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Analytical analysis of a vesicle tumbling under a shear flow

F. Rioual, T. Biben, and C. Misbah
Groupe de Recherche sur les Phénomènes Hors Equilibres, LSP, Université Joseph Fourier, CNRS (UMR 5588), Boîte Postale 87,
F-38402 Saint Martin d'Hères cedex, France

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Vesicles under a shear flow exhibit a tank-treading motion of their membrane, while their long axis points with an angle $<\pi/4$ with respect to the shear stress if the viscosity contrast between the interior and the exterior is not large enough. Above a certain viscosity contrast, the vesicle undergoes a tumbling bifurcation, a bifurcation which is known for red blood cells. We have recently presented the full numerical analysis of this transition. In this paper, we introduce an analytical model that has the advantage of being both simple enough and capturing the essential features found numerically. The model is based on general considerations and does not resort to the explicit computation of the full hydrodynamic field inside and outside the vesicle.

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I. INTRODUCTION

Vesicles are closed membranes, which are suspended in an aqueous solution. They represent an attractive biomimetic system, which has revealed several interesting static and dynamical features that bear a strong resemblance with some behavior of real cells. Among these features we can cite equilibrium shapes [1] revealing forms similar to red blood cells, and tumbling known for these cells [2]. It is known that red cells, as well as vesicles [3], orient themselves at a given angle with respect to the shear flow at high hematocrit (high enough concentration of red cells), while at low hematocrit (where cells behave as being individual) both *in vitro* and *in vivo* observations reveal a tumbling motion, where the long axis of the red cell rotates in a periodic fashion. It has been recognized for a long time that the viscosity ratio between the internal fluid and the ambient one is a decisive factor (the more viscous is the internal fluid in comparison to the external one, the easiest is the tumbling). Another relevant ingredient is the swelling ratio: a flatten out cell would tumble more easily than a swollen one. Several attempts in understanding the tumbling transition have been made in the literature, the most prominent one is the work of Keller and Skallak [4]. This work uses the solution of the hydrodynamical equations in the Stokes regime (inertial effects are negligibly small for biological blood transport) around an ellipsoid which involve quite complex expressions. But still several assumptions had to be made in order to solve the problem. Recently, a full numerical analysis has been presented [5] and provided the boundaries in the parameter space (basically the viscosity contrast, and the swelling ratio) separating the regions of tumbling and those of tank treading. That work focused on vesicles that correspond to a simplified model of red blood cells, and especially ignored the elastic properties of the membrane, a fact which though turns out to lead to some interesting qualitative changes will not be accounted for here either.

Due to the interplay of several effects in the tumbling transition, it is highly desirable to have at our disposal an analytical theory, which, on the one hand, should reproduce the basic essential features of the tumbling transition and, on the other, should be simple enough in order to shed light on the various competing phenomena leading to tumbling. It is the main aim of the present paper to deal with this question.

The present theory bypasses the tedious computation of the velocity field around the ellipsoid (note that in the general case, no analytical solution of the Stokes flow is known), and is based on the assumption that the forces acting on each piece of the vesicle membrane are proportional to the actual relative velocity at the membrane with respect to the applied flow. It follows from our study that simple enough notions account remarkably well for many features and render each effect transparent. In addition, this work offers a promising basis for more elaborate models, including, for example, the effect of membrane stretching or shear elasticity.

The scheme of this paper is as follows. In Sec. II, we present the basic ingredients of the model. Section III is devoted to the derivation of the dynamical equation that governs the motion of the vesicle. This part is based on a torque balance. Section IV presents a complementary ingredient that serves to put the evolution equation in a closed form. This is based on an energy balance between the inner fluid of the

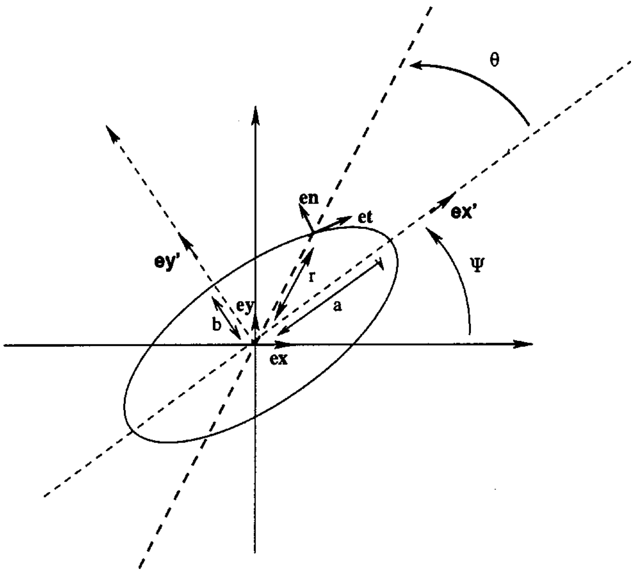

FIG. 1. Decomposition of the shear flow (S) in a rotational part (R) and an elongational part (E).

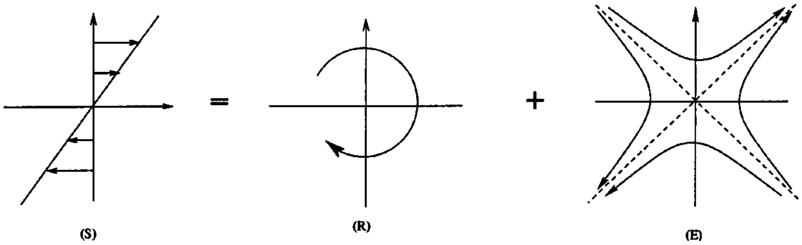

FIG. 2. Decomposition of the velocity field around the vesicle subjected to a tumbling motion and a tank-treading motion of its membrane in a simple shear flow.

vesicle and the work provided by the ambient one. The main outcomes of the analytical theory together with their confrontation with the full numerical analysis are presented in Sec. VI.

II. BASIC INGREDIENTS OF THE MODEL

(a) As in Ref. [4], we will assume the shape of the vesicle to be an undeformable ellipse, with the long and the short axes denoted by a and b, respectively. It will be recognized that the theory can be used for arbitrary prescribed shapes. For definitness we shall, however, specialize our discussion to an elliptical shape. The enclosed area is denoted by S and the perimeter by P. The fluid embedded into the vesicle has a viscosity μ_{in} and the ambient one μ_{out}. τ is the swelling ratio of the vesicle defined in two dimensions (2D) as $\tau = 4\pi S/P^2$. For a circle $\tau = 1$ and it is smaller than one otherwise.

(b) The vesicle is subjected to a linear shear flow ($v_x = \gamma y, v_y = 0$) where γ is the shear rate. Since the vesicles of interest have a fluid membrane, each material point on the membrane will be transported by the flow, so that the membrane moves in a tank-tread fashion.

Let us make a remark, which will prove to be useful later in this paper. A simple shear flow characterized by the (2×2) shear rate matrix

$$\begin{pmatrix} 0 & \gamma \\ 0 & 0 \end{pmatrix}$$

can be decomposed into two parts: a symmetric one given by

$$\begin{pmatrix} 0 & \gamma/2 \\ \gamma/2 & 0 \end{pmatrix}$$

and an antisymmetric one given by

$$\begin{pmatrix} 0 & \gamma/2 \\ -\gamma/2 & 0 \end{pmatrix}.$$

As shown in Fig. 1, the antisymmetric part provides a rigid like clockwise rotation of the vesicle (R), while the symmetric part corresponds to an elongational (or strain) flow, which tends to orient the vesicle along $\pi/4$ (E).

Our calculation is based on the following two properties of the Stokes equations.

(1) Due to the linearity of the Stokes equations, the superposition principle for given boundary conditions applies: the velocity field around a vesicle subjected to a tank treading and a tumbling motion in a simple shear flow is the sum of the velocity fields obtained for the three following configurations (see Fig. 2):

(i) A simple shear flow acting on a rigid body fixed in the flow at a constant orientation angle ψ with a fluid velocity equal to zero on the contour of the vesicle.

(ii) The flow created by a rigid elliptic body rotating at a rotation velocity $d\psi/dt$ in a quiescent fluid.

(iii) The flow created by an elliptic body subjected to a tank-treading motion of its contour and fixed at a constant orientation ψ in a quiescent fluid.

(2) The second ingredient, which follows from the previous one, is an extension of a general result valid in Stokes flows for a solid which is in relative motion at a velocity V with respect to the surrounding fluid. The drag force on the solid scales as $F_{drag} = \mu\lambda V$, where λ is (a drag coefficient) a function of the geometry of the body.[1] There is a linear relation between the force and the relative velocity of the body with respect to the applied flow. We view the elliptic contour as being represented by adjacent segments. The key hypothesis of the following analysis is to apply this property, i.e., the linearity between forces and relative velocities, on each segment of the membrane. Let us make some important comments about the meaning of this assumption. The external force applied on an elementary segment of the membrane is provided, on the one hand, by the flow imposed externally, and, on the other hand, by the backflow due to the presence of the vesicle. This retroaction of the vesicle on the applied flow is a complex piece of study and an exact determination of its effect requires sophisticated numerical treatments such

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[1] More precisely, the Stokes force exerted on a solid of typical length L in a translational motion at speed U, in a quiescent Newtonian fluid of viscosity μ, scales indeed as

$$F \approx \mu U L.$$

More formally, we can write a linear relation between the force and the velocity:

$$F_i = -\mu A_{ij} U_j. \tag{1}$$

A_{ij} is a tensor which is symmetrical for a Newtonian fluid, and in a specific frame linked to the solid, one can write

$$F_i = -\mu\lambda_i U_i \tag{2}$$

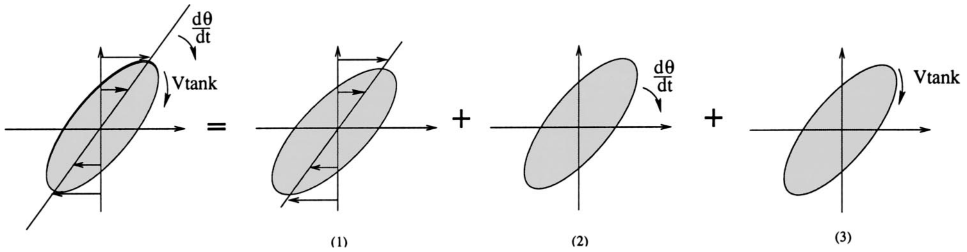

FIG. 3. The different frames involved in the model.

as the boundary integral method [6,7]. In our model, the basic assumption stated above takes into account this complex interaction in an effective manner: the effect of the backflow is included in the coefficient λ, which links the effective force to the relative velocity of the segment with respect to the applied flow. In the framework of our model, this coefficient is chosen to be independent of the particular elementary segment considered. This is reminiscent of a "mean-field"-like approximation. This coefficient is also *a priori* nonisotropic, i.e., takes different values depending on whether we consider the normal direction or the transverse direction of the elementary segment considered. These two values will be denoted as λ_t and λ_n and their determination will be discussed in Sec. VI. To some extent this model is akin to the Rouse model for polymer rods [8], where hydrodynamical interactions between adjacent pieces are ignored.

III. MECHANICAL EQUILIBRIUM FOR THE VESICLE IN THE SHEAR FLOW

As stated above, the main idea is to use the linear generalized Stokes law at the local level of each segment of the contour, and to compute the torque associated with the force. Since we shall decompose the velocity field into an applied shear, a tank-treading motion, and a tumbling one, we shall have to deal with three types of forces separately. Once each torque is evaluated, we sum up the three contributions, and set the resultant to be zero, owing to the absence of inertia. Once the expressions of the forces are specified, the remaining pieces of the work are purely algebraic with some specific integrals involving the geometry of the vesicle.

Since the Stokes law relating the force to the relative velocity is local, we find it convenient to first, write it in the frame linked to the vesicle, and then, to express the torque elements in the laboratory frame for ease of computations. We refer to Fig. 3 for the different frames used here. The laboratory frame has the basis denoted as $(\mathbf{e_x},\mathbf{e_y})$. The rotating frame, which is linked to the principal axes of the ellipse, is specified by its basis denoted as $(\mathbf{e'_x},\mathbf{e'_y})$. The local frame associated to an elementary segment on the elliptic contour is specified by $(\mathbf{e_t},\mathbf{e_n})$.

In the local frame $(\mathbf{e_t},\mathbf{e_n})$, the components of the local force (or drag) applied on the segment per unit length in the transverse direction can be expressed as functions of the relative velocities (V_t,V_n) exerted upon a membrane element:

$$dF_t=-\mu_{out}\lambda_t V_t dl,$$

$$dF_n=-\mu_{out}\lambda_n V_n dl, \tag{3}$$

where λ_t and λ_n are phenomenological parameters of the model associated, respectively, to the transverse and the normal motions to the segment dl. λ_t and λ_n have positive values with the choice of Eqs. (3). They have a dimension of the inverse of a length. The crux of the analysis is to decompose the local velocity in three pieces as stated above, and evaluate various torques.

A. Torque of the force acting on the body in a simple shear flow

In the laboratory frame $(\mathbf{e_x},\mathbf{e_y})$, the velocity field of a simple shear flow takes the form

$$v_x=\gamma y,$$

$$v_y=0.$$

γ is the shear rate, which fixes the time scale of the flow. Written in the local coordinate system $(\mathbf{e_t},\mathbf{e_n})$, the relative velocity reads

$$V_{shear_t}=-\gamma y\mathbf{e}_x\cdot\mathbf{e_t},$$

$$V_{shear_n}=-\gamma y\mathbf{e}_x\cdot\mathbf{e_n}.$$

Using Eq. (3), we determine the associated forces denoted as dF_{shear_t} and dF_{shear_n}, from which the torque is computed as

$$\mathbf{M}_{\text{shear}}=\oint_C \mathbf{r}\times d\mathbf{F}_{\text{shear}}. \tag{4}$$

Using the coordinates linked with the natural axes of the ellipse (for a convenient calculation), we easily find

$$M_{\text{shear}}=\mu_{out}\gamma\left[\frac{L_{s1}^2+L_{s2}^2}{2}+\frac{L_{s1}^2-L_{s2}^2}{2}\cos(2\psi)\right], \tag{5}$$

with the convention that a positive torque corresponds to a clockwise rotation (see Fig. 1). L_{s2} and L_{s1} are elliptic integrals:

$$L_{s2}^2=[\lambda_t f(a,b)-\lambda_n f(b,a)]+\left(\frac{b}{a}\right)^2[\lambda_t g(a,b)+\lambda_n f(b,a)],$$

$$L_{s1}^2=[\lambda_t f(a,b)-\lambda_n f(b,a)]+\left(\frac{a}{b}\right)^2[\lambda_t g(b,a)+\lambda_n f(b,a)]$$

with

$$f(a,b)=\oint_C \frac{x'^2y'^2}{\left(\frac{a}{b}\right)^2y'^2+\left(\frac{b}{a}\right)^2x'^2}dl,$$

$$g(a,b)=\oint_C \frac{x'^4}{\left(\frac{a}{b}\right)^2y'^2+\left(\frac{b}{a}\right)^2x'^2}dl.$$

According to the linear decomposition of Fig. 2, we can identify from Eq. (5) the torque associated with the rotational part of the flow

$$M_{rot}=\mu_{out}\gamma\frac{L_{s1}^2+L_{s2}^2}{2} \tag{6}$$

and the torque associated with the elongational part of the flow

$$M_{elong}=\mu_{out}\gamma\frac{L_{s1}^2-L_{s2}^2}{2}\cos(2\psi). \tag{7}$$

B. Torque of the force acting on a rigid ellipse with a rotation speed $d\psi/dt$

The tumbling velocity at a position r of the membrane is given by

$$\mathbf{V}_{\text{tumble}}=\mathbf{w}\times\mathbf{r}, \tag{8}$$

where $\mathbf{w}=(d\psi/dt)\mathbf{e_z}$ is the instantaneous angular velocity of the vesicle $d\psi/dt$ and its components in the local frame are

$$V_{\text{tumble}_t}=\left(x'\frac{d\psi}{dt}\mathbf{e}_{\mathbf{y}'}-y'\frac{d\psi}{dt}\mathbf{e}_{\mathbf{x}'}\right),$$

$$V_{\text{tumble}_n}=\left(+x'\frac{d\psi}{dt}\mathbf{e}_{\mathbf{y}'}-y'\frac{d\psi}{dt}\mathbf{e}_{\mathbf{x}'}\right).$$

We use Eq. (3) to determine the force and then we compute the torque as

$$\mathbf{M}_{\text{tumble}}=\oint_C \mathbf{r}\times d\mathbf{F}_{\text{tumble}}.$$

This yields, after elementary integration, to

$$M_{\text{tumble}}=\mu_{out}\frac{d\psi}{dt}(L_{s1}^2+L_{s2}^2). \tag{9}$$

C. Torque of the force acting on the ellipsoid related to the tank-treading motion

The tank-treading velocity is tangential to the membrane:

$$\mathbf{V}_{\text{tank}}=V_{\text{tank}}\mathbf{e_t} \tag{10}$$

and the force is simply

$$\mathbf{F}_{\text{tank}}=-\mu_{out}\lambda_t V_{\text{tank}}\mathbf{e_t}. \tag{11}$$

The associated torque is

$$\mathbf{M}_{\text{tank}}=\oint_C \mathbf{r}\times d\mathbf{F}_{\text{tank}}.$$

The integration provides us with

$$M_{\text{tank}}=-\mu_{out}V_{\text{tank}}(L_1+L_2), \tag{12}$$

where

$$L_1=\lambda_t\oint_C\left(\frac{b}{a}x'^2\right)\Bigg/\sqrt{\left[\left(\frac{a}{b}\right)^2x'^2+\left(\frac{b}{a}\right)^2y'^2\right]}dl,$$

$$L_2=\lambda_t\oint_C\left(\frac{a}{b}y'^2\right)\Bigg/\sqrt{\left[\left(\frac{a}{b}\right)^2x'^2+\left(\frac{b}{a}\right)^2y'^2\right]}dl.$$

Because the inertial effects are small (and thus neglected), the sum of the three torques must vanish. Summing up the three contributions [Eqs. (5), (9), and (12)], one finds the evolution equation for the angular velocity of the vesicle:

$$\frac{d\Psi}{dt}=\omega_{rot}+\omega_c+\omega_{elong}, \tag{13}$$

where we have defined the three quantities on the right-hand side of Eq. (13) as

$$\omega_{rot}=-\frac{\gamma}{2}, \tag{14}$$

where ω_{rot} represents the rotational velocity (i.e., a torque in the Stokes framework), arising from the rotational part of the flow and is responsible for the global rotation of the shape.

$$\omega_c=V_{\text{tank}}\frac{L_1+L_2}{L_{s1}^2+L_{s2}^2}, \tag{15}$$

where ω_c is the contribution of the tank-treading motion of the membrane to the effective angular velocity $d\psi/dt$ of the vesicle.

$$\omega_{elong}=-\frac{\gamma}{2}\frac{L_{s1}^2-L_{s2}^2}{L_{s1}^2+L_{s2}^2}\cos(2\psi), \tag{16}$$

where ω_{elong} is the effective elongational velocity which represents the main contribution of the elongational flow and tends to orient the vesicle along a direction making an angle $\psi=\pi/4$ with respect to the applied flow.

It is interesting to note at this point that for a sphere, the various integrals can easily be computed

$$L_1+L_2=2\pi\lambda_t a^2; \quad L_{s1}^2+L_{s2}^2=2\lambda_t \pi a^3.$$

Reporting into Eqs. (14) and (15), and requiring in Eq. (13) that $d\Psi/dt=0$ (since for a sphere the contribution to tumbling vanishes[2]), we obtain

$$V_{\rm tank}=\frac{\gamma}{2}a. \tag{17}$$

This is the expected value of the tank-treading velocity in the case of a sphere with a radius a. Interestingly, this result holds whatever the prescription for the parameters λ_n and λ_t is.

Inspection of Eqs. (13)–(16) reveals, in particular, that for a rigid membrane where $V_{\rm tank}=0$, no stationnary solution is possible: a rigid elliptic body should always tumble, as one expects. This can be interpreted by the fact that the rotational velocity $|\omega_{rot}|$ is always bigger than the elongational velocity $|\omega_{elong}|$. If allowance is made for a tank-treading motion (due to the membrane fluidity and the finite viscosity of the internal liquid) then $\omega_c \neq 0$. Equations (13)–(15) show indeed that the tank-treading motion described by the velocity ω_c results in an effective reduction of the global rotation ω_{rot}, provided that the tank-treading velocity $V_{\rm tank}$ has a positive value. A stationary (nontumbling) tank-treading motion of the shape is thus possible if the velocity $|\omega_{elong}|$, representing the elongational part of the flow, can balance the effective tumbling velocity $|\omega_{rot}+\omega_c|$. This can occur for sufficiently high values of the tank-treading velocity. Hitherto, the tank-treading velocity has been introduced as a phenomenological quantity, and it must be computed independently. This step is necessary in order to have an evolution equation in a closed form. The tank-treading velocity is clearly limited by the viscous friction of the internal fluid, and this piece of information must be evoked in order to complete the analysis.

IV. DETERMINATION OF THE TANK-TREADING VELOCITY

Following Ref. [4], the tank-treading velocity $V_{\rm tank}$ can be determined by considering the energy dissipated in the system. The energy injected by the flow is dissipated by viscous friction in the fluid inside the vesicle. The energy rate (or power) provided by the fluid to an elementary segment in the laboratory frame is equal to $d\mathbf{F}\cdot\mathbf{V_t}$.

The velocity $\mathbf{V_t}$ at a point $\mathbf{r}$ of the membrane can be written in the same frame as

$$\mathbf{V}_t=V_{\rm tank}\mathbf{e}_t+\mathbf{w}\times\mathbf{r}, \tag{18}$$

where $\mathbf{w}=(d\psi/dt)\mathbf{ez}$ is the instantaneous angular velocity of the vesicle.

An elementary force $d\mathbf{F}$ acting on an element dl of the membrane can be decomposed according to the preceding section as

$$d\mathbf{F}=d\mathbf{F}_{\rm shear}+d\mathbf{F}_{\rm tumble}+d\mathbf{F}_{\rm tank}.$$

The sum of the torques applied on the vesicle is equal to zero, entailing

$$\oint d\mathbf{F}\cdot(\mathbf{w}\times\mathbf{r})dl=\oint \mathbf{w}\cdot(\mathbf{r}\times d\mathbf{F})dl=0. \tag{19}$$

Hence, only the first contribution of the velocity in Eq. (18) matters. The total power provided by the flow has the following contributions:

$$E_{tot}=E_{\rm shear}+E_{\rm tumble}+E_{\rm tank}. \tag{20}$$

(a) The contribution from the simple shear flow is $E_{\rm shear}=\oint d\mathbf{F}_{\rm shear}\cdot V_{\rm tank}\mathbf{e}_t$ and upon integration on the contour, we find

$$E_{\rm shear}=\mu_{out}V_{\rm tank}\gamma\left[\frac{L_1+L_2}{2}+\frac{L_1-L_2}{2}\cos(2\psi)\right], \tag{21}$$

where the lengths L_1 and L_2 have been defined previously [Eqs. (12)]. Following the spirit of the last section, we write $E_{\rm shear}=E_{rot}+E_{elong}$ in order to identify the contributions from the rotational part of the shear flow

$$E_{rot}=\mu_{out}V_{\rm tank}\gamma\frac{L_1+L_2}{2}$$

and the elongational part of the shear flow

$$E_{elong}=\mu_{out}V_{\rm tank}\gamma\frac{L_1-L_2}{2}\cos(2\psi).$$

This decomposition will be useful in the discussion of the results.

(b) The contribution from the tumbling motion is $E_{\rm tumble}=\oint d\mathbf{F}_{\rm tumble}\cdot V_{\rm tank}\mathbf{e_t}$, yielding

$$E_{\rm tumble}=\mu_{out}V_{\rm tank}\frac{d\psi}{dt}(L_1+L_2). \tag{22}$$

(c) The contribution from the tank-treading motion is $E_{\rm tank}=\oint d\mathbf{F}_{\rm tank}\cdot V_{\rm tank}\mathbf{e_t}$, and upon integration one finds

$$E_{\rm tank}=-\mu_{out}V_{\rm tank}^2 P', \tag{23}$$

where $P'=\oint_c \lambda_t dl=\lambda_t P$

By using the above results, the total power (20) takes the form

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[2] Distinguishing between tumbling and tank treading for a sphere might seem a bit confusing. The case of a sphere is degenerate, since one can view the dynamics as being of pure tank-treading or pure tumbling nature. Indeed requiring either that $d\Psi/dt=0$, as we did here, or $V_{\rm tank}=0$, provides the same velocity along the contour. For continuity reasons with the case where there is a slight deviation from a sphere, we interpret the motion under question as being of tank-treading type.

$$E_{tot}=\mu_{out}(\alpha V_{\text{tank}}^2+\beta V_{\text{tank}}), \tag{24}$$

where

$$\alpha=\left[\frac{(L_1+L_2)^2}{L_{s1}^2+L_{s2}^2}-P'\right], \tag{25}$$

$$\beta=\gamma\left[\frac{L_2-L_1}{2}-\frac{L_1+L_2}{2}\,\frac{L_{s2}^2-L_{s1}^2}{L_{s2}^2+L_{s1}^2}\cos(2\Psi)\right]. \tag{26}$$

In the particular case of a circular shape, the total power provided by the external fluid to the internal one can easily be determined: indeed, we have $(L_1+L_2)^2=4\lambda_t^2(\pi a^2)^2$; $L_{s1}^2+L_{s2}^2=2\lambda_t\pi a^3$; $P'=2\lambda_t\pi a$, and $L_1=L_2$, $L_{s1}=L_{s2}$. This implies that both coefficients α and β vanish, and so does the total power. This result is conforting since inside a sphere the fluid executes a rigidlike rotation (there is no dissipation) and thus no energy can be transferred. It is only when the shape deviates from a circle (or a sphere in 3D) that dissipation is permissible. Note that we arrived at this result before using any information about dissipation in the enclosed fluid, and this points to a consistency of the model.

The energy dissipated by viscous friction in the volume of the vesicle is of the form

$$\epsilon=\frac{1}{2}\mu\oint_S\left(\frac{\partial V_i}{\partial x_j}+\frac{\partial V_j}{\partial x_i}\right)^2 ds. \tag{27}$$

In general, we have to determine the velocity field, which satisfies the Stokes equations inside the vesicle and subjected to boundary conditions at the surface of the ellipse. Our aim is not to determine the velocity field exactly, which is not an easy task in general (and an exact result is the exception rather than the rule). Rather we wish to capture the main ingredients and remain within a heuristic analysis. For that purpose, it will be sufficient to make use of an approximate solution inferred from simple considerations based on the result relative to a spherical shape. In order to anticipate the main ingredient, we shall take the case of a slightly deformed circle as a reference in order to serve as a guide for our reasoning. Consider $e=(b-a)/a$ to be small. The following velocity field fulfills the prescribed conditions (i.e., to be a solution of the Stokes equations in the inner domain of the vesicle):

$$V_{\mathbf{x}'}=V_{\text{tank}}\frac{y'}{b},$$

$$V_{\mathbf{y}'}=-V_{\text{tank}}x'\frac{b}{a^2}.$$

It must be noted that despite the fact that the velocity is not exactly constant along the contour, the velocity remains collinear to the tangent at the membrane[3] and this continues to represent a reasonable approximation. Let us estimate the energy dissipated in the vesicle. This is given by

$$\epsilon=\mu_{in}\alpha' V_{\text{tank}}^2, \tag{28}$$

where α' is a constant depending on a and b: $\alpha'=\frac{1}{2}\pi ab(b/a^2-1/b)^2$ in the present case.

Using Eqs. (24) and (28), we arrive at

$$V_{\text{tank}}=-\frac{f_3}{f_2-\dfrac{\mu_{in}}{\mu_{out}}f_1}\gamma\cos(2\Psi), \tag{29}$$

where

$$f_1=\alpha'=\frac{1}{2}\pi ab\left(\frac{1}{b}-\frac{b}{a^2}\right), \tag{30}$$

$$f_2=\frac{(L_1+L_2)^2}{L_{s1}^2+L_{s2}^2}-P', \tag{31}$$

$$f_3=\frac{L_2-L_1}{2}-\frac{L_1+L_2}{2}\,\frac{L_{s2}^2-L_{s1}^2}{L_{s2}^2+L_{s1}^2}. \tag{32}$$

As could be anticipated, the tank-treading velocity is directly proportional to γ which fixes the time scale of the imposed flow. We also note that the tank-treading velocity enjoys the same symmetry as the elongational flow does: it vanishes for $\psi=\pm\pi/4$ and is maximal for $\psi=0$.

Some remarks are in order. As explained in Sec. III, a shear flow can always be split into a rotational part and an elongational one (see Fig. 2). In order to understand the origin of the tank-treading motion, it is appropriate to specify the role of both the elongational and the rotational components of the flow.

On the one hand, for a purely rotational flow, Eq. (24) shows that $E_{tot}=\mu_{out}\alpha V_{\text{tank}}^2$ since $\beta=0$. Equating Eqs. (24) and (28) leads to the condition $V_{\text{tank}}=0$, provided that the shape is not circular. This corresponds to a global solidlike rotation. On the other hand, for a purely elongational flow, Eqs. (24) and (28) lead to $V_{\text{tank}}\sim\cos(2\psi)$. A nonzero tank-treading velocity is possible with the proviso that the orientation angle is different from $\psi=(\pi/4)$ $[\cos(2\psi)\neq 0]$. The torque applied on the vesicle arising from the elongational flow is [see Eq. (7)] $M_{elong}\sim\cos(2\psi)$. An inspection of the balance of the torques for the elongational flow, as done in Sec. III, leads to the dynamical equation $d\psi/dt\sim\cos(2\psi)$.

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[3] Other prescriptions for the flow could have been used. In particular,

$$V_{\mathbf{x}'}=V_{\text{tank}}\frac{y'}{b},$$

$$V_{\mathbf{y}'}=-V_{\text{tank}}\frac{x'}{a}.$$

This flow ensures a constant value for the tank-treading velocity along the contour but the velocity is not collinear to the tangential direction of the contour.

$\psi = \pi/4$ is thus, the only steady equilibrium position, with a tank-treading velocity equal to zero. Hence, the existence of a tank-treading motion of the membrane is only a consequence of the coupling between the rotational and the elongational part of the flow. The total effect of the shear can be interpreted as follows: the rotational part tends to push the orientation angle of the vesicle axis towards lower values than $\psi = \pi/4$. As soon as this is achieved the vesicle acquires a nonzero tank-treading velocity since there, the elongational part enters into action [see Eq. (16)].[4]

V. DYNAMICAL EQUATION FOR THE ORIENTATION ANGLE

Plugging Eq. (29) into Eq. (13), we can express explicitly ω_c (which involves the tank-treading motion of the vesicle) and this leads to the general dynamical equation for the orientation angle ψ of the vesicle:

$$\frac{d\psi}{dt} = A + B\cos(2\psi), \tag{33}$$

where

$$A = -\frac{\gamma}{2}, \tag{34}$$

$$B = -\frac{\gamma}{2}\left[\frac{L_{s2}^2 - L_{s1}^2}{L_{s1}^2 + L_{s2}^2} + (L_2 + L_1)\frac{(L_2 - L_1) - (L_1 + L_2)\dfrac{(L_{s2}^2 - L_{s1}^2)}{(L_{s2}^2 + L_{s1}^2)}}{(L_1 + L_2)^2 - \left(P' + \dfrac{\mu_{in}}{\mu_{out}}\alpha'\right)(L_{s1}^2 + L_{s2}^2)}\right]. \tag{35}$$

A purely tank-treading motion corresponds to the situation where the inclination angle is constant. This is expressed by $d\psi/dt = 0$ which implies the condition $-A/B < 1$. This constraint leads, in particular, to a condition on the viscosity ratio between the inner and the outer fluid:

$$\frac{\mu_{in}}{\mu_{out}} < \frac{1}{\alpha'}\left[(L_1 + L_2)\left(1 + \frac{L_{s1}^2}{L_{s2}^2}\right)\frac{L_2}{L_{s2}^2} - P'\right]. \tag{36}$$

This is the general condition which can be tabulated numerically, provided that the two drag coefficients λ_t and λ_n are known, which is exactly the case for several shapes (disks, ellipses, and spheres). Thus, the condition relates uniquely the viscosity contrast to geometrical quantities which are functions of the swelling ratio. In order to gain more insight towards an analytical progress we can explore the situation of a small deformation around the spherical shape. This proves to be sufficient to capture the essential features. For that purpose, we set $e = b - a$ and treat e as a small parameter. The integrals $L_1, L_2 \ldots$, that enter in Eq. (36) can be evaluated explicitly, so that the critical condition for tumbling is expressed in a simple form in terms of the viscosity ratio and the swelling ratio τ:

$$\frac{\mu_{in}}{\mu_{out}} = \frac{1/4\lambda_t a}{1 - \tau} \tag{37}$$

and the dissipation rate (28) scales as

$$\epsilon = \mu_{in} V_{\text{tank}}^2 (1 - \tau). \tag{38}$$

This law for the dissipation rate is in a good agreement with previous numerical results (see Ref. [5]). We find here that the closer is the shape to a sphere, the more difficult does tumbling occur; the viscosity contrast for tumbling diverges as $1/(1 - \tau)$.

VI. QUANTITATIVE AND QUALITATIVE ANALYSES OF THE MODEL

We have seen that the model presented here captures the essential features and sheds light on the various competing effects that fix the tank-treading and tumbling motions. We may ask the question whether the model can be made more quantitative. As stated before, the model requires the introduction of two drag parameters λ_t and λ_n, which are the proportionality constants relating the force and velocity in the normal and the tangential directions. Let us recall that these two drag coefficients describe the effect of the hydrodynamic interaction felt by a membrane element. This involves the geometry of the shape around a given element of membrane and these drag parameters are *a priori* function of the position of the element considered on the contour. If one wishes to go beyond a qualitative discussion we must determine these two drag parameters, which can be made in general only numerically. For a sphere with a radius a moving in a Stokes flow, it is known that on a local segment of the spherical contour we have $\lambda_t = \lambda_n = 3/2a$ (see Ref. [9]). Instead of evaluating the exact values of these parameters for each elementary elements of the membrane, we shall rather estimate them from the best fit with the full numerical simulations obtained previously [5]. Note that each membrane portion can be approximated locally as an arc of a circle. Thus, as in the case of a sphere we chose equal values for the drag coefficients in the normal and in the transverse directions with respect to the contour: $\lambda_t = \lambda_n$. We consider now a vesicle with an aspect ratio $\tau = 0.8$ and determine several quantities.

The results have been compared to the full numerical

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[4] Note that the tank-treading velocity is the result of an energy balance which involves the coupling between the rotational and the elongational part of the flow. Since energetic quantities are quadratic functions of the velocity field, the tank-treading velocity is not simply the sum of the tank-treading motions associated, respectively, to the elongational component and the rotational component considered independently. Such a summation would result in a vanishing tank-treading velocity.

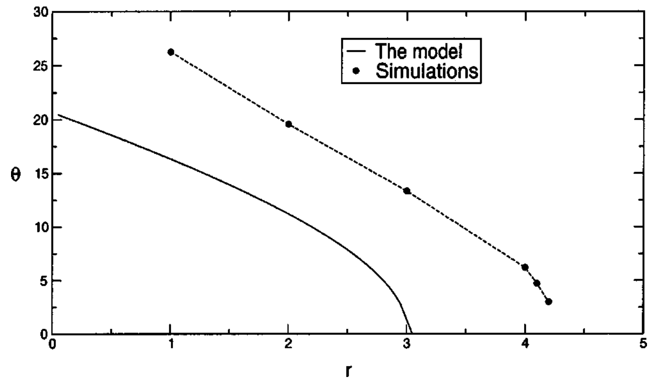

FIG. 4. Equilibrium angle as a function of the viscosity ratio: the saddle-node bifurcation ($\tau = 0.84$–model; $\tau = 0.8$–simulations).

computation and the values of λ_t and λ_n have been guessed. For various tests made so far, we found that $\lambda_t = \lambda_n \simeq 4$ per unit length in the transverse direction provide the most reasonable fit. We present in Fig. 4 the evolution of the equilibrium angle as a function of the viscosity ratio r, which corresponds to the stable branch of the saddle-node bifurcation [10]. The prediction of the model qualitatively reproduces the bifurcation branch (this is always the case regardless of the chosen parameter), and is fairly in reasonable agreement on the quantitative level. The point at which the angle is zero corresponds to the threshold of the tumbling bifurcation. This threshold depends on the swelling ratio. Consequently, the two parameters controlling the bifurcation are the viscosity contrast and the swelling ratio. Figure 5 represents the boundary between the region of the phase diagram where pure tank-treading motion takes place (low r and high τ) and that, where the motion is of tumbling type (which is favored at large r and small τ). The results are compared with the full numerical calculation. It is also worthwhile to represent some other physical quantities. Of particular interest are the global rotation velocity and the tank-treading velocity (Figs. 6–9).

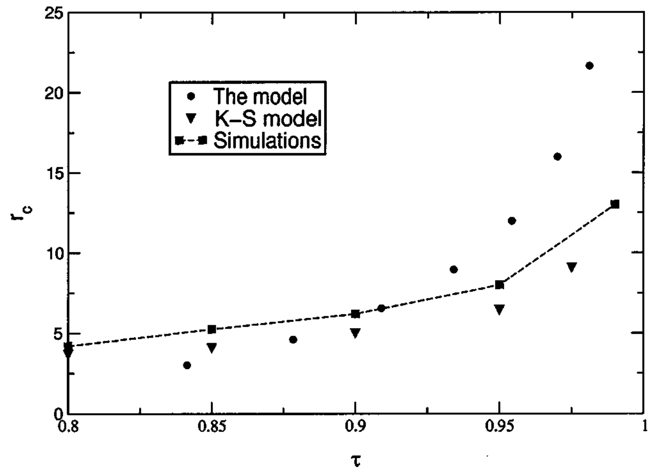

FIG. 5. Evolution of the critical viscosity ratio rc as a function of the swelling ratio τ for $a = 1$.

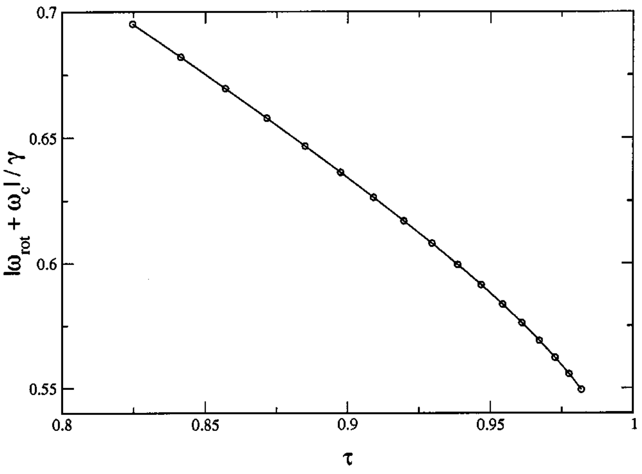

FIG. 6. Evolution of the effective tumbling velocity ($|\omega_{rot} + \omega_c| / \gamma a$) as a function of the swelling ratio τ, $r = \mu_{in} / \mu_{out} = 2$.

Before concluding some additional comments are worth to mention. Following the considerations in Sec. IV, the tank-treading motion is a result of the competition between the rotational part of the flow and the elongational component. More precisely, the rotational component pushes the vesicle axis away from the elongational main axis ($\psi < \pi/4$), allowing the membrane to acquire a nonzero tank-treading motion. One may say that part of the rotation torque is transferred to the tank-treading one. Increasing the viscosity of the inner fluid results in a global reduction of the tank-treading velocity since the internal dissipation penalizes velocity gradients inside the vesicle (see Fig. 9). From Fig. 8 the effective tumbling velocity should thus increase, reducing further the value of ψ. However, thanks to the $\cos(2\psi)$ variation of the tank-treading velocity, a new equilibrium position can be found at a value of ψ which is a decreasing function of the viscosity ratio. In the extreme limit where $\psi_{eq} = 0$, the elongational velocity ω_{elong} reaches its maximum and cannot overcome the rotational velocity on further increase of the

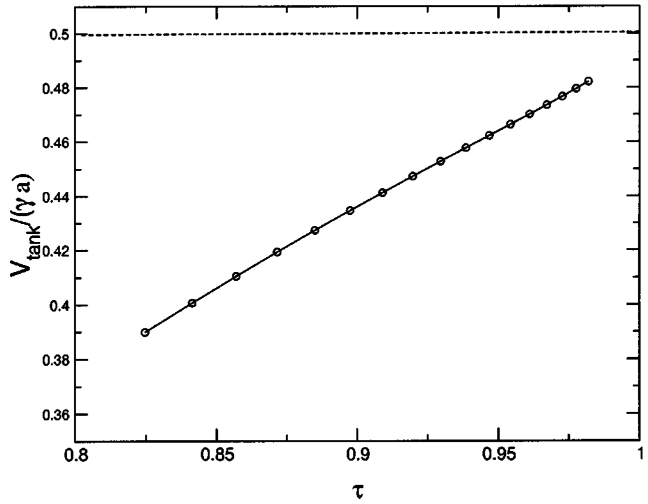

FIG. 7. Evolution of the tank-treading velocity $V_{\text{tank}} / \gamma a$ as a function of the swelling ratio τ.

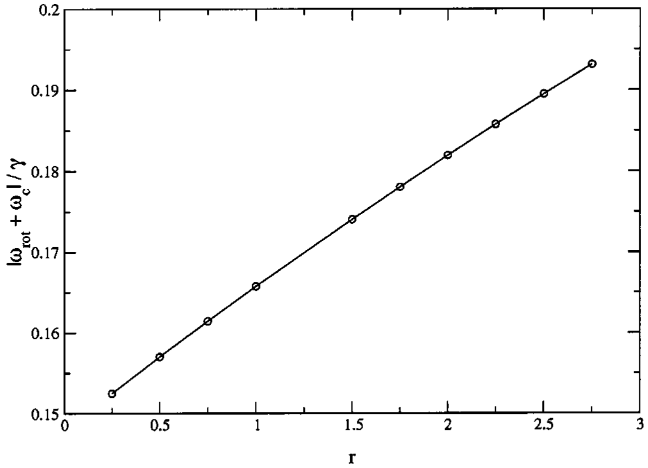

FIG. 8. Evolution of the effective tumbling velocity ($|\omega_{rot}+\omega_c|/\gamma a$) as a function of the viscosity ratio *r*, the swelling ratio is equal to $\tau = 0.84$.

internal viscosity: the steady-state solution does not exist anymore whereby a new dynamical solution takes place in the form of tumbling. Figure 4 illustrates the evolution of the equilibrium angle as a function of the viscosity ratio.

The above discussion was made on the assumption that the swelling ratio is constant. The swelling ratio is a measure of the deviation from a spherical shape. For the particular case of a circular shape (corresponding to a swelling ratio $\tau = 1$), the total velocity arising from the rotational part of the flow is completely transferred in the tank-treading motion of the membrane so that the effective tumbling velocity $|\omega_{rot}+\omega_c| = 0$ (in reality, as commented above, this situation is degenerate and there is no distinction between rigid rotation and tank treading). For a circular shape, the tank-treading velocity is maximal and equal to $V_{\text{tank}} = (\gamma/2)a$, where a is the radius of the circle. This result has already been obtained directly in Sec. III.

Figures 6 and 7 represent the evolution of the tank-treading velocity and the effective tumbling velocity $|\omega_{rot}+\omega_c|$ as a function of the swelling ratio τ. As the shape deviates from a circular one, the effective velocity responsible for tumbling $|\omega_{rot}+\omega_c|$ increases (Fig. 6) since the tank-treading velocity decreases (Fig. 7). This explains that the transition to a tumbling regime can be achieved for lower values of the viscosity ratio as the swelling ratio decreases. This is indeed what is observed in Fig. 5.

VII. CONCLUSION

We have presented a simple model bypassing the calculation of the Stokes flow. We have captured the essential features of the transition tank treading/tumbling, and have a transparent view of the various competing phenomena. This work has added a piece to our understanding of tumbling.

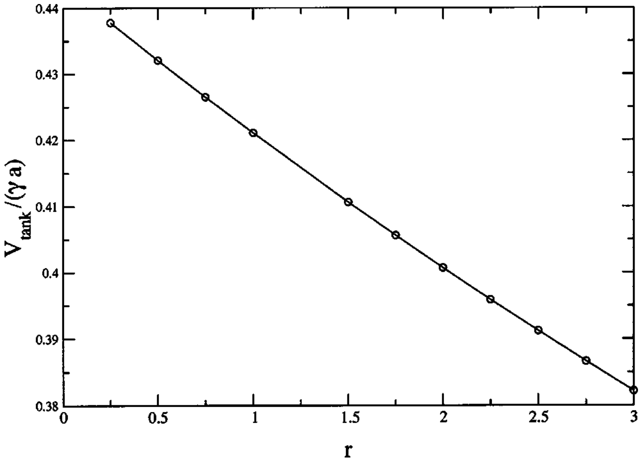

FIG. 9. Evolution of the tank-treading velocity $V_{\text{tank}}/\gamma a$ as a function of the viscosity ratio *r*, $\tau = 0.84$.

There are several important effects that have been disregarded, however. We have restricted most of our discussion to 2D shapes. In view of the result of Keller and Skallak [4] we do not expect a qualitative change when 3D shapes are considered, provided that the shape is prescribed. If the shape is free to evolve, the shear may induce a shape transformation, such as a prolate/oblate transition, and this constitutes an important task for future investigations. In addition, we did not include the fact that the two monolayers forming the vesicle membrane may slide with respect to each other [11]. In that case one has to include two tank-treading velocities, one for each layer, and evaluate the membrane internal dissipation. It will be an interesting point to clarify the influence of this fact on tumbling. For biological cells, such as red cells, further refinement of the model is clearly necessary. For example, red blood cells tumble *in vivo* in the same manner as vesicles do. There is however a notable difference between vesicles and red cells. The transition to tumbling depends on the shear rate [2]. This dependence is completely absent for vesicles since there is only one time scale $1/\gamma$ which is imposed by the flow. This points to the fact that there should exist a relevant intrinsic time scale for red cells. A natural candidate is the elastic (or even viscoelastic) response of the cytoskeleton. A natural time scale is μ/G, where G is the (2D) shear modulus of the spectrin network forming the red cell cytoskeleton, and μ is the membrane viscosity. Available data on G [12] and μ [13] provide us with μ/G of the order of $10^{-2}-10^{-1}$ s, which is not far from $1/\gamma$ in ordinary experiments [2]. We are presently using a simple model for elasticity in order to analyze the qualitative features of this effect [14].

ACKNOWLEDGMENTS

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