Mechanical resonances of bacteria cells

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The quality of the natural vibrations of specific bacteria is investigated using a shell model which accounts for the elastic properties of the membrane and the associated viscosities of the cytoplasma and the surrounding fluid. The motion of the membrane is approximated in terms of the distribution of internal forces over the shell thickness, which is assumed to be much less than the size of the cell. Flexural moments and intersecting stresses are neglected. Using experimentally obtained values for the membrane properties, high-quality resonances are predicted for several types of bacteria which have radii greater than 5 μm. Viscous shear waves are the main source of energy dissipation as has been previously reported in other studies on the natural oscillations of red blood cells, drops, and bubbles. Implications for the acoustic mediated destruction of bacteria are discussed.

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I. INTRODUCTION

Ultrasound has been shown to be an effective means for killing bacteria [1–4]. To better understand the biophysical effects of ultrasound on the bacteria it is necessary to analyze the physical and mechanical phenomena which occur during the ultrasound scattering [5]. Such an analysis encompasses a study of the spectrum of the natural mechanical vibrations. The theoretical analysis of the natural oscillation of biological cells follows from an extension of the theory of drop oscillations, which was studied by Rayleigh and Lamb [6]. An expression for the frequency of natural oscillations of a drop in air was obtained by Rayleigh, and for a drop in an inviscid fluid by Lamb. The general dispersion equation of the viscous drop oscillations in a viscous fluid was obtained by Miller and Scriven [7]. Like a drop, if a cell is deformed slightly by some external force which is subsequently removed, the cell will return to its original shape. Depending on the viscoelastic properties of the cytoplasm and the elasticity of the cell's membranes this process may involve either a series of oscillations about a spherical shape with continuously decreasing amplitude (resonance oscillations) or else an aperiodic direct return to the spherical shape (an aperiodic relaxation movement). In this paper, we examine the possibility of resonance oscillations of bacteria cells.

The question of resonance in mechanical oscillations of cells was investigated by Ackerman [8]. Based on early works of Rayleigh and Lamb [6], Ackerman estimated resonance frequencies and qualities of red blood cells modeling the cells as spherical, isotropic elastic shells filled with and surrounded by viscous fluids [9,10]. In order to estimate the possibility of detecting the resonance of a cell, Ackerman considered the effect of viscous damping on the quality of the natural oscillations of the cell [11]. However, his simplified cell model and the mathematical errors in the derivation of the quality of the natural cell's oscillations [11–13] impose limitations on potential applicability of his work [14–16] (see also Refs. [17,18]). His experimental results have never, to our knowledge, been reproduced; nevertheless, they cannot be completely disregarded. A more rigorous theory of the natural oscillations of biological cells based on a more complete understanding of the elasticity of cellular materials was subsequently developed [19]. The dispersion equation obtained in Ref. [19] has a complex form and only simple approximations were obtained for red blood cells (RBCs). It was found that due to small values of the shear elastic modulus of the RBCs and the high viscosity of the internal fluid, the natural oscillations of the RBCs were always aperiodic relaxation movements. Meanwhile, estimations of the quality of natural vibrations of biological cells revealed that natural oscillations with a relatively high quality factor were possible for cells with a rigid wall (such as plant cells or bacteria). Qualitative estimations obtained in Ref. [19] were in agreement with experimental data. Aperiodic relaxation movements of the RBCs have been studied experimentally [20,21]. Resonance oscillations were observed [22] in algae hydrodiction at 1 MHz by Miller [22]. Also, resonancelike phenomena has been observed in a suspension of brine shrimp [23] (see also Refs. [24–26]). The possibility of resonances in viruses has been discussed recently [27–29]. Virus particles have been modeled as liquid drops, elastic spheres, and cylinders [27,30]. The error and limitations in an undamped elastic sphere formulation has been outlined in Ref. [31].

This work seeks to analyze the spectra of the natural oscillations of different types of bacteria by numerically solving the dispersion equation derived in Ref. [19] for recent data for the mechanical properties of bacteria [32–35]. The dispersion equation for the mechanical oscillations of the cell was derived using a shell model of the cell that takes into account the elasticity of the bacterium shell and viscoelastic properties of the surrounding and internal fluid of the bacterium. This shell model has been shown to adequately describe the attenuation of sound in RBC suspensions [5].

It is demonstrated that the characteristic natural movements of the cell are determined both by the elastic properties of the shell and the associated viscosities of the system. Natural oscillations of sufficiently high quality factor seem possible for several types of bacteria which have a rigid wall.

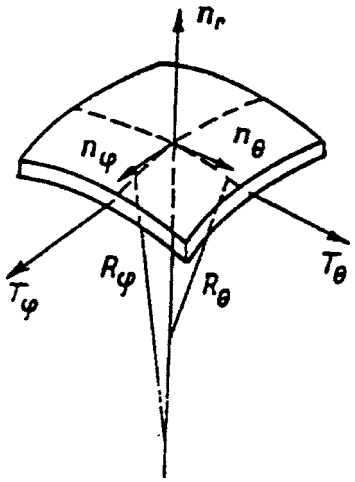

FIG. 1. Stresses on the element of the spherical shell.

II. MODEL

The pioneering measurements of the elastic moduli of the erythrocyte's membrane by Evans and his colleagues [36] fostered the development of realistic mechanical models of cell. The cell, as a mechanical system, resists change both in volume and shape. For most cells the intracellular contents can be represented by an aqueous solution, a solid, or gel of density ρ and volumetric elasticity modulus K_V, which are close to the values of the same parameters in the ambient fluid. Resistance to change in the shape of the cells of different structure may be due to a variety of factors. We shall consider only those cells in which the shape is maintained by a thin cortical surface layer. Such surface elasticity is characteristic of plant cells and many bacteria or protozoa but not erythrocytes and adipose cells. Plant cells and bacteria possess a rigid cell wall [37], but in erythrocytes the elastic properties of the shell are determined by the bilipid membrane and its polymer network [36]. A theoretical study of the spectrum of the natural vibrations may be based on a simplified cell model, the "shell model" [19]. Within the shell model (Fig. 1), a bacterium is assumed to have a spherical shape of radius a. Resistance to change in shape of the bacteria is due to a rigid cell wall [35]. For the shell model the motion of the cell is composed of the motion of three components: the internal fluid, the shell, and the surrounding fluid [5,19]. A spherical shape of the cell is assumed for two reasons. First, it is possible to obtain an analytical solution for spherical objects. Second, many bacteria indeed have a spherical shape (cocci). Since the thickness of the shell is small as compared with the cell radius, the shell is regarded as a simple elastic surface separating two fluids. The frequency of the natural oscillations of bacteria can be obtained by solving the equations of motion of a viscous fluid, where the equations of motion of an elastic shell, are incorporated into the boundary conditions [6].

In reality, the cell's shell is not uniform in thickness [36], it is a stratified system which is composed of at least three layers differing in mechanical properties: bilipid membrane, external shell, and internal polymer network. Each layer makes a unique contribution to the resistance of the shell undergoing different forms of deformation. However, for the cells considered here, the thickness of the shell h is much less than the characteristic size of the cell a; $h \ll a$. For analyzing the movement of the shell an approximation in which the equations of motion include the total values of the internal forces distributed over the thickness of the shell may be used [38]. Within such an approximation the flexural moments and the intersecting stresses in the membrane may be neglected [38].

A. Wave equations

The fluid within and outside the cell is characterized by a density ρ, a velocity of sound c, a compressional or bulk viscosity ζ, and a shear viscosity η. The values relating to the internal fluid will be designated by the subscript i and the values associated with the external fluid by o. The motion of the fluids is described by the particle velocity fields V_i and V_o and the pressure p_i and p_o determined by a standard system of equations consisting of the equation of continuity, the Navier-Stokes equation, and the linearized equation of state [6]. As usual, we assume that perturbation of the fluid density ρ' and pressure p' caused by cell vibrations are small in comparison with static values of the density ρ and pressure p: $p_{\text{total}}=p'+p$, $\rho_{\text{total}}=\rho'+\rho$; $\rho' \ll \rho$; $p' \ll p$. In the linear approach, the equation of continuity can be written as [39]

$$\frac{\partial \rho'}{\partial t} + \rho \,\mathrm{div}(\mathbf{V}) = 0, \tag{1}$$

the Navier-Stokes equation as

$$\rho \frac{\partial \mathbf{V}}{\partial t} = -\,\mathrm{grad}(p') + \eta \Delta \mathbf{V} + (\zeta + \eta/3)\mathrm{grad}\,\mathrm{div}(\mathbf{V}) = 0, \tag{2}$$

where c is the sound velocity in fluid, Δ is the Laplacian, and the linear equation of state is

$$p' = c^2 \rho'. \tag{3}$$

The velocity field in the fluid may be represented as a superposition of two parts: the potential part described by a scalar field Φ, and the vortical part described by a vector field $\mathbf{A}$ [6,39],

$$\mathbf{V} = -\,\mathrm{grad}\Phi + \mathrm{rot}\mathbf{A}. \tag{4}$$

Solutions for the potentials Φ^i and Φ^o are sought in the form of the diverging and standing spherical waves; and for $\mathbf{A}^i$ and $\mathbf{A}^o$ in the form of viscous shear waves, which exponentially attenuate on both sides of the shell due to viscous dissipation. Substituting Eq. (4) into Eq. (3), the wave equation can be expressed as follows:

$$(\Delta + k^2)\Phi = 0, \tag{5}$$

$$(\Delta + \varkappa^2)\mathbf{A} = 0, \tag{6}$$

where $k=\omega/c$, $\varkappa=\sqrt{(i\omega\rho)/\eta}$, ω is the angular frequency. The analysis of a shell of arbitrary shape poses considerable mathematical difficulties; therefore we confine ourselves in

this work to the vibrations of a spherical shell. The V_r and V_θ components of the vector velocity $\mathbf{V}$ can be written in spherical coordinate system as

$$V_r = -\frac{\partial \Phi}{\partial r} + \frac{1}{r}\nabla_\theta A, \tag{7}$$

$$V_\theta = -\frac{1}{r}\frac{\partial \Phi}{\partial \theta} - \frac{1}{r}\frac{\partial (rA)}{\partial r}, \tag{8}$$

where

$$\Delta_\theta A = \frac{1}{\sin\theta}\frac{\partial}{\partial \theta}(\sin\theta A). \tag{9}$$

B. Motion of shell and the boundary value problem

The shell resists deformation due both to constant tension T_o and to the force of surface elasticity. The resistance to change in the surface area is characterized by the area compression modulus K_A, and the resistance to the shear deformation by modulus μ [35,36,40]. The radii of curvature which describe the cell's shell are much larger than the thickness of the membrane structure ($h/a \ll 1$). Due to the small thickness of the shell, the equation of motion of shell can be replaced by the equilibrium equations (Fig. 1). The equation of mechanical equilibrium for an element for the spherical thin shell may be expressed in the form [38]

$$\sigma^o_{rr} - \sigma^i_{rr} - \left(\frac{T_\theta}{R_\theta} + \frac{T_\phi}{R_\phi}\right) = 0, \tag{10}$$

$$\sigma^o_{\theta r} - \sigma^i_{\theta r} + \frac{1}{a}\left(\frac{\partial T_\theta}{\partial \theta} + \cot\theta (T_\theta - T_\phi)\right) = 0, \tag{11}$$

where T_θ, T_ϕ are the normal tension in the shell, R_θ, R_ϕ are the local radii of curvature. The components of the tensor of viscous stress acting on the shell on part of the fluid σ^o_{rr}, σ^i_{rr}, $\sigma^o_{\theta r}$, $\sigma^i_{\theta r}$, have the form [39]

$$\sigma_{rr} = \left[-p' + 2\eta\frac{\partial V_r}{\partial r} + \left(\zeta - \frac{2}{3}\eta\right)\mathrm{div}\,\mathbf{V}\right]_{r=a}, \tag{12}$$

$$\sigma_{\theta r} = \eta\left[\frac{1}{a}\frac{\partial V_r}{\partial \theta} + \frac{\partial V_\theta}{\partial r} - \frac{V_\theta}{a}\right]_{r=a}. \tag{13}$$

Equations (10) and (11) must be supplemented by relationships between the deformations and the internal forces in the shell. The equations of motion are written in an instant local system of coordinates associated with the perturbed surface; its radii of curvature R depends on the relative movement of the shell W ($V = \partial W/\partial t$). Therefore, for the magnitudes R one may use their values for the unperturbed surface taking into account the linear corrections [38]. In the linear approximation, this dependence is fundamental only when the tension the T_θ, T_ϕ contain a constant component determined by the isotropic tension of the shell T_o. The relations between the tensions T_θ and T_ϕ and the strains $e_{\theta\theta}$ and $e_{\phi\phi}$ for a thin spherical shell have the following form [36,41]:

$$T_\theta = K_A(e_{\theta\theta} + e_{\phi\phi}) + \mu(e_{\theta\theta} - e_{\phi\phi}) + T_o, \tag{14}$$

$$T_\phi = K_A(e_{\theta\theta} + e_{\phi\phi}) - \mu(e_{\theta\theta} - e_{\phi\phi}) + T_o. \tag{15}$$

Here $(e_{\theta\theta} + e_{\phi\phi}) = e_S$ is the relative change in the area of the element of the surface, K_A is the area compression modulus which represents the resistance of the shell to change in its surface area; μ is the surface shear modulus. For bacteria, the moduli μ and K_A are comparable in magnitude [35]. For cells without walls, the surface shear modulus is smaller by many orders than K_A: $\mu \ll K_A$ [36]. In Eq. (15) the contribution of the viscous stresses in the shell can be accounted for by allowing the moduli K_A and μ complex values:

$$\tilde{K}_A = K_A - i\omega\eta_K, \tag{16}$$

$$\tilde{\mu} = \mu - i\omega\eta_\mu. \tag{17}$$

The strains are expressed in terms of the displacement W_r and W_θ of surface points:

$$e_{\theta\theta} = \frac{1}{a}\left(W_r + \frac{\partial W_\theta}{\partial \theta}\right), \tag{18}$$

$$e_{\phi\phi} = \frac{1}{a}(W_r + W_\theta \cot\theta). \tag{19}$$

The radii of curvature of a perturbed spherical shell are expressed as

$$\frac{1}{R_\theta} = \frac{1}{a}\left(1 - \frac{W_r}{a} - \frac{1}{a}\frac{\partial^2 W_r}{\partial \theta^2}\right),$$

$$\frac{1}{R_\phi} = \frac{1}{a}\left(1 - \frac{W_r}{a} - \frac{1}{a}\cot\theta\frac{\partial^2 W_r}{\partial \theta}\right). \tag{20}$$

Using Eqs. (15), (19), and (20), we can write the equations of motion of the shell in the following form:

$$\sigma^o_{rr} - \sigma^i_{rr} + \frac{T_o}{a^2}\left(2W_r + \Delta_\theta\frac{\partial W_r}{\partial \theta}\right) - \frac{2K_A}{a^2}(2W_r + \Delta_\theta W_\theta) = 0,$$

$$\sigma^o_{\theta r} - \sigma^i_{\theta r} + \frac{K_A}{a^2}\frac{\partial}{\partial \theta}(2W_r + \Delta_\theta W_\theta) + \frac{\mu}{a^2}\left(2W_\theta + \frac{\partial}{\partial \theta}\Delta_\theta W_\theta\right) = 0, \tag{21}$$

where

$$\Delta_\theta W = \frac{1}{\sin\theta}\frac{\partial}{\partial \theta}(\sin\theta W).$$

The above equations determine the dynamic conditions between the motion of the shell and that of interior and surrounding fluid. It is assumed that both surfaces of the shell move at the same velocity which is also the velocity of the shell itself:

$$\mathbf{V}^i|_{r=a} = \mathbf{V}^o|_{r=a} = \frac{\partial \mathbf{W}}{\partial t} \tag{22}$$

or $V_r^o = V_r^i$, $V_\theta^o = V_\theta^i$. Therefore four undetermined coefficients A_n, B_n, C_n, D_n can be determined from the four boundary condition equations (21) and (22).

III. SOLUTION

We introduce a system of spherical coordinates r, θ, and φ; with the origin at the center of the shell (Fig. 1), and consider only oscillations possessing axial symmetry. For the case of axial symmetry Eqs. (5) and (6) are solved in terms of series expansions of spherical Bessel functions with four undetermined coefficients A_n, B_n, C_n, D_n. We may write these for the surrounding fluid as follows:

$$\Phi^o = \sum_{n=0}^{\infty} A_n h_n(k_o r) P_n(\cos\theta) e^{-i\omega t},$$

$$A^o = \sum_{n=0}^{\infty} C_n h_n(\varkappa_o r) \frac{\partial P_n(\cos\theta)}{\partial \theta} e^{-i\omega t}$$

and for internal phase

$$\Phi^i = \sum_{n=0}^{\infty} B_n j_n(k_i r) P_n(\cos\theta) e^{-i\omega t},$$

$$A^i = \sum_{n=0}^{\infty} D_n j_n(\varkappa_i r) \frac{\partial P_n(\cos\theta)}{\partial \theta} e^{-i\omega t}, \tag{23}$$

where $P_n(\cos\theta)$ are the Legendre polynomials [42], $h_n(kr)$ is the spherical Hankel function of the first kind, $j_n(kr)$ are the spherical Bessel functions [42], and A is the φ component of vector potential $\mathbf{A}: \mathbf{A} = \mathbf{A} i_\phi$. The response of the cell to the external force is determined by the set of A_n, B_n, C_n, D_n. For each value of n these amplitudes are linked by four linear algebraic equations arising from Eqs. (21) and (22),

$$G^m * X^n = 0, \tag{24}$$

where G^n is a 4×4 matrix, the components are given in the Appendix A, and X^n is the following vector:

$$X^n = \begin{bmatrix} A_n \\ B_n \\ C_n \\ D_n \end{bmatrix}. \tag{25}$$

Every partial term, describing the nth mode of oscillations, is determined by the corresponding Legendre polynomials. The linear system given by Eq. (24) has a unique solution if the determinant of the matrix G^n equals zero. The corresponding equation is

$$\det(G^n) = 0. \tag{26}$$

As it was pointed out by Ackerman [11], the wavelength of the longitudinal waves at the frequency of mechanical resonances of the cell are much longer than the radius of the cell: the long-wave approximation, $a/\lambda \ll 1$; where λ is the length of the acoustic wave. In the long-wave approximation the solution of the dispersion equation (26) can be simplified as shown in Appendix A. The solutions of the dispersion equation (26) give the frequencies of the natural oscillations of cells ω_n. Equation (26) can be written in a more compact, closed analytical form as outlined in Ref. [19],

$$d^n(\omega) = d_D^n(\omega) + \frac{\omega_{Kn}^2}{\omega^2} d_C^n(\omega), \tag{27}$$

where

$$d_D^n(\omega) = \left(1 - \frac{\omega_{Tn}^2}{\omega^2}\right)\left(\frac{\rho_o}{\rho_*}\mathcal{H}_n(\xi_o) + \frac{\rho_i}{\rho_*}\mathcal{J}_n(\xi_i) - \Delta\xi\right) \tag{28}$$

$$-\left((2n+1)\frac{\rho_i}{\rho_*}\mathcal{J}_n(\xi_i) - \Delta\xi n(n+2)\right)\left((2n+1)\frac{\rho_o}{\rho_*}\mathcal{H}_n(\xi_o) + \Delta\xi(n^2-1)\right) \tag{29}$$

$$d_C^n(\omega) = \frac{(\omega^2 - \omega_{Tn}^2)(1+\beta) - 4\omega_{\mu n}^2}{\omega^2} - \frac{\rho_i}{\rho_*}\mathcal{J}_n(\xi_i)[(n-1)^2 + \beta(n+1)^2] \tag{30}$$

$$-\frac{\rho_o}{\rho_*}\mathcal{H}_n(\xi_o)[(n+2)^2 + \beta n(n+1)] - 2\Delta\xi[(n-1)(n+2) - \beta n(n+1)], \tag{31}$$

where $\xi_i = \varkappa_i a$, $\xi_o = \varkappa_o a$. The mechanical oscillations of the cell are determined by characteristic frequencies of the cell ω_μ, ω_T, ω_R, ω_K,

$$\omega_{Kn}^2 = \frac{n(n+1)K_A}{\rho_* a^3},$$

$$\omega_{\mu n}^2 = \frac{(n-1)(n+2)\mu}{\rho_* a^3},$$

$$\omega_{Tn}^2 = \frac{(n-1)n(n+1)(n+2)T_o}{\rho_* a^3}, \tag{32}$$

which represent the frequency characterizing the restoring forces in the shell, $\beta = \omega_{\mu n}^2/\omega_{Kn}^2$, and $\rho_* = (n+1) * \rho_i + n\rho_o$. For convenience, we also introduce the relaxation frequency ω_R,

$$\omega_R = \frac{\eta}{\rho a^2}.$$

At this frequency, the depth of viscous wave penetration in fluids coincides with the radius of the particle.

The parameter

$$\Delta\xi = \frac{2(\eta_i - \eta_o)}{i\omega\rho_* a^2} = 2\left(\frac{\rho_i}{\rho_*\xi_i^2} - \frac{\rho_o}{\rho_*\xi_o^2}\right) \tag{33}$$

expresses the process of mechanical relaxation due to the viscous forces in the fluid where the following notation has been introduced:

$$\mathcal{J}_n(\xi_i) = \frac{j_n(\xi_o)}{j_{n+1}(\xi_i)\xi_i}, \tag{34}$$

$$\mathcal{H}_n(\xi_o) = \frac{h_n(\xi_o)}{h_{n-1}(\xi_o)\xi_o}. \tag{35}$$

These functions can be calculated using the iterative relations

$$\mathcal{J}_{n+1}(\xi_i) = \frac{1}{[2n+3-\mathcal{J}_n(\xi_i)]}, \tag{36}$$

$$\mathcal{H}_{n+1}(\xi_o) = \frac{1}{\xi_o^2}\left(2n+1-\frac{1}{\mathcal{H}_n(\xi_o)}\right), \tag{37}$$

where

$$\mathcal{H}_0(\xi_o) = -\frac{i}{\xi_o},$$

$$\mathcal{J}_0(\xi_i) = \frac{1}{1-\xi_i \cot \xi_i}. \tag{38}$$

It is noted that the dispersion equation in a matrix (26) or its analytical forms (27) are equivalent. The form of Eq. (27) can be simplified for two limiting cases. If $K_A=0$, Eq. (27), the dispersion equation of the natural oscillations of drops in immiscible fluids [7,43], $d_D^n(\omega)=0$ is obtained. For cells with a shell such as RBCs or vesicles surrounded by bilipid membranes where $\omega_K \gg \omega_T \gg \omega_\mu$ ($K_A \simeq 1$ N/m, $\mu \simeq 10^{-5}$ N/m [35,36]), the dispersion equation has a form $d_C^n(\omega)=0$. Here the constant tension T_o appears due to turgor pressure inside bacteria. Its maximum value $T_o = e_K K_A$ can be evaluated from the maximally permitted value of change in the area of the membrane, $e_K \sim 5\%$, obtained from experiments on osmotic shock of erythrocytes [36].

A dispersion equation similar to Eq. (27) was obtained in the form of a determinant by Miller and Scriven [7] in the analysis of the free vibrations of a fluid drop where the surface possessed rigidity from a film of surfactants ($\mu=0$). Solutions of the dispersion equation of drops [$d_D^n(\omega)=0$] do not have analytical forms. Prosperetti [43–45] performed a numerical analysis of the solution for drop without the surfactant film. For a more general case of viscous drop in elastic thin shell, the associated dispersion equation was obtained by Zinin *et al.* [19] and later by Lu and Apfel [46,47]. For an accuracy to terms of first order in the parameter $1/|\xi|$, the solution of Eq. (27) was obtained by Miller and Scriven [7], and to terms of second order by Marston [48].

IV. RESULTS AND DISCUSSION

First, it is interesting to qualitatively analyze the overall characteristics of the natural vibrations of different types of cells. In the inviscid limit ($\eta_i, \eta_i \to 0, 1/\xi \to 0$), when the depth of viscous wave penetration tends to zero, the frequencies of the natural cell oscillations are determined by the equation

$$(\omega^2 - \omega_{Tn}^2)(\omega_{Kn}^2 + \omega_{\mu n}^2) - 4\omega_{Kn}^2\omega_{\mu n}^2 = 0. \tag{39}$$

This follows from the substitution of the asymptotic representation of functions $\mathcal{J}_n(\xi_i)$ and $\mathcal{H}_n(\xi_o)$ for the large complex argument ξ,

$$\mathcal{H}_n(\xi_o) \approx -\frac{i}{\xi_o} + \frac{n}{\xi_o^2}, \tag{40}$$

$$\mathcal{J}_n(\xi_i) \approx -\frac{i}{\xi_i} + \frac{(n+1)}{\xi_i^2}. \tag{41}$$

For negligible viscosity, $\xi \to \infty$, $\mathcal{H}_n(\xi_o)$ and $\mathcal{J}_n(\xi_i) \to 0$, and the natural frequencies depend on the elastic frequencies ω_{Kn}^2, $\omega_{\mu n}^2$, ω_{Tn}^2,

$$\omega_n^2(\eta=0) = \omega_{Tn}^2 + \frac{4\omega_{Kn}^2\omega_{\mu n}^2}{\omega_{Kn}^2 + \omega_{\mu n}^2}. \tag{42}$$

For a cell in which the shell is deformed mainly due to the shear deformation ($K_S \gg \mu$), the natural frequency will be close to the frequencies ω_{Tn}^2 and $\omega_{\mu n}^2$:

$$\omega_n^2 \simeq \omega_{Tn}^2 + 4\omega_{\mu n}^2.$$

For cells with a rigid wall such as bacteria, the natural frequencies are close to the values ω_{Kn}. The character of the natural oscillations is determined by the relationship between the cell size and the depth of penetration δ of a viscous wave,

$$\delta = \sqrt{\frac{2\eta}{\omega\rho}} \tag{43}$$

$$\text{such that } \xi = (1+i)\frac{a}{\delta}. \tag{44}$$

At the resonance frequency, the depth of penetration δ is small as compared with the cell size such that $\delta < a$, $|\xi| \gg 1$, so the region the viscous shear wave occupies is a small part of the cell volume and the cell behaves as an elastic system with low damping. If the viscous wave fills the bulk of the volume such as $\delta > a$, $|\xi| \ll 1$, the cell behaves as an aperiodic system and its response is relaxational. The region of the vibratory behavior corresponds to the frequencies $\omega_n \gg \omega_R$ and the region of relaxational to the frequencies $\omega_n \lesssim \omega_R$. Table II shows the characteristic frequencies ω_K, ω_μ (for the quadrupole mode $n=2$), the frequencies of relaxation for different cell types of bacteria, and Bakery yeast cells. In these calculations, it was assumed that the density of the fluid is equal to 10^3 kg/m^3 and its shear viscosity is that of water, $\eta = 10^{-3}$ Pl. The elastic moduli of the bacteria and B. yeast cells are evaluated from a known value of Young's modulus (see Table I) and using the following expressions:

$$K_A = \frac{Eh}{2(1-\nu)}, \tag{45}$$

TABLE I. Elastic shell properties of specific bacteria.

Cell	E (MPa)	Poisson's ratio	Radius (μm)	Thickness (nm)	T (N/m)	Turgor pres. (MPa)
E. coli[a]	25	0.16	0.50	6	7.5×10^{-3}	0.3
M. hungatei[b]	$2-4\times10^{4}$		0.22		3.5–5	30–40
C. eugametos[c]			8	60	38	9.5
B. emersonii[c]			10	450	32	6.5
D. Carota[c]			30	100	45	3
Yeast[d]	0.6	0.5	1.5–8			
Yeast[e]	K_S=12.9 (N/m)	0.5		90		

[a]Reference [34]. Method: AFM.
[b]Reference [33]. Method: AFM.
[c]Reference [32]. Method: gas decompression.
[d]Reference [53]. Method: AFM.
[e]Reference [54]. Method: micromanipulation.

$$\mu = \frac{Eh}{2(1+\nu)}, \tag{46}$$

where ν is Poisson's ratio. The derivation of Eqs. (45) and (46) is given in Appendix B. For most plant cells the thickness h amounts to approximately one percent of the size of the cell, $h/a \approx 10^{-2}$. In its natural surroundings, the wall of the bacteria cell experiences a constant tension T_o through the intracellular pressure (turgor). The known magnitude of the turgor pressure (Table I) allows the evaluation of T_o from Laplace's law for the equilibrium of a curved surface:

$$T_o = P_T a/2. \tag{47}$$

The corresponding characteristic frequency is of the same order as ω_K; $\omega_T/\omega_K \sim (1+\nu)/(1-\nu)$. A change in the ionic composition of the external medium of the turgor pressure and tension may decrease the magnitude of ω_T such that it is substantially smaller than ω_K. From current understanding of the microstructure of the wall, measured properties of its component, data on the shear elasticity, and internal friction of the wood at low frequency [49], in the resonance region it is assumed that the elasticity of the wall exceeds its viscosity, and the viscous dissipation inside the cell wall can be neglected. The wood values offer an estimate of the acoustic attenuation.

The existence of natural vibrations for cells with soft shell even with a low quality factor is an exceptional phenomenon [19]. For most cells (intact erythrocytes; adipose cells, etc.) free motion is of an aperiodic character since the depth of penetration of the viscous shear wave at frequency close to ω_n is either comparable with the size of cell ($|\xi| \approx 1$) or is much larger than it ($|\xi| \ll 1$) (Table II). However, the situation may be different for bacteria. Recent studies have shown that certain bacteria have a stiff elastic shell, meaning that high quality resonances are possible (see Table I). For the high frequency natural oscillations, the depth of penetration δ is small as compared with the cell size $\delta < a$, $|\varkappa a| = |\xi| \gg 1$, the region of the viscous shear wave occupies a small part of the cell volume and the cell behaves as an elastic system with low damping. Simulations of the a/δ ratio at the resonance frequency (Table II) for these types of cells indicate that resonances are impossible for an intact RBC, however, they should be pronounced in Carota bacteria, and exist in B. yeast cells. From Table II, we also conclude that a strong resonance can be expected in cells which are relatively large and rigid.

For resonance natural oscillations Eq. (27) has only one (ω_n) complex solution [43], which can be written in a form

$$\omega_n = \Omega_n - i\alpha_n, \tag{48}$$

where Ω_n and α_n are positive real numbers: Ω_n determines the frequency of oscillations and α_n the rate of their decay. The decaying oscillations may be characterized by another variable, called the quality of oscillation given by the equation (Ref. [50], Chap. 3):

$$Q_n = \frac{\Omega_n}{2\alpha_n}. \tag{49}$$

Hence a solution is sought in the following form:

TABLE II. Frequencies ω_K, ω_μ, ω_{Ri} computed for different cells (n=2).

Cell type	Radius (μm)	$\omega_K/2\pi$ (MHz)	$\omega_\mu/2\pi$ (MHz)	$\omega_{Ri}/2\pi$ (KHz)	ω_K/ω_{Ri}	ω_μ/ω_{Ri}	Ratio
RBC	5	0.331	0.00127	0.0318	10.4	0.04	a/δ_μ=0.14
B. yeast	4.5	0.142	0.0667	0.0078	18.0	8.48	a/δ_K=3.0
Carota	30	0.318	0.152	1.768×10^{-4}	1800	859.8	a/δ_K=30.0

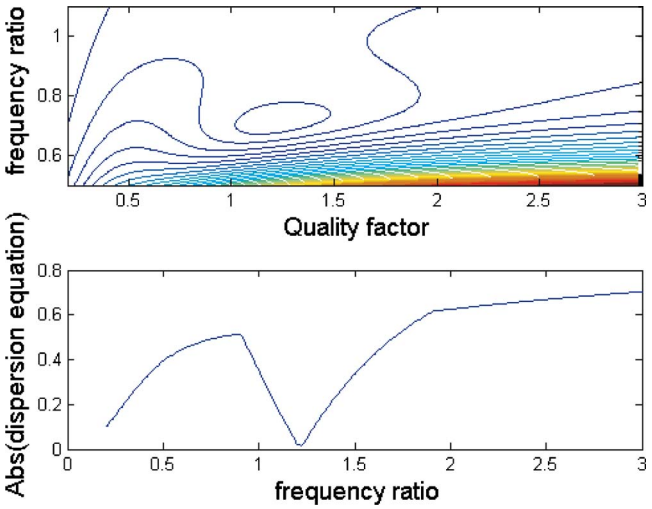

FIG. 2. (Color online) Projection of the minimum of the surface $|d_D^n(\omega)|^2$. Upper plot: two-dimensional image of the surface $|d_D^n(\omega)|^2$ near minimum as a function of quality factor (Q) and nondimensional frequency $\Omega_n/\omega_n(\eta=0)$; lower image: the behavior of the minimum of the $|d_D^n(\omega)|^2$ as a function of Q_n ($n=2$).

$$\omega_n = \Omega_n\left(1 - \frac{i}{2Q_n}\right). \tag{50}$$

To find the solution of the form (50), a MATLAB code was written to determine the zeroes of the function: $|d_D^n(\omega)|^2$ (Fig. 2) on the complex plane. Figure 2 shows contours of the $|d_D^n(\omega)|^2$ surface near the minimum. For clarity we have introduced the nondimensional frequency Ω_n/ω_n ($\eta=0$) [see Eq. (42)]. Results of the computations are shown in the Table III. All computations were done for the mode $n=2$ (Fig. 3), which is thought to be the most important in drop breakup [51]. Figure 3 illustrates the quadrupole and octupole modes.

Table III shows the resonance frequencies and the qualities of natural oscillation for different types of bacteria. For the calculations, it was assumed that the density of the fluid is equal to 10^3 kg/m^3 ($\rho_o=\rho_i=10^3$ kg/m^3) and its shear viscosity is equal to the viscosity of water; $\eta_i=\eta_o=10^{-3}$ Pl. For E. coli and M. hungatei cells, K_A and μ moduli were calculated using Eq. (45) and (46), and Poisson's ratio for M. hungatei shell was assumed to be 0.16. For bacteria, C. eugametos, B. emersonii, and D. carota, the breaking (turgor) pressure, radius, and thickness of the cell shell have been

TABLE III. Natural frequencies Ω_n and qualities of the quadrupole vibrations for different types of cells ($n=2$).

Cell type	a (μm)	$\Omega_n/2\pi$ (MHz)	Q_2
E. coli	0.5	4.58	0.8
M. hungatei	0.22	646.8	6.1
C. eugametos	8	3.41	15.7
B. emersonii	10	2.24	15.8
Carota	30	0.517	23.2
B. yeast (AFM)	4.5	0.16	1.2
B. yeast (micromanipulation)	4.5	2.06	6.6

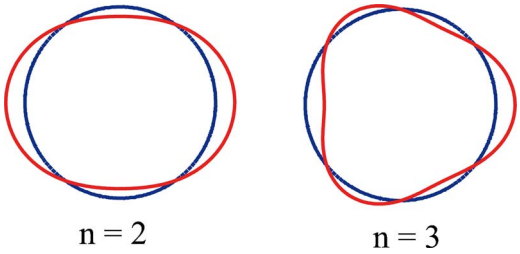

FIG. 3. (Color online) Shape of the quadrupole ($n=2$) and octupole ($n=3$) oscillations.

measured [32]. For these bacteria, we estimated the surface tension using Laplace's law (47), and K_A was estimated assuming that $T=0.5K_A$ (Ref. [35] p. 236), and the modulus μ was computed using expressions (45) and (46) assuming a Poisson's ratio equal to 0.49 [35]. As indicated in Table III, high quality resonances can be expected for the spherical cell C. eugametos, B. emersonii, and D. carota, and for M. hungatei. Though the viscosity of the internal fluid inside bacteria is unknown, some variations in its value should not change the quality sufficiently. Our simulations demonstrate that by increasing the internal viscosity inside B. emersonii by 10 μm in the radius by a factor of 5 ($\eta_i=5\times10^{-3}$ Pl) decreases the quality of the resonance by 26% (from $Q=15.8$, $f=2.24$ MHz to $Q=12.5$, $f=2.23$ MHz). Therefore even a high viscosity value of the cytoplasm will not completely eliminate mechanical resonances of the bacteria shown in Table I. Our simulations also show that the surface tension T_o does not have strong effect on the quality of the mechanical vibration of a cell with a rigid shell. Likewise, an increase of the T_o from 0 to 38 N/m increases the corresponding quality Q from 15.8 to 10.5.

Recently, the mechanical behavior of Bakery yeast cells has received attention because resonance vibrations of the yeast cell membrane at 1 KHz have been detected by atomic force microscope (AFM) [52]. Using this theory we can investigate whether observed resonance is related to the shape resonance oscillations of the cells. Bakery yeast cells are 3–15 μm in diameter with a cell wall thickness of 100–1000 nm. Elastic properties of Bakery yeast cells are given in Table I. We consider oscillations of the cell with the following elastic parameters: $a=8$ μm, $\rho_o=10^3$ kg/m^3, $\rho_i=10^3$ kg/m^3, $E=0.6$ MPa, $h=0.1$ μm, $\nu=0.5$. Moduli K_A and μ were calculated using expressions (45) and (46). Natural frequencies of the Bakery yeast cells can be calculated (Table III). From Table III, it is noted that resonances of $Q=1.2$ are possible at 160 KHz. The frequency of the resonance oscillations of the B. yeast cells is much higher than that detected by Pelling *et al.* [52]. It is believed that the resonances detected by AFM are not related to the mechanical resonances of cell vibration.

We mention that despite the fact that the quality factor for specific types of bacteria can be high these resonances have not been readily observed in numerous biological cell experiments. To our knowledge, there is only one experimental observation of the resonances in algae hydrodiction at 1 MHz by Miller [22]. Resonancelike phenomena have been reported in suspensions of brine shrimp [23] (see also Refs. [24–26]). A physical explanation for these has been sug-

gested in the original Ackerman paper [13] and also in the publication by Marston and Apfel [51]. They suggested that the sound scattering cross section of the cells at the frequency of the cell's shape resonance was fairly small. Indeed, the wavelength of the sound wave in water at the resonance frequency for a 30-μm Carota bacterium cell is 1.67 mm. This is 55 times higher than the radius of the bacterium. Since the cross section of the sound scattering by a small particle like a bacterium is proportional to the fourth power of the ratio $(a/\lambda)^4$, the effect of the sound wave on the bacteria at the frequency of the shape resonance is negligible. Marston and Apfel suggested the excitation of the quadrupole resonance of drops using modulated acoustic radiation pressure, where the wavelength of the carrier wave was close to the radius of the drop and the frequency of modulation was close to the frequency of the quadrupole surface resonance [51]. This method applied to bacteria may facilitate their destruction by ultrasound, though further experimental and theoretical investigations are needed.

A critical issue in the study of the natural oscillations of the bacteria and other biological cells is obtaining appropriate and realistic values for the viscoelastic properties of the cells. In experiments, it is difficult to obtain proper values of the elastic properties of the cell's shell which are approximately 10 nm thick. This is particularly the case with certain bacteria since these cells have a stiff shell and the established method used for measuring elastic properties of RBCs and vesicles [35,36] cannot be applied. Thus discrepancies exist in the literature on the associated values. For instance, the Young modulus of the B. yeast cells measured by AFM [53] ($E=0.6$ MPa) is two orders of magnitude lower than that measured by micromanipulation techniques [54] ($E=110$ MPa). The corresponding qualities determined from these experiments are different (Table III). The more precise measurements of the elastic properties of bacteria will assist in future investigations on the possibility of natural resonances of these cells.

V. CONCLUSIONS

We applied a shell model for a biological cell to estimate the quality of the natural vibrations of the specific types of bacteria. The shell model of a cell takes into account elastic properties of bacteria shells and the viscosities of the cytoplasm and the surrounding fluid. Previously, the successful application of the model to the sound attenuation in RBC suspensions was reported [5]. In this paper, the natural frequencies and corresponding qualities were computed for specific types of bacteria whose elastic properties of shell have been measured experimentally. As in the case of sound attenuation in RBC suspensions, and natural vibrations of drops and bubbles, the main source of the energy dissipation was found to be due to the generation of shear viscous waves. High quality resonances are possible for several types of bacteria, which have radii greater than 5 μm. It is more likely that Gram positive bacteria would have resonances than Gram negative bacteria because the cell wall (shell) of the Gram-positive bacteria is much stiffer than that of Gram negative bacteria [35]. It may be possible to achieve optimized ultrasound destruction of specific bacteria with the modulated acoustic radiation pressure technique developed for exciting shape resonances in drops by Marston and Apfel [51]. This topic along with the interaction of bacteria with acoustic cavitation bubbles are subjects for further studies.

APPENDIX A

With the notations $z_o=k_o a$, $z_i=k_i a$, $\xi_o=\varkappa_o a$, $\xi_i=\varkappa_i a$, the coefficients g_{ij}^n are the elements of matrix G^n given as follows:

$$g_{11}^n = -z_o h_n'(z_o), \tag{A1}$$

$$g_{12}^n = -z_i j_n'(z_i),$$

$$g_{13}^n = n(n+1)h_n(\xi_o),$$

$$g_{14}^n = -n(n+1)j_n(\xi_i),$$

$$g_{21}^n = -h_n(z_o),$$

$$g_{22}^n = j_n(z_i),$$

$$g_{23}^n = \xi_o h_n'(\xi_o) + h_n(\xi_o),$$

$$g_{24}^n = -[\xi_i j_n'(\xi_i) + j_n(\xi_i)],$$

$$g_{31}^n = \frac{\rho_o}{\rho_*} h_n(z_o),$$

$$g_{32}^n = -\left[\left(\frac{\rho_i}{\rho_*} + \frac{2\omega_{Kn}^2}{\omega^2} - n(n+1)\Delta\xi\right) j_n(z_i) - \left(\frac{4\omega_{Kn}^2 + \omega_{Tn}^2}{n(n+1)\omega^2} - 2\Delta\xi\right) z_i j_n'(z_i)\right],$$

$$g_{33}^n = 0, \tag{A2}$$

$$g_{34}^n = \left[\left(\frac{2\omega_{Kn}^2}{\omega^2} - n(n+1)\Delta\xi\right)\xi_i j_n'(\xi_i) - \left(\frac{2\omega_{Kn}^2 + \omega_{Tn}^2}{\omega^2} - n(n+1)\Delta\xi\right) j_n(\xi_i)\right],$$

$$g_{41}^n = 0, \tag{A3}$$

$$g_{42}^n = \left[\left(\frac{\omega_{Kn}^2 + \omega_{\mu n}^2}{\omega^2} - \Delta\xi\right) j_n(z_i) - \left(\frac{2\omega_{Kn}^2}{n(n+1)\omega^2} - \Delta\xi\right) z_i j_n'(z_i)\right],$$

$$g_{43}^n = -\frac{\rho_o}{\rho_*} h_n(\xi_o),$$

$$g_{44}^n = \left[\left(\frac{\omega_{Kn}^2 - \omega_{\mu n}^2}{\omega^2} + \frac{\rho_i}{\rho_*} - (n^2 + n - 1)\Delta\xi \right) j_n(\xi_i) - \left(\frac{\omega_{Kn}^2 + \omega_{\mu n}^2}{\omega^2} - \Delta\xi \right) \xi_i j_n'(\xi_i) \right].$$

In the long-wave approximation, the elements of the matrix can be simplified taking into account the following relationships ($n \geqslant 1$) [42]:

$$z_i j_n'(z_i) \approx n j_n(z_i), \tag{A4}$$

$$z_o h_n'(z_o) \approx -(n+1) h_n(z_o). \tag{A5}$$

The matrix G^n can be further simplified if the third column of the third column of the matrix G^n is divided by the function $h_n(\xi_o)$, and the forth column by the function $j_n(\xi_i)$. The new matrix G^n will contain functions such as $\xi_i j_n'(\xi_i)$ and $\xi_o h_n'(\xi_o)$. These function terms can be easily expressed in terms of $\mathcal{J}_n(\xi_i)$ and $\mathcal{H}_n(\xi_o)$. Indeed, using interactive expression for derivatives of the spherical functions [42] we obtain

$$\frac{\xi_i j_n'(\xi_i)}{j_n(\xi_i)} = -\frac{\xi_i j_{n+1}(\xi_i)}{j_n(\xi_i)} + n = n - \frac{1}{\mathcal{J}_n(\xi_i)}, \tag{A6}$$

$$\frac{\xi_o h_n'(\xi_o)}{h_n(\xi_o)} = \frac{\xi_o h_{n-1}(\xi_o)}{h_n(\xi_o)} - (n+1) = \frac{1}{\mathcal{H}_n(\xi_i)} - (n+1). \tag{A7}$$

If the third column of the matrix G^n is divided by function $h_n(z_o)$, and the second column by the function $h_n(\xi_o)$, and taking into account Eqs. (A4)–(A7), the matrix G^n will have the simple form

$$g_{11}^n = n + 1, \tag{A8}$$

$$g_{12}^n = n,$$

$$g_{13}^n = n(n+1),$$

$$g_{14}^n = -n(n+1),$$

$$g_{21}^n = -1,$$

$$g_{22}^n = 1,$$

$$g_{23}^n = \frac{1}{\mathcal{H}_n(\xi_i)} - n,$$

$$g_{24}^n = \frac{1}{\mathcal{J}_n(\xi_i)} - (n-1),$$

$$g_{31}^n = \frac{\rho_i}{\rho_*},$$

$$g_{32}^n = -\left(\frac{\rho_i}{\rho_*} + \frac{2(n-1)\omega_{Kn}^2 - \omega_{Tn}^2}{(n+1)\omega^2} - n(n-1)\Delta\xi \right),$$

$$g_{33}^n = 0, \tag{A9}$$

$$g_{34}^n = \left(\frac{2\omega_{Kn}^2}{\omega^2} - n(n+1)\Delta\xi \right) \left((n-1) - \frac{1}{\mathcal{J}_n(\xi_i)} \right) - \frac{\omega_{Tn}^2}{\omega^2},$$

$$g_{41}^n = 0, \tag{A10}$$

$$g_{42}^n = \frac{(n-1)\omega_{Kn}^2}{(n+1)\omega^2} + \frac{\omega_{\mu n}^2}{\omega^2} + (n-1)\Delta\xi,$$

$$g_{43}^n = -\frac{\rho_o}{\rho_*},$$

$$g_{44}^n = \frac{\rho_i}{\rho_*} + \frac{\omega_{Kn}^2}{\omega^2} \left(1 - n + \frac{1}{\mathcal{J}_n(\xi_i)} \right) - \frac{\omega_{\mu n}^2}{\omega^2} \left(n + 1 - \frac{1}{\mathcal{J}_n(\xi_i)} \right) - \left(n^2 - 1 + \frac{1}{\mathcal{J}_n(\xi_i)} \right) \Delta\xi.$$

APPENDIX B

Hooke's law written in Eq. (15) for a plane configuration,

$$T_x = K(e_{xx} + e_{yy}) + \mu(e_{xx} - e_{yy}), \tag{B1}$$

$$T_y = K(e_{xx} + e_{yy}) + \mu(e_{yy} - e_{xx}), \tag{B2}$$

can be expressed for isotropic materials in terms of the stress [55],

$$e_{xx} = \frac{1}{E}[\sigma_{xx} - \nu(\sigma_{yy} + \sigma_{zz})], \tag{B3}$$

$$e_{yy} = \frac{1}{E}[\sigma_{yy} - \nu(\sigma_{xx} - \sigma_{zz})]. \tag{B4}$$

If the shell is thin and the tension distribution is homogeneous over the membrane thickness, we can assume

$$T_x = h\sigma_{xx},$$

$$T_x = h\sigma_{xx}.$$

Considering the case where $\sigma_{xx} = \sigma_{xx} = \sigma$; $\sigma_{zz} = 0$, combining Eqs. (B1) and (B2) we obtain

$$h\sigma = K(e_{xx} + e_{yy}). \tag{B5}$$

Adding Eq. (B3) to Eq. (B4) results in

$$(e_{xx} + e_{yy}) = \frac{2\sigma}{E}[1 - \nu] \tag{B6}$$

and by combining Eqs. (B5) and (B6), we obtain Eq. (45).

Let us consider a case when $\sigma_{xx} = \sigma$; $\sigma_{xx} = \sigma_{zz} = 0$. Substracting Eq. (B2) from Eq. (B1),

$$h\sigma = 2\mu(e_{xx} - e_{yy}). \tag{B7}$$

Likewise from Eqs. (B1) and (B2), we obtain

$$(e_{xx} - e_{yy}) = \frac{\sigma}{E}[1 + \nu]. \tag{B8}$$

By combining Eqs. (B7) and (B8), Eq. (46) is recovered.

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