

## INFLUENCE OF EXTERNAL ELECTRIC FIELDS ON MEMBRANE POTENTIALS

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UDC 536  
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General notions of the thermodynamics of irreversible processes are used to study membrane potentials in the presence of external electric fields. A formula for the Nernst concentration potential is derived giving the dependence of membrane potential not only on ion concentrations and external fields, but also on the electrodynamic characteristics on both sides of membranes. The calculation of the electrodiffusive distribution of ion concentrations under the action of an external electric field and the derivatives of permittivity with respect to the concentration allows us to estimate the numerical values of membrane potentials in the presence of external electric fields.

Modern theories which describe the electric properties of membranes were constructed, as a rule, in the case where external fields are absent (see, e.g., [1–3]). At the same time, the study of the effects of external fields on membrane potentials is of great importance now not only in the theoretical aspect, but also in the practical one. This is related, first of all, to the wide use of such methods as diathermy, hyper- and hypothermia, microwave resonance therapy, etc. in contemporary medical practice. In this case, by studying the electric properties of membrane structures, it is necessary to consider the presence of artificially created external fields such as temperature gradients, electric and magnetic fields, in particular electromagnetic millimeter radiation. For example, works [4, 5] studied the influence of temperature gradients on the membrane potentials of cells and on the diffusion processes related to the participation of the transport of ions through membrane structures. The formulas for the Nernst concentration potential and the stationary membrane potential with regard for thermodiffusion effects and those describing the conditions for ion balance and the redistribution of ion concentrations under nonisothermic conditions were deduced.

The purpose of the present work is to study the influence of an external electric field on membrane potentials. As known, one of the main membrane potentials is the so-called Nernst equilibrium

concentration potential [1–3]

$$\varphi_m = \frac{RT}{zF} \ln \frac{C_i}{C_e}, \quad (1)$$

where  $\varphi_m$  is the difference of electric potentials on the membrane,  $C_i$  and  $C_e$  are the ion concentrations inside and outside the medium limited by the membrane, respectively,  $R$  is the universal gas constant,  $T$  is the absolute temperature,  $z$  is the valency, and  $F$  is the Faraday constant. It follows from (1) that the Nernst concentration potential depends on temperature and the difference of ion concentrations (as a rule, ions  $K^+$  are considered) on the both sides of the membrane.

We consider the external “ $e$ ” and internal “ $i$ ” sides of the membrane as different phases with respect to the medium enclosed by it. The condition of balance between these phases is satisfied if the equalities of temperatures  $T_e = T_i$ , pressures  $P_e = P_i$ , and chemical potentials of the phases  $\mu_e = \mu_i$  are established. We assume that the first two conditions are satisfied. If an external electric field is present, then the third condition must be written with regard for not only the osmotic and electric contributions from dissolved ions, but the supplementary contributions to the chemical potentials which are caused directly by the external field. To this end, by considering firstly the general case with the presence of electric field, we use the well-known expression for the chemical potential of a dielectric medium in an external electric field [6, 7],

$$\mu = \mu_0^* - \frac{\varepsilon_0}{2} \frac{\partial \varepsilon}{\partial C} E^2 - \frac{\tilde{\mu}_0}{2} \frac{\partial \tilde{\mu}}{\partial C} H^2, \quad (2)$$

where  $\mu_0^*$  is the chemical potential of the medium without electromagnetic field,  $\varepsilon_0$  and  $\tilde{\mu}_0$  are the electric and magnetic constants,  $\varepsilon$  and  $\tilde{\mu}$  are, respectively, dielectric and magnetic permeability of the given medium, and  $E$  and  $H$  are the electric and magnetic field intensities.

In view of (2), we write the generalized formula for electrochemical potential in an external electromagnetic

field,

$$\mu^{E,H} = \mu_0 + RT \ln C + zF\varphi - \frac{1}{2}(\varepsilon_0 \varepsilon' E^2 + \tilde{\mu}_0 \tilde{\mu}' H^2), \quad (3)$$

where we introduced the designations  $\varepsilon' = \partial\varepsilon/\partial C$ ,  $\tilde{\mu}' = \partial\tilde{\mu}/\partial C$ . Here,  $\mu_0$  is the chemical potential of the pure solvent (we assume its value to be identical on the both sides of the membrane),  $RT \ln C$  is the term describing the osmotic contribution from dissolved ions, and  $zF\varphi$  is the term describing the contribution from the electric field created by ion charges ( $\varphi$  is the potential of the electric field).

In the presence of an external electromagnetic field, the condition for ion balance is the equality of the generalized electrochemical potentials of both phases, i.e.,  $\mu_e^{E,H} = \mu_i^{E,H}$ . This yields the following formula for the Nernst concentration potential:

$$\varphi_m^{E,H} = \frac{RT}{zF} \ln \frac{C_i}{C_e} + \frac{\varepsilon_0 E^2}{2zF} (\varepsilon'_e - \varepsilon'_i) + \frac{\tilde{\mu}_0 H^2}{2zF} (\tilde{\mu}'_e - \tilde{\mu}'_i). \quad (4)$$

It is seen from (4) that the membrane potential in the presence of an external electromagnetic field is defined not only the difference of concentrations on both sides of the membrane, but also the difference of the derivatives of dielectric and magnetic permeability of these media with respect to concentration.

In this work, we consider a special case with only an external electric field. Then the Nernst membrane potential is described by the first two terms in (4). The second is directly related to the presence of the external electric field, and its value is defined by the field intensity and the dielectric parameters of the given medium (by the difference of derivatives,  $\varepsilon'_e - \varepsilon'_i$ ).

With the purpose to determine the change in the ion concentrations in the first term in (4) which depends on the presence of the external electric field, we used the following reasoning. For some section of the membrane which has geometry of a plane-parallel layer with thickness  $L$ , let the intensity vector of the external electric field  $\mathbf{E}_{\text{ext}}$  be directed from phase “ $i$ ” to phase “ $e$ ”. Then, taking into account that the ion concentrations on both sides of the membrane are changed by the same value  $\Delta C$ , we can write the ion concentrations in the presence of the external electric field as follows:  $C_i^E = C_i^0 - \Delta C$  and  $C_e^E = C_e^0 + \Delta C$  (we consider ions with positive charge). But if the external electric field has the opposite direction, a change in the ion concentrations reads as  $C_i^E = C_i^0 + \Delta C$  and  $C_e^E = C_e^0 - \Delta C$ . Respectively, in the general case, the Nernst

concentration potential has the following form:

$$\varphi_m^E = \frac{RT}{zF} \ln \frac{C_i^0}{C_e^0} + \frac{RT}{zF} \ln \frac{1 \mp \frac{\Delta C}{C_i^0}}{1 \pm \frac{\Delta C}{C_e^0}} + \frac{\varepsilon_0 E^2}{2zF} (\varepsilon'_e - \varepsilon'_i). \quad (5)$$

Here we separated the term which corresponds to the initial value of the membrane potential (the first term which we will denote as  $\varphi_m^0$ ). In (5), the second term is the supplementary contribution to the membrane potential at the expense of the influence of the external electric field on the distribution of ion concentrations (we will denote it as  $\Delta\varphi_m^{\text{conc}}$ ). The third term in (5) which appears directly due to the presence of the external electric field will be denoted as  $\Delta\varphi_m^E$ . Thus, in these designations, formula (5) takes the form

$$\varphi_m^E = \varphi_m^0 + \Delta\varphi_m^{\text{conc}} + \Delta\varphi_m^E. \quad (6)$$

The electric field intensity in which charged particles (ions) are situated is defined as the total intensity of the electric field created by the charges of ions  $\mathbf{E}_{\text{int}}$  and the external field  $\mathbf{E}_{\text{ext}}$ , i.e.,  $\mathbf{E}_{\text{sum}} = \mathbf{E}_{\text{int}} + \mathbf{E}_{\text{ext}}$ . We suppose that the internal electric field of the membrane (we will denote it as  $\mathbf{E}_{\text{int}}^0$ ) existed prior to the appearance of the external field. Moreover, the internal medium of the region limited by the membrane is charged negatively relative to the environment, and the vector  $\mathbf{E}_{\text{int}}^0$  is directed inward this region. Such a situation is valid for biological membranes where  $E_{\text{int}}^0$  is of order of  $10^6 \div 10^7$  V/m. For example, the Nernst concentration potential for ions  $\text{K}^+$  at the temperature  $T = 293$  K in the giant calmar’s axone is  $\varphi_m^0 = 72.67$  mV, and, respectively, the intensity of the internal electric field at  $L = 10^{-8}$  m is  $E_{\text{int}}^0 \approx 7.3 \cdot 10^6$  V/m.

The quantity  $E_{\text{int}}^0$  is defined in terms of the initial ion concentrations  $C_i^0$  and  $C_e^0$ . If an external electric field  $\mathbf{E}_{\text{ext}}$  is present, the ion concentrations are changed, which leads to a new value of the “new” internal field. This means that  $\mathbf{E}_{\text{int}} = \mathbf{E}_{\text{int}}^0 + \mathbf{E}_{\text{int}}^{\text{conc}}$ , where  $\mathbf{E}_{\text{int}}^{\text{conc}}$  is the supplementary contribution to the intensity of the internal field which arises due to a change in the ion concentrations. Thus, the total electric field intensity in which ions are situated is defined as follows:

$$\mathbf{E}_{\text{sum}} = \mathbf{E}_{\text{int}}^0 + \mathbf{E}_{\text{int}}^{\text{conc}} + \mathbf{E}_{\text{ext}}. \quad (7)$$

This formula should be compared with formula (6) for the difference of electric potentials by considering the connection of the electric field potential with its intensity.

We calculate the redistribution of ion concentrations occurred at the expense of the external electric field. First, we express the flow of charged particles

(ions) in the form of the well-known Nernst–Planck electrodiffusion equation [1–3],

$$\mathbf{I} = -D\nabla C - Cb\nabla\varphi, \tag{8}$$

where  $D$  and  $b$  are the coefficients of diffusion and mobility for the given sort of ions.

By index “0”, we denote the concentration gradient existed on the membrane before the appearance of the external electric field, i.e.,  $\nabla_0 C \approx (C_e^0 - C_i^0)/L$ . The external field induces a change in concentrations, and the gradient takes other value. In other words, the action of the external field leads to a supplementary contribution to the total concentration gradient. We separate this contribution, i.e.,  $\nabla C = \nabla_0 C + \nabla_E C$ . The first term in the last formula is the initial gradient, and the second is defined by the change of ion concentrations relative to their initial values. We represent the gradient of the electric field potential in the second term of (8) as the sum of two terms  $\nabla\varphi = \nabla_0\varphi + \nabla_E\varphi$  where the first term corresponds to the initial (prior to the appearance of the external field) potential gradient ( $\nabla_0\varphi \approx \varphi_m^0/L$ ). Thus, according to the above-presented formulas, the ion flow can be written as  $\mathbf{I} = \mathbf{I}_0 + \mathbf{I}_E$ , where  $\mathbf{I}_0 = -D\nabla_0 C - Cb\nabla_0\varphi$  is the ion flow without external electric field and  $\mathbf{I}_E = -D\nabla_E C - Cb\nabla_E\varphi$  is the supplementary ion flow caused by the presence of the external electric field. By using the Einstein relation for the coefficients of diffusion and mobility (see, e.g., [3]), we may represent the ion flow as

$$\mathbf{I} = -D \left( \nabla_0 C - C \frac{e\mathbf{E}_{\text{int}}^0}{kT} \right) - D \left( \nabla_E C - C \frac{e(\mathbf{E}_{\text{int}}^{\text{conc}} + \mathbf{E}_{\text{ext}})}{kT} \right), \tag{9}$$

where  $k$  is the Boltzmann constant and  $e$  is the elementary charge value. In (9) and below, we consider, for definiteness, ions for which  $z = 1$ .

To find a change in the concentrations on both sides of the membrane, we use the ion balance condition, i.e., we take that the full flow of ions through the membrane is zero. Without external field,  $\mathbf{I}_0$  equals zero because the system was in the state of ion balance before the “switching on” of the external field. After the appearance of the external field, the full flow became  $\mathbf{I} = \mathbf{I}_0 + \mathbf{I}_E$ . Thus, to satisfy the ion balance condition, it is necessary now that the additional ion flow be also zero, i.e.,  $\mathbf{I}_E = 0$ . This yields

$$\nabla_E C = C \frac{e(\mathbf{E}_{\text{int}}^{\text{conc}} + \mathbf{E}_{\text{ext}})}{kT}. \tag{10}$$

The difference of concentrations between two phases “ $i$ ” and “ $e$ ” which appears due to the presence of the additional electric field equals  $2\Delta C$ . The value of this difference of concentrations can be found by using the approach used in [5]. According to it, the ion balance condition reads

$$\int_{C_i^0 - C_e^0 - \Delta C}^{C_i^0 - C_e^0 + \Delta C} \frac{dC}{C} = \frac{e(E_{\text{int}}^{\text{conc}} + E_{\text{ext}})}{kT} \int_0^L dx. \tag{11}$$

The limits of integration on the left-hand side of (11) correspond to the case where  $\mathbf{E}_{\text{ext}}$  is directed from phase “ $i$ ” to phase “ $e$ ”. For the opposite direction of  $\mathbf{E}_{\text{ext}}$ , the integration limits must be interchanged, which does not affect the absolute value of  $\Delta C$  in the general case. Thus, by integrating relation (11), we get

$$\Delta C = (C_i^0 - C_e^0) \frac{\exp \left\{ \frac{e(E_{\text{int}}^{\text{conc}} + E_{\text{ext}})}{kT} L \right\} - 1}{\exp \left\{ \frac{e(E_{\text{int}}^{\text{conc}} + E_{\text{ext}})}{kT} L \right\} + 1}. \tag{12}$$

Formula (12) allows us to calculate  $\Delta C$  if the numerical values of the intensities  $E_{\text{ext}}$  and  $E_{\text{int}}^{\text{conc}}$  are known. However, the value of  $E_{\text{int}}^{\text{conc}}$  would be determined through the already known values of  $\Delta C$ . With regard for this circumstance, we apply the method of successive approximations, i.e., we find firstly  $\Delta C$  in the zero approximation [by setting  $E_{\text{int}}^{\text{conc}} = 0$  in formula (12)]:

$$\Delta C^{(0)} = (C_i^0 - C_e^0) \frac{\exp \left\{ \frac{eE_{\text{ext}}}{kT} L \right\} - 1}{\exp \left\{ \frac{eE_{\text{ext}}}{kT} L \right\} + 1}. \tag{13}$$

In Table 1, we present the numerical estimates of  $\Delta C^{(0)}$  by (13) for various intensities of the external field. We note that all numerical estimates in the present work are carried out for the giant calmar’s axone (a nerve fiber) for which the initial concentrations of ions  $\text{K}^+$  outside and inside of the axon are well known:  $C_e^0 = 22$  mmol/l and  $C_i^0 = 392$  mmol/l [1]. In this case, we assume the temperature to be equal to 293 K and the membrane thickness  $L = 10^{-8}$  m.

**Table 1**

$E_{\text{ext}}, \text{V/m}$	$\Delta C^{(0)}, \text{mmol/l}$
$10^2$	$7.3 \cdot 10^{-3}$
$10^3$	$7.3 \cdot 10^{-2}$
$10^4$	0.73
$10^5$	7.32
$10^6$	72.26

By using the data of Table 1 and the formula for  $\Delta\varphi_m^{\text{conc}}$  [see formula (5)], we calculated  $E_{\text{int}}^{\text{conc}}$  at various values of  $E_{\text{ext}}$ :

$$E_{\text{int}}^{\text{conc}} = \frac{\Delta\varphi_m^{\text{conc}}}{L} = \frac{1}{L} \frac{RT}{F} \ln \frac{1 \mp \frac{\Delta C^{(0)}}{C_i^0}}{1 \pm \frac{\Delta C^{(0)}}{C_e^0}}. \quad (14)$$

Table 2 presents the numerical estimates of the supplementary contribution to the internal field intensity due to a change in ion concentrations  $E_{\text{int}}^{\text{conc}}$  calculated by (14). In Table 2 and in Tables 3 and 4, the field  $\mathbf{E}_{\text{ext}}$  is antiparallel to  $\mathbf{E}_{\text{int}}^0$  in the first case which corresponds to upper signs in formulas (5) and (14). In this case, the redistribution of ion concentrations occurs in such a way that the initial internal field is weakened, i.e.,  $E_{\text{int}} = E_{\text{int}}^0 - E_{\text{int}}^{\text{conc}}$  ( $E_{\text{int}}^{\text{conc}} < 0$ ). The field  $\mathbf{E}_{\text{int}}^{\text{conc}}$  is directed contrarily to  $\mathbf{E}_{\text{int}}^0$  and, at the same time, is parallel to the external field  $\mathbf{E}_{\text{ext}}$ . In the second case which corresponds to lower signs in formulas (5) and (14), the field  $\mathbf{E}_{\text{ext}}$  has the same direction as  $\mathbf{E}_{\text{int}}^0$ . In this case, the internal field increases due to the redistribution of ion concentrations, i.e.,  $E_{\text{int}} = E_{\text{int}}^0 + E_{\text{int}}^{\text{conc}}$  ( $E_{\text{int}}^{\text{conc}} > 0$ ). Respectively, the vectors  $\mathbf{E}_{\text{int}}^0$  and  $\mathbf{E}_{\text{int}}^{\text{conc}}$  have the identical direction. Like the first case, the field  $\mathbf{E}_{\text{int}}^{\text{conc}}$  is parallel to the field  $\mathbf{E}_{\text{ext}}$ .

Thus, given the value of  $E_{\text{int}}^{\text{conc}}$  at various intensities of the external field, we can calculate a change in ion concentrations  $\Delta C$  in the first approximation, i.e., by formula (12) in which  $E_{\text{int}}^{\text{conc}}$  is defined by (14). Table 3 includes the relevant numerical estimates of  $\Delta C^{(1)}$ . In the first case,  $\Delta C^{(1)}$  is negative. This is related to the fact that a change of the concentrations by  $\Delta C$  on both sides of the membrane leads to a decrease in the initial gradient. In the second case, the concentration gradient increases due to the redistribution of ions, and therefore  $\Delta C$  is positive.

Thus, by using the results of Table 3, we can calculate the contribution of the redistribution of ions to the membrane potential. Table 4 presents the numerical estimates of  $\Delta\varphi_m^{\text{conc}}$  for various intensities of the external field.

We consider now the third term in (5). The electric field intensity, for which the breakdown of biological membranes happens, is about  $3 \cdot 10^7$  V/m. In view of this fact, we implement the numerical estimates for an external electric field whose intensity varies in the limits  $E_{\text{ext}} = 1 \cdot 10^2 \div 2 \cdot 10^7$  V/m. In this interval, the coefficient  $\varepsilon_0 E^2 / 2F$  of the difference of the derivatives of permeability takes the values  $4.6 \cdot 10^{-16} \div 1.84 \cdot 10^{-5}$  V·mol/l. The derivatives of dielectric permeability with

respect to concentration can be determined by the Lorentz–Lorentz formula. For the giant calmar’s axone, this formula gives  $\varepsilon'_e - \varepsilon'_i = 3 \cdot 10^2$  l/mol. Thus, for the indicated interval of variation in the external field, the numerical value of  $\Delta\varphi_m^E$  is in the limits  $1.4 \cdot 10^{-10} \div 5.52$  mV. This yields that the third term in (5) will significantly contribute to the membrane potential only in the external field whose intensity is of order of  $10^7$  V/m. At considerably less intensities, e.g., in the interval  $E_{\text{ext}} = 10^2 \div 10^5$  V/m, the value of  $\Delta\varphi_m^E$  will be by 6–8 orders less than the value of the concentration contribution described by the second term in (5).

Of course,  $\Delta\varphi_m^E$  can be considered as a distinctive energy contribution to the membrane potential. Moreover, since the internal electric field is of order of  $10^6 \div 10^7$  V/m, one may expect a remarkable contribution to the membrane potential from  $\Delta\varphi_m^E$  at the same intensities of the external field. We note that dissolved ions react to external electric fields with significantly less intensities (the redistribution of ion concentrations occurs), which explains such a great difference of numerical values of  $\Delta\varphi_m^{\text{conc}}$  and  $\Delta\varphi_m^E$ .

Thus, based on the numerical estimates performed, we may infer that 1) variations of the membrane potential equal  $0.07 \div 10.7$  mV at external fields of  $10^2 \div 10^4$  V/m, 2) the main contribution to the membrane potential from the external electric field is caused by the redistribution of the ion concentrations between the interior and exterior media limited by the membrane, and 3) the membrane potential decreases on membranes where the external electric field is directed to the exterior phase. On the contrary, the membrane potential

**Table 2**

$E_{\text{ext}}, \text{V/m}$	$E_{\text{int}}^{\text{conc}}, \text{V/m}$ (the 1st case)	$E_{\text{int}}^{\text{conc}}, \text{V/m}$ (the 2nd case)
$10^2$	$-8.8 \cdot 10^2$	$8.8 \cdot 10^2$
$10^3$	$-8.8 \cdot 10^3$	$8.9 \cdot 10^3$
$10^4$	$-8.7 \cdot 10^4$	$9.0 \cdot 10^4$
$10^5$	$-7.7 \cdot 10^5$	$10.7 \cdot 10^5$

**Table 3**

$E_{\text{ext}}, \text{V/m}$	$\Delta C^{(1)}, \text{mmol/l}$ (the 1st case)	$\Delta C^{(1)}, \text{mmol/l}$ (the 2nd case)
$10^2$	$-5.7 \cdot 10^{-2}$	$7.2 \cdot 10^{-2}$
$10^3$	$-5.7 \cdot 10^{-1}$	$7.2 \cdot 10^{-1}$
$10^4$	$-5.64$	$7.32$

**Table 4**

$E_{\text{ext}}, \text{V/m}$	$\Delta\varphi_m^{\text{conc}}, \text{mV}$ (the 1st case)	$\Delta\varphi_m^{\text{conc}}, \text{mV}$ (the 2nd case)
$10^2$	$-6.9 \cdot 10^{-2}$	$8.7 \cdot 10^{-2}$
$10^3$	$-6.8 \cdot 10^{-1}$	$8.9 \cdot 10^{-1}$
$10^4$	$-6.12$	$10.67$

increases on membranes with the opposite direction of the external electric field.

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Received 04.02.03.

Translated from Ukrainian by V. V. Kukhtin

#### ВПЛИВ ЗОВНІШНЬОГО ЕЛЕКТРИЧНОГО ПОЛЯ НА МЕМБРАННІ ПОТЕНЦІАЛИ

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#### Резюме

Для вивчення мембранних потенціалів в присутності зовнішніх електричних полів використовуються загальні положення

термодинаміки необоротних процесів. Отримано формулу для концентраційного потенціалу Нернста, яка описує залежність мембранного потенціалу не лише від концентрації іонів та величини зовнішнього поля, а й від електродинамічних характеристик середовищ по обидва боки мембрани. Розрахунок електродифузійного розподілу іонних концентрацій під дією зовнішнього електричного поля, а також похідних діелектричної проникності по концентрації дозволяє зробити чисельні оцінки мембранних потенціалів в присутності зовнішніх електричних полів.

#### ВЛИЯНИЕ ВНЕШНЕГО ЭЛЕКТРИЧЕСКОГО ПОЛЯ НА МЕМБРАННЫЕ ПОТЕНЦИАЛЫ

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#### Резюме

Для изучения мембранных потенциалов в присутствии внешних электрических полей используются общие положения термодинамики необратимых процессов. Получена формула для концентрационного потенциала Нернста, которая описывает зависимость мембранного потенциала не только от концентрации ионов и величины внешних полей, но и от электродинамических характеристик сред по обе стороны мембраны. Вычисление электродиффузионного распределения ионных концентраций под воздействием внешнего электрического поля, а также производных диелектрической проницаемости по концентрации позволяет сделать численные оценки мембранных потенциалов в присутствии внешних электрических полей.