Role of membrane viscosity in the orientation and deformation of a spherical capsule suspended in shear flow

By D. BARTHES-BIESEL AND H. SGAIER

Départment de Génie Biologique, Université de Technologie de Compiègne, B.P. 233, 60206 Compiègne, France

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Red blood cells or artificial vesicles may be conveniently represented by capsules, i.e. liquid droplets surrounded by deformable membranes. The aim of this paper is to assess the importance of viscoelastic properties of the membrane on the motion of a capsule freely suspended in a viscous liquid subjected to shear flow. A regular perturbation solution of the general problem is obtained when the particle is initially spherical and undergoing small deformations. With a purely viscous membrane (infinite relaxation time) the capsule deforms into an ellipsoid and has a continuous flipping motion. When the membrane relaxation time is of the same order as the shear time, the particle reaches a steady ellipsoidal shape which is oriented with respect to streamlines at an angle that varies between 45° and 0° , and decreases with increasing shear rates. Furthermore it is predicted that the deformation reaches a maximum value, which is consistent with experimental observations of red blood cells.

1. Introduction

A red blood cell (r.b.c.), freely suspended in another fluid subjected to simple shear flow, exhibits very peculiar behaviour. When the suspending fluid viscosity is high enough, the r.b.c. takes a stable deformed shape while its membrane continuously rotates around this profile: this is the so-called 'tank-treading motion' (Fischer & Schmid-Schonbein 1977). Direct microscopic observation of this behaviour indicates that the apparent deformation of the cell increases with shear rate, until it reaches a maximum value. Furthermore, the particle is oriented with respect to streamlines. This orientation has not been measured up to now, but is known to exist because of two phenomena: the impossibility to focus simultaneously on both extremities of the cell, and the distortion of the diffraction spectrum of a laser beam crossing a sheared suspension of r.b.c.s.

It is very difficult to model correctly the behaviour of such a particle, owing to its high overall deformability. When the cell is suspended in a shear flow, it deforms under the influence of the viscous stresses exerted by the suspending medium as well as by the internal liquid (the haemoglobin solution). Those stresses themselves depend on the overall shape of the particle and on the motion. Consequently the problem belongs to the free-interface class and is highly nonlinear. The situation is further complicated by the peculiar mechanical properties of the r.b.c. membrane. The latter is a very thin bilayer, lined with a protein network. Because of this structure, it behaves as a two-dimensional incompressible elastic sheet with nonlinear constitutive behaviour. Furthermore, because the shear elastic modulus has a very low value, the membrane is easily shearable and can probably attain quite large deformations. This certainly complicates the formulation of the membrane-mechanics equations. Finally, a number of experiments (Evans & Hochmuth 1976; Chien *et al.* 1978; Tozeren *et al.* 1982) have shown unambiguously that this membrane exhibits a measurable viscosity.

These considerations may explain why up to now there have been relatively few mechanical models of r.b.c.s in general, and of their trank-treading motion in particular, and also why the presently existing models are still quite approximate and are all open to some sort of criticism.

For example, a tank-treading ellipsoidal cell has been studied by Keller & Skalak (1982). Such a model represents qualitatively the general features of the motion of a r.b.c. suspended in shear flow, in particular the transition from a solid-body rotational motion to a tank-treading behaviour. However, the wall mechanics are not treated in detail, and consequently the shape of the deformed cell, which obviously must depend on the shear rate, is an independent parameter of the model. A different approach has been proposed by Barthes-Biesel (1980), who tried to understand the physical phenomena involved into cell behaviour by considering the motion of a spherical capsule suspended in shear flow (a capsule consists of a liquid drop surrounded by an elastic deformable skin). This type of model can only give qualitative informations, since a spherical cell is not a realistic representation of a r.b.c., which, in its natural shape, is a biconcave disk. However, the advantage of this simple geometry is that it is amenable to fairly straightforward analytical solutions into which all the features of the membrane behaviour can be taken into account and from which the main physical parameters can be identified. For example, when the capsule wall has elastic properties and when the deformation Dis small $(D \leq 1)$, it is then predicted that, to first order, the particle reaches a steady ellipsoidal shape, oriented at 45° with respect to streamlines, while the membrane continuously rotates around this profile. Increasing the flow strength results in a slight decrease of the orientation angle, but this is an $O(D^2)$ effect. The deformation can be computed exactly and is found to be a monotonic increasing function of shear rate.

Up to now, all models have only considered cells surrounded by a purely elastic skin, devoid of bending resistance. Now, if one takes into account the fact that the membrane does have a finite viscosity, one should expect the above results to become different and to depend on the ratio of viscous to elastic forces acting in the wall. Indeed, because of the conjugate effects of the tank-treading motion and of the steady global shape, a membrane element is subjected to a cyclic time-dependent load, and thus viscosity should play an important role. It is the objective of the present paper to study the influence of the membrane viscosity upon the motion, deformation and orientation of an initially spherical capsule suspended in a linear simple shear flow.

Since the problem is time-dependent, it is convenient to use the Cartesian tensor formulation of membrane mechanics developed by Barthes-Biesel & Rallison (1981, hereinafter referred to as I) and by Secomb & Skalak (1982). To the elastic constitutive law of I the viscous term of Secomb & Skalak will be added linearly, so that the viscoelastic model chosen for the cell wall is of the Kelvin–Voigt type. The fluid-mechanical problems of the flows of the internal and external liquids are solved under the condition of kinetic and dynamic equilibrium of the membrane. This is done by means of a regular perturbation analysis developed in the case where the deformation is small.



FIGURE 1. Definition of the different domains.

In §2, the equations of the problem are given, together with a short outline of the membrane mechanics. The general solution in the case of a linear shear flow and of a spherical capsule subjected to small deformations may be found in §3. The particle motion is discussed for simple shear flow in §4, while the types of behaviour obtained for different membrane properties are shown in §§5–7. The relevance of the results to r.b.c. mechanics is discussed in §8.

2. Statement of the problem

Consider a capsule of characteristic dimension a, filled with an incompressible Newtonian liquid of viscosity $\lambda \mu$ and surrounded by a two-dimensional membrane with a surface shear elastic modulus E^s , and a surface viscosity μ^s . This capsule is suspended in another Newtonian incompressible liquid of viscosity μ , which is subjected to a linear shear flow $G(\boldsymbol{E} + \boldsymbol{\Omega})$, where \boldsymbol{E} and $\boldsymbol{\Omega}$ are respectively the symmetric and skew-symmetric parts of the velocity gradient. Non-dimensional quantities are used: lengths are scaled by a, time by G^{-1} and viscous stresses by μG .

2.1. General equations

Assuming the particle to be very small, the Reynolds number based on its dimensions is much smaller than unity, so that inertial effects may be neglected. The fluid mechanics is described by the Stokes equations. Denoting by V^1 , V^e and S respectively the internal domain, the suspending fluid and the surface of the particle (figure 1), the non-dimensional governing equations with respect to a set of axes moving with the centre of mass of the cell are:

$$\nabla \cdot \boldsymbol{v} = 0, \quad \nabla \cdot \boldsymbol{\sigma} = 0, \tag{2.1}$$

$$\boldsymbol{\sigma} = -\boldsymbol{p}\boldsymbol{I} + (\boldsymbol{\nabla}\boldsymbol{v} + \boldsymbol{\nabla}\boldsymbol{v}^{\mathrm{T}}) \quad \text{in } \boldsymbol{V}^{\mathrm{e}},$$

$$\boldsymbol{\sigma} = -p\boldsymbol{I} + \lambda(\boldsymbol{\nabla}\boldsymbol{v} + \boldsymbol{\nabla}\boldsymbol{v}^{\mathrm{T}}) \quad \text{in } V^{1},$$

$$v \to (\boldsymbol{E} + \boldsymbol{\Omega}) \cdot \boldsymbol{x} \quad \text{as } |\boldsymbol{x}| \to \infty,$$
 (2.3)

$$[\boldsymbol{v}]_{S} = 0, \tag{2.4}$$

$$[\boldsymbol{\sigma} \cdot \boldsymbol{n}]_S + \boldsymbol{f} = 0, \tag{2.5}$$

where v and p are respectively the velocity and pressure fields, I is the unit tensor, n is the outward unit normal vector to S and f is the force exerted by the membrane on the fluids. The notation $[]_S$ denotes the jump of the enclosed quantity across the boundary.

Conditions (2.4) and (2.5) correspond respectively to the kinetic and dynamic equilibria of the membrane. The exact expression for f depends on the wall mechanics, which is now specified.

2.2. Membrane mechanics

A formulation of membrane mechanics in terms of Cartesian tensors has been proposed in I for the elastic behaviour and by Secomb & Skalak (1982) for the viscous one. We briefly outline the theory and show how a linear viscoelastic constitutive law for the membrane may be constructed. For the sake of clarity, dimensional quantities are used first; the non-dimensionalization will be performed when the coupling between fluid and solid mechanics is completed.

The material points of the membrane are labelled by their position X in some reference configuration (unstressed). After application of a load, they are displaced to position x(X, t). The three-dimensional displacement gradient is thus

$$C = \frac{\partial x}{\partial X}$$

Since all the points belong to a surface, it is necessary to define a projection tensor P, which maps three-dimensional space into the two-dimensional subspace of the cell surface. If n is the unit normal to the deformed surface then

$$\boldsymbol{P} = \boldsymbol{I} - \boldsymbol{n}\boldsymbol{n}. \tag{2.6}$$

Similarly, the projection tensor onto the undeformed surface is

$$P_0 = I - NN$$

where N is the unit normal to the reference configuration. Consequently, the two-dimensional deformation gradient is defined as

$$\boldsymbol{A} = \boldsymbol{P} \cdot \boldsymbol{C} \cdot \boldsymbol{P}_{0}. \tag{2.7}$$

For a purely elastic material, its mechanical behaviour is completely determined by a strain-energy function $W(\Lambda_1, \Lambda_2)$ which depends only on the strain invariants Λ_1 and Λ_2 given by

$$\Lambda_{1} = \log \lambda_{1} \lambda_{2} = \frac{1}{2} \log \{ \frac{1}{2} [\operatorname{tr} (\boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}})]^{2} - \frac{1}{2} \operatorname{tr} [(\boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}})^{2}] \},$$

$$\Lambda_{2} = \frac{1}{2} (\lambda_{1}^{2} + \lambda_{2}^{2}) - 1 = \frac{1}{2} \operatorname{tr} (\boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}}) - 1,$$

$$(2.8)$$

where λ_1 and λ_2 are the principal stretch ratios. With such definitions, the invariant Λ_1 is linked to local surface variations, and is thus zero when the membrane is incompressible. Then the two-dimensional Cauchy stresses in the membrane are given by

$$\boldsymbol{\sigma}^{\mathrm{e}} = \mathrm{e}^{-A_{1}} \left[\frac{\partial W}{\partial A_{1}} \boldsymbol{P} + \frac{\partial W}{\partial A_{2}} \boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}} \right].$$
(2.9)

The viscous behaviour of the membrane has been studied by Secomb & Skalak, who show that the proper definition of the rate of strain is

$$\boldsymbol{\theta} = \frac{1}{2} \boldsymbol{\mathcal{P}} \cdot \left[\frac{\partial \boldsymbol{v}^{\mathrm{m}}}{\partial \boldsymbol{x}} + \left(\frac{\partial \boldsymbol{v}^{\mathrm{m}}}{\partial \boldsymbol{x}} \right)^{\mathrm{T}} \right] \cdot \boldsymbol{\mathcal{P}}, \qquad (2.10)$$
$$\boldsymbol{v}^{\mathrm{m}} = \frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t}.$$

where

At this stage it is sufficient to postulate a linear constitutive law for the viscous behaviour of the membrane. However, following Secomb & Skalak, it is necessary to separate in the viscous stress σ^{v} the contributions from the shear viscosity μ^{s} and from the expansion viscosity μ'^{s} :

$$\boldsymbol{\sigma}^{\mathbf{v}} = \boldsymbol{\mu}^{\prime \mathbf{s}} \operatorname{tr} \left(\boldsymbol{\theta} \right) \boldsymbol{P} + 2\boldsymbol{\mu}^{\mathbf{s}} \left[\boldsymbol{\theta} - \frac{1}{2} \operatorname{tr} \left(\boldsymbol{\theta} \right) \boldsymbol{P} \right].$$
(2.11)

If the shell is incompressible, as is the case for many biological membranes with a bilayer structure, then the first term in (2.11) identically vanishes, and only the pure shear components of \boldsymbol{e} are relevant. But, if the membrane material can undergo surface variations, then two viscosity coefficients are needed in principle. Since there is very little information on the relative magnitudes of μ^s and μ'^s , we have chosen here for the sake of simplicity to make them equal, in order to characterize viscous effects with a single parameter μ^s . Thus the constitutive relation (2.11) reduces to

$$\boldsymbol{\sigma}^{\mathrm{v}} = 2\mu^{\mathrm{s}}\boldsymbol{\theta},\tag{2.12}$$

which is the correct form for an incompressible membrane.

In the present analysis it was decided to describe the membrane behaviour by means of a simple Kelvin–Voigt model, where the stress tensor is the sum of the elastic and of the viscous contributions:

$$\boldsymbol{\sigma} = \boldsymbol{\sigma}^{\mathbf{e}} + \boldsymbol{\sigma}^{\mathbf{v}},$$

$$\boldsymbol{\sigma} = e^{-A_{1}} \left(\frac{\partial W}{\partial A_{1}} \boldsymbol{P} + \frac{\partial W}{\partial A_{2}} \boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}} \right) + 2\mu^{\mathrm{s}} \boldsymbol{\theta}.$$
(2.13)

To complete the description of the problem, there remains to express the equilibrium equations of the membrane, which, in the absence of inertia, may be written as

$$\boldsymbol{P} \cdot \boldsymbol{\nabla} \cdot \boldsymbol{\sigma} = \boldsymbol{f}, \tag{2.14}$$

where f is the load exerted by the shell on the external medium.

There are two kinds of coupling between fluid and solid mechanics. The first one is kinematic and follows from the continuity of velocities between the liquids and the membrane:

$$\boldsymbol{v}^{\mathrm{f}} = \boldsymbol{v}^{\mathrm{m}} = \frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t} \quad (\boldsymbol{x} \in S), \tag{2.15}$$

where v^{t} represents the fluid velocity on the surface. Using again a and G^{-1} respectively as length and timescales, (2.15) remains unchanged when nondimensional quantities are used.

The second coupling arises through the force f which appears both in (2.5) and in (2.14). This leads also to the question of the proper scaling of f. If tensions (forces per unit length) in the shell are scaled by E^8 when they have an elastic origin and by $\mu^8 G$ when they are viscous, then, combining (2.5) and (2.14) and now using non-dimensional quantities, we find

$$[\boldsymbol{\sigma} \cdot \boldsymbol{n}]_{S} = -k\boldsymbol{f}^{\mathrm{e}} - \eta \boldsymbol{f}^{\mathrm{v}}, \qquad (2.16)$$

with

5

$$\boldsymbol{f}^{\mathrm{e}} = \boldsymbol{P} \cdot \boldsymbol{\nabla} \cdot \left\{ \mathrm{e}^{-A_{1}} \left[\frac{\partial W}{\partial A_{1}} \boldsymbol{P} + \frac{\partial W}{\partial A_{2}} \boldsymbol{A} \cdot \boldsymbol{A}^{\mathrm{T}} \right] \right\}, \qquad (2.17)$$

$$\boldsymbol{f}^{\mathrm{v}} = \boldsymbol{P} \cdot \boldsymbol{\nabla} \cdot (2\boldsymbol{e}). \tag{2.18}$$

Consequently, it appears that the problem depends on three main parameters:

 λ , the ratio of bulk viscosities of the internal and external liquids;

 $k = E^{s}/\mu Ga$, the ratio of elastic forces in the membrane to viscous forces exerted by the suspending fluid; $\eta = \mu^{s}/\mu a$, the ratio of membrane viscosity to the bulk viscosity of the suspending liquid (since μ^{s} is a surface viscosity, it has the dimensions of a bulk viscosity multiplied by a length).

Obviously, for any capsule (and particularly for a r.b.c.), subjected to any shear flow, this problem is highly nonlinear and no general solution presently exists. However, in the particular situation of an initially spherical capsule, limited to small deformations, it is possible to develop a regular perturbation expansion of the solution.

3. Solution in a general linear shear flow

From now on, we consider the special case of an initially spherical capsule of radius a. Owing to the vorticity of the shear flow, the particle both rotates and deforms. However, as was pointed out by Barthes-Biesel (1980) and also in I, it is possible to take advantage of the initial isotropy of the shape and to subtract out the rotation from the problem. Let Y label the material points in a reference configuration (t = 0) such that $Y \cdot Y = 1$.

At time t the points occupy position x(t) resulting from a total displacement which may be decomposed into a rotation and a stretch. If Q(t) is the rotation matrix of the membrane during time t, it obeys the following relations:

$$\boldsymbol{Q}\cdot\boldsymbol{Q}^{\mathrm{T}}=\boldsymbol{I},\quad \boldsymbol{\dot{Q}}=\boldsymbol{\omega}\cdot\boldsymbol{Q},$$

where $\boldsymbol{\omega}$ is the rotation rate of the wall. Since the initial shape is isotropic, a new reference configuration may be defined where the material points are labelled by X, such that $\mathbf{X} = \mathbf{O} : \mathbf{Y} = \mathbf{W} : \mathbf{Y}$ (3.1)

$$\boldsymbol{X} = \boldsymbol{Q} \cdot \boldsymbol{Y}, \quad \dot{\boldsymbol{X}} = \boldsymbol{\omega} \cdot \boldsymbol{X}. \tag{3.1}$$

Consequently, X may be viewed as the Eulerian position of the points before deformation. Since the solid-body rotation generates no stresses, and since the material is assumed to be isotropic, we may use X rather than Y as the reference configuration of the membrane.

Now we assume that the deformations of the sphere are limited, and we denote their magnitude by $\epsilon \ll 1$. Consequently, the displacement may be written as

$$\boldsymbol{x} = \boldsymbol{X} + \boldsymbol{\epsilon} \boldsymbol{g}(\boldsymbol{X}) + O(\boldsymbol{\epsilon}^2).$$

Then, following a standard procedure (Cox 1969; Frankel & Acrivos 1972; Barthes-Biesel 1980), all equations are expanded in terms of ϵ . Thus for each order in ϵ the problem to be solved becomes linear.

3.1. The purely elastic membrane

When the membrane is purely elastic its time-dependent deformation has been obtained to $O(\epsilon)$ in I. It is shown that the displacement of the material points depends on two second-order tensors J and K, which are symmetric and traceless:

$$\boldsymbol{x} = \boldsymbol{X} + \boldsymbol{\epsilon} \boldsymbol{K} \cdot \boldsymbol{X} + \boldsymbol{\epsilon} \boldsymbol{X} \cdot (\boldsymbol{J} - \boldsymbol{K}) \cdot \frac{\boldsymbol{X} \boldsymbol{X}}{\boldsymbol{X}^2} + O(\boldsymbol{\epsilon}^2).$$
(3.2)

The overall distortion of the profile of the particle is determined by J, since the surface equation is given by $r = (\mathbf{x} \cdot \mathbf{x})^{\frac{1}{2}} = 1 + \epsilon \mathbf{X} \cdot \mathbf{J} \cdot \mathbf{X} + O(\epsilon^2)$. (3.3)

whereas K measures in-plane deformations of the membrane elements. Using (3.2),

it is straightforward to determine P, A, σ^{e} and ultimately f^{e} . The procedure then consists in expressing the solution to the Stokes equations in terms of spherical harmonics (of order 2 in this approximation):

$$v = 2\mathbf{S}^{\mathbf{e}} \cdot \frac{x}{r^5} - 5\mathbf{x} \cdot \mathbf{S}^{\mathbf{e}} \cdot \mathbf{x} \frac{x}{r^7} + \frac{1}{2}\mathbf{x} \cdot \mathbf{T}^{\mathbf{e}} \cdot \mathbf{x} \frac{x}{r^5} \quad (\mathbf{x} \in V^{\mathbf{e}}),$$

$$v = 2\mathbf{S}^{\mathbf{i}} \cdot \mathbf{x} - \frac{2}{2\mathbf{i}}\mathbf{x} \cdot \mathbf{T}^{\mathbf{i}} \cdot \mathbf{x} \mathbf{x} + \frac{5}{2\mathbf{i}}r^2\mathbf{T}^{\mathbf{i}} \cdot \mathbf{x} \quad (\mathbf{x} \in V^{\mathbf{i}}).$$
(3.4)

The coefficients of the harmonics S^{e} , T^{e} , S^{i} and T^{i} are second-order symmetric and traceless tensors which follow from boundary conditions (2.3)-(2.5), where f is replaced by f^{e} . Their values are given in I. The dynamic coupling between the fluid and the membrane is thus realized, and there remains to express the kinematic condition (2.15), which leads to two differential equations defining the time evolution of \boldsymbol{J} and \boldsymbol{K} :

$$\begin{aligned}
\mathbf{J} &= a_0 \mathbf{E} + k \epsilon [b_0 \mathbf{L} + (b_1 + b_2) \mathbf{M}] + O(k \epsilon^2), \\
\mathbf{\mathring{K}} &= a_0 \mathbf{E} + k \epsilon [b_0 \mathbf{L} + b_1 \mathbf{M}] + O(k \epsilon^2).
\end{aligned}$$
(3.5)

where " denotes a Jaumann derivative defined for any second-order tensor as

$$\dot{J} = \frac{\partial J}{\partial t} + \boldsymbol{\omega} \cdot \boldsymbol{J} + \boldsymbol{J} \cdot \boldsymbol{\omega}.$$

$$b_0 = \frac{1}{2\lambda + 3}, \quad a_0 = 5b_0,$$

$$b_1 = \frac{2(3\lambda + 2)}{(19\lambda + 16)(2\lambda + 3)}, \quad b_2 = \frac{2}{19\lambda + 16}.$$

L and M are two homogeneous linear combinations of J and K

a/a) / a)

The coefficients α_i depend on the specific elastic properties of the material, whose strain-energy function W is expanded as follows:

$$W = W_0 + \alpha_1 \Lambda_1 + \frac{1}{2}(\alpha_1 + \alpha_2) \Lambda_1^2 + \alpha_3(\Lambda_2 - \Lambda_1) + O(\epsilon^3).$$

3.2. The purely viscous membrane

The problem to be solved is given by (2.1) and (2.2), with which the following boundary conditions are associated:

$$v \to 0$$
 as $|x| \to \infty$, (3.7)

$$[\boldsymbol{v}]_{S} = 0, \tag{3.8}$$

5-2

$$[\boldsymbol{\sigma} \cdot \boldsymbol{n}]_S = -\eta \boldsymbol{f}^{\mathbf{v}},\tag{3.9}$$

and f^{v} is given by (2.18).

The first step consists in determining $\boldsymbol{\theta}$. We assume that the position of each material point is given by (3.2). This will be justified a posteriori. The velocity of the membrane then follows from (3.2) and (3.1):

$$\boldsymbol{v}^{\mathbf{m}} = \frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t} = \boldsymbol{\omega} \cdot \boldsymbol{X} + \boldsymbol{\epsilon} (\dot{\boldsymbol{K}} + \boldsymbol{K} \cdot \boldsymbol{\omega}) \cdot \boldsymbol{X} + \boldsymbol{\epsilon} \boldsymbol{\omega} \cdot \boldsymbol{X} \cdot (\boldsymbol{J} - \boldsymbol{K}) \cdot \frac{\boldsymbol{X}}{X^2} + \frac{\boldsymbol{\epsilon} \boldsymbol{X}}{X^2} [\boldsymbol{X} \cdot (\dot{\boldsymbol{J}} - \dot{\boldsymbol{K}}) \cdot \boldsymbol{X} + \boldsymbol{\omega} \cdot \boldsymbol{X} \cdot (\boldsymbol{J} - \boldsymbol{K}) \cdot \boldsymbol{X} + \boldsymbol{X} \cdot (\boldsymbol{J} - \boldsymbol{K}) \cdot \boldsymbol{\omega} \cdot \boldsymbol{X}] + O(\boldsymbol{\epsilon}^2). \quad (3.10)$$

However, to compute the velocity gradient \boldsymbol{e} we must first express \boldsymbol{v}^{m} in terms of the instantaneous deformed position \boldsymbol{x} . This is achieved by solving (3.2) by successive approximations and then by replacing \boldsymbol{X} by \boldsymbol{x} in (3.10). The final result for \boldsymbol{e} becomes

$$\boldsymbol{e} = \epsilon \left[\boldsymbol{\mathcal{K}} + \boldsymbol{x} \cdot \boldsymbol{\mathcal{K}} \cdot \frac{\boldsymbol{x} \boldsymbol{x} \boldsymbol{x}}{r^4} - (\boldsymbol{\mathcal{K}} \cdot \boldsymbol{x} \boldsymbol{x} + \boldsymbol{x} \boldsymbol{x} \cdot \boldsymbol{\mathcal{K}}) \frac{1}{r^2} + \boldsymbol{\mathcal{P}} \boldsymbol{x} \cdot (\boldsymbol{\mathcal{J}} - \boldsymbol{\mathcal{K}}) \cdot \frac{\boldsymbol{x}}{r^2} \right] + O(\epsilon^2), \quad (3.11)$$

from which it follows that (3.9) can be written as

$$[\boldsymbol{\sigma} \cdot \boldsymbol{n}]_{S} = -2\eta\epsilon \left[(2\boldsymbol{J} - 5\boldsymbol{\mathcal{K}}) \cdot \frac{\boldsymbol{x}}{r} - 4\boldsymbol{x} \cdot (\boldsymbol{J} - 2\boldsymbol{\mathcal{K}}) \cdot \frac{\boldsymbol{x}\boldsymbol{x}}{r^{3}} \right] + O(\eta\epsilon^{2}).$$
(3.12)

The general solution to (2.1) and (2.2) is again obtained in terms of second-order harmonics (3.4). Using these expressions, and the corresponding values of the viscous stresses in the boundary conditions (3.7), (3.8) and (3.12), the expressions of the harmonics S^e and T^e can be obtained:

$$\begin{split} \boldsymbol{S}^{\mathbf{e}} &= -\frac{\eta \boldsymbol{\epsilon}}{c_0} \left(c_3 \boldsymbol{J} + c_4 \boldsymbol{K} \right) \\ \boldsymbol{T}^{\mathbf{e}} &= 2\eta \boldsymbol{\epsilon} b_0 (2 \boldsymbol{J} - 9 \boldsymbol{K}). \end{split}$$

The velocity field of the suspending fluid may then easily be computed, and the kinematic condition (2.15) leads to two differential equations in J and K:

$$\epsilon \mathbf{\mathring{J}} = -\frac{2\eta\epsilon}{c_0} (c_1 \mathbf{\mathring{J}} + c_2 \mathbf{\mathring{K}}) + O(\eta\epsilon^2),$$

$$\epsilon \mathbf{\mathring{K}} = -\frac{2\eta\epsilon}{c_0} (c_3 \mathbf{\mathring{J}} + c_4 \mathbf{\mathring{K}}) + O(\eta\epsilon^2),$$

$$(3.13)$$

with

$$\begin{split} c_0 &= (2\lambda+3)\,(19\lambda+16), \quad c_1 = 2(\lambda+4), \quad c_2 = 15\lambda, \\ c_3 &= -\,2(7\lambda+8), \quad c_4 = 47\lambda+48. \end{split}$$

Furthermore, it also appears that

$$\boldsymbol{\omega} = \boldsymbol{\Omega} + O(\boldsymbol{\epsilon}),$$

which means that the rotation rates of the membrane and of the fluids are equal to this order.

3.3. The viscoelastic membrane

In the case of a viscoelastic membrane, because of the linearizing procedure, to first order in ϵ , the viscous behaviour simply adds up to the elastic one. Consequently the time evolution of the deformation is obtained by adding (3.5) and (3.13):

$$e\hat{\boldsymbol{J}} = a_0 \boldsymbol{E} + k\epsilon [b_0 \boldsymbol{L} + (b_1 + b_2) \boldsymbol{M}] - \frac{2\eta\epsilon}{c_0} (c_1 \boldsymbol{J} + c_2 \boldsymbol{K}) + O(k\epsilon^2, \eta\epsilon^2),$$

$$e\hat{\boldsymbol{K}} = a_0 \boldsymbol{E} + k\epsilon (b_0 \boldsymbol{L} + b_1 \boldsymbol{M}) - \frac{2\eta\epsilon}{c_0} (c_3 \boldsymbol{J} + c_4 \boldsymbol{K}) + O(k\epsilon^2, \eta\epsilon^2).$$

$$(3.14)$$

Because of the appearance of the Jaumann derivative in (3.14), it follows that J and K are not parallel to E. As a consequence, it may be expected that the particle will orient itself at an angle with respect to the principal direction of shear. Furthermore, to this order of approximation and for steady states, it is clear that no higher-order tensors should be included in the equation of the profile of the particle, since they would contribute to transient states only.

4. Deformation and orientation in simple shear flow

The underlying hypothesis in the derivation of the solution was that the deformation was *small* and measured by a parameter called ϵ . There remains now to relate ϵ to the physical parameters of the system as they were listed in §2.

The deviation of the shape from sphericity will be small in three asymptotic situations:

 $k \ge 1$, $\eta = O(1)$, $\epsilon = k^{-1}$: this case corresponds to weak flows or to strong elastic forces. It is the only one to have already been solved (I);

 $k = O(1), \eta \ge 1, \epsilon = \eta^{-1}$: this case corresponds to a very viscous membrane with low elasticity;

 $k \ge 1$, $\eta \ge 1$, $\epsilon = k^{-1}$ or η^{-1} : this case corresponds to a very viscous membrane, and strong elastic forces or weak flows.

It is useful to introduce a new parameter β , which measures the relative magnitude of k and η :

$$\beta = \frac{\eta}{k} = \frac{\mu^{\mathbf{s}}G}{E^{\mathbf{s}}}.$$
(4.1)

This parameter is the ratio of the characteristic relaxation time of the membrane $\mu^{\rm s}/E^{\rm s}$ to the shear time G^{-1} . As such, it is identical with the Deborah number, commonly used for viscoelastic fluids, which measures the relative magnitudes of the flow time and of the liquid time. The three cases mentioned above may be treated simultaneously if we let β vary between 0 and infinity and if we choose

$$\epsilon = \frac{k^{-1}}{1+\beta},$$

keeping in mind that for the analysis to be valid, when β is O(1) or less, then k must be very large. It is then obvious that, in the system (3.14), the left-hand side is negligible with respect to the leading terms of the right-hand side; consequently this system reduces to:

$$\beta \mathbf{J} = 5(\beta + 1) \mathbf{E} + \mathbf{L} + \frac{5}{8} \mathbf{M} \\ \beta \mathbf{\mathring{K}} = \frac{5}{2}(\beta + 1) \mathbf{E} + \frac{1}{2} \mathbf{L} + \frac{1}{4} \mathbf{M} \right\} + O(k^{-1}, k^{-1}\beta^{-1}).$$
(4.2)

Once the type of elastic behaviour is specified, the above equations describe the time evolution of the capsule shape for any given shear field \boldsymbol{E} .

The situation of interest clearly occurs when the flow has a non-zero vorticity, since, in this case, the rotation of the membrane creates a time-dependent load on each material point. One should thus expect to observe an influence of the membrane viscosity even at steady state. Consequently, the solution to (4.2) will be sought in the case of a steady simple shear flow given by

$$E_{12} = E_{21} = \Omega_{12} = -\Omega_{21} = \frac{1}{2}, \tag{4.3}$$

all other components being zero. We assume that at time t = 0 the capsule is spherical and that the flow is suddenly started from rest. The components of interest for J and for K are the 11, 22 and 12 ones, since the others vanish. Furthermore, from the condition of tracelessness, it follows that

$$J_{11} = -J_{22}, \quad K_{11} = -K_{22}$$

The equation of the capsule profile is obtained from (3.3), and may be rewritten as

$$r^{2} = 1 + 2\epsilon [2J_{12}x_{1}x_{2} + J_{11}(x_{1}^{2} - x_{2}^{2})] + O(\epsilon^{2}).$$

$$(4.4)$$



FIGURE 2. Profile in the 12 plane of a deformed capsule subjected to a simple shear flow. The departure from sphericity is exaggerated for clarity.

This equation is that of an ellipsoid with principal semidiameters A_1 , A_2 and A_3 . The diameters A_1 and A_2 are in the 12 plane and make an angle θ with the axes Ox_1 and Ox_2 , while A_3 is along Ox_3 (see figure 2). From (4.4) it then follows that

$$A_1 = 1 + \epsilon (J_{11}^2 + J_{12}^2)^{\frac{1}{2}}, \quad A_2 = 1 - \epsilon (J_{11}^2 + J_{12}^2)^{\frac{1}{2}}, \quad \tan 2\theta = J_{12}/J_{11}. \tag{4.5}$$

Since the resulting profile is non-symmetric, its deviation from sphericity cannot be measured by a single quantity. It is clear that the larger deformation is found in the 12 plane. It can be defined in the classical way as

$$D_{12} = \frac{A_1 - A_2}{A_1 + A_2}, \quad D_{12} = \epsilon (J_{11}^2 + J_{12}^2)^{\frac{1}{2}} + O(\epsilon^2).$$

However, in the experimental devices designed to observe and to measure the deformation of r.b.c.s the line of sight is parallel to the axis Ox_2 , so that only an apparent deformation D_a is measured. It corresponds to the projection of the profile on the 13 plane and follows from (4.4):

$$D_{\mathbf{a}} = \frac{1}{2} \epsilon J_{11} + O(\epsilon^2),$$

whereas the true deformation in a section containing the diameters A_1 and A_3 is expressed as

$$D_{13} = \frac{1}{2}\epsilon (J_{11}^2 + J_{12}^2)^{\frac{1}{2}} + O(\epsilon^2) = \frac{1}{2}D_{12}.$$

The difference between D_a and D_{13} is only due to orientation effects.

The types of motion are now studied for membranes with different constitutive behaviours.

5. Case of three-dimensional incompressible isotropic elasticity

Here it is assumed that the elasticity of the membrane corresponds to that of an infinitely thin sheet of a three-dimensional isotropic, incompressible material. As shown in I, this leads to the following values of the coefficients α_i :

$$\alpha_1 = 0$$
 (no prestress),
 $\alpha_2 = 2\alpha_3 = \frac{2}{3}$.

The characteristic surface modulus E^s is identified with the product of the bulk Young modulus of the material with the thickness of the sheet:

$$E^{s} = Eh$$

Then, replacing L and M by their values given by (3.6), the system (4.2) becomes

$$\beta \begin{bmatrix} J_{11} \\ J_{12} \\ \dot{K}_{11} \\ \dot{K}_{12} \end{bmatrix} = \begin{bmatrix} -1 & \beta & 1 & 0 \\ -\beta & -1 & 0 & 1 \\ 0 & 0 & -\frac{1}{3} & \beta \\ 0 & 0 & -\beta & -\frac{1}{3} \end{bmatrix} \begin{bmatrix} J_{11} \\ J_{12} \\ K_{11} \\ K_{12} \end{bmatrix} + \begin{bmatrix} 0 \\ \frac{5}{2}(\beta+1) \\ 0 \\ \frac{5}{4}(\beta+1) \end{bmatrix} + O(k^{-1}, \beta^{-1}k^{-1}).$$
(5.1)

Its general solution is straightforward:

$$\begin{bmatrix} K_{11} \\ K_{12} \end{bmatrix} = e^{-t/3\beta} \begin{bmatrix} c_1 \sin t - c_2 \cos t \\ c_1 \cos t + c_2 \sin t \end{bmatrix} + \frac{5}{4} \frac{\beta + 1}{\beta^2 + \frac{1}{9}} \begin{bmatrix} \beta \\ \frac{1}{3} \end{bmatrix},$$
(5.2)
$$\begin{bmatrix} J_{11} \\ J_{12} \end{bmatrix} = e^{-t/\beta} \begin{bmatrix} c_3 \sin t - c_4 \cos t \\ c_3 \cos t + c_4 \sin t \end{bmatrix} + e^{-t/3\beta} \frac{3}{2} \begin{bmatrix} c_1 \sin t - c_2 \cos t \\ c_1 \cos t + c_2 \sin t \end{bmatrix}$$
$$+ \frac{5}{2} \frac{\beta + 1}{(\beta^2 + 1)(\beta^2 + \frac{1}{9})} \begin{bmatrix} \beta(\beta^2 + \frac{7}{9}) \\ \frac{1}{2}(\beta^2 + \frac{5}{9}) \end{bmatrix}.$$
(5.3)

The dynamic response of the particle has two relaxation times β and 3β . This is due to the fact that two independent modes of deformation are allowed for the surface: pure shear and area dilatation. Furthermore, after an initial transient behaviour, which has a duration of order β , the capsule reaches a steady profile defined by

$$J_{11} = \frac{5}{2} \frac{\beta(\beta+1)(\beta^2 + \frac{7}{9})}{(\beta^2+1)(\beta^2 + \frac{1}{9})}, \quad J_{12} = \frac{5}{4} \frac{(\beta+1)(\beta^2 + \frac{5}{9})}{(\beta^2+1)(\beta^2 + \frac{1}{9})}.$$
 (5.4)

It follows from (5.4) and (4.5) that the orientation of the particle is given by

$$\theta = \frac{1}{2} \operatorname{Arctan} \frac{\beta^2 + \frac{5}{9}}{2\beta(\beta^2 + \frac{7}{9})}.$$
(5.5)

Consequently θ varies between 0° and 45°.

The very small values of β correspond to membranes with negligible viscosity subjected to weak flows $(k \ge 1)$. This case has already been solved by Barthes-Biesel, by Brunn (1980) and in I. It is found indeed that, to $O(k^{-1})$, the capsule deforms into an ellipsoid oriented at 45° with respect to streamlines. When $\beta \rightarrow 0$ the asymptotic values of J are obtained from (5.4):

$$\lim_{\beta \to 0} J_{11} = 0, \quad \lim_{\beta \to 0} J_{12} = \frac{25}{4},$$

which is consistent with the aforementioned results. Consequently, the low-shear deformation of the capsule is given in this case by

$$\lim_{\beta \to 0} D_{13} = \frac{25}{8} k^{-1} + O(k^{-2}).$$
(5.6)

The relaxation times of the particle are very small, $O(k^{-1})$, so that the steady profile is reached almost instantaneously, the time delay being due essentially to the viscosity of the internal fluid.

For O(1) values of β ($k \ge 1$ and $\eta \ge 1$) the membrane viscosity begins to play an important role. The orientation is then a decreasing function of β . For a capsule of given properties, with a non-zero viscosity, increasing β is equivalent to increasing the shear rate G ((4.1)). Consequently, taking the membrane viscosity into account



FIGURE 3. Variation of the orientation angle with respect to streamlines, as a function of β . The parallel scale in shear rates is computed for a capsule that has physical properties similar to those of a r.b.c. (5.9).



FIGURE 4. Deformation of the capsule defined by (5.9) versus β or, equivalently, shear rate. The dashed line is the true deformation D_{13} , whereas the full line is the apparent deformation D_{a} .

leads to an O(1) effect in the orientation of the capsule as shown on figure 3. The true deformation of the particle is given by

$$D_{13} = \frac{5k^{-1}}{4} \frac{1}{(\beta^2 + 1)(\beta^2 + \frac{1}{9})} \left[\beta^2 (\beta^2 + \frac{7}{9})^2 + \frac{1}{4} (\beta^2 + \frac{5}{9})^2\right]^{\frac{1}{2}},\tag{5.7}$$

whereas the observed deformation is

$$D_{a} = \frac{5k^{-1}}{4} \frac{\beta(\beta^{2} + \frac{7}{9})}{(\beta^{2} + 1)(\beta^{2} + \frac{1}{9})}.$$
 (5.8)

For small β , D_{13} and D_a are distinct and increase with shear rate. For large values of β , D_{13} and D_a have a common upper bound given by

$$\lim_{\beta \to \infty} D_{13} = \lim_{\beta \to \infty} D_{a} = \frac{5}{4} \eta^{-1}$$

This behaviour is very different from that predicted for capsules with elastic membranes, where the deformation is an ever-increasing function of G. The evolution of deformation with shear rate can only be plotted for a specific capsule, since it involves both k and β . If we choose a particle that has physical properties similar to those of a r.b.c. suspended in a 20 cP medium, i.e.

$$a = 3 \,\mu\text{m}, \quad E^{s} = 5 \times 10^{-3} \,\text{dyn/cm}, \quad \mu^{s} = 5 \times 10^{-4} \,\text{dyn s/cm},$$
 (5.9)

then the variations of D_{13} and D_a with β are shown on figure 4. As already pointed

out, the deformation is an increasing function of shear rate, but it is limited. This result is in qualitative agreement with the experimental observations of Pfafferott, Wenby & Meiselman (1982).

6. The r.b.c.-type elasticity

It is assumed now that the elastic properties of the material are similar to those of a r.b.c. This means that the membrane strongly resists area changes, but has a relatively low shear modulus. The variation of the local surface area is measured by the invariant Λ_1 . The constancy of this quantity is ensured to $O(\epsilon)$ if

$$\begin{split} \boldsymbol{\Lambda}_1 &= \boldsymbol{\epsilon} \boldsymbol{x} \cdot (2\boldsymbol{J} - 3\boldsymbol{K}) \cdot \boldsymbol{x} + O(\boldsymbol{\epsilon}^2) = \boldsymbol{0}, \\ \boldsymbol{J} &= \frac{3}{2}\boldsymbol{K} + O(\boldsymbol{\epsilon}). \end{split}$$

or

A form of the strain-energy function for a r.b.c. membrane has been proposed by Skalak *et al.* (1973) as

$$W = \frac{1}{8}B[4(1+\Lambda_2)^2 - 4(1+\Lambda_2) - 2 e^{2\Lambda_1}] + \frac{1}{8}C(e^{4\Lambda_1} - 2 e^{2\Lambda_1}).$$

This means for small deformations that

$$\alpha_1 = 0, \quad \alpha_2 = C, \quad \alpha_3 = \frac{1}{2}B,$$
$$C = 5 \text{ dyn/cm}, \quad B = 5 \times 10^{-3} \text{ dyn/cm}.$$

with

If the value of B is chosen as the characteristic modulus E^{s} then

$$\alpha_2 = 10^3, \quad \alpha_3 = \frac{1}{2}.$$

Following I, we introduce a second-order tensor F, which becomes $O(\alpha_2^{-1})$ on a rapid timescale and which is defined by

$$J = \frac{3}{2}K + F.$$

Then, eliminating $\alpha_2 F$ terms from the system (4.2), we obtain a single differential equation for J:

$$\beta \boldsymbol{J} = \frac{15}{4} (\beta + 1) \boldsymbol{E} - \frac{1}{2} \boldsymbol{J}$$

Thus the capsule, being restricted in the deformations it can achieve, has only one relaxation time, equal to 2β . After an initial transient behaviour, the particle reaches a steady deformation and orientation given by

$$D_{13} = \frac{15}{16}k^{-1}\frac{1}{(\beta^2 + \frac{1}{4})^{\frac{3}{2}}}, \quad D_a = \frac{15}{16}k^{-1}\frac{\beta}{\beta^2 + \frac{1}{4}}, \quad \theta = \frac{1}{2}\operatorname{Arctan}\frac{1}{2\beta}.$$

It appears that the deformation is smaller for such a membrane than for one made of a three-dimensional elastomer. This can be attributed to the surface incompressibility condition, which limits the deformation modes. However, the deformation curves present qualitatively the same features as those on figure 4. The same phenomenon of rapid alignment with streamlines is observed.

7. Purely viscous membrane

When the membrane elasticity is altogether negligible $(\eta \ge 1, k = O(1))$ the viscosity becomes the dominant effect. The time evolution of the profile follows from (4.2) and is given by $\mathbf{j} = m\mathbf{E} + O(\beta^{-1}, k^{-1}),$ (7.1)



FIGURE 5. Time evolution of the orientation and of the deformation in the 12 plane of a capsule with a very viscous membrane. When elastic forces are not taken into account, no steady state exists, and the membrane continuously inflates and deflates, while oscillating between -45° and $+45^{\circ}$ orientations with respect to streamlines.



FIGURE 6. Successive profiles in the 12 plane of a capsule with a very viscous membrane. The departure from sphericity is exaggerated for clarity.

with m = 5 for an elastomer elasticity and $m = \frac{15}{4}$ for r.b.c. elasticity. The solution to this set of equations is periodic:

$$\begin{bmatrix} J_{11} \\ J_{12} \end{bmatrix} = \frac{m}{2} \begin{bmatrix} 1 - \cos t \\ \sin t \end{bmatrix}.$$
 (7.2)

It corresponds to the asymptotic behaviour of solution (5.3) when β becomes infinitely large, time remaining finite (then the time-exponential functions become unity at leading order, and the constants c_i are computed from the condition that at time t = 0the shape is spherical). This means that the particle's shape is an ellipsoid, with time-dependent principal diameters given by

$$A_1 = 1 + m\eta^{-1} |\sin \frac{1}{2}t|, \quad A_2 = 1 - m\eta^{-1} |\sin \frac{1}{2}t|, \quad A_3 = 1.$$

The angle of inclination of this profile is then

$$\theta = \frac{1}{4}\pi - \frac{1}{4}t, \quad t \in [0, 2\pi] \mod 4\pi,$$
$$\theta = \frac{3}{4}\pi - \frac{1}{4}t, \quad t \in [2\pi, 4\pi] \mod 4\pi.$$

The deformation becomes

$$D_{13} = \frac{1}{2}m\eta^{-1} |\sin \frac{1}{2}t| = \frac{1}{2}D_{12}.$$

The time evolutions of θ and of the observed deformation are shown on figure 5. The capsule's profile oscillates between 45° and -45°, while periodically elongating and deflating. The different stages of the shape are shown on figure 6. This behaviour is similar to the one observed by Rallison (1980) for very viscous droplets, and may also be attributed to the dominant effect of viscosity forces.

8. Discussion

It is striking to note how much the overall motion of a capsule suspended in shear flow is affected by the membrane viscosity. The previous studies on spherical capsules, which had only considered a purely elastic skin $(k \ge 1)$, found to $O(k^{-1})$ a 45° orientation. After long and tedious calculations, Barthes-Biesel (1980) has obtained the $O(k^{-2})$ terms and has shown that the angle slightly decreases with increasing shear rate. Also, the deformation is found to be a quadratic function of G and thus to increase without bound (this is of course an artefact of the expansion procedure). When the membrane viscosity is taken into account, the simple first-order analysis presented here changes the picture completely: orientation effects are important for low shear rates, but for high values of G all particles are parallel to the lines of flow. Also, the deformation is limited when the viscous load is increased. This phenomenon is explained by the role of membrane viscosity, which hinders the continuous flow of the interface during tank-treading motion. Finally, when the particle viscosity (whether it be the internal or the parietal one) is much higher than that of the suspending medium, an oscillatory motion is predicted.

The question that arises now is the relevance of this model to r.b.c. behaviour. When the suspending medium viscosity is of the order of 1 cP it is experimentally observed that the r.b.c.s behave as flexible elastic solids, and have a 'flipping' motion even at very high shear rates. In such a fluid, with the values of the parameters given by (5.9), we find

$$\eta \approx 167, \quad k \approx \frac{1670}{G}, \quad \lambda \approx 10.$$

Viscous effects are dominant, and the capsule deformation is limited by the high value of η . This may correspond to the oscillatory motion predicted in §7. It is, of course, more easily observable when the particle is a disk rather than a sphere. The ratio λ of internal to external viscosities is also large, which further enhances the phenomenon.

In a 20 cP medium, the value of η , although still large, is more modest:

$$\eta \approx 8.3, \quad k \equiv \frac{83}{G}, \quad \lambda \approx 0.5.$$

The deformation is 20 times larger than in the previous case, and results at low shear from both viscous and elastic effects. Consequently tank-treading is predicted, and the deformation curve has the same qualitative behaviour as the one published by Pfafferott *et al.* (1982).

In high-viscosity media ($\mu \ge 100 \text{ cP}$) the value of η is too small for the present analysis to apply. Elastic effects are dominant, and the previously existing models, with their shortcomings, become relevant.

Altogether, deformation is predicted to increase with the suspending-fluid viscosity, which is consistent with the experimental observations of r.b.c.s.

Another question of interest is the proper definition of the value of the membrane viscosity. Indeed, Chien et al. (1978) carefully measured μ^{s} from micropipette suction recovery experiments. They found that μ^{s} had first a low value of the order of 10^{-4} dyn s/cm, corresponding to an initial recovery phase and probably to high shear rates. During a secondary slow recovery phase μ^{s} had a higher value of the order of the one used in this study. Obviously, the membrane shear rate, as given by (3.11), is a function of position. The inclusion in the model of a shear-thinning behaviour of the interface would certainly have complicated the solution, and it is not obvious that this would have resulted in a great change in the overall predictions. Recently, Tran-Son-Tay, Sutera & Rao (1984) have used the Keller & Skalak approach to infer from experimental observations the value of the membrane viscosity of a tank-treading cell. They thus obtain very low values of the average membrane viscosity, of the order of $(1-0.6) \times 10^{-4}$ dyn s/cm, which might be justified for their high-shear experiments, but seems a little low for the low-shear ones. However, as was pointed out by Keller & Skalak themselves, their model is only roughly approximate, especially in the choice of a linear velocity field for the membrane rotation. Tran-Son-Toy et al. have reevaluated their computations using a more realistic velocity field, and have found that their membrane-viscosity estimates were then increased by 40-70%. This was done without taking into account the corresponding modifications of the internal and external flow fields. It thus seems that there is a large uncertainty in this method of determination of μ^{s} , and that the question of the proper value of this parameter remains open.

In conclusion, it is clear that the choice of an initial spherical geometry limits the applicability of this model to r.b.c.s. Indeed the membrane incompressibility imposes very small departures from sphericity. For a diskoidal cell, the membrane incompressibility does not prevent large deformations, but determines the type of tank-treading motion. This is obviously a very complicated process, which has not yet been completely modelled. The simple model presented here, despite its shortcomings, has many of the features of r.b.c. behaviour and shows clearly that membrane viscosity is an important intrinsic parameter which should be included in studies of tank-treading cells.

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