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Membrane hydrodynamics at low Reynolds number

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A general theory of the low Reynolds number hydrodynamics of membranes immersed in Newtonian fluids is derived. The basic result is a linear relation between membrane stress and membrane velocity, involving two singular integral operators A and B on the membrane. Methods for computing A and B are given in the case where the membrane is azimuthally symmetric. Explicit formulas for incorporating a wall boundary condition are given. The small amplitude shape dynamics of a vesicle near a wall is described. The method is computationally efficient because it pulls the description of the three-dimensional fluid flows back to the two-dimensional membrane boundary using the classical integral representation of Stokes flows in terms of their boundary values.

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I. INTRODUCTION

The low Reynolds number flow of an incompressible Newtonian fluid is described by the Stokes equations [1]

$$\vec{\nabla}\cdot\vec{v}=0 , \tag{1}$$

$$-\vec{\nabla}P+\eta\nabla^2\vec{v}=\vec{0} , \tag{2}$$

where $\vec{v}$ is the velocity vector field, P is the pressure, and η is the viscosity of the fluid. The physical content of the Stokes equations is that the inertial term in Newton's second law is negligible compared to the viscous and pressure forces on each element of fluid, which therefore balance each other everywhere in the interior of the fluid region. We will call solutions of these equations Stokes flows. The most familiar and useful Stokes flow is the flow in the exterior of a rigid sphere, leading to the well known expression for the net force $\vec{F}$ on a sphere of radius R moving with constant velocity $\vec{V}$ through an otherwise stationary fluid [2]

$$\vec{F}=-6\pi\eta R\vec{V} . \tag{3}$$

This result is verified experimentally to good accuracy when the Reynolds number $\rho VR/\eta<1$ (see Ref. [2]). For such low Reynolds number flows the Stokes equations are an appropriate description. The example of the moving sphere illustrates that time dependence may enter the Stokes equations through the boundary conditions, even though time does not appear explicitly in the equations themselves.

This paper is concerned with computing Stokes flows in regions with membrane boundaries, such as those that arise, for example, in biological problems. Blood, to name one example, poses such problems, being a suspension of deformable fluid vesicles (from the purely mechanical point of view). One approach to modeling Stokes flows would be to integrate the (three dimensional) Stokes equations, which are, after all, an especially simple case of the Navier-Stokes equation, for which an enormous computational literature exists. This paper suggests an alternative approach, in which all integration is pulled back to the (two-dimensional) membrane boundaries. This reduces the problem from three to two dimensions, a very significant simplification. If the membranes have azimuthal symmetry, the problem is simplified still more, becoming essentially one dimensional. This method also isolates the role of the mechanical properties of the membrane, making it, as it should be, a problem separate from the three-dimensional flow to which the moving membrane gives rise.

The method relies entirely on Green's identity, as applied by Oseen to this problem [3]. Oseen pointed out that the Stokes flow $\vec{v}$ in a bounded region D has an integral representation in terms of the boundary values of $\vec{v}$ and its normal derivative. (It is analogous to the representation of the eletrostatic potential by a combination of single layer and double layer potentials.) That Stokes flows can be represented by boundary values tells us that we do not have to regard them as essentially three dimensional.

Let M be a membrane surface, separating two regions D_1 and D_2, and consider the Stokes flows on each side. One may approach the surface M from either side, and it is clear that the velocity is continuous on M, but that its normal derivative is typically discontinuous. The discontinuity is related to internal stresses in the membrane. This observation, in conjunction with the above mentioned integral representation, leads to a linear relation between the internal membrane stresses and the membrane velocity, the main result of the paper, Eq. (19). The rest of the paper is detailed methods for computation. Azimuthal symmetry is treated in Sec. III. Wall boundary conditions are treated in Sec. IV. The small amplitude shape dynamics of vesicles is treated in Sec. V.

Of course, the idea of deriving singular integral equations from Green's function representations is absolutely classical in mathematical physics. It is not widely appreciated, though, that this leads to computationally practical schemes. One must deal with singular operators, it is true, but one lowers the dimensionality of the problem from three dimensions to two.

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II. MEMBRANE STRESS AND VELOCITY

Oseen's integral representation for a Stokes flow in an open bounded region D in terms of boundary data on the smooth boundary M is given by [3]

$$v_k(\vec{r}_0)=\frac{1}{8\pi\eta}\int\int_M \left[t_{jk}\left[\eta\frac{dv_j}{dn}-Pn_j\right] -v_j\left[\eta\frac{dt_{jk}}{dn}-p_k n_j\right]\right]dA \ . \tag{4}$$

Here $\vec{r}_0$ is a fixed (interior) point of D, and j and k are indices running from 1 to 3, labeling Cartesian components of several vectors and tensors. The vector with components n_j is the unit outer normal $\hat{n}$ on M, as in Fig. 1. The derivative d/dn is best understood as *minus* the partial derivative in the direction $-\hat{n}$, since it is not clear from this representation that the flow exists outside of D. The tensor t_{jk} and the vector p_k should be thought of as known quantities, depending on the variable of integration $\vec{r}$ and the parameter $\vec{r}_0$. They are three Stokes flows (labeled by k) with a Green's function singularity at $\vec{r}=\vec{r}_0$, and may be taken to be [3]

$$t_{jk}(\vec{r},\vec{r}_0)=\frac{\delta_{jk}}{|\vec{r}-\vec{r}_0|}+\frac{(x_j-x_{0j})(x_k-x_{0k})}{|\vec{r}-\vec{r}_0|^3} \ , \tag{5}$$

$$p_k(\vec{r},\vec{r}_0)=2\eta\frac{(x_k-x_{0k})}{|\vec{r}-\vec{r}_0|^3} \ . \tag{6}$$

Here x_j is a Cartesian component of $\vec{r}$, etc. One may equally well add to these singular Stokes flows, for each k, regular Stokes flows in $\bar{D}$, i.e., the representation Eq. (4) is far from being unique. In Sec. IV this freedom is used to build in no-slip boundary conditions on a plane wall.

The continuity properties of the integrals in Eq. (4) are as follows. Let M be a smooth (orientable) surface with unit normal $\hat{n}$ and $\vec{P}$ a point of M. Let $\vec{r}_0=P\pm\epsilon\hat{n}_0$, where $\epsilon>0$. Then

$$\lim_{\epsilon\to 0}\int_M f_j t_{jk}\,dA=A[\vec{f}\,]_k \tag{7}$$

and

$$\lim_{\epsilon\to 0}\int_M v_j\left[\eta\frac{dt_{jk}}{dn}-n_j p_k\right]dA=\pm 4\pi\eta v_k+\eta B[\vec{v}\,]_k \ . \tag{8}$$

Here A and B are linear functionals taking vector functions on M to vector functions on M. A and B are *defined* here as singular integral operators. They depend on the surface M. The functional B also depends on the orientation of M (through $\hat{n}$). The determination of A and B turns out to be the main computational task in using this method. Initially, however, the important thing to notice is the discontinuity in the second integral, indicated by the $\pm$ sign: the limit as $\vec{r}_0\to P$ depends on which side of M one approaches from.

It is worth digressing to see how this works in the only really familiar Stokes flow, that around a rigid sphere translating with constant velocity V. Specifically, let M be a rigid spherical shell of radius R with fluid outside and inside, having viscosities η_0 and η_i. In this case the integrands are known and the integrals elementary. (It is permissible to use the integral representation even in the unbounded exterior of the sphere because the integrands fall off as r^{-3}, so that one could add a large spherical boundary giving arbitrarily small contribution.) For this flow there is a physical meaning to the combination

$$\eta\frac{dv_j}{dn}-pn_j=-f_j \ . \tag{9}$$

In fact, f_j is the stress due to the fluid on the sphere (either outside or inside, depending on the direction of $\hat{n}$, which points *out* of the region). It happens to be a constant vector field [2] in either case, i.e.,

$$f_j=\frac{F_j}{4\pi R^2} \ , \tag{10}$$

where F_j is the *net* force due to the fluid (either outside or inside) on the sphere. The velocity of the fluid on M is also a constant vector field V_j because the rigid M is moving with this velocity. Then, using Eq. (4) and taking the limit as $\vec{r}_0$ approaches M from the outside, one has

$$8\pi\eta_0 V_k=-\frac{16\pi R}{3}f_k^{\text{out}}+4\pi\eta_0 V_k-4\pi\eta_0 V_k \ ; \tag{11}$$

taking the limit as $\vec{r}_0$ approaches M from the inside one has

$$8\pi\eta_i V_k=-\frac{16\pi R}{3}f_k^{\text{in}}+4\pi\eta_i V_k+4\pi\eta_i V_k \ . \tag{12}$$

In going from the exterior case to the interior case the orientation of $\hat{n}$ reverses because the integral representation requires that $\hat{n}$ point out of the domain where the representation is valid. In the first term on the right-hand side this sign is swallowed up in the definition of f_k, but in the last two terms it appears as an explicit reversal of sign. In particular, the first term on the right-hand side is the result of the functional A and the last term is the result of the functional B. One notices that the constant vector field on the sphere is an eigenfunction of A with eigenvalue $16\pi R/3$ and of B with eigenvalue -4π. These two statements, which refer to a computation over

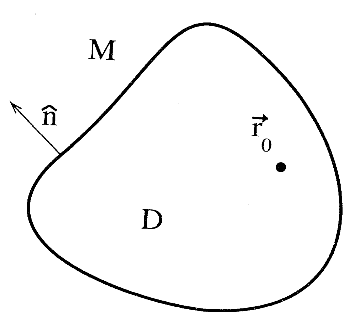

FIG. 1. Stokes flow in D can be represented at an interior point $\vec{r}_0$ by an integral over the boundary M.

the two-dimensional surface of the sphere only, turn out to imply the usual conclusions about the three-dimensional Stokes flow.

It is clear from Eq. (11) that

$$F_k^{\text{out}}=4\pi R^2 f_k^{\text{out}}=-6\pi\eta_0 R V_k \tag{13}$$

and from Eq. (12) that

$$F_k^{\text{in}}=4\pi R^2 f_k^{\text{sin}}=0 \ . \tag{14}$$

This is, of course, the usual conclusion, Eq. (3). In getting to it, though, one has used the already known solution in Eq. (10) to assert that the stress f_i is a constant vector field on M. This is not at all obvious initially and in the usual derivation is something one learns only after the problem is essentially solved. In general, one would not know what f_j corresponds to the boundary values V_j of the velocity. The situation is suddenly different, however, if one simply adds Eqs. (11) and (12). One finds

$$8\pi\eta_0\vec{V}=A[-\vec{f}^{\text{out}}-\vec{f}^{\text{in}}] \ , \tag{15}$$

with *no* assumptions about the stresses. Now, by the usual assumptions of low Reynolds number hydrodynamics, the net force on every fluid element vanishes, including elements of the membrane, i.e.,

$$\vec{f}^{\text{out}}+\vec{f}^{\text{in}}+\vec{f}_M=\vec{0} \ , \tag{16}$$

where $\vec{f}_M$ is the stress on an element of the membrane due to the rest of the membrane. This quantity, unlike the other stresses, has nothing intrinsically to do with Stokes flows and depends only on the viscoelastic properties of the membrane under deformation. (A rigid membrane is, unfortunately for the exposition, a degenerate case.) The example of the sphere then takes the form

$$8\pi\eta_0\vec{V}=A[\vec{f}_M] \ . \tag{17}$$

The problem reduces to inverting the linear functional A. A study of A, especially its spectral properties, would reveal that the inverse image of a constant vector field under A is a constant vector field

$$\vec{f}_M=\frac{3\pi\eta_0}{2R}\vec{V}=\frac{1}{4\pi R^2}6\pi\eta_0 R\vec{V} \ , \tag{18}$$

implying, since clearly $\vec{f}^{\text{in}}=\vec{0}$ in rigid translation, the usual result, Eq. (13). The above argument is an unorthodox derivation of the Stokes result Eq. (3) involving only computations on the sphere itself.

The example of the sphere has served its purpose. The general statement is only a slight generalization from this example: its derivation is exactly the same

$$4\pi(\eta_0+\eta_i)\vec{V}=A[\vec{f}_M]+(\eta_0-\eta_i)B[\vec{V}] \ , \tag{19}$$

where M is any membrane surface, f_M is the internal stress in the membrane, and $\vec{V}$ is its velocity. This singular integral equation on M relates the velocity of the membrane to its internal stress. It is the main result of this paper. Of course, by linearity, solutions to this equation can be superimposed on other Stokes flows that are regular across M.

The next section gives a practical method for computing the singular integral operators A and B for azimuthally symmetric membranes. These operators determine the first-order hydrodynamics theory of arbitrary (even nonsymmetric) perturbations of azimuthally symmetric membranes.

III. AZIMUTHALLY SYMMETRIC MEMBRANES

Let M be generated by rotating a curve

$$C=\{(x(s),0,z(s))|0\le s\le\pi\} \tag{20}$$

in the x-z plane about the z axis, where the parameter s is the arclength on C. It is useful also to define the angle $\theta(s)$ to be the angle between the tangent to C and the z axis, so that

$$dz/ds=\cos\theta \ , \tag{21}$$

$$dx/ds=\sin\theta \ . \tag{22}$$

For definiteness suppose that $x(0)=x(\pi)=0$ and that M has the topology of a sphere, as in Fig. 2, although nothing essential depends on this. (s,ψ) are coordinates on M, where ψ is the azimuthal angle, and the unit vectors $(\hat{\vec{n}},\hat{\vec{s}},\hat{\vec{\psi}})$ are a right-handed orthonormal system at each point of M. The membrane stress is best represented in these coordinates, in order to take advantage of azimuthal symmetry. Detailed methods for doing this have been given elsewhere [4]. It is enough to note that the membrane stress can be represented as (complex) linear combinations of symmetric stresses in the form

$$\vec{f}_M=(f_n\hat{\vec{n}}+f_s\hat{\vec{s}}+if_\psi\hat{\vec{\psi}})e^{im\psi} \ , \tag{23}$$

where m is an integer labeling the azimuthal symmetry class and f_n, f_s, and f_ψ are real functions of s only. The

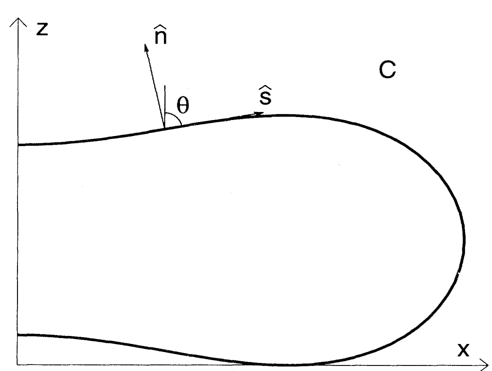

FIG. 2. Azimuthally symmetric membrane M generated by a curve C in the x-z plane by rotation about the z axis. The arclength s on C and the azimuthal angle ψ are coordinates on M.

corresponding membrane velocity takes the same form

$$\vec{V}=(V_n\hat{n}+V_s\hat{s}+iV_\psi\hat{\psi})e^{im\psi} , \tag{24}$$

where V_n, V_s, and V_ψ are real functions of s.

The functionals A and B, according to Eqs. (7) and (8), are obtained as limits of integrals over M, i.e., integrals over s and ψ, but the ψ dependence of $\vec{f}$ and $\vec{V}$ is always the same, $e^{im\psi}$ for some m. Thus the ψ integrals can be done once and for all.

The ψ integrals that occur are linear combinations of the integrals

$$I_{pm}(s,s_0,\epsilon)=\int_0^{2\pi}\Delta^{-p}e^{im\psi}d\psi , \tag{25}$$

where

$$\Delta^2=R^2+4A^2\sin^2\frac{\psi}{2} , \tag{26}$$

$$R^2=[z(s)-z_0-\epsilon\sin\theta_0]^2+[x(s)-x_0+\epsilon\cos\theta_0]^2 , \tag{27}$$

$$A^2=x(s)(x_0-\epsilon\cos\theta_0) . \tag{28}$$

Here $(x,0,z)$ and $(x_0,0,z_0)$ are points on C, with $x_0=x(s_0)$, etc., defining s_0. These expressions are less mysterious when one notes that $\Delta=|\vec{r}-\vec{r}_0|$ with $\vec{r}_0=(x_0,0,z_0)+\epsilon\hat{n}_0$ and $\vec{r}$ is on the circle generated by $(x,0,z)$ and parametrized by ψ. By a contour integral technique one expresses these integrals in terms of the Gauss hypergeometric function F (see Ref. [5]):

$$I_{pm}=w^{m+p/2}\frac{2\Gamma(m+p/2)\Gamma(1-p/2)}{A^p\Gamma(m+1)} \times F(p/2,m+p/2;m+1;w^2) , \tag{29}$$

where

$$w=1+\frac{R^2}{2A^2}-\frac{R}{A}\left[1+\frac{R^2}{4A^2}\right]^{1/2} \tag{30}$$

is the root of $A^2w^2-(2A^2+R^2)w+A^2$, which is smaller than 1. As $\epsilon\to 0, I_{pm}(s,s_0,\epsilon)$ develops a singularity at $s=s_0$, corresponding to $\vec{r}=\vec{r}_0$, or, in Eq. (29), $w=1$, Asymptotic expansions of the hypergeometric function near $w=1$ are available [5], which make it possible to isolate this singularity so that the singular parts of the integrals over s can be done analytically, leaving nonsingular integrals to do numerically. This, in outline, is the method for evaluating the singular integral operators. Details are given in Appendix A.

It is worth emphasizing here that numerical computations of this kind can be done with complete confidence. The singular nature of the integrals is very unforgiving, from the numerical point of view, and this makes any mistake obvious. An integrand that is supposed to be nonsingular, because two singularities have been made to cancel by subtraction, will not look nonsingular if there is a mistake. The limiting value of a nonsingular integrand at $s=s_0$ will be out of place if any detail is wrong. Finally, if M is a sphere, A and B can be computed analytically. From the numerical point of view the sphere is not special, so it is a very strong check that the algorithm sketched above correctly computes A and B in this case.

Since A and B can be evaluated on a suitable (truncated) basis of vector fields on M, they should be regarded as matrices. This reduces Eq. (19) to linear algebra.

IV. WALL BOUNDARY CONDITIONS

Most real experimental situations include not only membrane boundaries but also nearby fixed walls. The effect of these walls can be included by modifying the tensors t_{jk} and p_k in Oseens' representation, Eq. (4). For this purpose it is useful to recognize

$$t_{jk}(\vec{0},\vec{r})=\frac{2\cos\zeta_j}{r}\hat{r}_k-\frac{\sin\zeta_j}{r}\hat{\zeta}_{jk} . \tag{31}$$

Here r and ζ_j are spherical polar coordinates and the angle ζ_j is measured from the jth Cartesian coordinate axis. (The flow is azimuthally symmetric, so the third coordinate does not occur in this expression.) These are singular Stokes flows originating from a point source orientated along each coordinate axis in turn. To solve wall boundary value problems, it is enough to add nonsingular Stokes flows T_{jk}, which exactly cancel t_{jk} on the walls, and to add the corresponding nonsingular pressures to the p_k. Then no-slip boundary conditions are built into the Oseen representation. For a single infinite plane wall those flows are well known [1]. They have a "reflected" point singularity on the unphysical side of the wall.

If an azimuthally symmetric membrane's symmetry axis coincides with the normal of the nearby wall (say the wall is $z=0$), then the hydrodynamics problems still has azimuthal symmetry and can still be solved by the method of Sec. III. The effect of the wall is to add regular integrals involving T_{jk} to the singular integrals involving t_{jk}. Again, the azimuthal integrals can be done once and for all. The situation is as pictured in Fig. 3, looking down along the symmetry axis at the x-y plane. The contribution at $\vec{r}_0$ of the reflection in the wall of a point source at $\vec{r}$ involves the projected distance $\rho(\psi)$ and the angle $\alpha(\psi)$. Here the following convention is used:

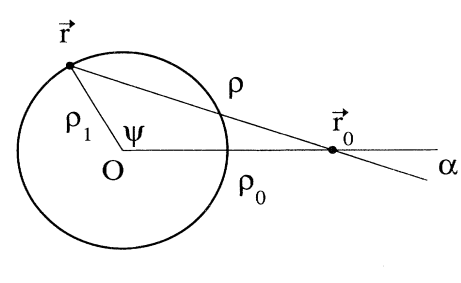

FIG. 3. Integral operators A and B involve integration over the azimuthal angle ψ. The contribution at $\vec{r}_0$ of a source at $\vec{r}$ may include a flow "reflected" from a rigid wall (here considered to be in a plane parallel to the plane of the figure). This flow is best represented in cylindrical coordinates centered on the point $\vec{r}$.

$$\cos(\alpha)=(\rho_0-\rho_1 \cos\psi)/\rho \ , \tag{32}$$

$$\sin(\alpha)=-(\rho_1 \sin\psi)/\rho \ , \tag{33}$$

i.e., the α shown in the figure is negative. Introduce the Cartesian vectors

$$\hat{z}=(0,0,1) \ , \tag{34}$$

$$\hat{e}(\alpha)=(\cos(\alpha),\sin(\alpha),0) \ . \tag{35}$$

Then T_{jk} is given by

$$T=H_0\hat{z}\otimes\hat{z}+H_1\hat{z}\otimes\hat{e}(\psi-\alpha)+F_0\hat{e}(\alpha)\otimes\hat{z} +F_1\hat{e}(\alpha)\otimes\hat{e}(\psi-\alpha) +G_1\hat{e}(\alpha+\pi/2)\otimes\hat{e}(\psi-\alpha-\pi/2) \tag{36}$$

and operates on Cartesian vector fields by the usual Cartesian inner product with the second factor in the tensor product. The functions F, G, and H, with subscripts indicating their azimuthal symmetry class, are nonsingular Stokes flows in cylindrical coordinates, which just cancel the singular Stokes flows on the wall $z=0$. For example, the flow that cancels t_{3k} (due to a source at $\vec{r}$ pointing in the direction of $\hat{z}$) is $H_0\hat{z}+F_0\hat{\rho}$. The significance of the other functions can be deduced similarly. These functions are given in Appendix B, along with the corresponding pressures. The normal derivative of T_{jk} on the membrane, which is needed for the functional B, can be found using

$$\frac{\partial}{\partial n}=\sin[\theta(s)]\frac{\partial}{\partial z}-\cos[\theta(s)]\frac{\partial}{\partial \rho_1} \ . \tag{37}$$

The explicit formulas for these derivatives, which are rather lengthy, were generated in MATLAB-useable form using MATHEMATICA. MATHEMATICA was also used to check that the nonsingular flows really do satisfy the Stokes equations. The numerical cancellation on the wall after integration is a good check of this part of the computation.

V. SHAPE DYNAMICS OF VESICLES

The equilibrium shapes of vesicles and their equilibrium statistical mechanics have received much attention in recent years (see, for example, the review by Peliti [6]). By contrast the dynamics of vesicles is discussed very little, although, as the above theory demonstrates, the observable motions of membranes are very directly related to their elastic properties. In this section the small amplitude dynamics of vesicles will be sketched. An example of this dynamics is the erythrocyte flicker phenomenon, the Brownian shape fluctuations of the human red blood cell. Quantitative investigations of erythrocyte flicker typically involve an azimuthally symmetric erythrocyte resting, and perhaps adhering, on a rigid horizontal substrate. This is exactly the situation worked out above. As emphasized, one can treat each azimuthal symmetry class separately. Of course the remarks below apply to the shape dynamics of any vesicle.

Expand the membrane elastic energy to second order about its minimum in a basis of allowed deformations and diagonalize the resulting quadratic form. This gives "normal modes" U_j and a positive definite diagonal energy matrix D_{jk} containing generalized Hooke's law constants. Here the indices $j,k,\ldots$ label the modes, which serve as a (truncated) basis for the space of deformations. These modes and the corresponding eigenvalues are accessible experimentally through equilibrium statistical mechanics. Evaluate the matrices A_{jk},B_{jk}, which represent the linear functional A and B in this basis. Represent an arbitrary membrane deformation in this basis:

$$U=U_jc_j(t) \ . \tag{38}$$

Then the membrane stress is

$$f_M=-DU=-U_kD_{kj}c_j \tag{39}$$

and the membrane velocity is

$$V=\dot{U}=U_j\dot{c}_j(t) \ . \tag{40}$$

Equation (19) says

$$4\pi(\eta_0+\eta_i)\dot{c}_j=-A_{jk}D_{kn}c_n+(\eta_0-\eta_i)B_{jk}\dot{c}_k \ . \tag{41}$$

Let $C_j(s)$ be the Laplace transform of $c_j(t)$. Then Eq. (41) becomes an inhomogeneous linear equation for $C_j(s)$ in the form

$$(M_{jk}+sN_{jk})C_k=-N_{jk}c_k(0) \ , \tag{42}$$

where

$$M=AD \ , \tag{43}$$

$$N=4\pi(\eta_0+\eta_i)I-(\eta_0-\eta_i)B \ . \tag{44}$$

The solution of this problem is a linear combination of eigenvectors of $N^{-1}M$, each relaxing at a rate that is the corresponding eigenvalue. Thus the hydrodynamic modes are readily found.

A membrane may have an appreciable two-dimensional shear viscosity η_M. Its effect on the hydrodynamic modes can be computed easily. The matrix S of the elastic shear energy will have been found in the first part of the computation, since it is typically part of the elastic energy. An intrinsic membrane viscosity means there is an additional membrane stress

$$f_M=-2\eta_M SV \ . \tag{45}$$

The result is to change N by

$$N\rightarrow N+2\eta_M AS \ . \tag{46}$$

This exactly accounts for membrane shear viscosity. Viscosities associated with bending or dilation, if they were important, could be brought in just as easily because the corresponding matrices would already have been computed as elastic energy terms.

The matrix $N^{-1}M$, which determines the hydrodynamic modes, is not self-adjoint in the natural inner product on modes (integrate the Cartesian dot product of vector fields over the membrane). Thus, unlike the normal modes of equilibrium statistical mechanics, the hydrodynamic modes are not in general orthogonal. These modes and their time dependences are observable and contain more information than equilibrium quantities. The theory outlined in this paper is an accurately computable description of them. Experimental results in this direction may help elucidate the sometimes puzzling mechanical properties of membranes.

ACKNOWLEDGMENT

I wish to thank Erich Sackmann for suggesting this problem and for hospitality while this work was done.

APPENDIX A: COMPUTING SINGULAR INTEGRALS

The method for doing singular integrals in the case where the membrane is azimuthally symmetric is illustrated by an example. According to Eqs. (8) and (5), the integrals that define B include integrals over

$$\frac{dt_{jk}}{dn}=-\frac{\hat{n}\cdot(\vec{r}-\vec{r}_0)}{|\vec{r}-\vec{r}_0|^3}+\frac{n_j(x_k-x_{0k})+n_k(x_j-x_{0j})}{|\vec{r}-\vec{r}_0|^3}-3\frac{\hat{n}\cdot(\vec{r}-\vec{r}_0)(x_j-x_{0j})(x_k-x_{0k})}{|\vec{r}-\vec{r}_0|^5} . \quad (A1)$$

The integral is over the membrane M, where $\vec{r}$ is the variable of integration, $\hat{n}$ is the unit normal at $\vec{r}$, $\vec{r}_0$ is at $\vec{P}+\epsilon\hat{n}_0$, where $\vec{P}$ is a point in M, and the limit as $\epsilon\rightarrow 0$ is to be found. There are many terms and many components. Consider only the last term in Eq. (A1), without the factor -3, and consider the particular component obtained by dotting with $\hat{n}$ and $\hat{n}_0$ (since such coordinates, rather than Cartesian coordinates, are best adapted to representing membrane motions). One is led to the integral

$$I(s,s_0,\epsilon)=\int_0^{\pi}\int_0^{2\pi}\frac{[\hat{n}\cdot(\vec{r}-\vec{r}_0)]^2\hat{n}_0\cdot(\vec{r}-\vec{r}_0)}{|\vec{r}-\vec{r}_0|^5}\times V_n(s)e^{im\psi}d\psi\, x(s)ds , \quad (A2)$$

where one is working in the space of motions with azimuthal symmetry labeled by m. Since M is generated by a curve $(x(s),0,z(s))$, making an angle $\theta(s)$ with the z direction, as described in Sec. III, the dot products are

$$\hat{n}\cdot(\vec{r}-\vec{r}_0)=\alpha(s,\epsilon)-2\beta(s,\epsilon)\sin^2(\psi/2) , \quad (A3)$$

$$\hat{n}_0\cdot(\vec{r}-\vec{r}_0)=\gamma(s,\epsilon)-2\delta(s,\epsilon)\sin^2(\psi/2) , \quad (A4)$$

where

$$\alpha=(z-z_0-\epsilon\sin\theta_0)\sin\theta-(x-x_0+\epsilon\cos\theta_0)\cos\theta , \quad (A5)$$

$$\beta=(x_0-\epsilon\cos\theta_0)\cos\theta , \quad (A6)$$

$$\gamma=(z-z_0)\sin\theta_0-(x-x_0)\cos\theta_0-\epsilon , \quad (A7)$$

$$\delta=-x\cos\theta_0 . \quad (A8)$$

Then

$$I(s,s_0,\epsilon)=\int_0^{\pi}[\alpha^2\gamma I_{5m}-2(2\alpha\beta\gamma+\alpha^2\delta)I_{5m}^{(2)}+4(2\alpha\beta\delta+\beta^2\gamma)I_{5m}^{(4)}-8\beta^2\delta I_{5m}^{(6)}]V_n(s)x(s)ds , \quad (A9)$$

where

$$I_{pm}^{(r)}=\int_0^{2\pi}\frac{\sin^r(\psi/2)e^{im\psi}}{\Delta^p}d\psi , \quad (A10)$$

extending somewhat the definition of Eq. (25) and using the definition of Δ in Eq. (26). (Note that $I_{pm}=I_{pm}^{(0)}$.) However,

$$I_{pm}^{(2)}=-(I_{p,m-1}-2I_{pm}+I_{p,m+1})/4 , \quad (A11)$$

$$I_{pm}^{(4)}=(I_{p,m-2}-4I_{p,m-1}+6I_{p,m}-4I_{p,m+1}+I_{p,m+2})/16 , \quad (A12)$$

etc., so that, in fact, only the integrals in Eq. (25) are needed and only with $p=5$.

Using the result in Eq. (29) and the quantities R, A defined in Eqs. (27) and (28), one deduces the asymptotic expression for small R [5]

$$I_{5m}\sim\frac{4}{3AR^4}\left[1-\frac{(mR)^2}{4A^2}+\frac{(mR)^4}{12A^4}+\cdots\right]+\frac{2}{A^5}J_{5m}+\cdots , \quad (A13)$$

where

$$J_{5m}=(m-\tfrac{3}{2})(m-\tfrac{1}{2})(m+\tfrac{1}{2})(m+\tfrac{3}{2})\times[\ln(1-w^2)-\psi(1)-\psi(5)+\psi(\tfrac{5}{2})+\psi(m+\tfrac{5}{2})]/4! \quad (A14)$$

and ψ is the digamma function. Omitted terms are irrelevant for a discussion of the singularity at $R=0$ (equivalently $w=1$). [In the square brackets of Eq. (A13), multiplying each positive power of R, there are other terms of lower degree in m that have also been omitted, for reasons that will become clear.]

In the integral

$$I_0=\int_0^{\pi}I_{5m}\alpha^2\gamma V_n(s)x(s)ds \quad (A15)$$

the leading singularity in I_{5m} is R^{-4} or, equivalently, $[(s-s_0)^2+\epsilon^2]^{-2}$. This suggests writing

$$I_0=\int_0^{\pi}\left[I_{5m}-\frac{4}{3A}\frac{1}{[(s-s_0)^2+\epsilon^2]^2}\right]\times\alpha^2\gamma V_n(s)x(s)ds+J_0 , \quad (A16)$$

where

$$J_0=\int_0^{\pi}\frac{4}{3A}\frac{\alpha^2\gamma V_n(s)x(s)}{[(s-s_0)^2+\epsilon^2]^2}ds . \quad (A17)$$

The first integral in Eq. (A16), I_0-J_0, is actually nonsingular because, with the leading singularity subtracted off, the dangerous factor is only R^{-2}, which is ϵ^{-2} at

$s=s_0$, while the factor $\alpha^2\gamma$ in the numerator is $-\epsilon^3$. The limit as $\epsilon\to 0$ can be taken by simply setting $\epsilon=0$ where $s\neq s_0$ and defining the integrand to be zero at $s=s_0$ (where it would otherwise be undefined). This integrand is actually continuous. Next write

$$J_0=\int_0^\pi \left[\frac{4\alpha^2\gamma V_n(s)x(s)}{3A}+\frac{4}{3}\epsilon^3 V_n(s_0)\right] \times \frac{1}{[(s-s_0)^2+\epsilon^2]^2}ds+K_0 , \quad (A18)$$

where

$$K_0=-\int_0^\pi \frac{4}{3}\epsilon^3 V_n(s_0)\frac{1}{[(s-s_0)^2+\epsilon^2]^2}ds . \quad (A19)$$

The first integral in Eq. (A18), J_0-K_0 is actually nonsingular. The integrand at $s=s_0$ is zero for any nonzero ϵ and hence also in the limit as $\epsilon\to 0$. The integrand is continuous in this limit. Hence J_0-K_0 can be evaluated numerically. Finally, K_0 is an elementary integral and one easily computes

$$\lim_{\epsilon\to 0} K_0=-\text{sgn}(\epsilon)\frac{2\pi}{3}V_n(s_0) . \quad (A20)$$

Thus

$$\lim_{\epsilon\to 0} I_0=-\text{sgn}(\epsilon)\frac{2\pi}{3}V_n(s_0)+(I_0-J_0)+(J_0-K_0) , \quad (A21)$$

where the last two integrals are to be done numerically with $\epsilon=0$ and the appropriate limiting value of the integrand supplied at $s=s_0$. One sees in Eq. (A21) the form of Eq. (8) emerging.

The next piece of the integral Eq. (A2) involves

$$I_2=\int_0^\pi I_{5m}^{(2)}(2\alpha\beta\gamma+\alpha^2\delta)V_n(s)x(s)ds . \quad (A22)$$

Using Eq. (A11) and the asymptotic series Eq. (A13), one finds that the leading singularity in $I_{5m}^{(2)}$ is R^{-2} for small R. The linear combination in Eq. (A11) essentially takes two derivatives with respect to m, at least on polynomials. Thus terms of degree 0 and 1 in m are eliminated, including the R^{-4} term in Eq. (A13) and lower degree terms multiplying R^{-2}, which were omitted there just for this reason. Thus one is led to write

$$I_2=\int_0^\pi \left[I_{5m}^{(2)}-\left[\frac{1}{6A^3}\right]\frac{1}{(s-s_0)^2+\epsilon^2}\right] \times(2\alpha\beta\gamma+\alpha^2\delta)V_n(s)x(s)ds+J_2 , \quad (A23)$$

where

$$J_2=\int_0^\pi \left[\frac{1}{6A^3}\right]\frac{1}{(s-s_0)^2+\epsilon^2} \times(2\alpha\beta\gamma+\alpha^2\delta)V_n(s)x(s)ds . \quad (A24)$$

The first integral in Eq. (A23), I_2-J_2, has only a $\ln(R)$ singularity at $R=0$, since the leading singularity has been subtracted off. This would be an integrable singularity in any case, but in fact both α and γ vanish like $(s-s_0)^2$ at s_0 if $\epsilon=0$, so I_2-J_2 can be done numerically, setting $\epsilon=0$ if $s\neq s_0$ and setting the integrand zero at $s=s_0$. The integral J_2 can be done similarly. Set $\epsilon=0$ in the integrand and make the integrand continuous at $s=s_0$ by defining it to be zero there. Then

$$\lim_{\epsilon\to 0} I_2=(I_2-J_2)+J_2 , \quad (A25)$$

where it is understood that on the right-hand side ϵ is set zero and the integrands are defined to be zero at $s=s_0$. Both terms represent nonsingular integrals, which can be done numerically.

The next contribution to Eq. (A2) involves

$$I_4=\int_0^\pi I_{5m}^{(4)}(2\alpha\beta\delta+\beta^2\gamma)V_n(s)x(s)ds . \quad (A26)$$

Using Eq. (A12) and the asymptotic series Eq. (A13), one finds that the leading singularity in $I_{5m}^{(4)}$ is logarithmic. Since α and γ vanish at $R=0$, this integral has a continuous integrand at $s=s_0$ if one defines it to be zero there (setting $\epsilon=0$) and so can be done numerically. Finally, $I_{5m}^{(6)}$ has a continuous integrand if one defines it to be zero at $s=s_0$, so it presents no numerical problems.

This almost completes the prescription for computing the integral in Eq. (A2). All the integrals in the functionals A and B follow this pattern, and it is just a question of repeating the same ideas. The example is atypical only in that the limiting values of integrands were always 0 at $s=s_0$. It remains to point out that if $x_0=0$, the azimuthal integrals are trivial and should be done directly, not as limiting cases of the above algorithm.

APPENDIX B: REFLECTED FLOWS AT A WALL

Let $z=0$ be a rigid boundary and introduce cylindrical coordinates (ρ,α,z). Complex Stokes flows with definite azimuthal symmetry can be represented as

$$\vec{V}_m=[F_m(\rho,z)\hat{\rho}+iG_m(\rho,z)\hat{\alpha}+H_m(\rho,z)\hat{z}]e^{im\alpha} . \quad (B1)$$

Of course, the real part or imaginary part separately is also a Stokes flow.

Consider the flow t_{jk} of Eq. (31), originating at the point $(0,0,h)$, i.e., the singularity of the flow is a height h above the wall. If $j=3$, corresponding to a source pointed in the $\hat{z}$ direction, then the nonsingular flow that just cancels it on the wall is the $m=0$ flow

$$F_0=(h^3\rho+h\rho^3-5h^2\rho z-\rho^3 z-7h\rho z^2-\rho z^3)/D^5 , \quad (B2)$$

$$G_0=0 , \quad (B3)$$

$$H_0=(-2h^4-3h^2\rho^2-\rho^4-12h^3 z-4h\rho^2 z -20h^2z^2-3\rho^2z^2-12hz^3-2z^4)/D^5 , \quad (B4)$$

where

$$D^2=\rho^2+(h+z)^2 . \quad (B5)$$

The pressure in this flow (for unit viscosity) is

$$P_0 = \frac{1}{D^7}(-10h^5 - 8h^3\rho^2 + 2h\rho^4 - 42h^4 z - 20h^2\rho^2 z - 2\rho^4 z - 68h^3 z^2 - 16h\rho^2 z^2 - 52h^2 z^3 - 4\rho^2 z^3 - 18hz^4 - 2z^5) \ . \qquad \text{(B6)}$$

If $j=1$ or 2, the nonsingular Stokes flow, which cancels t_{jk} on the wall, is the $m=1$ flow, oriented appropriately,

$$F_1 = -(h^4 + 3h^2\rho^2 + 2\rho^4 + 6h^3 z + 2h\rho^2 z + 10h^2 z^2 + 3\rho^2 z^2 + 6hz^3 + z^4)/D^5 \ , \qquad \text{(B7)}$$

$$G_1 = -(h^4 + 2h^2\rho^2 + \rho^4 + 6h^3 z + 6h\rho^2 z + 10h^2 z^2 + 2\rho^2 z^2 + 6hz^3 + z^4)/D^5 \ , \qquad \text{(B8)}$$

$$H_1 = (h^3\rho + h\rho^3 + 7h^2\rho z - \rho^3 z + 5h\rho z^2 - \rho z^3)/D^5 \ . \qquad \text{(B9)}$$

The corresponding pressure (which also has $m=1$ symmetry) is

$$P_1 = (10h^4\rho + 8h^2\rho^3 - 2\rho^5 + 28h^3\rho z + 4h\rho^3 z + 24h^2\rho z^2 - 4\rho^3 z^2 + 4h\rho z^3 - 2\rho z^4)/D^7 \ . \qquad \text{(B10)}$$

These functions are used in representing flows that vanish on $z=0$, as described in Sec. IV. There the role of z is taken by z_0 and the role of h by z.

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