BLOCKING OF IMPULSE BY AN INHOMOGENEITY IN AN ELECTROCHEMICAL NERVE MODEL

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A recently published paper [1] was devoted to an analytical investigation of the conduction of the nerve impulse through an inhomogeneous fiber in a model incorporating current sources [2]. It is of interest to consider the corresponding problem for various physical models of the nerve fiber, particularly the Lillie-Bonhoeffer model [3-5], with specific physicochemical characteristics. The Lillie model is an iron wire contained in a tube filled with strong nitric acid. This model has been used to investigate impulse conduction through a smooth [6] and myelinated [7] fiber. Below we investigate the movement of the activation impulse in an inhomogeneous Lillie model and compare the results with experimental data [8].

1. Abrupt Inhomogeneity. The state of the system is described by a potential $\varphi(x, t)$, the fraction of the surface free from the passivating oxide film $\alpha(x, t)$, and the concentration $c(x, t)$ of one of the reaction products — nitrous acid. In this problem we can neglect the change in the last quantity and put $c(x, t) = c_0 = \text{const}$, since the change in $c(x, t)$ has a significant effect only in the tail region, which extends far back (in the repassivation process).

The changes in potential and the fraction of active surface are given by the equations

$$\frac{\partial^2\varphi}{\partial x^2} + R(j_i + j_f + j_a) = 0, \tag{1}$$

$$\frac{\partial \alpha}{\partial t} + \frac{1}{Q} j_f = 0, \tag{2}$$

where $R = R_1 = \rho\sigma_1/S_1$ when $x < 0$, and $R = R_2 = \rho\sigma_2/S$ when $x > 0$. The letters $\sigma_{1,2}$ and $S_{1,2}$ denote, respectively, the sectional perimeter of the wire and the sectional area of the electrolyte in the tube. In other words, we assume that the inhomogeneity is localized at the point $x = 0$.

The expressions for the equivalent currents of active solution of iron, destruction and formation of the passivating film, and reduction of nitric acid to nitrous acid have the form (in a linear approximation)

$$\begin{gathered} j_i = A(\varphi_1 - \varphi)\alpha; \\ j_f = A\cdot\begin{cases}(\varphi_* - \varphi)(1-\alpha) & \text{for } \varphi > \varphi_*, \\ (\varphi_* - \varphi)\alpha & \text{for } \varphi < \varphi_*;\end{cases} \\ j_a = \begin{cases} 0 & \text{for } \varphi = 0, \\ -Jc_0 & \text{for } \varphi > 0.\end{cases} \end{gathered} \tag{3}$$

The threshold potential φ_* is characterized by the fact that when $\varphi > \varphi_*$ the film is destroyed, and when $\varphi < \varphi_*$ the film is formed.

The aim of the problem was to determine the conditions in which the activation impulse is blocked by an inhomogeneity. We can answer this question by investigating the steady states of the system.

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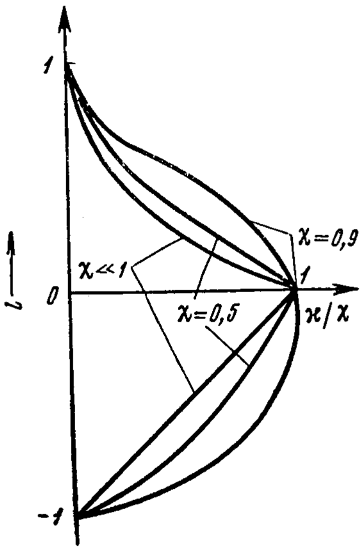

Fig. 1. Relationship $l(\varkappa)$ for some values of parameter χ. For convenience we have chosen different (characteristic for each region) units of length for $l > 0$ and $l < 0$.

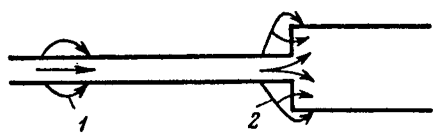

Fig. 2. Local currents in activation impulse. 1) Impulse front far from junction; 2) impulse front in region of junction.

From the condition $\partial\alpha/\partial_t = 0$ and using (2) and (3) we easily obtain the general form of the steady-state solution either $\alpha = 0$ and $\varphi < \varphi_*$, or $\alpha = 1$ and $\varphi > \varphi_*$. For definiteness we will consider an impulse arriving from the left. In accordance with the condition $c(x, t) = c_0$ (absence of repassivation) it is simply an activation wave. It is clear that when $t \to \infty$ such a wave can lead to steady states of two types: either $\alpha \equiv 1$, which corresponds to passage of the impulse, or

$$\alpha = \begin{cases} 1 & \text{when } x < l, \\ 0 & \text{when } x > l, \end{cases} \tag{4}$$

which corresponds to blocking (stoppage of the impulse front at the point $X = l$).

The method of solving the problem is as follows. If we put in form (4) in equation (1) we obtain a linear equation with piecewise-constant coefficients. In addition to the condition of boundedness of φ and continuity with the first derivative, which determines the definite solution of this equation for any l, we also have the condition $\varphi(l) = \varphi_*$. This "superfluous" condition determines l in relation to the parameters of the problem. The corresponding formulas are rather unwieldy and, hence, it is convenient to express this relationship graphically. Figure 1 shows the graph of l as a function of the geometric parameter $\varkappa = \sigma_1 S_1/\sigma_2 S_2$ for several values of the refractoriness parameter $\chi = 2A\varphi_* Jc_0/[A(\varphi_1 - \varphi_*) - Jc_0]^2$, which in real conditions is much less than unity. For clarity we can assume that the tube with the acid is much thicker than the wire, so that $S_1/S_2 \approx 1$. Then $\varkappa$ will simply be the ratio of the diameter of the wire left of the inhomogeneity to its diameter right of the inhomogeneity.

Figure 1 shows that when $\varkappa > \chi$ the point $l(\varkappa)$ does not exist, i.e. the impulse passes the inhomogeneity. On the other hand, when $\varkappa < \chi$, i.e., when the diameter of the right part of the wire exceeds that of the left part by a sufficiently high factor, there will be two values of $l(\varkappa)$: $l_- < 0$ and $l_+ > 0$. It can be shown that the impulse stops at l_- and does not reach the junction of the thin and thick wires. This is due to the fact that the steady state with $l = l_-$ is stable, and that with $l = l_+$ is unstable.

The physical explanation of the blocking of the impulse is that as the impulse approaches the inhomogeneity the subthreshold zone encroaches onto the thicker wire and the current consumption in it increases, since it is forced to spread over a larger area. At the same time, the activation zone present in the thin wire generates a constant activating current (Fig. 2). If the difference in diameters is large enough the activating current is not high enough and the impulse stops.

2. Inhomogeneity with an Electrochemically Inert Gap In real conditions the order of magnitude of the parameter χ is 10^{-4}. Hence, blocking will be observed if one half of the wire is tens of thousands of times thicker than the other, i.e., in real conditions this effect will hardly ever occur. One-way conductivity, however, will be observed in a slightly modified system, viz., if the junction region is covered with an insulator. Figure 3 shows a synapse model from [8], consisting of a long wire to which a bunch of several short wires is attached. One end of the bunch is embedded in paraffin. For the theoretical calculation of such a model we can use the arguments of the preceding section, the only difference being that in the interval (0, h) we must put $j_i + j_f + j_a = 0$. This interval corresponds to the portion of wire embedded in the paraffin. The calculation leads to curves of $l(\varkappa)$ similar to the curves in Fig. 1. However, the maximum value of $\varkappa$ at which blocking can still occur now depends on h:

$$\varkappa_{cr} = \chi(1 + h\sqrt{R_i A})^2.$$

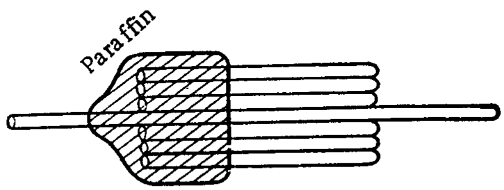

Fig. 3

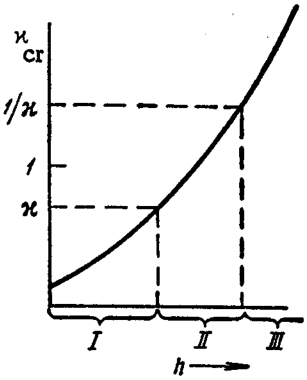

Fig. 4

Fig. 3. One-way conduction system from [8].

Fig. 4. Critical thickness ratio as function of h and regions of two-way, one-way, and no conduction.

It is clear from this formula that the blocking effect of the inhomogeneity rapidly increases with increase in length of the inert region. Since the characteristic length $(R_1A)^{-1/2}$ of the wires usually used is of the order of 0.1 cm, then the values of $\varkappa_{cr}$ obtained in the case of an inert region several centimeters in length will be a little less than unity. Hence, in the system shown in Fig. 3 an impulse coming from the left will be blocked even when the bundle contains a small number of wires.

By using the graph of relationship (5), shown in Fig. 4, we can easily obtain the region of values of h corresponding to two-way (region I), one-way (region II), and no (region III) conduction. All we have to do to obtain the last region in the case of an impulse arriving from the right is to replace $\varkappa$ by $1/\varkappa$.

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