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HYPERBOLIC WAVE FEATURES OF AN EXACT SOLUTION TO A MODEL FOR NERVE PULSE TRANSMISSION

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Abstract. Nerve pulse transmission through an excited fibre is investigated by means of an exact solution to a hyperbolic governing model which can also take into account cumulative nonlinear effects different from those due to the ion current mechanisms. It is shown that if the initial pulse is localized, the resulting signal propagates at finite velocity along the fibre perturbing the initial nonequilibrium state. The behaviour of signal velocity and the role played in the wave process by the characteristic speeds, provided by the hyperbolic governing model, are highlighted.

Key words: reduction procedure, nerve fibre.

1. INTRODUCTION

Within the theoretical framework of wave propagation the hyperbolic governing models play a prominent role because they provide finite speeds (characteristic speeds) to propagating wave disturbances such as acceleration (weak discontinuity) waves or simple waves. Furthermore, assumption of hyperbolicity is relevant in the study of shock waves and in the investigation of quasilinear and conservative models reducible to symmetric and conservative form (see [1,2] and references quoted there). Based upon assumption of hyperbolicity is also the approach proposed in [3] for constructing classes of exact solutions to quasilinear systems of partial differential equations (PDEs) endowed by differential constraint equations [4].

In this paper we aim at getting an insight into the hyperbolic model proposed in [5] for describing nerve pulse transmission. Actually, within the present context, it is relevant to point out how an initial pulse modifies along the fibre in the course of time. Such an investigation has been carried out for some celebrated parabolic models as those of Hodgkin and Huxley [6], Fitz-Hugh [7], and Nagumo et al. [8] mainly by means of numerical solutions and under the assumption that the pulse was propagating into an equilibrium (constant) state. In particular, those models were proved to be consistent with action potential-like behaviour which is supported by well-known experimental evidence [9,10] and is mainly related to activation and inactivation of different ion currents through the axon membrane of the nerve fibre. For a large body of literature on nerve fibre physiology and on the related experimental results, we refer to [9–11].

In order to describe nerve pulse transmission within a well-posed wave theory, a number of hyperbolic models have been proposed [12,13].

In [5] the following hyperbolic system of first-order PDEs was considered:

$$\pi a^2 C \frac{\partial u}{\partial t} + \frac{\partial i}{\partial x} = -2\pi a I, \tag{1.1}$$

$$\frac{L}{\pi a^2}\frac{\partial i}{\partial t} + \frac{\partial u}{\partial x} = \frac{R}{\pi a^2} i, \tag{1.2}$$

$$\frac{\partial w}{\partial t} + \phi(u, w)\frac{\partial u}{\partial t} = \psi(u, w), \tag{1.3}$$

where x denotes the distance along the axon, t the time, u the potential difference across the membrane, i the axon current, w a recovery variable modelling the sodium inactivation and the potassium activation [8], a the axon radius, C the self-capacitance, L the specific self-inductance, R the specific resistance. Moreover, $\phi(u, w)$ and $\psi(u, w)$ are material response functions while $I(u, w)$ represents the ion current density.

In passing we notice that the parabolic Fitz-Hugh–Nagumo model is recovered from Eqs. (1.1)–(1.3) when $L = \phi(u, w) = 0, \quad \psi = \psi_0 + \psi_1 u + \psi_2 w$ (ψ_0, ψ_1, and ψ_2 being constants) and $I(u, w) = \varphi(u) + w$, where $\varphi(u) = k_1 u + k_3 u^3$ (k_1 and k_3 are constants), takes the sodium activation into account [8].

The need for modelling nerve pulse transmission by means of the set of equations (1.1)–(1.3) in view of the structural complexity of a nerve fibre was motivated in [5,14]. Here we remark only that through (1.3) the governing system under concern can model memory effects as well as cumulative nonlinear effects different from those due to the ion current mechanisms.

The system of equations (1.1)–(1.3) is hyperbolic with characteristic wave speeds given by

$$\lambda^{(1)} = 0; \quad \lambda^{(2),(3)} = \lambda = \pm\frac{1}{\sqrt{CL}}. \tag{1.4}$$

This striking feature was used in [14] to construct classes of exact solutions to initial and/or boundary value problems described by (1.1)–(1.3) by means of the general approach outlined in [3]. Within such a framework here we are interested to point out whether, for the model at hand, it is possible to characterize solutions, different from travelling wave or self-similar solutions, which exhibit the distinguishing features of a wave propagating at finite speed. In particular, we are able to highlight the role played by the characteristic speeds in transmitting a signal along the fibre. In fact, given a solution of a hyperbolic model, in general the corresponding signal is transmitted at a velocity which is different from the characteristic speeds.

2. ACTION POTENTIAL

Provided the material response functions $I(u,w)$, $\phi(u,w)$, and $\psi(u,w)$ adopt a special form, some of the exact solutions to (1.1)–(1.3) determined in [14] are capable of describing certain material behaviour, such as the well-known "action potential", which is usually expected to occur in nerve fibre. Here, our analysis is devoted to considering pulse-like exact solutions to the system (1.1)–(1.3) which represent a nerve signal transmitting along the fibre into a nonconstant state. In particular, we aim at describing the action potential propagation into a nonequilibrium state. To accomplish such a plan, we focus our attention on the following "model constitutive laws":

$$\phi(u,w) = \frac{F_u + \nu_0 - 2k}{F_w}, \qquad \psi(u,w) = \frac{1}{F_w}\left(\nu_0 F - k^2 u\right), \tag{2.1}$$

where k is an arbitrary constant, $\nu_0 = -\frac{R}{L}$, and $F(u,w) = -\frac{2}{aC} I(u,w)$. Moreover, here and in the following, subscripts denote partial derivative with respect to the indicated arguments.

It is easy to ascertain that the quasilinear system of equations (1.1)–(1.3), supplemented by (2.1) in terms of the field variables u, i, F, writes under the linear form

$$\pi a^2 C \frac{\partial u}{\partial t} + \frac{\partial i}{\partial x} = \pi a^2 C F, \tag{2.2}$$

$$\frac{L}{\pi a^2}\frac{\partial i}{\partial t} + \frac{\partial u}{\partial x} = \frac{R}{\pi a^2} i, \tag{2.3}$$

$$\frac{\partial F}{\partial t} + (\nu_0 - 2k)\frac{\partial u}{\partial t} = \nu_0 F - k^2 u. \tag{2.4}$$

Before proceeding further, we make a remark about the linear governing system (2.2)–(2.4). We notice that in the original system (1.1)–(1.3) the mechanism of different ion currents through the axon membrane is taken into account through the recovery variable w whose role is similar to that played by internal variables in continuum models, whereupon the quantity w cannot be directly measured. In the linear system (2.2)–(2.4) the switching on and the switching off of the potassium and sodium ion currents are characterized by means of the field variable F, namely by means of the total ion current which can be determined experimentally [9,15].

The system (2.2)–(2.4), after eliminating i and F, produces the second-order hyperbolic equation for the potential u

$$\frac{\partial^2 u}{\partial t^2} - \lambda^2 \frac{\partial^2 u}{\partial x^2} - 2k\frac{\partial u}{\partial t} + k^2 u = 0, \tag{2.5}$$

which by means of the variable transformation $\overline{u} = e^{-k}u$ reduces to the classical wave equation

$$\frac{\partial^2 \overline{u}}{\partial t^2} - \lambda^2 \frac{\partial^2 \overline{u}}{\partial x^2} = 0, \tag{2.6}$$

whereupon the general solution of (2.5) is given by

$$u = e^{kt}\left(f(\sigma) + g(\xi)\right), \tag{2.7}$$

where $\sigma = x - \lambda t$, $\xi = x + \lambda t$, while $f(\sigma)$ and $g(\xi)$ are arbitrary functions of integration.

The availability of the free functions f and g makes the solution (2.7) flexible to fit with prescribed initial and/or boundary conditions for the problem of interest. Here we assume that at $t = 0$ the fibre is excited and we try to model how a pulse generated by the boundary condition at $x = 0$ is transmitted along the fibre perturbing the initial nonequilibrium state.

In view of characterizing the evolution of an action potential-like pulse, we set

$$f(\sigma) = \frac{1}{2}\omega(\sigma)\tanh(c\sigma), \qquad g(\xi) = \omega(\xi)\,\mathrm{sech}(c\xi)\left(e^{-c\xi} + \frac{1}{2}\sinh(c\xi)\right), \tag{2.8}$$

where $c = -\frac{k}{\lambda}$, while the function ω is to be determined and it represents the initial state of the fibre. Next, we assume that the fibre is excited in a region close to the origin ($x = 0$) while far from the origin the fibre is initially at rest. Hence, the initial pulse (i.e. $u(x, 0)$) must be localized and we choose

$$\omega(x) = u(x, 0) = \mathrm{sech}^2(z_0\,(x - z_1)), \tag{2.9}$$

where z_0 and z_1 are constants. Therefore the solution (2.7) specializes to

$$\begin{aligned} u \;=\; & \frac{1}{2}e^{kt}\left\{\mathrm{sech}^2(z_0(\xi - z_1))\tanh(c\xi) + \mathrm{sech}^2(z_0(\sigma - z_1))\tanh(c\sigma)\right\} \\ & + e^{-cx}\mathrm{sech}^2(z_0(\xi - z_1))\,\mathrm{sech}(c\xi) \end{aligned} \tag{2.10}$$

and it describes the full wave process along the fibre for the problem at hand.

From (2.10), if $k < 0$, it results that $u \to 0$ as $t \to +\infty$ or $x \to -\infty$; if $k > 0$, $u \to 0$ as $x \to +\infty$; as $t \to +\infty$, $u \to 0$ provided that $2|z_0|\lambda > k$; $u \to +\infty$ provided that $2|z_0|\lambda < k$, and u tends to $4\cosh[2z_0(x - z_1)]$ provided that $2|z_0|\lambda = k$.

The pulse evolution is illustrated by means of plots of u versus t at different x kept fixed, as shown in Figs. 1 and 2 where we set $k = 0.9$, $\lambda = 0.7$, $z_0 = 1.5$, $z_1 = 1$.

First, we notice that, owing to (2.10), the stimulus at the origin of the fibre $u(0, t)$ (see Fig. 1) is qualitatively in accordance with the usual boundary condition considered in several experiments. Moreover, Fig. 1 points out that, by fixing x in the interval where the initial pulse is sensitively nonzero (e.g. $0 < x < 3$), the resulting plot of u versus t represents a damping of the potential, whereas the plot of u versus t obtained for x outside the initial nonequilibrium region (see Fig. 2) (e.g. $x > 3$) makes evident the typical action potential behaviour which is expected to propagate along the fibre. In fact, at x far from the origin the potential is at rest until a certain time in which the localized impulse originated at $t = 0$ in $x = 0$ arrives, assuming a characteristic action potential-like behaviour; in other words, the signal originated at the boundary is transmitted along the fibre at finite velocity perturbing the initial nonequilibrium state.

On the latter concern we remark that, owing to the hyperbolicity, the original governing model (1.1)–(1.3) provides the characteristic speeds (1.4), namely the speeds at which wave disturbances such as acceleration waves propagate. Hence, it

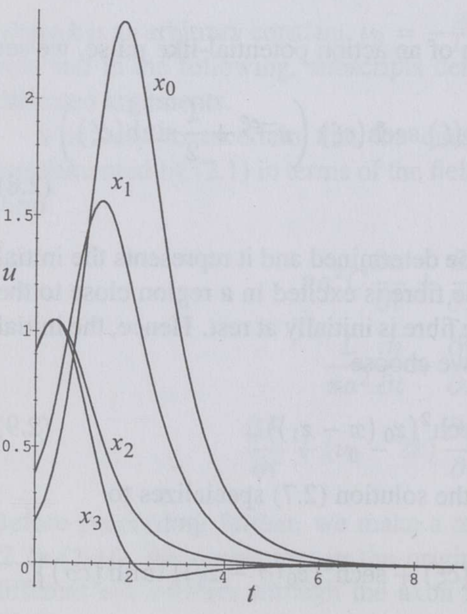

Fig. 1. Plot of u versus t at $x_0 = 0$, $x_1 = 0.3$, $x_2 = 0.8$, $x_3 = 1.2$.

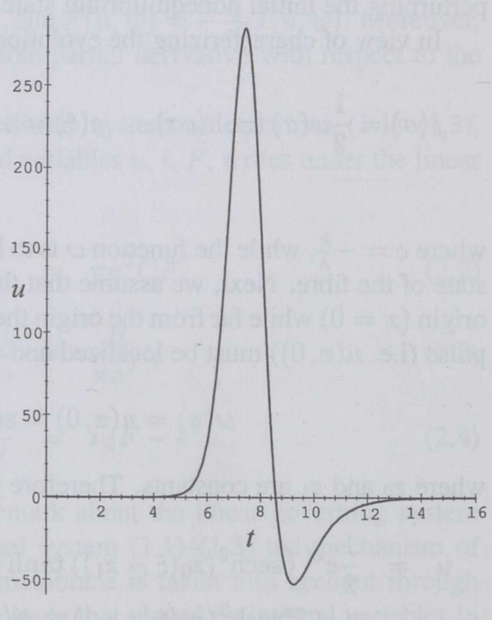

Fig. 2. Plot of u versus t at $x = 6$.

is of interest to point out how the inherent features of the hyperbolic model (1.1)–(1.3) reflect into the wave process described by the solution (2.10). Such an analysis will be accomplished in the next section.

3. NERVE SIGNAL VELOCITY

As well known, given a wave solution $u = u(x,t)$ of a governing model, the velocity v at which a signal $u = u_0$ is transported along the curves (trajectories) defined by $u(x,t) = u_0$ is determined by

$$v(x,t) = -\left(\frac{u_t}{u_x}\right)_{u=u_0}. \tag{3.1}$$

In the present case it is straightforward to see that the solution (2.7) is the superposition of two solutions representing two pulses travelling in opposite directions. As far as the initial value problem (2.9) is concerned, we notice that the two pulses in point interact in a region near the origin of the fibre (e.g. $0 < x < 3$), but they are separate outside the initial nonequilibrium region (e.g. $x < 0$ or $x > 3$), so that each of them behaves as a far field [16,17]. Therefore, in order to define the effective speed of the signal under interest in the region $x > 0, t > 0$, we can, in fact, neglect the contribution of the function $g(\xi)$ to the solution (2.7). Consequently, the relation (2.7) reduces to

$$u = e^{kt} f(\sigma) \tag{3.2}$$

with $f(\sigma)$ given by $(2.8)_1$ and, in turn, v specializes to

$$v = \lambda - k\frac{f(\sigma)}{f\prime(\sigma)}. \tag{3.3}$$

Here and in the following prime stands for ordinary differentiation.

In order to clarify the role played by the characteristic speeds (1.4) in the present wave process, we notice that the behaviour of the signal speed v is strictly connected to that of the level curves (trajectories in the (x,t) plane) associated to the solution (3.2). In the following we limit our analysis to the region of the (x,t) plane, where $x > 0, t > 0$.

By direct inspection it is easily seen that the value $u = 0$ is transported by the characteristic straight line $x - \lambda t = 0$, while the trajectories (which are not characteristic curves) transporting the values $u(x,t) > 0$ and $u(x,t) < 0$ are located in the regions of the (x,t) plane, where $x > \lambda t$ and $x < \lambda t$, respectively.

A parametric description of a trajectory, where $u \neq 0$, is achieved by means of the family of characteristic straight lines $x - \lambda t = \sigma$.

Actually, it is simple to ascertain that any level curve, where $u = u_0 \neq 0$, is defined by the relations

$$t = \frac{1}{k} \log \left(\frac{u_0}{f(\sigma)} \right), \tag{3.4}$$

$$x = \sigma + \lambda t, \tag{3.5}$$

where the parameter $\sigma \in]0, +\infty[$ if $u_0 > 0$ or, alternatively, $\sigma \in]-\infty, 0[$ if $u_0 < 0$.

Figure 3 shows the general picture of the trajectories under investigation.

Next let us focus our attention on the effective speed of the signal. For the sake of simplicity we limit our analysis to the case $u_0 > 0$.

Owing to the parametric representation (3.4), (3.5), the signal speed v given by (3.3) does not depend on the value u_0, so that the corresponding trajectories are parallel. Moreover, according to the behaviour of the trajectories for $\sigma \to +\infty$ and $\sigma \to 0^+$, we have

$$\lim_{\sigma \to +\infty} v = \lambda + \frac{k}{2z_0}, \qquad \lim_{\sigma \to 0^+} v = \lambda. \tag{3.6}$$

The limit values (3.6) can be easily related to the pulse profile. Actually, to a given value u_0 there correspond two points on the pulse, as shown in Fig. 2 in the case of a plot of u versus t at x kept fixed. Of course, the position on the profile of these points changes with x and in the (x, t) plane the corresponding trajectories lie on the level curve associated with the given value u_0. It is easily seen that (3.6) represent the asymptotic values of the velocities of the points under interest along the corresponding trajectories. Such a situation is summarized in Fig. 4 which shows the plot of v versus x.

Similar results hold in the case $u_0 < 0$, where the limit values of the signal velocity are given by

$$\lim_{\sigma \to -\infty} v = \lambda - \frac{k}{2z_0}, \qquad \lim_{\sigma \to 0^-} v = \lambda. \tag{3.7}$$

Thus the velocity v is bounded as x or t grow large.

Moreover, the limit values (3.6) and (3.7) depend upon the parameter z_0 which, on account of (2.9), characterizes the thickness of the initial nonequilibrium region of the fibre. It is straightforward to see that the limit values (3.6) and (3.7) of the velocity v get closer to one another as z_0 grows large. Hence, if the thickness of the initial region becomes smaller (z_0 large), then the resulting pulse asymptotically behaves like a travelling wave propagating with the characteristic velocity λ.

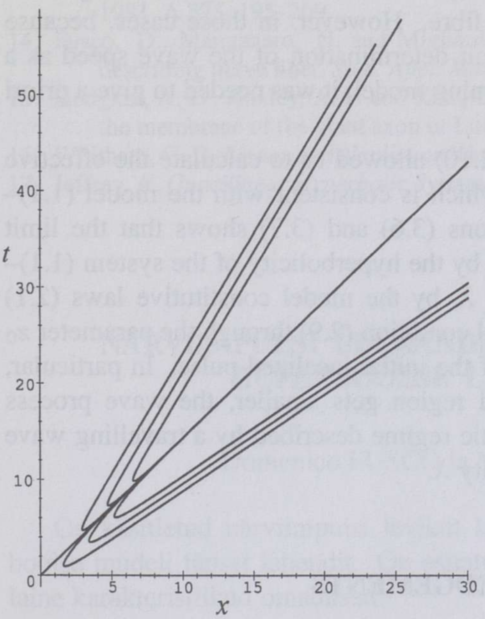

Fig. 3. Level curves defined by (3.4), (3.5).

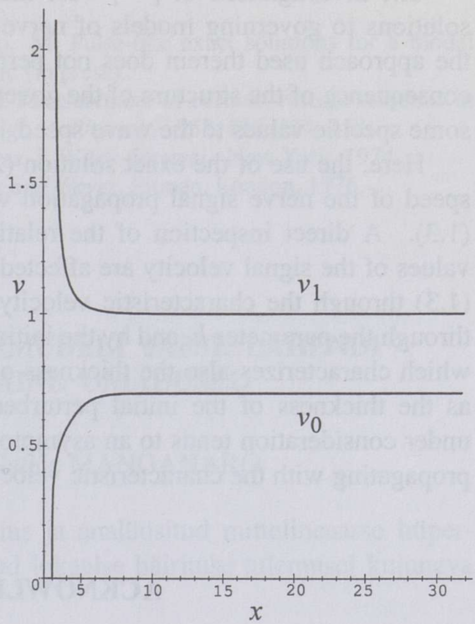

Fig. 4. Plot of v versus x with $v_0 = \lambda$ and $v_1 = \lambda + \frac{k}{2z_0}$.

4. CONCLUSIONS

Mathematical modelling of nerve pulse transmission has been carried out mainly by means of numerical solutions and by assuming the signal to propagate into an equilibrium (constant) state [6–8].

Here, the propagation of an action potential-like pulse into a nonequilibrium state was studied by means of an exact solution which was obtained for the governing model (1.1)–(1.3) via the general approach developed in [3] for quasilinear hyperbolic systems of first-order PDEs.

The initial pulse was assumed to be localized in order to describe a fibre which is excited in a region close to the origin and initially at rest far from the origin. The subsequent analysis showed that the signal originated at the boundary propagates along the fibre at a finite velocity, which is different from the characteristic speeds provided by the hyperbolic model (1.1)–(1.3). At any station x fixed outside the initial nonequilibrium region the expected action potential behaviour was obtained. Moreover, the role the characteristic speeds played in the nerve signal transmission was highlighted by investigating the behaviour of the level curves associated with the exact solution (3.2), and the results were also related to the pulse profile.

The investigations of [7,8] were mainly aimed to search for travelling wave solutions to governing models of nerve fibre. However, in those cases, because the approach used therein does not permit determination of the wave speed as a consequence of the structure of the governing model, it was needed to give a priori some specific values to the wave speed.

Here, the use of the exact solution (2.10) allowed us to calculate the effective speed of the nerve signal propagation which is consistent with the model (1.1)–(1.3). A direct inspection of the relations (3.6) and (3.7) shows that the limit values of the signal velocity are affected by the hyperbolicity of the system (1.1)–(1.3) through the characteristic velocity λ, by the model constitutive laws (2.1) through the parameter k, and by the initial condition (2.9) through the parameter z_0 which characterizes also the thickness of the initial localized pulse. In particular, as the thickness of the initial perturbed region gets smaller, the wave process under consideration tends to an asymptotic regime described by a travelling wave propagating with the characteristic velocity λ.

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NÄRVIIMPULSI ÜLEKANDEMUDELI TÄPSE LAHENDI HÜPERBOOLSE LAINE OMADUSED

Domenico FUSCO ja Natale MANGANARO

On käsitletud närviimpulsi levikut kius ja analüüsitud mittelineaarse hüperboolse mudeli täpset lahendit. On esitatud lokaalse häirituse tulemusel kujuneva laine karakteristlikud omadused.