The behavior of closed inextensible membranes in linear and quadratic shear flows

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Abstract

The dynamics of a spheroidal vesicle, bounded by an inextensible membrane, is analyzed in function of the enclosed fluid viscosity, and of the membrane mechanical properties. The two situations in which a bending rigidity and a shear elasticity are the potential energy source in the membrane have been compared, and the stability properties of quasi-spherical vesicle shapes discussed. The transition from tank-treading to flipping motion in an external shear flow, has been studied in function of the vesicle internal viscosity and of the strength of the shear quadratic component. The transverse lift strength has been calculated in both cases of a tank-treading and of a flipping motion regime.

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I. Introduction

Vesicles (closed membranes) can exhibit, in an external fluid flow, a variety of behaviors, which are consequence of their ability to change shape in response to the stresses from the suspending fluid. These behaviors are important to understand the rheology of emulsions and other suspensions of deformable particles, which play an important role especially in the biological realm (think of blood). Depending on the viscosity of the membrane and of the fluid it contains, a non-spherical vesicle in a shear flow may either behave as a rigid object, carrying on a kind of flipping motion, or it could maintain a more or less fixed shape and orientation, while its interior carries on a circulating "tank-treading" motion.

It is well known that deformable objects, e.g. droplets \([1]\), in channel and Couette flows are able to migrate transversally to the flow lines and away from the channel walls. In small blood vessels, this phenomenon has long been known and carries the name of Fahraeus-Lindqwist effect \([2]\). The role of tank-treading motions in the transverse migration of vesicles in bounded shear flows has been considered in \([3, 4]\) focusing on the problem of a fixed shape ellipsoidal cell and to the interaction with a wall bounding the fluid. In the case of droplets, in which the interface dynamics is governed by surface tension, a tank-treading regime, and hence transverse migration, occurs irrespective of the droplet fluid viscosity \([5]\).

A tank-treading regime and a stationary ellipsoidal shape has been observed by means of direct numerical simulation \([6]\) also in the case of inextensible closed membranes with a finite bending rigidity, confirming previous experimental results presented \([7]\). The same result has been obtained analytically in the quasi-spherical regime, including the effect of thermal fluctuations \([8]\). In all cases, however, identical values for the viscosity inside and outside the membrane, were considered.

In practical situations, this is not the case. In blood, for instance, the ratio of hemoglobin and plasma viscosities, inside and outside a red cell, is of the order of five, and to this, the cell membrane viscosity must be added.

Theoretical analysis, given a prescribed ellipsoidal cell shape \([9]\), leads to expect the transition to flipping motion in a red cell, for a ratio of inner to outer viscosities between three and five. In fact, experimental observations tell us that red cells in-vivo do not stay in a tank-treading motion condition \([10]\). It is to be noticed that the transition threshold mentioned before is a decreasing function of the cell departure from spherical shape, so that, for a fixed viscosity ratio, a cell will always be able to tank-tread, provided its shape is sufficiently close to spherical.

Given this state of affair, the migration of objects like red cells in small blood vessels must be governed by a mechanism more complex than the one valid in the case of droplets, which is based essentially on orientation fixing by tank-treading motions. Recently, a simplified mechanism for the transverse migration of red cells in small blood vessels has been discussed in \([11]\), based on the stabilizing effect that quadratic shear has on cell orientation and on the contribution to lift from the kind of deformations this produces in the cell. Contrary to what happens in the case of a rigid object \([12]\), this lift acts also in the external portion of the blood vessel, in which flipping motions prevail.

It is clear that an explanation of this mechanism in terms of membrane dynamics must take into account the inextensibility of the membrane itself. This condition prevents the vesicle from reacting against the excess of stiffness in its structure by simply decreasing the amount of non-sphericity of its shape, which would allow maintaining its ability to tank-tread. This leaves out any model based on isotropic elastic membranes \([13]\) or on analogy with droplet dynamics, in which the vesicle rest shape is a sphere. Likewise, any model based on a prescribed vesicle shape, like the one considered in \([4, 9]\) is excluded, due to the need to study the flow produced deformations.

Helfrich \([14]\) and Zhong-can & Helfrich \([15, 16]\), introduced a vesicle model characterized by a membrane bending rigidity dominated dynamics, and with the total area conservation constrain imposed through a Lagrange multiplier term added to the energy of the system. Similar approaches were used in the context of fluctuating micro-emulsions in \([17, 18]\). More recently, the local inextensibility constrain was taken into account, in \([19]\) introducing a finite compressibility in the
membrane dynamics, and in $\mathbb{S}$ by means of a local Lagrange multiplier coupled with the metric tensor of the surface element expressed in spherical coordinates. In the present paper, a different approach will be used, considering the dynamics of a finite thickness membrane and taking the zero thickness limit at the end of the calculation; this with the aim of retaining in the analysis, the effect of the membrane shear elasticity and viscosity. The range of vesicle dimensions and shear strengths that will be considered is such that creeping flow conditions can be assumed, but, at the same time, that thermodynamical fluctuations, both at the vesicle and at the membrane scale can safely be neglected.

This paper is organized as follows. In section II, the equation for the membrane shape dynamics will be derived, starting from a Lamb representation for the fluid flow \cite{20} and for the deformation field inside the membrane. In section III the transition from flipping to tank-treading motion will be analyzed taking into account the effect of a quadratic contribution to shear. In the tank-treading motion regime, the vesicle shape, orientation and transverse drift velocity will be given in the flipping motion regime. Section V will be devoted to discussion of the results and conclusions. The appendix is devoted to discussion of the relative importance of torque and deformation in leading to vesicle alignment in the middle of a channel flow.

II The role of shear stresses inside the membrane

Consider a spheroidal vesicle of volume $\frac{4}{3}\pi R^3$ and area $(4\pi + S)R^2$; $S$ is the dimensionless excess area parametrizing the deviation from spherical shape. Indicate with $\delta$ the membrane thickness, which will be sent to zero at the end of the calculation, and with $\Delta(x)$ the displacement of the membrane element with respect to an initial position on the spherical surface $x = R$. Since attention is concentrated here only on the deformations, that part of the dynamics associated with bulk translations and rotations is eliminated by working in the proper reference frame. For simplicity, the particle is supposed to be neutrally buoyant, so that the reference frame is, to the medium: $\nabla \cdot s = 0$ can be split into the two independent pieces:

$$
\nabla^2 \Delta + \nabla(\nabla \cdot \Delta) = \frac{\delta}{\kappa_s} \nabla P \kappa, \quad \nabla^2 \tilde{\Delta} + \nabla(\nabla \cdot \tilde{\Delta}) = \frac{\delta}{\lambda_s} \nabla P \lambda
$$

(2.1)

with $P\kappa + P\lambda = P$. It is expedient to expand the displacement field $\Delta$ into vector spherical harmonics:

$$
\Delta(x) = \sum_{lm} \left[ \Delta^{e}_{lm}(x) Y^{e}_{lm}(\hat{x}_i) + \Delta^{m}_{lm}(x) Y^{m}_{lm}(\hat{x}_i) + \Delta^{m}_{lm}(x) Y^{m}_{lm}(\hat{x}_i) \right],
$$

(2.2)

where $x_i = x_i/x$ are the cosines of $x$ in an appropriate reference frame and the superscripts \{sem\}, standing for scalar, electric and magnetic, come from the origin of this basis as a tool in the study of electromagnetic waves (see \cite{23}). In terms of standard spherical harmonics, the functions $Y^{a}_{lm}$ are defined as

$$
Y^{e}_{lm}(\hat{x}_i) = \hat{x} Y^{e}_{lm}(\hat{x}_i), \quad Y^{m}_{lm}(\hat{x}_i) = \frac{x \nabla Y^{m}_{lm}(\hat{x}_i)}{\sqrt{l(l+1)}}, \quad Y^{m}_{lm}(\hat{x}_i) = \left[ \frac{x \nabla Y^{m}_{lm}(\hat{x}_i)}{\sqrt{l(l+1)}} \right].
$$

(2.3)
where $\hat{x} = x^{-1}x$. The radial component $\Delta_s^{im}$ gives therefore the vesicle shape deviation from spherical. In particular, it is possible to write for the excess area $S$:

$$
S = \frac{1}{2} \sum_{lm} (l^2 + l - 2) |\Delta_s^{im}|^2
$$

(2.4)

It is easy to show that $\Delta_{00} = O(S)$, while $\Delta_{lm} = O(S^{1/2})$ for $l > 0$. Also, $l = 1$ terms are associated with translation of the vesicle centre, so that all sums over spherical harmonics components actually start at $l = 2$. Substituting Eqns. (2.2-3) into Eqn. (2.1) gives for the pressure:

$$
P = \frac{1}{\hat{\delta}} \sum_{lm} \left[ x^{-4} (x^4 \hat{\Delta}_s^{im})' + \frac{(x \hat{\Delta}_s^{im})''}{\sqrt{l(l+1)}} - \frac{2}{x} \sqrt{l(l+1)} \hat{\Delta}_s^{im} \right] Y_{lm}^{*}
$$

(2.5)

where primes indicate derivation with respect to the radial coordinate $x$, and $\hat{\Delta} \equiv \kappa \Delta + \lambda \hat{\Delta}$. From here, the force densities $\mathbf{f}^{out}$ and $\mathbf{f}^{out}$ exerted by the fluids outside and inside the membrane, on the membrane itself, are given, to lowest order in $\Delta$, by $\hat{x} \cdot \mathbf{s}^{out}$ and $-\hat{x} \cdot \mathbf{s}^{in}$; using Eqns. (2.2-3) and (2.5):

$$
\hat{x} \cdot \mathbf{s} = \frac{1}{\hat{\delta}} \sum_{lm} \left[ \left( x^4 \hat{\Delta}_s^{im}/x^4 \right)' - \frac{(x \hat{\Delta}_s^{im})''}{\sqrt{l(l+1)}} + \frac{2}{x} \sqrt{l(l+1)} \hat{\Delta}_s^{im} \right] Y_{lm}^{*}
$$

$$\left[ x(\hat{\Delta}_s^{im}/x)' + \sqrt{l(l+1)} \hat{\Delta}_s^{im} \right] Y_{lm}^{*} + x(\hat{\Delta}_s^{im}/x)Y_{lm}^{*} \right] \right) \right) \right)
$$

(2.6)

The constitutive equation for the medium must coincide in the zero thickness limit with the inextensibility condition $\nabla_{\bot} \cdot \Delta(x) = 0$, where $\nabla_{\bot}$ is the angular part of the nabla operator in spherical coordinates $[22]$; for $\hat{\delta}$ finite, the constitutive equation must be therefore in the form:

$$
\nabla_{\bot} \cdot \Delta(x) = \gamma^\mu(\hat{x})(x-1); \quad \nabla_{\bot} \cdot \Delta(x) = \gamma^\mu(\hat{x})(x-1).
$$

(2.7)

where the function $\gamma$ is still arbitrary. Putting to system with Eqn. (2.1) and using Eqns. (2.2-3) and (2.5), leads to the following radial dependence for $\Delta$:

$$
\begin{align*}
\hat{\Delta}_s^{im} &= \frac{\sqrt{l(l+1)} \hat{\Delta}_s^{im}}{2} + \gamma_{lm}(x-1) \\
\hat{\Delta}_s^{im} &= \frac{\sqrt{l(l+1)} \hat{\Delta}_s^{im}}{2} + \frac{a_{lm}}{2^{l+1}} x^l + \frac{b_{lm}}{2^{l+1}} x^{-l} + \frac{c_{lm}}{2^{l+1}} \left( x - \frac{4 - l(l+1)}{2 - l(l+1)} \right) + \frac{d_{lm}}{2^{l+1}} x^{2 - l - 2} \\
\gamma_{lm} &= \frac{2^{l+1}}{2^{l+1}} c_{lm} \\
\hat{\Delta}_s^{im} &= \frac{\sqrt{l(l+1)} \hat{\Delta}_s^{im}}{2} + \frac{e_{lm}}{2^{l+1}} x^l \end{align*}
$$

(2.8)

The function $\gamma$ in Eqn. (2.7), therefore, is in general non-zero and provides one of the six parameters necessary for establishing a force balance at the outer and inner membrane surfaces. The total force exerted by the inner and outer fluids on the membrane is given by, to lowest order in $\hat{\delta}$: $\mathbf{f}^{out} + \mathbf{f}^{in} = \delta \partial_x (\hat{x} \cdot \mathbf{s})$. The difference between the force exerted on the outer and inner fluids, associated with purely internal shear and compression of the membrane, is given instead by $\mathbf{f}^{out} - \mathbf{f}^{in} = 2 \hat{x} \cdot \mathbf{s}$. Substituting into Eqns. (2.6) and (2.8) and taking the $\delta \to 0$ limit leads to the following simple expression for the field $\Delta(x)$:

$$
\begin{align*}
\hat{\Delta}_s^{im} &= \frac{\sqrt{l(l+1)} \hat{\Delta}_s^{im}}{2^{l+1}} \left( 2f_{lm}^{in} + \frac{4f_{lm}^{out}}{\sqrt{l(l+1)}} \right) \\
\hat{\Delta}_s^{im} &= \frac{2\hat{\Delta}_s^{im}}{\sqrt{l(l+1)}} \left( \frac{2f_{lm}^{out}}{2^{l+1}} - \frac{2f_{lm}^{in}}{2^{l+1}} \right) \\
\hat{\Delta}_s^{im} &= \frac{\sqrt{l(l+1)} \hat{\Delta}_s^{im}}{2^{l+1}} \left( 2f_{lm}^{out} + \frac{4f_{lm}^{in}}{\sqrt{l(l+1)}} \right) \\
\hat{\Delta}_s^{im} &= \frac{2\hat{\Delta}_s^{im}}{\sqrt{l(l+1)}} \left( \frac{2f_{lm}^{out}}{2^{l+1}} - \frac{2f_{lm}^{in}}{2^{l+1}} \right)
\end{align*}
$$

(2.9)

The first of Eqn. (2.9) is the equation for the membrane shape dynamics. The force terms at its right hand side are just the opposite of the ones produced on the membrane by the fluid stresses and
by possible other mechanical effects within the membrane, which are not accounted for by Eqn. (2.6). These last contributions are basically two: the tension force produced by the total area conservation constrain and the curvature dependent force produced by the membrane bending rigidity. The necessity a tension force associated with the total area conservation constrain, in addition to the local inextensibility condition produced pressure [Eqn. (2.5)], is due to the fact that the excess area \( S \) depends quadratically on \( \Delta \), while the local area changes are linear. The total area conservation constrain can be imposed introducing a Lagrange multiplier term proportional to \( S \) in the membrane potential energy; this leads to a contribution to the force

\[
T \partial S / \partial \Delta_{lm} = (l^2 + l - 2)T \Delta_{lm},
\]

where the Lagrangean multiplier \( T \) plays the role of a tension. The effect of finite bending rigidity can be accounted for adding to the membrane energy a curvature term \([14, 15, 16]\), which leads to the contribution to the force \( \tilde{\lambda} \):

\[
-\kappa_b(l^2 + l - 2)(l + 1)\Delta_{lm},
\]

where \( \kappa_b \) is the membrane bending rigidity (in terms of the dimensional counterpart \( \tilde{\kappa}_b \): \( \kappa_b = \frac{4\tilde{\kappa}_b}{\tilde{\rho}^2} \)).

Of course, a dissipation term due to bending could easily be added by considering an analogous term with \( \lambda_b \Delta \) in place of \( \kappa_b \Delta \), where \( \lambda_b = \mu_b / \mu \) is the ratio of the bending viscosity \( \mu_b \) with respect to the viscosity of the external fluid.

The boundary conditions for the velocity on the membrane are obtained combining the second of Eqn. (2.9) with the requirement that the velocity on the inner and outer membrane surfaces coincide in the limit \( \delta \rightarrow 0 \). Indicating with \( \hat{U}, U \) and \( \hat{U} \), respectively, the value calculated at \( x = R \) of the external velocity field, of the perturbation induced outside, and of the one induced inside the membrane, the boundary conditions will be:

\[
\begin{align*}
\hat{U}_{lm} &= \hat{\Delta}_{lm}^s; & U_{lm} &= \hat{\Delta}_{lm}^s - \hat{U}_{lm}^s, \\
\hat{U}_{lm}^e &= \frac{2\Delta_{lm}}{\sqrt{l(l+1)}}; & U_{lm}^e &= \frac{2}{\sqrt{l(l+1)}}(\hat{U}_{lm}^s + \hat{\Delta}_{lm}^s) - \hat{U}_{lm}^e.
\end{align*}
\]

It is then possible to write for the force entering the first of Eqn. (2.9):

\[
\begin{align*}
\mathbf{f}_m \rightarrow -\kappa_b(l^2 + l - 2)(l + 1)T \Delta_{lm}^s + g_{lm}^s(\hat{U}) - h_{lm}^s(\hat{U}) + \hat{\lambda}_m h_{lm}^s(\hat{U})
\end{align*}
\]

where \( \hat{\lambda} = \hat{\mu} / \mu \) is the inner to outer fluid viscosity ratio, and \( g \) and \( h \) are the force densities per unit viscosity, on a spherical surface bounding a fluid flow from the inside and the outside, calculated respectively in the case of a velocity field decaying at infinity and at zero. These can be obtained starting from a Lamb representation for the velocity field \( \hat{U} \). In explicit form \([12]\), for \( \hat{U}(x \rightarrow \infty) = 0 \):

\[
\begin{align*}
g_{lm}^s &= -\frac{2l^2 + 3l + 4}{l+1}U_{lm}^s + 3\sqrt{\frac{l}{l+1}}U_{lm}^e \\
g_{lm}^e &= 3\sqrt{\frac{l}{l+1}}U_{lm}^s - (2l + 1)U_{lm}^e
\end{align*}
\]

while, for \( \hat{U}(x \rightarrow 0) = 0 \):

\[
\begin{align*}
h_{lm}^s &= -\frac{2l^2 + l + 3}{l+1}U_{lm}^s + 3\sqrt{\frac{l}{l+1}}U_{lm}^e \\
h_{lm}^e &= 3\sqrt{\frac{l}{l+1}}U_{lm}^s - (2l + 1)U_{lm}^e
\end{align*}
\]

The equation for the membrane shape dynamics can now be obtained substituting Eqns. (2.10-14) into the first of Eqn. (2.9), and the result is, indicating \( \Delta_{lm} = \Delta_{lm}^s \):

\[
\begin{align*}
\Delta_{lm} + Ai \Delta_{lm} &= c_{lm} \\
\sum_{lm} d_l |\Delta_{lm}|^2 = S
\end{align*}
\]
where

\[ d_l = \frac{1}{2}(l^2 + l - 2); \quad c_{lm} = \frac{1}{\alpha_l} \left( \frac{4l^3 + 6l^2 - 4l - 3}{l(l+1)} \bar{U}_{lm} + \frac{2l+1}{(l+1)} \bar{U}_{lm} \right); \]

\[ A_l = a_l + b_l \bar{T}; \quad a_l = \frac{2d_1}{\alpha_l} (\bar{\kappa}_n(l+1) + \frac{4c_n}{l(l+1)}); \quad b_l = \frac{2d_2}{\alpha_l}; \]

\[ \alpha_l = \frac{2d^2 + 3d^2 + 4}{l(l+1)} + \frac{2l^3 + 5l^2 + 6l + 4}{l(l+1)} \lambda_{s} + \frac{4l^4 - l^2 - 2l - 1}{4} \lambda_{b}. \]  

(2.16)  

This is a constrained relaxation equation, in which the forcing \( c_{lm} \) comes from the external shear and the relaxation coefficient \( A_l \) at \( a_l + b_l \bar{T} \) from the membrane elastic properties and the inextensibility produced tension \( T \). In all this, the viscosity dependent coefficient \( \alpha_l \) plays the role of a mass matrix setting the time scale for the membrane response to internal and external forces. Notice that there is an ordering between the contribution to viscous and elastic forces coming from different \( l \), in that terms coming from shear are important only at low \( l \), while the tension and the bending rigidity dominate at large \( l \). It is to be noticed that the fact that (2.15) is a first order differential equation comes from the proportionality relation existing between electric and scalar components, in the second of Eqn. (2.9), and this is at the end just a consequence of the local inextensibility condition given by Eqn. (2.7).

### III. Membrane shape dynamics in viscous shear flow

To fix the ideas, imagine that the vesicle is immersed in a channel flow. It is then easy to show that the velocity field in the reference frame translating with the vesicle is:

\[ \bar{v} = e_3(x_2 + q^{-1}(\frac{1}{3} - x_2^2)), \quad q = L_r - L_l \]  

(3.1)  

where, \( x_2 = -L_l \) and \( x_2 = L_r \) are the coordinates of the walls. Back to dimensional units, the flow vorticity will thus be:

\[ \omega_0 = \frac{(L_r - L_l)\bar{v}_0}{L_0^2} \]  

(3.2)  

with \( 2L_0 = L_r + L_l \) the channel width and \( \bar{v}_0 \) the fluid velocity at the channel axis, measured in the laboratory reference frame. The analysis in the previous section was carried out in the reference frame of the rotating rigid particle (i.e. of the rigid particle with shape equal, at the given instant, to that of the vesicle). In order to proceed, it is necessary to write the vesicle shape equation in the laboratory frame. As previously discussed, the particle reference frame rotates with angular frequency, in dimensionless units: \( \frac{1}{2} + O(\Delta) \). Indicating with superscripts \( l \) and \( r \) components in the laboratory and rotating reference frames, one will have the relation:

\[ \Delta^l(x_l^r) = \Delta^r(x_l^r) = \exp(\frac{t}{2}M_1)\Delta^r(x_l^r) \]  

(3.3)  

and similar expressions for \( c_{lm} \), where \( \mathbf{M} = -i\mathbf{x} \times \nabla \) is basically the quantum mechanical angular momentum operator and \( x_2^r = x_2^l \cos(t/2) + x_3^l \sin(t/2) \), \( x_3^r = x_3^l \sin(t/2) + x_2^l \cos(t/2) \). Substituting into Eqn. (2.15) will lead then to the following equation in the laboratory frame:

\[ \begin{align*}
\Delta^l + A_l \Delta^l + \sum_m \sum_{m'} \bar{\Omega}_{mm'}^l \Delta^l_{mm'} &= c_{lm} \\
\sum_{lm} d_l |\Delta_{lm}|^2 &= S
\end{align*} \]  

(3.4)  

where \( \bar{\Omega}_{mm'}^l = -\frac{1}{2} \langle lm|M_1|lm' \rangle \); in explicit form \( \mathbb{E} \):

\[ \langle lm|M_1|l, m + 1 \rangle = \langle l, m - 1|M_1|lm \rangle = -\frac{i}{2} \sqrt{(l-m)(l+1+m)} \]  

(3.5)  

Thus, \( \bar{\Omega}_{mm'}^l \) gives nothing else than the variation rate of the components \( \Delta_{lm} \) due to solid rotation at frequency 1/2. The tension \( T \) is obtained multiplying the first of Eqn. (3.2) by \( d_l \Delta^*_lm \), summing
over \(lm\) and using the constrain \(\dot{S} = 0\); the result is:

\[
T = \frac{\sum_{lm} a_l b_l (c_{lm} \Delta_{lm}^2 - a_l |\Delta_{lm}|^2)}{\sum_{lm} a_l b_l |\Delta_{lm}|^2} \tag{3.6}
\]

It is important to notice that, in the absence of an external flow, the tension is negative. Now, in order for a stable shape configuration to be possible, it is necessary that the coefficients \(A_l\) in Eqn. (2.15) be positive. This imposes the condition on the relative importance of membrane elasticity and of the tension, that the ratio \(a_l/b_l\), varying \(l\), must be bounded below by some positive constant. Looking at Eqn. (2.15), one realizes therefore that a membrane dynamics, based purely on shear elasticity, is unstable in the quasi-spherical regime, and would require a non-perturbative treatment. In the case the elasticity due to bending dominates the one due to shear (it is enough that \(\kappa_b > \kappa_s/3\)) one finds instead that the configuration in which all the excess area is concentrated in modes \(l = 2\) is linearly stable.

**A. Flipping and tank-treading motion regime in linear shear flow**

Away from the channel center, the linear part of the shear is dominant. From the analysis carried on in \([9]\), it is known that, in the case of a prescribed ellipsoidal shape, a vesicle undergoes a transition from tank-treading to flipping motion, which depends on the inner to outer fluid viscosity ratio and on the cell non-sphericity. It is interesting to consider the same problem taking fully into account the membrane shape dynamics.

For the flow given in Eqn. (4.1), the only non-zero components are \(\bar{U}_2,\pm 1 = i \sqrt{\frac{2\pi}{5}}\) and \(\bar{U}_2,\pm 1 = i \sqrt{\frac{2\pi}{3}}\). This leads to:

\[
c_{lm} = i \delta_{l2} (\delta_{m1} + \delta_{m,-1}) c_2 \quad \text{where} \quad c_2 = \frac{2}{\alpha_2} \sqrt{\frac{10\pi}{3}} \tag{3.7}
\]

Tank-treading solutions to Eqn. (3.2) correspond to a constant shape configuration. Imposing the condition \(\Delta_{lm} = 0\) in the first of Eqn. (3.2), and using Eqns. (3.3,5) leads then to the following solution:

\[
\begin{align*}
\Delta_{20} &= \sqrt{\frac{3/2}{1 + A_2^*}}; \\
\Delta_{2,\pm 1} &= \sqrt{\frac{A_2 c_2}{1 + A_2^*}}; \\
\Delta_{2,\pm 2} &= \frac{c_2}{2(1+A_2^*)}
\end{align*} \tag{3.8}
\]

and \(\Delta_{lm} = 0\) for \(l \neq 2\). The coefficient \(A_2\) is obtained substituting Eqn. (3.6) into Eqn. (3.4):

\[
A_2 = \frac{\alpha_2 b_2}{2S} \sum_m c_{2m} \Delta_{2m}^2 = \frac{4}{S} \frac{A_2 c_2^2}{1 + A_2^*} \quad \Rightarrow \quad A_2 = \left( \frac{160}{3\alpha_2^2 S} - 1 \right)^{\frac{1}{2}} \tag{3.9}
\]

From Eqns. (2.15) and (3.5), reality of \(A_2\) fixes then the condition on the viscosity ratios \(\dot{\lambda}, \lambda_s\) and \(\lambda_b:\)

\[
\alpha_2 (\dot{\lambda}, \lambda_s, \lambda_b) < \alpha_2^{\text{MAX}} = 4 \sqrt{\frac{10}{3S}} \tag{3.10}
\]

and, as in \([9]\), in no way do the membrane elastic properties affect the transition from flipping to tank-treading motion.

For \(\alpha_2 > \alpha_2^{\text{MAX}}\), no stationary configurations are possible. One can modify the analysis leading to Eqn. (3.8) to calculate the rotation velocity of the vesicle at \(\theta = 0\) (i.e. the stationary orientation at the crossover \(\alpha_2 = \alpha_2^{\text{MAX}}\); see below). In this case, it is easy to show that \(\Delta_{2,\pm 1} = 0\), while \(\Delta_{20}\) and \(\Delta_{2,\pm 2}\) are extremal. This last fact implies that \(\dot{\Delta}_{2m} \neq 0\) only for \(m = \pm 1\). Repeating the calculation leading to Eqn. (3.6) with \(c_2 + i2\Delta_{21}\) in place of \(c_2\), and imposing the condition \(A_2 = 0\) (from \(\Delta_{21} = 0\)) leads then to the result:

\[
\dot{\Delta}_{2,\pm 1} = i\left( \frac{2\pi}{2} - c_2 \right) = i\left( \frac{2\pi}{3\alpha_2} \right).
\]
The vesicle shape is described by the equation \( X(x) = 1 + \sum_m \Delta_{2m} Y_{2m}(\hat{x}) \). It is simple at this point to find the semi-axes lengths and orientation of this ellipsoid. If \( \{x'_1, x'_2, x'_3\} \) indicates the reference frame in which the ellipsoid is diagonal, with \( x'_1 = x_1 \) and with \( \theta \) the orientation angle of \( x'_2 \) with respect to \( x_2 \), one can write:

\[
X(x) = Ax_1^2 + Bx_2^2 + 2Cx_2x_3 + Dx_3^2 = A'x'_1^2 + B'x'_2^2 + 2C'x'_2x'_3 + D'x'_3^2
\]

(3.11)

where \( A' = A \) and:

\[
\begin{align*}
B' &= \frac{B+D}{2} + \frac{B-D}{2} \cos 2\theta + C \sin 2\theta \\
C' &= 2C \cos 2\theta - (B - D) \sin 2\theta \\
D' &= \frac{B+D}{2} - \frac{B-D}{2} \cos 2\theta - C \sin 2\theta
\end{align*}
\]

(3.12)

The orientation angle is then fixed requiring \( C' = 0 \). Using the standard spherical harmonics expressions \( Y_{20} = \frac{1}{\sqrt{2}} \left( \frac{3}{2} \hat{x}_3 - \frac{1}{2} \hat{x}_1 \right) \), \( Y_{2,\pm1} = \frac{\sqrt{15}}{2\pi} \hat{x}_3 (\mp \hat{x}_1 - i\hat{x}_2) \) and \( Y_{2,\pm2} = \frac{1}{\sqrt{2}} \left( \frac{3}{2} \hat{x}_3^2 - \frac{3}{2} \hat{x}_1 \hat{x}_2 \pm 2i\hat{x}_1 \hat{x}_2 \right) \), together with Eqns. (3.6-7) and (3.9-10) leads then to the result for \( \theta \):

\[
\theta = -\frac{1}{2} \tan^{-1} \left( \frac{160}{3\alpha^2 S} - 1 \right)^{\frac{1}{2}}
\]

(3.13)

and for the ellipsoid semi-axes:

\[
\begin{align*}
R_1^2 &\equiv A' = 1 \\
R_2^2 &\equiv B' = 1 - \frac{3x_2x_3}{2\pi \cos 2\theta} \\
R_3^2 &\equiv D' = 1 + \frac{3x_2x_3}{2\pi \cos 2\theta}
\end{align*}
\]

(3.14)

Thus, one has \( \theta \in [-\pi/4, 0] \), with \( \theta = -\pi/4 \) corresponding to the limit \( S \to 0 \) and \( \theta = 0 \) to the transition from tank-treading to flipping motion, for \( \alpha_2 = O(S^{-\frac{1}{2}}) \). From Eqn. (3.12) and \( \theta < 0 \), this corresponds to the vesicle major axis (i.e. \( R_3 \)) oriented between the stretching direction of the shear flow and that of the velocity \( u \) itself. These results reproduce those obtained in [9], in the case of a fixed shape ellipsoidal vesicle, and in [25] in that of the rigid ellipsoid.

**B. The effect of quadratic shear**

The same approach can be used to study the transition to tank-treading motion induced by quadratic shear. From Eqn. (3.1), the quadratic component of the flow produces \( l = 1, 2, 3 \) contributions to \( U \) in the form:

\[
\begin{align*}
U_{10}^q &= \frac{4\sqrt{3\pi}}{45q}, & U_{10}^e &= -\frac{2\sqrt{6\pi}}{45q}, & U_{30}^q &= \frac{2\sqrt{7\pi}}{35q}, & U_{30}^e &= \frac{4\sqrt{70\pi}}{105q}, \\
U_{3,\pm2}^q &= \frac{1}{q} \sqrt{\frac{2\pi}{105}}, & U_{3,\pm2}^e &= \frac{2\sqrt{70\pi}}{105q} & U_{2,\pm2}^m &= \frac{2\sqrt{5\pi}}{15}.
\end{align*}
\]

(3.15)

As it is clear from Eqn. (2.9), the magnetic component \( U_{2,\pm2}^m \) does not contribute to shape dynamics. Substitution into \( c_m \), using Eqn. (2.15) gives, as expected, \( c_{10} = 0 \) and the only components which survive are:

\[
c_{30} = \frac{c_3}{q}, \quad \text{and} \quad c_{3,\pm2} = \sqrt{\frac{5}{6}} \frac{c_3}{q} \quad \text{where} \quad c_3 = \frac{5\sqrt{7\pi}}{6\alpha_3};
\]

(3.16)

Substituting this result, together with Eqn. (3.5) into the first of Eqn. (3.4), and imposing again stationarity, leads to the following solution for \( \Delta_{3m} \):

\[
\begin{align*}
\Delta_{30} &= -\frac{4A_3c_3}{q^2} (1 - 4A_3^2) \\
\Delta_{31} &= -\frac{6}{\sqrt{3}q^2} (9 + 44A_3^2) \\
\Delta_{32} &= \frac{40A_3c_3}{q^2} (3 + 4A_3^2) \\
\Delta_{33} &= -\frac{6\sqrt{3}c_3}{q^2} (3 + 4A_3^2)
\end{align*}
\]

(3.17)
where $\beta = 16A_3^4 + 40A_3^2 + 9$, and again $\Delta_{3m} = \Delta_{4,-m}$. The tension $T$ and then the coefficients $A_2$ and $A_3$ in Eqns. (3.8) and (3.17) could be obtained by substituting the result of these equation into Eqn. (3.6). The resulting expression for the general situation in which the quadratic and linear shear components are comparable, corresponding to $q \sim 1$, is rather complicated. A simpler expression is obtained for small $q$. In this regime, most of the excess area is stored in the $\Delta_{l=3}$ components, which leads to: $A_3 \approx \frac{5}{3} \sum_m c_{3m} \Delta_{3m}$, and, together with Eqn. (3.17), to the following equation for $A_3$:

$$A_3^4 + 10 \left( \frac{1}{4} - \frac{4c_3^2}{3S^2} \right) A_3^2 + \left( \frac{9}{16} - \frac{5c_3^2}{8q^2} \right) = 0$$  (3.18)

This equation admits real solutions when $\frac{9}{16} < \frac{5c_3^2}{8q^2}$, which leads to the condition on $q$:

$$q < q_{\text{MAX}} = \frac{10}{9\alpha_3} \sqrt{\frac{35\pi}{S}}$$  (3.19)

and again, the membrane elastic properties do not play any role. One thus notices that the condition of $q_{\text{MAX}}$ small means nothing but the fact that the viscosity of the inner fluid or of the membrane are large, so that the vesicle, stays in a state of flipping motion when placed in a linear shear flow. In correspondence to the transition, one has $A_3 = 0$ and the vesicle shape is given by:

$$\begin{cases}
\Delta_{30} = \Delta_{32} = 0; \\
\Delta_{31} = -\frac{i}{4} \sqrt{\frac{3S}{8}}; \\
\Delta_{33} = -\frac{i\sqrt{S}}{4}; 
\end{cases}$$  (3.20)

meaning that the particle fore-aft line is in the direction of the $x_2$ axis. In the case $q = 0$, i.e. at the middle of a channel flow, one has instead, from Eqn. (3.18) $A_3 = \sqrt{\frac{80S^2}{9q}}$ and then:

$$\begin{cases}
\Delta_{31} = \Delta_{33} = 0 \\
\Delta_{30} = \sqrt{\frac{10S}{16}} \\
\Delta_{32} = \sqrt{\frac{S}{16}} 
\end{cases}$$  (3.21)

corresponding to the particle fore-aft line along the $x_3$ axis, with the particle tip in the direction of the flow. Now, the error in the approximation $\Omega_{mm}' \approx \frac{i}{2} \langle lm|M_1|lm' \rangle$ [see definition after Eqn. (3.4)] is proportional to the part of the torque on the vesicle coming from the deviation of its shape from spherical. In the present case, a contribution to the torque comes from the interaction between the $\Delta_{l=3}$ components and the quadratic shear and is directed towards alignment of the particle with the direction of the flow (i.e. $\Delta_{3,\pm 2}$ and $\Delta_{30} > 0$ are the only components remaining). This torque is $O(q^{-1}S^4)$ at the transition and then, for $\alpha_3 > S^{-1}$, the transition to flipping motion occurs for a value of $q$ larger than the one set by Eqn. (3.19). A quantitative evaluation of this effect is presented in the appendix.

IV. Transverse drift in the tank-treading and flipping motion regimes

Once the vesicle shape and membrane motions are known, it is possible to calculate the lift forces originating from interaction with the shear flow and the walls. The transverse drift dependence on the particle shape, on the presence of walls bounding the fluid and characteristics of the shear flow was analyzed in [12] in the case of rigid particles. The results presented therein can be summarized as follows. A fore-aft symmetric particle will drift transversally due to interaction with the walls mediated by the linear part of the shear flow. In the case of asymmetric particles, there will also be one contribution from interaction with the wall, this time mediated by the quadratic part of
the shear, and another from direct interaction with the linear part of the flow, without the walls playing any role in this case.

The most important difference, in the case of a vesicle, is the possibility of fixed orientation provided by tank-treading, but the global picture is not modified. There are, however, additional contributions to the lift from the internal motions of the vesicle. The drift velocity $\mathbf{v}^d$ can be calculated as an adequate combination of components of the velocity perturbation $\mathbf{U}$ around the vesicle. Given the channel flow configuration described by Eqns. (3.1-2), one has $\mathbf{v}^d = \mathbf{v}^k e_2$, with:

$$v^k = \langle L | \mathbf{U} | \frac{1}{L_1^2} - \frac{1}{L_2^2} \rangle + \langle f | \mathbf{U} \rangle$$  \hspace{1cm} (4.1)

where

$$|L| = \frac{15}{16\pi} [-x_1 x_2^2, (1-x_2^2)x_2, -x_2^2 x_3] \quad \text{and} \quad |f| = (4\pi)^{-1} e_2 \hspace{1cm} (4.2)$$

and the bra-ket notation $\langle \cdot | \rangle$ stands for the integral over solid angle, of the arguments scalar product, calculated at $x = 1 \hspace{0.5cm} [13]$. Using Lamb representation, one writes then Eqn. (4.1) in function of the external flow $\mathbf{U}$ and the velocity on the membrane $\mathbf{U}$; working to $O(\Delta)$:

$$\langle Z | \mathbf{U} \rangle = \langle Z | \{ \mathbf{U}^{(0)} - \mathbf{U} \} + \langle Z | \mathbf{U}^{(1)} \rangle + \sum_{\mu m} \langle Z | \Delta | \mu m \rangle U^\mu_{lm} \rangle$$  \hspace{1cm} (4.3)

where $Z = L, f, |\mu m\rangle = \mathbf{Y}^\mu_{lm}$ and:

$$\begin{pmatrix}
U^s_{lm} \\
U^e_{lm} \\
U^m_{lm} = -2 \frac{l+1}{R} \bar{U}^m_{lm} + \frac{i+1}{R} \hat{U}^m_{lm}
\end{pmatrix} = \begin{pmatrix}
\frac{3}{l(l+1)} - 2 \bar{U}^e_{lm} \\
2 \frac{l+1}{R} \bigg( \sqrt{\frac{l(l+1)}{r}} \bigg) \bigg( \frac{3}{l(l+1)} - 2 \bar{U}^e_{lm} \bigg) + 2i \bar{U}^e_{lm} \\
0
\end{pmatrix} \hspace{1cm} (4.4)$$

The first term to right hand side of Eqn. (4.3) is identically zero, corresponding to the fact that neutrally buoyant spherical particles do not undergo transverse drift.

A. Tank-treading motion regime

In the case of a rigid particle, the velocity term $\mathbf{U}$ gives simply the bulk rotation of the particle following the flow vorticity, and the only non-zero components are $\Delta^\mu_{lm}$. In the case of a tank-treading vesicle, this is true only for $\mathbf{U}^{(0)}$, while $\mathbf{U}^{(1)}$ contains contributions which arise from the necessity to maintain constant area locally in the tank-treading process. The drift $\mathbf{v}^d$, therefore, differs from that of a rigidly rotating particle, by the amount $\Delta^\mu_{lm}$. Calculated at $x = \frac{1}{2}$, the bra-ket notation $\langle \cdot | \rangle$ stands for the integral over solid angle, of the arguments scalar product, calculated at $x = 1 \hspace{0.5cm} [13]$. Using Lamb representation, one writes then Eqn. (4.1) in function of the external flow $\mathbf{U}$ and the velocity on the membrane $\mathbf{U}$; working to $O(\Delta)$:

$$\mathbf{U}^{(1)}(\mathbf{x}) = \sum_{lm} \left( \mathbf{e}_1 \cdot [\mathbf{x} \times \nabla] \Delta \right) \frac{\mathbf{Y}^\mu_{lm}}{\sqrt{l(l+1)}} \frac{\sqrt{32\pi}}{3\alpha_2 S} \left( \frac{3}{160\pi} - 1 \right) \left( \hat{x}_2 \hat{x}_3 \right) \hspace{1cm} (4.6)$$

plus possible magnetic $l = 1$ components, associated with renormalization of the tank-treading frequency. In the case of a linear shear flow, the vesicle has the ellipsoidal shape described by the following equation; from Eqns. (3.5-7):

$$\Delta(\mathbf{x}) = \frac{3\alpha_2 S}{32\pi} \left( \hat{x}_3^2 - \hat{x}_2^2 + 2 \left( \frac{160\pi}{3\alpha_2 S} - 1 \right) \frac{1}{2} \hat{x}_2 \hat{x}_3 \right) \hspace{1cm} (4.7)$$

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The lift velocity can then be calculated substituting Eqns. (4.2-7) into Eqn. (4.1). The result close to the left wall, in dimensional units, is the following; after some algebra:

\[
v^L = \frac{129}{224\pi} \frac{a_2 S \bar{v}_0 R^3}{L_0 L_1^2} \left( \frac{160\pi}{3a_2 S} - 1 \right)^{\frac{1}{2}}
\]  

Thus, as expected, the lift goes to zero at the transition to flipping motion.

The quadratic shear dominated regime described by Eqn. (3.19), corresponds to the region \( L_i \sim L_f \). The width \( 2y^{\text{MAX}} \) of this region can be obtained from Eqns. (3.1) and (3.19): \( y^{\text{MAX}} = \frac{5R}{9a_3} \sqrt{\frac{15\pi}{S}} \) and is, as it could easily be guessed, inversely proportional to the non-sphericity and internal viscosities of the cell. It is easy to see that the contributions to lift coming from the interaction of the \( \Delta l = 3 \) terms with the linear shear, from that of the \( \Delta l = 3 \) terms with the walls, through the quadratic shear, and from that of the \( \Delta l = 2 \) terms with the walls, through the linear part of the shear, are respectively \( O(S^{\frac{1}{2}}) \), \( O(S^{\frac{1}{2}} L^{-3}) \) and \( O(S^{\frac{1}{2}} q L_0^{-2}) \) \[26\]. The first contribution is therefore dominant. Repeating the same calculations leading to Eqn. (4.8) gives now the result:

\[
v^L = \frac{1}{14} \sqrt{\frac{7}{\pi}} \Delta_{30} + \frac{1}{42} \sqrt{\frac{210}{\pi}} \Delta_{32}
\]

Back to dimensional units, from inspection of Eqns. (3.16-18):

\[
v^L = \frac{R^2 \bar{v}_0 f(q/q^{\text{MAX}})}{L_0^2 a_3}
\]

where the function \( f \) is obtained using in Eqn. (3.17) the value for \( A_3 \) obtained from solution of Eqn. (3.18). The plot of the function \( f \) is shown in Fig. 1 below.

![Figure 1: Plot of the contribution from quadratic shear to the transverse drift in function of the distance of the vesicle from the channel axis. On vertical axis, \( f \) is the transverse drift \( v^L \) normalized to \( \frac{R^2 \bar{v}_0}{L_0^2 a_3} \). On horizontal axis, \( q/q^{\text{MAX}} \) is just the vesicle distance to the channel axis, normalized to the half width of the channel region in which tank-treading motions are possible.](image)

**B. Flipping motion regime**

Away from the channel axis, the external shear is dominated by its linear component and the vesicle excess area is expected to be concentrated in the \( \Delta l = 2 \) modes. In a flipping motion regime, there are two possible sources of lift forces, associated with the vesicle deformability. One is the possibility of the linear strain, stretching or compressing the cell in such a way that components
\( \Delta_{2,\pm 1} \) with a non-zero average, necessary for a wall induced drift, be present. The other is that the shear quadratic piece be able to induce \( \Delta_{30} \) and \( \Delta_{3,\pm 2} \) components in the vesicle shape, with non-zero average, leading to lift from interaction both with the linear part of the shear, and with the walls, through the quadratic part of the shear.

An idea of this effect can be obtained by means of a perturbation theory in \( \alpha_l^{-1} \): \( \Delta = \Delta^{(0)} + \Delta^{(1)} + \ldots \), with \( \Delta^{(n)}_{lm} = O(\alpha_l^{-n}) \). The quadratic part of the shear must still be taken small enough to be in the flipping motion regime: \( q \ll q^{\text{MAX}} \sim \alpha_l^{-1} S^{-\frac{3}{2}} \). From inspection of Eqns. (2.15-16) and (3.4), one finds immediately \( \Omega_{mm'}^{(i)} = O(1) \) and \( \zeta_{lm} = O(\alpha_l^{-1}) \). To obtain the order of magnitude of \( A_1 \), one needs the tension \( T \). As it will be checked a posteriori, to lowest order in \( \alpha_l^{-1} \), only \( l = 2 \) components contribute to \( \Delta \). To lowest order one finds therefore, for the tension:

\[
T = \frac{4}{3 \alpha_2} c_{21} \Delta^{(0)*}_{21} - \frac{10}{9} \]

Thus, the effect of the membrane elasticity begins to be felt when it comes to extracting excess area from the \( l = 2 \) modes and passing it to the higher harmonics. It is interesting to consider the case in which the viscous and the elastic time scales are comparable, i.e. \( \kappa_b - \kappa_s / 3 = O(\alpha_l) \). In this way, \( A_2 = O(\alpha_l^{-1}) \), while \( A_3 \simeq \frac{1}{\alpha_3} (\kappa_b - \kappa_s / 3) = O(1) \). Hence, to zeroth order, Eqn. (3.4) will read (the convention of summation over repeated indices is adopted from now on):

\[
\begin{aligned}
\Delta^{(0)}_{2m} + \Omega^{(2)}_{mm'} \Delta^{(0)}_{2m'} &= 0 \\
\Delta^{(0)}_{3m} &= 0.
\end{aligned}
\]  

(4.11)

while, to \( O(\alpha_l^{-1}) \):

\[
\begin{aligned}
\Delta^{(1)}_{3m} + \Omega^{(2)}_{mm'} \Delta^{(1)}_{3m'} &= \epsilon_{2m} - A_2 \Delta^{(0)}_{2m} \\
\Delta^{(1)}_{3m} + \Omega^{(3)}_{mm'} \Delta^{(1)}_{3m'} + A_3 \Delta^{(3)}_{3m'} &= \epsilon_{3m} \\
\end{aligned}
\]  

(4.12)

The solution to Eqns. (4.11-12) can be written in the form:

\[
\begin{aligned}
\Delta^{(0)}_{2m}(t) &= d^{(0)}_{mm'}(t) \Delta^{(0)}_{2m}(0) \\
\Delta^{(1)}_{2m}(t) &= d^{(1)}_{mm'}(t) \Delta^{(1)}_{2m}(0) + \int_t^\infty \tau \, d^{(2)}_{mm'}(t - \tau) \epsilon_{2m'} - A_2(\tau) \Delta^{(0)}_{2m'}(\tau) \\
\Delta^{(3)}_{3m}(t) &= \int_{-\infty}^t \tau \, d^{(3)}_{mm'}(t - \tau) \exp(-A_3(\tau) \Delta^{(0)}_{3m'}(\tau) \\
\end{aligned}
\]  

(4.13)

where \( d^{(i)}_{mm'}(t) \) is the matrix element of the rotation operator:

\[
d^{(i)}_{mm'}(t) = \langle lm | \exp \left( \frac{t}{2} M_1 \right) | lm' \rangle = \int d\Omega \hat{Y}^*_{lm'}(\hat{x}'_i) \hat{Y}_{lm}(\hat{x}'_i).
\]  

(4.14)

In the equation above, as in Eqn. (3.3), superscripts \( l \) and \( r \) indicate components in the laboratory and the rotating reference frame and \( \hat{M}_1 = -i \mathbf{x} \times \nabla \). (Hence: \( \Delta^{(0)}_{lm} = d^{(0)}_{mm'}(\Delta^{(0)}_{lm}) \).

From Eqn. (4.13), one obtains the following results. The lowest order solution \( \Delta^{(0)}_{1m} \) is exact in the limit of a cell with an infinitely viscous interior and, as expected, it gives just a rigid rotation at constant angular velocity of the initial shape. Thus, if initially only \( l = 2 \) components are present, no higher harmonics will be generated at later times. This means that the relaxation term \( A_2 \) entering the second of Eqn. (4.13), i.e. the equation for \( \Delta^{(1)}_{2m} \) will have a purely oscillatory behavior. Then, all factors in the integrand of that equation will be oscillatory and the corresponding integral will either grow linearly in time or be itself an oscillating function. Actually, secular behaviors could signal the presence of some selection rule for the possible shape of the vesicle at order zero. However, it turns out that all factors in the integral are out of phase and no secular terms are present irrespective of the vesicle shape (as it might have been expected, perhaps, from the equivalence, from the energetical point of view of shapes, with different contributions from the different \( m \)’s but identical value of \( l \)). To be convinced of this fact, it is enough to notice that
small renormalization of the membrane elasticity and of the vesicle inner viscosity, concentrated at dynamics. In the presence of a strong bending rigidity, shear elasticity and viscosity provide only more towards the presence of limitations in an approach based on a quasi-spherical approximation, change, is a well known feature of vesicle dynamics \[27\]. The present situation, however, hints given shape does not correspond any more to an energy minimum, after an appropriate parameter change, is a well known feature of vesicle dynamics \[27\]. The third of Eqn. (4.13) becomes:

\[
\Delta_{l}^{(1)}(t) = \left( \frac{5}{6} \right) \int_{0}^{\infty} d\tau \exp(-A_{3}\tau) \left( d_{m0}^{(3)}(\tau) + \left( \frac{5}{7} \right) (d_{m-1}^{(3)}(\tau) + d_{m2}^{(3)}(\tau)) \right)
\]  

(4.15)

From Eqn. (4.9), the contribution to lift from \(\Delta_{l=3}\) terms is due only to \(m = 0, \pm 2\). After some algebra, one obtains for the rotation matrix coefficients:

\[
\begin{align*}
    d_{00}^{(3)}(\tau) + \left( \frac{5}{6} \right) (d_{0-2}^{(3)}(\tau) + d_{02}^{(3)}(\tau)) &= (5\cos^{2}(\tau/2) - 4)\cos(\tau/2) \\
    d_{20}^{(3)}(\tau) + \left( \frac{5}{6} \right) (d_{2-2}^{(3)}(\tau) + d_{22}^{(3)}(\tau)) &= \sqrt{3}(\frac{1}{4} \cos^{2}(\tau/2) - \frac{1}{4})\cos(\tau/2)
\end{align*}
\]

(4.16)

Substituting into Eqn. (4.15) and then into Eqn. (4.9), taking for simplicity \(\kappa_{s} = 0\), so that \(A_{3} = \frac{10\kappa_{s}}{\kappa_{c}} \simeq \frac{5\kappa_{s} k^{2} L_{m}^{6}}{\mu \alpha_{3}}\), gives then the final result, in dimensional units:

\[
v^{t} = \begin{cases} 
    \frac{20A_{3}(8A_{3}^{2} + 3)R^{2}v_{0}}{9(4A_{3}^{2} + 9)(4A_{3}^{2} + 1)L_{m}^{2} \alpha_{3}} & \text{for } A_{3} \rightarrow 0 \\
    \frac{2\mu \alpha_{3}^{2} L_{m}^{6}}{9 \kappa_{s} L_{m}^{6}} & \text{for } A_{3} \rightarrow \infty
\end{cases}
\]

(4.17)

Notice that the \(A \rightarrow 0\) limit in the first case of Eqn. (4.17) forbids the unphysical possibility of a finite drift in the absence of a fluid flow, suggested by vanishing of the \(v^{t}\) dependence on \(v_{0}\). As it was to be expected, a transverse drift in the flipping motion regime is hindered by a bending rigidity that is too large. Somewhat less intuitive is the fact that the same thing occurs also in the opposite \(\kappa_{b} / \alpha_{3} \rightarrow 0\) limit. In this case, \(\Delta_{m}^{(1)}\) becomes periodic like \(\Delta_{m}^{(1)}\) and the average contribution to drift is zero.

V. Conclusion

The study carried on in this paper has been directed towards three separate goals: understanding the effect of shear elasticity and viscosity on the dynamics of an inextensible membrane; obtaining quantitative informations on the tank-treading vs. flipping motion behaviors of vesicles in viscous flow; determining what are the consequence as regards the possibility of transversal drifts in channel flow configurations.

As regards the first problem, the tension generated from the global area conservation constrain, as it is clear from Eqns. (2.14-15) and (3.4), produces a renormalization of the elastic forces acting on the membrane, which may actually lead to a change of their sign and hence, to the absence of equilibrium stable configurations. Stability requires that the contributions to elastic force \(f_{l}\) coming from higher harmonics in the deformation \(\Delta\), be weighted by high enough powers of the spherical harmonics index \(l\), specifically, \(f_{l} \sim l^{2}\Delta_{l}\) with \(z \geq 2\). It turns out that the case of an elastic force purely due to shear leads to unstable membrane behaviors: the excess area is transferred to the modes with the highest \(l\) available. The presence instabilities signaling that a given shape does not correspond any more to an energy minimum, after an appropriate parameter change, is a well known feature of vesicle dynamics \[27\]. The present situation, however, hints more towards the presence of limitations in an approach based on a quasi-spherical approximation, than towards inability of membrane shear stresses to provide by themselves an acceptable vesicle dynamics. In the presence of a strong bending rigidity, shear elasticity and viscosity provide only a renormalization of the membrane elasticity and of the vesicle inner viscosity, concentrated at small \(l\). On the other hand, a small shear modulus implies the presence of deformation modes,
proportional to \([\mathbf{x} \times \nabla]Y_{lm}\) [see Eqn. (2.9)], which become easier to excite than the other modes, which involve changes of shape and therefore membrane bending. It is then to be remembered that different effective elastic constants for deformations at large and small scales, are actually observed in red cells, although perhaps in consequence of more complex mechanisms [28].

Concerning the problem of the behavior of a vesicle with a stiff but deformable interior in a viscous shear flow, the main motivation to the study is to be able to properly model red cell dynamics. One of the aspects is understanding in which way such a system differs from others more or less similar, like for instance droplets, elastic micro-capsules, or even rigid non-spherical particles. One crucial aspect is then the presence of transitions from tank-treading to flipping motion behaviors.

The picture that comes out of the analysis confirms that of Keller and Skalak [9] in which a fixed ellipsoidal shape was assumed. Basically, at least in the quasi-spherical regime considered, the transition to tank-treading appears to be independent of the membrane elastic properties. One can understand in a crude way what happens in terms of a balance between external and internal viscous stresses. In a tank-treading regime, the internal motions will have a typical time scale given by the external flow vorticity \(\omega_0\), while the part of the external flow maintaining the fixed orientation will be equal at most to the strain \(s\) (it will approach \(s\) for a strongly viscous vesicle). Given a deviation from spherical shape \(\Delta\) and a vesicle size \(R\), the balance between external and internal stresses will have the form: 

\[
\frac{\hat{\mu}\Delta}{\mu R^2} \lesssim \frac{\mu_s}{R},
\]

where \(\hat{\mu}\) and \(\mu\) are the external and internal dynamic viscosities. In the case considered in this paper, the ratio \(s/\omega_0\) can be large if the quadratic part of the shear is large, i.e., in terms of the parameter \(q\) introduced in Eqn. (3.1), if \(s/\omega_0 \sim q^{-1} > 1\). The condition for tank-treading becomes therefore:

\[
\frac{\hat{\mu}\Delta}{\mu R} \lesssim q^{-1}
\]

which gives basically the physical content of Eqns. (3.10) and (3.19): tank-treading is possible either when the cell is not too strongly non-spherical, or when its interior is not too viscous, or when the quadratic part of the shear dominates.

In real blood cells, the situation is complicated by the presence of a network, composed mainly of spectrin [29], providing an elastic skeleton for the membrane, and it is not clear whether tank-treading could take place without actually destroying the network. Nonetheless, in the middle part of the channel, it is likely that the cell reaches the channel axis before having the time to actually carry out a whole tank-treading cycle, so that the problem is likely not to be a real issue. Clearly, in all this, effects due to the strongly non-spherical shape, in particular, the torque produced by interaction between odd harmonics in the vesicle shape and quadratic shear, are likely to become important and should be taken into account in a realistic model of red cell dynamics.

Knowledge of the membrane dynamics becomes essential when it comes to understanding cell deformation. It is well known that within a quasi-spherical approximation, no distinction is made between different shapes involving spherical harmonics \(Y_{lm}\) with the same \(l\) [16]. Such an approximation has been sufficient, however, to determine the \(l = 3\), quadratic shear produced deformation of a vesicle with an ellipsoidal rest shape, and to understand its effect in terms of the possibility of transverse drifts in a flipping motion regime. The interesting result is that such deformations have a preferential orientation, and contribute therefore to transverse drift, only if the membrane elasticity and the vesicle inner viscosity have comparable characteristic frequencies, which is the content of Eqn. (4.17). In other words the membrane must be neither too stiff nor too “loose”. The presence of non-zero average \(l = 3\) shape components corresponds to the picture of the vesicle trying to offer to the parabolic flow a parachute kind of shape, with the concave side towards the coming fluid. In the simplified model presented in [11], this effect was parametrized as a contribution to the vesicle angular velocity, odd in the angle between vesicle symmetry axis and flow direction. In the present analysis, this contribution appears to be of higher order in the shape non-sphericity, and the dominant contribution is the direct interaction of the average \(l = 3\) shape component with the external shear linear part. This effect, however, may play an important role
in the case of strongly non-spherical vesicles like real red cells.

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**Appendix A. Torque on non-spherical vesicle in quadratic shear**

The presence of a torque $t = te_1$ on the vesicle is equivalent to a change in the vorticity of the external flow, in dimensional units, from $\omega_0$ to $\omega_0 + \Delta \omega$, with $\Delta \omega = \frac{t}{8\pi \mu R^2}$. This corresponds to a redefinition of $q$ in Eqn. (3.1):

$$q = L_r - L_l + \Delta q$$

(A1)

where $\Delta q = \Delta \omega/\omega_0$. In a way perfectly analogous to the case of the drift velocity [see Eqns. (4.1-4)], it is possible to express this vorticity renormalization using a bra-ket notation [12]. Back to dimensionless units:

$$\Delta q = \langle t|\hat{U}^{(1)} + \sum_{\mu \ell m} \langle t|\Delta X|\mu \ell m \rangle U^\mu_{\ell m} \rangle$$

(A2)

where $U^\mu_{\ell m}$ is given by Eqn. (4.4), and the ket $|t\rangle$ is given by:

$$|t\rangle = \frac{3}{8\pi} [0, x_3, -x_2].$$

(A3)

which is proportional to $Y^m_{11} + Y^m_{1,-1}$. The velocity correction $\hat{U}^{(1)}$ is given, as in the calculation of $v^L$ by Eqn. (4.6) and is therefore proportional to a combination of electric components $Y^\mu_{\ell m}$, which are orthogonal to $Y^m_{1,\pm 1}$. For this reason, $\hat{U}^{(1)}$ does not contribute in Eqn. (A1). Substituting Eqn. (3.15) into Eqn. (4.4) and carrying out the angular integrals in the term $\langle t|\Delta X|\mu \ell m \rangle$ leads then to the result, after some algebra:

$$\Delta q = -\frac{i}{112} \left( \frac{7}{\pi} \right)^\frac{3}{4} (23\sqrt{3} \Delta_{31} + 15\sqrt{5} \Delta_{33})$$

(A4)

At the transition to flipping motion regime, $q = q^{\text{MAX}}$; hence, using the expression for $\Delta$ provided by Eqn. (3.20), one obtains:

$$-\Delta q = \frac{47}{32} \sqrt{\frac{S}{35\pi}},$$

(A5)

that is the amount by which, the width of the region at the channel center where tank-treading dominate, gets increased. From comparison with Eqn. (3.19), this effect will begin to be important when $\alpha_3 \sim 70\pi/S$.

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