

Electrostriction of dry films of purple membranes and their piezoelectric effect

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Introduction

Specific membrane proteins can be considered as molecular machines converting the electronic excitation energy into other forms convenient for utilization in multiple enzymatic reactions or in active ion pumping and signal transduction [1, 2]. Membranes containing proteins are, as a rule, asymmetric, since electric dipole moments (polarization) are inherent for proteins. Bacteriorhodopsin (BR) is one of the simplest examples of such proteins performing active transmembrane proton pumping [3]. Knowledge of the structural organization of the BR with less than 3 Å resolution (see for instance [4 – 7]) enables to relate the details in structural changes to the intermediate states in proton translocation from the intracellular to extracellular sides of the membrane. Spectroscopically these intermediates are well defined; their sequential evolution from one to another arranged in a photocycle has been demonstrated. However, despite a large number of experimental data collected during more than two decades of investigations of the relationship between the structure and function of BR [8, 9], the detailed mechanism of proton pumping in BR is not fully elucidated yet. Due to the proton translocation during this photocycle of BR, the electrogenicity of the intermediates was determined or postulated under various external conditions [8, 10, 11].

The active transport of protons in BR and the increase of the electric conductivity of the purple membranes (PM) stimulated by light are usually considered as separate phenomena not related to each other on the common physical ground. The conductivity problem is in general more complex since in addition to the proton transfer via the intermediate states it can also be sensitive to the reorganization of internal charged groups and dipoles present in the membrane. BR rapidly reacts to the external electric field, which causes deformation of the protein as it was recently demonstrated by the atomic force microscope [12, 13]. There has been shown that the protein dynamics initiated by light consists of the initial increase of the volume of the protein and a subsequent decrease of it on the microsecond/millisecond timescale. These changes of the volume are also related to the local structural changes in the vicinity of the proton translocation path resulting in more favorable arrangement of the protein for the proton transfer [14, 15]. According to our suggestions based on the studies of the piezoelectric effect of PM [16, 17, 18] such a protein dynamics (local as well as global) could be a determining factor of the driving force for the proton

pumping. However, the origin of piezoelectricity of BR still remains unclear.

Discussion of the origin of the driving force of the proton translocation across the membrane is the main issue of this paper. On the basis of the data presented here it is shown that the piezoelectricity can be attributed to the electrostriction of the films.

Materials and Methods

Non-oriented films of purple membranes (PM) of *Halobacterium salinarium* were produced by dropping the PM suspension on the rotating glass tray covered with the layer of SnO₂. Oriented PM films containing BR were electrophoretically precipitated on a glass plate coated with the same SnO₂ layer according to the standard procedure [19]. The voltage generated by the actinic light ($\lambda=570$ nm, illumination intensity around 400 W/m²), is about 5 to 15 V depending on a particular PM film. This variation is attributed to the differences in the degree of orientation of PM's in various films and thus can be used for the estimation of the latter value.

The load resistance of the potential measuring equipment was chosen to be 10¹² Ω. The thickness of the film was estimated from the optical density (D) using the relation $D = n\kappa d$, where n is the molar concentration of chromophores, κ is the extinction coefficient ($\kappa=6.3 \cdot 10^3$ m²/M for BR at 570 nm) and d is the thickness of the film. By substituting the concentration n (calculated as the inverse of the BR molecule volume divided by the Avogadro number) it can easily be shown that the thickness of the film with the optical density of 2 optical units is ≈ 14 μm. The optical density of the film was adjusted to $D \approx 2$ optical units by repeatedly dropping the suspension and drying it layer by layer.

For measuring the electromechanical response of PM films, a home-built setup schematically shown in Fig. 1, was used. The AC voltage from the oscillator producing the 1.2 MHz harmonic signal $U_{1\omega}$ with the amplitude U_{10} (less than 2V) was applied on the film. The DC voltage source is also applied for the generation of the bias signal U_0 in the interval from –80 to 80 V. The positive sign of the voltage is attributed to the positive electrode to be connected with the external side of the membrane (see Fig.1). The harmonic deformation S_{ω} of the film resulted from electrostriction or piezoelectricity [18] was directed by the glass waveguide to the BaTiO₃ piezoelectric transducer (PET) with the resonance frequency equal to

that of the external harmonic signal, i. e. 1.2 MHz. Static (time-independent) deformations of the PM film have no influence on the PET.

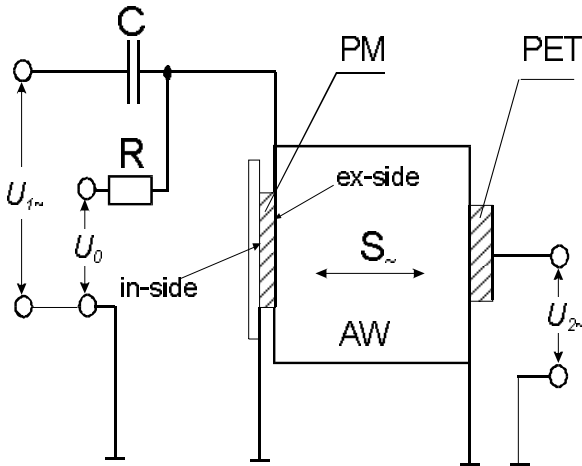


Fig.1. Experimental setup. PM – the film of dry purple membranes with electrodes connected to the surfaces, AW – acoustic waveguide, PET – BaTiO₃ piezoelectric transducer. AC voltage $U_{1\sim}$ is imposed on the sample via the capacitor C (100 pF). Bias voltage U_0 is connected to the resistor R (100 kΩ). The response to the external electric field is obtained as $U_{2\sim}$.

To improve the acoustic contact between the film and the waveguide the latter was moistened with transformer oil. The BaTiO₃ transducer is sensitive to the longitudinal acoustic modes and generates the electric signal $U_{2\sim}$. The DC voltage U_0 generates static deformation, which has no influence on the PET. However, by changing U_0 it is possible to scan volt-deformation characteristic of the film. If this characteristic is non-linear, the transfer function of the AC signal

$$k_{1\rightarrow 2}(U_0) = \frac{U_{20}}{U_{10}} \quad (1)$$

is dependent on the DC voltage U_0 . Here U_{20} denotes the amplitude of the $U_{2\sim}$ signal and U_{10} is the amplitude of $U_{1\sim}$. From this dependence, volt-deformation characteristics of the film can be obtained using the following arguments.

By imposing both the DC (U_0) and AC ($U_{1\sim} = U_{10} \cos \omega t$) voltages, the resulting voltage creating the deformation $S = S(U)$ then is a sum of both these values, i. e. $U = U_0 + U_{1\sim}$. In the case of a small AC field ($U_{10} \ll U_0$) the amplitude of the deformation S_0 can be estimated as

$$S_0 = \left. \frac{dS}{dU} \right|_{U=U_0} U_{10}. \quad (2)$$

The latter relationship enables us to determine experimentally the derivative of the unknown deformation function at a fixed value of the applied voltage U_0 as a ratio S_0/U_{10} . Since the PET signal U_{20} is proportional to the deformation, i.e. $U_{20} \sim S_0$, considering also Eq. 1 and Eq. 2 we can derive the deformation function from the dependence of the transformation coefficient $k_{1\rightarrow 2}(U_0)$ on the bias voltage:

$$S(U_0) \sim \int k_{1\rightarrow 2}(U_0) dU_0 + const. \quad (3)$$

where the integration constant can be determined from the chosen boundary condition. The natural boundary condition in our case is to set the deformation equal to zero at the bias value where the transformation function is zero. Eq. 3 describes the general dependence of the deformation on the applied voltage; i.e. it defines the volt-deformation characteristic of the PM film.

Results

The dependence of the transformation function defined by Eq. 1 on the DC voltage U_0 is shown in Fig. 2 for oriented and non-oriented films of PM's.

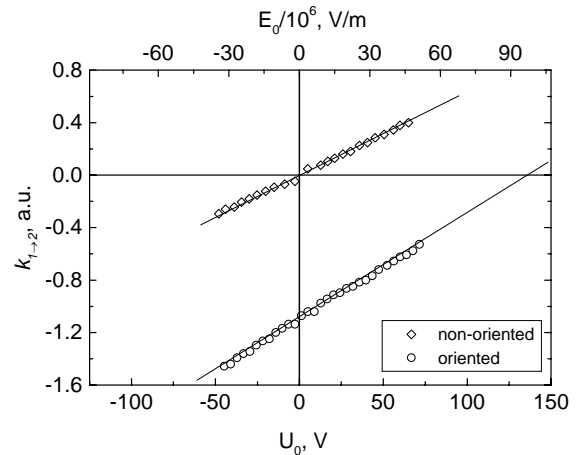


Fig. 2. The dependence of the electrical-to-acoustical transformation function in non-oriented and oriented PM films on the applied bias voltage U_0 . On the top axis, the values of the bias voltage are given recalculated into the cross-membrane electric field ($E_0 = U_0/d$)

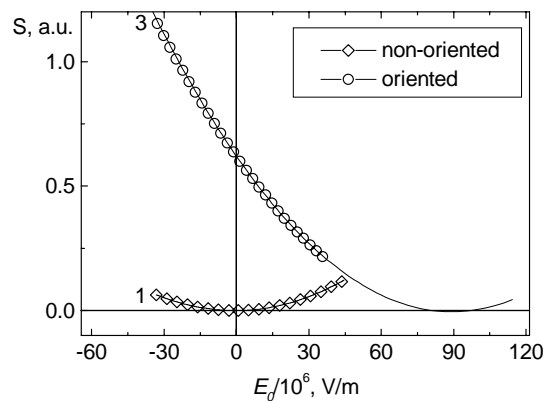


Fig. 3. Deformation of PM films with various degrees of orientation plotted as a function of the cross-membrane electric field

The phase difference of 180° between the input signal $U_{1\sim}$ and the detected signal $U_{2\sim}$ is reflected in the data by the minus sign of the transfer function. Evidently, at the values of the bias voltage, where the flip of this phase difference occurs, the transfer function is zero. The

position of this zero-crossing point on the U_0 axis depends on the degree of orientation of PM's and is well distinguished for non-oriented films. In the case of oriented films, this point could not be reached because it is at $U_0 > 100$ V, i.e. at values of the electric field higher than those where the electrical damage of the sample occurs. By integrating the experimentally obtained transfer function according to Eq. 3 and considering phase changes of the signal, the volt-deformation characteristic of the oriented and non-oriented PM films are obtained (see Fig.3).

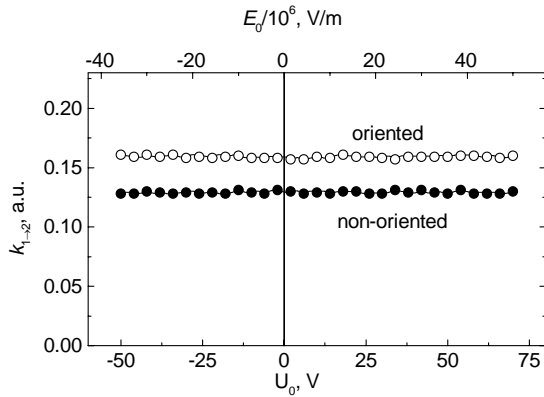


Fig. 4. Frequency doubling efficiency of PM films plotted as a function of the applied bias voltage. The top axis shows the bias values recalculated into the cross-membrane electric field

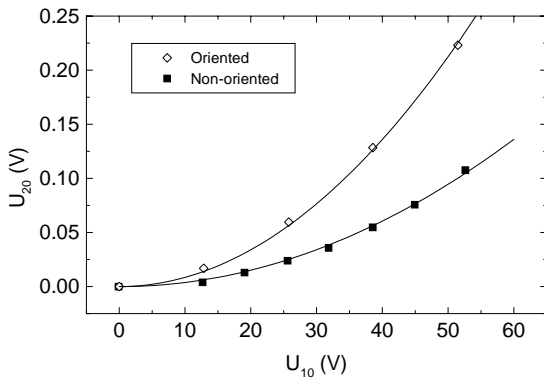


Fig. 5. The dependence of the second harmonic amplitude U_{20} on the amplitude of the input signal U_{10} . Solid lines show the fits of the measured datasets with parabolic functions

Since the measured signal $U_{2\sim}$ is proportional to the deformation of the film S_{\sim} , the results are presented in arbitrary units. It is noteworthy that the volt-deformation characteristic of non-oriented films is a parabolic function, symmetric with respect to the point $U_0 = 0$. From the comparison of the response of PM films with the known piezoelectric material (e.g., quartz crystal) the sign of the deformation can be determined. It shows that both positive and negative external fields create positive deformation (the thickness of the film decreases). The increase in the degree of PM orientation in the film changes the parabolic characteristic so that the minimum of the parabola is then

at some positive value of U_0 . For oriented films, however, this minimum is not reachable experimentally because of the electric damage of the sample.

Volt-deformation characteristics shown in Fig. 3 are evidently non-linear. This means that the sample can generate higher harmonics of the excitation signal. Therefore measurements directed to detect the second harmonics have been carried out. When the PM film is excited by the AC voltage $U_{1\sim}$ at 600 kHz, and PET is tuned to 1.2 MHz, the second harmonic signal is obtained as $U_{2\sim}$. For both types of the films, the ratio between amplitudes of the second harmonic (U_{20}) and the excitation signal (U_{10}) does not depend on U_0 (see Fig. 4), while the value U_{20} itself shows a quadratic dependence on the amplitude of the excitation signal U_{10} (see Fig. 5). The latter allows us to conclude that the volt-deformation characteristic is completely defined by the quadratic dependence on the external DC field. The difference between the oriented and non-oriented films can be attributed to the differences in electromechanical properties of these films.

Discussion

The quadratic dependence of the deformation in the measurements of the indirect piezoelectricity on the external electric field (see Fig. 3) can be explained in terms of the electrostriction effect which determines the electromechanical properties of BR. The change of the position of the minimum of volt-deformation parabola depending on the orientation degree of the films can be caused by the presence of the internal cross-membrane electric field. This is the basic concept which is used for the interpretations of the experimental data.

Electrostriction and inverse piezoelectric effect

The change of the position of the minimum of the transformation function on the U_0 (or E_0) axis depending on the degree of PM orientation (see Fig. 2) can be attributed to the internal electric field present in the PM. This field can result from the dipole moment of the BR molecule, or, in other terms, from the electric asymmetry of a separate purple membrane. In non-oriented films the internal electric fields from each single PM sheet compensate each other, resulting in the zero overall electric field, and, thus, the parabola shown in Fig. 3 is symmetric with respect to $E_0 = 0$. This compensation effect is evidently absent in orientated films and, consequently, the resultant electric field across the film is non-zero. The external DC voltage applied compensates this resultant electric field. In the experiment, this manifests itself as a shift of the corresponding parabola along the E_0 axis.

These observations can be understood in terms of electrostriction (see Appendix and [20] for details). Let us assume now that PM films compose a mixture of two fractions characterized by different (opposite to each other) orientations of the resultant electric field with

respect to the external field. Then the resulting electric field in the film can be determined as follows:

$$E = E_0 + E_{1\sim} + \alpha E_m - (1 - \alpha)E_m \quad (4)$$

where E_m is the intrinsic electric field of a single membrane, α is the fraction of membranes in the film, oriented so that their electric field is directed along E_0 . The electric field $E_{1\sim} = U_{1\sim}/d$ created by the AC external voltage $U_{1\sim}$ can be written as: $E_{1\sim} = E_{10} \cos \omega t$. By substituting Eq. 4 into Eq. A.3 and neglecting time-independent terms that determine the static deformation (the latter is not registered by PET), the variable deformation can be determined as

$$S_{\sim} = \frac{\xi}{c} \left\{ [E_0 + (2\alpha - 1)E_m] E_{10} \cos \omega t + \frac{1}{2} E_{10}^2 \cos 2\omega t \right\} \quad (5)$$

where c is the elasticity of the PM and $\xi = \epsilon_0 \rho \frac{d\epsilon}{d\rho}$ is the electrostriction coefficient (see Appendix for exact definitions of ξ and c).

For non-oriented films $\alpha = 0.5$. Thus, by substituting this value into Eq. 5 it follows that

$$S_{\sim} = \frac{\xi}{c} \left(E_0 E_{10} \cos \omega t + \frac{1}{2} E_{10}^2 \cos 2\omega t \right), \quad (6)$$

i.e. the first harmonics of the deformation (as well as the transformation function $k_{1 \rightarrow 2}(U_0)$ according to its definition in Eq. 1) is proportional to the applied external field E_0 . It is evident that non-oriented films do not emit the first-harmonic acoustic waves when $E_0 = 0$. The phase difference between the excitation signal $E_{1\sim}$ and the deformation response S_{\sim} changes by 180° , when the direction of E_0 is changed, which is reflected in Eq. 6 as the change of the sign of the amplitude of the first harmonics. The second harmonics of the deformation (see Eq. 6) is independent on the applied external DC voltage U_0 (as well as E_0) as it is seen in Fig. 4. Eq. 6 also implies the quadratic dependence of the amplitude of the second harmonics of deformation on the amplitude of the excitation signal U_{10} , which is indeed observed (see Fig. 5).

The dependence of deformation on the electric field in PM's can be entirely described as a parabolic function (see Eq. 5). Considering the fact that the deformation is positive (the thickness of the film decreases) regardless of the direction of the external electric field, according to Eq. A.2 the electrostriction coefficient has to be positive ($d\epsilon/d\rho > 0$).

For oriented films, $\alpha = 1$ can be roughly assumed. In this case, the minimum of the first harmonics amplitude corresponds to the condition $E_0 = -E_m$, which means that the external DC voltage has to compensate for the internal cross-membrane electric field. Due to very high values of the latter, this minimum was not reached experimentally. However, by extrapolating the experimental data to the intersection point with the E_0 axis, the cross-membrane field can be determined. It was estimated to be equal to $E_m \approx -10^8$ V/cm. The minus sign means that the external (endoplasmic) surface of the PM has to be charged

negatively. The accuracy of the value of the cross-membrane field determined in this way depends entirely on how well PM's are oriented within the film. Imperfections in the orientation of PM films can lead to the underestimation of this value. Furthermore, in the absence of the external field E_0 , for the first harmonics of deformation Eq. 5 yields

$$S_{\sim} = \frac{\xi}{c} \cdot E_m E_{1\sim}. \quad (7)$$

This result demonstrates the relationship between the piezoelectricity and the electrostriction effect for the PM films with charged surfaces. The piezoelectric coefficient is then proportional to the value of the cross-membrane field.

General

Referring to the above considerations, piezoelectric properties of PM films shown in Figs. 1–6 can be understood as a result of i) electrostriction and ii) electric asymmetry of purple membranes. Thus, by taking into account Eq. 5, the following relationship of the first harmonics of deformation (generalization of Eq. 7) in the presence of the external electric field for the oriented films can be obtained:

$$S_{\sim} = \frac{\xi}{c} (E_m + E_0) E_{1\sim}. \quad (8)$$

Mechanical tension (T), deformation (S) and the electric field (E) are related by the equation of inverse piezoelectric effect:

$$T = cS - eE \quad (9)$$

Assuming that $T = 0$ in Eq. (9), the following relationship is obtained in the case of E is the alternating electrical field:

$$S_{\sim} = \frac{e}{c} E_{\sim}, \quad (10)$$

where c is elasticity and e is piezoelectric constant. By comparing Eq. 8 with Eq. 10, it follows, that

$$e = \xi (E_m + E_0), \quad (11)$$

i.e. the piezoelectric constant of oriented films of BR can be modulated by the external DC field E_0 .

Protein molecules are built of amino acids with different hydrophobic and hydrophilic properties. Polar (hydrophilic) amino acids have large dielectric susceptibility and electric conductivity as compared with the hydrophobic segments. Dry films consist of mono PM's. The model of inhomogeneous condensed medium where the dielectric constant depends on the deformation is proposed in order to explain the observed electrostriction of PM films and to interpret the deformation-induced charge transfer. By applying the composite matter approach to the films of PM's, the electrostriction coefficient for the oriented films can be determined according to Eq. 11, where:

$$\xi = \epsilon_0 \epsilon_1^{\theta_1} \epsilon_2^{\theta_2} \theta_1 \theta_2 \ln\left(\frac{\epsilon_1}{\epsilon_2}\right) \frac{c_1 - c_2}{c_2 \theta_1 + c_1 \theta_2}, \quad (12)$$

All parameters in Eq. 12 are defined in Appendix.

Conclusions

Considering piezoelectric properties of PM films revealed by the experiments presented in this study, we can conclude that the films of oriented PM's can (at least, theoretically) be used as electric-to-acoustic (and vice-versa) converter with a variable piezoelectric constant. This constant depends on the external DC field, which can be considered as the control parameter. Due to the fact that external illumination also changes cross-membrane field in PM (BR transfers the protons from the internal to the external side of the membrane), the control factor can also be the light.

Appendix.

The main expressions for electrostriction

Let us briefly describe the main standpoint of the electrostriction. The force f acting on the unit area of the dielectric medium in the electric field is determined by [20]:

$$f = -\frac{1}{2}\varepsilon_0 E^2 \nabla \varepsilon + \frac{\varepsilon_0}{2} \nabla \left(\rho \frac{d\varepsilon}{d\rho} E^2 \right), \quad (\text{A.1})$$

where ε_0 is the dielectric constant, ρ is the mass density of the film, ε is the dielectric susceptibility, E is the strength of the electric field inside the dielectric media. The first term results from the spatial inhomogeneity of the dielectric susceptibility. For the dielectric plate present in the electric field this force would appear at the separating boundary between the plate and its environment. The second term in Eq. A.1 is caused by the dependence of the dielectric susceptibility on the density of the material ρ . The integral of the second term over the whole volume of the dielectric body is zero so that this force cannot change the position of the body in space. However, this force causes the mechanical tension of the dielectric medium in the presence of the external electric field; this phenomenon is known as electrostriction. The density of electrostriction forces in the homogeneous medium is evenly distributed within the volume and in this sense this phenomenon is similar to the inverse piezoelectric effect. For one-dimensional plate, the mechanical tension T per surface unit can be calculated from Eq. A.1 as follows:

$$T = \frac{\varepsilon_0}{2} \rho \frac{d\varepsilon}{d\rho} E^2. \quad (\text{A.2})$$

This force of the mechanical stress is compensated by the hydro-dynamical pressure in fluids and gases, and by elasticity in solids.

According to the Hooke's law, $T = cS$, where c is the elasticity and S is the deformation. Then by using Eq. A.2 it follows that

$$S = \frac{\xi}{2c} E^2, \quad (\text{A.3})$$

where

$$\xi = \varepsilon_0 \rho \frac{d\varepsilon}{d\rho} \quad (\text{A.4})$$

is the so-called electrostriction coefficient. The positive sign of the deformation ($S > 0$) means the contraction of the dielectric plate, while in the opposite case ($S < 0$) it is expanded. Since this sign is independent of the direction of

the external electric field for the media characterized by $\frac{d\varepsilon}{d\rho} > 0$, the thickness decreases in the presence of the external electric field. Materials characterized by the negative electrostriction coefficient ($\frac{d\varepsilon}{d\rho} < 0$) expand in the electric field.

Electrostriction in the composite matter

The dielectric susceptibility of heterogeneous matter is dependent on its density. This can be demonstrated by using the following model of the composite material, which is constructed by small fragments of one material with the dielectric susceptibility ε_1 dispersed in the other material with the dielectric susceptibility ε_2 (see Fig. 6).

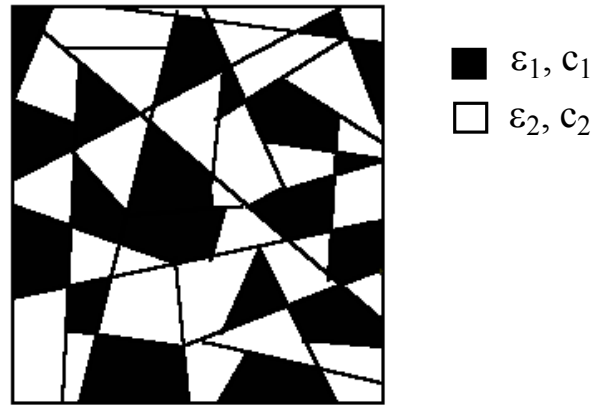


Fig. 6. The model of composite matter, consisting of two different fractions characterized by dielectric permeabilities ε_1 and ε_2 and elasticities c_1 and c_2

The total dielectric susceptibility then is expressed as follows [20]:

$$\varepsilon_{ef} = \varepsilon_1^{\frac{V_1}{V}} \varepsilon_2^{\frac{V_2}{V}}, \quad (\text{A5})$$

where V_1 and V_2 are the volumes of each component in the mixture and $V = V_1 + V_2$ is the total volume of the

mixture. To calculate the derivative $\frac{d\varepsilon_{ef}}{dV}$, we use

Hooke's law. For the inhomogeneous medium $T_1 = c_1 \frac{dV_1}{V_1}$ and $T_2 = c_2 \frac{dV_2}{V_2}$ determine the Hooke's law

for each of the component, where c_1 and c_2 are the elasticity moduli of the respective components of the medium. Under the conditions of equilibrium, the mechanical tension is constant within the whole volume of the material, i. e. $T_1 = T_2$. Thus, the additional conditions

that allow us to calculate the derivative $\frac{d\varepsilon_{ef}}{dV}$ are as follows:

$$c_2 \frac{dV_2}{V_2} = c_1 \frac{dV_1}{V_1}, \quad V = V_1 + V_2, \quad (\text{A6})$$

and the full derivative is:

$$\frac{d\varepsilon_{ef}}{dV} = \frac{1}{V} \varepsilon_1^{\theta_1} \varepsilon_2^{\theta_2} \theta_1 \theta_2 \ln\left(\frac{\varepsilon_1}{\varepsilon_2}\right) \frac{c_2 - c_1}{c_2 \theta_1 + c_1 \theta_2}, \quad (\text{A7})$$

where $\theta_1 = \frac{V_1}{V}$ and $\theta_2 = \frac{V_2}{V}$ are the relative volumes of different components of the composite material.

By using the definition $\rho = \frac{m}{V}$ we obtain that

$$\frac{dV}{V} = -\frac{d\rho}{\rho}. \quad \text{Thus, multiplying both sides by } \varepsilon_0 \text{ and}$$

using Eqs. A4 and A7, we obtain the following relationship:

$$\xi = \varepsilon_0 \varepsilon_1^{\theta_1} \varepsilon_2^{\theta_2} \theta_1 \theta_2 \ln\left(\frac{\varepsilon_1}{\varepsilon_2}\right) \frac{c_1 - c_2}{c_2 \theta_1 + c_1 \theta_2}. \quad (\text{A8})$$

This expression shows that the electrostriction of the composite medium in the electric field can manifest itself as piezoelectricity, if the elasticities and dielectric permeabilities of different components are different, i. e. $\varepsilon_1 \neq \varepsilon_2$ and $c_1 \neq c_2$.

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Sausų purpurinių membranų plėvelių elektrostrikiacija ir jų pjezoelektrinis efektas

Reziumė

Tirtos sausų purpurinių membranų plėvelių pjezoelektrinės savybės. Elektroakustinio keitiklio, sukurto iš šių plėvelių, generuojamų akustinių bangų amplitudė priklauso nuo išorinio nuolatinio elektrinio lauko bei plėvelių orientacijos laipsnio. Neorientuotoms plėvelėms perdavimo koeficiento priklausomybė nuo išorinio elektrinio lauko yra tiesinė ir simetriška nulinio atžvilgiu; nesant išorinio elektrinio lauko, akustinės bangos negeneruojamos. Orientuotose plėvelėse šis simetrijos taškas yra pasislinkęs priklausomai nuo plėvelių orientacijos laipsnio. Išorinis apšvietimas taip pat gali valdyti keitiklio parametrus, keisdamas transmembraninį elektrinį lauką. Pateiktas purpurinių membranų plėvelių elektroakustinio keitiklio veikimo modelis, paremtas elektrostrikiacijos reiškiniu.

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