

## Theoretical plotting of the action potential curve of *Characeae* cells

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### Abstract

This paper gives a theoretical analysis of the action potential of cells of *Characeae* based on the Chizmadzhev-Markin equation.

### INTRODUCTION

Since the character of the electric processes in the cells of *Characeae* is similar to those in nerve cells, attempts have been undertaken to apply the theoretic descriptions used for nerve cells also for those of plants. As example may be quoted the paper by Platonov and Volkov (1970) in which the electric parameters of *Nitella flexilis* cells were determined on the basis of the cable theory concerning the neurone. *Characeae* cells exhibit action potentials which have been repeatedly studied (Hope 1961; Mailman and Mullins 1966; Findlay and Hope 1964). The action potential in these cells is initiated by the influence of chlorine ions. According to other opinions it is elicited by the sudden influence of calcium ions.

In the initial phase of the action potential the potential of the cell wall rises from the resting value amounting to about — 130 mV to about 10 mV. In the next phase the potential returns to its initial value. The rise of the cell wall potential is due to the influence of negative chlorine ions (Mailman and Mullins 1966), we thus are dealing with the flow of electric current into cells. The flow of potential into the cell during the first phase of the action potential, and in the second phase the outflow of current from the cell is in agreement with the principles of the model described by Chizmadzhev and Markin (1967) so that this model may be utilised in the case of these cells.

### THEORY

The action potential equation of Chizmadzhev and Markin has the following form:

$$\frac{d^2 \varphi}{d\xi^2} + v RC \frac{d\varphi}{d\xi} - R j_m(\xi) = 0$$

where

$\varphi$  — cell wall potential

$j_m$  — current flowing through unit of cell wall

$\xi = x - vt$

$x$  — coordinate parallel to cell axis,  $t$  — time

$v$  — action potential velocity.

When  $\xi$  is introduced, equation 1 describes the spread of the action potential.  $R, C$  — resistance and capacity of cell wall unit.

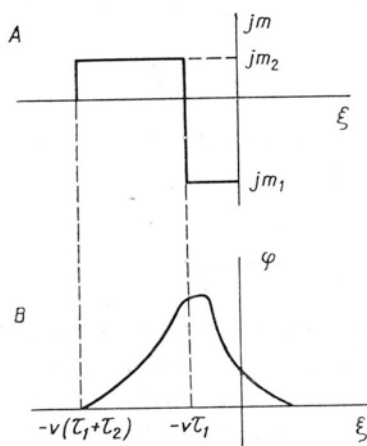


Fig. 1. A — Curve of current passing through cell wall; B — Action potential curve

$\xi$  — coordinate along cell;  $\varphi$  — action potential value;  $j_m$  — current through cell wall,  $\tau_1$  and  $\tau_2$  times of current inflow and outflow from cell

Fig. 1 shows schematically the cell wall potential and the action potential in dependence on the coordinate  $\xi$ , under the assumption that  $x$  is equal to zero. The coordinate  $\xi$  is the distance along the cell.

For  $-v\tau_1 \leq \xi \leq 0$  the current flows into the cell. For  $-v(\tau_1 + \tau_2) \leq \xi \leq -v\tau_1$  the current flows out of the cell. Equation 1 for the particular interval of  $\xi$  has the following solution:

For  $\xi \geq 0$

$$\varphi(\xi) = \frac{1}{v^2 RC^2} [j_{m1} + j_{m2} e^{-v^2 RC(\tau_1 + \tau_2)} - (j_{m1} + j_{m2}) e^{-v^2 RC\tau_1}] e^{-v RC\xi}$$

For  $-v\tau_1 \leq \xi \leq 0$

$$\varphi(\xi) = \frac{1}{v^2 RC^2} [j_{m2} e^{-v^2 RC(\tau_1 + \tau_2)} - (j_{m1} + j_{m2}) e^{-v^2 RC\tau_1}] e^{-v RC\xi} - \frac{j_{m1} \xi}{vC} + \frac{j_{m1}}{v^2 RC^2}$$

For  $-v(\tau_1 + \tau_2) \leq \xi \leq -v\tau_1$

$$\varphi(\xi) = \frac{j_{m2}}{v^2 RC^2} e^{-v^2 RC(\tau_1 + \tau_2)} e^{-v RC\xi} + \frac{j_{m2}\xi}{vC} + \frac{\tau_1(j_{m1} + j_{m2})}{C} - \frac{j_{m2}}{v^2 RC^2}$$

For  $\xi \leq -v(\tau_1 + \tau_2)$

$$\varphi(\xi) = \frac{j_{m1}\tau_1 - j_{m2}\tau_2}{C}$$

The foregoing solutions overlap on limits of the intervals.

## RESULTS

In calculations the following values were used: cell wall resistance  $R = 54,000 \Omega/\text{cm}^2$  (Platonova, Volkov 1970), action potential velocity  $v = 2.3 \text{ cm/s}$  (Gorchakov, Sinyukhin 1966), cell wall specific capacitance  $C = 1 \mu\text{F}/\text{cm}^2$  (Mailman and Mullins 1966).

Table 1

Values of adopted times  $t$ , times  $\tau_1$  and  $\tau_2$ , length  $\xi$ , currents  $j_{m1}$  and  $j_{m2}$  and calculated maximum action potential values

$t$ s.	$\tau_1$ s.	$\tau_2$ s.	$\xi_1$ cm	$j_{m2}$ $\mu\text{A}/\text{cm}^2$	$j_{m1}$ $\mu\text{A}/\text{cm}^2$	$\varphi$ mV
2	0.7	1.3	1.61	0.06	0.11	141
2	0.5	1.5	1.15	0.05	0.16	259
3	1	2	2.3	0.04	0.08	96
3	0.75	2.25	1.72	0.03	0.1	152
4	1.33	2.66	3.05	0.03	0.06	73
4	1	3	2.3	0.02	0.08	128

The duration of the action potential, the times of inflow and outflow of the current into and from the cell, and the currents flowing in and out of the cell, are shown in table 1. The currents  $j_{m1}$  and  $j_{m2}$  were chosen so as to fulfill the relation

$$j_{m1}\tau_1 = j_{m2}\tau_2 = 0.08 \mu\text{C}/\text{cm}^2$$

that is so that the charges inflowing and outflowing into and out of the cell be the same and equal about  $0.08 \mu\text{C}/\text{cm}^2$  for all the three times of duration of the action potential. For the times of action potential duration  $t = \tau_1 + \tau_2$  equality: 2s, 3s and 4s, in compliance with experimental values, Hope (1961), Findlay and Hope (1964) notice that there is a strong relation between the maximum action potential value and the time of inflow of the current into the cell  $\tau_1$ . This is indicated by the results shown in figs 2-4. The maximum value of the action potential is higher for respective shorter times  $\tau_1$ . Moreover, higher maximum action potential values were obtained for shorter times  $t$ .

If we assume equal values of the outflowing charges for all the three times  $t$ , the value of the peak action potential depends on the ratio of the inflowing current

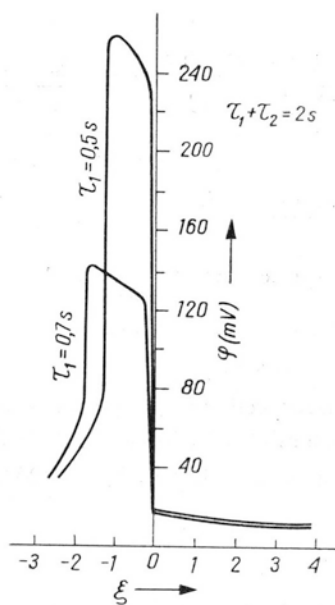


Fig. 2

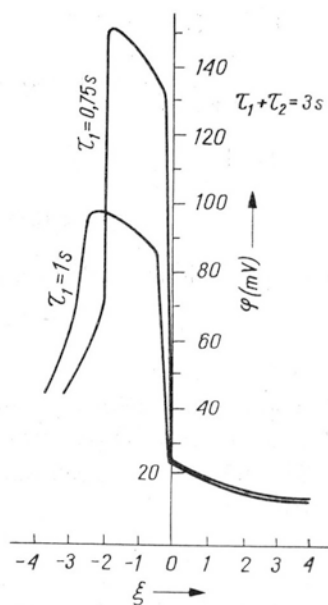


Fig. 3

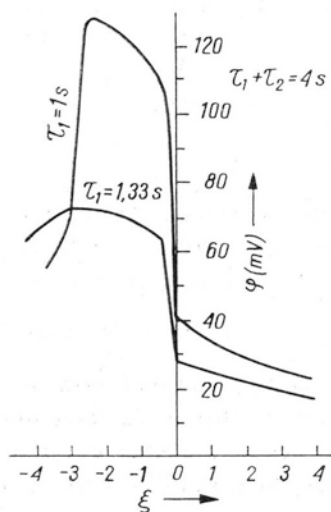


Fig. 4

Fig. 2. Curves of calculated action potentials for durations  $t=2s$ . Notations as in fig. 1

Fig. 3. Curves of calculated action potentials for durations  $t=3s$ . Notations as in fig. 1

Fig. 4. Curves of calculated action potentials for durations  $t=4s$ . Notations as in fig. 1

value to the time of its inflow, that is on the acceleration of charge inflow. For shorter times  $\tau_1$  the acceleration is greater, the current grows more rapidly. The current increase occurs also in shorter segment of the cell length  $\xi_1$ , thus, the action potential peak is higher. If current inflow occurs on a shorter segment of cell length  $\xi_1$ , then the same value of inflowing charge produces a higher concentration of positive ions in the cell and a larger potential difference on both sides of the cell wall, or in the units adopted in Chizmadzhev and Markin's model a higher  $\phi$  value.

Inflow of current into the cell during the action potential is measured by the voltage clamping technique (Findlay 1962), in which depolarisation of the cell wall was stabilised, its level maintained while the current flow was measured.

The values of current flow through the cell wall obtained in this way are higher, amounting to about  $10 \mu\text{A}/\text{cm}^2$ , and do not agree with those calculated in the present paper. In order to adopt higher current values  $j_{m1}$  and  $j_{m2}$ , the cell wall resistance  $R$  should be changed.

Resistance  $R$  is a value which has not been univocally determined, experimenters obtain widely varying values. It is also known that resistance  $R$  during the action potential decreases to several hundred  $\Omega/\text{cm}^2$ .

In the model of Chizmadzhev and Markin the change of cell wall resistance during depolarisation is not taken into account.

The times  $\tau_1$  and  $\tau_2$ , the sum of which is known from experiment attain during the action potential values difficult to assay.

The maximum action potential value also depends on the choice of time  $\tau_1$  and  $\tau_2$ . They could be evaluated exactly when the current and charge outflowing from the cell are known. Depolarisation of the cell wall during the action potential is due to the influence of chlorine ions. Mailman and Mullins (1966) report the outflow of chlorine ions from the cell to be  $114 \text{ pmoles}/\text{cm}^2$  per impulse. In other papers higher values are quoted.

The charge calculated from the above given chlorine outflow is higher than that adopted for calculations. The latter made possible to obtain correct cell wall potentials in the process of action potential by utilising Chizmadzhev and Markin's model.

In true action potentials there is no such course of action potential in the cell wall as shown in the model in fig. 1. The courses of the current through the cell wall obtained by the voltage clamping technique change with time in a different manner. Chizmadzhev and Markin's model describes, as regards the plant cell, an ideal case.

The adoption of higher currents for calculation gives maximum action potential values higher than the experimental ones.

Processes occurring inside the cell wall, not taken into account in modelling, are essential for the discussion.

Calculations were carried out adopting  $v$ ,  $R$ ,  $C$  values from various sources and obtained for various cells.

An "Odra 1204" computer was used for calculation.

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*Teoretyczne wyznaczanie krzywej potencjału czynnościowego komórek Characeae*

## Streszczenie

W pracy podano teoretyczną analizę potencjału czynnościowego komórek *Characeae* używając równań Czizmadzewa—Markina.

Wartość maksymalna obliczonego potencjału czynnościowego zależy w dużym stopniu od doboru czasu wpływu jonów do komórki, czasu trwania potencjału czynnościowego oraz prądów błonowych. Dzięki temu aparatowi matematycznemu można poprzez przyjęcie eksperymentalnego przebiegu potencjału czynnościowego wyznaczyć dyskusyjne wartości prądów błonowych.