SALTATORY EXCITATION IN A MYELINATED LILLIE-BONHOEFFER NERVE-FIBER MODEL

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In this paper we discuss the myelinated variant of the Lillie-Bonhoeffer nerve-fiber model [1-7]. It consists of an iron wire composed of alternating segments of length L covered with a thin layer of insulator and bare portions of length l ("Ranvier nodes"). This wire is enclosed in a capillary filled with concentrated nitric acid (Fig. 1).

The model is characterized by the resistivity ρ of the electrolyte, the cross-sectional area S of the electrolyte, and the perimeter σ of the cross section of the wire. We will assume that $L \gg l$, and, hence, within the limits of one node the potential and other parameters are constant. We can then use the results of the theory developed for the spatially uniform case (unpublished data).

Thus (see Fig. 2), let node 1 (N1) be in an active state (active-surface fraction $\alpha = 1$) at potential $\varphi^{(1)}$, close to φ_1 – the equilibrium potential of active iron – and node 2 (N2) be in the passive state ($\alpha = 0$, $0 < \varphi^{(2)} < \varphi_*$) † Then from the first to the second node there flows a current $I = (\varphi^{(1)} - \varphi^{(2)})\,S/\rho L$, approximately equal to $(\varphi_1 - \varphi_*)\cdot S/\rho L$ (it will be clear from what follows that potential $\varphi^{(2)}$ from the instant of activation of N1 to the instant of activation of N2 will be close to the value of φ_* almost all the time). The absolute density of the current leaving N1 and entering N2 is $i \approx (\varphi_1 - \varphi_*)\,S/\rho L l \sigma$.‡

The current flowing into N2 is the reason for the activation of N2 some time after the activation of N1. When a passive iron specimen is activated by an external current of density $-i$**, the process is described by the equations for the change of potential

$$C\,d\varphi/dt - j_i - j_f + i_r - i = 0 \tag{1}$$

and the decay of the passivating film

$$\frac{d\alpha}{dt} = -\frac{1}{Q}\,j_f\,. \tag{2}$$

Here j_i is the density of the active iron solution current; j_f is the density of the film decay current; i_r (rheobase) is the maximum current density transmitted by the unactivated system (it is due to the formation of HNO_2 on the passive surface when $\varphi > 0$; for simplicity we neglect the variation in HNO_2 concentrations at the surface). Current–voltage curves for these processes are given in [3]. For the quantitative analysis they are approximated here by straight lines. It can be shown that at the stage of activation the term $C\,d\varphi/dt$ can be neglected in Eq. (1).

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† Below the threshold potential φ_* the passivating film is unstable. As the origin of φ we took the equilibrium potential of the passive surface.

‡ For simplicity we neglect the leak from N2 to the right. This leak is not more than half of I (since $\varphi_* = 0.3$ V, and $\varphi_1 - \varphi_* = 0.6$ V); in addition, there are other grounds for believing that $\varphi^{(2)} - \varphi^{(3)} \ll \varphi^{(1)} - \varphi^{(2)} \approx \varphi_1 - \varphi_*$.

** A current flowing from the iron to the electrolyte is regarded as positive.

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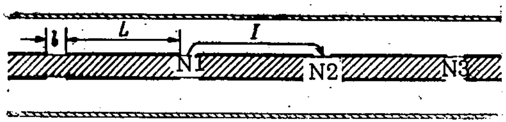

Fig. 1

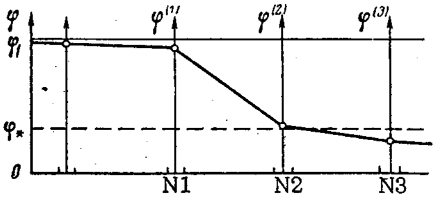

Fig. 2

Fig. 1. Schematic illustration of Lillie model with "myelin."

Fig. 2. Electrolyte potential distribution along wire.

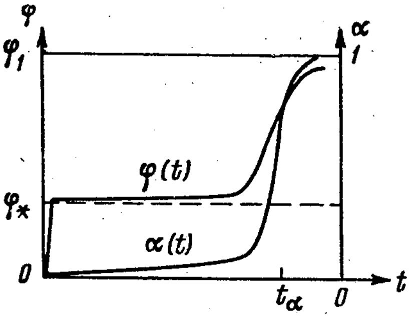

Fig. 3

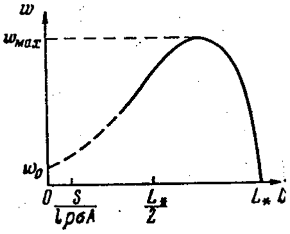

Fig. 4

Fig. 3. Potential φ and active-surface fraction α as functions of time during activation by external current.

Fig. 4. Velocity of propagation as function of length L of "myelinated" parts with prescribed l.

The analytical expressions for j_i and j_f are*:

$$j_i = A\alpha(\varphi_1 - \varphi), \quad j_f = A(1-\alpha)(\varphi_* - \varphi). \tag{3}$$

Substituting them in Eqs. (1) and (2) and using the initial condition $\alpha(0) = 0$, we find the relationship between the active-surface fraction and the time

$$\alpha = \frac{\exp\left[\frac{A(\varphi_1-\varphi_*)}{Q}\left(1+\frac{i-i_r}{A(\varphi_1-\varphi_*)}\right)t\right]-1}{\exp\left[\frac{A(\varphi_1-\varphi_*)}{Q}\left(1+\frac{i-i_r}{A(\varphi_1-\varphi_*)}\right)t\right]+\frac{A(\varphi_1-\varphi_*)}{i-i_r}}.$$

An analysis of the formula shows that when $(i-i_r)/A(\varphi_1-\varphi_*) \ll 1$ the value of α changes in the following way. Initially α increases very slowly and then increases rapidly from almost 0 to 1. The time of rapid increase of α is equal in order of magnitude to $Q/A(\varphi_1-\varphi_*)$, and the "acceleration" time is

$$t_a = \frac{Q}{A(\varphi_1-\varphi_*)}\ln\frac{A(\varphi_1-\varphi_*)}{i-i}. \tag{4}$$

A comparison of these quantities shows that most of the activation time is taken up by the "acceleration period" when $\alpha \ll 1$ and $\varphi-\varphi_* \ll \varphi_1-\varphi_*$, and activation can be regarded as saltatory at instant t_a (Fig. 3).

We now proceed directly to find the velocity of propagation. The activating current I is switched on at the instant when N1 changes to the active state. The time taken for the excitation to jump from N1 to N2 is obviously given by formula (4). From this formula it is easy to find the velocity of propagation of activation

$$w = LA(\varphi_1-\varphi_*)/Q\ln\frac{1}{S/Ll\rho\sigma A - i_r/A(\varphi_1-\varphi_*)}. \tag{5}$$

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* The slopes of the current–voltage characteristics for solution of iron and formation/decay of the film happened to be very similar. Hence, for the sake of simplicity we took the same value for them: $A = 20\ \mathrm{A/cm^2 \cdot V}$.

This expression shows that as the density $S(\varphi_1-\varphi_*)/Ll\rho\sigma$ of the activating current approaches i_r the velocity decreases to zero, and when $S(\varphi_1-\varphi_*)/Ll\rho\sigma < i_r$ the expression ceases to have sense. The physical meaning of this is that the length L of the "myelinated" region can be increased only up to a certain limit L_*, above which the effect of N1 on N2 is reduced so much that propagation of the activation impulse becomes impossible. A more thorough investigation of the relationship between w and L shows that w(L), when $i_r/A(\varphi_1-\varphi_*) < e^{-2}$, has a maximum between L_* and $L_*/2$. For w_{max} we can write

$$w_{max} \approx \frac{AS(\varphi_1-\varphi_*)}{Q} \Big/ l\rho\sigma i_r \ln\frac{A(\varphi_1-\varphi_*)}{i_r},$$

which is valid when $i_r/A(\varphi_1-\varphi_*) \ll 1$. For real values of the parameters this condition is always fulfilled.

We will indicate the region of applicability of the expounded theory. If excitation transfer mainly involves two neighboring nodes, we must have

$$(\varphi_1-\varphi^{(1)})/(\varphi_1-\varphi_*) \ll 1 \qquad (6)$$

all the time, except for the short periods in which the node changes from the passive to the active state. Since the current flowing from N1, where $\alpha = 1$, is produced by active solution of the iron, then $i = A(\varphi_1-\varphi^{(1)})$ [see (3)] and condition (6) gives

$$i/A(\varphi_1-\varphi_*) \ll 1 \quad \text{or} \quad Ll\rho\sigma A/S \gg 1. \qquad (7)$$

This inequality is the condition for existence of the situation illustrated in Fig. 2.

The above-described propagation of excitation in the electrochemical model of a myelinated fiber was investigated experimentally [1, 7], and a considerable increase in the velocity due to "myelination" of the fiber was discovered. The main reason for this increase is as follows.

If we ignore the weak logarithmic relationship, then for the velocity for L not too close to L_* we can, on the basis of (5), write the expression $w \sim LA(\varphi_1-\varphi_*)/Q$. At the same time, knowing the characteristic length of the activation zone on a "nonmyelinated wire" $\lambda = \sqrt{S/\rho\sigma A}$ and the characteristic activation time $Q/A(\varphi_1-\varphi_*)$, we can estimate the velocity of the impulse on a bare wire $w_0 \sim A(\varphi_1-\varphi_*)\sqrt{S/\rho\partial A}/Q$. (We note that this estimate is in good agreement with the results of [4].) The velocity increase $w/w_0 \sim L/\lambda \gg 1$, which follows from the conditions $L \gg l$ and (7).

In the case opposite to that considered in this paper, viz., when $Ll \ll \lambda^2$, many nodes are in intermediate states between the active and passive state. Hence, the problem reduces approximately to the case of a bare wire with Q replaced by the "smeared" quantity $Ql/(l+L)$. In this case also the velocity is many times greater:

$$w/w_0 = (l+L)/l \gg 1.$$

The velocity increase can thus be attributed to "myelination," eliminating the need for activation of a large part of a wire surface.

The developed theory qualitatively predicts the experimental results of [1, 7].

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