 0$). We thus arrive at a contradiction which proves that $h_u, h_z > 0$. Now, if we suppose that $h_k = 0$ for some $k = 1, \dots, n$, we will have. Hence we must have $h_k \neq 0$ for all k . Now, let us suppose that $\lambda < 0$ and $h_z \leq 0$ whereas $h_u, h_k \geq 0$. Then $\lambda h_u = h_z$. As before, this implies that either $h_u = 0$ or $h_u, h_z > 0$. It is easily seen that we can repeat the rest of the proof almost *verbatim* to conclude that also for $\lambda < 0$ the claim of the lemma is true. \square

Additional properties of the eigenvalues of the matrix L at the points corresponding to P_1 and P_3 can be proved.

LEMMA 11. *Assume that $a < 0$. If $q > 0$, then the matrix L has one negative eigenvalue and $n + 1$ positive eigenvalues. If $q < 0$, then the matrix L has one positive eigenvalue and $n + 1$ negative eigenvalues.*

The lemma is in fact identical with Lemma 5.2, p. 255 in [12].

Below, we will need also the following auxiliary lemma.

LEMMA 12. *Consider system (1.9)–(1.10) (with $D_i > 0$). If one of the functions $z = u', z_i = v'_i$, $i \in \{1, \dots, n\}$, attains a minimum equal to zero for some $\xi = \xi_0$ then $z(\cdot), z_1(\cdot), \dots, z_n(\cdot) \equiv 0$. The same is true for system (1.21)–(1.22).*

\square

P r o o f. Let us suppose that for some $i \in \{1, \dots, n\}$ the function $z_i(\xi_0)$ attains a minimum. Then $z_i'(\xi_0) = 0$ and $z_i''(\xi_0) \geq 0$. Thus differentiating the equation for v_i we obtain the relation

$$D_i z_i''(\xi_0) = G_{i,u}(u(\xi_0), v_i(\xi_0))z + G_{i,v_i}(u(\xi_0), v_i(\xi_0))z_i.$$

As $G_{i,u}(u(\xi_0), v_i(\xi_0)) < 0$ hence $z_i''(\xi_0) = 0$ and $z(\cdot)$ must attain a minimum equal to zero at $\xi = \xi_0$. By differentiating the equation for u we infer that $z_j(\xi_0) = 0$ for all $j = 1, \dots, n$ and the source terms of all the equations are equal to zero. Hence the lemma is proved. If the value zero is attained by the function $z(\cdot)$ then the proof is the same. For system (1.21)–(1.22) the proof can be carried out along the same lines. \square

For $\alpha, \beta = 0, 1, 2, 3$, let

$$(5.5) \quad B_{\alpha\beta}(\mathbb{R}^1) = S_\alpha \times \underbrace{S_\beta \times \dots \times S_\beta}_{n \text{ times}}$$

where, for $\gamma = 1, 2, 3$,

$$S_\gamma = \{f \in C^\gamma(\mathbb{R}^1) : \lim_{\xi \rightarrow \pm\infty} f(\xi) \text{ exist, } \lim_{\xi \rightarrow \pm\infty} f^{(j)}(\xi) = 0, 1 \leq j \leq \gamma\},$$

whereas

$$S_0 = \{f \in C^0(\mathbb{R}^1) : \lim_{\xi \rightarrow \pm\infty} f(\xi) \text{ exist}\}.$$

Here, by $f^{(j)}$ we mean the j -th derivative of f . $B_{\alpha\beta}$ are the Banach spaces under the norm. To be more precise

$$\|(u, v_1, \dots, v_n)\|_{B_{\alpha\beta}} = \|u\|_{S_\alpha} + \sum_{k=1}^n \|v_k\|_{S_\beta}, \quad \|\cdot\|_{S_\gamma} = \|\cdot\|_{C^\gamma(\mathbb{R}^1)}.$$

Note, that the heteroclinic solutions to system (1.21)–(1.22) are determined only up to a shift in ξ . To get rid of the translational symmetry, we impose the condition of the form

$$(5.6) \quad u(0) = (u_1 + u_2)/2,$$

where u_1, u_2 are defined in the Assumption 2. Let $D_i = D_i(\varepsilon)$, $i = 2, \dots, n$, with

$$D_i(\varepsilon) \rightarrow 0$$

as $\varepsilon \rightarrow 0$, and let $\varepsilon = 1/l$ with $l \in \{1, 2, \dots\}$. For simplicity, we will use below the notation introduced in (1.17). Let us enumerate the solutions to system (1.9)–(1.10) assigned to $\varepsilon = 1/l$ (i.e. to $D_i = D_i(1/l)$, $i = 2, \dots, n$), satisfying

conditions (1.16) and condition (5.6) by $\{U_{[l]}\}_{l=1}^{l=\infty}$, whereas the corresponding speeds by $\{q_l\}_{l=1}^{l=\infty}$.

By means of Lemma 4, $(q_l, U_{[l]}) \in \mathbb{R}^1 \times B_{32}$ with $(\|U_{[l]}\|_{B_{32}} + |q_l|)$ bounded uniformly with respect to l . Using the Arzela–Ascoli lemma we conclude that in every compact interval $I_{\mathcal{J}}$ of the form $I_{\mathcal{J}} = [-\mathcal{J}, \mathcal{J}]$, where $\mathcal{J} > 0$, we may find a subsequence $\{k_l\}_{l=1}^{l=\infty}$ such that both $U_{[k_l]}$ and q_{k_l} are converging in $B_{21}(I_{\mathcal{J}})$ and \mathbb{R}^1 respectively. (Here $B_{21}(I_{\mathcal{J}}) := \{f \in B_{21}(\mathbb{R}^1)|_{I_{\mathcal{J}}}\}$.) Next, out of this subsequence we can choose another subsequence (denoted for simplicity in the same way) such that the sequences $U_{[k_l]}$ and q_{k_l} are convergent in the norms of the spaces $B_{21}(I_{\mathcal{J}+1})$ and \mathbb{R}^1 . This procedure can be continued. It follows that on every compact subset of the form $I_{\mathcal{J}} = [-\mathcal{J}, \mathcal{J}]$ with natural \mathcal{J} arbitrarily large, we can find subsequences $\{U_{[k_l]}\}_{l=1}^{l=\infty}$ and $\{q_{k_l}\}_{l=1}^{l=\infty}$ converging to the solutions of the system (1.21)–(1.22). By differentiation of the equations of this system we easily conclude that the limiting pair (Q, Ψ) belongs to the space $\mathbb{R}^1 \times B_{32}$. One can prove that the function $\Psi(\cdot)$ connects the constant steady states P_1 and P_3 as it was desired. So, according to the fact that the first derivatives of the functions $U_{[l]}$, $l = \{1, 2, \dots\}$, are positive in \mathbb{R}^1 and tend to zero at infinities, $\Psi'(\xi)$ must tend to 0 for $|\xi| \rightarrow \infty$. Moreover, as $\xi \rightarrow \pm\infty$, due to the monotonicity, the functions $\Psi_1(\cdot), \Psi_2(\cdot), \dots, \Psi_{n+1}(\cdot)$ must attain their limits. Due to condition (5.6), $\lim_{\xi \rightarrow -\infty} \Psi(\xi) = P_1$. Now, if it were not true that $\lim_{\xi \rightarrow \infty} \Psi(\xi) = P_3$, we would have $\Psi(\xi) \rightarrow P_2$ as $\xi \rightarrow \infty$. But it is easy to note that then we would have another wave $\tilde{\Psi}$ such that $\tilde{\Psi}(\xi) \rightarrow P_2$ and P_3 as $\xi \rightarrow \pm\infty$ respectively, that is to say there would exist two waves (of the same speed q) joining the states P_1 with P_2 and P_2 with P_3 , consecutively. (Let us note that every $U_{[l]}(\cdot)$ is a $C^1(\mathbb{R}^1)$ function of its argument and $\lim_{\xi \rightarrow \infty} U_{[l]}(\xi) = P_3$. For the detailed considerations the reader is referred to [4] p. 478.) When $Q \neq 0$ then this possibility should be however excluded due to Lemma 9. If $Q = 0$, the first equation decouples from the rest. It is easy to note that for this equation, an analogous to Lemma 9 property holds (even for $q = 0$). Thus $\lim_{\xi \rightarrow \infty} \Psi_1(\xi) = u_3$ and consequently $\lim_{\xi \rightarrow \infty} \Psi(\xi) = P_3$ also in this case.

From the first equation it follows that $\Psi_1''(\xi) \rightarrow 0$ as $\xi \rightarrow \pm\infty$, whereas Ψ_i , $i = 2, \dots, n+1$, satisfy the reduced equations

$$Q\Psi_i' - G_{i-1}(\Psi_1, \Psi_i) = 0.$$

Let us remind that by q_r we denoted the speed of the unique (in the sense of profile) monotonically increasing heteroclinic solution for the scalar equation

$$(5.7) \quad Du'' + qu' + f(u) = 0$$

joining the states u_1 and u_3 .

Our existence result is contained in the following theorem.

THEOREM 3. *Suppose that the Assumption 2 is satisfied. Then there exists a heteroclinic solution to system (1.21)–(1.22), i.e. a speed q and a vector function $(u, v_1, \dots, v_n) : \mathbb{R}^1 \rightarrow \mathbb{R}^{n+1}$ satisfying conditions (1.16). This solution pair is a limit of the unique (up to a translation in ξ), heteroclinic pairs for systems (1.9)–(1.10) with $D_i > 0$ as $D_i \rightarrow 0$ for $i = 1, \dots, n$. If $q_r \neq 0$ then also $q \neq 0$.* \square

P r o o f. According to what we have said above, we only need to show the last statement concerning the relations between q and q_r . This follows from Lemma 13, which is formulated and proved below. \square

LEMMA 13. *Assume that $q_r \neq 0$. Then for $\varepsilon \geq 0$ sufficiently small, the heteroclinic pairs (q, u) to systems (1.9)–(1.10) must satisfy the condition $q \neq 0$.* \square

P r o o f. Suppose that there exists a subsequence $\{k_l\}_{l=1}^{l=\infty}$ such that $\{q_{k_l}\}_{l=1}^{l=\infty} \rightarrow 0$ as $l \rightarrow \infty$. Thus, according to Lemma 4, for every $\rho > 0$ arbitrarily small there exists l_ρ such that $|q_{k_l} v'_{k_l i}(\xi) + D_i(1/k_l) v''_{k_l i}(\xi)| < \rho$, $i = 1, \dots, n$ for all $l > l_\rho$ (and all $\xi \in \mathbb{R}^1$). Using these estimations in the first equation of the system, we obtain Eq. (1.24) perturbed by terms of the order $O(\rho)$. For $\rho = 0$ (or $l = \infty$) we obtain exactly Eq. (1.24) (since from the last n equations it would follow that $G_i(u(\xi), v_i(\xi)) \equiv 0$, $i = 1, \dots, n$). This equation has a unique, monotonically increasing heteroclinic solution joining the states u_1 and u_3 corresponding to the speed q_r which, according to our assumption, is different from zero. Hence we arrive at contradiction with the fact that $q_{k_l} \rightarrow 0$. \square

Let us note that for $q_r = 0$ the existence of a solution is straightforward.

LEMMA 14. *Suppose that $q_r = 0$. Then there exists a unique heteroclinic pair $(0, U)$ of system (1.21)–(1.22). This pair is unique (up to a translation in ξ) in the class of solutions with $q = 0$ and monotone U .* \square

P r o o f. Take $q = 0$. Then, the first equation separates from the rest. This equation has a unique, monotonically increasing heteroclinic solution corresponding to the speed $q_r = 0$ and joining the states u_1 and u_3 . The remaining n equations have the form

$$G_i(u(\xi), v_i(\xi)) = 0, \quad i = 1, \dots, n + 1.$$

Given $u(\xi)$, according to the form of the functions, G_i equations can be solved explicitly with respect to $v_i(\xi)$. \square

Uniqueness of the travelling wave solutions to system connecting the states P_1 and P_3 is stated and proved in the paper of [12] (see Theorem 1 p. 247). The travelling wave solution is also stable with respect to perturbations of the initial conditions. This result is stated in Theorem 3 p. 250 in [12].

6. Conclusions

The main result of the paper is the proof of the existence of travelling wave solutions to the system of partial differential equations describing the concentration of intracellular calcium and concentrations of different kinds of buffer particles with zero diffusion coefficients. Mechanical effects are also taken into account by introducing an appropriate modification of the source term in the equation for calcium. The form of this additional term is obtained under the assumption that the viscosity phenomena are negligible with respect to the elastic effects. The method of proof requires to use the classical theory for non-degenerate systems from [13] and then to pass to the limit with the diffusion coefficients of the buffers. It is worthwhile to note that the influence of the buffers on the mechanics is also essential. It comes through the term $\gamma\theta_0(u, \sigma)$. This term does not depend explicitly on the concentrations of buffers v_i , $i = 1, \dots, n$. However, their presence modifies the profile of the travelling wave of free calcium concentration. Having the profile $c(\cdot)$ of the calcium travelling wave we may, in principle, find the profile of the dilation travelling wave $\theta(\cdot)$ moving with the same speed.

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