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Time Evolution of the Action Potential in Plant Cells

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Abstract. In this paper we extend and reconsider a solitonic model of the action potential in biological membranes for the case of plant cells. Aiming to give at least a qualitative description of the K^+, Cl^- and Ca^{2+} driven process of propagation of the action potential along plant cells we put forward the hypothesis of three scalar fields $\phi_i(\mathbf{x})$, i = 1, 2, 3 which represent K^+, Cl^- and Ca^{2+} ions, respectively. The modulus squared of these fields carries the usual quantum-mechanical (probabilistic) interpretation of the wave function. On the other hand, the fields are described themselves by the Lagrangian densities $\mathcal{L}_{\phi_i}$. Moreover, the interaction and self-interaction term $\mathcal{L}_{(\phi_i,\phi_j)}$ between the fields is considered. The Lagrangian densities $\mathcal{L}_{\phi_i}$ include a *double-well* potential (which is proportional to ϕ_i^4) that leads to *spontaneous symmetry breaking* which may produce structures with non-zero topological charge, e.g. *longitudinal solitons*. In order to describe the transversal motion of the ions of concern we need to assume only non-uniform solutions of the system of equation of motion. Hence we seek for solutions (*travelling waves*) which preserve the shape and which move without dissipation and in this way we reconstruct the main dynamical features of the action potential in plants.

Key words: Action potentials, Plants, Ion fluxes, Longitudinal solitons

1. Introduction

It is suggested (Davies, 1987) that action potentials which occur in most, if not all, plants play a major role in intercellular and intracellular communication. Long distance communication is achieved through the transmitted changes in membrane potential, whereas local signalling is accomplished by changes in the subcellular localization of ions K^+, Cl^- and Ca^{2+}, and perhaps by membrane depolarization and current flow (Shimmen & Tazawa 1980; Shiina & Tazawa 1986; Fromm & Bauer 1994). These local changes in ion concentration can lead to modified activities of enzymes in the cell wall, the plasma membrane and the cytoplasm. In particular, the elevated concentration of cytoplasmatic Ca^{2+} is shown to play a major role especially in the modulation of translation. On the other hand, the plasma membrane of higher plants contains a H^+-ATPase as its major ion pump. The plasma membrane H^+-ATPase generates an electric potential and pH gradient across the plasma membrane by extruding protons from the cell. The energy bound in this electrochemical gradient is thought to be the driving force for solute carriers and channels that are responsible for nutrient uptake and maintenance of cell turgor.

The occurence of action potentials (AP) in plants is quite common (see Davies 1987). Action potentials are generated in fungi (Slayman et al. 1976), algae (Hope & Walker 1975; Gradmann & Mummert 1980; Abe et al. 1980; Williamson & Ashley 1982; Beilby 1984), excitable higher plants (van Sambeek & Pickard 1976; Samejima & Sibaoka 1980; Abe 1981; Simons 1981), and 'normal' higher plants (Zawadzki 1980; Zawadzki et al. 1991; Davies & Schuster 1981a, b; Roblin 1985) in response to light (Stolarek & Pazurkiewicz-Kocot 1980), heat, cold, chemicals, electrical stimulus and wounding (Gradmann & Mummert 1980; Stolarek et al. 1984; Filek et al. 1993). A role for action potentials is rather obvious in plant movements such as leaf folding in *Mimosa* and insect trapping in *Dionea* (Pickard 1973); their role, according to Davies (1987), is less obvious in 'normal' plants, but suggestions have included regulation of ion transport, turgor and phloem functioning, as well as intercellular and intracellular signalling (Pickard 1973; Gradmann & Mummert 1980; Fromm & Eschrich 1993; Fromm & Spanswick 1993; Fromm & Bauer 1994), although their role as long distance signals has also been questioned (Goldsworthy 1983).

According to Trębacz (1989) the course of events during the 'metabolic' action potential is to be as follows: "interruption of illumination causes a temporary insufficiency of the ATP available for the power supply of Cl^- pumps, this causes their breakdown and then reversal of their action. The passage of Cl^- outside the cell causes depolarization to about –50 mV which brings about the exit of K^+ as a consequence of exceeding the equilibrium potential for these ions. As a result of the efflux of K^+ from the cell, repolarization to about –90 mV occurs. Meanwhile, the ion pump regains its previous direction and begins to import Cl^- to the cell and after 30–90 seconds restores the equilibrium at a resting potential of –170 mV" (Gradmann 1976).

In the plasmalemma of *Charophytes* there are Cl^- channels activated by depolarization, which are responsible for a component of the action potential (Gaffey & Mullins 1958; Beilby & Coster 1979). These channels may be activated by cytoplasmic Ca^{2+} (Shiina & Tazawa 1987) the concentration of which increases during the action potential (Williamson & Ashley 1982; Kikuyama & Tazawa 1983). By using the patch-clamp technique on the plasmalemma, Coleman (1986) demonstrated unitary currents of Cl^- channels which open more frequently with membrane hyperpolarization. The average current through these channels measured by conventional voltage clamping is also activated by low external pH (Tyerman et al. 1986a) and it was proposed that their function is to regulate voltage and to keep the proton-motive force across the plasmalemma constant at different external pH (Tyerman et al. 1986b). It is not known whether the depolarization and hyperpolarization activated Cl^- currents are the result of the same population of channels or two different populations of channels (Tyerman & Findlay 1989). Experiments in which the patch-clamp technique was used reveal the I–V curves of single Cl^- channels in the cytoplasmatic droplet membrane that we tentatively assume to be tonoplast. The Cl^- channel coexists with two K^+ channels: the high conductance

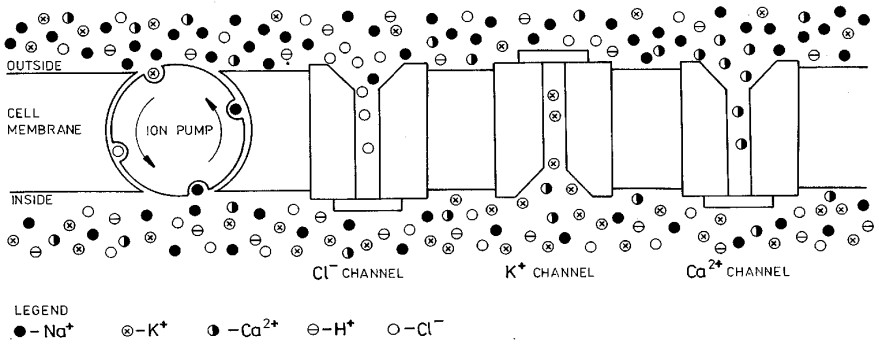

Figure 1. Schematic representation of transverse membrane ionic fluxes. An energy-dependent ion (proton) 'pump' driven by the hydrolysis of ATP transports chloride (empty dots) and potassium (crossed dots) ions against electrical gradient and establishes concentration gradients of these ions across the membrane. The second type of channels enables the ionic flow with the gradient in response to changes in the voltage across the membrane. The separate potassium, chloride and calcium channels are shown in the resting state – the gates held closed by the membrane potential. When the resting potential is reduced, the channels open and give rise to a pulse of current that propagates down the cell. Our theoretical description concerns the channels that allow ion movements along with the electrical gradient (based on Keyens 1979).

channel and K^+ channel with a smaller conductance which displays marked voltage dependence (Tyerman & Findlay 1989).

In maize (Fromm & Bauer 1994), action potentials are elicited by electrical stimulation and the K^+ and Cl^- concentrations of the sieve elements decrease sharply while Ca^{2+} may increase. From these ion displacements, it is assumed that Cl^- also carries the inward and K^+ the outward current in the maize action potential. Since Ca^{2+} is present at lower concentrations than K^+ and Cl^-, its role during excitation might involve stimulation, as was already proposed for the *Characeae* action potential (Lunevsky et al. 1983). It was shown (Fromm & Spanswick 1993) that stimulation of the plant was followed by ion shifts which were most striking in the phloem cells. While the concentration of potassium and chloride was diminished after stimulation, the amount of cytoplasmic calcium increased slightly. These displacements lead to the conclusion that Ca^{2+} influx as well as K^+ and Cl^- efflux are involved in the propagation of action potentials (see Figures 1 and 2).

To conclude, the ionic mechanism of excitation in plants is based on the observation that chloride carries the inward current (Gaffey & Mullins 1958) and potassium the outward current. However, calcium also plays a significant role during the action potential (Beilby & Coster 1979; Kikuyama & Tazawa 1983). It has been suggested that entry of calcium stimulates the opening of chloride channels (Lunevsky et al. 1983; Tsutsui et al. 1986; Kikuyama 1987).

Linear and two dimensional (membrane) structures seem to be the most fundamental elements of living cells (Odell 1980; Barrett 1981; Lakshminarayanaiah

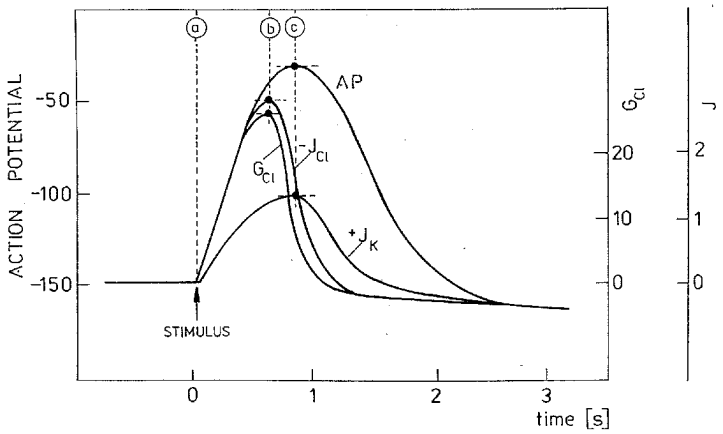

Figure 2. Illustration of the sequence of events of the action potential (AP) (voltage) across plasmalemma in *Chara corallina* and the corresponding ionic currents (conductances) (r.h.s. scales) of of Cl^- and K^+. (a) The excitation and the rapid growth of G_{Cl} (electrical conductivity) for chloride ions is accompanied by a sudden rise of inward electrical current J_{Cl} which is brought about by the efflux of Cl^- and the depolarization of the resting potential; (a–b) Slow depolarization still enhances the G_{Cl}; (b–c) Outward potassium current G_K; K^+ efflux increases during the depolarization of the resting potential; (c) The depolarization reaches its maximum value when $-G_{Cl} = G_K$ which keeps decreasing and results in a resting potential recovering to the initial level; J_{Cl} and J_K diminish – at the moment the membrane looses excitability.

1984; Mańka & Ogrodnik 1991; Nossal & Lecar 1991). Propagation of the action potential along such quasi one-dimensional structures due to transversal current of potassium and sodium ions and due to the gradient of the electrochemical potential caused by its relative deficiency inside or outside of the membrane was first described on the basis of a phenomenological model due to Hodgkin, Huxley and Katz (Hodgkin & Huxley 1952; Hodgkin & Huxley 1952; Hodgkin et al. 1952) with the help of a second order nonlinear differential equation. They elucidated the basic events underlying the generation of the action potential on the squid giant axon at the Marine Biological Association of the United Kingdom in Plymouth (a contribution for which they shared a Nobel prize in 1963). They showed (see Keynes 1979) that the electrical excitability of the nerve membrane depends on its possession of a voltage-sensitive ionic permeability system that enables it to utilize energy stored in the ionic concentration gradients set up by the energy-dependent ion pump. This description gave first insight into possible inward and outward flows of K^+ and Na^+ gated currents and thus propagation of the membrane potential along such structures. In Pietruszka (1993), we considered how such a system evolves, i.e. we have treated similar system dynamically. The propagation of the action potential along the axon was of our main concern. Our investigation in a series of subsequent time instants provided an insight into mutual relations between the action potential and the ionic transmissions across excitable membranes. It was possible to observe

changes in both the action potential amplitude and ionic currents as a sequence of events along such one-dimensional structures as axons.

The aim of this communication is to reconsider and generalize an alternative description (a 'per analogia' model) of the action potential when applied to plants (regarding its evolution in time) by means of field-theoretical methods. We propose here that the transmitted action potential as a whole may act as a major intercellular signal. We expand some tentative suggestions put forward earlier (Maśka & Pietruszka 1995). We develop the idea of treating the transmission of the action potential as a well-known physical phenomenon (which was first observed and described by John Scott Russell who was riding along Union Canal in Scotland once in the morning in 1834 and followed a solitary wave uniformly moving on the water surface (Scott Russell 1844) which in mathematical description results from non-linear time-dependent partial differential equations – the soliton propagation.[1] The scope of this paper is as follows: The second section addresses providing a physical model of the action potential propagation in plant cells while the remainder of our paper presents short conclusions and remarks.

2. The model

Let us consider the full Lagrangian density function, which includes the kinetic and potential energies of the scalar fields ϕ_i ($i = 1, 2, 3$) as well as the $\phi_i - \phi_j$ interactions (we omit the role of a proton (ion) pump for the sake of simplicity):

$$\mathcal{L} = \sum_{i=1}^{3} \mathcal{L}_{\phi_i} + \sum_{i,j=1}^{3}{}' \mathcal{L}_{(\phi_i,\phi_j)}, \tag{1}$$

where $\sum'$ denotes summation over different indices ($i \neq j$). Trying to give at least a qualitative description of the biological process presented in the first section we introduce three scalar fields[2] ϕ_i ($i = 1, 2, 3$) in 1+1 dimensional space (vt, x), representing K^+, Cl^- and Ca^{2+} ions, respectively; c is here the maximum transport velocity in the medium (it is *not* to be confused with the light velocity). v which is unequal to c, $v \neq c$, in our *pseudorelativistic* formalism describes the propagation velocity. The fields are described by the Lagrangian densities $\mathcal{L}_{\phi_i}$:

$$\mathcal{L}_{\phi_i} = \tfrac{1}{2}\partial_\mu \phi_i \partial^\mu \phi_i - U_i(\phi_i), \tag{2}$$

where μ = 0, 1, hence $\partial_\mu = (\partial_0, \partial_1)$ and $\partial_0 = \frac{1}{v}\frac{\partial}{\partial t}$, $\partial_1 = \frac{\partial}{\partial x^1}$, with the (fields) self-interactions given by

$$U_i(\phi_i) = \frac{\lambda_i}{4}\left(\phi_i^2 - u_i^2\right)^2, \tag{3}$$

and the interaction between ϕ_i and ϕ_j described by the second term in (1) $\mathcal{L}_{(\phi_i,\phi_j)}$:

$$\mathcal{L}_{(\phi_i,\phi_j)} = \frac{\lambda_{ij}}{2}\phi_i^2\phi_j^2. \tag{4}$$

The Lagrangians $\mathcal{L}_{\phi_i}$, $(i = 1, 2, 3)$ posses reflection symmetry ($\phi_i \leftrightarrow -\phi_i$). Presumably, the ground state of the system described by e.g. $\mathcal{L}_{\phi_1}$ is either $\phi_1 = -u_1$ or $\phi_1 = +u_1$ and the $\mathcal{Z}_2$ symmetry present in the Lagrangian is not respected by the vacuum state (ground state energy). When a symmetry of the Lagrangian is not respected by the vacuum, the symmetry is said to be *spontaneously broken*. However, *the symmetry can be broken* by obtaining a vacuum expectation value (VEV) $\phi_i = -u_i$ as well as $\phi_i = +u_i$ with equal probability. Thus one can imagine, that in one region (e.g., for $x \to +\infty$) the configuration is close to one of the minima (e.g., $\phi_i \approx +u_i$), whereas in the another region (e.g., for $x \to -\infty$) the configuration is close to the other one (i.e., $\phi_i \approx -u_i$). It is obvious that there must be also a region where $U_i(\phi_i) > 0$. It is easy to find a static ($\partial\phi/\partial t = 0$) solution of a system described by the Lagrangian $\mathcal{L}_{\phi_i}$ with the boundary value conditions $\phi_i(-\infty) = -u_i,\ \phi_i(\infty) = u_i$. Equation of motion for the field ϕ_i (Euler-Lagrange equation) takes the form:

$$\frac{\partial^2 \phi_i}{\partial x^2} = U_i'(\phi_i), \tag{5}$$

which has the *topological soliton* solution – the kink: $\phi_i(x) = \pm u_i \tanh(x/\Delta_i)$ where Δ is the 'thickness' of the wall, given by $\Delta_i = (\lambda_i)^{1/2} u_i^{-1}$. The finite, but non-zero thickness of the wall may be understood in the following way: The terms contributing to the energy include a gradient term (kinetic) and a potential energy term; the gradient term is minimized by making the wall as thick as possible, and the potential term is minimized by making the wall as thin as possible, i.e., by minimizing the distance over which ϕ_i is away from $\pm u_i$; the balance between these terms results in a wall of thickness Δ_i.

The total energy of the kink configuration can easily be calculated for non-interacting fields:

$$\begin{aligned} \mathcal{E}_i &= \int_{-\infty}^{\infty} \mathcal{H}_i dx = \int_{-\infty}^{\infty} \left[\frac{1}{2} \left(\frac{\partial \phi_i}{\partial x} \right)^2 + U_i(\phi_i) \right] dx \\ &= \int_{-u_i}^{u_i} \sqrt{2U_i(\phi_i)} d\phi_i = \frac{4}{3} \sqrt{\frac{\lambda_i}{2}} u_i^3 \end{aligned} \tag{6}$$

and eventually reads $E_{Tot} = \sum_i \mathcal{E}_i$.

We find that such a solution is topologically stable, i.e., there are no continuous transformations which lead to a field configuration without the region of finite density of energy. This is a consequence of conservation of topological charge Q, which is different from zero for all topologically non-trivial configurations. In general, topological charge takes values from a (sub)set of integer numbers. In our example $Q = \pm 1$ for kink-type solutions and $Q = 0$ for homogeneous solutions (i.e., for $\phi_i = u_i$ or $\phi_i = -u_i$). Let us remind that the topological charge Q is connected with a conserved current j^μ ($\partial_\mu j^\mu = 0,\ \mu = 0, 1$) given by

$$j_i^\mu = \frac{1}{2u_i} \epsilon^{\mu\nu} \partial_\nu \phi_i^\nu, \tag{7}$$

where $\epsilon^{\mu\nu}$ is the fully antisymmetric tensor ($\epsilon^{01} = 1$). Integrating the zeroth component of the above equation we get

$$\begin{aligned} Q_i &= \int_{-\infty}^{\infty} j_i^0 dx = \frac{1}{2u_i} \int_{-\infty}^{\infty} \frac{\partial \phi_i}{\partial x} dx \\ &= \frac{1}{2u_i}[\phi(\infty) - \phi(-\infty)] = \pm 1 \end{aligned} \tag{8}$$

for non-homogeneous field configurations. Note, that the current j_i^μ is not a consequence of any continuous symmetry (it is not a Noether current). The simple model described by the Lagrangian $\mathcal{L}_{\phi_i}$ has stable non-homogeneous solutions because of the existence of disconnected vacuum states.

Now, we look for a more realistic model with kink-type stable solutions that involve potassium, chloride and calcium fields. The full Lagrangian (1) can be rewritten in the following form:

$$\mathcal{L} = \frac{1}{2} \sum_{i=1}^{3} \sum_{\mu=0}^{1} \partial_\mu \phi_i \partial^\mu \phi_i - W(\phi_i, \phi_j), \tag{9}$$

where the potential $W(\phi_i, \phi_j)$ is given by

$$W(\phi_i, \phi_j) = \sum_{i=1}^{3} \frac{\lambda_i}{4} \left(\phi_i^2 - u_i^2\right)^2 + \sum_{i \neq j} \frac{\lambda_{ij}}{2} \phi_i^2 \phi_j^2 \tag{10}$$

($i, j = 1, 2, 3$).

For some values of the parameters λ_i and u_i – when we focus our attention only on potassium and chloride fields – the potential $W(\phi_i, \phi_j)$ does not have disconnected minima, and then we do not expect topologically stable solutions. For instance, for $\lambda_1 = \lambda_2 = \lambda_3 = u_1 = u_2 = 1$ the manifold of equivalent vacuum states constitutes a circuit in the $\phi_1 - \phi_2$ plane with a radius $R^2 = \phi_1^2 + \phi_2^2 = 1$ (Figure 3). However, for most values of these parameters (for $\lambda_3 > \lambda_1, \lambda_3 > \lambda_2$) $W(\phi_1, \phi_2)$ has four disconnected minima for $(\phi_1, \phi_2) \in \{(u_1, 0),\ (-u_1, 0),\ (0, u_2),\ (0, -u_2)\}$ (Figure 4).

Once we wish to reconstruct the shape of the action potential we look for solutions which fulfill the following boundary value data conditions: $\phi_1(-\infty) = 0$, $\phi_1(\infty) = u_1$, $\phi_2(-\infty) = u_2$, $\phi_2(\infty) = 0$, where u_1 and u_2 are the VEVs of ϕ_1 and ϕ_2 in the potassium-rich and chloride-rich regions, respectively. The values of the coupling constants $\lambda_1,\ \lambda_2,\ \lambda_3$ and the vacuum expectation values $u_1,\ u_2$ can be determined with the help of the fit to experimentally obtained data.

Recalling at this point the Euler-Lagrange equations

$$\partial_\mu \frac{\partial \mathcal{L}}{\partial(\partial_\mu \phi_i)} = \frac{\partial \mathcal{L}}{\partial \phi_i} \tag{11}$$

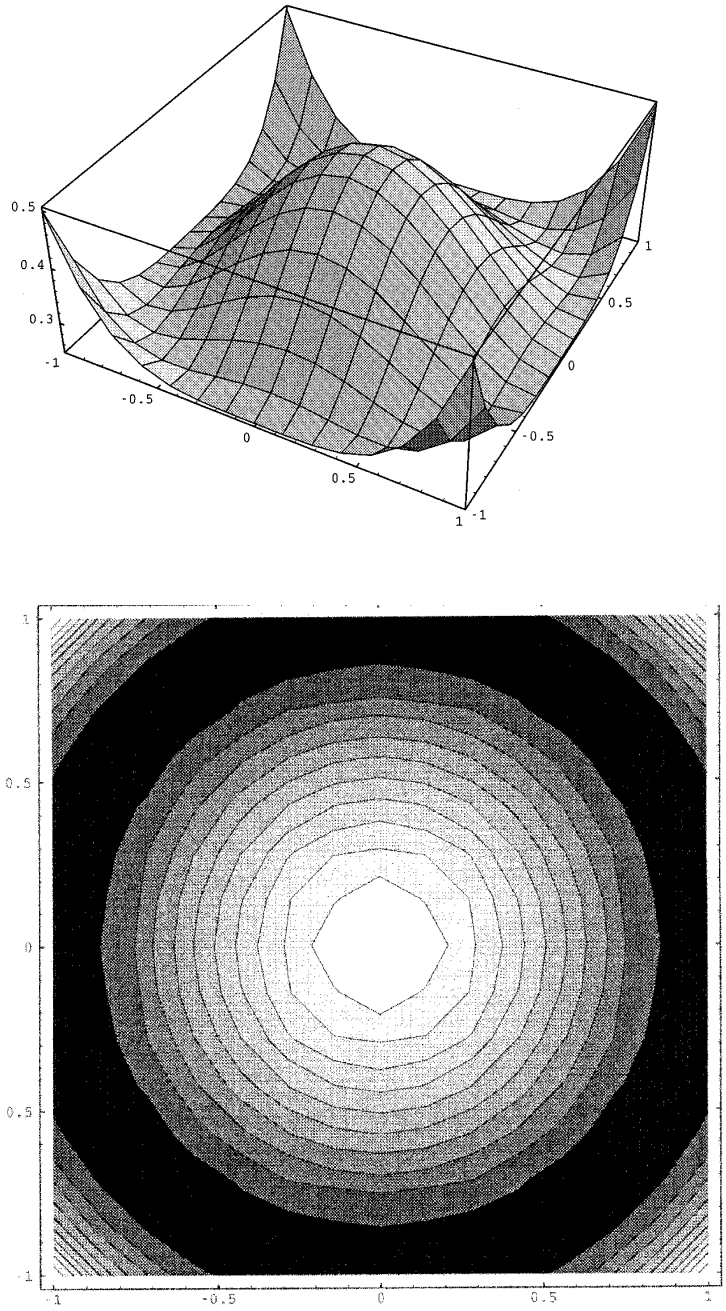

Figure 3. The 3-dimensional plot (top) of the potential $W(\phi_i, \phi_j)$ for the set of parameters: $\lambda_1 = \lambda_2 = \lambda_3 = u_1 = u_2 = 1$. The bottom figure shows the corresponding contour plot of isoenergetic curves.

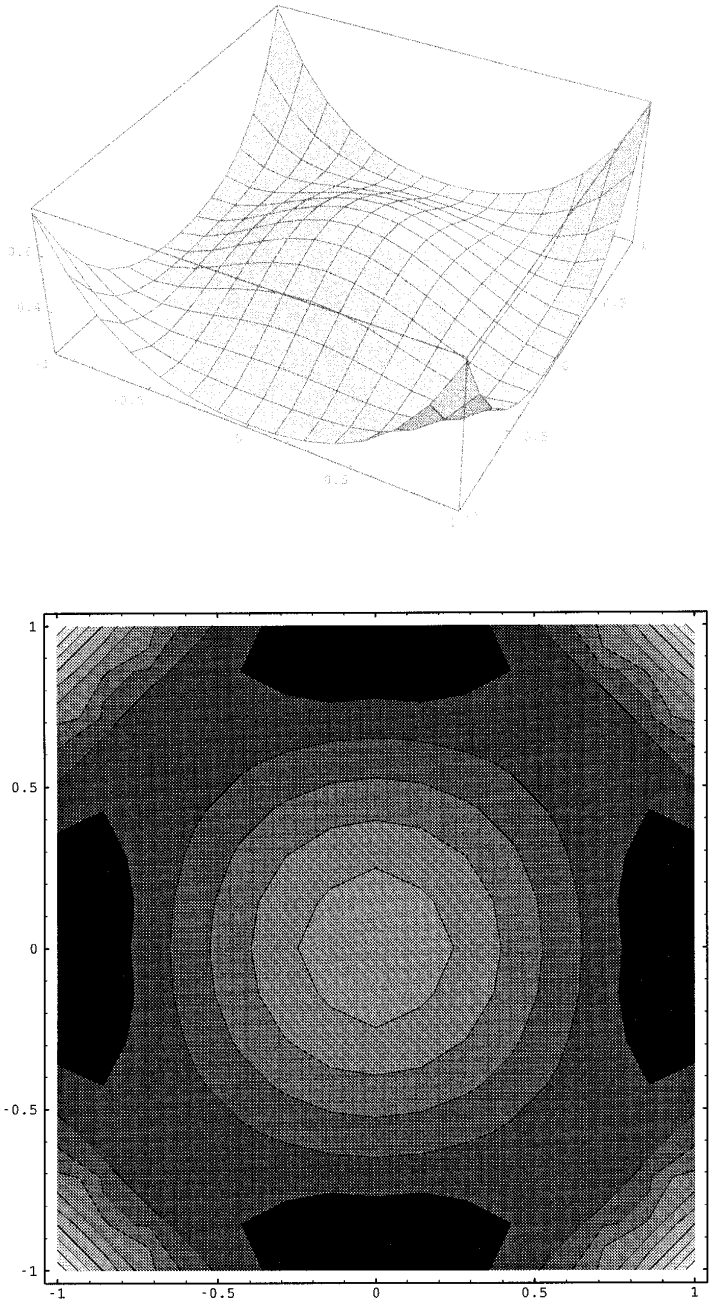

Figure 4. The 3-dimentional plot (top) of the trial potential $W(\phi_i, \phi_j)$, when the interaction strength (λ_3) between the fields increases, for $\lambda_1 = \lambda_2 = u_1 = u_2 = 1,\ \lambda_3 = 1.5$. The bottom figure shows the corresponding contour plot of isoenergetic curves.

($i = 1, 2, 3$), or, here, equivalently $\partial_\mu \partial^\mu \phi_i = -W'(\phi_i)$, and after inserting the total Lagrangian density $\mathcal{L}$ (9) we end up with the set of three partial differential equations for the scalar fields ϕ_1 and ϕ_2 and ϕ_3:

$$\begin{aligned}
\Box\phi_1 &= -\phi_1[\lambda_1(\phi_1^2 - u_1^2) + \lambda_{12}\phi_2^2 + \lambda_{13}\phi_3^2], \\
\Box\phi_2 &= -\phi_2[\lambda_2(\phi_2^2 - u_2^2) + \lambda_{21}\phi_1^2 + \lambda_{23}\phi_3^2], \\
\Box\phi_3 &= -\phi_3[\lambda_3(\phi_3^2 - u_3^2) + \lambda_{31}\phi_1^2 + \lambda_{32}\phi_3^2],
\end{aligned} \tag{12}$$

where we have utilized the following (d'Alambertian) notation

$$-\partial_\mu \partial^\mu = \Box = \frac{\partial^2}{\partial x_1^2} - \frac{1}{v^2}\frac{\partial^2}{\partial t^2}. \tag{13}$$

For symmetry reasons we put $\lambda_{ij} = \lambda_{ji}$. Moreover, if we assume interaction constants $\lambda_{13} = \lambda_{23} \cong 0$ and we change the notation suitably we are left with

$$\begin{aligned}
\partial_\mu \partial^\mu \phi_1 - \phi_1(\lambda_1\phi_1^2 + \lambda_3\phi_2^2 - \lambda_1 u_1^2) &= 0, \\
\partial_\mu \partial^\mu \phi_2 - \phi_2(\lambda_2\phi_2^2 + \lambda_3\phi_1^2 - \lambda_2 u_2^2) &= 0, \\
\partial_\mu \partial^\mu \phi_3 - \phi_3(\lambda_3\phi_3^2 + \lambda_3 u_3^2) &= 0,
\end{aligned} \tag{14}$$

for $\mu = 0, 1$. The first two equations couple *via* coupling constants λ_i. The third one describes the dynamics of the free calcium field ϕ_3 – since calcium is present at lower concentrations than potassium and chloride we retain relevant interactions (we neglect Ca^{2+} ions) and we put (in the 'zeroth' approximation) $\phi_3 = 0$ hereafter. Because of the 'Lorentz invariance' of the Euler-Lagrange equations we seek static solutions (by, e.g., discretizing the space variable and by use of central difference approximation for the second order space derivative), and then apply the Lorentz transformation to obtain the time-dependent solution. In the static case ($\partial\phi_i/\partial t = 0$, $i = 1, 2$) the system of equations of motion (12) takes the following form:

$$\begin{aligned}
\frac{d^2\phi_1(x)}{dx^2} &= \phi_1(\lambda_1\phi_1^2 + \lambda_3\phi_2^2 - \lambda_1 u_1^2), \\
\frac{d^2\phi_2(x)}{dx^2} &= \phi_2(\lambda_2\phi_2^2 + \lambda_3\phi_1^2 - \lambda_2 u_2^2),
\end{aligned} \tag{15}$$

with the boundary conditions given as above.[3] For arbitrary values of the coupling constants and the vacuum expectation values the above system of equations is too complicated to be solved analytically. (For some specific values of these parameters, when the system is analytically solvable, there are no topologically non-trivial solutions.) Thus we have adopted some numerical procedures in order to find the solutions, namely a variable order, variable step size finite-difference method with deferred corrections used.

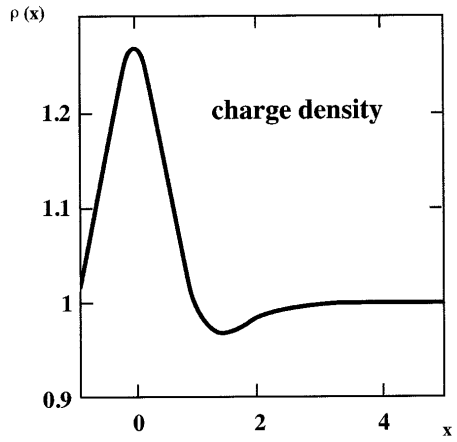

Figure 5. The density of charge inside the cell for the field configuration calculated from the example solution for the system of equations of motion for the potassium and chloride fields.

According to the standard interpretation of the wave function we can finally calculate (taking into account the solutions for some values of parameters of the system of equations) the *charge density* (the spatial density of K^+ and Cl^- ions times the single ion charge) in the cell in the following form:

$$\varrho(x) = \sum_{i=1}^{2} q_i \, |\phi_i(x)|^2, \tag{16}$$

where q_i stands for the *i*-th single ion charge. Figure 5 shows how the density of charge changes along the cell. The shape of the charge density function resembles a shape of the action potential impulse.

Up to this point we have presented a static picture but we can still explore the relativistic invariance of the Euler-Lagrange equations of motion in order to find time-dependent solutions. Observe that if $\phi_1(x)$ and $\phi_2(x)$ are solutions to the equations (13), then so are the boosted configurations:

$$\Phi_i(x,t) = \phi_i \left[(x + vt)\gamma\right], \tag{17}$$

$$\gamma = \frac{1}{\sqrt{1 - \frac{v^2}{c^2}}}, \tag{18}$$

which describe the *solitary wave* moving *along* the x axis with a constant velocity v. Thus, also the region of depolarized cell membrane can propagate down the length of the cell *without attenuation* or *change in shape*.

3. Conclusions

In this paper we have presented a simple solitonic model for the action potential travelling along the plant cell. We started our considerations with three scalar

fields (for potassium, chloride and calcium channels, respectively) which were described by the Lagrange function that includes both interactions between these fields and self-interactions in the kinetic and potential terms. The interactions and self-interactions result in non-linear terms in the equations of motions for the potassium and chloride fields, allowing stable and non-homogeneous structures - topological defects, e.g. longitudinal solitons. We observe that these *solitons* can propagate down the cell qualitatively in the same manner (without the energy loss – dissipation – and with preserving the shape of the moving spike) as does the action potential.

Acknowledgments

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Notes

1. We seek solutions of the form $\phi(x,t) = f(x-vt)$ what is called *travelling wave*. Especially, we are interested in travelling waves with finite energy, i.e., if we introduce the variable $\xi = x - vt$, then f must satisfy the boundary conditions $\lim_{\xi\to\pm\infty} f(\xi) = \phi_{\pm\infty}$. As f is essentionally constant sufficiently far away we say that such a wave is *localized*. A solution of the form $\phi(x,t) = f(\xi)$ which satisfies such boundary conditions is called a *solitary wave*.
2. In general $\phi = \phi_0 + \delta\phi$ where ϕ_0 stands for the mean-field value of ϕ and $\delta\phi$ describes deviation about ϕ_0. In our derivation we omit the second component.
3. By making the substitution $y_1 = \phi_1$, $y_2 = \phi_1'$, $y_3 = \phi_2$ and $y_4 = \phi_2'$ (where prime denotes derivatives over x) we obtain a set of ordinary differential equations of the first order

$$\begin{aligned} y_1' &= y_2, \\ y_2' &= y_1(\lambda_1 y_1^2 + \lambda_3 y_3^2 - \lambda_1 u_1^2), \\ y_3' &= y_4, \\ y_4' &= y_3(\lambda_2 y_1^2 + \lambda_3 y_3^2 - \lambda_2 u_2^2) \end{aligned}$$

for unknown functions $y_1(x)$ and $y_3(x)$ and their derivatives. The above system of equations may be solved numerically with the help of the multiple shooting method (e.g., BVPMS/DBVPMS, IMSLMD Fortran Library; MUSN, etc.).

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