ROTATION OF DIELECTRICS IN A ROTATING ELECTRIC HIGH-FREQUENCY FIELD

Model Experiments and Theoretical Explanation of the Rotation Effect of Living Cells

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ABSTRACT Model experiments are carried out to clarify the mechanism of rotation of living cells in a rotating electric field. According to classical investigations of the rotation of macroscopic bodies in external fields, the rotation of spherical glass vessels or metal cylinder filled with electrolyte solutions was investigated. The relation of the calculations of Lertes (1921*a*,*b*) to the recent paper of Arnold and Zimmerman (1982) and our new derivations lead to equations explaining the rotation of objects. The results are compared with measurements using mesophyll protoplasts and data from the literature.

INTRODUCTION

Following various observations indicating that cells can rotate in an alternating electric field (Pohl and Cranes, 1971; Pohl, 1978) and the theoretical explanation of this phenomenon (Holzapfel et al., 1982), Arnold and Zimmermann (1982) introduced a new technique that induces rotation in a four-electrode chamber. In this case the electrodes are driven with sinusoidal voltages having a progressive 90° phase difference. As a result, in the center of the measuring chamber a constant electric field vector (**E**) rotates. This method allows easy measurement of the rotation speed of several kinds of cells (Arnold and Zimmermann, 1982; Glaser et al., 1983). The rotation depends on the frequency of the applied field as well as on the field strength, membrane capacity, and resistance. Therefore, this method may become important in biophysical cell analysis.

Holzapfel et al. (1982) and Arnold and Zimmermann (1982) used dipole theory for the physical interpretation of this rotation phenomenon. Their theory predicts that the sense of rotation should be the same as that of the applied field vector (**E**). In all experiments (Arnold and Zimmermann, 1982; Glaser et al., 1983), however, the cells spun in the opposite direction. This indicates that basic principles of this phenomenon have not bee interpreted completely.

An investigation of classical physical papers indicates that the first suggestion of the rotation of physical bodies in changing fields came from Heinrich Hertz (1881). Quincke (1896, 1897), Heydweiller (1897), and v. Schweidler (1906) worked experimentally and theoretically in the field. To generate alternating electric fields Quincke, for instance, used nearly 1,200 galvanic elements, Leyden jars as capacitors and mannitol solutions for calibration of the resistances. In 1921 Lertes produced rotating fields in MHz-range, using nearly the same wiring diagram as we did, despite our modern transistors. The wiring diagram was developed by Görges (1898) and Lang (1906). The aim of this paper is to demonstrate the rotation phenomenon with macroscopic bodies, well defined in geometrical and electrical properties to show how rotation experiments can be used to determine membrane properties.

MATERIAL AND METHODS

Electric Field

Four sinusoidal voltage with 90° phase differences were produced according to the method of Arnold and Zimmermann (1982). By using conventional transistors we obtained output voltages from 0 to 250 V in the 100 Hz to 500 kHz range.

Measuring Chamber for Macroscopic Objects

The distances between the two electrode-couples were each 5 cm and the chamber was square. Each stainless steel electrode had an area of 10 cm^2. The measuring object was fixed by a 2-m–long filament of thread in the middle of the chamber. The frictional forces were very small and could be neglected up to five revolutions of the object. The rotation speed was registered automatically by using a photoelement (Fig. 1). The conductivity of the bathing electrolyte solutions was adjusted with KCl. The volume

(For definitions of A_1, A_2, B_1, B_2, C_1, and C_2, see Appendix)

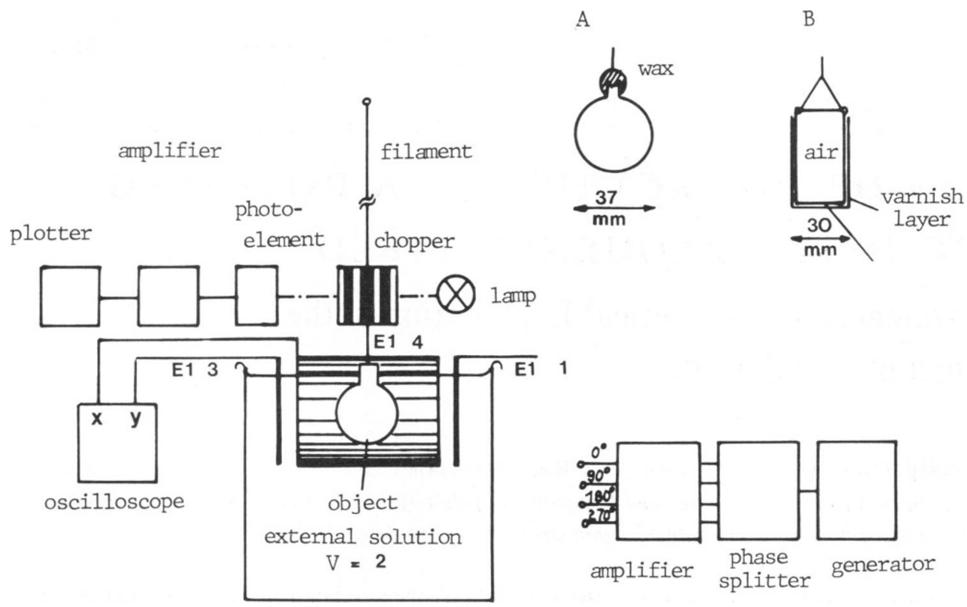

FIGURE 1 Schematic diagram of the experimental setup for rotation measurement (object *A*: hollow glass sphere; object *B*: hollow aluminum cylinder isolated by varnish layer (Nitro-black) on the surface).

of the measuring chamber amounted to 2 l. As a result the conductivity was constant over a long period.

Measurement for Microscopic Objects

For protoplasts a measuring chamber as described by Arnold and Zimmermann (1982) was used.

Measuring Objects

For our experiments we used three different objects. At first a hollow glass sphere (diameter 3.7 cm) with an opening for changing the solution inside. The second object was an aluminum cylinder (diameter 3 cm, length 4 cm) with a thin varnish layer (Nitro-black) on the surface. In one case we used a cylinder (diam 4 cm, length 6 cm) covered by a rubber membrane. The third object was mesophyll protoplasts from *Avena sativa* prepared according to Hampp and Ziegler (1980).

EXPERIMENTAL RESULTS

For all objects used in our experiments, rotation in a rotating electric field was observed. The direction of rotation, as in the experiments with living cells (Arnold & Zimmermann, 1982; Glaser et al., 1983), was opposite to the spin of the field vector. Only in the case where the external medium was air did we observe slow rotation of the objects in the same direction as the electric field. Fig. 2 indicates measurements of the angular velocity (ω_z) of the objects as a function of the applied field strength (**E**) for four different objects. The plot using the square of the field strength as abscissa indicates clearly that the parameter $R = \omega_z/\mathbf{E}^2$ is constant. We called the parameter R "rotation," in analogy to the "mobility" ($v/\mathbf{E}$) in cell electrophoresis (Glaser et al., 1983). Corresponding to single-cell experiments, rotation is a function of the frequency (f) of the alternating electric field (Fig. 3). The points could be fitted by the function:

$$R = R_{max} \frac{2f/f_0}{1 + (f/f_0)^2}, \tag{1}$$

where f_0 is frequency of maximum rotation.

Table I indicates results of various experiments with glass spheres. Knowing the frequency (f_0) for maximal rotation (R_{max}), we can calculate the capacity of the dielectric layer (glass) according to the equation

$$C_m = \frac{1}{2 \cdot \pi \cdot r \cdot f(1/G_i + 1/2 \cdot G_e}, \tag{2}$$

where r is the radius, G_i is the internal conductivity and G_e is the external conductivity. (Pauly and Schwan, 1959; Arnold and Zimmermann, 1982).

For cylinders the term ($2G_e$) in the denominator must be replaced by G_e. As Table I indicates, these values correspond well to the capacity measured separately using a Wheatstone-bridge with the glass sphere in mercury or in 0.1 M KCl solution.

For plant protoplasts we get $C_m \approx 5 \cdot 10^{-3}\ F/m^2$ for both the combined system of tonoplast and plasmalemma membranes. Thus for each membrane the well-known value of nearly $10^{-2}\ F/m^2$ is obtained. Table II shows direction of spin for objects in relation to the electric field rotation under several conditions. In the first three cases there is water inside and outside the sphere. Depending on the ratio of external to internal conductivity the spin direction can be opposite to or equidirectional with the electric field. All experiments with living cells are examples of the first case and therefore the spin direction of all cells is opposite to the electric field vector. From the literature (Lertes, 1921 *a*, *b*)

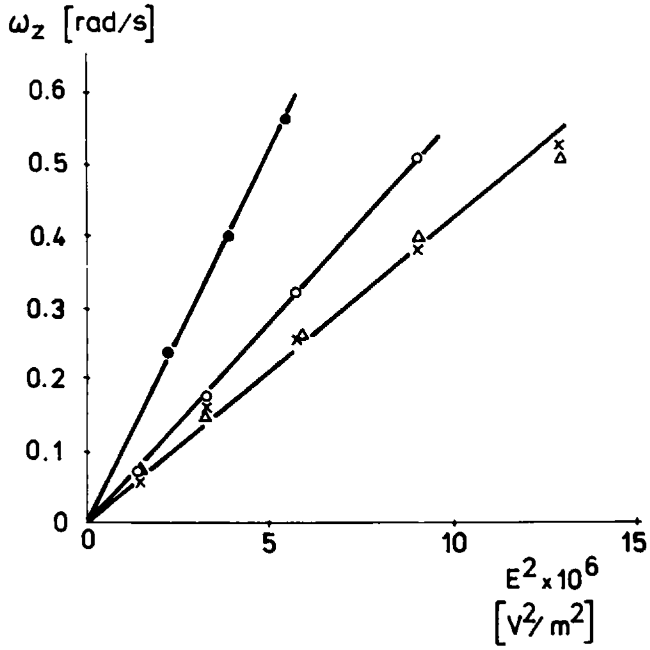

FIGURE 2 Angular velocity (ω_z) in dependence on field strength (E) (X) cylinder with rubber membrane, $G_i = 10^{-1}$ S/m, $G_e = 5 \cdot 10^{-4}$ S/m, diameter 4 cm. (Δ) glass sphere, $G_i = 10^{-1}$ S/m, $G_e = 5 \cdot 10^{-4}$ S/m, diameter 3.7 cm. (O) aluminum cylinder isolated with varnish layer, $G_e = 5 \cdot 10^{-4}$ S/m, diameter 3 cm. (●) protoplast of *Avena sativa*, $G_e = 5 \cdot 10^{-4}$ S/m, diameter 30 μm.

and our own experiments we know that in air dielectric spheres and cylinders filled with solutions rotate in the direction of the field, but the rotation speed of the object rotating in the same direction as the electric field is very small.

DISCUSSION AND THEORETICAL INTERPRETATION

From the literature we know of three approaches. The first calculation made by Lampa (1906) was based on the assumption that two dielectrics (a sphere and the surrounding medium) are located in a rotating field, or as another possibility, a sphere rotating in a stationary field. These calculations do not include a membrane or another dielectric layer on the surface of the body. Lampa (1906) proceeds from the assumption that part of the current produces a polarization charge on the surface of the rotating body. The current consists of conducting and displacement components

$$i = G \cdot \mathbf{E} + \frac{\epsilon - 1}{4 \cdot \pi} \dot{\mathbf{E}}, \tag{3}$$

where ϵ is the dielectric constant, and G is the conductivity.

At the interface of the dielectrics the difference between influx and efflux should be equal to the increase of surface charge density. From the polarization and conduction components the surface charge density (σ) on the interface of the two dielectrics can be calculated by way of the magnetically effective current. The interactions of these surface charges and the electric field yield the desired torque (N) (for a more detailed description see the derivation by Lampa, 1906 and Lertes, 1921*a*).

Lampa's equation for the torque leading to rotation is

$$N = \mathbf{E}^2 \cdot r^3 \cdot \frac{4 \cdot \pi}{\omega} \cdot \frac{3(\epsilon_e \cdot G_i - \epsilon_i \cdot G_e)}{\frac{16\pi^2}{\omega^2}(2 \cdot G_e + G_i)^2 + (2\epsilon_e + \epsilon_i)^2} \tag{4}$$

or

$$N = 3\mathbf{E}^2 r^3 \frac{(\epsilon_e G_i - \epsilon_i G_e) \cdot (\omega/\omega_o)}{(2G_e + G_i)(2\epsilon_e + \epsilon_i) \cdot [1 + (\omega/\omega_o)^2]}, \tag{5}$$

where $\omega = 2\,\pi f$. In the case where inside and outside the object are aqueous solutions with various conductivities in the milliSiemens-per-meter range, $\epsilon_e \sim \epsilon_i$. Eq. 5 can be written in the following form:

$$N = \mathbf{E}^2 \cdot r^3 \frac{(G_i - G_e)}{(2 \cdot G_e + G_i)} \cdot \frac{\omega/\omega_o}{[1 + (\omega/\omega_o)^2]}. \tag{6}$$

Arnold and Zimmermann (1982) calculate the torque (N) by using dipole theory. For this interpretation a dipole

TABLE I
CHANGE OF THE CHARACTERISTIC FREQUENCY (f_o) AND THE MAXIMUM ROTATION (R_{max}) BY SEVERAL COMBINATIONS OF EXTERNAL AND INTERNAL CONDUCTIVITY (G_e) AND (G_i)

G_i [S/m]	G_e [S/m]	G_i/G_e	f_o [kHz]	$R_{max} \cdot 10^{-7}$ $\left[\frac{\text{rad m}^2}{V^2\text{s}}\right]$	C_m [F/m^2]	Relative regression [%]
0.28	$5 \cdot 10^{-4}$	560	22.32	0.5314	$3.84 \cdot 10^{-7}$	96.3
0.05	$5 \cdot 10^{-4}$	100	25.27	0.4571	$3.35 \cdot 10^{-7}$	98.3
0.013	$4.9 \cdot 10^{-4}$	26.5	17.43	0.4374	$4.58 \cdot 10^{-7}$	97.4
0.002	$5 \cdot 10^{-4}$	4	13.37	0.2350	$4.28 \cdot 10^{-7}$	66.0
$4.9 \cdot 10^{-4}$	$4.9 \cdot 10^{-4}$	1	6.20	0.1510	$4.63 \cdot 10^{-7}$	98.9

Average: $4.24 \cdot 10^{-7}$ F/m^2.
Capacity measured in mercury: $4.88 \cdot 10^{-7}$ F/m^2.

TABLE II
SPIN DIRECTION OF OBJECTS BY CHANGING EXTERNAL AND INTERNAL CONDUCTIVITY (G_e) AND (G_i) IN RELATION TO THE ELECTRIC FIELD VECTOR (E)

Object	Situation		Direction of field and object rotation
Glass sphere	G_i	$> G_e$	↗ ↙
Glass sphere	G_i	$= G_e$	↗ ↙
Glass sphere	G_i	$\ll G_e$	no rotation
Glass sphere	G_i	$G_e = 0$ $\epsilon_e = 1$ (air)	↗ ↗ (Lertes, 1921*a*, *b* and own experiments)
Aluminum cylinder isolated by varnish layer	air	G_e-liquid	↗ ↙
Dielectric sphere	G_i	$G_e = 0$ $\epsilon_e = 1$ (air)	↗ ↗
Protoplast	G_i	$> G_e$	↗ ↙

inside the object is generated that follows the electric field vector with angle φ. The exact form of the torque is

$$N = 4 \cdot \pi \cdot \epsilon_o \cdot \epsilon_e \cdot \mathbf{E}^2 \cdot r^3 \frac{(G_i - G_e)}{(2 \cdot G_e + G_i)} \cdot \frac{\omega/\omega_o}{[1 + (\omega/\omega_o)^2]}. \quad (7)$$

The term $(4 \cdot \pi \cdot \epsilon_o)$ is only the result of using another physical unit system. Nevertheless it is easy to see that Eqs. 6 and 7 are identical. The interpretation of this equation in relation to our experiments leads to the following results: The dependence of the torque (N) and therefore also the angular velocity (ω_z) on the field strength (E) is quadratic. This is in good agreement with the results represented in Fig. 2 and in the literature (Arnold and Zimmerman, 1982; Glaser et al., 1983).

The dependence of rotation (R) on the frequency (f) of the electric field is described by the term

$$\frac{\omega/\omega_0}{1 + (\omega/\omega_0)^2} = \frac{\omega\tau}{1 + (\omega\tau)^2}, \quad (8)$$

where τ is the time constant. The maximum rotation is reached at $\omega = \omega_o$. The fitting of this function has been plotted in Fig. 3. Table I shows that the calculated curves are in good agreement with the experimental data (relative regression >90%).

However, the predictions of these questions for the rotation (R) as a function of the ratio of G_i/G_e are not correct. Both equations show that for $G_i = G_e$ the torque is zero, but, in several experiments under these conditions, we observed rotation of a glass sphere (Tables I and II). Fig. 4 shows the theoretical curve (A) predicted by Eq. 7. The experimental points could be fitted only for $G_i/G_e > 3$.

From the derivation of Lampa's equation it is easy to understand why at $G_i = G_e$ the torque should be zero. The membrane as a dielectric barrier between the two solutions is neglected. Therefore in the case that $G_i = G_e$ there is no difference between the sphere and the surrounding medium. This means that effectively no sphere exists and, consistently, there can be no torque.

Another shortcoming of Lampa's approach is the calculation of the maximum angular velocity (ω_o)

$$\omega_o = \frac{4 \cdot \pi \cdot (2 \cdot G_e + G_i)}{(\epsilon_i + 2\epsilon_e)}; \qquad \epsilon = \epsilon_e = \epsilon_i, \quad (9)$$

or in SI

$$\omega_o = \frac{(2 \cdot G_e + G_i)}{3 \cdot \epsilon_0\epsilon_e}.$$

Thus, if $G_i \gg G_e$ and G_i = constant, a change in G_e should produce no change in ω_0. However, our experimental results show the contrary effect (see Tables I, III). For the

TABLE III
THEORETICAL AND EXPERIMENTAL VALUES OF THE CHARACTERISTIC FREQUENCY (f_o) AFTER EQ. 2

G_i (S/m)	G_e (S/m)	f_o Theoretical (kHz)	f_o Experimental (kHz)	Δf_o
0.28	$5 \cdot 10^{-4}$	20.23	22.32	−2.09
0.05	$5 \cdot 10^{-4}$	19.90	25.27	−5.37
0.013	$4.9 \cdot 10^{-4}$	18.49	17.43	+1.06
0.002	$5 \cdot 10^{-4}$	13.53	13.37	+0.16
$4.9 \cdot 10^{-4}$	$4.9 \cdot 10^{-4}$	6.63	6.195	+0.43

Glass sphere, $C_m = 4.24 \cdot 10^{-7}$ F/m^2, diameter $3.7 \cdot 10^{-2}$m.

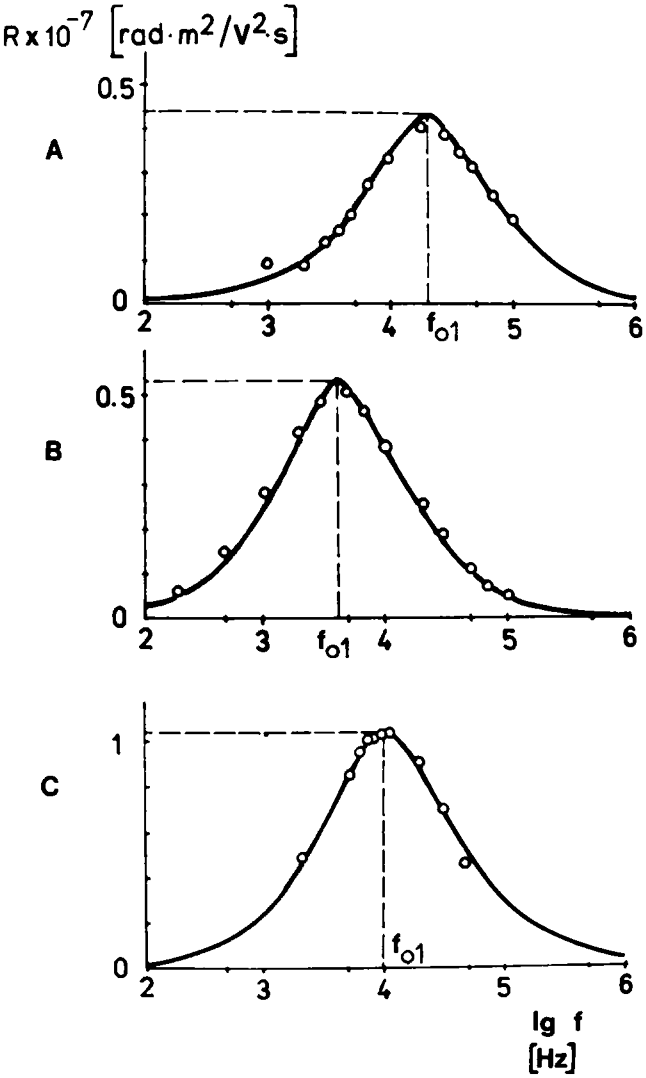

FIGURE 3 Rotation (R) of metal cylinder, glass sphere and protoplast as a function of frequency (f). (A) hollow glass sphere, $G_i = 2.8 \cdot 10^{-1}$ S/m, $G_e = 5.1 \cdot 10^{-4}$ S/m. (B) aluminum cylinder isolated by varnish layer, $G_e = 5.1 \cdot 10^{-4}$ S/m. (C) protoplast of *Avena sativa*, $G_e = 2.2 \cdot 10^{-3}$ S/m, diameter 30 μm. Relative regression: (A) 95.3%; (B) 97.9%; (C) 97.2%.

special case $G_i \gg G_e$, Arnold and Zimmerman (1982) obtain for torque

$$N = 2\pi \cdot \epsilon_o \cdot \epsilon_e \cdot \mathrm{E}^2 \cdot r^3 \frac{\omega/\omega_o}{1 + (\omega/\omega_o)^2}. \tag{10}$$

Additionally, they introduced the following term for ω_o (Arnold and Zimmermann, 1982)

$$\omega_o = \frac{1}{r \cdot C_m (1/G_i + 1/2 \cdot G_e)}. \tag{11}$$

This discussion indicates that a more detailed description of the rotation phenomenon is necessary. The results show that the influence of the membrane cannot be neglected. The derivation should take into consideration

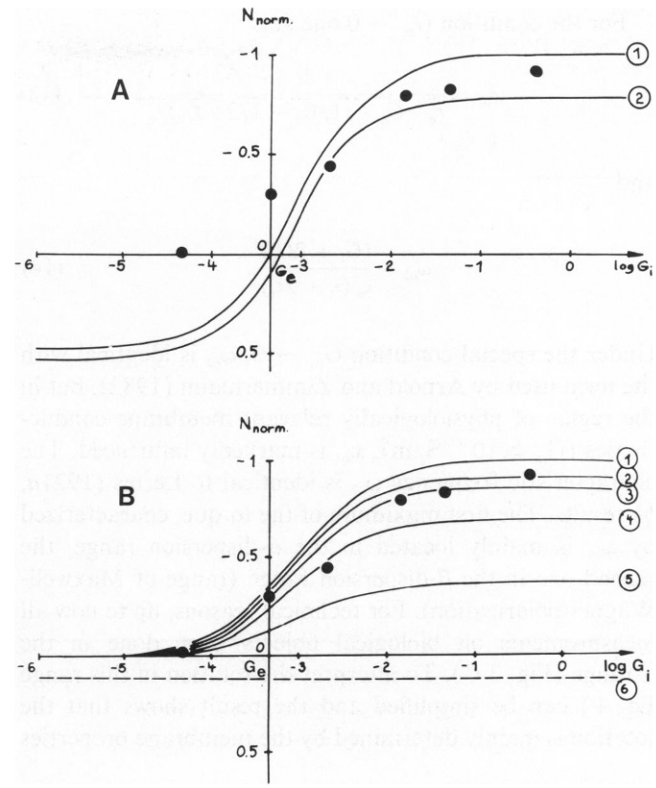

FIGURE 4 The torque (N) and the rotation (R), respectively, normalized as a function of the ratio of the conductivities G_i/G_e. (A) comparison with Lertes result (2) and Eq. 7 (1). (B) comparison with Eq. 15, 1 - $d = r_e - r_i = 1$ μm; 2 - $d = 50$ μm; 3 - $d = 100$ μm; 4 - $d = 250$ μm; 5 - $d = 1000$ μm.

the following three-component system: (a) Outside medium (ϵ_e; G_e); (b) a dielectric barrier or membrane (ϵ_m; G_m); and (c) inside medium (ϵ_i; G_i) (Fig. 6).

Such a calculation was described by Lertes (1921a) but he considered only the special situation where $\epsilon_e = 1$ (air) and concluded that the membrane is without effect. For this reason the equations given by Lertes are not suitable for cells. Following Lertes we also use three-component system for our derivation of the torque (for a short derivation see Appendix). For the torque (N) we obtain the following equation:

$$N = 4\pi \cdot \epsilon_o \cdot \epsilon_e \mathrm{E}_o^2 \cdot r^3 \left\{ \frac{(B_2C_1 - B_1C_2)}{B_2 \cdot C_2} \cdot \frac{\omega/\omega_{o1}}{[1 + (\omega/\omega_{o1})^2]} + \frac{(A_2B_1 - B_2A_1)}{A_2 \cdot B_2} \cdot \frac{\omega/\omega_{o2}}{[1 + (\omega/\omega_{o2})^2]} \right\}, \tag{12}$$

where

$$\omega_{o1} = \frac{C_2}{\epsilon_o B_2} \quad \text{and} \quad \omega_{o2} = \frac{-B_2}{\epsilon_o A_2}.$$

For the condition $G_m \rightarrow 0$ one gets

$$\omega_{o1} = \frac{1}{r_e \cdot C_m \cdot (1/G_i + 1/2 \cdot G_e)} \tag{13}$$

and

$$\omega_{o2} = \frac{(G_i + 2G_e)}{\epsilon_o\,(\epsilon_i + 2\epsilon_e)}. \tag{14}$$

Under the special condition $G_m \rightarrow 0$, ω_{o1} is identical with the term used by Arnold and Zimmermann (1982), but in the region of physiologically relevant membrane conductivities ($G_m \geqq 10^{-7}$ S/m), ω_{o1} is markedly influenced. The characteristic frequency ω_{o2} is identical to Lertes (1921*a*, *b*) results. The first maximum of the torque, characterized by ω_{o1} is mainly located in the α-dispersion range, the second one in the β-dispersion range (range of Maxwell-Wagner polarization). For technical reasons, up to now all measurements on biological objects were done in the α-range (Fig. 3 *C*). To interpret the rotation in this range Eq. 12 can be simplified and the result shows that the rotation is mainly determined by the membrane properties

$$N = 4\pi \cdot \epsilon_o \cdot \epsilon_e \cdot E_o^2 \cdot r_e^3 \left\{\frac{(C_1B_2 - C_2B_1)}{B_2C_2} \cdot \frac{\omega/\omega_{o1}}{[1 + (\omega/\omega_{o1})^2]}\right\}. \tag{15}$$

In accordance with our experimental results the torque (N) is proportional to E^2 and r^3, the dependency on frequency is correct and also for $G_i = G_e$ and $r_i < r_e$ (existence of a membrane) the torque remains finite (Fig. 4 *B*).

Regarding the spin direction of the objects, the results of Arnold and Zimmermann (1982) support our observation that the sense of cell rotation in the frequency range up to 1 MHz is contrary to the spin of the electric field. Lertes (1921*a*, *b*) observed that at higher frequencies (1 to 100 MHz), hollow liquid-filled glass spheres in air follow the field. In analogous experiments using a glass sphere filled with distilled water, paraffin, or alcohol and suspended in air at a field strength of 10^4 V/m we confirmed this result. In general, according Eq. 12 the polarity of the field-induced dipole and also the polarity of object rotation is determined by the relations between ϵ and G in the internal, external, and boundary spaces. Our experimental observations agree with Eq. 12, which predicts a positive torque for glass spheres in air whereas for the same frequencies <1 MHz biological objects in solutions should have a negative torque (Fig. 5). Of special interest is the fact that the simplification made by Arnold and Zimmermann (1982) leading to ψ_{o1} is only applicable if the conductivity of the cell membrane is zero. Our calculations show that even membrane conductivities of 10^{-7} S/m influence the behavior of cells in rotating electric fields. Because such conductivities are in the physiological range, the rotation technique may play a growing role in investigation of membrane properties, such as distinguishing living cells from dead ones. Furthermore, it should be possible to detect the action of ionophores on the membrane. This technique could be applied in cell-fusion experiments, in separating cell species, and in testing the compatibility of biomaterials.

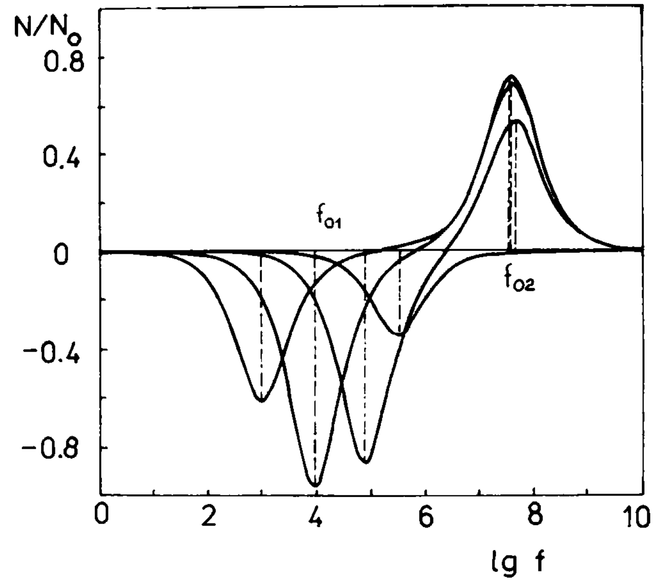

FIGURE 5 Torque (N) of a shell surrounded sphere in dependence on the frequency (f) of the external rotating field under the conditions $G_m < (G_i; G_e)$; $\epsilon_m < (\epsilon_i; \epsilon_e)$ for different conductivities G_e (from left to right: $G_e = 5 \cdot 10^{-4}$S/m; $G_e = 5 \cdot 10^{-3}$S/m; $G_e = 5 \cdot 10^{-2}$S/m; $G_e = 5 \cdot 10^{-1}$S/m.

Finally, some remarks on the model used. We started from the fact that the dielectrics are homogeneous. Existing membrane potentials and surface charges were not considered. To a first approximation our model describes cells with one membrane system. Protoplasts and cells with walls represent much more complicated systems. For those objects one must first check what kind of simplifications are allowed. In spite of this, the results show that the

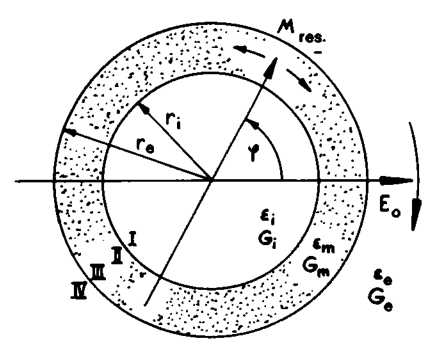

FIGURE 6 Model with induced dipole leading to the object rotation.

method of cell rotation is highly suitable for measuring membrane properties.

APPENDIX

Short form of the calculation of the torque (N) leading to object rotation (for the principles and a more detailed derivation of the resulting electrical dipole moment (m_{el}) see Lertes, 1921*a,b*; Dänzer, 1934; Pauly and Schwan, 1959; Holzapfel et al., 1982). The electrical dipole moment of a sphere is

$$\vec{m}_{el} = \iint dA\sigma(r)\vec{r}, \tag{A1}$$

where σ is surface charge density. In case of a shell surrounded sphere and an electric field of the form

$$\vec{\mathbf{E}} = \vec{\mathbf{E}}_o \exp(j\omega t) \tag{A2}$$

the calculation of the resulting dipole moment leads to

$$\vec{\mathbf{m}}_{el} = 4\pi\epsilon_o\epsilon_e\vec{\mathbf{E}}r_e^3 \cdot \left\{\frac{3\bar{\epsilon}_m(\bar{\epsilon}_e - \bar{\epsilon}_i) + x[(\bar{\epsilon}_i - \bar{\epsilon}_m)(2\bar{\epsilon}_m + \bar{\epsilon}_e)]}{-3\bar{\epsilon}_m(\bar{\epsilon}_i + 2\bar{\epsilon}_e) - 2x[(\bar{\epsilon}_i - \bar{\epsilon}_m)(\bar{\epsilon}_e - \bar{\epsilon}_m)]}\right\}, \tag{A3}$$

where ϵ_e is the real part of the external dielectric constant; $\bar{\epsilon}_i$; $\bar{\epsilon}_m$; $\bar{\epsilon}_e$ are complex dielectric constants; d is the thickness of the membrane; and $x = 3d/r_e$ (see also Pauly and Schwan, 1959).

Eq. A3 has to be transformed to

$$\vec{\mathbf{m}}_{el} = 4\pi\epsilon_o\epsilon_e\vec{\mathbf{E}}r_e^3\left\{\frac{A_1\epsilon_o^2\omega^2 + jB_1\epsilon_o\omega + C_1}{A_2\epsilon_o^2\omega^2 + jB_2\epsilon_o\omega + C_2}\right\} \tag{A4}$$

where

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

$$A_2 = -\epsilon_m(\epsilon_i + 2\epsilon_e) - \frac{2 \cdot d}{r_e}[(\epsilon_i - \epsilon_m)(\epsilon_e - \epsilon_m)]$$

$$B_1 = -\left\{G_m(\epsilon_e - \epsilon_i) + \epsilon_m(G_e - G_i) + \frac{d}{r_e}[(G_i - G_m)(2\epsilon_m + \epsilon_e) + (2G_m + G_e(\epsilon_i - \epsilon_m)]\right\}$$

$$B_2 = G_m(\epsilon_i + 2\epsilon_e) + \epsilon_m(G_i + 2G_e) + \frac{2 \cdot d}{r_e}[(\epsilon_i - \epsilon_m)(G_e - G_m) + (\epsilon_e - \epsilon_m)(G_i - G_m)]$$

$$C_1 = -G_m(G_e - G_i) - \frac{d}{r_e}(G_i - G_m)(2G_m + G_e)$$

$$C_2 = G_m(G_i + 2G_e) + \frac{2d}{r_e}(G_i - G_m)(G_e - G_m).$$

Following Arnold and Zimmermann (1982), it can be shown that in the rotating electric field the torque

$$\vec{N} = R_e[\vec{m}_{el}\exp(j\omega t)] \times R_e[\vec{\mathbf{E}}_o\exp(j\omega t)] \tag{A5}$$

develops. Using Eq. A4 one obtains

$$\vec{N} = 4 \cdot \pi \cdot \epsilon_o \cdot \epsilon_e\vec{\mathbf{E}}_o^2 r_e^3 \cdot \left\{\frac{(B_2C_1 - B_1C_2)}{B_2 \cdot C_2} \cdot \frac{\omega/\omega_{o1}}{[1 + (\omega/\omega_{o1})^2]} + \frac{(A_2B_1 - A_1B_2)}{A_2B_2} \cdot \frac{\omega/\omega_{o2}}{[1 + (\omega/\omega_{o2})^2]}\right\} \cdot \vec{e}_z, \tag{A6}$$

where $\hat{\mathbf{e}}_z$ is a unit vector in the z-direction.

The characteristic frequencies ω_{o1} and ω_{o2} can be calculated from

$$\omega_{o1} = \frac{C_2}{\epsilon_o B_2}$$

and

$$\omega_{o2} = \frac{-B_2}{A_2 \cdot \epsilon_o}. \tag{A7}$$

The comparison of C_2 and B_2 in Eq. A7 with the terms in Eq. A4 shows that ω_{o1} is essentially determined by the membrane properties.

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