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INTERPRETATION OF ELECTROROTATION OF PROTOPLASTS

I. Theoretical considerations

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This paper contains the theoretical fundament of the rotation of protoplasts in high-frequency rotating electric fields (electrorotation). The protoplasts have to be calculated as three-shell spheres, considering their composition of vacuole, tonoplast, cell plasma, and plasmalemma. In contrast to the behaviour of single-shell bodies, the electrorotation spectrum indicates a rather complicated shape, depending on the dielectric properties of their compounds. This is demonstrated on theoretical rotation spectra which are calculated for typical parameters of protoplasts.

1. Introduction

Cells placed in a rotating high-frequency field start to spin in a rate which, however, is much slower than the frequency of the applied field (ELECTROROTATION). The reasons for this rotation are interactions between time-dependent polarizations of all dielectric constituents of the cell and the external electric field /1,3,4,7,10/. In order to understand the experimentally observed rotation of the cells against the spin direction of the electric field in the lower frequency range and the co-field spin at higher frequencies, one must consider at least a single-shell model, i.e. a dielectric surrounded by a single membrane /3,7,10,11/. In this case the electrorotation spectrum clearly indicates two resonance peaks (i.e. two characteristic frequencies) usually located in the kHz and in the MHz range, respectively. The first characteristic frequency depends mainly on electric membrane properties, whereas the second one reflects the parameters of the internal medium.

Both peaks were investigated experimentally on liquid filled glass spheres, erythrocytes and plant protoplasts /3,4,7/. The results of these experiments correspond to our theory.

Biological particles behaving like single-shell spheres are such cells the interior of which can be considered as being a more or less homogeneous electrolyte medium, surrounded by an isolating membrane. (For example unnucleated erythrocytes and to some extent even other animal cells as well as isolated vacuoles.)
In most cases, however, cells consist of more than two electrically separated phases, which influence the electrorotation.
From this point of view, cells without large organelles but, surrounded by a cell wall can be considered to be a double-shell sphere. Protoplasts with a central vacuole have to be regarded as three-shell spheres, consisting of a vacuole surrounded by the tonoplast (shell 1), the cytoplasm (shell 2) and the plasmalemma (shell 3). Finally, cells covered by a cell wall and containing also a large central vacuole are examples for a four-shell body /3/. Additionally, the electric double layers in cellular systems may be considered to be conductive shells too. Corresponding correlations, however, have shown that the influence of the double layers on the electrorotation of cells actually is very small and practically not measurable /3,6/.
In a first step we investigated the electrorotation of cells considering them as single-shell bodies /3,4,7,10/. This is possible to some extent even for a number of morphologically multi-shell cells. This reduction is of special interest even in the case of protoplasts, because each dielectric phase, i.e. the interior of the sphere and each shell surrounding it, takes three additional variables (dielectric constant, conductivity, thickness) into calculation. For a three-shell sphere this means 4 dielectric phases and, therefore, 12 more or less unknown parameters. Recently we demonstrated how the cellular parameters can be evaluated in practical cases for single-shell particles /7/.
Experimental data of protoplasts indicate that in most cases their treatment as single-shell bodies is inadequate. The purpose of this publication is the theoretical investigation of the electrorotation spectrum of three-shell spheres in comparison with experimental results, which will be published in a following paper /Gimsa et al, studia biophysica in press/.

2. Torque calculations

In Fig. 1 the model of a three-shell sphere is demonstrated, containing the central dielectric (phase 1) and the shells, the parameters of which are numbered from index 2 to 4. The parameters with the index e denote the external medium.

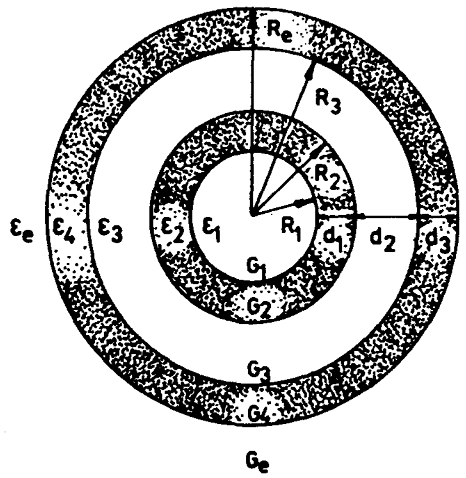


FIG. 1
Diagram of the protoplast geometry, assumed in the analysis of the electric field and charge separations.
$\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4, \varepsilon_e$ - diel. const.
G_1, G_2, G_3, G_4, G_e - conductivities
1 - interior, 2 - tonoplast,
3 - cytoplasm, 4 - plasmalemma
e - external medium,
d_1, d_2, d_3 - corresp. thicknes.

For calculating the torque of such a body the interactions between the electric field created by the induced dipoles inside the various phases and the applied external field have to be described /3,6,9/. This deviation only considers conductivity and polarization effects. The dipole rotation effect, occurring in parallel /2/ is not taken into consideration. This simplification is possible, because those dipole effects only occur in extremely high frequencies, which are not used for measurements.

In order to solve the LAPLACE equation

$$\mathrm{div\ grad}\varphi = 0 \qquad (1)$$

(φ- potential) the following potential equations can be used /9/:

$$\begin{aligned}
\varphi_1 &= \vec{A}\,\vec{r} && (r < R_1) \\
\varphi_2 &= \vec{B}\,\vec{r} + (\vec{C}\,\vec{r}) / 4\pi\varepsilon_o r^3 && (R_1 < r < R_2) \\
\varphi_3 &= \vec{D}\,\vec{r} + (\vec{F}\,\vec{r}) / 4\pi\varepsilon_o r^3 && (R_2 < r < R_3) \\
\varphi_4 &= \vec{H}\,\vec{r} + (\vec{J}\,\vec{r}) / 4\pi\varepsilon_o r && (R_3 < r < R_e) \\
\varphi_5 &= -\vec{E}\,\vec{r} + (\vec{m}\,\vec{r}) / 4\pi\varepsilon_o {}_e r^3 && (r < R_e)
\end{aligned} \qquad (2)$$

In these equations $\vec{A}$, $\vec{B}$, $\vec{C}$, $\vec{D}$, $\vec{F}$, $\vec{H}$, $\vec{J}$ and $\vec{m}$ are vectors. $\vec{r}$ denotes the polar vector and $\vec{E}$ the external field strength applied by the electrodes.

At the interfaces, two boundary conditions for the potential function (r) must be fulfilled:

$$\varphi_i = \varphi_{i-1}; \quad \varepsilon_i \frac{\partial \varphi_i}{\partial r} = \varepsilon_{i+1} \frac{\partial \varphi_{i+1}}{\partial r} \text{ ; for: } i=1 \text{ to } 4 \tag{3}$$

Using:

$$C = C^* \, 4\pi \varepsilon_o R_1^3 \; ; \qquad J = J^* 4\pi \varepsilon_o R_3^3$$
$$F = F^* \, 4\pi \varepsilon_o R_2^3 \; ; \qquad m = m^* 4\pi \varepsilon_o \varepsilon_e R_e^3 \tag{4}$$

We find:

$$A - B - C^* = 0$$
$$B + C^*(R_1/R_2)^3 - D - F^* = 0$$
$$D + F^*(R_2/R_3)^3 - H - J^* = 0$$
$$H + J^*(R_3/R_e)^3 - m^* = - E$$
$$\varepsilon_1 A - \varepsilon_2 B + 2\varepsilon_2 C^* = 0 \tag{5}$$
$$\varepsilon_2 B - 2\varepsilon_2 C^*(R_1/R_2)^3 - \varepsilon_3 D + 2\varepsilon_3 F^* = 0$$
$$\varepsilon_3 D - 2\varepsilon_3 F^*(R_2/R_3)^3 - \varepsilon_4 H + 2\varepsilon_4 J^* = 0$$
$$\varepsilon_4 H - 2\varepsilon_4 J^*(R_3/R_e)^3 + 2\varepsilon_e m^* = - E\varepsilon_e$$

Under consideration of the following complex terms:

$$A = A' + j A''$$
$$B = B' + j B''$$
$$C = C^{*\prime} + j C^{*\prime\prime} \tag{6}$$
$$\vdots$$
$$m = m^{*\prime} + j m^{*\prime\prime}$$

(where $j^2=-1$) and complex dielectric constants:

$$\bar{\varepsilon} = \varepsilon - j \frac{G}{\varepsilon_o \omega} \tag{7}$$

a system of equations can be developed, consisting of 16 equations, according to:

$$A * B = S \tag{8}$$

The matrices have the following meaning:

$$A = \begin{bmatrix}
1 & 0 & -1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & -1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & K_1 & 0 & -1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & K_1 & 0 & -1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & K_2 & 0 & -1 & 0 & -1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & K_2 & 0 & -1 & 0 & -1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & K_3 & 0 & -1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & K_3 & 0 & -1 \\
X_1 & X_2 & X_3 & X_4 & X_5 & X_6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
-X_2 & X_1 & -X_4 & X_3 & -X_6 & X_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & -X_3 & -X_4 & X_7 & X_8 & X_9 & Y_1 & Y_2 & Y_3 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & X_4 & -X_3 & -X_8 & X_7 & -Y_1 & Y_9 & -Y_3 & Y_2 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & -X_9 & -Y_1 & Y_4 & Y_5 & Y_6 & Y_7 & Y_8 & Y_9 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & Y_1 & -X_9 & -Y_5 & Y_4 & -Y_7 & Y_6 & -Y_9 & Y_8 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -Y_6 & -Y_7 & Z_1 & Z_2 & Z_3 & Z_4 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Y_7 & -Y_6 & -Z_2 & Z_1 & -Z_4 & Z_3
\end{bmatrix}$$

Whereas the symbols stand for the following expressions:

$$K_1 = \left(\frac{R_e - (d_1 + d_2 + d_3)}{R_e - (d_2 + d_3)}\right)^3; \quad K_2 = \left(\frac{R_e - (d_2 + d_3)}{R_e - d_3}\right)^3; \quad K_3 = \left(\frac{R_e - d_3}{R_e}\right)^3$$

$X_1 = \varepsilon_1$; $X_2 = G_1/\varepsilon_0\omega$; $X_3 = -\varepsilon_2$; $X_4 = -G_2/\varepsilon_0\omega$; $X_5 = 2\varepsilon_2$;

$X_6 = 2G_2/\varepsilon_0\omega$; $X_7 = -2\varepsilon_2 K_1$; $X_8 = -2G_2 K_1/\varepsilon_0\omega$; $X_9 = -\varepsilon_3$;

$Y_1 = -G_3/\varepsilon_0\omega$; $Y_2 = 2\varepsilon_3$; $Y_3 = -2G_3/\varepsilon_0\omega$; $Y_4 = -2\varepsilon_3 K_2$;

$Y_5 = -2G_3 K_2/\varepsilon_0\omega$; $Y_6 = -\varepsilon_4$; $Y_7 = -G_4/\varepsilon_0\omega$; $Y_8 = 2\varepsilon_4$;

$Y_9 = 2G_4/\varepsilon_0\omega$; $Z_1 = -2\varepsilon_4 K_3$; $Z_2 = -2G_4 K_3/\varepsilon_0\omega$; $Z_3 = 2\varepsilon_e$;

$Z_4 = 2G_e/\varepsilon_0\omega$;

$$S = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ -E \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ -\varepsilon_e E \\ G_e E \end{pmatrix} \qquad B = \begin{pmatrix} A' \\ A'' \\ B' \\ B'' \\ C^{*\prime} \\ C^{*\prime\prime} \\ D' \\ D'' \\ F^{*\prime} \\ F^{*\prime\prime} \\ H' \\ H'' \\ J^{*\prime} \\ J^{*\prime\prime} \\ m^{*\prime} \\ m^{*\prime\prime} \end{pmatrix}$$

For calculating particular curves we solved the following equation numerically:

$$B = A^{-1} * S \tag{9}$$

The torque leading to electrorotation is proportional to the imaginary part of the resulting electrical dipole moment (m") (see:/1,3,7,9/):

$$N = -E\, m'' \tag{10}$$

respectively:

$$N = -E\, 4\pi \varepsilon_o \varepsilon_e R^3 m^{*\prime\prime} \tag{11}$$

In the following calculations we normalized the external field strength to 1 V/m in all cases to get homogeneous curves demonstrating the dielectric properties of the measured dielectric only. In special cases the absolute value of N can be calculated by using the Eqn. (11). The torque (N) is proportional to the angular velocity (ω_c). For the case of exact smooth spheres the angular velocity ω_c can be calculated by using the Stokes frictional torque:

$$N_f = 8\pi\eta R_e^3 \omega_c \tag{12}$$

$$\omega_c = \frac{N}{8\pi R_e^3 \eta} = -\frac{E\varepsilon_o\varepsilon_e m^{*''}}{2\eta} \tag{13}$$

Where η means the viscosity of the external medium.
For particular application we used a parameter $R = \omega_c/E^2$ (rotation) allowing to relate experimental results performed under different field strength conditions. In the curves of the following chapter we used a dimensionless spin-number (N'), defined in the following way:

$$N' = \frac{m^{*''}}{E} \tag{14}$$

For finding out superpositions of different resonances in the rotation spectrum the plot of the imaginary over the real part of the resulting dipole moment (m', m") is very useful. In this case half circles describe each resonance according to the Cole-Cole's function.
In principle the system of equations (8) and consequently the matrices A, B, and S can be expanded for a four or even for a multi-shell system. Such particles, however, are rather complicated disregarded from four-shell systems (cells with vacuole and additionally a cell wall) and without direct biological relevance.

3. Particular Calculations

Using the equations derived in the previous chapter, the electrorotation spectrum of protoplasts treated as three-shell spheres will be demonstrated. We will compare this function with the electrorotation spectrum of single-shell models to find out situations where significant deviations occur.
Let us consider a protoplast with a radius of 25 µm indicating the following typical parameters:

	CONDUCTIVITY (S/m)	DK	RADIUS	THICKNESS
vacuole:	0.8	70	22.5µm	
tonoplast:	10^{-5}-10^{-6}	6		8 nm
cytoplasm:	0.1	50		2.5 µm
plasmalemma:	10^{-7}	6	25.0µm	8 nm
external medium:	0.01	75		

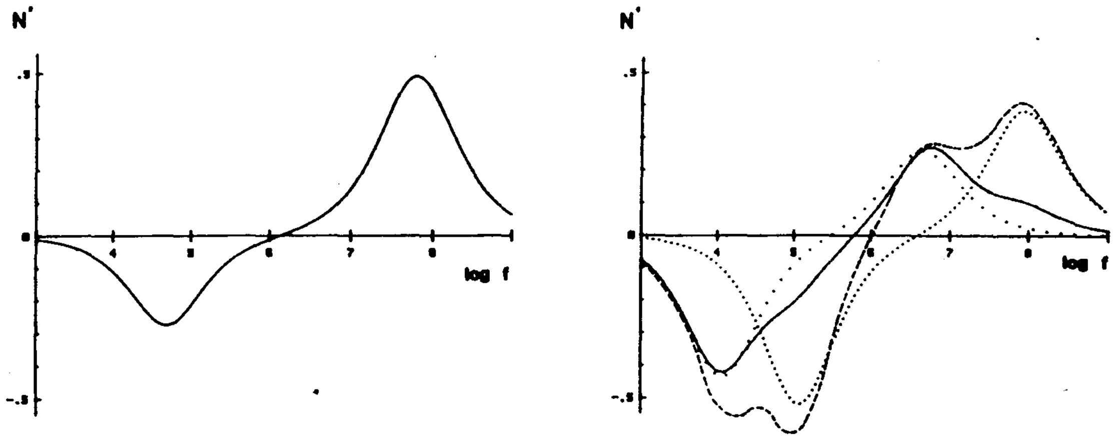
In comparison with this protoplast we use a vacuole as an example for a single-shell cell with the following parameters:

	CONDUCTIVITY (S/m)	DK	RADIUS	THICKNES
vacuole:	0.8	70	25.0µm	
tonoplast:	10^{-5}	6		8 nm
external medium:	0.01	75		

Fig. 2A indicates an electrorotation spectrum of an isolated vacuole. This curve shows the typical two peaks with opposite polarities as discussed before. The first peak at the characteristic frequency f_{c1} is strongly determined by the electrical membrane properties, whereas the second peak at the frequency f_{c2} is related to the internal and external conductivities.

It is to be noticed that the electrorotation spectrum of cells is mostly determined by their conductivities and to a much lower extent by their dielectric constants. This is caused by the circumstance that the conductivities vary between 10^{-1} and 10^{-8} S/m or less, whereas the dielectric constants may vary in the region between 1 and 80 only.

Before discussing special cases of the behaviour of a protoplast as a three-shell sphere, the general composition of such a curve will be considered. As already published /3,4,7,10/, the torque of single shell spheres indicates two resonance frequencies (see Fig. 2A), a two-shell sphere has three and, consequently, the protoplast, being a three-shell sphere, produces four resonance peaks. Only in special cases, all resonances are expressed in the curves as separate extrema. In Fig. 2B such a special case is plotted (curve ——). Additionally two curves are demonstrated, representing the torque of single-shell spheres. In



A B

Fig. 2

A. Electrorotation spectrum of a single-shell sphere (according to the parameters of the vacuole given above)

B. Electrorotation spectrum of a three-shell sphere (protoplast) and the interpretation of the resonances using two single-shell models.

——— - three-shell sphere for the above demonstrated protoplast parameters except the values: G_2=10 µS/m, G_3=0.03 S/m, radius of the vacuole = 15 µm.

..... - single shell model of the vacuole interior and tonoplast (G_1=0.8 S/m, G_2=10 µS/m, G_3=0.03 S/m, ε_1=70, ε_2=6, ε_3=50, vacuole radius =15 µm)

. . . - single shell model of the cytoplasma and plasmalemma (G_1=0.03 S/m, G_2=0.1 µS/m, G_3=0.01 S/m, ε_1=50, ε_2=6, ε_3=75, radius=25 µm)

- - - - mathematical addition of curves (....) and (. . . .)

one case (......) the cytoplasm is considered the external medium, whereas the vacuole, surrounded by the tonoplast represents the internal space. This case resembles the situation of an isolated vacuole. In the other curve (. . . .) the single-shell model is represented by the homogeneous cytoplasm, surrounded by the plasmalemma and the external solution. This simulates the protoplast without a vacuole. Furthermore the mathematical addition of both curves is plotted (- - - -). Therefore, the dotted curve represents the case in which the protoplast is formally divided into two single-shell spheres.

From the physical point of view such a division, obviously, cannot be the correct way of calculating the rotational behaviour of multi-layered particles. On the other hand, to some extent it helps to understand the electrorotation spectra of protoplasts qualitatively. As we know, the first resonance peak of the curve (.....) positioned in the kHz range is related to the electric relaxation process of the tonoplast, whereas the second peak reflects the properties of the internal conditions of the vacuole. Analogously in the curve (. . . . .) the first resonance peak is greatly determined by the plasmalemma, whereas the second one is related to the properties of the cytoplasm. All those resonances are reflected in the three-shell protoplast curve (----) too.

By comparing the electrorotation curve of a single-shell model (Fig. 2A) with that of a three-shell model of the protoplast (Fig. 2B), the following conclusion can be drawn: The dielectric properties of all components of a multi-shell model (i.e. plasmalemma. tonoplast, cytoplasm, vacuole interior) are reflected in the electrorotation spectrum in particular cases. The separation of the multi-shell model as a sum of single shell spheres helps to understand the electrorotation curve of the whole system, even if a simple addition of those curves is incorrect.

Let us consider now the influence of variations of special parameters for multi-shelled systems:

A. Variation of the thickness of the cytoplasm (Fig. 3):

To understand these situations, it has to be considered that the highly conductive cytoplasm strongly weakens the electric field, applied by the electrodes, inside the protoplast. As demonstrated in Fig. 3, the electrorotation spectrum of protoplasts with a large thickness of the cytoplasm layer (---- d_2=20µm) resembles the situation of a single-shell model. Therefore, the dielectric properties of the tonoplast have nearly no effect on the shape of the curve. The properties of the tonoplast influence the curve in the frequency range up to 1 MHz more and more with decreasing value of d_2. The interpretation of Arnold and Zimmermann /1/, considering the two membranes as capacitors connected in series, is fulfilled only in the case in which both membranes have identical electric properties and d_2 is extremely low (see also Fig. 4).

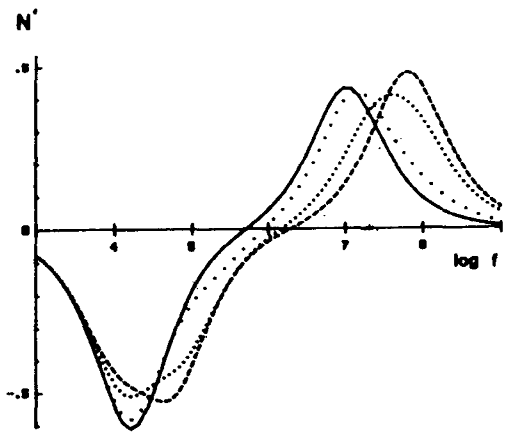


Fig. 3
Variation of the thickness of the cytoplasm (d_2) of the protoplast, corresp. to the above defined parameters.
(——— = 20 µm, ... = 10 µm
.... = 2.5 µm, - - - = 0.02 µm.

B. Variations of the membrane conductivities (Fig. 4):
The discussion of this situation is of particular interest, since the electrorotation is especially applied to investigate electrical membrane properties/1,3,8,11/. The curves in Fig. 4 reflect the typical parameters for a protoplast, i.e. a thin but highly conductive cytoplasm layer. Let us first consider the influence of the variation of the tonoplast conductivity (Fig. 4A). At low conductivities of the tonoplast (10^{-6}S/m) the first characteristic frequency is determined by the plasmalemma as well as by the tonoplast. If the tonoplast conductivity increases, the electrorotation spectrum in the low frequency range is more or less determined by the plasmalemma only. In this case a single-shell model can be applied. In the range of the second characteristic frequency no influence of the membrane conductivities occurs, because they are short-circuited. This maximum results from the superposition of the resonances of the cytoplasm and the vacuole content.
In contrast to the curves in Fig. 4A, the increase of the plasmalemma conductivity indicates not only a shift of the first characterstic frequency and a modification of the shape of the curves, but additionally a remarkable decrease in the rotation itself. Under these conditions plasmalemma conductivities in the range of 10^{-4} to 10^{-8} S/m produce significant effects. In those cases no single-shell approach is applicable.

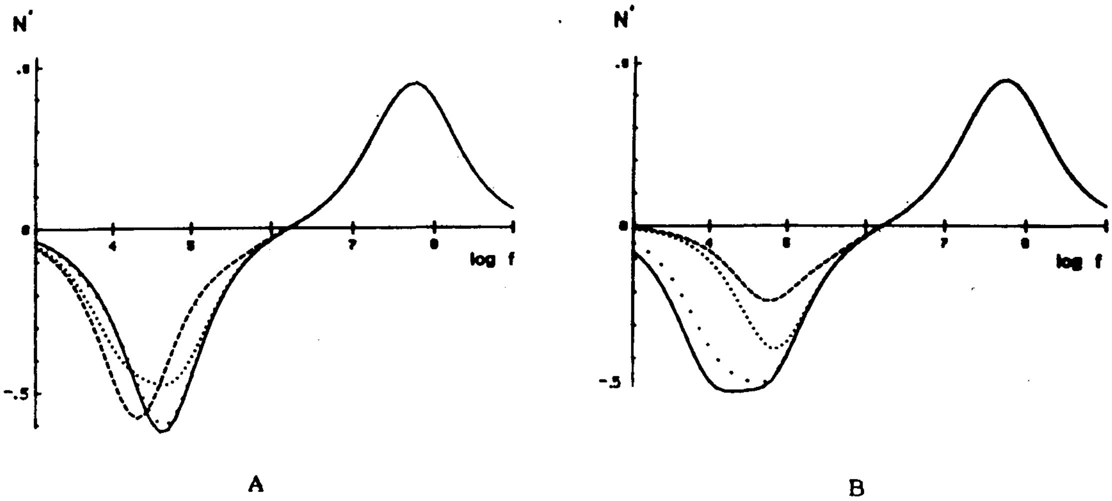


Fig. 4.
A. Variation of the tonoplast conductivity (G_2), whereas:
d_2= 1 µm. G_4= 1 µS/m.
——— = 0.01 µS/m, . . . = 1 µS/m, ...= 10 µS/m, - - -= 100 µS/m
B. Variation of the plasmalemma conductivity (G_4), whereas
G_2=10 µS/m.
——— = 0.01 µS/m, . . .= 1 µS/m, ...= 10 µS/m, - - -= 100 µS/m

C. Variation of the internal and external conductivities (Fig. 5):

In contrast to the modifications of the membrane parameters a change of the conductivities influences the first as well as the second characteristic frequency of the electrorotation spectrum. By increasing the conductivity of the vacuole interior the spin number increases and the behaviour of the vacuole is expressed more extensively in the shape of the curve (Fig. 5A). Under conditions of physiologically real values (large internal conductivities) a variation of this parameter influences the curve in the region of the first characteristic frequency only slowly.

The variation of the external conductivity (Fig. 5B) is of particular practical interest, since this parameter can be chosen freely in the experiments. It is remarkable that not only the position of the peaks, but also the character of the curves depends on the external conductivity. This circumstance can be demonstrated even better by using a sort of Cole-Cole plot (Fig. 5C). In this case the imaginary part of the induced dipole moment is plotted over its real part. This plot leads to half circles for each resonance, the centres of which are located on the abscissa. The curves in Fig. 5C, directly corresponding to those of Fig. 5B, indicate more clearly that more than two resonances are superimposed. In this plot the deviation from the single shell case is expressed better.

D. Variation of the cell size (Fig. 6):

All calculations, which were demonstrated here, actually reflect special situations in a multidimensional parameter space. This can be demonstrated, e.g. by changing the radius of the cell, whereas the geometrical proportions (R_e/d_2) remain the same. These curves show that a shift of the first characteristic frequency occurs as well as a change of the shape of the curves.

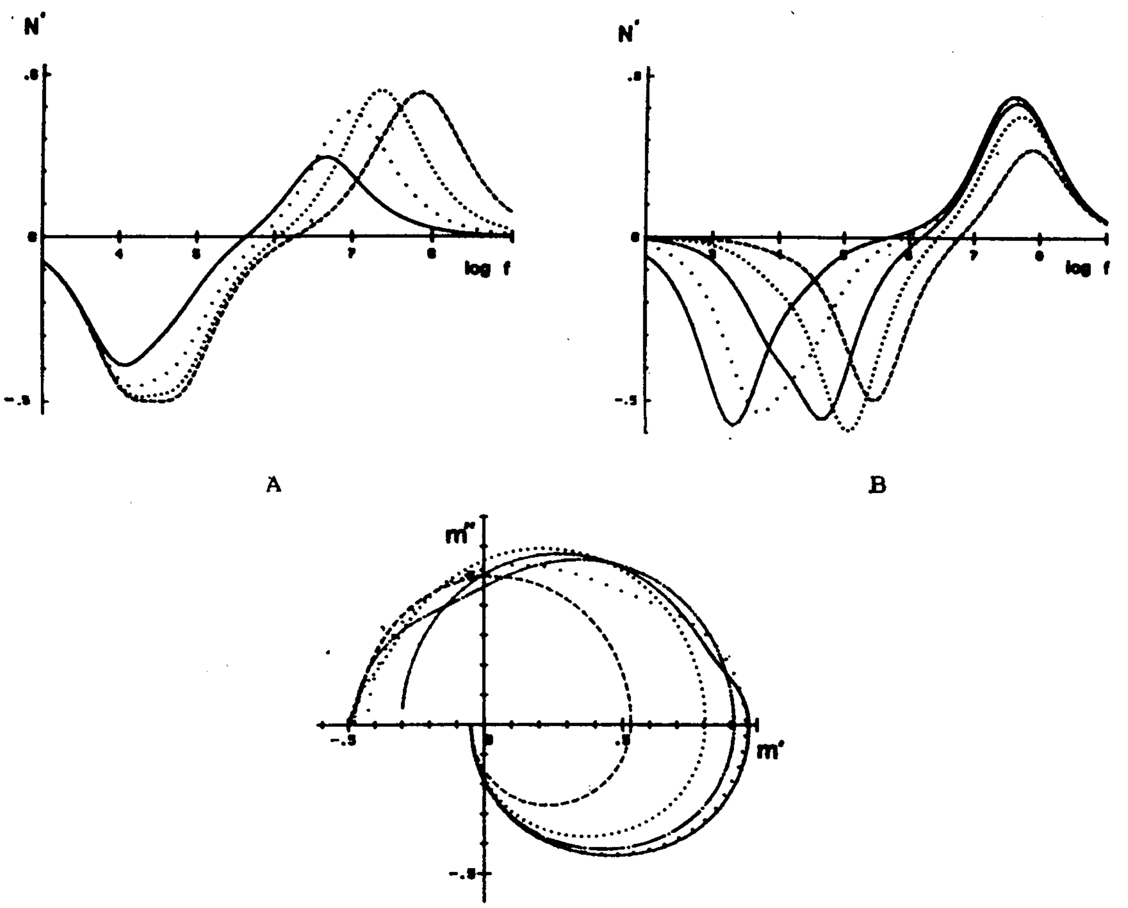


Fig. 5. C

A. Variation of the inside conductivity (G_i) (d_2=1 µm).
——= 0.03 S/m, ...= 0.1 S/m, ...= 0.3 S/m, - - -= 1S/m.

B. Variation of the external conductivity (G_e), whereas:
d_2= 2 µm, G_2= 1µS/m
——= 1 mS/m, ...= 3 mS/m, -.-.-= 10mS/m, ...= 30 mS/m,
- - -= 100 mS/m

C. Cole-Cole plot of the parameters of the cases B.

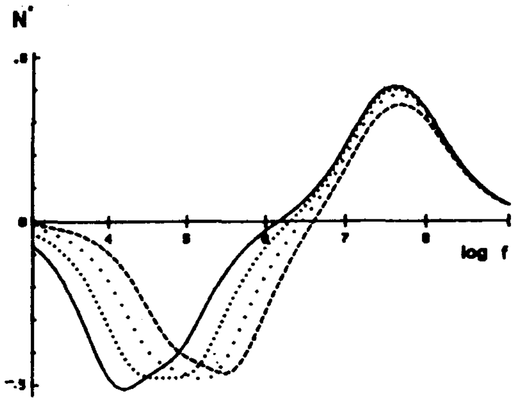


Fig. 6
Variation of the cell radius
——— = 25µm, ... = 12.5 µm
. . . . = 6.25 µm, - - - = 3.125 µm
($d_2 = R_e e/20$)

In a number of cases demonstrated here, the electrorotation spectrum resembles that of a single shell model. This, however, does not allow to calculate all parameters using equations for this simplified case. The error, resulting from such an approach is demonstrated in Fig. 7. In this case the curves of Fig. 5, representing a plasmalemma capacity of 6.6 mF/m², were evaluated using a single-shell model. As indicated in the Figure, the apparent capacity found in this way can be both higher and lower than the real value. In the conductivity range between 10^{-3} and 10^{-2} S/m the capacity seems to decrease. This is exactly the range where measurements were taken /1,7,8,11,12,13/.

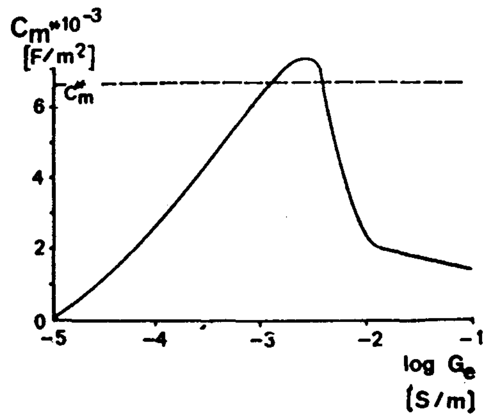


Fig. 7
The apparent plasmalemma capacity used for the calculation of a single-shell model in dependence on the external conductivity. (c_m corresponds to the real value of the specific capacity used to calculate the electrorotation spectra).

4. Discussion

The evaluation of the equations describing the electrorotation of three-shell spheres indicates that one has to expect that cells containing large organelles and/or cell wall show a more or less complicated electrorotational spectrum. Such curves have already been measured for various cells /3,10,11/. In the second part of this publication we will demonstrate such experimentally determined curves and discuss them in relation to this theoretical approach.

The particular calculations discussed here should be considered as selected examples only. The calculation of a three-shell sphere already contains 14 independent parameters, most of them variing in a large scale. It is hard to find out rules describing this multi-dimensional parameter space in general.

Under some conditions even the multi-layer cell may indicate a single-shell spectrum. However, the parameters calculated by this simplified approach can be incorrect, as demonstrated in Fig. 7 for a particular case. Possibly membrane capacities calculated in this way previously /1,7,8/ are only to be considered as effective parameters. The particular case in which tonoplast and plasmalemma can be considered simply as two capacitors in series /1/ is realized only if the two membranes have identical dielectric properties and the protoplasm thickness is very small. Moreover, the calculations show that the electrorotational analysis of cells demands the determination of the complete curve. It seems to be a loss of information if only the first characteristic frequency is determined. Especially the measurement of the high frequency part of the electrorotation spectrum contains important additional information.

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