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Motion of a tank-treading ellipsoidal particle in a shear flow

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A theoretical model is developed for the motion of a human red blood cell in a shear field. The model consists of a tank-treading ellipsoidal membrane encapsulating an incompressible Newtonian liquid immersed in a plane shear flow of another incompressible Newtonian liquid. Equilibrium and energy considerations lead to a solution for the motion of the particle that depends on the ellipsoidal-axis ratios and the ratio of the inner- to outer-liquid viscosities. The effect of variation in these parameters is explored and it is shown that, depending on their values, one of two types of overall motion is exhibited: a steady stationary-orientation motion or an unsteady flipping motion. A qualitative agreement of the predicted behaviour of the model with experimental observations on red blood cells is found.

1. Introduction

Problems in which a viscous fluid interacts with a deformable particle are of considerable interest in the study of liquids such as blood, polymer solutions, and suspensions of liquid droplets. An understanding of the mechanics of the interaction between the liquid and the particle is important both for investigating phenomena of interest at the level of a single particle and for the bulk rheology of the suspension. One problem of this type that has received considerable attention, both experimental and theoretical, is the response of a human red blood cell to a viscous shear field. In recent years improving experimental techniques have enabled the behaviour of red blood cells in a shear field to be directly observed. To complement these experimental observations several efforts have been made to model the problem theoretically. While the existing theoretical analyses provide some insight, they fall considerably short of adequately explaining all of the observed phenomena. In this paper a theoretical analysis is developed for the motion of a human red blood cell in a shear field that provides a more complete model for understanding the observed behaviour. The qualitative results may also be applicable to problems involving other deformable particles.

The resting shape of the human red blood cell may be described as a biconcave disk having a diameter of about 8 μm. The cell consists of a thin (70 Å) biological membrane which encloses a Newtonian solution of haemoglobin (Cokelet & Meiselman 1968). The mechanical properties of the membrane material are such that it deforms easily at constant area but strongly resists any change in area (Skalak *et al.* 1973). The total

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surface area of the red-cell membrane is about 40 % greater than that necessary to enclose the same volume by a sphere. Primarily owing to this 'excess' surface area, the thinness and mechanical properties of the cell membrane, and the liquid nature of the cell interior, the red blood cell is able to exhibit remarkable deformability. This deformability is of physiological significance because it enables the cell to pass through capillaries with diameters as small as 3 μm, contributes to reducing the bulk viscosity of blood in the larger vessels, and enhances oxygen transport to the tissues by allowing mixing of the haemoglobin (Chien 1975; Schmid-Schönbein 1975).

Several investigators have observed individual red blood cells in a Couette or Poiseuille flow field (Schmid-Schönbein & Wells 1969; Goldsmith & Marlow 1972; Fischer & Schmid-Schönbein 1977; Fischer, Stöhr-Liesen & Schmid-Schönbein 1978*a*). It is found that a human red blood cell subjected to a shear field may exhibit one of two types of overall motion: an unsteady motion in which the shape of the cell remains essentially unchanged from its resting shape while the cell undergoes a flipping motion, or a steady motion in which the cell deforms into an ellipsoid-like particle at a stationary orientation with the membrane circulating about the cell interior similar to the motion of a tank tread. For example, Goldsmith & Marlow (1972) observed that human red blood cells in plasma at shear stresses less than about 1 dyn/cm^2 will exhibit a flipping motion with little evidence of deformation (such as bending while flipping). However, in an isotonic medium having a viscosity about 30 times that of plasma at shear stresses greater than 1 dyn/cm^2 they observed that the cells appeared as slightly deformed ellipsoids and oriented themselves at a constant angle with respect to the flow with their membranes appearing to tank-tread about the cell interior. The experiments indicate that, as the viscosity or shear stress of the external fluid is increased, the elongation of the cell increases and there is a transition from the flipping type of motion to the tank-treading. These observations have been supported by indirect optical diffractometric evidence on dilute suspensions of red cells (Bessis & Mohandas 1975; Morris & Williams 1979).

Existing theoretical analyses of a red blood cell when subjected to a shear field fall considerably short of adequately representing the observed physical phenomena. Using the fundamental solution of Jeffery (1922), several studies have compared the behaviour of a red cell to that of a rigid ellipsoid in a shear flow (Goldsmith 1967; Goldsmith & Mason 1967; Brenner & Bungay 1971; Goldsmith & Marlow 1972). While an ellipsoid may be a reasonable approximation for the shape of the red cell in a shear field, Jeffery's theory for a rigid particle predicts only the observed unsteady flipping motion. The theory does not explain the steady motion in which the principal axes of the cell remain fixed with the membrane tank-treading about the cell interior.

To account for this steady motion, a number of investigations have employed the theoretical work of Taylor (1932, 1934), Cox (1969), and others to model the behaviour of the red cell in a shear field as that of a liquid droplet (Brenner & Bungay 1971; Gauthier, Goldsmith & Mason 1972; Kline 1972; Fischer, Stöhr & Schmid-Schönbein 1978*b*). While this approach sheds some light on the steady motion, its validity for the non-spherical red blood cell is limited because the underlying theory is based upon the assumption of small deviations from a spherical shape.

There have been a few analyses of the red cell in a shear flow using thin-shell theory. Brennen (1975), Guerlet, Barthès-Biesel & Stoltz (1977) and Barthès-Biesel (1980) have considered elastic or viscoelastic liquid-filled and initially spherical membranes in plane Couette flow. Richardson (1974) has considered the motion of a linearly elastic and initially ellipsoidal membrane in a shear flow. These papers, in which the deformed shape of the particle was determined as part of the solution, are limited by the assumption of small deviations from the initial shape and do not assess the conditions under which the red cell undergoes the transition between unsteady and steady motion.

This transition has been considered by Kholeif & Weymann (1974) in a two-dimensional model. The red cell was assumed to maintain a fixed shape resembling the cross-section of a resting red cell while immersed in a plane Couette flow. The cell was further assumed to contain a Newtonian liquid and to be bounded by an inextensible infinitesimally thin membrane that was allowed to have a tank-treading motion along the perimeter of the cell. The analysis predicted both the stationary orientation motion and the unsteady periodic flipping motion, with the type of motion exhibited depending on the shape of the cross-section and the ratio of the viscosities of the inner and outer liquids. While this two-dimensional study demonstrates the transition between the two modes of motion, its validity for the three-dimensional red cell is not entirely clear.

Recently Keller (1979*a*) and Keller & Skalak (1980) have considered the effect of a prescribed tank-treading surface velocity on an ellipsoid immersed in a shear flow. This parametric approach demonstrates how tank-treading affects both the stationary orientation and flipping motion of a three-dimensional particle, but it does not consider the effect of an internal liquid or the mechanics of an enveloping membrane. In this approach the problem is not closed in the sense that the motion depends on an arbitrarily assigned free parameter (the tank-tread frequency).

To overcome some of these limitations, the present investigation considers the motion of an ellipsoidal membrane encapsulating an incompressible Newtonian liquid immersed in a plane Couette flow of another incompressible Newtonian liquid. One axis of the ellipsoid is assumed to be aligned with the vorticity vector of the undisturbed flow. The tank-tread motion of the membrane is given by a prescribed surface velocity that is kinematically similar to the experimentally observed tank-treading motion. The principal advantage of this approach is that it allows a relatively complete mathematical analysis that exhibits many of the essential features of the problem. Furthermore, since the deformed shape of the particle is regarded as an independent rather than dependent entity, it is possible to explore how large changes in shape affect the overall motion.

The motion of the particle is determined by equilibrium and energy considerations. The formulation of the problem is set forth in § 2. The particle is assumed to be neutrally buoyant, and because the Reynolds numbers characteristic of red-cell motion are much less than unity, inertial effects are neglected. Then Stokes' equations govern the fluid motions. In § 3 a solution to these equations for the external liquid satisfying the appropriate boundary conditions based upon Roscoe's (1967) adaptation of the classical work of Jeffery (1922) is employed to find an expression for the resultant moment exerted on the particle by the outer liquid. The condition that the total moment on a freely suspended neutrally buoyant particle must vanish then yields an equation of motion for the particle.

In addition to satisfying equations of equilibrium, the particle must also satisfy conservation of energy, i.e. the rate of dissipation of energy inside the particle must

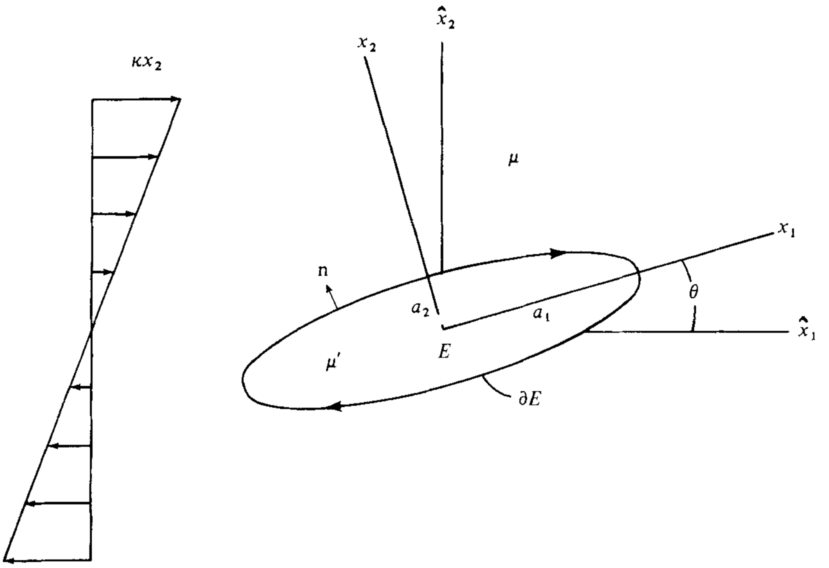

FIGURE 1. Schematic drawing of a tank-treading fluid-filled ellipsoidal membrane in a shear flow.

equal the rate at which work is done by the external fluid on the particle. The internal liquid motion and the rate of energy dissipation in the inner liquid is given in § 4.

In the present analysis, the mechanics of the membrane deformation is not specifically considered. Rather it is assumed that it is such that the ellipsoidal shape and prescribed surface motion results. Furthermore the rate of energy dissipation in the membrane is taken to be zero, which is equivalent to assuming that the membrane has no shear viscosity. While this assumption is almost certainly not valid for the red-cell membrane, it is made for the sake of simplicity and clarity. A method for modifying the analysis to include the energy dissipation in the membrane is given in § 4.

To assess the effects of changes in shape on the motion of the red cell, the particle representing it is assumed to be a member of the one-parameter family of ellipsoids having the same volume and surface area as the red cell. This family is determined in § 5. Finally, in § 6 the effects of particle shape and the ratio of inner- to outer-liquid viscosities on the steady and unsteady motions are evaluated.

2. Formulation of the problem

Let $\hat{x}_i$ denote co-ordinates in a fixed Cartesian co-ordinate system and let x_i denote co-ordinates in a second Cartesian system having origin coinciding with the fixed frame. The x_3 axis is assumed to coincide with the $\hat{x}_3$ axis, but the x_1 and x_2 axes are rotated through an angle θ with respect to the $\hat{x}_1$ and $\hat{x}_2$ axes (see figure 1). A positive value of θ is taken to mean a counterclockwise rotation of the x_1 and x_2 axes as shown. In general θ will be a function of time and $\dot{\theta} = d\theta/dt$ is the angular velocity of the x_1 and x_2 axes with respect to the $\hat{x}_1$ and $\hat{x}_2$ axes.

Consider the ellipsoidal surface ∂E having semi-axes a_i $(i = 1, 2, 3)$ defined by

$$x_i^2/a_i^2 = 1. \tag{1}$$

The co-ordinate axes x_i are the principal axes of the ellipsoidal body E interior to ∂E, and will be referred to as the body frame.

The components of the velocity vector of the fluid external to ∂E relative to the fixed frame but referred to the body frame will be denoted by $\hat{v}_i$, and those relative to the body frame and referred to the body frame will be denoted by v_i. The corresponding components of the velocity of the internal fluid will be denoted by $\hat{v}'_i$ and v'_i. The external and internal velocity fields must satisfy Stokes' equations and the continuity equation, which have the same form in both a fixed frame and a rotating frame. Thus

$$\mu v_{i,jj} = p_{,i} \quad v_{i,i} = 0, \tag{2}$$

$$\mu' v'_{i,jj} = p'_{,i}, \quad v'_{i,i} = 0, \tag{3}$$

where p and p' are the pressures and μ and μ' are the viscosities associated with the outer and inner fluids respectively. A comma followed by subscript i denotes differentiation with respect to x_i.

Far from the particle, the velocity field relative to the fixed frame is assumed to approach a plane Couette flow with shear rate κ. The components of the undisturbed shear flow referred to the fixed frame are denoted by $\hat{u}_i^0$:

$$\hat{u}_1^0 = \kappa \hat{x}_2, \quad \hat{u}_2^0 = 0, \quad \hat{u}_3^0 = 0. \tag{4}$$

Referred to the body frame this undisturbed motion is

$$\left.\begin{aligned} \hat{v}_1^0 &= \kappa(x_1 \sin\theta \cos\theta + x_2 \cos^2\theta), \\ \hat{v}_2^0 &= -\kappa(x_1 \sin^2\theta + x_2 \sin\theta \cos\theta), \\ \hat{v}_3^0 &= 0. \end{aligned}\right\} \tag{5}$$

Relative to the body frame and referred to the body frame the undisturbed motion is

$$v_i^0 = \hat{v}_i^0 - \dot{\theta}\epsilon_{i3k} x_k, \tag{6}$$

where ϵ_{ijk} is the alternator tensor.

In order to study the possible motions of the ellipsoid E, its surface ∂E is assumed to have a type of tank-tread motion. The surface velocity v_i^{m} relative to and referred to the body frame is assumed to be

$$v_1^{\mathrm{m}} = \nu(-a_1/a_2)\, x_2, \quad v_2^{\mathrm{m}} = \nu(a_2/a_1)\, x_1, \quad v_3^{\mathrm{m}} = 0, \tag{7}$$

where ν is a parameter having the dimensions of frequency. In general, ν may be a function of time. It will be determined later as part of the solution. Considering the model as a red blood cell, the velocity v_i^{m} is a prescribed motion of the membrane. Relative to the fixed frame but referred to the body frame this membrane motion is

$$\hat{v}_i^{\mathrm{m}} = v_i^{\mathrm{m}} + \dot{\theta}\epsilon_{ijk} x_k. \tag{8}$$

It is readily shown that v_i^{m} represents a tank-tread motion. First note that the components in the body frame of the unit outer normal to ∂E are

$$n_i = (x_i/a_i^2)\,(x_j^2/a_j^4)^{-\frac{1}{2}} \quad \text{(sum on } j\text{, no sum on } i\text{)}. \tag{9}$$

Thus $v_i^{\mathrm{m}} n_i = 0$, i.e. v_i^{m} is everywhere tangent to ∂E. Further, since $v_3^{\mathrm{m}} = 0$, material surface points move along elliptical paths in planes parallel to the (x_1, x_2)-plane. For

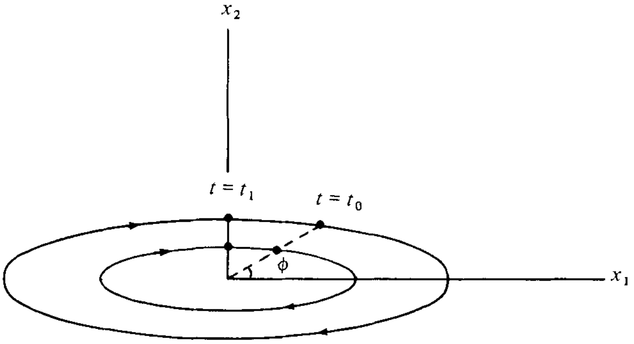

FIGURE 2. Kinematics of the surface velocity. Material-surface points move along elliptical paths in planes parallel to the (x_1, x_2)-plane. Material-surface points having the same polar angle ϕ at any initial instant have equal polar angles at all future times and remain in a plane.

positive and negative values of ν the membrane motion is respectively in the counterclockwise and clockwise sense when viewed from the positive x_3 axis. It may be shown that the Lagrangian description corresponding to (7) is given by

$$\left.\begin{aligned} x_1(\mathbf{x}^0, t) &= x_1^0 \cos\omega - (a_1 x_2^0/a_2)\sin\omega, \\ x_2(\mathbf{x}^0, t) &= x_2^0 \cos\omega + (a_2 x_1^0/a_1)\sin\omega, \\ x_3(\mathbf{x}^0, t) &= x_3^0, \end{aligned}\right\} \tag{10}$$

where

$$\omega = \int_0^t \nu(t')\,dt', \tag{11}$$

and $\mathbf{x}^0 = (x_i^0)$ is the position of a material surface point at time $t = 0$. Equations (10) and (11) imply that if ν is constant the membrane moves completely around the cell interior with period $\tau = 2\pi/|\nu|$. From (10) it may be shown that the polar angle describing the angular position of a material surface point is

$$\phi = \arctan(x_2/x_1) = \arctan\left\{\frac{\tan\phi_0 \cos\omega + (a_2/a_1)\sin\omega}{\cos\omega - (a_1/a_2)\tan\phi_0 \sin\omega}\right\}, \tag{12}$$

where $\phi_0 = \arctan(x_2^0/x_1^0)$ is the polar position angle at $t = 0$. Equation (12) shows that the membrane motion is synchronous in the sense that material surface points having the same ϕ_0 (i.e. lying in a plane containing the x_3 axis at $t = 0$) have the same ϕ at time t, and so again lie in a plane containing the x_3 axis (see figure 2).

While (7) represents a tank-treading motion, it may be shown that it is not locally area-conserving (Secomb & Skalak 1981), and as such cannot precisely represent the actual motion of the red-cell membrane. Nevertheless, it is similar to the experimental observations, and this simplified motion allows explanation of several aspects of the problem. Accordingly, the boundary conditions imposed on the outer and inner liquids are

$$v_i = v_i^{\mathrm{m}} \quad \text{on } \partial E, \tag{13}$$

$$v_i \to v_i^0 \quad \text{as} \quad |x| \to \infty, \tag{14}$$

$$v_i' = v_i^{\mathrm{m}} \quad \text{on } \partial E. \tag{15}$$

3. External flow and equilibrium

Roscoe (1967) has shown how the classical work of Jeffery (1922) may be adapted to derive a solution to the external-flow problem posed by (2), (13) and (14) for the case $\dot{\theta} = 0$. His approach rests upon the observation that the disturbance velocity created by an ellipsoid immersed in a linear flow with a surface motion that depends linearly on x_i is the same as the disturbance velocity created by a rigid ellipsoid immersed in another linear flow. Thus Jeffery's result for rigid ellipsoids in linear flows can be used to find the velocity field and surface-stress vector for ellipsoids having a surface motion that depends linearly on x_i. Roscoe's solution can be readily extended to the more-general case $\dot{\theta} \neq 0$ by adding the solution for a rigid ellipsoid rotating in an otherwise quiescent fluid. This solution can also be obtained from Jeffery's original result.

The external velocity field for the general case $\dot{\theta} \neq 0$ will not be given explicitly here, but for equilibrium and energy considerations the stress vector exerted by the external liquid on the particle will be given in some detail. It can be shown that the components of the surface-stress vector referred to the body frame are given by

$$T_i = -p'' n_i + \mu(A^*_{ij} + 2e^{\mathrm{m}}_{ij})\, n_j, \tag{16}$$

where p'' is an arbitrary constant pressure and e^{m}_{ij} is defined by

$$e^{\mathrm{m}}_{ij} = \tfrac{1}{2}(v^{\mathrm{m}}_{j,i} + v^{\mathrm{m}}_{i,j}), \tag{17}$$

where v^{m}_i is the velocity field (7) taken as applying for all x_i. The strain rate e^{m}_{ij} and the tensor A^*_{ij} are independent of x_i. The element A^*_{11} is

$$A^*_{11} = \frac{4}{3}\,\frac{2g_1 e^*_{11} - g_2 e^*_{22} - g_3 e^*_{33}}{g''_2 g''_3 + g''_3 g''_1 + g''_1 g''_2}, \tag{18}$$

where

$$e^*_{ij} = e^0_{ij} - e^{\mathrm{m}}_{ij}, \tag{19}$$

$$e^0_{ij} = \tfrac{1}{2}(\hat{v}^0_{j,i} + \hat{v}^0_{i,j}). \tag{20}$$

The symbols $g_i, g'_i, g''_i, \ldots$ denote certain integrals that depend only on the shape of the ellipsoid. The integrals g_1, g'_1 and g''_1 are given by

$$\left.\begin{aligned} g_1 &= \int_0^\infty \frac{ds}{(\alpha_1^2 + s)\,\Delta}, \\ g'_1 &= \int_0^\infty \frac{ds}{(\alpha_2^2 + s)(\alpha_3^2 + s)\,\Delta}, \\ g''_1 &= \int_0^\infty \frac{s\,ds}{(\alpha_2^2 + s)(\alpha_3^2 + s)\,\Delta}, \\ \text{where}\quad \Delta^2 &= (\alpha_1^2 + s)(\alpha_2^2 + s)(\alpha_3^2 + s). \end{aligned}\right\} \tag{21}$$

Here, the α_i are the dimensionless axes defined by

$$\alpha_i = a_i / a_0, \tag{22}$$

where $a_0 = (a_1 a_2 a_3)^{\frac{1}{3}}$. The elements A^*_{22} and A^*_{33} and the integrals $g_2, g'_2, g''_2, g_3, g'_3$ and g''_3 may be obtained by the appropriate permutation of the subscripts in (18) and (21). For the off-diagonal terms of A^*_{ij} the typical element is

$$A^*_{12} = 4\,\frac{g_1 e^*_{12} - \alpha_2^2 g'_3(\zeta^*_{12} - \epsilon_{12k}\omega_k)}{g'_3(\alpha_1^2 g_1 + \alpha_2^2 g_2)}, \tag{23}$$

where
$$\zeta^{*}_{ij} = \zeta^{0}_{ij} - \zeta^{\mathrm{m}}_{ij}, \tag{24}$$
with
$$\zeta^{0}_{ij} = \tfrac{1}{2}(\hat{v}^{0}_{j,i} - \hat{v}^{0}_{i,j}), \tag{25}$$
$$\zeta^{\mathrm{m}}_{ij} = \tfrac{1}{2}(v^{\mathrm{m}}_{j,i} - v^{\mathrm{m}}_{i,j}). \tag{26}$$

Here ω_k is the angular velocity of the ellipsoid with respect to the fixed frame. The other off-diagonal terms may be obtained by the appropriate permutation of the subscripts in (23).

Equation (16) is valid for an ellipsoid immersed in any undisturbed velocity $\hat{v}^{0}_i$ that is linear in x_i, where the ellipsoid has any surface velocity v^{m}_i that is linear in x_i and has any angular velocity ω_i. For the present problem $\hat{v}^{0}_i$ is given by (5), v^{m}_i by (7), and ω_i by
$$\omega_1 = 0, \quad \omega_2 = 0, \quad \omega_3 = \dot{\theta}. \tag{27}$$

The stress vector T_i may be written as
$$T_i = c_{ij} n_j, \tag{28}$$
where
$$c_{ij} = -p'' \delta_{ij} + \mu(A^{*}_{ij} + 2e^{\mathrm{m}}_{ij}). \tag{29}$$
By virtue of the linearity of $\hat{v}^{0}_i$ and $\hat{v}^{\mathrm{m}}_i$ in x_i, c_{ij} is independent of x_i. In the present case it may be shown that in general
$$c_{13} = c_{31}, \quad c_{23} = c_{32}, \tag{30}$$
but
$$c_{12} \neq c_{21}. \tag{31}$$

The components of the resultant force exerted by the external liquid on the ellipsoidal particle at any instant in the body frame are given by
$$F_i = \int_{\partial E} c_{ij} n_j \, dA. \tag{32}$$
However, as the integral of any odd function of x_i over the ellipsoidal surface is zero,
$$F_i = 0. \tag{33}$$
This result is obvious from the antisymmetry of the problem. The components of the resultant moment about the origin exerted by the external liquid on the ellipsoidal surface at any instant in the body frame are
$$M_i = \int_{\partial E} \epsilon_{ijk} x_j c_{kl} n_l \, dA, \tag{34}$$
where ϵ_{ijk} is the alternator tensor. To evaluate (34) it is very helpful to make use of the fact that
$$\int_{\partial E} x_i n_i \, dA = V \quad \text{(no sum)}, \tag{35}$$
where V is the volume of the ellipsoid. Equations (30), (31) and (35) lead to the result that the only non-vanishing moment component is
$$M_3 = V(c_{21} - c_{12}). \tag{36}$$
After substituting for c_{21} and c_{12} using (29) and some algebraic manipulation, it may be shown that
$$M_3 = M^{\mathrm{S}}_3 + M^{\mathrm{F}}_3 + M^{\mathrm{T}}_3, \tag{37}$$

where
$$M_3^{\mathrm{S}} = -\tfrac{1}{2}C\kappa[a_1^2(1-\cos 2\theta)+a_2^2(1+\cos 2\theta)], \tag{38}$$
$$M_3^{\mathrm{F}} = -C\dot{\theta}(a_1^2+a_2^2), \tag{39}$$
$$M_3^{\mathrm{T}} = -C2a_1a_2\nu, \tag{40}$$
with
$$C = \frac{4\mu V}{a_1^2g_1+a_2^2g_2}. \tag{41}$$

The term M_3^{S} is the moment, due to the shear flow (4), acting on a stationary rigid ellipsoid inclined at an angle θ (i.e. $\dot{\theta} = \nu = 0$); M_3^{F} is the moment acting on a rigid ellipsoid flipping about the x_3 axis with angular speed $\dot{\theta}$ in a fluid at rest at infinity (i.e. $\nu = \kappa = 0$); and M_3^{T} is the moment acting on a stationary ellipsoid undergoing the tank-treading motion (7) in an otherwise-quiescent liquid ($\dot{\theta} = \kappa = 0$).

Now consider a membrane-enclosed fluid-filled particle of arbitrary shape immersed in an external flow. Assume that the particle is neutrally buoyant and that no forces or couples are exerted by any external agency. Further assume that inertial effects are neglected throughout. Under these conditions the stress distribution in the internal fluid is such that every volume element of the internal fluid is in equilibrium. It follows that the internal fluid cannot exert a resultant force or moment on the membrane. Now the entire membrane, considered as a free body, is also in equilibrium at each instant in time. Consequently the resultant force and moment exerted by the external liquid on the membrane must vanish at every instant. For the present solution, the only force or moment component that does not vanish identically is M_3. Therefore equilibrium requires
$$M_3 = M_3^{\mathrm{S}}+M_3^{\mathrm{F}}+M_3^{\mathrm{T}} = 0. \tag{42}$$
Substituting (38)–(40) into (42) yields an equation for the flipping velocity:
$$\dot{\theta} = \tilde{A}+\tilde{B}\cos 2\theta, \tag{43}$$
where
$$\tilde{A} = -\left(\tfrac{1}{2}\kappa+\frac{2a_1a_2}{a_1^2+a_2^2}\nu\right), \tag{44}$$
$$\tilde{B} = \tfrac{1}{2}\kappa\frac{a_1^2-a_2^2}{a_1^2+a_2^2}. \tag{45}$$

Equation (43) was first given by Keller (1979*a*). Notice that the semi-axis length a_3 and the viscosity μ of the external liquid enter in the expression for each of the moments (38)–(40), but as a consequence of the cancellation of C from each term in (42) they do not appear in the equation of motion (43).

4. Internal flow and conservation of energy

The solution for the internal velocity field v_i' is the surface velocity (7) extended to the interior of the ellipsoid:
$$v_1' = \nu(-a_1/a_2)x_2, \quad v_2' = \nu(a_2/a_1)x_1, \quad v_3' = 0 \quad \text{in } E. \tag{46}$$
It is easily verified that v_i' given by (46) satisfies (3) and (15) with p' constant. This solution for the internal liquid motion is unique for the given surface motion (cf. Skalak 1970).

The dissipation function corresponding to v_i' is

$$\Phi' = \mu' f_1 \nu^2, \tag{47}$$

where

$$f_1 = (r_2 - r_2^{-1})^2, \tag{48}$$

and r_2 is the first of the two axis ratios defined by

$$r_2 = a_2/a_1, \quad r_3 = a_3/a_1. \tag{49}$$

Since Φ' is spatially homogeneous, the rate at which energy is dissipated in the inner liquid is simply Φ' times the volume of the ellipsoid:

$$D' = V\mu' f_1 \nu^2. \tag{50}$$

Energy is also dissipated within the red-cell membrane. Although the membrane volume is two orders of magnitude smaller than the haemoglobin solution volume, because of its high shear viscosity (Evans & Hochmuth 1976; Chien *et al.* 1978) the energy dissipated in the membrane may exceed that in the haemoglobin solution. Fischer (1980) has recently made preliminary estimates of the rate of energy dissipation in the membrane and in the haemoglobin solution for a tank-treading human red blood cell over a range of external-flow shear rates (28–575 s^{-1}). His calculations are based upon kinematic data for the membrane motion and the reported values for the membrane and haemoglobin solution viscosities. He found that, although both dissipation rates showed a strong increase with increasing external, flow shear rate, their ratio was essentially constant and of the order of 1.

In the present analysis, for the sake of simplicity and clarity, the energy dissipated in the membrane is assumed to be zero. However, if it is assumed, as Fischer's results seem to indicate, that the ratio of the rate of energy dissipation in the membrane to that in the inner liquid is a constant (that is, independent of the shape of the cell and the external-flow shear rate), then it is a simple matter to account for the energy dissipated in the membrane by replacing μ' in (50) with an apparent internal viscosity μ'_{app} defined by

$$\mu'_{\mathrm{app}} = (1+d)\mu', \tag{51}$$

where d is the ratio of the rate of energy dissipation in the membrane to that in the inner liquid. The quantity D' in (50) would then represent the rate at which energy is dissipated in the inner liquid and in the membrane.

The energetics of the system provide a constraint on the possible motions. The energy dissipated inside the cell must be supplied by the external fluid. The rate at which the external flow does work on the element of area dA of the ellipsoid is $T_i \hat{v}_i^{\mathrm{m}}\, dA$. By employing (28), the total rate at which the external flow does work on the particle may be expressed by

$$W_{\mathrm{p}} = \int_{\partial E} c_{ij} n_j \hat{v}_i^{\mathrm{m}}\, dA. \tag{52}$$

By employing (8), (52) may be written as

$$W_{\mathrm{p}} = \int_{\partial E} c_{ij} n_j v_i^{\mathrm{m}}\, dA + \dot{\theta} \int_{\partial E} \epsilon_{3jk} x_j c_{kl} n_l\, dA. \tag{53}$$

The last integral in (53) is M_3, and vanishes because of the equilibrium condition (42). Therefore

$$W_{\mathrm{p}} = \int_{\partial E} c_{ij} n_j v_i^{\mathrm{m}}\, dA. \tag{54}$$

Note, that for a non-tank-treading ellipsoid ($v_i^{\mathrm{m}} = 0$), (54) implies $W_{\mathrm{p}} = 0$. This means that the external flow would not do any work on the particle. However, as is well-known (Jeffery 1922), there would be additional energy dissipation in the external flow due to the presence of the particle.

By substituting for c_{ij} in (54) and employing (7), (35) and (43), it may be shown that

$$W_{\mathrm{p}} = V\mu(f_2\nu^2 + f_3\,\kappa\nu\cos 2\theta), \tag{55}$$

where f_2 and f_3 are functions of the axis ratios r_2 and r_3 given by

$$f_2 = 4z_1^2(1-2/z_2), \quad f_3 = -4z_1/z_2, \qquad (56), (57)$$

where

$$z_1 = \tfrac{1}{2}(r_2^{-1} - r_2), \quad z_2 = g_3'(\alpha_1^2 + \alpha_2^2). \qquad (58), (59)$$

Although the integrals g_i, g_i', g_i'' from (21) and (59) are most conveniently expressed using the dimensionless axes α_i (22), they also may be regarded as functions of r_2 and r_3 alone, since

$$\alpha_1 = r_2^{-\frac{1}{3}} r_3^{-\frac{1}{3}}, \quad \alpha_2 = r_2^{\frac{2}{3}} r_3^{-\frac{1}{3}}, \quad \alpha_3 = r_2^{-\frac{1}{3}} r_3^{\frac{2}{3}}. \qquad (60), (61), (62)$$

Conservation of energy requires that the rate at which work is done on the particle be equal to the rate at which energy is being dissipated inside the particle. This condition is expressed by the equation

$$W_{\mathrm{p}} = D'. \tag{63}$$

Equation (63) provides a constraint on the allowable motions of the particle and it must be simultaneously satisfied along with (43). By substituting (50), (51) and (55) into (63) it is found that either

$$\nu = 0 \tag{64}$$

or

$$\nu = -f_3[f_2 - (\mu'/\mu)f_1]^{-1}\kappa\cos 2\theta. \tag{65}$$

Equation (64) corresponds to a rigid (non-tank-treading) ellipsoid which does not dissipate energy. In this case W_{p} and D' are both zero. On the other hand, (65) gives the circular frequency of tank-treading for an ellipsoidal particle of fixed shape with viscosity ratio μ'/μ. This equation implies that, if the particle is stationary (i.e. θ = const.), the circular frequency of tank-treading is constant. However, if the particle is flipping, ν varies with time or equivalently with θ. In this case the direction of the tank-treading motion changes as θ passes through odd multiples of $\frac{1}{4}\pi$. For r_2 and r_3 less than 1, the coefficient of $\kappa\cos 2\theta$ in (65) is negative, and the sense of the tank-tread motion is indicated in figure 3. Experimental observation of this type of oscillatory tank-tread motion has apparently not been reported. This may be because of difficulty in observing a membrane motion on a flipping red cell.

By substituting (65) into (44) ν can be eliminated and the equation of motion of the tank-treading particle becomes

$$\dot{\theta} = A + B\cos 2\theta, \tag{66}$$

where

$$A = -\tfrac{1}{2}\kappa, \tag{67}$$

$$B = 2\kappa\{\tfrac{1}{2} + z_1^{-1} f_3[f_2 - (\mu'/\mu)f_1]^{-1}\}\, z_1/(r_2^{-1} + r_2). \tag{68}$$

Integration of (66) indicates how, for a given shear rate κ, the motion of the particle depends on r_2, r_3 and μ'/μ.

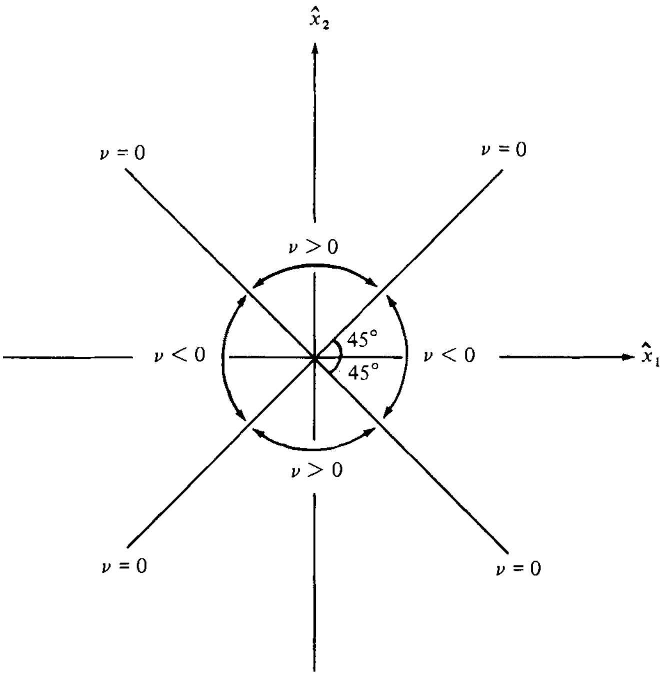

FIGURE 3. Direction of the tank-tread motion in different octants of the $(\hat{x}_1, \hat{x}_2)$-plane for $1 \geqslant r_3 \geqslant r_2$. For $\nu < 0$, the tank-treading is in the clockwise sense.

5. Ellipsoids of constant sphericity index

To apply the above theory as a model of a red blood cell in a shear flow it is pertinent to consider a family of ellipsoids having constant volume and constant surface area. The volume of the resting human red blood cell is about 94 μm^3 and its surface area is about 135 μm^2 (Evans & Fung 1972). Under most conditions a red cell will have the same volume and surface area as its resting shape. Experimental observations suggest that the shape of a red cell in a shear flow may be approximated by an ellipsoid (Fischer & Schmid-Schönbein 1977). At low shear stress the red cell is only slightly deformed from its resting shape and resembles an oblate spheroid. At higher shear stress the cell is an elongated but flat ellipsoid. At still-higher shear stress the cell resembles a prolate spheroid (Sutera, Mehrjardi & Mohandas 1975).

With the assumption that the red cell is an ellipsoid of known volume and surface area, specifying any one of the semi-axes determines the other two. The surface area of an ellipsoid is a function of its three semi-axes but no simple closed-form expression exists for the area when $a_1 \neq a_2 \neq a_3$. Keller (1979*b*) has developed a convergent series for the surface area of a triaxial ellipsoid. If $a_1 \geqslant a_3 \geqslant a_2$, the surface area is given by

$$S(a_i) = \frac{2\pi a_1 a_2}{n} \sum_{j=1}^{n} \frac{a_2}{a_1} + \frac{1-\tau_j}{[(1-a_1^2/a_2^2)-\tau_j]^{\frac{1}{2}}} \arcsin \frac{[(1-a_2^2/a_1^2)-\tau_j]^{\frac{1}{2}}}{(1-\tau_j)^{\frac{1}{2}}}, \tag{69}$$

where

$$\tau_j = (1-a_2^2/a_3^2)\cos^2[(2j-1)\pi/(2n)], \tag{70}$$

and n is an integer. As $n \rightarrow \infty$, the formula converges to the exact surface area and with $n = 40$ it is accurate to 10 significant digits for most cases. The volume of any ellipsoid is given by

$$V(a_i) = \tfrac{4}{3}\pi a_1 a_2 a_3. \tag{71}$$

a_1	a_2	a_3	$r_2 = a_2/a_1$	$r_3 = a_3/a_1$
4·296	1·229	4·296	0·286	1·000
4·488	1·230	4·110	0·274	0·916
4·680	1·232	3·935	0·263	0·841
4·872	1·235	3·770	0·253	0·774
5·064	1·238	3·617	0·244	0·714
5·255	1·244	3·468	0·237	0·660
5·447	1·251	3·328	0·230	0·611
5·639	1·258	3·196	0·223	0·567
5·831	1·268	3·068	0·217	0·526
6·023	1·278	2·946	0·212	0·489
6·215	1·290	2·830	0·208	0·455
6·407	1·303	2·718	0·203	0·424
6·599	1·319	2·606	0·200	0·395
6·791	1·337	2·498	0·197	0·368
6·983	1·358	2·392	0·194	0·343
7·174	1·383	2·286	0·193	0·319
7·366	1·414	2·178	0·192	0·296
7·558	1·452	2·066	0·192	0·273
7·750	1·513	1·934	0·195	0·250
7·942	1·690	1·690	0·213	0·213

TABLE 1. Semi-axes (in μm) of 20 ellipsoids having volume 95 μm^3 and surface area 135 μm^2 (sphericity index = 0·746)

If the specified surface area and volume are S_0 and V_0, then (69) and (71) give a pair of equations

$$S(a_i) = S_0, \quad V(a_i) = V_0 \tag{72), (73}$$

that define implicitly a one-parameter family of ellipsoids having the given surface area and volume. For given values of S_0 and V_0, (72) and (73) can be solved by numerical iteration for a_2 and a_3 with the major semi-axis a_1 as a parameter. However, a solution exists only for a finite range of values of a_1. The ellipsoid with the smallest major axis is an oblate spheroid ($a_1 = a_3 > a_2$), while the ellipsoid with the largest major axis is a prolate spheroid ($a_1 > a_3 = a_2$). Table 1 indicates the results for $V_0 = 95\,\mu m^3$, $S_0 = 135\,\mu m^2$, and a number of a_1 values.

In the red-blood-cell literature one measure of the shape of the cell often used is the sphericity index s defined by

$$s = (6\pi^{\frac{1}{2}}V)^{\frac{2}{3}}/S. \tag{74}$$

The sphericity index is unity for a sphere and less than one for any other shape. For the set of ellipsoids having a constant sphericity index, say s_0, it can be shown that

$$s(r_2, r_3) = s_0, \tag{75}$$

where r_2 and r_3 are the axis ratios (49), and the function $s(r_2, r_3)$ is obtained by substituting (69) and (71) into (74). Values of r_2 and r_3 in table 1 are solutions of (75) for $s_0 = 0·746$.

6. Motion of the particles

The angular motion of the ellipsoid is governed by the differential equation (66). For a given shear rate κ the coefficient A (67) is determined, and the coefficient B (68) is a function of the axis ratio r_3, viscosity ratio μ'/μ and sphericity index s_0. The axis

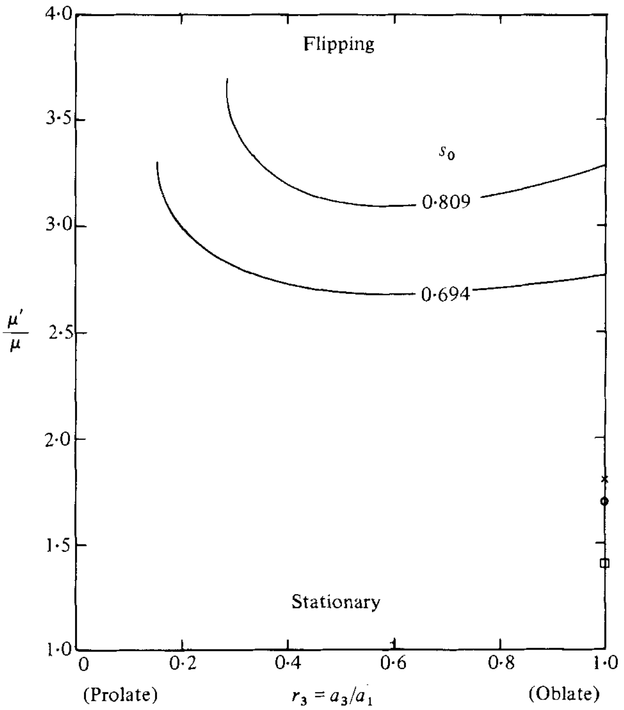

FIGURE 4. Transition value of viscosity ratio μ'/μ as a function of axis ratio r_3 for fixed values of the sphericity index s_0. Also shown are points representing experimental observations of Bessis & Mohandas (1975) (×, μ' = 8·9 cP; □, 18·4 cP) and of Morris & Williams (1979) (○, μ' = 10·3 cP).

ratio r_2 is implicitly determined from (75). It is assumed for convenient discussion that $1 \geqslant r_3 \geqslant r_2$ and that κ is positive. It may then be shown that B is always positive.

There are two types of solutions to (66). If $B > -A$, the solution for $\theta(t)$ is transient, with the angle $\theta(t)$ asymptotically approaching a constant value θ^*. If $B < -A$ the solution for $\theta(t)$ is periodic, corresponding to a flipping motion of the ellipsoid. The transition between flipping motion and stationary orientation occurs when $B = -A$. This equation specifies a relationship between r_3, μ'/μ and s_0 at which this transition takes place. Figure 4 is a plot of the transition value of μ'/μ as a function of r_3 for two values of s_0. Each curve represents a threshold for stationary orientation (or flipping). The region above each curve corresponding to a fixed value of s_0 yields solutions for which the particle would be flipping. For values of μ'/μ below the curve, the particle would assume a stationary orientation. The curves begin at a non-zero value of r_3 because there is a non-zero minimum of r_3 for any given s_0 (corresponding to the prolate spheroid with that s_0).

The curves indicate that for a given s_0 the transition value of μ'/μ is fairly insensitive to the value of r_3 until the particle is quite elongated, say $r_3 < 0{\cdot}4$. For $r_3 < 0{\cdot}4$ the threshold value of μ'/μ increases with increasing elongation (i.e. r_3 decreasing). Furthermore, it can be seen from figure 4 that increasing the sphericity index or the elongation tends to promote a stationary orientation, while increasing the viscosity ratio drives the particle toward flipping like a rigid ellipsoid.

Also shown in figure 4 are points representing the threshold values of μ'/μ obtained from the experimental observations of Bessis & Mohandas (1975) and Morris & Williams (1979). These investigators found, through diffractometric observations on dilute suspensions of human red cells in viscometric flows at constant shear stress, that there was a threshold value of suspending liquid viscosity μ below which no elongation was observed. These observed thresholds are assumed to correspond to the transition from flipping to stationary orientation. To interpret the experimental data in the terms used here, the values for μ' were taken from haemoglobin viscosities reported in the literature (Cokelet & Meiselman 1968; Chien, Usami & Bertles 1970), and were adjusted for the reported temperature and osmolarity. It is assumed that the red-blood-cell shape at the threshold value of μ'/μ could be approximated by an oblate spheroid, and hence the points are plotted for $r_3 = 1$.

The experimental values of μ'/μ at the threshold between flipping and stationary orientation are in the range of about 1·4 to about 1·8. The theoretically predicted thresholds for ellipsoidal membranes without shear viscosity are in the range of about 2·8 to about 3·2. The difference between theory and experiment may be due to dissipation in the membrane. To account for the effect of the membrane in an approximate fashion the theoretical curves might be regarded as specifying the ratio of the apparent internal viscosity μ'_{app} (51) to the external viscosity μ. This then determines the dissipation ratio d, via (51). The results indicate that d is of the order of 1·0. If d is taken to be 1 (as suggested by Fischer's work), then the theoretically predicted value of the threshold viscosity ratio μ'/μ is in the range of about 1·4 to about 1·6, which is in reasonable agreement with the experimental observations.

For $B > -A$ the solution to (66) is

$$\theta(t) = \arctan\left[\frac{B+A}{(B^2-A^2)^{\frac{1}{2}}}\,\frac{D\exp[2(B^2-A^2)^{\frac{1}{2}}t]+1}{D\exp[2(B^2-A^2)^{\frac{1}{2}}t]-1}\right], \tag{76}$$

where

$$D = \frac{(B^2-A^2)^{\frac{1}{2}}\tan\theta_0+A+B}{(B^2-A^2)^{\frac{1}{2}}\tan\theta_0-A-B} \tag{77}$$

and θ_0 is the initial value of θ at $t = 0$. It may be shown from (76) that

$$\lim_{t\to\infty}\theta(t) = \theta^*, \tag{78}$$

where

$$\theta^* = \tfrac{1}{2}\arccos(-A/B). \tag{79}$$

Since $0 \leqslant -A/B \leqslant 1$, it is seen from (79) that

$$0 \leqslant \theta^* \leqslant \tfrac{1}{4}\pi. \tag{80}$$

Figure 5 is a plot of the angle of inclination θ^* versus r_3 for three pairs of viscosity ratio μ'/μ and sphericity index s_0. It is seen that the angle of inclination generally decreases with decreasing r_3, increasing μ'/μ and decreasing s_0. As indicated in (51) the variation of θ^* with d would be in the same sense as with μ'/μ. Also shown are estimates of θ^* made by Fischer (1980) from experimental observations on a human red blood cell with $\mu'/\mu = 0{\cdot}44$ and $s_0 = 0{\cdot}679$. The general range of θ^* values and trend with decreasing r_3 of the present analysis exhibit a qualitative agreement with Fischer's estimates.

By substituting (79) into (65) it may be shown that the circular frequency of tank-treading for the stationary-orientation case ($B > -A$) is given by

$$\nu^* = f_3[f_2-(\mu'/\mu)f_1]^{-1}\kappa A/B. \tag{81}$$

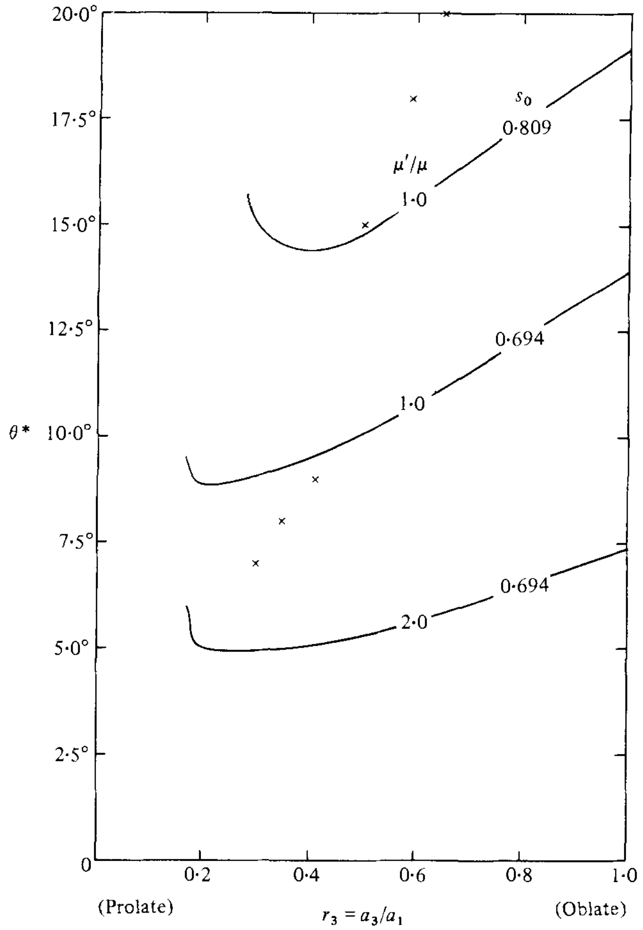

FIGURE 5. Plot of stationary angle of inclination θ^* *vs.* axis ratio r_3 for three pairs of viscosity ratio μ'/μ and sphericity index s_0 with the dissipation ratio $d = 1$. Also shown (×) are points estimated by Fischer (1980) from experimental observations with $\mu'/\mu = 0{\cdot}44$ and $s_0 = 0{\cdot}679$.

The sign of ν^* is negative, and thus the tank-tread motion is always in the clockwise sense when the particle assumes a stationary orientation. Figure 6 is a plot of $-\nu^*/\kappa$ versus r_3 for three pairs of μ'/μ and s_0. The dimensionless circular frequency of tank-treading $-\nu^*/\kappa$ generally decreases with decreasing r_3, increasing μ'/μ and decreasing s_0. This predicted behaviour is consistent with the experimental observations of Fischer *et al.* (1978*b*). Also shown are points corresponding to the experimental observations by Fischer (1980) for $\mu'/\mu = 0{\cdot}44$ and $s_0 = 0{\cdot}679$. The theoretical prediction of tank-treading frequency is seen to agree qualitatively with the experimental observations.

For $B < -A$ the solution to (66) is

$$\theta(t) = \arctan\left\{\frac{A+B}{(A^2-B^2)^{\frac{1}{2}}}\tan\left[(t-t_0)\pi/T\right]\right\}, \tag{82}$$

where t_0 is the time at which $\theta = 0$, and T is the period of flipping through an angle π. It is given by

$$(T = \pi A^2 - B^2)^{-\frac{1}{2}}. \tag{83}$$

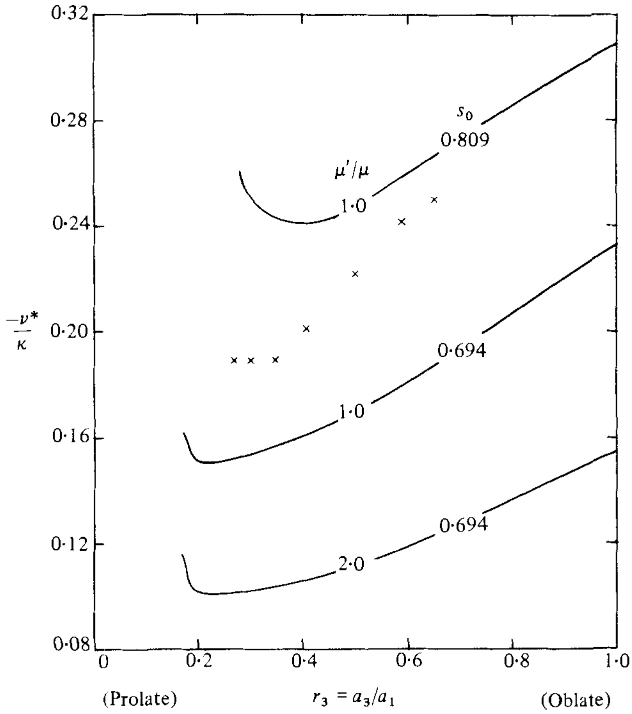

FIGURE 6. Plot of non-dimensional circular tank-treading frequency $-\nu^*/\kappa$ *vs.* axis ratio r_3 for three pairs of viscosity ratio μ'/μ and sphericity index s_0. Also shown (×) are the experimental observations by Fischer (1980) on a human red blood cell with $\mu'/\mu = 0{\cdot}44$ and $s_0 = 0{\cdot}679$.

It is seen from (66) that for positive κ the flipping motion is in the clockwise sense, so $\dot{\theta}(t)$ is negative. Figure 7 shows $-\theta/\pi$ over one flipping period for three viscosity ratios with $r_3 = 1$ and $s_0 = 0{\cdot}694$. The r_2 corresponding to this r_3 and s_0 is 0·245. As μ'/μ increases, the angular motion of the particle approaches that of a rigid ellipsoid. For $\mu'/\mu = 100$, the curve is indistinguishable from Jeffery's solution for a rigid particle. As μ'/μ approaches the threshold for stationary orientation (about 2·78 in this case, cf. figure 4), the motion becomes more jerky, with the particle spending a greater proportion of its temporal period with its major axis aligned with the flow.

Figure 8 is a plot of the dimensionless flipping period κT *vs.* the viscosity ratio μ'/μ for an oblate spheroid ($r_3 = 1$) with $s_0 = 0{\cdot}694$ ($r_2 = 0{\cdot}245$). For large values of the viscosity ratio it is easily shown from (67), (68) and (83) that the flipping period becomes Jeffery's result for a rigid ellipsoid:

$$\kappa T = \pi(r_2 + r_1^{-2}), \tag{84}$$

which is equal to 13·59 for $r_2 = 0{\cdot}245$. As the viscosity ratio decreases it is seen that the period of flipping increases and becomes infinite as μ'/μ approaches the transition value, which is 2·78 for the case shown.

7. Summary and concluding remarks

The present theoretical analysis provides a useful model for understanding several features of the observed motions of human red blood cells in a shear field. The most striking feature of the observed behaviour is that, under the proper circumstances,

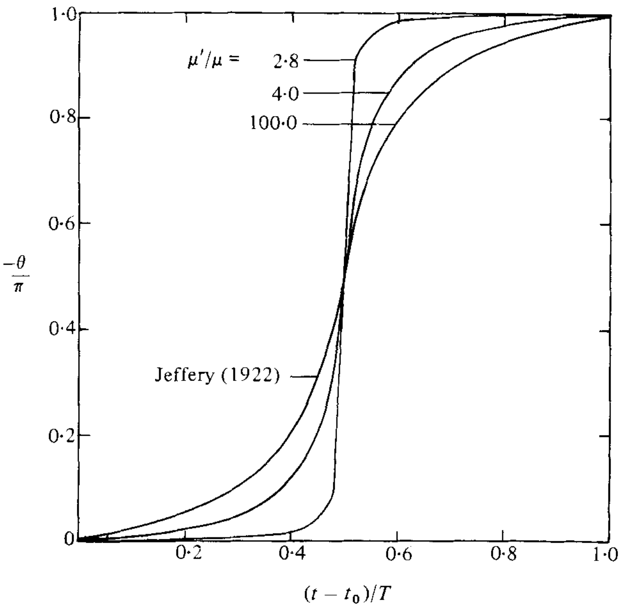

FIGURE 7. Angular orientation of an oblate spheroid ($r_3 = 1\cdot000$) over one flipping period for three viscosity ratios with $s_0 = 0\cdot694$ ($r_2 = 0\cdot245$). The curve $\mu'/\mu = 100$ coincides with Jeffery's (1922) solution for rigid ellipsoids.

a red blood cell may assume a stationary shape and orientation while the membrane and cell contents perform a tank-tread motion. Under other circumstances, the red cell is observed to have a flipping motion. The theoretical analysis indicates that the type of motion that occurs may be determined from a knowledge of the values of three parameters. These are: the ratio of the middle to major axes of an ellipsoid which represents the red cell, the sphericity index, and the ratio of the internal to external liquid viscosities.

The theory indicates that decreasing the viscosity ratio or increasing the elongation of the particle promotes a stationary orientation, with the opposite variations inducing the flipping motion. This is in agreement with the observation that increasing the suspending-medium viscosity, which is the usual experimental technique, brings about tank-treading of a human red cell at a stationary orientation. Decreasing the sphericity index is predicted to favour the flipping motion, with the opposite variation tending to cause the stationary orientation. The effect of these variations on the type of motion exhibited by a red cell has not yet been experimentally examined.

When the model particle assumes a stationary orientation, the angle of inclination is between 0° and 45°, and the tank-treading frequency is constant. The theory implies that the angle and tank-treading frequency generally decrease with increasing elongation. The range of the predicted angles and tank-treading frequencies and their behaviour with increasing elongation are in agreement with experimental observations on the human red cell. The theory also suggests that the angle of inclination and tank-treading frequency decrease with increasing viscosity ratio or decreasing sphericity index. These trends are consistent with the experimental observations.

When the model particle flips, it also tank-treads, with the direction and frequency of the tank-tread motion varying with the angular position of the particle. The exist-

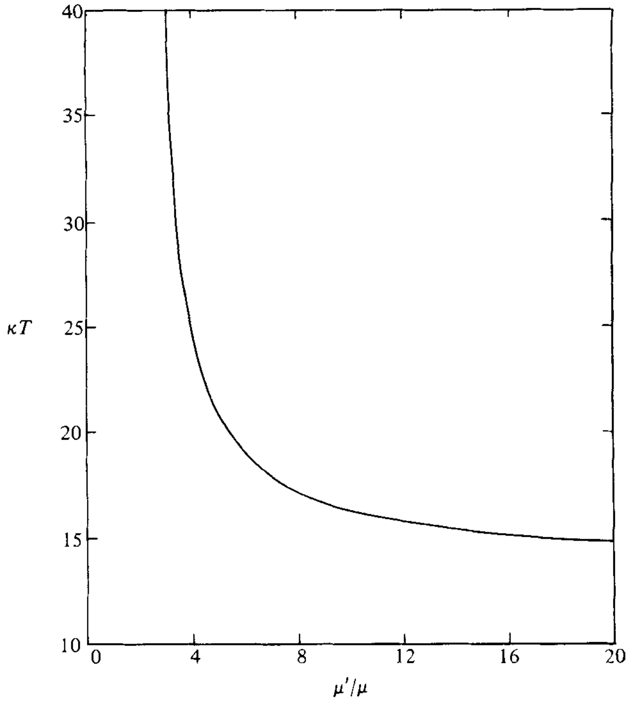

FIGURE 8. Dimensionless flipping period κT for an oblate spheroid (r_3 = 1·000) with s_0 = 0·694 (r_2 = 0·245) *vs.* viscosity ratio μ'/μ.

ence of this oscillatory tank-tread motion while a red blood cell is flipping has not been observed, although flipping is easily seen. The theory indicates that as the viscosity ratio increases the particle flips increasingly like a rigid ellipsoid, and in the limit the motion becomes Jeffery's solution. As the viscosity ratio decreases, however, the period of flipping and time spent aligned with the flow are predicted to increase, with the particle eventually assuming a stationary orientation. The details of this transition from flipping motion to stationary orientation also have not yet been experimentally investigated.

The present analysis might be made a more realistic model for red blood cells by several improvements which have to do mostly with the shape and properties of the membrane. In the present study, the shape of the particle has been assumed to be an ellipsoid. In a more-complete theory, this shape would be determined instead by the stresses acting on the membrane and its elastic properties. This is a formidable problem in large-deformation shell theory, but an approximate treatment considering the net axial force exerted on each half of the cell might provide a sufficiently accurate solution.

In addition, the rate of energy dissipation in the membrane should be included in a more complete model. This perhaps can be calculated directly from the membrane motion and its viscous properties. Also, to be realistic, the membrane motion itself needs to be revised so that it is area-preserving in a local sense because this is a salient feature of red-blood-cell membranes.

The improvements mentioned above are not expected to alter the qualitative nature of the results predicted and may have relatively small quantitative effects.

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