Shear Deformation of the Spherical Shell Acted on by an External Alternating Electric Field: Possible Applications to Cell Deformation Experiments

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Shape deformation of the thin, area non-compressible spherical shell separating two different media, subjected to an external, alternating, homogeneous electric field is considered. The function relating shape deformation of the shell to the shear stress in its plane is presented. Shear stress develops as a result of Maxwell stress acting on both shell surfaces. All media are considered as lossy. The theoretical model predicts that the shear stress reaches its maximal value at the shell "equator" in relation to the field direction. The magnitude of the shear stress depends on the strength and frequency of the electric field, on the geometric parameters of the shell, and on the electric parameters of the system studied.

The foregoing was applied to an analysis of cell deformation, *e.g.*, an erythrocyte in an electric field. The analysis predicts that the maximal shear stress in the membrane develops at field frequencies close to $f = 10^7$ Hz. This is comparable to the electrocompression stress of the same membrane, maximal at the cell "pole". At lower frequencies, compression predominates over shear stress.

Introduction

The technique of measuring cell deformation in a periodic electric field was recently applied to evaluation of rheological properties of cells and cellular membranes [1–7]. Theoretical analysis, following experimental observations, was based on evaluation of electric stresses and deformation of the membrane, treated as a thin spherical or elipsoidal shell surrounding the internal medium [8, 9].

In a previously published analysis [10] deformations and stresses in the shell were averaged over a volumetrically homogeneous and isotropic shell, hence simplyfying real membrane structure. In the present study, area homogeneity and isotropy of the shell is assumed and an analytical solution of the distribution of deformations and stresses in the shell is proposed. This analysis is based on equilibrium equations for a thin spherical shell, where the electric part is described by a Maxwell stress tensor in lossy medium. Deformation is related to stress by the constitutive equation defining shear elastic response in the plane of the shell. This theoretical model can be applied to analysis of deformation of such experimental models as large unilamellar vesicles, as well as, roughly spherical living cells.

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Theoretical model

Infinitesimal deformations of the thin spherical shell separating the internal and external media and subjected to an external, homogeneous, alternating electric field were considered. R denotes mean shell radius, and d is shell thickness.

In a proposed mechanical model the shell was treated as area homogeneous, isotropic, non-compressible, elastic body. External and internal media were treated as homogeneous isotropic, weakly compressible, non-viscous liquids. In a respective electrical model all media were considered as electrically homogeneous, isotropic and characterized by conductive properties of non-piezoelectric lossy dielectrics. Zero volumetric density of free charge was assumed. Variations in shell dielectric permeability, resulting from shape deformation, and stress arising from the magnetic field, were neglected. The behaviour of the system was described on a time scale greatly exceeding the reciprocal of the electric field frequencies, and so deformations and stresses were averaged over the field period. Deformation was analyzed taking into account displacement of points situated at a mid-distance between both, non-deformed shell surfaces. Consequently, the system of spherical coordinates r, ϑ, φ, was chosen, where the surface including initial position of points subjected to analysis is described by the equation $r = R$. In this system of coordinates ϑ is the angle between a given shell site and the field direction. Then, due to rotational symmetry, the description of a given situation is independent of φ.

The equation for a deformed shell is of the vectorial form

$$\vec{r}_{def} = R\,\vec{e}_r + u_r\,\vec{e}_r + u_\vartheta\,\vec{e}_\vartheta \tag{1}$$

where $\vec{r}_{def}$ is the position vector for sites in the deformed shell, u_r, u_ϑ are radial and tangential resultants of the displacement vector, respectively, $\vec{e}_r$, $\vec{e}_\vartheta$ are radial and tangential versors in a system of spherical coordinates. Therefore the goal of the study, shape determination of the deformed shell, reduces to determination of the u_r and u_ϑ constituents of the displacement vector. They are related to components of the shell deformation tensor, ε_{ij}, by following relations

$$\begin{aligned} \varepsilon_{\vartheta\vartheta} &= \frac{1}{R}\frac{\partial}{\partial\vartheta}u_\vartheta + \frac{1}{R}u_r \\ \varepsilon_{\varphi\varphi} &= \frac{1}{R}\operatorname{ctg}(\vartheta)u_\vartheta + \frac{1}{R}u_r. \end{aligned} \tag{2}$$

Constituents $\varepsilon_{\vartheta\vartheta}$, $\varepsilon_{\varphi\varphi}$ allow for description of two types of deformation in the shell plane: due to pure shear, ε_s, and to uniform extension, ε_d.

The following notations were used

$$\begin{aligned} \varepsilon_s &= \frac{1}{2}(\varepsilon_{\vartheta\vartheta} - \varepsilon_{\varphi\varphi}) \\ \varepsilon_d &= \frac{1}{2}(\varepsilon_{\vartheta\vartheta} + \varepsilon_{\varphi\varphi}). \end{aligned} \tag{3}$$

The expression $\varepsilon_{\vartheta\vartheta} + \varepsilon_{\varphi\varphi}$ denotes relative alterations in the shell area. In a case of area non-compressible shell

$$\varepsilon_d = 0. \tag{4}$$

Deformation results from the shell internal stress, characterized by mechanical stress tensor in the shell, σ_{ij}. Similarly, its components $\sigma_{\vartheta\vartheta}$, $\sigma_{\varphi\varphi}$ allow for the description of two types of stress in a shell plane: shear stress, σ_s, and extension stress, σ_d.

Use was made of the following expressions

$$\begin{aligned} \sigma_s &= \frac{1}{2}(\sigma_{\vartheta\vartheta} - \sigma_{\varphi\varphi}) \\ \sigma_d &= \frac{1}{2}(\sigma_{\vartheta\vartheta} + \sigma_{\varphi\varphi}). \end{aligned} \tag{5}$$

Based on the assumption of area elasticity and isotropy of the shell, the constitutive equation relating shear deformation, ε_s, to shear stress, σ_s, is of the form

$$\varepsilon_s = \frac{1}{2\mu}\sigma_s \tag{6}$$

where μ is the elastic shear modulus in a plane of the shell. In an external homogeneous electric field, as shown in Appendix 1

$$\sigma_s = \sigma_s^{extr}\sin^2(\vartheta) \tag{7}$$

where σ_s^{extr} is an extremal magnitude of shear stress, depending on the frequency and intensity of the electric field, and on geometric and electric parameters of the system. According to Eqns. (1–4, 6, 7) the description of the shape of the deformed shell is of the form

$$\vec{r}_{def} = R\,\{1 + \varepsilon_s^{extr}(3\cos^2(\vartheta) - 1)\}\,\vec{e}_r - R\,\varepsilon_s^{extr}\sin(2\vartheta)\,\vec{e}_\vartheta \tag{8}$$

where

$$\varepsilon_s^{extr} = \frac{1}{2\mu}\sigma_s^{extr} \tag{9}$$

is an extremal shear deformation in the shell plane.

By introducing

$$\begin{aligned} z &= \vec{r}_{def}(\vartheta = 0^\circ) \\ x &= \vec{r}_{def}(\vartheta = 90^\circ) \end{aligned} \tag{10}$$

where denotes vector length, one obtains, by virtue of (8)

$$\begin{aligned} \frac{z - R}{R} &= 2\,\varepsilon_s^{extr} \\ \frac{x - R}{R} &= -\varepsilon_s^{extr}. \end{aligned} \tag{11}$$

Relations (11) can be useful in the description of experimental results where deformation of the spherical shell is observed.

Discussion

The foregoing theoretical analysis is considered valid for the description of deformation of cells acted on by a periodic electric field. Two different approaches to this problem were previously presented. The first [8] identifies shape deformation of the cell with homogeneous area alterations, the other [9] assumes area non-compressibility of the membrane and relates shape alterations to the area shear deformation. It is easy to show that equations (11) are particular cases for the general relations of the form

$$\frac{z-R}{R} = \frac{1}{2}\left(\frac{\Delta A}{A}\right)_z + 2\varepsilon_s^{extr}$$
$$\frac{x-R}{R} = \frac{1}{2}\left(\frac{\Delta A}{A}\right)_x - \varepsilon_s^{extr} \tag{12}$$

where $\left(\frac{\Delta A}{A}\right)_z$, $\left(\frac{\Delta A}{A}\right)_x$ are relative alterations in membrane surface at sites with coordinate $\vartheta = 0°$, $\vartheta = 90°$, respectively. The relative alteration of the total cell surface $\frac{\Delta A}{A}$ can be presented in the form

$$\frac{\Delta A}{A} = \frac{2}{3}\frac{(z+2x-3R)}{R} = \frac{1}{3}\left(\frac{\Delta A}{A}\right)_z + \frac{2}{3}\left(\frac{\Delta A}{A}\right)_x. \tag{13}$$

It is evident that both types of membrane deformation can contribute simultaneously and equally to shape deformation. This fact escaped the attention of Bryant and Wolfe when they assumed in their analysis of cell deformation that $\varepsilon_s^{extr} = 0$ [8]. It follows from indetermined character of Eqns. (12, 13) that based on direct measurements of cell elongation in main directions ($\vartheta = 0°$, $\vartheta = 90°$) only relative alteration of the total cell area, $\frac{\Delta A}{A}$, can be determined, whereas local changes $\left(\frac{\Delta A}{A}\right)_z$, $\left(\frac{\Delta A}{A}\right)_x$ as well as shear deformation, ε_s^{extr}, can be determined unequivocally only when including further assumptions.

As established in the previous study [7], the relative alteration in the cell area $\frac{\Delta A}{A}$ is at least one order of magnitude lower than relative elongations $\frac{z-R}{R}$, $\frac{x-R}{R}$. For this reason the assumption $\left(\frac{\Delta A}{A}\right)_z$, $\left(\frac{\Delta A}{A}\right)_x = 0$ in Eqn. (12) seems valid and more useful than the condition $\varepsilon_s^{extr} = 0$. It corresponds to the assumption of area non-compressibility and is consistent with widely accepted model of a cellular membrane as a two-dimensional liquid-mosaic structure. As such it would be susceptible to shear deformation and resistant to extension.

For cells with the radius $R \cong 10^{-5}$ m the contribution of bending deformation to the total one [11, 12] can be neglected. The bending elasticity dominates shear elasticity in spherical objects with the radius $R < 10^{-7}$ m, only [13].

Equations describing relative extension of the shell in parallel, (z), and perpendicular, (x), directions to the external electric field (11) are identical with the equations describing homogeneous deformation of volumetrically non-compressible sphere to ellipsoid. Fig. 1 shows variations of the shell shape, initial radius R = 1 (a.u.), as a function of the magnitude of extreme shear deformation in a shell plane, ε_s^{extr}. In spite of similarities of both shapes, the shell deformation in an electric field is not homogeneous, as we assumed previously [10], therefore its shape (*cf.* Eqn. (8)) can not be simply described by the equation for an ellipsoid.

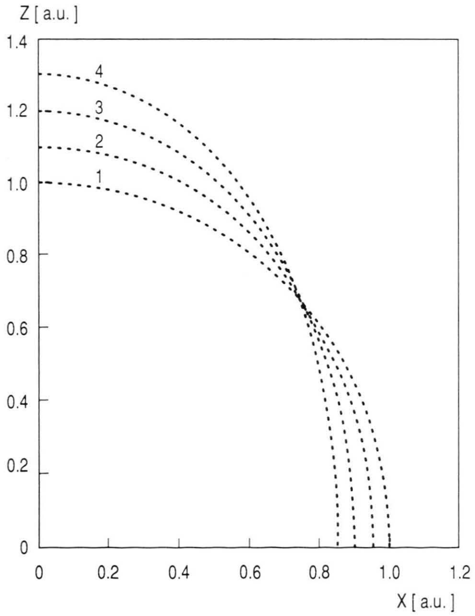

Fig. 1. Variations of cell shape as a function of the extreme shear deformation magnitude: 1, $\varepsilon_s^{extr} = 0$; 2, $\varepsilon_s^{extr} = 0.05$; 3, $\varepsilon_s^{extr} = 0.10$; 4, $\varepsilon_s^{extr} = 0.15$. z is the direction of the electric field.

It is pertinent to note that the measurements of the relative extension of the cell along electric field lines, $\frac{z-R}{R}$, expand the linear range of the deformation: stress relationship twice as much as analogous measurements perpendicular to the field direction; therefore the first are recommended in experiments.

Experimental determination of ε_s^{extr} opens two roads to investigations. First – knowledge of the external electric field intensity and frequency, and of the electric and geometric parameters of the system, allow determination of the extremal shear stress in the shell plane, σ_s^{extr}, and, when applying Eqn. (9) – for determination of the elastic shear modulus, μ. On the other hand, when μ is known, it is possible to estimate electric and geometric parameters of the system.

Another set of experiments seems plausibel, *e.g.* exploring the dependence of σ_s^{extr} on electric field frequency $f = \frac{\omega}{2\pi}$. The analytical model proposed above considers the full spectrum of forces and stresses in the shell. As shown below (Appendix 1) shear stress, σ_s^{extr}, is proportional to both normal, $(\Delta\sigma_{rr})^{var}$ and tangential, $(\Delta\sigma_{r\vartheta})^{var}$, stress increments and to the normal stress, $(\sigma_{rr})^{var}$, as well (14)

$$\sigma_s^{extr} = \frac{1}{4}\frac{(1+K)}{(1-K)}[(\Delta\sigma_{rr})^{var} - (\Delta\sigma_{r\vartheta})^{var}] + (\sigma_{rr})^{var}. \quad (14)$$

As an example, predictions for shear stress developed in the membrane of human red blood cells (Appendix 3) subjected to an alternating electric field were made. Based on proportionality of stress to vacuum dielectric permittivity (ε_o) and to the square of the electric field strength, (E_0^2), the stress was normalized relative to the electric field pressure in vacuum ($\bar{\sigma} = 4\sigma/\varepsilon_o E_0^2$).

The function sought for, shown in Fig. 2 (1, continuous line), can be devided tentatively into three domains: conductive, $f < 10^5$ Hz, dielectric, $f > 10^9$ Hz and intermediate. The dotted line (2) shows the same dependence calculated according to the theoretical approach of Engelhardt and Sackmann [9], which took into account the increment of normal stress only. The figure shows that application of the latter model is limited to frequencies $f > 10^7$ Hz.

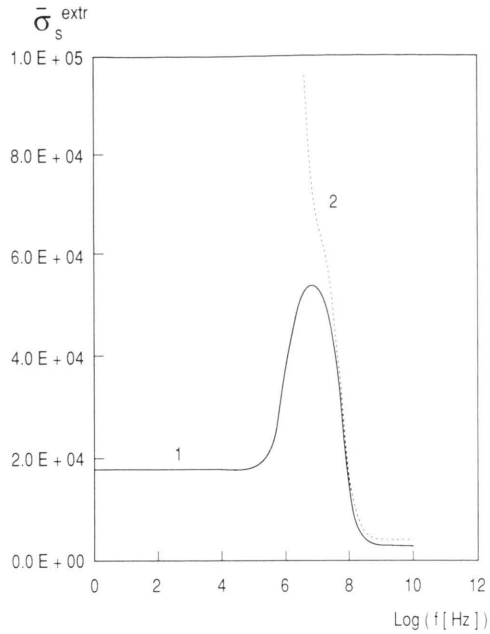

Fig. 2. Dependence of shear stress in a human red blood cell membrane on the frequency of an external periodic electric field. Presented model (1, continuous line), Engelhardt and Sackmann's model [9] (2, dotted line).

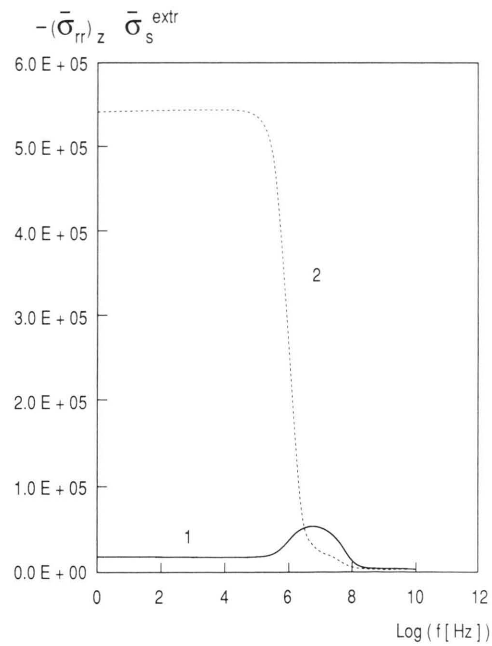

Fig. 3. Magnitude of shear and radial stresses in a human red blood cell membrane as a function of electric field frequency. Shear extreme stress (1, continuous line), and radial stress, calculated for the shell site with coordinate $\vartheta = 0°$ (2, dotted line).

The model presented above allows for comparison of contribution of shear stress and other stresses to the total stress imposed by the electric field. As an example, radial stress, $(\bar{\sigma}_{rr})_z = (\bar{\sigma}_{rr}^{con} + 2\,\bar{\sigma}_{rr}^{var})$, when $\overset{i}{p} = 0$ and $\overset{e}{p} = 0$, was considered in a shell site with coordinate $\vartheta = 0°$. The stress in question has a negative value and corresponds to normal compression of the shell. The results are shown on Fig. 3.

At low electric field frequencies, compression predominates and could be the main cause for experimentally observed electrodestruction of cellular membrane. The observed effects impede measurements of cell deformation, the more so in that shear stress and corresponding deformation decrease in this frequency range.

The model presented above is a follow-up to our previous approach [10] to the analysis of cell deformation provoked by an electric field. As our calculations show, for a given cell and under given conditions (*cf.* [7], p. 369) predictions of both models differ, albeit remaining in the same range of magnitude. We believe that the present model is based on more realistic assumptions, and as such should be recommended for analysis of experimental data. This work is going on in our laboratory.

To sum up, we have presented a theoretical model describing thin spherical shell deformation in an external alternating electric field. This model is an alternative to [8], and more general than that suggested in [9]. It can be useful in determinations of rheological, or electric and geometric, parameters of cellular membranes.

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Appendix 1

Shear stress in a plane of the shell, averaged over the electric field period

To determine shear stress, σ_s, analysis of stress distribution in a spherical shell was performed.

For forces acting on a shell subjected to an alternating electric field, and neglecting mass acceleration effects, Newton's second law can be presented in tensor form

$$\sum_{j=1}^{3} \frac{\partial}{\partial x_j} \sigma_{ij} + f_i^{el} = 0, \qquad (A\,1.1)$$

where σ_{ij} is a symmetric tensor of mechanical stress in the shell, f_i^{el} is the volumetric density of electric forces, x_j is the Cartesian coordinate of the deformed shell.

Assumptions about electric properties of the system (see text) allow for neglecting volumetric density of electric forces ($f_i^{el} = 0$). Then, under approximation for infinitesimal deformations, and for points situated in the middle of the shell thickness ($r = R$) equations (A 1.1), expressed in spherical coordinates r, ϑ, φ, become

$$\frac{\partial}{\partial r}\sigma_{rr} + \frac{1}{R}\frac{\partial}{\partial\vartheta}\sigma_{r\vartheta} + \frac{1}{R}[2\sigma_{rr} - (\sigma_{\vartheta\vartheta} + \sigma_{\varphi\varphi}) + \sigma_{r\vartheta}\mathrm{ctg}(\vartheta)] = 0$$
$$\frac{\partial}{\partial r}\sigma_{r\vartheta} + \frac{1}{R}\frac{\partial}{\partial\vartheta}\sigma_{\vartheta\vartheta} + \frac{1}{R}[3\sigma_{r\vartheta} + (\sigma_{\vartheta\vartheta} - \sigma_{\varphi\varphi})\,\mathrm{ctg}(\vartheta)] = 0. \quad (A\,1.2)$$

Under natural orientation of the system of coordinates, a description of the situation does not depend on the angular coordinate φ (see text).

According to definition,

$$\sigma_s = \frac{1}{2}(\sigma_{\vartheta\vartheta} - \sigma_{\varphi\varphi}). \quad (A\,1.3)$$

Shear stress, σ_s, can be calculated by solving the system of Eqns. (A 1.2) when constituents σ_{rr}, $\sigma_{r\vartheta}$ and their radial gradients $\frac{\partial}{\partial r}$ are determined.

In the case of a thin spherical shell, unknown constituents and their gradients can be substituted respectively for

$$\sigma_{rr} = \frac{\sigma_{rr}^{int} + \sigma_{rr}^{ext}}{2}$$
$$\sigma_{r\vartheta} = \frac{\sigma_{r\vartheta}^{int} + \sigma_{r\vartheta}^{ext}}{2}$$
$$\frac{\partial}{\partial r}\sigma_{rr} = \frac{\sigma_{rr}^{ext} - \sigma_{rr}^{int}}{d}$$
$$\frac{\partial}{\partial r}\sigma_{r\vartheta} = \frac{\sigma_{r\vartheta}^{ext} - \sigma_{r\vartheta}^{int}}{d}, \quad (A\,1.4)$$

where upper indexes denote points on the internal (int) and external (ext) surfaces of the shell, respectively, at a fixed angular coordinate ϑ.

By definition, stresses on the shell surface equal respective constituents of the area density of forces, $\vec{f}^{int}$, $\vec{f}^{ext}$, acting on internal and external shell surfaces, respectively.

$$\sigma_{rr}^{ext} = \vec{f}^{ext}\cdot\vec{e}_r$$
$$\sigma_{r\vartheta}^{ext} = \vec{f}^{ext}\cdot\vec{e}_\vartheta$$
$$\sigma_{rr}^{int} = -\vec{f}^{int}\cdot\vec{e}_r$$
$$\sigma_{r\vartheta}^{int} = -\vec{f}^{int}\cdot\vec{e}_\vartheta. \quad (A\,1.5)$$

In the presence of an electric field, conditions for force equilibrium on boundary surfaces can be presented as

$$\vec{f}^{int} = \left(\overset{s}{\Pi}_m - \overset{i}{\Pi}_m + \overset{i}{p}\delta\right)\cdot\vec{e}_r$$
$$\vec{f}^{ext} = \left(\overset{e}{\Pi}_m - \overset{s}{\Pi}_m - \overset{e}{p}\delta\right)\cdot\vec{e}_r \quad (A\,1.6)$$

where Π_m is Maxwell electric stress tensor, p is a constant pressure [14], δ is a unit tensor, i, s, e – upper indexes denote internal medium, shell and external medium, respectively.

In complex notation, where induction of the electric field $\vec{D} = \mathrm{Re}\{\varepsilon\vec{E}\,\exp(i_u\omega t)\}$ (see Appendix 2) constituents of the Maxwell stress tensor can be expressed as

$$(\Pi_m)_{ij} = \frac{1}{4}\mathrm{Re}\{\varepsilon\}\left[E_i^*E_j + E_iE_j^* - \left(\sum_{k=1}^{3}E_kE_k^*\right)\delta_{ij}\right]$$
$$(i, j = 1, 2, 3) \quad (A\,1.7)$$

where * denotes complex conjugation.

When the distribution of the electric field in a shell and in the surrounding medium is known. Eqns. (A 1.5–A 1.7) lead to relations of the form

$$\frac{\sigma_{rr}^{int} + \sigma_{rr}^{ext}}{2} = \sigma_{rr}^{con} + 2\sigma_{rr}^{var}\cos^2(\vartheta)$$
$$\frac{\sigma_{r\vartheta}^{int} + \sigma_{r\vartheta}^{ext}}{2} = 2\sigma_{r\vartheta}^{var}\sin(\vartheta)\cos(\vartheta)$$
$$\sigma_{rr}^{ext} - \sigma_{rr}^{int} = (\Delta\sigma_{rr})^{con} + 2(\Delta\sigma_{rr})^{var}\cos^2(\delta)$$
$$\sigma_{r\vartheta}^{ext} - \sigma_{r\vartheta}^{int} = 2(\Delta\sigma_{r\vartheta})^{var}\sin(\vartheta)\cos(\vartheta), \quad (A\,1.8)$$

where

$$\sigma_{rr}^{con} = -\frac{1}{2}(\overset{i}{p} + \overset{e}{p}) + \frac{1}{2}(\beta_1 + \beta_2)E_0^2$$
$$\sigma_{rr}^{var} = \frac{1}{4}(\alpha_1 + \alpha_2 + \gamma_1 + \gamma_2)E_0^2$$
$$\sigma_{r\vartheta}^{var} = -\frac{1}{4}(\alpha_1 + \alpha_2)E_0^2$$
$$(\Delta\sigma_{rr})^{con} = \overset{i}{p} - \overset{e}{p} + (\beta_2 - \beta_1)E_0^2$$
$$(\Delta\sigma_{rr})^{var} = \frac{1}{2}(\alpha_2 - \alpha_1 + \gamma_2 - \gamma_1)E_0^2$$
$$(\Delta\sigma_{r\vartheta})^{var} = -\frac{1}{2}(\alpha_2 - \alpha_1)E_0^2 \quad (A\,1.9)$$

and where

$$\alpha_1 = \frac{1}{2}\,\mathrm{Re}\{\overset{i}{\varepsilon}\}\,|\overset{i}{m}|^2 - \frac{1}{2}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,\left(|\overset{s}{m}|^2 + \mathrm{Re}\{\overset{s}{m}\overset{s}{n}{}^*\} - 2\,|\overset{s}{n}|^2\right)$$

$$\beta_1 = \frac{1}{4}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,|\overset{s}{m} - \overset{s}{n}|^2 - \frac{1}{4}\,\mathrm{Re}\{\overset{i}{\varepsilon}\}\,|\overset{i}{m}|^2$$

$$\gamma_1 = -\frac{9}{4}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,|\overset{s}{n}|^2 \qquad \text{(A 1.10)}$$

$$\alpha_2 = \frac{1}{2}\,\mathrm{Re}\{\overset{e}{\varepsilon}\}\,\left(1 + \mathrm{Re}\{\overset{e}{n}\} - 2\,|\overset{e}{n}|^2\right) - \frac{1}{2}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,\left(|\overset{s}{m}|^2 + \mathrm{Re}\{\overset{s}{m}\overset{s}{n}{}^*\}\,K^3 - 2\,|\overset{s}{n}|^2K^6\right)$$

$$\beta_2 = \frac{1}{4}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,|\overset{s}{m} - \overset{s}{n}\,K^3|^2 - \frac{1}{4}\,\mathrm{Re}\{\overset{e}{\varepsilon}\}\,|1 - \overset{e}{n}|^2$$

$$\gamma_2 = \frac{9}{4}\,\mathrm{Re}\{\overset{e}{\varepsilon}\}\,|\overset{e}{n}|^2 - \frac{9}{4}\,\mathrm{Re}\{\overset{s}{\varepsilon}\}\,|\overset{s}{n}|^2K^6$$

where E_0 is the real amplitude of the external electric field, K is the geometric parameter of a shell, $|\;\;|$ is a complex number modulus. Complex numbers n, m with upper indexes are coefficients of the field distribution, which depend on its frequency, on electric parameters of the system and on K. For details see Appendix 2.

In Eqns. (A 1.8), the constant part (con) and varying with angular coordinate ϑ part (var) (for $\vartheta = 45^\circ$) were separated from the mean stresses and from their radial increments.

Use is made of Eqns. (A 1.2–A 1.4, A 1.8) to obtain

$$\sigma_s = 2\sigma_s^{var}\sin^2(\vartheta) \qquad \text{(A 1.11)}$$

where shear stress in a plane of the shell, for $\vartheta = 45$, equals

$$\sigma_s^{var} = \frac{1}{2}\left\{\frac{(1+K)}{4(1-K)}\left[(\Delta\sigma_{rr})^{var} - (\Delta\sigma_{r\vartheta})^{var}\right] + (\sigma_{rr})^{var}\right\}. \qquad \text{(A 1.12)}$$

Extreme shear stress in a plane of the shell, σ_s^{extr} becomes

$$\sigma_s^{extr} = 2\sigma_s^{var} \qquad \text{(A 1.13)}$$

and is attained for shell points with angular coordinate $\vartheta = 90$.

Appendix 2

Electric field distribution

The description of an alternating electric field in lossy media makes use of complex notation, where induction of the electric field, $\vec{D}$, is in the form

$$\vec{D} = \mathrm{Re}\{\varepsilon\vec{E}\exp(i_u\omega t)\} \qquad \text{(A 2.1)}$$

where $\vec{E}$ is a complex electric field amplitude, ε is the complex dielectric permittivity of the medium, $\frac{\omega}{2\pi}$ is the field frequency, t is time, i_u is an imaginary unit, $\mathrm{Re}\{\;\}$ is the real component of a complex number.

In the electric model it is assumed that all media are homogeneous, isotropic and neutral, according to Maxwell's laws. For complex values, we can write

$$\mathrm{div}(\varepsilon\vec{E}) = 0 \qquad \text{(A 2.2)}$$

$$\mathrm{div}[(\sigma + i_u\omega\varepsilon)\vec{E}] = 0, \qquad \text{(A 2.3)}$$

where σ is the complex conductivity of the medium, $\mathrm{div} = \sum_{j=1}^{3}\frac{\partial}{\partial x_j}$.

Equation (A 2.3) gives the boundary conditions on a boundary between medium a and medium b in the form

$$\overset{a}{\xi}\,\overset{a}{\vec{E}}\cdot\vec{n} = \overset{b}{\xi}\,\overset{b}{\vec{E}}\cdot\vec{n}, \qquad \text{(A 2.4)}$$

where

$$\xi = \varepsilon - i_u\,\frac{\sigma}{\omega}, \qquad \text{(A 2.5)}$$

where $\vec{n}$ is a vector normal to the boundary surface.

Assuming homogeneity of the external electric field $\vec{E}_0$ considered far from the cell, or in the cell's absence, and assuming zero phase displacement, the complex field amplitude $\vec{E}_0$ is of the form

$$\vec{E}_0 = E_0\,\vec{e}_f \qquad \text{(A 2.6)}$$

where E_0 is the real amplitude of the external electric field $\vec{e}_f$ is a versor of the field direction.

In a system of spherical coordinates, r, ϑ, φ, (*cf.* Theoretical Model) solving equation (A 2.2) with boundary conditions (A 2.4) and condition at infinity (A 2.6) leads to the description of the distribution of the complex electric field amplitude in a shell and in the surrounding media in the vectorial form

$$\overset{\alpha}{\vec{E}} = \left(\overset{\alpha}{m} - \frac{\overset{\alpha}{N}}{r^3} \right) E_0 \vec{e}_{\mathrm{f}} + 3 \frac{\overset{\alpha}{N}}{r^3} \cos(\vartheta)\, E_0 \vec{e}_{\mathrm{r}} \quad \text{(A 2.7)}$$

where the upper index α denotes the respective medium.

Factors of field distribution, m, N, are of the form – internal medium $\left(r < R - \frac{d}{2} \right)$

$$\overset{\mathrm{i}}{m} = \frac{9}{(b_{\mathrm{is}} + 3)(b_{\mathrm{se}} + 3) + 2\, b_{\mathrm{is}} b_{\mathrm{se}} K^3}$$

$$\overset{\mathrm{i}}{N} = 0 \quad \text{(A 2.8)}$$

– shell $\left(R - \frac{d}{2} < r < R + \frac{d}{2} \right)$

$$\overset{\mathrm{s}}{m} = \frac{1}{3} (b_{\mathrm{is}} + 3)\, \overset{\mathrm{i}}{m}$$

$$\overset{\mathrm{s}}{N} = \overset{\mathrm{s}}{n} \left(R - \frac{d}{2} \right)^3 \quad \text{(A 2.9)}$$

$$\overset{\mathrm{s}}{n} = \frac{1}{3} b_{\mathrm{is}}\, \overset{\mathrm{i}}{m}$$

– external medium $\left(r > R + \frac{d}{2} \right)$

$$\overset{\mathrm{e}}{m} = 1$$

$$\overset{\mathrm{e}}{N} = \overset{\mathrm{e}}{n} \left(R + \frac{d}{2} \right)^3 \quad \text{(A 2.10)}$$

$$\overset{\mathrm{e}}{n} = \frac{1}{9} [(b_{\mathrm{is}} + 3) b_{\mathrm{se}} + b_{\mathrm{is}} (2\, b_{\mathrm{se}} + 3) K^3]\, \overset{\mathrm{i}}{m}$$

where

$$\mathrm{b}_{\alpha\beta} = \frac{\overset{\alpha}{\xi} - \overset{\beta}{\xi}}{\overset{\beta}{\xi}} \quad \text{(A 2.11)}$$

and geometric parameter of the shell, K, is the ratio of the internal to external radii

$$K = \frac{R - \frac{d}{2}}{R + \frac{d}{2}} \,. \quad \text{(A 2.12)}$$

Appendix 3

Electric and geometric parameters used for calculations of stresses developed in red blood cell membrane (taken from [9]).

$$\begin{aligned}
\mathrm{Re}\{\overset{\mathrm{i}}{\varepsilon}\} &= 60\ \ \varepsilon_o \\
\mathrm{Re}\{\overset{\mathrm{s}}{\varepsilon}\} &= 1.5\, \varepsilon_o \\
\mathrm{Re}\{\overset{\mathrm{e}}{\varepsilon}\} &= 80\ \ \varepsilon_o \\
\mathrm{Re}\{\overset{\mathrm{i}}{\sigma}\} &= 0.5 \left[\frac{S}{m} \right] \\
\mathrm{Re}\{\overset{\mathrm{e}}{\sigma}\} &= 0.02 \left[\frac{S}{m} \right] \\
\mathrm{Re}\{\overset{\mathrm{s}}{\sigma}\} &= Im\{\overset{\mathrm{i}}{\varepsilon}, \overset{\mathrm{s}}{\varepsilon}, \overset{\mathrm{e}}{\varepsilon}, \overset{\mathrm{i}}{\sigma}, \overset{\mathrm{s}}{\sigma}, \overset{\mathrm{e}}{\sigma}\} = 0 \\
\varepsilon_o &= 8.8542 \cdot 10^{-12} \left[\frac{F}{\mathrm{m}} \right] \\
R &= 4 \cdot 10^{-6}\, [m] \\
d &= 10^{-8}\, [m].
\end{aligned} \quad \text{(A 3.1)}$$