Fields and forces acting on a planar membrane with a conducting channel

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Modeling electric fields and forces around a channel in a planar membrane is still an open problem. Until now, most of the existing theories have oversimplified the electric field distribution by placing the electrode directly at the entry of the channel. However, in any relevant experimental setup the electrodes are placed far away in the electrolyte solution. We demonstrate that long-range deformation of the electric field distribution appears around the membrane, spanning on distances of the order of the distance between the membrane and the electrode. The forces acting due to this distribution are in most of the cases negligible. They can be important for channels with radii of the order of the thickness of the layer of structured water at the oil-water interface.

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I. INTRODUCTION

One of the basic functions of a biological membrane is to control the permeation of specific substrates between separated compartments by modifying the properties of the membrane channels. Examples of such channels and the detailed description of the electric field distribution in such systems are of great interest (Refs. [1,2], and the references therein).

In biotechnology, cell walls are permeabilized with short external electric pulses [3–5]. Such pulses induce fluctuating defects (pores) in the lipid matrix which allow the transfer of giant molecules. Many models of the electroporation were already developed, but until now a final model is not established [6–20]. More complete reviews on this subject can be found, e.g., in Ref. [21].

Many experiments were performed on planar lipid bilayers [22]. Such membranes have typically a conductance of less than a few pS/mm^2. A single defect of a few angstrom in size would be easily detectable. Conducting channels modify the electric field distribution and, consequently, the forces acting on a membrane. In what follows, all conducting structures in the membrane will be described as channels.

An essential characteristic of a channel is its effective resistance (i.e., the ratio between the potential difference, applied to its two ends and the current through it). This quantity depends on the dimensions of the channel, its shape [23] and the Faxen correction factor which takes into account frictional interactions between the charge carriers and the channel [24]. When studying protein channels in electrolyte solution, the distribution of charges on the surface of the pore and the screening effects must be taken into account [25,26]. This can give as a consequence nonlinear effects even for the so called large water-filled channels, i.e., dependence of the effective channel resistance on (i) the potential difference applied to the channel [27–29], (ii) the bulk conductivity (or the absolute electrolyte concentration) [27,29]. Other effects such as a resistance asymmetry under reversed polarity have been observed experimentally and with computational methods [27–29].

In the present work we consider the stationary case of the current flows. We also neglect the magnetic field effects due to the current flows. Consequently, all forces under consideration are of electrostatic origin. Hence, first of all we have to calculate the electric field distribution between the two electrodes. This gives readily the electric field forces which depend on the channel radius.

Until now, it was usually assumed that the perturbation of the electric field due to the presence of a microscopic conducting channel is of short range. This implies that in the direction parallel to the membrane the perturbation spans on a distance of the order of a few channel radii. The forces thus obtained depend only on the dimensions of the channel. Applying implicitly the idea that the electrodes are very near the membrane and that the channel is part of a circular cylinder with radius r_0 and height d, Abidor *et al.* [8] derived the electric field contribution to the energy of the pore, permitting to obtain the electric force $F^{Ab}(r_0)$ (defined as the taken with negative sign derivative of this energy with respect to the pore radius r_0) acting on the edge of the pore and tending to open it:

$$F^{Ab}(r_0)=\frac{\pi r_0}{d}(\varepsilon_w-\varepsilon_d)(U_0)^2, \tag{1}$$

where ε_w and ε_d are the permittivities of the water and the membrane, respectively, and U_0 is the potential difference, applied to the electrodes. Later, Pastushenko and Chizmadzhev [9] took into account the redistribution of U_0 between the bulk electrolyte and the channel, but to derive their results, once again they placed implicitly the electrodes near the membrane, applying potential difference to them, equal to the potential difference on the channel.

In the present paper we demonstrate that the electric field perturbation depends on the distance between the membrane and the electrodes, while for narrow channels (with radii,

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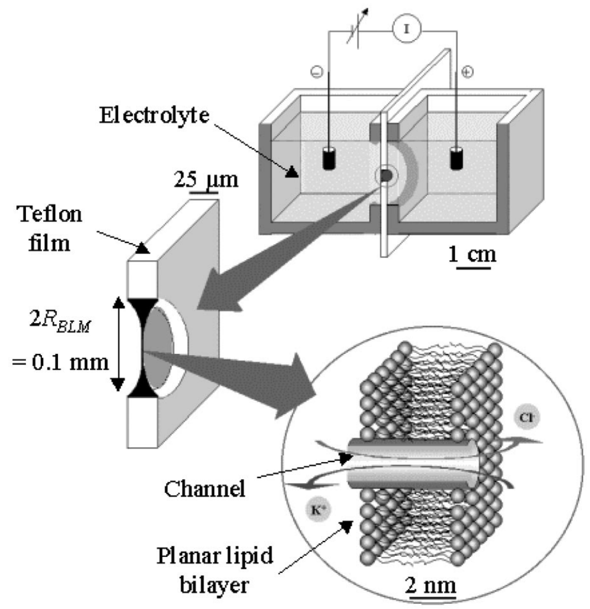

FIG. 1. Experimental setup for conductance recording of planar model membranes. The two chambers are approximately ~1 cm in size and are separated by a Teflon sheet containing a hole with dimensions ~0.1 mm. The cuvette is filled with electrolyte and a lipid bilayer is formed across the Teflon hole using one of the established techniques (see, e.g., Ref. [2]). Into the lipid membrane of about $d=4$ nm thickness a single conducting channel can be inserted. A transmembrane voltage U_0 is applied via two electrodes at a distance L from the membrane.

considerably less than the thickness of the membrane) the related forces depend on the dimensions of the channel.

II. ELECTRIC FIELD BETWEEN TWO ELECTRODES SEPARATED BY A PLANAR MEMBRANE CONTAINING A SINGLE CONDUCTING CHANNEL

First of all, we revisit certain earlier electric field calculations for the idealization of the experimental setup shown in Fig. 1. It consists of a flat infinite dielectric layer of thickness d, placed at a distance L between two parallel flat electrodes at a voltage U_0. The dielectric layer contains a conducting axisymmetric channel of a mean radius r_0, filled with the electrolyte. The channel is not necessarily part of a circular cylinder. If the area of the cross section changes along its axis, r_0 is the radius of a cylinder with the property that the volume of a part of such a cylinder with the height of the channel is equal to the volume of the channel. The effective channel radius r_0 can be written as: $r_0 = [(1/\pi d)\int_{-d/2}^{d/2} S(z)dz]^{1/2}$, where $S(z)$ is the cross section of the channel at distance z from the midplane of the membrane.

We assume a homogeneous conductivity throughout the aqueous space and no conductivity of the hydrophobic dielectric layer. As a consequence the relation between the electric field $\boldsymbol{E}$ and the current density $\boldsymbol{j}$ in the electrolyte is $\boldsymbol{j}=\sigma\boldsymbol{E}$, where σ is the bulk conductivity of the electrolyte. We restrict ourselves to the stationary case where the bulk charge density is zero. Under these conditions the electric field $\boldsymbol{E}$ in the bulk of the electrolyte and its potential U satisfy the equations $\operatorname{div}\boldsymbol{E}=0$ and $\boldsymbol{E}=-\operatorname{grad} U$. The potential $U(\boldsymbol{r})$ satisfies the Laplace equation and is caused by the surface charges on the borders of the electrolyte including those of the channel.

As it was already pointed out, most of the theoretical models calculate the electric forces by placing the electrode directly at the channel entrance. However, in the real experiments the electrode is kept at some macroscopic distance. For example, the channel size is typically less than a few nanometers, while the electrode is placed at a distance of a few millimeters. A planar lipid bilayer can be treated as an insulator, because a reasonably good preparation does not show (on average) any conducting defect within a bilayer. The presence of a conducting channel will obviously lead to an electric field perturbation. Relatively few attempts have been made to account for such effects [30,31,9,10]. Therein it was assumed that the distance between the electrodes tends to infinity and that the thickness of the dielectric layer tends to zero. In this particular case it was shown that in each of the half-spaces on both sides of the layer the electric field distribution coincides with that of a conducting charged disk with a radius r_0, equal to that of the channel, placed in dielectric medium with dielectric permittivity ε_w equal to that of the electrolyte. On the surface, presenting the dielectric layer, there is a change of the sign of the electric potential and of the electric field. Let a reference frame be placed with origin in the center of the channel and with plane XY parallel to the dielectric layer and the electrodes. Let (r,z) be the cylindrical coordinates of a point with coordinates (x,y,z), i.e., the relation $r=\sqrt{x^2+y^2}$ holds. Then a potential was obtained of the kind [10]:

$$U(r,z)=\operatorname{sgn}(z)\frac{U_0}{\pi}\operatorname{arccot}\left[\frac{r_0}{R}\right], \tag{2}$$

where

$$R^2=\tfrac{1}{2}\{[r^2+z^2-(r_0)^2]+\sqrt{[r^2+z^2-(r_0)^2]^2+4(r_0)^2z^2}\}. \tag{3}$$

From these equations it follows that for $R \gg r_0$ the field distribution in the electrolyte coincides with this of a point charge equal to the total charge of the disk. It can be shown, that if $\sqrt{x^2+y^2+z^2}>10r_0$, the deviation of the equipotential lines from these of a point charge is less than 1%. The perturbation of the field due to the presence of the channel decreases as $1/\sqrt{x^2+y^2+z^2}$, i.e., it is a long-range perturbation.

This model is suitable for the description of channels with effective diameters much greater than the thickness of the membrane.

In the present work we deal with channel radii which are much less than the thickness of the membrane, and neglect any particular molecular details characterizing the channel. In addition we also expect that the field distribution at some distance, sufficiently greater than the mean radius r_0 of the channel, does not depend on the detailed shape of the channel. To verify this hypothesis, we calculated numerically the

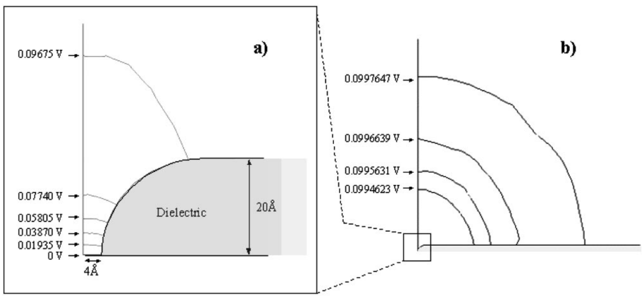

FIG. 2. Numerically calculated distribution of the potential field in the electrolyte to the side of the positively charged electrode. The electrodes are placed at a distance $L=1$ cm on the two sides of the membrane. The channel has the form of the inner half of tore with small diameter equal to the thickness $d=40$ Å of the membrane and throat radius equal to 4 Å. The voltage applied to the upper (positive) electrode is $U_0/2=0.1$ V, (a) the domain of distances of the order of the channel radius, (b) the domain of distances much greater than the channel radius and much less than the distance between the membrane and the electrode.

potential distribution for the case of a channel modeled by the inner half of a tore with a small diameter equal to the thickness of the dielectric. The potential distribution is a solution of the Laplace equation $\Delta U=0$ with the following boundary conditions for the upper half of the electrolyte: (1) $U=0$ on the part of the plane of symmetry (in the middle of the membrane) inside the electrolyte, (2) $U=U_0/2$ on the positive electrode, (3) $(\partial U/\partial \boldsymbol{n})=0$ on the borders of the dielectric. Where $\boldsymbol{n}$ is the normal to the border of the dielectric in the point under consideration. The third boundary condition is a consequence of the fact that the ion current is tangential to the borders of the dielectric.

The results of the numerical calculation presented in Fig. 2 show that, for distances larger than some channel radii, the equipotential lines have the form of a hemisphere. This is in agreement with the earlier analytical calculation of Newman [30].

The next step is to search for an explicit expression of the electric field distribution shown in Fig. 2. In the setup, shown in Fig. 1, we introduce a reference frame $X'Y'Z'$ with origin O' on the axis of the channel, with a plane $X'Y'$ coinciding with the upper boundary of the membrane, and axis Z' directed to the positive electrode (see Fig. 3). The cylindrical coordinates in this last frame are denoted by (r',φ',z'). The electric potential $U(r',z')$ is axisymmetric (it does not depend on φ). Let S_p be an equipotential hemisphere, situated in the electrolyte, with a center O', radius R_0, and $z'>0$ (see Fig. 3). R_0 is of the order of some channel radii and much less than the distance between the membrane and the electrode (i.e., $R_0/L \ll 1$). The distribution of the potential $U(r',z')$ in the electrolyte between the electrode and the hemisphere satisfies the following boundary conditions, (1) $U=U_0/2$ on the upper electrode, (2) $U=U_{R_0}/2$ on S_p, (3) $[\partial U(r',z')/\partial z']|_{z'=0}=0$ for $r'>R_0$.

Consider now a potential, created by an infinite sequence of point charges placed on the axis Z' with coordinates 0, $\pm 2L, \pm 4L, \ldots, \pm 2nL, \ldots$ (see Fig. 3). Let the charge in the point with the respective n be $(-1)^{n+1}q$, where q is determined from the following equation:

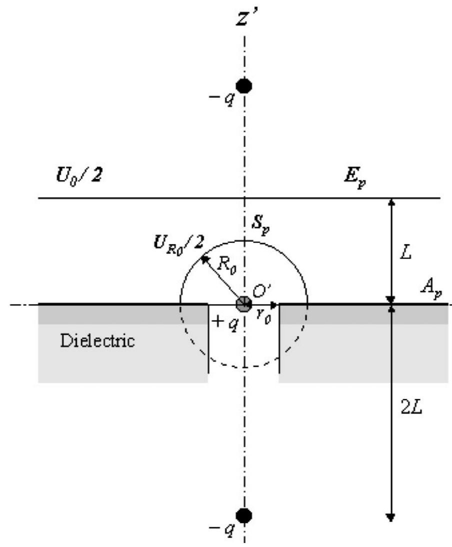

FIG. 3. Sequence of charges, creating the potential in the long distance range of the electrolyte above the membrane. The equipotential surface E_p determined by the equation $z'=L$ corresponds to the positive electrode and is kept at the potential $U_0/2$. The conditional boundary between long and short distances is a hemisphere S_p with center O' and radius R_0 and potential $U_{R_0}/2$. The upper boundary of the lipid membrane is indicated by A_p.

$$\frac{q}{4\pi\varepsilon_w R_0}=\frac{U_{R_0}}{2}-\frac{U_0}{2}+O\left(\frac{R_0}{L}\right), \tag{4}$$

where ε_w is the electric permittivity of the electrolyte. If the constant $U_0/2$ is added to the potential, created by these charges, we obtain the solution of the Laplace equation, satisfying the above boundary conditions.

This result allows to calculate the function $U(r',0)$, $r' \geqslant R_0$ permitting to estimate the range of the field perturbation in the lateral direction. The result thus obtained is

$$U(r',0)=\frac{U_0}{2}+\frac{qV\left(\frac{r'}{L}\right)}{4\pi\varepsilon_w r'} \tag{5}$$

with

$$V\left(\frac{r'}{L}\right)=1-\frac{r'}{L}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\sqrt{n^2+\left(\frac{r'}{2L}\right)^2}}. \tag{6}$$

The function $V(r'/L)$ is a decreasing function of the argument r'/L and satisfies the relation (this and all the other relations in the present work are obtained with the help of the software Maple):

$$\lim_{r'/L\to\infty}\frac{V\left(\frac{r'}{L}\right)}{\exp\left[-\ln(2)\frac{r'}{L}\right]}=0. \tag{7}$$

We chose this kind of the exponent because the functions $V(x)$ and $\exp[-\ln(2)x]$ have identical first and second term of their development in a Taylor series around $x=0$. It can be shown numerically, that the ratio $V(x)/\exp[-\ln(2)x]$ is in the interval $(0.8,1)$ for $0<x<1$ and tends to 1 when x tends to zero. Consequently, up to macroscopic distance $\sim L$ (much greater than the mean radius r_0 of the channel) the field near the plane A_p in the electrolyte (see Fig. 3) is practically equal to that of the charge q, i.e., a long-range perturbation of the electric field appears due to the presence of channel. For the points near the plane A_p at distances from the channel greater than L the perturbation of the electric field sharply decreases to zero. Because of the dependence in Eq. (7) this decrease is faster than the exponential one. As it was explained above, the equipotential surfaces in the electrolyte look like hemispheres for distances from the channel much greater than its radius. The deviation from a sphere will be essential when the function $V(r'/L)$ becomes substantially less than 1. This will happen for distances $r'\sim L$ (for $r'\ll L$ this function is practically equal to 1). Evidently, the positive electrode E_p can be situated on some of these spherelike equipotential surfaces at distance less than, but of the order of L from the channel. The change of the form of the electrode to a true hemisphere with a radius, equal to the average distance between the points of this equipotential surface and the channel, will keep the essential properties of the field in the electrolyte around the channel. The same is also valid for the negative electrode E_n.

In the following Sections the electric fields and forces acting on a membrane between electrodes of this kind will be calculated.

III. CALCULATION OF THE ELECTRIC FIELD FOR SPHERICAL FORM OF THE ELECTRODES

Later on, the electrodes E_p and E_n are assumed to be hemispheres with centers O_p and O_n on the axis of the channel and equatorial planes coinciding with the borders of the membrane (see Fig. 4). Let S_p and S_n be hemispheres, concentric with the electrodes E_p and E_n, and let they have radii R_0 of the order of some radii of the channel. They are assumed equipotential with potentials $\pm U_{R_0}/2$, respectively. The ensemble of points in the electrolyte between E_p and S_p and between E_n and S_n will be called long distance range, while the points between S_p and the channel and between S_n and the channel will be called short distance range.

Following the approach by Newman [30] the macroscopic ion current I between the spherical electrodes is

$$I=\frac{U_0}{\mathcal{R}_p+\mathcal{R}_{ch}+\mathcal{R}_n}, \tag{8}$$

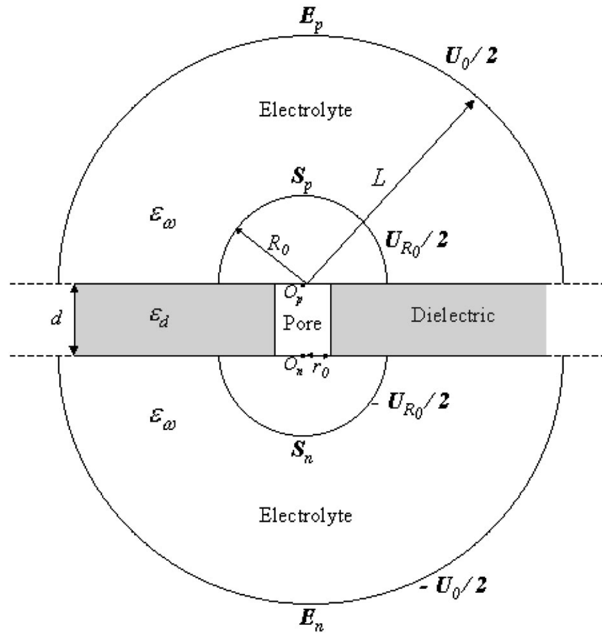

FIG. 4. Spherical electrodes, permitting the analytical calculation of the electric fields and the forces acting on the membrane. E_p and E_n are the positive and the negative electrodes having the form of hemispheres with radii L, with parallel equatorial planes situated at a distance d equal to the thickness of the membrane. The membrane is inserted in the gap between the hemispheres and contains a channel with an axis, determined by the centers O_p and O_n of the electrodes and a mean radius r_0. The channel is covered by two hemispheres S_p and S_n, with centers O_p and O_n and radii R_0 ($R_0 \ll L$). R_0 is of the order of some radii r_0. These two hemispheres are supposed equipotential with potentials $\pm U_{R_0}/2$, respectively. The borders of the dielectric to the side of the positively and the negatively charged electrodes are denoted with A_p and A_n, respectively.

where $\mathcal{R}_p=\mathcal{R}_n$ is the excess resistance of each of the spaces between the electrode and the corresponding equipotential hemisphere, covering the entrance of the channel, and $\mathcal{R}_{ch}$ is the resistance of the short distance ranges of the channel plus the resistance of the channel. The exact calculation of $\mathcal{R}_{ch}$ can be carried out if the structure of the channel is known.

The calculated resistances $\mathcal{R}_p$ and $\mathcal{R}_n$ are

$$\mathcal{R}_p=\mathcal{R}_n=\frac{\rho}{2\pi}\left(\frac{1}{R_0}-\frac{1}{L}\right), \tag{9}$$

where ρ is the bulk resistivity. The potential U_{R_0} can be expressed as

$$U_{R_0}=\frac{\mathcal{R}_{ch}}{\frac{\rho}{\pi}\left(\frac{1}{R_0}-\frac{1}{L}\right)+\mathcal{R}_{ch}}U_0. \tag{10}$$

Let r be the distance between the center O_p of the upper electrode and a point somewhere in the space between the hemispheres E_p and S_p. The potential $U(r)$, $R_0<r<L$ is

$$U(r)=\frac{\frac{\rho}{\pi}\left(\frac{1}{R_0}-\frac{1}{r}\right)+\mathcal{R}_{ch}}{\frac{\rho}{\pi}\left(\frac{1}{R_0}-\frac{1}{L}\right)+\mathcal{R}_{ch}}\frac{U_0}{2}. \quad (11)$$

For $r>R_0$, the function $U(r)$ must be independent from the arbitrary R_0. Consequently $\mathcal{R}_{ch}(r_0,R_0)$ can be presented in the form

$$\mathcal{R}_{ch}(r_0,R_0)=\frac{\rho}{\pi}\left(\frac{1}{r_0}-\frac{1}{R_0}\right)+\mathcal{R}^0_{ch}(r_0). \quad (12)$$

We define a length $l(r_0)$ via the relation

$$\frac{1}{l(r_0)}=\frac{1}{r_0}+\frac{\pi}{\rho}\mathcal{R}^0_{ch}(r_0). \quad (13)$$

Then the potential distribution $U(r)$ in the electrolyte in the long distance range to the side of the positive electrode can be presented as

$$U(r)=\frac{\frac{1}{l(r_0)}-\frac{1}{r}}{\frac{1}{l(r_0)}-\frac{1}{L}}\frac{U_0}{2}. \quad (14)$$

The calculation of $\mathcal{R}^0_{ch}(r_0)$ can be done by appropriate computer modeling [32,33].

The length $l(r_0)$ is a microscopic one, of the order of the thickness of the membrane and the radius of the channel, while L is the macroscopic distance between the electrodes and the membrane. The inequality $l(r_0)\ll L$ always holds. That is why in what follows we will omit the factor $1/L$, considering formally the distance L as equal to infinity. As L participates in the potential distribution inside the factor $[1/l(r_0)-1/L]$, this approximation will practically not influence the final results.

For the part of the space between the spheres E_n and S_n (see Fig. 4) the result for the potential distribution is antisymmetric with respect to the plane in the middle of the dielectric.

Later on in this section we calculate the electric field distribution for the case of a cylindrical channel with radius r_0 sufficiently smaller than the thickness d of the membrane. The opposite case of pores with radii, much greater than the thickness of the membrane is considered by Winterhalter and Helfrich [10].

The potential U inside the membrane must also satisfy the Laplace equation $\Delta U=0$. The dielectric layer is presented in Fig. 4. Let $X^dY^dZ^d$ be a frame of reference with origin O^d coinciding with the center of the channel and with plane X^dY^d parallel to the dielectric. Let (r^d,φ^d,z^d) be the cylindrical coordinates in this frame. Here the upper index d refers to the coordinates inside the dielectric part of the membrane. Due to the rotational symmetry, the potential distribution $U(r^d,z^d)$ does not depend on the coordinate φ. Because of the condition $r_0\ll d$, the long distance range is assumed to span up to the boundaries of the channel. As a consequence of this assumption and of Eq. (14), the boundary conditions for the solutions of the Laplace equations on the flat parts of the boundaries of the membrane are

$$U\left(r^d,\pm\frac{d}{2}\right)=\pm\left[1-\frac{l(r_0)}{r^d}\right]\frac{U_0}{2}. \quad (15)$$

On the surface of the pore the boundary condition is

$$U(r_0,z)=\frac{2z^d}{d}\left(1-\frac{l(r_0)}{r^d}\right)\frac{U_0}{2}. \quad (16)$$

These boundary conditions implicitly assume that inside the narrow channel the distribution of the potential is linear and that the perturbations of the electric field in the electrolyte around the entrances of the channel are of short range ($\sim r_0$) and their effect can be neglected. The exact distributions of the electric field in these zones are calculated by Neu, Smith, and Krassowska [34] via numerical solution of the Laplace equation.

The potential distribution function $U(r^d,z^d)$ inside the membrane is expanded in a Fourier series of the kind

$$U(r^d,z^d)=\left\{\frac{2z^d}{d}-\frac{l(r_0)}{r_0}\left[\frac{r_0}{r^d}\frac{2z^d}{d}+\sum_{n=1}^{\infty}A_n(r^d)\sin\left(\frac{2\pi n}{d}z^d\right)\right]\right\}\frac{U_0}{2}. \quad (17)$$

As shown in Appendix A, the values of the Fourier amplitudes $A_n(r^d)$ obtained from the Laplace equation and the presented above boundary conditions are

$$A_n(r^d)=4(-1)^{n+1}\frac{r_0}{d}\times\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_0\left(\frac{2\pi n}{d}r^d\right)-P\left(\frac{2\pi n}{d}r^d\right)\right], \quad (18)$$

where $K_0(x)$ is the modified Bessel function of zero order, and $P(x)$ is expressed by the modified Bessel functions $I_0(x)$ and $I_1(x)$ of the zero and first order and the modified Struve functions $L_0(x)$ and $L_1(x)$ of zero and first order as follows:

$$P(x)=\frac{1}{2x}\left\{-2xI_0(x)\int_x^{\infty}\left[-\frac{K_0(t)}{t^2}\right]\times dt-K_0(x)[(-x^2\pi L_1(x)-2x^2+2)I_0(x)+xI_1(x)\times(\pi xL_0(x)+2)]\right\}. \quad (19)$$

In this way, the distribution of the potential field in the electrolyte as well as inside the dielectric are determined when the membrane contains a narrow conducting channel and the electrodes have the form of hemispheres. These results will be used in the following section for the calculation of the forces, acting on the membrane.

IV. FORCES ACTING ON THE MEMBRANE DUE TO THE PRESENCE OF A CONDUCTING CHANNEL

To calculate the forces, acting on a membrane due to presence of a conducting channel we will use the Maxwell stress tensor [35], as it was done by Winterhalter and Helfrich [10] and Neu, Smith, and Krassowska [34].

The definition of the Maxwell stress tensor T in a point of a medium with electric permittivity ε and electrostatic field $\boldsymbol{E}$ is [35]

$$\mathsf{T}=\varepsilon(\boldsymbol{E}\boldsymbol{E}-\tfrac{1}{2}|\boldsymbol{E}|^2\mathsf{I}), \tag{20}$$

where with I is denoted the unit tensor and with $\boldsymbol{AB}$ is denoted the tensor product of the vectors $\boldsymbol{A}$ and $\boldsymbol{B}$. The forces, appearing in dielectric media due to presence of electric field can be described by the Maxwell tensor in the following way [35]. Let us consider some part of the dielectric and an infinitesimal area $d\boldsymbol{s}$ of its boundary ($d\boldsymbol{s}=\boldsymbol{n}ds$, where $\boldsymbol{n}$ is the normal to the surface in the patch under consideration, and this normal is directed outward the volume). The force $d\boldsymbol{f}$, acting on this area, is

$$d\boldsymbol{F}=\mathsf{T}\cdot d\boldsymbol{s}, \tag{21}$$

where the dot denotes the vector product of a tensor with a vector. This is the force due to the electric field inside the volume. Evidently, if on the boundary there are no charges and the permittivity ε is the same inside and outside the volume, the field outside the volume will create a force acting on the same infinitesimal area that is with the same modulus and the opposite direction. As it was noted above, the Laplace equation is valid inside the dielectric and inside the electrolyte. Consequently, the forces due to the electric field act on the boundary between these two media. In equilibrium of the system, they have to be compensated by mechanical stresses, created by the membrane in order to avoid its deformation. To calculate the electric forces, acting on an infinitesimal element with area ds of this boundary, two infinitesimally close and parallel to it surface elements with the same area in the electrolyte and in the dielectric have to be considered. The vector, presenting the surface element in the electrolyte is directed from the electrolyte to the dielectric while the vector presenting the surface element in the dielectric has the opposite direction. The force on the element ds is equal to the sum of the forces, acting on the two infinitesimally close to it elements. The ratio $\boldsymbol{f}=d\boldsymbol{F}/ds$ determines the surface force density, acting in a point of the boundary between the electrolyte and the dielectric.

The borders between the dielectric and the electrolyte are the surface of the channel and the points of the flat surfaces or the membrane that are at distances greater than r_0 from the axis of the channel.

The electric field in the electrolyte inside the channel is directed along the axis Z. Its projection $E_z^w(r,z)$, $r\leqslant r_0$ and $-d/2<z<d/2$, on the axis Z, equal to the projection on the same axis of the electric field on the surface of the channel $E_z^d(r_0,z^d)$ approaching it from the side of the dielectric, is calculated from Eq. (16):

$$E_z^w(r_0,z)=E_z^d(r_0,z^d)=-\frac{\partial U(r_0,z)}{\partial z}=-\left[1-\frac{l(r_0)}{r_0}\right]\frac{U_0}{d}. \tag{22}$$

In each point of the dielectric the projection $E_r^d(r^d,z^d)$ of the electric field $\boldsymbol{E}(r^d,z^d)$ on a ray, starting from the axis of the channel, parallel to the membrane, and passing through the point under consideration (later on we will refer to projection of this kind as the radial component of the vector) is

$$E_r^d(r^d,z^d)=-\frac{\partial U(r^d,z^d)}{\partial r^d}. \tag{23}$$

On the surface of the channel this component, calculated from Eqs. (17) and (18), is

$$E_r^d(r_0,z^d)=-\frac{l(r_0)}{r_0}\left(\frac{z^d}{r_0}-\frac{4\pi r_0}{d}\sum_{n=1}^{\infty}\times\left\{(-1)^{n+1}n\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_1\left(\frac{2\pi n}{d}r_0\right)-P'\left(\frac{2\pi n}{d}r_0\right)\right]\sin\frac{2\pi n}{d}z^d\right\}\right)\frac{U_0}{d}, \tag{24}$$

where

$$P'(x)=\frac{d}{dx}P(x) \tag{25}$$

and $K_1(x)$ is the modified Bessel function of first order.

Let ε_w and ε_d be the dielectric permittivity of the water solution (the electrolyte) and the dielectric (the membrane). The surface force density $\boldsymbol{f}$ acting in each point of the surface of the channel due to the electric field has two components. One of them f_z is along the Z axis and tends to change the thickness of the membrane. In the present work we will consider the case of a membrane with constant thickness and area. For such an object the forces, acting along the Z axis of the membrane, do not influence its properties. The other component is a radial one. As it is shown in Appendix B, this radial component $f_r(r_0,z^d)$ is

$$f_r(r_0,z^d)=\frac{1}{2}(\varepsilon_w-\varepsilon_d)[E_z^d(r_0,z^d)]^2+\tfrac{1}{2}\varepsilon_d[E_r^d(r_0,z^d)]^2, \tag{26}$$

where $E_z^d(r_0,z^d)$ and $E_r(r_0,z^d)$ are obtained from Eqs. (22) and (24), respectively. The general force $F^{ch}(r_0)$, acting on the channel, will be obtained by integration of $f_r(r_0,z)$ over the surface of the channel:

$$F^{ch}(r_0)=\int_S f_r(r_0,z^d)ds=2\pi r_0\int_{-d/2}^{d/2} f_r(r_0,z^d)dz^d. \tag{27}$$

As it is shown in Appendix B, for realistic values of the radii r_0, satisfying the inequality $r_0 \ll d$, the force $F^{ch}(r_0)$ can be presented as

$$F^{ch}(r_0)=\frac{\pi r_0}{d}(\varepsilon_w-\varepsilon_d)(U_0)^2+\alpha\frac{\pi r_0}{4d}\varepsilon_d(U_0)^2 + O\left(\left(\frac{r_0}{d}\right)^2\right)\varepsilon_d(U_0)^2, \tag{28}$$

where α is a numerical factor of the order of 1.

The same approach will be used for the calculation of the forces acting on the flat part of the boundaries of the membrane. Let us consider a point with cylindrical coordinates $(r^d,\varphi,d/2)$, $r>r_0$ on the surface of the membrane, taken for definiteness to the side of the positive electrode. From the side of the electrolyte the electric field has only a radial component $E_r^w(r^d,d/2)$, equal to the radial component $E_r^d(r^d,d/2)$, $r>r_0$, of the electric field when approaching the point from the side of he dielectric. It can be calculated from Eq. (14):

$$E_r^w\left(r^d,\frac{d}{2}\right)=E_r^d\left(r^d,\frac{d}{2}\right)=-\frac{\partial U\left(r^d,\frac{d}{2}\right)}{\partial r^d}=-\frac{l(r_0)}{(r^d)^2}\frac{U_0}{2}. \tag{29}$$

From the side of the dielectric the electric field has in addition a component $E_z^d(r^d,d/2)$, $r>r_0$, along the Z axis that can be calculated from Eq. (17):

$$E_z^d\left(r^d,\frac{d}{2}\right)=-\left.\frac{\partial U(r^d,z)}{\partial z}\right|_{z=\frac{d}{2}} = -\left(1-\frac{l(r_0)}{r_0}\left\{\frac{r_0}{r^d}-\frac{4\pi r_0}{d}\sum_{n=1}^{\infty} n \times\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_0\left(\frac{2\pi n}{d}r^d\right) - P\left(\frac{2\pi n}{d}r^d\right)\right]\right\}\right)\frac{U_0}{d}. \tag{30}$$

Due to the existence of these two components of the electric field in the dielectric, the density of the force field, acting on each of the surfaces of the membrane, contains a radial component $f_r(r^d,d/2)$, tending to close the channel. As it is shown in Appendix C, for narrow channels this radial component is

$$f_r\left(r^d,\frac{d}{2}\right)=-\frac{1}{2}\varepsilon_d E_r\left(r^d,\frac{d}{2}\right)E_z\left(r^d,\frac{d}{2}\right). \tag{31}$$

Let us consider a crown of the boundary of the membrane with a radius r^d, thickness dr^d and a center on the axis of the channel in the plane of the surface. The force dF^s acting on this crown and tending to decrease its radius is $2\pi r^d f_r(r^d,d/2)dr^d$. If the crown changes its radius with δr^d, because of the conservation of the area of the membrane the channel will change its radius r_0 with $\delta r_0 =(r^d/r_0)\delta r^d$. Consequently, the effective force dF_0^s, acting on the channel and having the same effect as the force dF^s is

$$dF_0^s=\frac{r_0}{r^d}f_r\left(r^d,\frac{d}{2}\right)dr^d. \tag{32}$$

The total effective force F_0^s acting on the channel and equivalent to the action of the electric forces on the surfaces of the membrane is

$$F_0^s=2\int_{r_0}^{\infty}dF_0^s, \tag{33}$$

where the multiplier 2 takes into account both surfaces (to the side of the positive electrode and to the side of the negative one) delimiting the membrane. As it is shown in Appendix C, this force is

$$F_0^s=-(\pi-\beta)\varepsilon_d\left(\frac{r_0}{d}\right)^2(U_0)^2+O\left[\left(\frac{r_0}{d}\right)^3\right]\varepsilon_d(U_0)^2, \tag{34}$$

where β is a numerical factor of the order of 0.1. The last result shows that contrary to the case of large pores [10], for the narrow pores this force is of higher order with respect to the ratio r_0/d and can be neglected.

Keeping the terms containing first order with respect to the ratio r_0/d we obtained the following expression for the total force $F^{tot}(r_0)$, appearing due to the existence of a narrow conducting channel with a radius r_0 and tending to open it:

$$F^{tot}(r_0)\approx\frac{\pi r_0}{d}(\varepsilon_w-\varepsilon_d)(U_0)^2+\frac{\pi r_0}{4d}\varepsilon_d(U_0)^2. \tag{35}$$

V. DISCUSSION

The first term on the right-hand side of Eq. (35) reproduces the well known result of Abidor *et al.* [8]. To estimate the second one the values of ε_w and ε_d must be taken. In the volume $\varepsilon_w \approx 80\varepsilon_0$, where ε_0 is the dielectric permittivity of the vacuum, while ε_d is in the interval $2\varepsilon_0$–$6\varepsilon_0$. With these values of the permittivities the calculated by us correction given by the second term on the right-hand side of Eq. (35) is negligible. Consequently, in the frames of the assumption that the bulk resistivity ρ and the dielectric permittivity ε_w are homogeneous (not depending on the place) throughout all the electrolyte, including the interior of the channel, the results of Abidor *et al.* [8] can be applied for narrow channels with radii greater than several times the dimension of one water molecule, in spite of the splay of the electric field around the channel and the long-range perturbation of the electric field near the membrane. It is necessary to note that in the real case the translational and rotational freedom of water molecules is substantially reduced inside a narrow channel relative to the bulk water [36,37]. As a consequence the water in the channel is highly structured and its permittivity is much less than that in the volume. Unfortunately, we did not find in the literature measured or simulated values of this quantity. What is known is that in the Helmholtz layer inside the diffuse part of the electric double layer the dielectric permittivity is $\approx 6\varepsilon_0$ [38]. This is of the order of the dielectric permittivity in the region of the hydrophilic heads of a lipid bilayer. For the case of equal permittivities of the dielectric part of the membrane and the water in the channel, the first addend on the right-hand side of Eq. (35) is zero and the second one becomes dominant. Evidently, in such a case additional investigation of the domain with inhomogeneous permittivity must be carried out in order to obtain the correct force acting on the channel.

Another effect that must be taken into account in the full description of the phenomena around the channel is the smearing of the surface charges on the dividing surface between the electrolyte and the membrane. Let D be the Debye length [39]:

$$D = \sqrt{\frac{\varepsilon_w kT}{2e^2(z_\nu)^2 Nc}}, \tag{36}$$

where ε_w is the dielectric constant of the water, k is the Botzmann constant, T is the temperature, e is the electronic charge, z_ν is the valency of the electrolyte (for simplicity, only symmetrical electrolytes will be considered), N is the Avogadro number, and c is the concentration of the electrolyte. In all the considerations so far it was assumed implicitly that this length is much smaller than the radius r_0 of the channel. In the typical experiments for measurements of the current flows through membrane channels [2] the used electrolyte is a water solution of KCL with concentration between 0.1 and 1 M. The Debye length for such an electrolyte is between 3 and 10 Å. It is comparable with the typical channel radius. In the short distance range, the numerical solution of the Poisson equation is a possibility to take this smearing into account.

In the long distance range the smearing of the charges in the diffuse layer has a twofold effect. The first one is the local increase of the ion concentration (and consequently the specific conductivity) near the dielectric. The numerical estimations of this increase for the mentioned above concentration ranges of the KCl solutions give a 2.5% change of the specific conductivity in the electrolyte. Consequently this effect can be neglected. The second effect is the redistribution of the potential $2U(r)$ [$U(r)$ determined from Eq. (11)], applied to the membrane at a distance r from the axis of the channel, between the diffuse layers and the dielectric. The potential drop on each of the double layers is $[\varepsilon_w \sigma(r)]/D$. Consequently, to take into account this effect, the thickness d of the dielectric must be replaced with the quantity $d[1+(\varepsilon_d D)/(\varepsilon_w d)]$. In the mentioned above concentration of the solute in the electrolyte, the Debye length is considerably smaller than the thickness of the membrane. If the dielectric permittivity ε_w of the water in the double layer is equal to that in the volume, this correction is of the order of several percent and can be neglected too. In the case when the permittivity in the vicinity of the membrane is inhomogeneous, the equation of Poisson has to be solved once again.

VI. CONCLUDING REMARKS

The results of the present work can be useful when computation of the electric field around the channel is carried out. If the electrodes are hemispherical with radii considerably greater than the typical dimension of the channel, but much less than the distance between the membrane and the electrodes, the electric field distribution around the channel will be the same as in the real case. This will facilitate studies of this kind.

The long-range distance perturbation of the electric field around a channel prompts that in a membrane with a more than one channel a long-range repulsion interaction will appear between them.

One of the main conclusions of the obtained results here is that when the bulk resistivity and the dielectric permittivity are homogeneous throughout all the electrolyte (the region of the channel included), and when the Debye length is much less than the radius of the channel, the forces, acting on a narrow channel are practically equal to those calculated by Abidor *et al.* [8]. The theoretical description of the real situation when these assumptions are not valid, rests in an open question.

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APPENDIX A: ELECTRIC POTENTIAL IN THE DIELECTRIC PART OF THE MEMBRANE

The potential $U(r^d, z^d)$ from Eq. (17) satisfies the Laplace equation. The function $2z^d/d$, defined in the interval $(-d/2, d/2)$ and considered as periodic with period d can be decomposed in a Fourier series in the following way:

$$\frac{2z^d}{d}=\sum_{n=1}^{\infty}\frac{2}{\pi n}(-1)^{n+1}\sin\left(\frac{2\pi n}{d}z^d\right). \tag{A1}$$

Writing the Laplace equation in cylindrical coordinates (r^d,φ^d,z^d), taking into account that the potential is axisymmetric, and using Eq. (A1), we obtained that the amplitudes $A_n(r^d)$ satisfy the equation

$$\frac{1}{r^d}\frac{\partial}{\partial r^d}r^d\frac{\partial}{\partial r^d}A_n(r^d)-\left(\frac{2\pi n}{d}\right)^2A_n(r^d)-\frac{(-1)^{n+1}}{\pi n}\frac{2r_0}{(r^d)^3}=0. \tag{A2}$$

The general solution of this equation is

$$A_n(r^d)=C_1^nI_0\left(\frac{2\pi n}{d}r^d\right)+C_2^nK_0\left(\frac{2\pi n}{d}r^d\right)-\frac{4(-1)^{n+1}r_0}{d}P\left(\frac{2\pi n}{d}r^d\right), \tag{A3}$$

where C_1 and C_2 are arbitrary coefficients, and $K_0(x)$ and $P(x)$ are defined after Eq. (18) and via Eq. (19). The function $P(x)$ is presented graphically in Fig. 5. When x tends to infinity it tends to zero as $1/x^3$. The function diverges at $x=0$ as $-1/x$.

To determine the coefficients C_1^n and C_2^n the boundary conditions have to be used. The Bessel function $I_0(x)$ tends to infinity when x tends to infinity, while the amplitudes $A_n(r^d)$ have to tend to zero in this limit. Consequently $C_1^n=0$.

From Eqs. (16) and (17) it follows that

$$\sum_{n=1}^{\infty}A_n(r^0)\sin\left(\frac{2\pi n}{d}z^d\right)=0. \tag{A4}$$

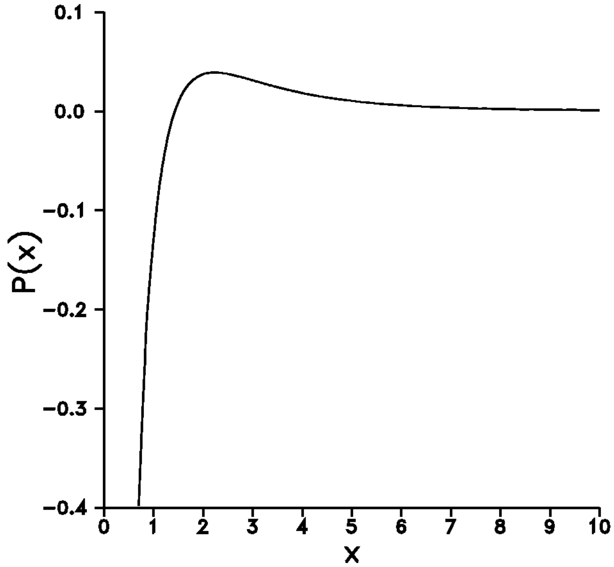

FIG. 5. Graphical presentation of the function $P(x)$ from Eq. (19).

Consequently, $A_n(r_0)=0$. The calculation of the coefficient C_2^n in a way assuring this requirement gives for the amplitudes $A_n(r^d)$ the expression presented by Eq. (18).

APPENDIX B: FIELDS AND FORCES ON THE SURFACE OF THE CHANNEL

Without loss of generality we will consider a point of the channel with cylindrical coordinates $(r_0,0,z^d)$. The Maxwell tensors $\mathsf{T}^{ch,d}$ and $\mathsf{T}^{ch,w}$ when approaching the point from the side of the dielectric and the side of the electrolyte are

$$\mathsf{T}^{ch,d}=\varepsilon_d\begin{pmatrix}\frac{1}{2}\{[E_r^d(r_0,z^d)]^2-[E_z^d(r_0,z^d)]^2\} & 0 & E_r^d(r_0,z^d)E_z^d(r_0,z^d)\\ 0 & -\frac{1}{2}\{[E_r^d(r_0,z^d)]^2+[E_z^d(r_0,z^d)]^2\} & 0\\ E_r^d(r_0,z^d)E_z^d(r_0,z^d) & 0 & -\frac{1}{2}\{[E_r^d(r_0,z^d)]^2-[E_z^d(r_0,z^d)]^2\}\end{pmatrix} \tag{B1}$$

and

$$\mathsf{T}^{ch,w}=\varepsilon_w\begin{pmatrix}\frac{1}{2}[E_z^d(r_0,z^d)]^2 & 0 & 0\\ 0 & -\frac{1}{2}[E_z^d(r_0,z^d)]^2 & 0\\ 0 & 0 & -\frac{1}{2}[E_z^d(r_0,z^d)]^2\end{pmatrix}, \tag{B2}$$

where $E_r^d(r_0,z^d)$, $E_z^d(r_0,z^d)$, and $E_z^w(r_0,z^d)$ are defined by Eqs. (24) and (22).

Using Eq. (20) and the approach described after that equation, we calculated the radial component $f_r(r_0,z^d)$ of the force density acting on this point. The final result is

$$f_r(r_0,z^d)=\frac{1}{2}(\varepsilon_w-\varepsilon_d)\{[E_z^d(r_0,z^d)]^2\}+\frac{1}{2}\varepsilon_d\{[E_r^d(r_0,z^d)]^2\}. \tag{B3}$$

In this way, Eq. (26) is deduced.

For narrow cylindrical channels with $r_0 \ll d$ the resistance $\mathcal{R}^0_{ch}(r_0)$ from Eq. (12) is

$$\mathcal{R}^0_{ch}(r_0)=\frac{\rho}{\pi}\frac{d}{(r_0)^2}. \tag{B4}$$

In this limit the quantity $l(r_0)$ from Eq. (13) is expressed via r_0 and d as

$$l(r_0)\approx\frac{(r_0)^2}{d}. \tag{B5}$$

The integration of $f_r(r_0,z^d)$ on the surface of the membrane permits to obtain the general force $F^{ch}(r_0)$ as this is done in Eq. (27). Using Eq. (B5), the result of the integration is

$$F^{ch}(r_0)=\frac{\pi r_0}{d}(\varepsilon_w-\varepsilon_d)(U_0)^2+\pi\varepsilon_d r_0\int_{-d/2}^{d/2}[E_r(r_0,z^d)]^2 dz^d. \tag{B6}$$

We denote with $g(r_0/d,z^d/d)$ the function:

$$g\left(\frac{r_0}{d},\frac{z^d}{d}\right)=\frac{z^d}{r_0}-\frac{4\pi r_0}{d}\sum_{n=1}^{\infty}\times\left\{(-1)^{n+1}n\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_1\left(\frac{2\pi n}{d}r_0\right)-P'\left(\frac{2\pi n}{d}r_0\right)\right]\sin\left(\frac{2\pi n}{d}z^d\right)\right\}. \tag{B7}$$

Let $I(r_0/d)$ be defined in the following way:

$$I\left(\frac{r_0}{d}\right)=\frac{4(r_0)^3}{d^4}\int_{-d/2}^{d/2}\left[g\left(\frac{r_0}{d},\frac{z^d}{d}\right)\right]^2 dz^d. \tag{B8}$$

Then $F^{ch}(r_0)$ from Eq. (B6) can be presented in the following way:

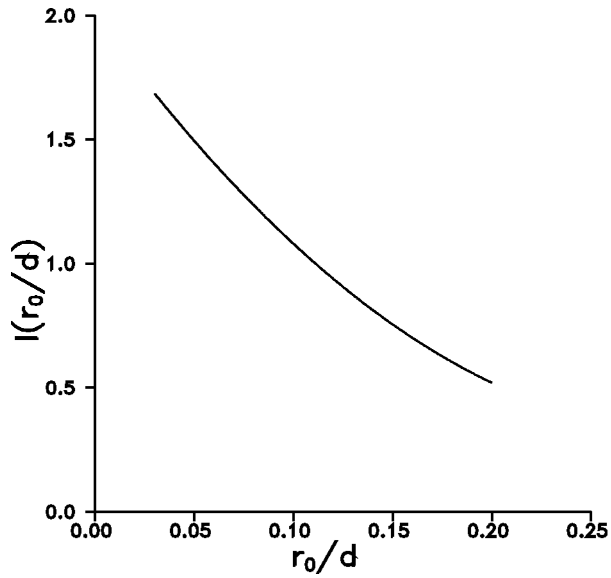

FIG. 6. Graphical presentation of the function $I(r_0/d)$ from Eq. (B8).

$$F^{ch}(r_0)=\frac{\pi r_0}{d}(\varepsilon_w-\varepsilon_d)(U_0)^2+I\left(\frac{r_0}{d}\right)\frac{\pi r_0}{4d}\varepsilon_d(U_0)^2. \tag{B9}$$

The thickness of the lipid bilayer is of the order of 40 Å. The radius of the channel must be at least several times the dimension of one water molecule. The minimal radii of the water channel, reported in the literature, are of the order of 1.3 Å [33]. Consequently in all the realistic cases the value of the ratio r_0/d is superior to 0.03. The numerically calculated values of the function $I(r_0/d)$ for values of its argument, belonging to the interval (0.03–0.2), are presented in Fig. (6). They are of the order of 1, and the function $I(x)$ can

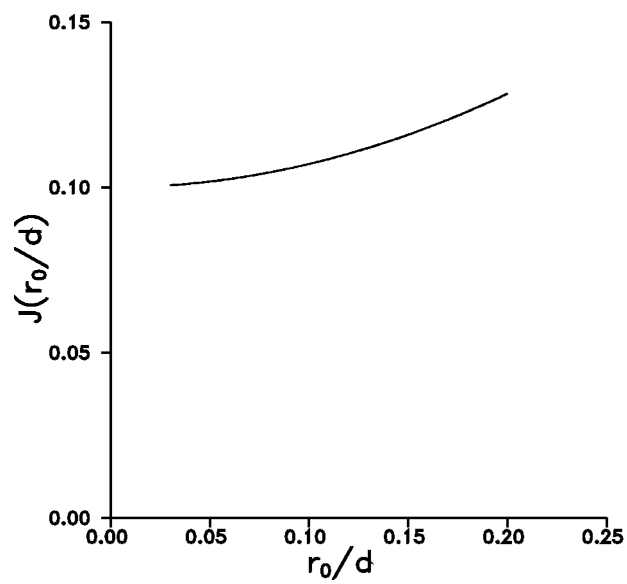

FIG. 7. Graphical presentation of the function $J(r_0/d)$ from Eq. (C5).

be fitted in this interval of values of its argument x by the quadratic polynomial:

$$I(x) = 2.0 - 11x + 18x^2. \tag{B10}$$

Replacing $I(r_0/d)$ in Eq. (B9) with the mean value α of this function, we obtain Eq. (28).

APPENDIX C: FIELDS AND FORCES ON THE SURFACE OF THE MEMBRANE OUT OF THE CHANNEL

Without a loss of generality we consider a point of the boundary of the membrane on its surface out of the channel, to the side of the positive electrode with cylindrical coordinates $(r^d, 0, d/2)$, $r^d > r_0$. The electric field around this point in the electrolyte and in the dielectric are given by Eqs. (29) and (30). The Maxwell tensors when approaching the point from the side of the dielectric, $\mathsf{T}^{s,d}$ and from the side of the electrolyte, $\mathsf{T}^{s,w}$, are

$$\mathsf{T}^{s,d} = \varepsilon_d \begin{pmatrix} \frac{1}{2}\left\{\left[E_r^d\left(r^d,\frac{d}{2}\right)\right]^2 - \left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2\right\} & 0 & E_r^d\left(r^d,\frac{d}{2}\right)E_z^d\left(r^d,\frac{d}{2}\right) \\ 0 & -\frac{1}{2}\left\{\left[E_r^d\left(r^d,\frac{d}{2}\right)\right]^2 + \left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2\right\} & 0 \\ E_r^d\left(r^d,\frac{d}{2}\right)E_z^d\left(r^d,\frac{d}{2}\right) & 0 & -\frac{1}{2}\left\{\left[E_r^d\left(r^d,\frac{d}{2}\right)\right]^2 - \left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2\right\} \end{pmatrix} \tag{C1}$$

and

$$\mathsf{T}^{s,w} = \varepsilon_w \begin{pmatrix} \frac{1}{2}\left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2 & 0 & 0 \\ 0 & -\frac{1}{2}\left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2 & 0 \\ 0 & 0 & -\frac{1}{2}\left[E_z^d\left(r^d,\frac{d}{2}\right)\right]^2 \end{pmatrix}. \tag{C2}$$

Using Eq. (20) and the approach described after that equation we calculated the radial component $f_r(r^d, d/2)$, of the force density acting on this point. The final result is

$$f_r\left(r^d,\frac{d}{2}\right) = -\varepsilon_d E_r^d\left(r^d,\frac{d}{2}\right)E_z\left(r^d,\frac{d}{2}\right). \tag{C3}$$

Using Eqs. (C3) and (B5), the force F_0^s from Eq. (33) can be presented in the form

$$F_0^s(r_0) = -\varepsilon_d (U_0)^2 \frac{\pi r_0}{d^2}\int_{r_0}^{\infty} \frac{(r_0)^2}{(r^d)^2}\left(1 - \frac{r_0}{d}\left\{\frac{r_0}{r^d} - \frac{4\pi r_0}{d}\sum_{n=1}^{\infty} n\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_0\left(\frac{2\pi n}{d}r^d\right) - P\left(\frac{2\pi n}{d}r^d\right)\right]\right\}\right)dr^d. \tag{C4}$$

We denote with $J(r_0/d)$ the following integral

$$J\left(\frac{r_0}{d^2}\right) = -\frac{4\pi^2 r_0}{d}\int_{r_0}^{\infty}\left(\frac{r_0}{r^d}\right)^2\left\{\sum_{n=1}^{\infty} n\left[\frac{P\left(\frac{2\pi n}{d}r_0\right)}{K_0\left(\frac{2\pi n}{d}r_0\right)}K_0\left(\frac{2\pi n}{d}r^d\right) - P\left(\frac{2\pi n}{d}r^d\right)\right]\right\}dr^d. \tag{C5}$$

Repeating the estimations of the preceding Appendix, we calculated numerically the value of this integral in the interval $0.03 \leqslant r_0/d \leqslant 0.2$. The results are presented on Fig. 7. In this interval the values of $J(r_0/d)$ are of the order of 0.1 and can be fitted by a polynomial of second degree:

$$J(x) = 0.10 + 0.71x^2. \tag{C6}$$

Doing in Eq. (C4) the integration with respect to r^d and replacing $J(r_0/d)$ with some mean value β, we obtain Eq. (34).

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