

# BEHAVIOR OF CELLS IN ROTATING ELECTRIC FIELDS WITH ACCOUNT TO SURFACE CHARGES AND CELL STRUCTURES

GÜNTER FUHR AND PIOTR I. KUZMIN

*Humboldt-University of Berlin, Berlin, German Democratic Republic, and Institute of Electrochemistry  
of the Academy of Sciences, Moscow, Union of Soviet Socialist Republics*

**ABSTRACT** The behavior of a single biological cell in a rotating electric field is investigated both theoretically and experimentally. The torque acting on the cell is calculated. The dependence of the torque on electric cell properties (the dielectric constants, the conductivities, and the surface charges of the cell components) and the field frequency is discussed. The dependence of the rotation velocity on the field frequency shows a typical resonance behavior. It is discussed in which manner the single rotation extrema are related to the different homogeneous cell compartments (cytoplasm, cell membrane, and cell wall). It is shown that the cell surface charge shifts the resonance frequency and influences the absolute value of rotation velocity.

## INTRODUCTION

Any body being different from external medium by its dielectric constant and/or its conductivity acquires an electric dipole moment if it is placed in an external electric field. The polarization of the body proceeds with a finite rate so that the dipole moment reaches its maximal value with some time delay after switching on the field. Due to this delay in case of a rotating field the direction of the induced dipole does not coincide with the field direction. Thus, the torque acting on the body arises. This effect, leading to the rotation of the body, was already investigated by Heydweiller (1897), Lampa (1906), Born (1920), and Lertes (1921). The inverse effect was described by Hertz (1880), who has predicted that a rotating sphere should be braked by an electrostatic field.

It was shown previously (Arnold and Zimmermann, 1982; Pohl and Braden, 1982; Glaser et al., 1983; Pohl, 1983) that single biological cells rotate continuously under the influence of the rotating electric field. This effect may be used as a method for determination of electric properties of cell wall and cell membrane. The functional dependence of the cell rotation on the applied field frequency shows a typical resonance behavior. Whereas in the earlier works (Mischel and Pohl, 1983; Hagedorn and Fuhr, 1984; Fuhr et al., 1985) simple models (homogeneous spheres or spheres with a single outer layer) were used, biological cells in most cases are multilayer systems (for example yeast cells—two layer systems, plant protoplasts with vacuole—three layer systems, and plant cells with large vacuole and

cell wall—four layer systems). Moreover, the cells are usually charged. Therefore, we want to discuss the more complicated case of multilayer and charged bodies here.

## MATERIAL AND METHODS

### Measuring Setup

The experimental setup was essentially the same as already described by Arnold and Zimmermann (1982). The rotation of cells was measured in a four-electrode system that employed sinusoidal voltages with variable amplitudes in the frequency range of 100 Hz up to 3 MHz in four phases, spaced by 90° and controlled by an oscilloscope. Four electrodes (platinum or stainless steel) form the walls of the square chamber fixed on a microscope coverslip. The electrode distance varied between 2 and 6 mm in different experiments. Microscopic observations were made by a normal objective (8×).

For rotation measurement the plant cells were fixed between two layers of solutions different in density (0.2 M metrizamid and 0.2 M mannitol). The conductivity of the solution was adjusted with KCl, the field strength ranged from  $0.5 \times 10^3$  to  $5 \times 10^3$  V/m (see also Glaser et al., 1983; Fuhr et al., 1984). The cell rotation speed was determined after reaching its stationary level.

### Cell Preparation

As object we used *Beta vulgaris* suspension-cultured cells. The cells were cultivated in an air-lift fermentor. Parameters like the cell growth, the concentration of different medium substances, the pH, and others were recorded automatically and allowed to characterize the cells. Cells were cultivated in a medium modified after Murashige and Skoog (1962) for 14 d. Small aggregates (4–10 cells) were mechanically and/or enzymatically (pectinase) divided in single cells. For the experiments we selected cells with small vacuoles and a large cytoplasm part.

### Influence of Multilayers on the Rotational Behavior (Torque and the Characteristic Frequencies) of Cells

As model for multilayered cells we used spheres as shown in Fig. 1. These spheres are two-shell systems consisting of three dielectrics; the first dielectric is the cytoplasm, the second dielectric and the first shell is the membrane, and the third dielectric and the second shell is the cell wall. This model describes the used suspension cultured cells. The detailed calculation of the rotational behavior of such bodies is given in the Appendix. Concerning the torque of an object in a rotating electric field, each homogeneous component of the object can be described by its conductivity and dielectric constant. From the calculation follows that a sphere with only one shell has two resonance frequencies. Each additional layer produces a further extremum: in case of a body surrounded by two shells, three characteristic frequencies  $\omega_{01}$ ,  $\omega_{02}$ , and  $\omega_{03}$  should be expected (see Appendix)

$$N = 4\pi\epsilon_0\epsilon_e R_c^3 E_0^2 \left[ K_1 \frac{\omega/\omega_{01}}{(1 + (\omega/\omega_{01})^2)} + K_2 \frac{\omega/\omega_{02}}{(1 + (\omega/\omega_{02})^2)} + K_3 \frac{\omega/\omega_{03}}{(1 + (\omega/\omega_{03})^2)} \right] \quad (1)$$

Here the quantities  $K_1$ ,  $K_2$ , and  $K_3$  are combinations of all material constants whose absolute sizes determine the amount of the torque ( $N$ ) at the different characteristic frequencies  $\omega_{01}$ ,  $\omega_{02}$ , and  $\omega_{03}$ .  $\epsilon_0 = 8.85 \times 10^{-12}$  F/m,  $\epsilon_e$  is the dielectric constant of the external solution,  $R_c$  is the cell radius,  $E_0$  the external field strength, and  $\omega$  is the angular frequency of the field.

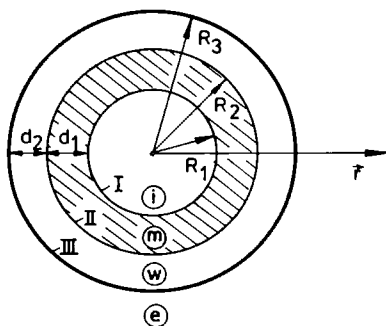


FIGURE 1 Model for multilayered cells:  $i$  = inside medium (e.g., cytoplasm) with conductivity ( $G_i$ ) and dielectric constant ( $\epsilon_i$ );  $m$  = membrane system ( $G_m$ ,  $\epsilon_m$ );  $w$  = cell wall ( $G_w$ ,  $\epsilon_w$ );  $e$  = external solution ( $G_e$ ,  $\epsilon_e$ );  $R_{1,2,3}$  = cell radii;  $d_1$  = membrane thickness;  $d_2$  = cell wall thickness; and I, II, III = boundary layers.

For multilayered spheres the torque is

$$N = 4\pi\epsilon_0\epsilon_e R_c^3 E_0^2 \sum_{s=1}^n \left[ K_s \frac{\omega/\omega_s}{(1 + (\omega/\omega_s)^2)} \right], \quad (2)$$

where  $s$  is the number of cell dielectrics.

In first approximation, plant cells with small vacuoles and large cytoplasm part and cell wall can be described as two-shell spheres. Therefore, we restricted ourselves to discuss this case as an example in a more detailed manner.

Whereas the amount of the torque depends on all material constants in a complicated manner, the expression for the characteristic frequencies and the torque can be specified and simplified for evident biological cases. In general we used biological cells whose membrane thickness and wall thickness are small in comparison with its radius. Furthermore we can suppose that we know roughly the dielectric constants of the object and also the internal conductivity (cytoplasm). Additionally we demand the external conductivity to be low in comparison with the internal one. For the calculation of the curve (Fig. 2) we have chosen the set of parameters in Table I.

Whereas slight changes of the dielectric constants up to 15% do not influence the frequency course of the torque visible, an increase of the cell wall conductivity shifts  $\omega_{01}$ , respectively,  $f_{01} = \omega_{01}/2\pi$  in a strong manner toward higher values (Fig. 6). As shown in Fig. 2, changes of the membrane conductivity act in the same direction and cannot be distinguished from the former one. This discrimination would only be possible if the torque extrema at  $\omega_{01}$  and  $\omega_{03}$  were not superimposed as they are in Fig. 3. To demonstrate the occurrence of three extrema we have chosen a more artificial set of parameters for the calculation of the curve (—) in Fig. 3.

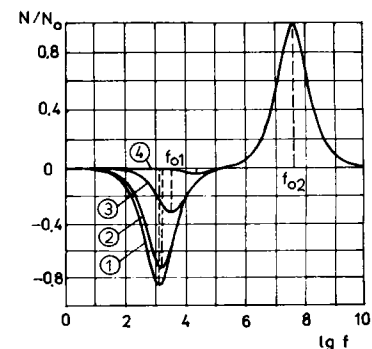


FIGURE 2 Torque ( $N$ ) of a two-shell sphere in dependence on the frequency ( $f$ ) for different membrane conductivities. (1:  $G_m = 0$ ; 2:  $G_m = 10^{-7}$  S/m; 3:  $G_m = 10^{-6}$  S/m; 4:  $G_m = 10^{-5}$  S/m) where  $G_i = 5 \times 10^{-1}$  S/m;  $\epsilon_i = 80$ ;  $R_3 = 6 \times 10^{-5}$  m;  $G_w = 5 \times 10^{-2}$  S/m;  $\epsilon_m = 9$ ;  $d_1 = 10^{-8}$  m;  $G_e = 10^{-3}$  S/m;  $\epsilon_w = 70$ ;  $d_2 = 10^{-6}$  m;  $\epsilon_e = 80$ ; normated with  $N_0 = /N_{max}/$ .

TABLE I

Cell part	Conductivity (S/m)	Dielectric constant
Cytoplasm	$G_i = 5 \times 10^{-1}$	$\epsilon_i = 80$
Cell membrane	$G_m = \text{variable}$	$\epsilon_m = 9$
Cell wall	$G_w = 5 \times 10^{-2}$	$\epsilon_w = 70$
External medium	$G_e = 10^{-3}$	$\epsilon_e = 80$

### Comparison between the Measurable and the Calculated Values of the Cell Rotation of Suspension Cultured Cells

If a sphere rotates stationarily in a liquid its driving torque is compensated by its frictional moment ( $N_f$ ). Using the Navier-Stokes expression for  $N_f$ , one can calculate the angular velocity ( $\omega_c$ ) of the object

$$\omega_c = \frac{N}{8\pi\eta R_c^3}, \quad (3)$$

where  $\eta$  is the viscosity of the external medium.

According to Eq. 1, one finds  $\omega_c \sim E_o^2$  in good agreement with the experimental findings (Fig. 4). The rotation ( $R^*$ ) of a *Beta vulgaris* cell in dependence on the applied field frequency is given in Fig. 5. To eliminate the influence of the field strength we use the quantity  $R^* = \omega_c/E_o^2$  (see Glaser et al., 1983). The circles in Fig. 5 represent measured values.

Finally we have measured the influence of the external conductivity on the characteristic frequency ( $f_{o1}$ ). As can be seen, an increasing external conductivity shifts  $f_{o1}$  toward higher values (Fig. 6, measured points are marked

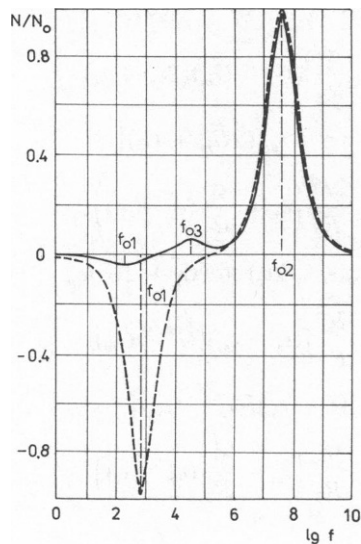


FIGURE 3 Torque ( $N$ ) of a two-shell sphere for two combinations of the dielectric constants and conductivities in dependence on the frequency ( $f$ ): curve (---)  $G_i = 5 \times 10^{-1}$  S/m;  $\epsilon_i = 80$ ;  $R_i = 6 \times 10^{-5}$  m;  $G_m = 10^{-8}$  S/m;  $\epsilon_m = 9$ ;  $d_i = 10^{-8}$  m;  $G_w = 5 \times 10^{-2}$  S/m;  $\epsilon_w = 70$ ;  $d_w = 10^{-6}$  m;  $G_e = 5 \times 10^{-4}$  S/m;  $\epsilon_e = 80$ ; curve (—) changed parameters  $G_m = 10^{-7}$  S/m;  $G_e = 10^{-3}$  S/m;  $G_w = 10^{-4}$  S/m;  $\epsilon_w = 60$ .

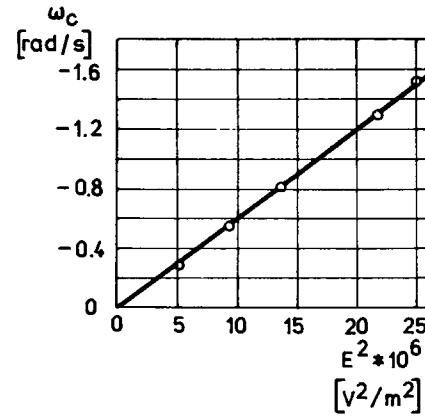


FIGURE 4 Dependency of the angular velocity of cells ( $\omega_c$ ) on applied field strength ( $E$ ) for suspension cultured cells of *Beta vulgaris* ( $G_e = 1.35 \times 10^{-3}$  S/m).

by circles). The curve in the upper part is calculated for a cell whose cell wall conductivity was assumed to be constant ( $G_w = 1$  S/m), the other curves for a cell wall conductivity of  $G_w = 10^{-1}$ ;  $5 \times 10^{-2}$  and  $10^{-2}$  S/m. It seems that the real cell wall conductivity lies between 1 and  $10^{-1}$  S/m. If one considered the cell wall conductivity as a function of the external one (see Donath, 1983) it would be possible to calculate the frequency course of the torque, provided the exact value of the membrane conductivity is known.

### Influence of Surface Charge

To study the influence of a surface charge on the rotational behavior of the cell, the simplest model was chosen (see Fig. 7). The zones  $i$  and  $e$  correspond to the internal and the external electrolyte solutions, the zone  $m$  is the cell shell (membrane). Near the charged cell surface a diffuse layer of counterion surplus exists that compensates the surface charge. Although the concentration of coions in this layer is lowered, the total concentration of ions in the diffuse double layer is higher than that in the bulk of the electrolyte solution. Usually the thickness of the diffuse layer  $\chi^{-1}$  ( $\chi$  is the parameter of the theory of Debye-Hückel) is

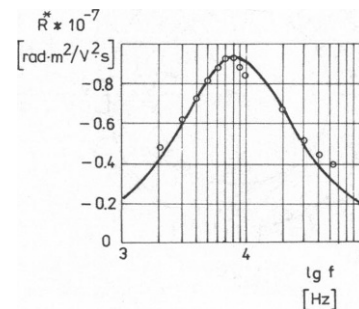


FIGURE 5 Rotation ( $R^*$ ) of single plant cells (*Beta vulgaris*) as a function of frequency ( $f$ ) ( $G_e = 1.35 \times 10^{-3}$  S/m; cell diameter, 90  $\mu$ m).

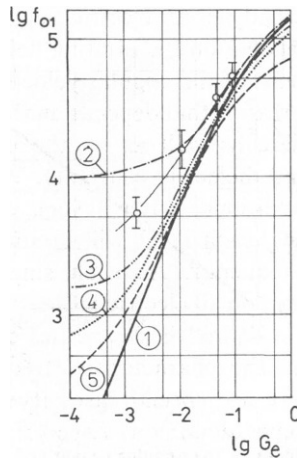


FIGURE 6 Characteristic frequency ( $f_{01}$ ) of a two-shell object in dependence on the external conductivity ( $G_e$ ) in comparison to experimental data (*Beta vulgaris*). 1: Object without surface structure (single-shell object). 2, 3, 4, and 5: objects with second shell of constant conductivity ( $G_m = 1; 0.1; 5 \times 10^{-2}$  and  $10^{-2}$  S/m) the other parameters:  $G_i = 0.1$  S/m;  $\epsilon_i = 70$ ;  $G_m = 10^{-7}$  S/m;  $\epsilon_m = 9$ ;  $d_1 = 10^{-8}$  m;  $\epsilon_w = 70$ ;  $d_2 = 10^{-6}$  m;  $\epsilon_e = 80$ ; (O) – measuring points (*Beta vulgaris*), radius of all objects  $r = 4.5 \times 10^{-5}$  m.

much smaller than the cell radius ( $r$ ):

$$\chi \cdot r \gg 1. \quad (4)$$

For sufficiently large cells ( $r > 3 \mu\text{m}$ ) in water electrolyte solutions this condition is always valid.

Thus, we can take into consideration the increasing conductivity ( $K_s$ ) that connects the surface density of electric current ( $I_s$ ) and the electric field strength ( $E_s$ )

$$I_s = K_s E_s. \quad (5)$$

The coefficient  $K_s$  depends on the external electrolyte concentration and the surface charge density (Dukhin, 1977). Then the surface charge of the object can be considered by a dimensionless parameter ( $Rel$ ) (Dukhin, 1977).

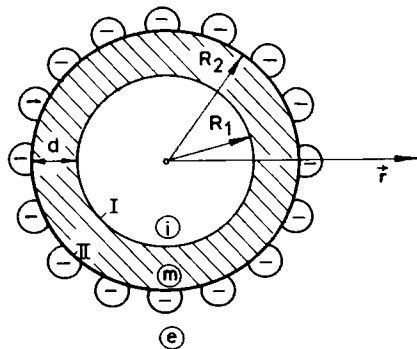


FIGURE 7 Model for cells with a surface charge:  $i$  – inside medium;  $R$  – cell radii;  $m$  – membrane system;  $d$  – membrane thickness;  $e$  – external solution.

$$Rel = K_s / (r G_e). \quad (6)$$

According to this equation a high external conductivity ( $G_e$ ) reduces the possible influence of a surface charge. For biological objects the quantity  $Rel$  ranges from 0 to 0.3 (Dukhin, 1977).

The calculation of the torque ( $N$ ) in this case is similar to that in the previous section (see Appendix); some simplifications connected with the absence of one layer are evident. Only the boundary condition for the complex dielectric displacement on the outer surface changes essentially. Now it assumes the form

$$\bar{\epsilon}_m \frac{\partial \varphi_m}{\partial r} = \bar{\epsilon}_e \frac{\partial \varphi_e}{\partial r} + j \frac{K_s}{\epsilon_e \omega} \text{div}_s E_s. \quad (7)$$

Here  $\text{div}_s$  is the surface divergence and  $\bar{\epsilon}$  are complex dielectric constants. This condition results from the charge balance analysis on the outer cell surface.

In the assumed case the general form of the torque ( $N$ ) is

$$N = 4\pi\epsilon_0\epsilon_e R_2^3 E_0^2 \left[ \left( \frac{C_1}{C_2} - \frac{B_1}{B_2} \right) \frac{\omega/\omega_{01}}{(1 + (\omega/\omega_{01})^2)} + \left( \frac{B_1}{B_2} - \frac{A_1}{A_2} \right) \frac{\omega/\omega_{02}}{(1 + (\omega/\omega_{02})^2)} \right], \quad (8)$$

where

$$A_1 = \epsilon_m(\epsilon_e - \epsilon_i) + \frac{d}{R_2}(\epsilon_i - \epsilon_m)(2\epsilon_m + \epsilon_e)$$

$$A_2 = -\epsilon_m(\epsilon_i + 2\epsilon_e) - \frac{2d}{R_2}(\epsilon_i - \epsilon_m)(\epsilon_e - \epsilon_m)$$

$$B_1 = -G_m(\epsilon_e - \epsilon_i) - \epsilon_m(G_e - G_i)$$

$$- \frac{d}{R_2} \{ (G_i - G_m)(2\epsilon_m + \epsilon_e) + (\epsilon_i - \epsilon_m)(2G_m + G_e) \}$$

$$+ \frac{2K_s}{R_2} \left( \epsilon_m - \frac{d}{R_2}(\epsilon_m - \epsilon_i) \right)$$

$$B_2 = G_m(\epsilon_i + 2\epsilon_e) + (G_i + 2G_e)\epsilon_m$$

$$+ \frac{2d}{R_2} [(\epsilon_e - \epsilon_m)(G_i - G_m) + (\epsilon_i - \epsilon_m)(G_e - G_m)]$$

$$+ \frac{2K_s}{R_2} \left( \epsilon_m - \frac{d}{R_2}(\epsilon_m - \epsilon_i) \right)$$

$$C_1 = -G_m(G_e - G_i) - \frac{d}{R_2}$$

$$\cdot (G_i - G_m)(2G_m + G_e)$$

$$+ \frac{2K_s}{R_2} \left( G_m - (G_m - G_i) \frac{d}{R_2} \right)$$

$$C_2 = G_m(G_i + 2G_e) + \frac{2d}{R_2}(G_i - G_m)(G_e - G_m) + \frac{2K_s}{R_2} \left[ G_m - (G_m - G_i) \frac{d}{R_2} \right].$$

In dependence on the field frequency the function shows two extrema at  $\omega_{01}$  and  $\omega_{02}$  (Fig. 8). For further simplification we assume that the conductivity of the shell (e.g., the conductivity of the cell membrane) is lower than  $10^{-7}$  S/m and can be neglected. In this case one gets

$$\omega_{01} = 2\pi f_{01} = \frac{d}{2\pi\epsilon_0\epsilon_m R_2 \left( \frac{1}{G_i} + \frac{1}{2G_e(1 + Rel)} \right)} \quad (9)$$

$$\omega_{02} = 2\pi f_{02} = \frac{G_i + 2G_e(1 + Rel)}{2\pi\epsilon_0(\epsilon_i + 2\epsilon_e)}. \quad (10)$$

In our experiments the condition  $G_i \gg G_e$  is valid. Therefore the surface charge, represented by the quantity ( $Rel$ ), shifts only  $\omega_{01}$  toward higher frequencies. On the other hand, an increasing surface charge decreases the torque and in this way also the cell angular velocity in the range of  $\omega_{01}$ . In Fig. 8 the dependency of the torque ( $N$ ) (according to Eq. 8) on the surface charge and on the field frequency is represented. Using realistic values for the surface charge ( $0 \leq Rel \leq 0.3$ ) a maximal frequency shift of  $\sim 30\%$  should be observable. Whereas this effect up to now has not been investigated experimentally, there is no doubt concerning the existence of two extrema (Fuhr et al., 1985).

## DISCUSSION

Both theoretical and experimental investigations show that the field-influenced rotation of biological cells is a complicated process. For the calculations, we consider the cell to be objects with homogeneous components (e.g., cytoplasm, cell membrane, and cell wall). As simplest model—but not suited for biological cells—one could use homogeneous spheres (Arnold and Zimmermann, 1982; Mischel and Pohl, 1983; Jones, 1984). In this case the rotational

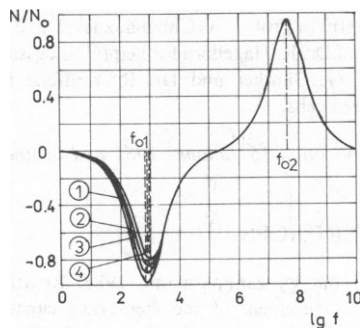


FIGURE 8 Torque ( $N$ ) of a shell-surrounded sphere with a surface charge in dependence on the frequency ( $f$ ) of the external rotating field for several values of the parameter ( $Rel$ ). 1:  $Rel = 0$ ; 2:  $Rel = 0.1$ ; 3:  $Rel = 0.2$ ; and 4:  $Rel = 0.3$ .

behavior of the body in an electric field would show one extremum, dependent on the exciting field frequency. For a maximal amount of the angular velocity ( $\omega_c$ ) one could calculate an expression that depends on the electric properties of the sphere as well as on the external medium (conductivity and dielectric constant). When considering spheres with additional outer layers, as necessary for biological objects, each layer will produce an additional characteristic frequency. As each single characteristic frequency depends on all electric properties of the object it is not possible to define the properties of one single cell component from the characteristic frequencies. On the other hand, there are special cases in which one single parameter becomes dominant. Especially in the case of cells  $\omega_{01}$  is mainly determined by the membrane conductivity and that of the cell wall. For this reason measurements of  $\omega_{01}$  can be used to clarify the conductivities of these cell components. As shown theoretically and experimentally, an increasing cell membrane conductivity shifts  $\omega_{01}$  toward higher values (Fuhr et al., 1985). On the other hand, an increasing of the surface charge acts in the same direction as an increase of the external conductivity; therefore, the external conductivity must be constant in all experiments. It is shown that realistic values for surface charges can affect the characteristic frequency ( $\omega_{01}$ ) by maximally 30%.

Summarizing, it can be stated that: (a) The absolute amount of the angular velocity is a quantity that depends on all electric properties of the cell in a complicated manner. Therefore, for multilayered objects it is difficult to relate the angular velocity to the conductivity or dielectric constant of a single cell component. (b) The characteristic frequencies, too, are described by expressions that contain all conductivities and dielectric constants of the object. But there are special cases in which one or two parameters become dominant. Especially in the case of biological objects (protoplasts, single plant or animal cells) the angular velocity of the cell can be used to determine the conductivities of cell envelopes—provided one determines the conductivity of the cytoplasm and/or inner space and that of the external solution. The calculations show that in the frequency range up to 1 MHz (the range of the first resonance) the cell rotation in a sensitive manner depends on the conductivities, whereas the dielectric constants play a subordinate role. (c) Surface charges act in the same direction as an increasing of the external conductivity: high values shift the characteristic frequency ( $\omega_{01}$ ) toward higher values and decrease the angular velocity. (d) The measurement of the rotational behavior of cells allows the determination of cell membrane and cell wall properties without destruction of the cell and is therefore a usable supplement to other methods.

## APPENDIX

As known (Stretton, 1941), the torque ( $N$ ) effecting on a body being placed in an electric field is expressed in terms of the maxwellian tension

(T):

$$\mathbf{N} = \oint_s [\mathbf{r}, \mathbf{T}] ds. \quad (\text{A1})$$

Here  $(\mathbf{r})$  is the radius-vector of a given point. The closed integration surface  $(s)$  lies in the electrolyte medium outside the body; its shape is arbitrary. The Maxwellian tension is expressed in terms of the electric field strength  $[\mathbf{E}(\mathbf{r}, t)]$  and the outward normal  $(\mathbf{n})$  to the surface  $(s)$ :

$$\mathbf{T} = \epsilon \epsilon_0 \left[ (\mathbf{E}, \mathbf{n}) \mathbf{E} - \frac{\mathbf{E}^2}{2} \mathbf{n} \right]. \quad (\text{A2})$$

Here  $\epsilon_0 = 8.8543 \times 10^{-12}$  F/m is the dielectric constant;  $\epsilon$  is a relative dielectric constant of the medium. Therefore, to calculate  $(\mathbf{N})$  one needs the electric field distribution outside the cell.

Since the external field effecting on the cell changes with the time harmonically, it is convenient to use the complex approach, writing the complex electric potential in the form

$$\hat{\varphi}(\mathbf{r}, t) = \varphi(\mathbf{r}) \exp(j\omega t); \quad (j^2 = -1). \quad (\text{A3})$$

Here  $\omega$  is the external field frequency,  $\varphi(\mathbf{r})$  is the complex amplitude of the potential.

The vector  $(\mathbf{E})$  in Eq. A2 is the negated real part of the gradient of the complex potential  $(\hat{\varphi})$ :

$$\mathbf{E} = -\text{Re} \{ \text{grad } \hat{\varphi} \}. \quad (\text{A4})$$

The model of the cell used for the calculations is shown in Fig. 1. We shall supply the corresponding subscript ( $i, m, w$ , or  $e$ ) to any electric quantity in each zone represented in Fig. 1. The amplitude  $(\varphi)$  must satisfy the Laplace equation in each zone in Fig. 1.

$$\Delta \varphi_k = 0; \quad k = i, m, w, e. \quad (\text{A5})$$

On the boundaries of the zones the potential is continuous

$$\begin{aligned} \varphi_i &= \varphi_m & (r = R_1) \\ \varphi_m &= \varphi_w & (r = R_2) \\ \varphi_w &= \varphi_e & (r = R_3). \end{aligned} \quad (\text{A6})$$

Here  $r = |\mathbf{r}|$ .

On the same boundaries the normal component of the complex dielectric displacement is continuous too

$$\begin{aligned} \bar{\epsilon}_i \frac{\partial \varphi_i}{\partial r} &= \bar{\epsilon}_m \frac{\partial \varphi_m}{\partial r} & (r = R_1) \\ \bar{\epsilon}_m \frac{\partial \varphi_m}{\partial r} &= \bar{\epsilon}_w \frac{\partial \varphi_w}{\partial r} & (r = R_2) \\ \bar{\epsilon}_w \frac{\partial \varphi_w}{\partial r} &= \bar{\epsilon}_e \frac{\partial \varphi_e}{\partial r} & (r = R_3), \end{aligned} \quad (\text{A7})$$

where  $\bar{\epsilon}_k = \epsilon_k - jG_k/\epsilon_0\omega$  is the complex relative dielectric constant (here  $\epsilon_k$  and  $G_k$  are the dielectric constant and the conductivity of the corresponding zone, respectively).

Far from the cell the electric field is uniform

$$\varphi_e \rightarrow -\mathbf{E}_0 \mathbf{r} \quad (r \rightarrow \infty), \quad (\text{A8})$$

where  $\mathbf{E}_0 = E_0(\mathbf{e}_x - j\mathbf{e}_y)$  is the rotating field amplitude ( $\mathbf{e}_x$  and  $\mathbf{e}_y$  are the unit vectors of the axes  $x$  and  $y$ ),  $E_0$  is the absolute value of the real rotating field.

We seek the solution to the problem (Eqs. A5–A8) in the form of

functions satisfying Eq. A4 in each of the zones in Fig. 1:

$$\begin{aligned} \varphi_i &= \mathbf{A} \mathbf{r} \\ \varphi_m &= \mathbf{B} \mathbf{r} + \mathbf{C} \mathbf{r}^3 \\ \varphi_w &= \mathbf{D} \mathbf{r} + \mathbf{F} \mathbf{r}^3 \\ \varphi_e &= -\mathbf{E}_0 \mathbf{r} + \mathbf{M} \mathbf{r} / (4\pi\epsilon_0\epsilon_e r^3). \end{aligned} \quad (\text{A9})$$

Here  $\mathbf{A}, \mathbf{B}, \mathbf{C}, \mathbf{D}, \mathbf{F}$ , and  $\mathbf{M}$  are vectors in question, independent on space coordinate  $(\mathbf{r})$ . Notice that the vector  $\mathbf{M} \exp(j\omega t)$  is the complex electric dipole moment. The observable dipole moment is represented by the quantity  $\text{Re} [\mathbf{M} \exp(j\omega t)]$ .

Substituting Eq. A9 into Eqs. A6 and A7 and solving the obtained system of linear equations, we obtain the expression for  $\mathbf{M}$

$$\mathbf{M} = \chi \mathbf{E}_0 \quad (\text{A10})$$

where:

$$\begin{aligned} \chi &= 4\pi\epsilon_0\epsilon_e R_3^3 \\ &\cdot \frac{\alpha_{we}\beta_{mi}\beta_{wm} + 2\alpha_{we}\alpha_{wm}\alpha_{mi}\rho_{12} + \alpha_{mw}\beta_{we}\beta_{mi}\rho_{23} + \alpha_{im}\beta_{we}\beta_{mw}\rho_{13}}{\beta_{ew}\beta_{mi}\beta_{wm} + 2\beta_{ew}\alpha_{wm}\alpha_{mi}\rho_{12} + 2\alpha_{ew}\alpha_{wm}\beta_{mi}\rho_{23} + 2\alpha_{ew}\alpha_{mi}\beta_{mw}\rho_{13}}. \end{aligned} \quad (\text{A11})$$

Here

$$\begin{aligned} \alpha_{sk} &= \bar{\epsilon}_s - \bar{\epsilon}_k; & \beta_{sk} &= 2\bar{\epsilon}_s + \bar{\epsilon}_k & (s, k = i, m, w, e) \\ \rho_{np} &= (R_n/R_p)^3 & (n, p = 1, 2, 3). \end{aligned}$$

Substituting the expression for  $\mathbf{M}$  from Eq. A10 into the formula for Eq. A9 and using Eq. A4, we obtain the real field strength  $(\mathbf{E})$  outside the cell. Then from Eqs. A1 and A2 we get the final expression for the torque

$$N = -E_0^2 \text{Im} \chi. \quad (\text{A12})$$

Here  $\text{Im}$  means the imaginary part,  $N$  is the torque projection to the axis that is perpendicular to the plane of the field rotation: if  $N > 0$ , then the rotation direction of the cell and the field coincide.

Eq. A12 may be presented in the form

$$N = 4\pi\epsilon_0\epsilon_e R_3^3 E_0^2 \sum_{s=1}^3 \left( K_s \frac{\omega/\omega_{0s}}{(1 + (\omega/\omega_{0s})^2)} \right), \quad (\text{A13})$$

where the coefficients  $K_1, K_2, K_3$  and the characteristic frequencies  $\omega_{01}, \omega_{02}, \omega_{03}$  depend on all the parameters  $\epsilon_k, G_k$  and the geometric dimensions of the cell. The corresponding expressions are voluminous, and for that reason they are omitted here.

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## REFERENCES

- Arnold, W. M., and U. Zimmermann. 1982. Rotating-field induced rotation and measurement of the membrane capacitance of single mesophyll cells of *Avena sativa*. *Z. Naturforsch.* 37c:908–915.
- Born, M. 1920. Über die Beweglichkeit der elektrolytischen Ionen. *J. Phys.* 1:221–249.
- Donath, E. 1984. Dissertation. Humboldt-Universität zu Berlin. 105.
- Fuhr, G., R. Glaser, and R. Hagedorn. 1986. Rotation of dielectrics in a

- rotating electric high frequency field. Model experiments and theoretical explanation of the rotation effect. *Biophys. J.* 49: 395–402.
- Glaser, R., G. Fuhr, and J. Gimsa. 1983. Rotation of erythrocytes, plant cells, and protoplasts in an outside rotating electric field. *Stud. Biophys.* 96:11–20.
- Hagedorn, R., and G. Fuhr. 1984. Calculation of rotation of biological objects in the electric rotation field. *Stud. Biophys.* 102:229–238.
- Hertz, H. 1881. Ueber die Vertheilung der Electricität auf der Oberfläche bewegter Leiter. *Wied. Ann.* 13:266–275.
- Heydweiller, A. 1897. Ueber Rotation im constanten elektrischen Felde. *Verh. Phys. Ges. (Berl.)*. 16:32–36.
- Holzapfel C., J. Vienken, and U. Zimmermann. 1982. Rotation of cells in an alternating electric field: theory and experimental proof. *J. Membr. Biol.* 67:13–26.
- Jones, Th. B. 1984. Quincke rotation of spheres. *IEEE (Inst. Electr. Electron. Eng.) Trans. Indus. Appl.* Vol. IA-20. 4:845–849.
- Lampa, A. 1906. Über Rotation im elektrostatischen Drehfelde. *Wien. Ber.* 115(2a):1659–1690.
- Lertes, P. 1921. Untersuchungen über Rotationen von dielektrischen Flüssigkeiten im elektrischen Drehfeld. *Z. Phys.* 4:315–336.
- Murashige, T., and F. Skoog. 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiol. Plant.* 15:473–497.
- Mischel, M., and H. A. Pohl. 1983. Cellular spin resonance: theory and experiment. *J. Biol. Phys.* 11:98–102.
- Pohl, H. A. 1983. Cellular spin resonance in pulsed rotating fields. *J. Biol. Phys.* 11:59–65.
- Pohl, H. A., and T. Braden. 1982. Cellular spin resonance of aging yeast and of mouse sarcoma cells. *J. Biol. Phys.* 10:17–30.
- v. Schweidler, E. 1897. Über Rotationen im homogenen elektrischen Felde. *Sitzungsber d k Akad d Wiss.* 106:526–532.
- Statton, J. A. 1940. *Electromagnetic Theory*. McGraw Hill Inc., New York.
- Zimmermann, U., and W. M. Arnold. 1983. *In Coherent Excitations in Biological Systems*. Springer Verlag, Berlin-Heidelberg. 211–221.