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GENERAL CABLE THEORY FOR CELLS OF ALGAE CHARACEAE

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SUMMARY

Cable theory is extended to objects of finite dimensions such as giant cells of the algae Characeae.

The solution of the cable equation is obtained taking into account the definite resistance of cell nodes for the general case of an applied current, the strength of which alters with time by any f(t) law. Two important cases for the function f(t) are considered in detail, *viz.* f(t) = f(0) = constant and f(t) = kt.

Practical formulae for determining the fundamental characteristics of the cell are obtained: membrane resistance and capacity (of plasmalemma), the nodal resistance and the characteristic length of the cell.

It has been shown that a simplified method for measuring membrane resistance suggested first by HOGG *et al.* (J. HOGG, E. J. WILLIAMS AND R. J. JOHNSTON, *J. Theor. Biol.*, 24 (1969) 317) can be used for the determination of the membrane time constant and hence the membrane capacity. Taking into account the nodal resistance of the cell gives an improved value for the electrode position in terms of the critical coordinate: $x_{cr} = 0.38\ l$, where $2\ l$ is the length of the cell. The current electrode has to be inserted in the middle of the cell.

INTRODUCTION

One of the most important problems of modern biology is the investigation of the biological membrane. Successful investigations in this field are impossible without the study of electrical characteristics of membranes and particularly of the outer cytoplasmic membrane of the internodal cell of algae Characeae. In this case it is necessary to consider so called cable properties as being the reflection of a certain morphological structure of that cell.

The distribution $U(x,t)$ of the membrane potential variation caused by an applied electric current, *i.e.* electrotonic potential (ETP), is expressed by the equation[1]:

$$\frac{\delta^2 U(x,t)}{\delta x^2} = \frac{U(x,t)}{\lambda^2} + \frac{\tau_m}{\lambda^2}\frac{\delta U(x,t)}{\delta t} \tag{1}$$

where x is the changing coordinate along the axis of the internodal cell, t is time τ_m is the membrane time constant and λ is the characteristic length:

$$\tau_m = r_m C_m, \qquad \lambda^2 = \frac{r_m}{r_i + r_o}$$

Abbreviation: ETP, electrotonic potential.

r_m, r_i, r_o are the resistances of the membrane (plasmalemma), the inner medium of the cell and the outer solution, respectively; C_m is the capacity of the membrane (plasma lemma), all per unit length.

In the previous paper[1] the equation was solved with regard to the finite length of the cell and the resistance of the cell nodes, both for transient and steady states for the applied direct current. On the basis of the obtained theoretical expressions and experimental data the main electrical characteristics of the *Nitella flexilis* cell have been determined.

The present work considers the solution of Eqn. 1 and its consequences when the applied current alters with time.

SOLUTION OF THE CABLE EQUATION

Suppose, the source of current is placed between the outer and inner sides of the outer cytoplasmic membrane at the point coincident with the middle of the cell length. The applied current is:

$$\mathscr{I}(0,t) = 2I(0,t) = \begin{cases} 0 & , t < 0 \\ 2I(0)\dfrac{f(t)}{f(0)} & , t > 0 \end{cases} \tag{2}$$

The initial condition for the solution of Eqn. 1 is:

$$U(x,0) = 0 \tag{3}$$

The boundary conditions will be the conditions for the flow of the current $I(o,t)$ and $I(l,t)$ at the point where $x = 0$ and across the node of the cell at the point where $x = l$, respectively, l being the half length of the cell:

$$\left.\frac{\delta U(x,t)}{\delta x}\right|_{x=0} = -(r_i + r_o)I(0)\frac{f(t)}{f(0)} \tag{4}$$

$$\left.\frac{\delta U(x,t)}{\delta x}\right|_{x=l} = -(r_i + r_o)I(l,t) \tag{5}$$

The latter expression with regard to the relation:

$$I(l,t) = \frac{U(l,t)}{(r_l + \Delta l r_o)}$$

where r_l is the resistance of the cell node and Δl the linear size of the node, may be presented in a more suitable form:

$$\left.\frac{\delta U(x,t)}{\delta x}\right|_{x=l} = -\frac{\xi}{\lambda}U(l,t) \tag{6}$$

The characteristic constant ξ, introduced in the previous paper[1], is related to the resistance of the cell node:

$$\xi = \frac{r_m}{\lambda(r_l + \Delta l r_o)}$$

In the case of $r_l \gg \Delta l r_0$ the latter expression is simplified:

$$\xi = \frac{r_m}{\lambda r_l} = \frac{1}{4}\frac{D}{\lambda}\frac{R_m}{R_l} \tag{7}$$

where D is the diameter of the cell and R_m and R_l are the membrane (plasmalemma) and the cell nodal resistances per unit area, respectively:

$$R_m = r_m \pi D, \qquad R_l = r_l \frac{\pi D^2}{4} \tag{8}$$

Let us introduce the new variables:

$$\psi = \frac{x}{\lambda}, \qquad \theta = \frac{t}{\tau_m} \tag{9}$$

and use the substitution:

$$U(\psi,\theta) = v(\psi,\theta)\exp(-\theta)$$

In this case for Eqn. 1, the initial and boundary conditions (Eqns. 5, 6 and 9) take the form:

$$\frac{\delta^2 v(\psi,\theta)}{\delta\psi^2} = \frac{\delta v(\psi,\theta)}{\delta\theta} \tag{10}$$

$$v(\psi,0) = 0 \tag{11}$$

$$\left.\frac{\delta v(\psi,\theta)}{\delta\psi}\right|_{\psi=0} = -\lambda(r_i + r_o)I(0)\frac{f(\theta)}{f(0)}\exp\theta, \quad \left.\frac{\delta v(\psi,\theta)}{\delta\psi}\right|_{\psi=l/\lambda} = -\xi v\left(\frac{l}{\lambda},\theta\right) \tag{12}$$

Applying Laplace's transformation with respect to θ to Eqns. 10–12 we obtain:

$$\frac{d^2\bar{v}(\psi,p)}{d\psi^2} = p\bar{v}(\psi,p) \tag{13}$$

$$\left.\frac{d\bar{v}(\psi,p)}{d\psi}\right|_{\psi=0} = -\lambda(r_i + r_o)I(0)\frac{f(p-1)}{f(0)}, \quad \left.\frac{d\bar{v}(\psi,p)}{d\psi}\right|_{\psi=l/\lambda} = -\xi\bar{v}\left(\frac{l}{\lambda},p\right) \tag{14}$$

The solution of the differential Eqn. 13 with the boundary conditions (Eqn. 14) has the form:

$$\bar{v}(\psi,p) = \lambda(r_i + r_o)I(0)\,\frac{f(p-1)}{f(0)}\left(\frac{\cosh\left(\frac{l}{\lambda}-\psi\right)\sqrt{p} + \frac{\xi}{\sqrt{p}}\sinh\left(\frac{l}{\lambda}-\psi\right)\sqrt{p}}{\sqrt{p}\sinh\frac{l}{\lambda}\sqrt{p} + \xi\cosh\frac{l}{\lambda}\sqrt{p}}\right)$$

Let us write the latter expression in the form:

$$\bar{v}(\psi,p) = \lambda(r_i + r_o)I(0)\left(\bar{v}_1(0,p)\bar{v}_2(\psi,p) - \bar{v}_2(\psi,p)\right) \tag{15}$$

where

$$\bar{v}_1(0,p) = (p-1)\frac{f(p-1)}{f(0)} - 1 \tag{16}$$

$$\bar{v}_2(\psi,p) = \frac{\cosh\left(\frac{l}{\lambda}-\psi\right)\sqrt{p} + \frac{\xi}{\sqrt{p}}\sinh\left(\frac{l}{\lambda}-\psi\right)\sqrt{p}}{(p-1)\left(\sqrt{p}\sinh\frac{l}{\lambda}\sqrt{p} + \xi\cosh\frac{l}{\lambda}\sqrt{p}\right)} \tag{17}$$

Inverting Eqn. 16 gives:

$$v_1(0,\theta) = \frac{1}{f(\theta)}\frac{df(\theta)}{d\theta}\exp\theta \tag{18}$$

The result of the inversion will be:

$$v_2(\psi,\theta) = \left(\frac{\cosh\left(\frac{l}{\lambda}-\psi\right) + \xi\sinh\left(\frac{l}{\lambda}-\psi\right)}{\sinh\frac{l}{\lambda} + \xi\cosh\frac{l}{\lambda}}\right)\exp\theta + \\ + \frac{2\lambda}{l}\sum_{p_\kappa}\frac{\cosh\psi\sqrt{p_\kappa}\exp p_\kappa\theta}{(p_\kappa-1)\left(1+\frac{\lambda}{2l\sqrt{p_\kappa}}\sinh\frac{2l}{\lambda}\sqrt{p_\kappa}\right)} \tag{19}$$

where p_κ is the root of the transcendental equation:

$$\coth\frac{l}{\lambda}\sqrt{p_\kappa} = -\frac{\sqrt{p_\kappa}}{\xi} \tag{20}$$

Since $\sqrt{p_\kappa}$ are purely imaginary values they may be presented in the form:

$$\frac{l}{\lambda}\sqrt{p_\kappa} = jq_\kappa \tag{21}$$

Then Eqn. 19 may be transformed into:

$$v_2(\psi,\theta) = \exp\theta\left(\frac{1}{A(\psi)} - \frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\Omega_\kappa(\psi,\theta)\right) \tag{22}$$

where

$$A(\psi) = \frac{\sinh\frac{l}{\lambda} + \xi\cosh\frac{l}{\lambda}}{\cosh\left(\frac{l}{\lambda}-\psi\right) + \xi\sinh\left(\frac{l}{\lambda}-\psi\right)} \tag{23}$$

$$\Omega_\kappa(\psi,\theta) = \frac{\cos\psi\frac{\lambda}{l}q_\kappa\exp\left(-\left(1+\frac{\lambda^2 q_\kappa^2}{l^2}\right)\theta\right)}{\left(1+\frac{\lambda^2 q_\kappa^2}{l^2}\right)\left(1+\frac{\sin 2q_\kappa}{2q_\kappa}\right)} \tag{24}$$

Also the next relations are true:

$$\frac{1}{A(0)} = \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \Omega_\kappa(0,0)$$
$$\frac{1}{A(\psi)} = \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \Omega_\kappa(\psi,0) \qquad , \psi > 0 \tag{25}$$

On the basis of Eqns. 20 and 21 we obtain:

$$\cot q_\kappa = q_\kappa \frac{\lambda}{l} \frac{1}{\xi} \tag{26}$$

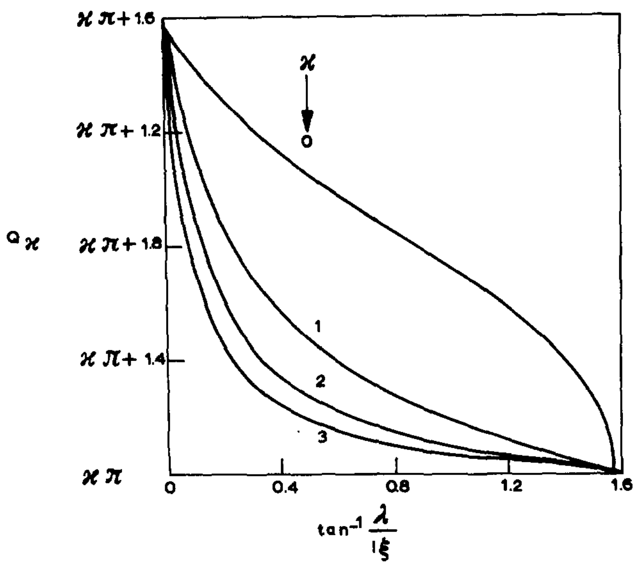

Fig. 1. Root values of Eqn. 26.

The roots of Eqn. 26 may be calculated directly or defined from Fig. 1.

Let us note that the roots q_κ may be stated with sufficient accuracy as follows:

$$q_\kappa = \pi\kappa + \xi \frac{l}{\lambda} \frac{1}{\pi\kappa} \qquad , \kappa = 1, 2, \cdots$$

and in the case of $\xi = 0$:

$$q_0 = 0, \qquad q_\kappa = \pi\kappa \qquad , \kappa = 1, 2, \cdots$$

The solution of Eqn. 1 is obtained by inverting Eqn. 15 with regard to Eqns. 18, 19, 22–24:

$$U(x,t) = \lambda(r_i + r_o)I(0)\left\{\frac{f(t)}{f(0)A(x)} - \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \Omega_\kappa(x,t) \times \right.$$
$$\left. \times \left(1 + \frac{1}{f(0)} \int_0^{t/\tau_m} \exp\left(1 + \frac{\lambda^2 q_\kappa^2}{l^2}\right) z \, df(z)\right)\right\} \tag{27}$$

where

$$A(x) = \frac{\sinh \frac{l}{\lambda} + \xi \cosh \frac{l}{\lambda}}{\cosh\left(\frac{l-x}{\lambda}\right) + \xi \sinh\left(\frac{l-x}{\lambda}\right)} \tag{28}$$

$$\Omega_\kappa(x,t) = \frac{\cos \frac{x}{l} q_\kappa \exp\left(-\left(1 + \frac{\lambda^2 q^2{}_\kappa}{l^2}\right)\frac{t}{\tau_m}\right)}{\left(1 + \frac{\lambda^2 q^2{}_\kappa}{l^2}\right)\left(1 + \frac{\sin 2q_\kappa}{2q_\kappa}\right)} \tag{29}$$

Obiously, Eqn. 2 for $t > 0$ should be rewritten as follows, if $f(0) = 0$:

$$I(0,t) = I(0)f(t)$$

and Eqn. 27:

$$U(x,t) = \lambda(r_i + r_o)I(0)\left(\frac{f(t)}{A(x)} - \frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\Omega_\kappa(x,t)\int_0^{t/\tau_m}\exp\left(1 + \frac{\lambda^2 q^2{}_\kappa}{l^2}\right) z\,\mathrm{d}f(z)\right) \tag{30}$$

Eqns. 27 and 30 describe the ETP distribution along the cell length caused by the alternating current.

SOME SPECIAL CASES FOR f(t)

The case of an applied direct current

In the case of $f(t) = f(0) = $ constant, Eqn. 27 is transformed to the form:

$$U(x,t) = \lambda(r_i + r_o)I(0)\left(\frac{1}{A(x)} - \frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\Omega_\kappa(x,t)\right) \tag{31}$$

Designating

$$U(x) = U(x,t)\Big|_{t\to\infty} = \lambda(r_i + r_o)\frac{I(0)}{A(x)} \tag{32}$$

we may write Eqn. 31 as follows:

$$U(x,t) = U(x)\,(1 - \varphi(x,t)) \tag{33}$$

where

$$\varphi(x,t) = A(x)\frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\Omega_\kappa(x,t) \tag{34}$$

When $t \to \infty$, $\varphi(x,t) \to 0$. Eqns. 31–34 are similar to those obtained before[1].

On the basis of Eqn. 32 we obtain

$$U(x)A(x) = U(0)A(0) \tag{35}$$

or with regard to Eqn 28:

$$\frac{U(x)}{U(0)} = \frac{\cosh\left(\frac{l-x}{\lambda}\right) + \xi \sinh\left(\frac{l-x}{\lambda}\right)}{\cosh\frac{l}{\lambda} + \xi \sinh\frac{l}{\lambda}} \tag{36}$$

When $r_l \to \infty$ ($\xi \to 0$), the distribution of ETP is determined by the relation, previously obtained by WILLIAMS *et al.*[2]:

$$\left.\frac{U(x)}{U(0)}\right|_{r_l \to \infty} = \frac{\cosh\left(\frac{l-x}{\lambda}\right)}{\cosh\frac{l}{\lambda}}$$

The case where the applied current increases in a linear fashion

In the case of $f(t) = kt$, Eqn. 30 is transformed to the form:

$$U(x,t) = \lambda(r_i + r_o)I(0)k\left[\frac{t}{A(x)} - \tau_m \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \frac{\Omega_\kappa(x,0) - \Omega_\kappa(x,t)}{\left(1 + \frac{\lambda^2 q^2_\kappa}{l^2}\right)}\right]$$

This expression is true for ETP variations with time:

$$\frac{\delta U(x,t)}{\delta t} = \lambda(r_i + r_o)I(0)k\left(\frac{1}{A(x)} - \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \Omega_\kappa(x,t)\right) \tag{37}$$

Let us designate:

$$\left[\frac{\delta U(x,t)}{\delta t}\right]_{st} = \left.\frac{\delta U(x,t)}{\delta t}\right|_{t \to \infty} = \frac{\lambda(r_i + r_o)I(0)k}{A(x)} \tag{38}$$

Then taking into account Eqn. 34 we obtain:

$$\frac{\delta U(x,t)}{\delta t} = \left[\frac{\delta U(x,t)}{\delta t}\right]_{st} (1 - \varphi(x,t))$$

In practice, $\varphi(x,t) = 0$ at $t >$ or $\approx 3\tau_m$ (ref. 1). Since at this moment the rate of change of ETP will remain constant, and the value of ETP will change with time according to the linear law:

$$U_{st}(x,t) = \lambda(r_i + r_o)I(0)k\left(\frac{t}{A(x)} - \tau_m \frac{2\lambda}{l} \sum_{\kappa=0}^{\infty} \frac{\Omega_\kappa(x,0)}{\left(1 + \frac{\lambda^2 q^2_\kappa}{l^2}\right)}\right) \tag{39}$$

From Eqn. 38 it follows directly:

$$\left[\frac{\delta U(x,t)}{\delta t}\right]_{st} A(x) = \left[\frac{\delta U(0,t)}{\delta t}\right]_{st} A(0)$$

and taking into account Eqn. 28 we obtain:

$$\frac{\left[\frac{\delta U(x,t)}{\delta t}\right]_{st}}{\left[\frac{\delta U(o,t)}{\delta t}\right]_{st}} = \frac{\cosh\left(\frac{l-x}{\lambda}\right) + \xi \sinh\left(\frac{l-x}{\lambda}\right)}{\cosh\frac{l}{\lambda} + \xi \sinh\frac{l}{\lambda}} \tag{40}$$

THE PRACTICAL RELATIONS IN THE MAIN ELECTRIC CHARACTERISTICS OF THE INTERNODAL CELL

The results of the previous section allow us to get some practical formulae. to determine the main electric characteristics of the internodal cell.

On the basis of Eqns. 7, 32 and 35 it may be written for the applied direct current:

$$r_m = \lambda A(o) \frac{U(o)}{I(o)} \tag{41}$$

$$r_l = \frac{A(o)}{\xi} \frac{U(o)}{I(o)} \tag{42}$$

$$r_i = \frac{A(o)}{\lambda} \frac{U(o)}{I(o)} - r_o \tag{43}$$

when the ionic composition of the external solution is known, the magnitude of the resistance r_0 may be calculated or measured directly by experiment.

The characteristic length λ and characteristic constant ξ are included in Eqn. 36 for the steady distribution of ETP. In many cases it appears more convenient to present this expression as a function of λ and $A(o)$. Combining Eqns. 28 and 36 we obtain:

$$\frac{U(x)}{U(o)} = \cosh\frac{x}{\lambda} - A(o) \sinh\frac{x}{\lambda} \tag{44}$$

As for the parameter $A(o)$, it is a function only of the characteristic constant ξ and the relation l/λ, *i.e.* it is also a characteristic parameter of the cell.

Eqn. 44 may be used for the practical determination of the values λ and $A(o)$. Actually, the steady ETP, caused by the applied direct current $I(o)$, will be $U(o)$, $U(a)$ and $U(2a)$ at the three points $x = o$, $x = a$ and $x = 2a$, respectively.
Then

$$A(o) = \frac{U(o)\,(U(o) - U(2a)) - 2U^2(a)}{U(o)\sqrt{(U(o) + U(2a))^2 - 4U^2(a)}} \tag{45}$$

$$\lambda = \frac{a}{\cosh^{-1}\left(\frac{U(o) + U(2a)}{2U(a)}\right)} \tag{46}$$

Finally, on the basis of Eqns. 28 and 45:

$$\xi = \frac{A(0) - \tanh \frac{l}{\lambda}}{1 - A(0) \tanh \frac{l}{\lambda}} \tag{47}$$

Substituting Eqns. 45–47 into Eqns. 41–43, we may express the values of the resistances r_m, r_l and r_i by $U(0)$, $U(a)$ and $U(2a)$ directly or by λ and $A(0)$. For example, the resistance of the node of the cell may be expressed:

$$r_l = A(0)\left(\frac{1 - A(0)\tanh \frac{l}{\lambda}}{A(0) - \tanh \frac{l}{\lambda}}\right)\frac{U(0)}{I(0)} \tag{48}$$

Thus, we determine by experiment the value of $A(0)$, λ, ξ, r_m, r_i, r_l by measuring the magnitudes of ETP at the three points $x = 0$, $x = a$ and $x = 2a$.

The value of ETP which may be obtained at any given point as a time multiple of the time constant of the membrane, *i.e.* for the time $t = n\tau_m$ (n is any whole positive number) and may be determined with respect to its steady value from:

$$\frac{U(x,n\tau_m)}{U(x)} = 1 - \varphi(x,n\tau_m)$$

or using Eqns. 24, 25 and 34:

$$\frac{U(x,n\tau_m)}{U(x)} = 1 - \frac{\sum_{\kappa=0}^{\infty} \Omega_\kappa(x,n\tau_m)}{\sum_{\kappa=0}^{\infty} \Omega_\kappa(x,0)} \tag{49}$$

Using the experimental values for the ETP variation with time at the corresponding point x and the value of the relation calculated with the help of Eqn. 49, we may determine the value of the membrane time constant τ_m and that of the membrane capacity C_m.

All the practical relations 41–48 given above are true in the case of an applied linearly increasing current when substituting $1/k\ [\delta U(x,t)/\delta t]_{st}$ for $U(x)$. This follows from direct comparison of Eqns. 37, 38 and 40 with 31, 32 and 36. Thus, in this case it is necessary to find the steady rate of the ETP increase from the experimental values of the ETP change with time at the three points $x = 0$, $x = a$ and $x = 2a$ to determine the values of $A(0)$, λ, ξ, r_m, r_i and r_l.

It is necessary to make use of the combination of Eqns. 38 and 39 to determine the membrane time constant:

$$\tau_m = \frac{t}{A(x)\frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\frac{\Omega_\kappa(x,0)}{\left(1 + \frac{\lambda^2 q^2{}_\kappa}{l^2}\right)}}\left(1 - \frac{U_{st}(x,t)}{t\left(\frac{\delta U(x,t)}{\delta t}\right)_{st}}\right)$$

Note, in the latter expression we may assume with sufficient accuracy:

$$A(x)\frac{2\lambda}{l}\sum_{\kappa=0}^{\infty}\frac{\Omega_\kappa(x,0)}{\left(1+\frac{\lambda^2 q_\kappa^2}{l^2}\right)} \approx \frac{1}{\left(1+\frac{\lambda^2 q_0^2}{l^2}\right)}$$

SIMPLE APPROXIMATE METHOD FOR DETERMINATION OF THE MEMBRANE RESISTANCE AND CAPACITY

Using Eqns. 8, 35 and 41, the expression for the full membrane resistance may be written as follows:

$$\frac{R_m}{\pi D l} = \frac{\lambda}{l} A(x) \frac{U(x)}{I(0)}$$

Obviously, if the critical coordinate $x = x_{cr}$ exists, for which $(\lambda/l)A(x_{cr}) = 1$, the full membrane resistance may be determined from the expression similar in its form to Ohm's law:

$$\frac{R_m}{\pi D l} = \frac{U(x)}{I(0)}$$

This method has been proposed by HOGG *et al.*[3]. The value of $x_{cr} = 0.42l$ was found for the case of an infinite resistance of the cell nodes, *i.e.* for $\xi = 0$.

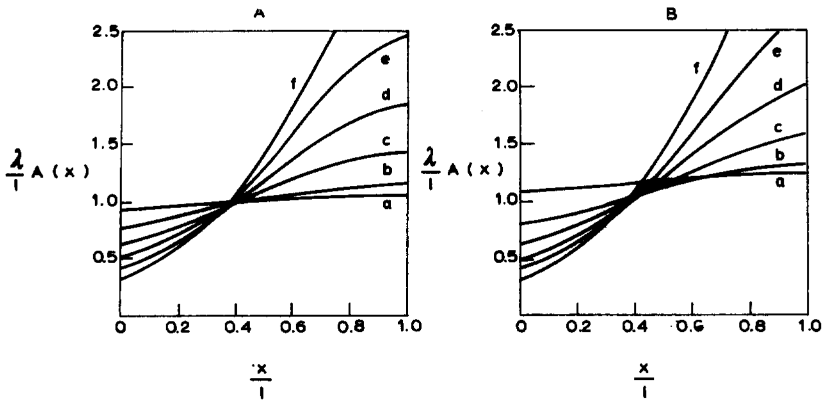

Fig. 2. The values of the function $(\lambda/l)A(x)$. A, $\xi = 0$; B, $\xi = 0.1$. $l/\lambda = 0.5$(a), 1.0(b), 1.5(c), 2.0(d), 2.5(e), 3.0(f). Eqn. 28 has been used for the calculations.

In Fig. 2 the values of the function $(\lambda/l)A(x)$ are shown for the cases of $\xi = 0$ and $\xi = 0.1$. The $\xi = 0.1$ corresponds to the real value of the nodal resistance determined for the cell *Nitella flexilis* placed in the normal solution [KCl] = 0.1 mM, [NaCl] = 1.0 mM and [$CaCl_2$] = 0.1 mM (ref. 1).

Taking into account the resistance of the nodes of the cell shifts the value of x_{cr}. It becomes $x_{cr} = 0.38l$. The maximum error in the magnitude of the defined membrane resistance R_m for $l/\lambda = 1.5$–3.0 does not exceed 2 %.

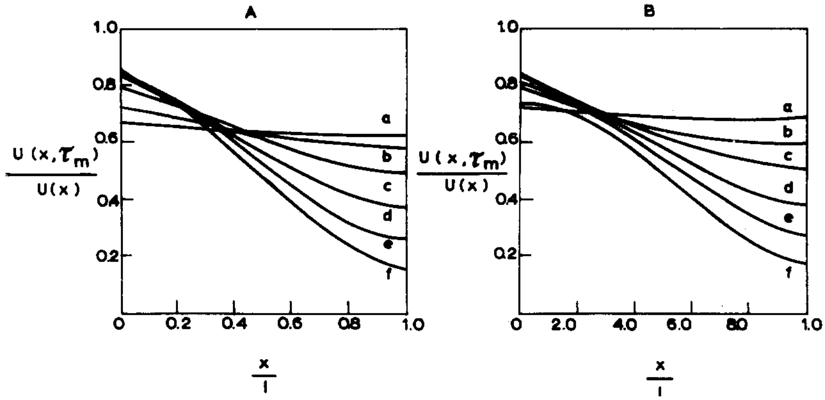

Fig. 3. The variation of electrotonic potential, the time being equal to the membrane time constant, in relation to its steady value. A, $\xi = 0$; B, $\xi = 0.1$. $l/\lambda = 0.5$(a), 1.0(b), 1.5(c), 2.0(d), 2.5(e), 3.0(f). Eqn. 49 for $n = 1$ and the root values of Eqn. 26 have been used for the calculations.

The records of the ETP variations with time at the point x_{cr} may be used for determination of the membrane time constant τ_m. As can be seen from the dependences shown in Fig. 3 the membrane time constant is equal to the time t necessary, for the value of ETP, to attain 63 % of its maximum value. That is, the potential change at the point x_{cr} is similar to the law of simple capacity charging. The error in the determination of the membrane time constant τ_m for $l/\lambda = 1.5$–3.0 may reach 4 %.

The values found in this way of the membrane resistance R_m and the membrane time constant τ_m allow the calculation of the value of the membrane capacity C_m.

It should be noted that there exists a better value of the coordinate x to determine the membrane time constant τ_m for the given values of the characteristic constant ξ. In this case, however, the error in determining the value of the membrane resistance R_m increases.

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