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Review

Calculation of action potential propagation in nerve fiber

N.M. Bogatov*, L.R. Grigoryan, E.G. Ponetaeva, A.S. Sinisyn

Kuban State University, Stavropolskaya Street, 149, Krasnodar 350040, Russian Federation

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ABSTRACT

This article introduces generalization of the action potential spreading model which considers generation of the action potential in each segment of the nerve fiber. Behavior of the impulse signal waveform during the propagation process was analyzed. A mechanism of distributed generation of the charge in nerve fiber results in decrease of phase velocity of signal spreading rate. Amplitude of the action potential decreases and pulse width increases in the action potential propagation process.

Contents

1. Introduction

Regular functioning of the living organism is impossible without the exchange of information between its subsystems. One of the ways of information transfer is propagation of electrical impulses in the nerve fiber. Electric character of nerve pulses is proved in researches done by Hodgkin and Rushton (1946); Hodgkin and Huxley (1952); Hodgkin (1965).

Modeling of bioelectrical effects is widely used in modern electrophysiology to study the processes occurring in living electro excitable structures (Frankenhaeuser and Huxley, 1964; Fomin and Berkinblit, 1973; Abbott and Kepler, 1990; Debanne, 2004). Soliton model of nerve fiber transmembrane potential change occurring in process of excitation propagation was developed in works (Maksimenko, 2003, 2004a,b; 2005). Accurate analytical solution of nerve impulse propagation within Hodgkin-Huxley's model, based on the integral Laplace transformation and Efros theorem when the input excitation pulse deviates from the Heaviside step function was obtained in (Selezov and Morozova, 2010).

Simulated results are generally consistent with the experimental data. Applied problems, e.g. bioprosthetics, require a solution of a general problem: an analysis of changes of arbitrary signals in nerve fiber. The problem of action potential propagation in nerve fiber for arbitrary input pulses was not solved.

The aim of this research is to generalize the model of action potential propagation considering potential generation in each fiber section and analyze signal change when form of excitation pulse corresponds to the actually observed.

2. The solution of the equation of action potential propagation in nerve fiber

Action potential is the change of the membrane potential between intracellular medium and extracellular substance, which moves with nerve signal propagation, when nerve cells are excited. Equation (1) described an action potential, $V(x,t)$, propagation in nerve fiber (Hodgkin and Rushton, 1946).

$$\frac{r}{2\rho_a}\frac{\partial^2 V}{\partial x^2} - C_m\frac{\partial V}{\partial t} - \frac{V}{\rho_m l} = 0, \tag{1}$$

where r is a radius of the axon, ρ_a is a resistivity of the axoplasm, C_m is a capacitance per unit area of membrane, ρ_m is a resistivity of

* Corresponding author. Tel.: +7 861 2199501x266.
E-mail addresses: bogatov@phys.kubsu.ru, physinf@phys.kubsu.ru (N.M. Bogatov).

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membrane material, l is a membrane thickness, the action potential is measured from the resting potential.

Now we generalize Equation (1) considering the generation of the potential in each fiber section. Voltage-gated ion channels play an important role in shaping the action potential. In vertebrates, they are concentrated in the nodes of Ranvier, which is generated by the input pulse $V_0(t)$. Ability to generate an action potential in each fiber section in nature is not excluded (Antonov et al., 2003). Defining rate of charge generation in a nerve fiber with uniformly distributed voltage-dependent ion channels on the part of a fiber of length dx as $G(V)\cdot dx$ where $G(V)$ is a generation function yields Equation (2).

$$\frac{r}{2\rho_a}\frac{\partial^2 V}{\partial x^2} - C_m\frac{\partial V}{\partial t} - \frac{V}{\rho_m l} + \frac{G(V)}{2\pi r} = 0. \quad (2)$$

In the first approximation we choose $G(V) = \beta\cdot V$, $\beta \geq 0$ is a generation constant.

We search for the solution of the Equation (2) when $x \in [0, \infty)$, $t \in [0, \infty)$ meeting next conditions:

$$V(x,t)|_{x=0} = V_0(t), \quad (3)$$

$$\lim_{x\to\infty} V(x,t) = 0, \quad (4)$$

$$V(x,t)|_{t=0} = 0. \quad (5)$$

We impose conditions (6) on the function $V_0(t)$.

$$\int_{-\infty}^{\infty} |V_0(t)|\mathrm{d}t = \mathrm{const}, \quad (6)$$

$$V_0(t) = 0 \quad \text{for} \quad t < 0 \quad (7)$$

And denote

$$\lambda = \sqrt{\frac{rl\rho_m}{2\rho_a}}, \tau = l\rho_m C_m, \gamma = 1 - \frac{\beta l \rho_m}{2\pi r}, \quad (8)$$

where λ is a constant of the neuron fiber length, τ is a constant of signal attenuation, $0 < \gamma \leq 1$. Condition $\gamma > 0$ preserves signal attenuation trend, $\gamma = 1$ corresponds to the absence of potential distributed generation.

Then Equation (2) takes a form (9).

$$\lambda^2\frac{\partial^2 V}{\partial x^2} - \tau\frac{\partial V}{\partial t} - \gamma V = 0 \quad (9)$$

We introduce dimensionless variables:

$$x' = \frac{x\sqrt{\gamma}}{\lambda}, t' = \frac{t\gamma}{\tau}, V' = \frac{V}{v_0}, \quad (10)$$

where v_0 is a resting potential.

In terms of dimensionless variables (10) the Equation (9) takes a form (11).

$$\frac{\partial^2 V'}{\partial x'^2} - \frac{\partial V'}{\partial t'} - V' = 0 \quad (11)$$

Then we represent the solution of the Equation (11) as a Fourier integral.

$$V'(x',t') = \int_{-\infty}^{\infty} U(\nu')\exp\{\alpha(\nu')x' + i2\pi\nu' t'\}\mathrm{d}\nu', \quad (12)$$

In Equation (12) $U(\nu')$ is a Fourier transform of the function $V_0'(t')$ which satisfies the condition (6).

$$U(\nu') = \int_{-\infty}^{\infty} V_0'(t')\exp\{-i2\pi\nu' t'\}\mathrm{d}t' \quad (13)$$

The characteristic equation follow from the Equations (11) and (12).

$$\alpha^2(\nu') - 2\pi i\nu' = 0. \quad (14)$$

$\alpha(\nu')$ is a complex function.

$$\alpha(\nu') = \mathrm{Re}\alpha(\nu') + i\mathrm{Im}\alpha(\nu'). \quad (15)$$

We can find imaginary part of $\alpha(\nu')$ from the Equation (15) considering condition (4). The result is:

$$\mathrm{Im}\alpha(\nu') = \begin{cases} -\frac{1}{\sqrt{2}}\sqrt{\sqrt{1+(2\pi\nu')^2}-1}, \nu' \geq 0 \\ \frac{1}{\sqrt{2}}\sqrt{\sqrt{1+(2\pi\nu')^2}-1}, \nu' < 0 \end{cases} \quad (16)$$

Similarly, we can find the real part of $\alpha(\nu')$.

$$\mathrm{Re}\alpha(\nu') = \frac{\pi\nu'}{\mathrm{Im}\alpha(\nu')}. \quad (17)$$

The Equation (16) shows that $Im\alpha(\nu')$ is an odd function of ν' and the Equation (17) shows that $Re\alpha(\nu')$ is an even function. We will have a solution of the Equation (11) with $x' \geq 0$ for input arbitrary excitation pulse $V_0'(t')$ if we insert (15–17) to the (12).

$$V'(x',t') = 2\int_0^{\infty} [\mathrm{Re}U(\nu')\cos(\mathrm{Im}\alpha(\nu')x' + 2\pi\nu t') - \mathrm{Im}U(\nu')\sin(\mathrm{Im}\alpha(\nu')x' + 2\pi\nu' t')]\exp\{\mathrm{Re}\alpha(\nu')x'\}\mathrm{d}\nu'. \quad (18)$$

3. Impulse response function

Let $V_0'(t') = \delta(t')$, where $\delta(t')$ is delta function. We denote the corresponding solution of (18) as $h(x',t')$ and name it impulse response function. From (13) we have $U(\nu') \equiv 1$ then:

$$h(x',t') = \begin{cases} 2\int_0^{\infty} \exp\{x'\mathrm{Re}\alpha(\nu')\}\cos(x'\mathrm{Im}\alpha(\nu') + 2\pi\nu' t')\mathrm{d}\nu', & t' \geq 0 \\ 0, & t' < 0 \end{cases}. \quad (19)$$