Propagation and Relaxation of Neuronal Membrane Mechanical Deformations in Mathematical Model

Maria R. Kotikova[1,2](✉) and Anton V. Chizhov[1,2]

[1] Ioffe Institute, Politekhnicheskaya Street, 26, 194021 St. Petersburg, Russia
kotikova.mr@yandex.ru

[2] Sechenov Institute of Evolutionary Physiology and Biochemistry of RAS, Torez pr., 44, 194223 St. Petersburg, Russia

Abstract. Neuronal membrane undergoes mechanical deformations in response to electrical pulse or mechanical influence. We propose a one-dimensional mathematical minimal model that describes propagation and dissipation of the deformations. The model is based on fluid dynamics equations and uses the Lippmann equation to connect electrical effects with membrane elasticity. The effects of internal heterogeneity of neuron, e.g. cytoskeleton, on mechanical deformations and pressure waves is investigated and specified as relaxation. The pressure in response to the mechanical disturbance of the neuron is compared to known experiment.

Keywords: Neuronal membrane · Mathematical modeling · Mechanical deformation · Pressure wave · Action potential

1 Introduction

Basic information in neural networks of the brain is transmitted using electrical pulses, named action potentials or spikes. Neuronal excitability is provided by the ionic channels that are gated by chemical mediators or membrane voltage. In classical Hodgkin and Huxley model [1], the excitability of neurons is described by a system of equations based on the diffusion equation and supplied with ordinary differential equations. This system reproduces action potentials, which can be approximate as an autowave process.

Experiments show that the generation of action potential is accompanied by small mechanical changes in the shape of neuron and pressure waves in the intracellular liquid [2]. The exact mechanism of such changes is unknown. However, it is shown that the change of the membrane potential affects the mechanical properties of the membrane.

Understanding of such processes will provide a deeper knowledge of the physical-chemical effects in neurons, and might help to develop an invasive technique of visualization of the electrical pulse spread.

A model based on the Lippmann equation [3], connecting membrane tension with membrane potential and the incompressible fluid dynamic equations was proposed in a previous work [4]. But model does not describe some effects, which was presented in experiments.

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Therefore, the previously presented mathematical model has been reconsidered. In previous version of model the dissipation was specified as a viscosity of intracellular liquid. But this mechanism cannot describe some of pressure wave effects, which was shown in experiment. Here we introduce a relaxation due to cytoskeleton.

2 Mathematical Model

We construct a one-dimensional model of a modeled neuron that is based on the fluid dynamics equations. In this consideration, a water-based electrolyte medium is surrounded by an elastic membrane of a cylindrical branch of the length L and the radius R_0, as shown in Fig. 1. Boundary conditions are specified as free surfaces. The membrane is supposed to be initially strengthened, so the surface tension is balanced by the osmotic and hydrostatic pressures.

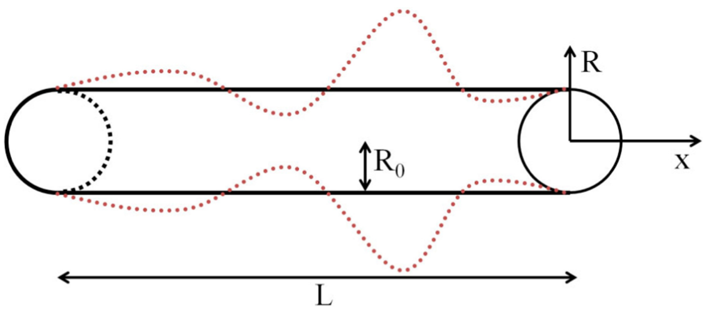

Fig. 1. Schematic of a cylindrical branch of a neuron and its deformations (dotted lines).

Taking the continuity equation for the incompressible fluid in the form of zeroed divergence of the velocity vector, we write it in the cylindrical coordinates and average across the radius. As a result, we obtain an equation for the average speed $\overline{u}$ and the radius $R(t)$:

$$\frac{2}{R}\frac{\partial R}{\partial t} + \frac{\partial \overline{u}}{\partial x} = 0 \tag{1}$$

The second equation is the momentum equation:

$$\frac{\partial \overline{u}}{\partial t} + \frac{1}{\rho}\frac{dp_i}{dx} = 0 \tag{2}$$

where p_i is the pressure inside the neuron; taking into account its balance with the osmotic and external pressure, it is equal to the membrane tension, i.e.

$$p_i = \Delta p_\sigma \tag{3}$$

According to the Laplace's law membrane tension calculated as

$$\Delta p_\sigma = \frac{\sigma}{R} \tag{4}$$

where σ is the membrane tension.

According to [5, 6], the membrane tension is calculated as a sum of voltage-dependent and voltage independent parts:

$$\sigma = \gamma + \sigma^{'}(V) \tag{5}$$

where γ is the membrane elasticity, $\sigma^{'}(V(t))$ is an additional membrane elasticity, that depends on membrane potential.

According to Hooke' law, pressure is calculated as

$$\Delta p_{\sigma} = \gamma \frac{R - R_0}{{R_0}^2} + \frac{\sigma^{'}(V(t))}{R_0} \tag{6}$$

where R_0 is the initial radius in the unperturbed state. Substituting the above relations in the main Eqs. (1,2), we obtain:

$$\begin{cases} \frac{\partial \overline{u}}{\partial t} + \frac{1}{\rho}\frac{\partial}{\partial x}\left(\frac{\gamma(R-R_0)}{R_0^2} + \frac{\sigma^{'}(t)}{R_0}\right) = 0 \\ \frac{2}{R_0}\frac{\partial R}{\partial t} + \frac{\partial \overline{u}}{\partial x} = 0 \end{cases} \tag{7}$$

This system of transport equations is of hyperbolic type. It describes the transport with the speed of propagation of the disturbances equal to:

$$a = \sqrt{\frac{\gamma}{2\rho R_0}} = \sqrt{\frac{hE}{2\rho R_0}} \tag{8}$$

where h is the effective membrane thickness and E is the Young's modulus.

The experiments reveal dissipation of membrane deformations. Neurons have cytoskeleton, which may provide the dissipation. Influence of cytoskeleton can be specified as a relaxation $-\nu\overline{u}$ in the momentum conservation equation. This term is similar to the one in hemodynamic equation [7].

Finally, system of equations, which describe mechanical deformation of neuronal membrane, is as follows:

$$\begin{cases} \frac{\partial \overline{u}}{\partial t} + \frac{1}{\rho}\frac{\partial}{\partial x}\left(\frac{\gamma(R-R_0)}{R_0^2} + \frac{\sigma^{'}(t)}{R_0}\right) = -\nu\overline{u} \\ \frac{2}{R_0}\frac{\partial R}{\partial t} + \frac{\partial \overline{u}}{\partial x} = 0 \end{cases} \tag{9}$$

3 Numerical Methods

We solved the above written equations numerically. The numerical scheme was obtained after the factorization of the equations according to physical processes, transport and dissipation. We then applied an explicit first-order TVD numerical scheme for the hyperbolic part of the equations. The TVD, or Godunov-like scheme was initially written for the Riemann invariants, which are the linear combinations of the velocity and a radius