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Mobility of particles embedded in a laterally bounded membrane

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The hydrodynamic analysis of motion of small particles (e.g. proteins) within lipid bilayers appears to be naturally suitable for the framework of two-dimensional Stokes flow. Given the Stokes paradox, the problem in an unbounded domain is ill-posed. In his classical paper, Saffman (*J. Fluid Mech.*, vol. 73, 1976, pp. 593–602) proposed several possible remedies, one of them based upon the finite extent of the membrane. Considering a circular boundary, that regularisation was briefly addressed by Saffman in the isotropic configuration, where the particle is concentrically positioned in the membrane. We investigate here the hydrodynamic problem in bounded membranes for the general case of eccentric particle position and a rectilinear motion in an arbitrary direction. Symmetry arguments provide a representation of the hydrodynamic drag in terms of 'radial' and 'transverse' coefficients, which depend upon two parameters: the ratio λ of particle to membrane radii and the eccentricity β. Using matched asymptotic expansions we obtain closed-form approximations for these coefficients in the limit where λ is small. In the isotropic case ($\beta = 0$) we find that the drag coefficient is $4\pi/(\ln(1/\lambda) - 1)$, contradicting the value $4\pi/(\ln(1/\lambda) - 1/2)$ obtained by Saffman. We explain the oversight in Saffman's argument.

Key words: membranes, colloids

1. Introduction

The calculation of hydrodynamic mobility of membrane-trapped particles is of obvious importance in interfacial rheology (Squires & Mason 2010; Fuller & Vermant 2012; Evans & Levine 2015). Using the Einstein relation, mobility expressions are readily translated to diffusivity formulae, the latter useful in modelling various biological processes

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(Saffman & Delbrück 1975). In his pioneering work, Saffman (1976) introduced a useful idealised description, treating the membrane as a zero-thickness fluid interface bounding one or two liquid domains and possessing a Boussinesq–Scriven rheology (Scriven 1960) characterised by surface viscosity μ_s (with dimensions of mass over time); the particle is consequently modelled as a disk of circular cross-section, stranded within the interface. (Saffman actually introduced a non-isotopic model of a finite-thickness liquid sheet with a transversely uniform velocity. His model is equivalent to that involving a zero-thickness membrane whose surface viscosity is provided by the product of the sheet thickness and viscosity; see Evans & Sackmann 1988).

The relative role of surface and bulk stresses is quantified by the Boussinesq number, namely the ratio of μ_s to the product of particle size and bulk viscosity. For small (e.g. integral membrane proteins) particles, that number is large, suggesting negligible bulk stresses. That simplification, however, leads to the Stokes paradox: there is no solution of two-dimensional (2-D) Stokes flow in an unbounded domain for the translation of a particle in an otherwise quiescent fluid. The standard procedure for dealing with the above problem (Leal 2007) involves the incorporation of fluid inertia, which substantially affects momentum transfer at large distances that are inversely proportional to the particle speed. Given the small speeds involved, regularisation in membrane problems takes place at shorter scales (still large compared with particle size), set by other mechanisms. Thus, rather than incorporating inertia, Saffman (1976) suggested the incorporation of bulk stresses; these become appreciable at the 'Saffman–Delbrück' distance, provided by the product of particle size with the Boussinesq number.

An alternative regularisation is simply provided by considering bounded membranes. The problem of particle motion in a bounded membrane is relevant to the modelling of protein diffusion in a plasma-membrane bleb (Charras *et al*. 2008). A bleb is a (typically circular) region of a cell membrane in which the connections from the membrane proteins to the cytoskeleton have been severed. In the remaining part of the membrane, the fixed proteins would screen hydrodynamic disturbances. If the screening length is small compared with the bleb radius, the edge of the bleb would come close to acting as a no-slip boundary. Similar phenomena may occur in lipid bilayers in which the proximity to a supporting substrate makes parts of the membrane nearly immobile (Stone & Ajdari 1998; Barentin *et al*. 1999), while polymeric spacers keep other parts away from the substrate.

The 2-D problem of particle motion in a bounded membrane was briefly considered by Saffman (1976), who assumed a circular boundary and focused upon the concentric geometry, where the centres of the particle and the membrane coincide. Assuming that the ratio λ of particle to membrane radii is small, Saffman concluded that the product of μ_s with particle mobility is $(4\pi)^{-1}(\ln(1/\lambda) - 1/2)$.

We consider the general eccentric configuration, allowing for particle velocity in an arbitrary direction in the plane. Symmetry arguments show that it suffices to solve two auxiliary problems: a 'radial' problem, where the particle moves along the radius vector that connects its centre to the membrane centre, and a 'transverse' problem, where the particle moves perpendicular to the radius vector. Following Saffman (1976) we address the limit of small particles. This limit is addressed systematically using matched asymptotic expansions.

2. Problem formulation

Our problem concerns Stokes flow within a circular membrane (radius $\mathcal{R}$, surface viscosity μ_s). The unit normal to the membrane is denoted by $\hat{\boldsymbol{k}}$. A rigid disk of radius $\lambda\mathcal{R}$ ($\lambda < 1$) is freely suspended within the membrane. The distance between the membrane centre O

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and the particle centre is $\beta\mathcal{R}$ (with $\beta < 1 - \lambda$). The instantaneous position of the particle in a laboratory reference frame is defined by a unit vector $\hat{\boldsymbol{\imath}}$ pointing from O to the particle centre. The particle translates with an arbitrary rectilinear velocity; it is written as $\mathcal{U}\hat{\boldsymbol{e}}$, $\hat{\boldsymbol{e}}$ being a unit vector in the membrane plane.

Our goal is the calculation of the hydrodynamic force on the particle. Since the flow problem is linear and homogeneous in the velocity $\mathcal{U}\hat{\boldsymbol{e}}$, that force must be linear in it. By dimensional and symmetry arguments, the force is of the form

$$-\mu_s\mathcal{U}\left[\hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}}\, F_{\parallel} + (\mathsf{I}_2 - \hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}})F_{\perp}\right]\boldsymbol{\cdot}\hat{\boldsymbol{e}}, \tag{2.1}$$

wherein $\mathsf{I}_2 = \mathsf{I} - \hat{\boldsymbol{k}}\hat{\boldsymbol{k}}$ (in which I is the idemfactor) is the surface idemfactor and $F_{\parallel}$, $F_{\perp}$ are dimensionless coefficients; the associated resistance tensor is

$$\mu_s\left[\hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}}\, F_{\parallel} + (\mathsf{I}_2 - \hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}})F_{\perp}\right]. \tag{2.2}$$

It is clear by symmetry that particle translation in the radial direction results in a radial force. It does not seem as intuitive that a velocity perpendicular to that direction does not result in a radial force.

The drag coefficients $F_{\parallel}$ and $F_{\perp}$ can only depend upon λ and β; standard thermodynamic arguments necessitate that both coefficients must be positive (Happel & Brenner 1965). In the concentric case $\beta = 0$ the problem is isotropic, whereby

$$\lim_{\beta\to 0} F_{\parallel} = \lim_{\beta\to 0} F_{\perp} (= F,\ \text{say}). \tag{2.3}$$

In that case, the hydrodynamic force on the particle is

$$-\mu_s\mathcal{U}F\,\hat{\boldsymbol{e}}. \tag{2.4}$$

This expression does not involve $\hat{\boldsymbol{\imath}}$, which is undefined for an isotropic configuration.

We employ a dimensionless notation, normalising length variables by $\mathcal{R}$, velocities by $\mathcal{U}$ and forces by $\mu_s\mathcal{U}$. We employ Cartesian (X, Y) coordinates with origin at O and the X axis passing through the particle centre, located at the point $(\beta, 0)$. Consistently with the definition of $\hat{\boldsymbol{\imath}}$, the unit vectors associated with X and Y are $\hat{\boldsymbol{\imath}}$ and $\hat{\boldsymbol{\jmath}} = \hat{\boldsymbol{k}} \times \hat{\boldsymbol{\imath}}$, respectively. The position vector $\hat{\boldsymbol{\imath}}X + \hat{\boldsymbol{\jmath}}Y$ is denoted by $\boldsymbol{X}$. We also employ the polar coordinates (R, θ), with $R = |\boldsymbol{X}|$ and θ measured anticlockwise from the X axis (see figure 1). The associated unit vectors are $\hat{\boldsymbol{e}}_R$ and $\hat{\boldsymbol{e}}_\theta$.

The 2-D flow is therefore governed by the continuity and Stokes equations together with the no-slip condition at boundaries of both the membrane

$$\boldsymbol{U} = \boldsymbol{0} \quad \text{at} \quad R = 1, \tag{2.5}$$

and the particle

$$\boldsymbol{U} = \hat{\boldsymbol{e}} \quad \text{for} \quad |\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| = \lambda. \tag{2.6}$$

Alternatively, we can use the biharmonic stream function Ψ, defined by (Happel & Brenner 1965)

$$\boldsymbol{U} = \boldsymbol{\nabla}\Psi \times \hat{\boldsymbol{k}}, \tag{2.7}$$

wherein

$$\boldsymbol{\nabla} = \hat{\boldsymbol{\imath}}\frac{\partial}{\partial X} + \hat{\boldsymbol{\jmath}}\frac{\partial}{\partial Y} \tag{2.8}$$

is the 2-D gradient. Thus, writing $\boldsymbol{U} = \hat{\boldsymbol{e}}_R U + \hat{\boldsymbol{e}}_\theta V$:

$$U = \frac{1}{R}\frac{\partial\Psi}{\partial\theta}, \qquad V = -\frac{\partial\Psi}{\partial R}. \tag{2.9}$$

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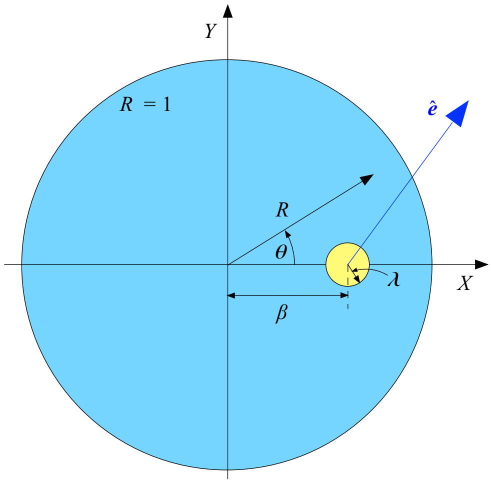

Figure 1. Dimensionless geometry and coordinate systems.

In particular, the no-slip condition (2.5) reads

$$\Psi = \frac{\partial \Psi}{\partial R} = 0 \quad \text{at} \quad R = 1. \tag{2.10}$$

Making use of the underlying linearity, it convenient to replace the general problem formulated above by two auxiliary problems, one where the particle translates with a unit velocity in the X-direction ($\hat{\boldsymbol{e}} = \hat{\boldsymbol{\imath}}$) and one where it translates with a unit velocity in the Y-direction ($\hat{\boldsymbol{e}} = \hat{\boldsymbol{\jmath}}$). From (2.1) we note that in the first 'radial' case the drag is $F_{\parallel}$, while in the second 'transverse' case it is $F_{\perp}$.

3. The limit of small particles

Hereafter we consider the limit of small particles:

$$\lambda \ll 1. \tag{3.1}$$

We address that limit using matched asymptotic expansions (Hinch 1991). Thus, the membrane size sets the 'outer' scale; on that scale, condition (2.6) does not apply. Rather, the solution on the outer scale must match a separate 'inner' solution, which is applicable on the particle scale. The inner region is described using the stretched position vector $\boldsymbol{x}$, measured from the particle centre and scaled by its size:

$$\boldsymbol{X} = \beta \hat{\boldsymbol{\imath}} + \lambda \boldsymbol{x}. \tag{3.2}$$

Writing $r = |\boldsymbol{x}|$, the particle boundary becomes $r = 1$. The inner velocity field is denoted by $\boldsymbol{u}$. As a function of $\boldsymbol{x}$, it satisfies the continuity and Stokes equations, together with the no-slip condition on the particle. The latter reads

$$\boldsymbol{u} = \hat{\boldsymbol{\imath}} \quad \text{at} \quad r = 1 \tag{3.3}$$

in the radial problem and

$$\boldsymbol{u} = \hat{\boldsymbol{\jmath}} \quad \text{at} \quad r = 1 \tag{3.4}$$

in the transverse problem.

In the inner region, condition (2.5) (or, equivalently, (2.10)) does not apply. To uniquely determine the inner velocity, we temporarily consider the drag as a prescribed quantity.

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Thus, we impose the requirement

$$\text{drag} = F_{\parallel} \tag{3.5}$$

in the radial problem and

$$\text{drag} = F_{\perp} \tag{3.6}$$

in the transverse problem. The unknown drag can only be determined via asymptotic matching.

In what follows we only seek the leading-order velocity fields. We abide by the Fraenkel convention (Fraenkel 1969), avoiding separation of asymptotic orders by logarithms of λ. The leading-order fields may therefore depend upon $\ln \lambda$. That approach allows for the use of the Van Dyke matching rule (Van Dyke 1964) and guarantees that the asymptotic error is algebraically small (i.e. asymptotically smaller than some positive power of λ). The Fraenkel convention was implicitly employed by Saffman (1976). It is indispensable in analysing the singular limit of small particles, regardless of the regularisation mechanism (see e.g. Henle & Levine 2010).

The solution of the leading-order inner problem is straightforward. It consists of a Stokeslet, an irrotational doublet and a uniform stream (Hinch 1991). In the radial case, the solution must satisfy (3.3) and (3.5). It is therefore given by

$$\boldsymbol{u} = \frac{F_{\parallel}}{4\pi}\left(-l_2 \ln r + \frac{\boldsymbol{x}\boldsymbol{x}}{r^2}\right)\boldsymbol{\cdot}\hat{\boldsymbol{\imath}} - \frac{F_{\parallel}}{8\pi r^2}\left(-l_2 + 2\frac{\boldsymbol{x}\boldsymbol{x}}{r^2}\right)\boldsymbol{\cdot}\hat{\boldsymbol{\imath}} + \left(1 - \frac{F_{\parallel}}{8\pi}\right)\hat{\boldsymbol{\imath}}. \tag{3.7}$$

In the transverse case, the solution must satisfy (3.4) and (3.6), and is accordingly

$$\boldsymbol{u} = \frac{F_{\perp}}{4\pi}\left(-l_2 \ln r + \frac{\boldsymbol{x}\boldsymbol{x}}{r^2}\right)\boldsymbol{\cdot}\hat{\boldsymbol{\jmath}} - \frac{F_{\perp}}{8\pi r^2}\left(-l_2 + 2\frac{\boldsymbol{x}\boldsymbol{x}}{r^2}\right)\boldsymbol{\cdot}\hat{\boldsymbol{\jmath}} + \left(1 - \frac{F_{\perp}}{8\pi}\right)\hat{\boldsymbol{\jmath}}. \tag{3.8}$$

The Stokes paradox is reflected by the logarithmic divergence at large r in both flow fields.

Considering now the leading-order outer problem, asymptotic matching with (3.7)–(3.8) implies a point-force singularity. In the radial problem, this imposes the limiting behaviour

$$\boldsymbol{U} \sim -\hat{\boldsymbol{\imath}}\frac{F_{\parallel}}{4\pi}\ln|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| \quad \text{as} \quad |\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| \to 0. \tag{3.9}$$

Similarly, in the transverse problem,

$$\boldsymbol{U} \sim -\hat{\boldsymbol{\jmath}}\frac{F_{\perp}}{4\pi}\ln|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| \quad \text{as} \quad |\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| \to 0. \tag{3.10}$$

The leading-order outer flow is uniquely defined by these conditions. It is simply the Green function for a Stokes flow inside a no-slip circle. That function was constructed by Daripa & Palaniappan (2001) for both the radial and transverse cases. (While those authors addressed a pair of Stokeslets, the requisite Green function is readily obtained from their formulae by setting one of the Stokeslet magnitudes to zero.)

For our purpose of calculating the leading-order drag, all we need is the refinement of (3.9)–(3.10); that is, we need the leading-order behaviour (in the aforementioned Fraenkel convention) of $\boldsymbol{U}$ as $\boldsymbol{X}$ approaches $\beta\hat{\boldsymbol{\imath}}$.

In what follows, we address the radial and transverse problems separately.

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4. Radial problem

It is convenient to employ the stream function formulation. Condition (3.9) reads

$$\Psi \sim -\frac{F_\parallel}{4\pi} Y \ln |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| \quad \text{as} \quad |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| \to 0, \tag{4.1}$$

which, together with (2.10), serves to uniquely define the biharmonic function Ψ in the disk $R < 1$. Our goal is the refinement of (4.1).

It is convenient to decompose Ψ as

$$\Psi = \frac{F_\parallel}{4\pi}(\Psi_S + \Psi_R), \tag{4.2}$$

where the 'singular' part

$$\Psi_S = Y(1 - \ln |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}|) \tag{4.3}$$

is a Stokeslet in the X direction. By restricting the 'regular' part Ψ_R to be smooth inside the circle $R = 1$, (4.1) is trivially satisfied. The regular part is therefore determined by the conditions (see (2.10))

$$\Psi_R = -\Psi_S, \quad \frac{\partial \Psi_R}{\partial R} = -\frac{\partial \Psi_S}{\partial R} \quad \text{at} \quad R = 1. \tag{4.4}$$

The biharmonic function that satisfies (4.4) was constructed by Daripa & Palaniappan (2001) using an image at the point $\boldsymbol{X} = \hat{\boldsymbol{\imath}}/\beta$, which lies outside the membrane. In the present notation,

$$\Psi_R = Y \left[\ln |\beta \boldsymbol{X} - \hat{\boldsymbol{\imath}}| - 1 - \frac{(1 - \beta^2)(1 - R^2)}{2|\beta \boldsymbol{X} - \hat{\boldsymbol{\imath}}|^2} \right]. \tag{4.5}$$

Taylor expansion about $\beta \hat{\boldsymbol{\imath}}$ simply gives

$$\Psi_R \sim Y \left[\ln(1 - \beta^2) - \frac{3}{2} \right] \quad \text{as} \quad |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| \to 0, \tag{4.6}$$

with an $O(|\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}|^2)$ error. Approximation (4.6) represents a uniform flow in the X direction. The local behaviour (3.9) near $\boldsymbol{X} = \beta \hat{\boldsymbol{\imath}}$ is accordingly refined to

$$\boldsymbol{U} \sim \frac{F_\parallel}{4\pi} \left\{ \left[-\mathsf{I}_2 \ln |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| + \frac{(\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}})(\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}})}{|\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}|^2} \right] \boldsymbol{\cdot} \hat{\boldsymbol{\imath}} + \left[\ln(1 - \beta^2) - \frac{3}{2} \right] \hat{\boldsymbol{\imath}} \right\}, \tag{4.7}$$

where the first term in the braces is due to the singular part (4.3) and the second term, a uniform stream in the X-direction, is due to (4.6). The asymptotic error in (4.7) is $O(\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}})$.

With algebraically small asymptotic error, the local behaviour (4.7) provides the requisite leading-order approximation (in the sense of Fraenkel). We may therefore directly employ the Van Dyke matching rule. Matching with (3.7) using (3.2) gives

$$F_\parallel = \frac{4\pi}{\ln \frac{1-\beta^2}{\lambda} - 1}. \tag{4.8}$$

5. Transverse problem

In the transverse case, the outer singularity is specified by condition (3.10). In terms of the stream function, it reads

$$\Psi \sim \frac{F_\perp}{4\pi}(X - \beta) \ln |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| \quad \text{as} \quad |\boldsymbol{X} - \beta \hat{\boldsymbol{\imath}}| \to 0. \tag{5.1}$$

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Our goal is the refinement of (5.1).

Similarly to (4.2) we decompose Ψ as

$$\Psi = \frac{F_\perp}{4\pi}(\Psi_S + \Psi_R), \tag{5.2}$$

where the singular part,

$$\Psi_S = (X - \beta)(\ln|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| - 1), \tag{5.3}$$

is a Stokeslet in the Y direction. Here, the regular part was found (Daripa & Palaniappan 2001) as

$$\Psi_R = X - \beta - (X - \beta)\ln|\beta\boldsymbol{X} - \hat{\boldsymbol{\imath}}| - \frac{(1-\beta^2)(1-R^2)R(\beta R - \cos\theta)}{2|\beta\boldsymbol{X} - \hat{\boldsymbol{\imath}}|^2}. \tag{5.4}$$

Our goal is the leading-order approximation of Ψ_R near $\boldsymbol{X} = \beta\hat{\boldsymbol{\imath}}$. At leading order, this approximation evidently represents a uniform velocity. Since symmetry arguments necessitate that this velocity is in the Y direction, it suffices to consider Ψ_R at $\theta = 0$ (where $R = X$) and then obtain a Taylor expansion up to ord$(X - \beta)$. This gives

$$\Psi_R \sim \frac{\beta(1-\beta^2)}{2} - (X - \beta)\left[\ln(1-\beta^2) + \beta^2 - \frac{3}{2}\right] + O(|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}|^2) \quad \text{as} \quad |\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| \to 0. \tag{5.5}$$

The first term in (5.5) is a constant of no physical significance. The second term represents a uniform stream in the Y direction.

The limiting form (3.10) near $\boldsymbol{X} = \beta\hat{\boldsymbol{\imath}}$ is accordingly refined to the asymptotic approximation:

$$\boldsymbol{U} \sim \frac{F_\perp}{4\pi}\left\{\left[-\mathsf{I}_2 \ln|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}| + \frac{(\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}})(\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}})}{|\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}}|^2}\right]\boldsymbol{\cdot}\hat{\boldsymbol{\jmath}} + \left[\ln(1-\beta^2) + \beta^2 - \frac{3}{2}\right]\hat{\boldsymbol{\jmath}}\right\}, \tag{5.6}$$

where the first term in the braces is due to the singular part (5.3) and the second term, a uniform stream in the Y-direction, is due to (5.5). As in (4.7), the asymptotic error is $O(\boldsymbol{X} - \beta\hat{\boldsymbol{\imath}})$. Matching with (3.8) using (3.2) gives

$$F_\perp = \frac{4\pi}{\ln\frac{1-\beta^2}{\lambda} - 1 + \beta^2}. \tag{5.7}$$

Note that (2.3) is indeed satisfied by (4.8) and (5.7).

6. Discussion

6.1. *The concentric limit*

The XY coordinates (and then too the associated unit vectors $\hat{\boldsymbol{\imath}}$ and $\hat{\boldsymbol{\jmath}}$) are undefined for $\beta = 0$. It is useful to employ an invariant notation in this case when describing the outer solution. For the singular part this gives, for both (4.3) and (5.3),

$$\Psi_S = (1 - \ln R)\,\hat{\boldsymbol{k}} \times \hat{\boldsymbol{e}}, \tag{6.1}$$

which is independent of $\hat{\boldsymbol{\imath}}$ and $\hat{\boldsymbol{\jmath}}$. The associated velocity field is

$$\frac{F}{4\pi}\left(-\mathsf{I}_2 \ln R + \hat{\boldsymbol{e}}_R\hat{\boldsymbol{e}}_R\right)\boldsymbol{\cdot}\hat{\boldsymbol{e}}. \tag{6.2}$$

While the (R, θ) polar coordinates are undefined for $\beta = 0$, we note that $\hat{\boldsymbol{e}}_R$ may be written in an invariant notation as $\boldsymbol{X}/R$.

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For the regular part this gives, for both (4.5) and (5.4),

$$\Psi_R = \frac{1}{2}(\hat{\boldsymbol{k}} \times \hat{\boldsymbol{e}}) \cdot \boldsymbol{X}(R^2 - 3), \tag{6.3}$$

which is independent of $\hat{\boldsymbol{\imath}}$ and $\hat{\boldsymbol{\jmath}}$. The associated velocity is

$$\frac{F}{8\pi}\left[(R^2-3)\hat{\boldsymbol{e}}_R\hat{\boldsymbol{e}}_R + 3(R^2-1)\left(\mathsf{I}_2 - \hat{\boldsymbol{e}}_R\hat{\boldsymbol{e}}_R\right)\right]\cdot\hat{\boldsymbol{e}}. \tag{6.4}$$

Evaluation at $R = 1$ reveals that the sum of (6.2) and (6.4) indeed satisfies (2.5).

6.2. *Comparison with Saffman (1976)*

The possibility of regularising the Stokes paradox by a finite membrane (as opposed to finite bulk viscosity) was briefly addressed by Saffman (1976), who only considered the isotropic case. Making use of the isotropy (2.3), the inner flow in that case follows from (3.7)–(3.8) as

$$\boldsymbol{u} = \frac{F}{4\pi}\left(-\mathsf{I}_2 \ln r + \frac{\boldsymbol{xx}}{r^2}\right)\cdot\hat{\boldsymbol{e}} - \frac{F}{8\pi r^2}\left(-\mathsf{I}_2 + 2\frac{\boldsymbol{xx}}{r^2}\right)\cdot\hat{\boldsymbol{e}} + \left(1 - \frac{F}{8\pi}\right)\hat{\boldsymbol{e}}. \tag{6.5}$$

In interpreting Saffman's arguments, it is evident that he estimated the inner flow field at large distances away from the particle, where the contribution of the doublet term is negligible. The velocity (6.5) at the membrane boundary (i.e. $r = 1/\lambda$) then consists of two contributions

$$\left(-\frac{F}{4\pi}\ln\frac{1}{\lambda} + 1 - \frac{F}{8\pi}\right)\hat{\boldsymbol{e}} + \frac{F}{4\pi}\hat{\boldsymbol{e}}_R\hat{\boldsymbol{e}}_R\cdot\hat{\boldsymbol{e}}, \tag{6.6}$$

which are of the same asymptotic order. (The first contribution, representing a uniform velocity, incorporates a $\ln\lambda$ term. In the Fraenkel interpretation, such a term does not imply a different asymptotic order.) By requiring the radial component of (6.6) to vanish, Saffman (1976) concluded that (see his (3.13))

$$F = \frac{4\pi}{\ln\frac{1}{\lambda} - \frac{1}{2}}. \tag{6.7}$$

Saffman's result is in contradiction with (4.8) and (5.7). This is hardly surprising: the tangential component of (6.6) does not vanish on the boundary. Indeed, it is impossible to find a value for F that would guarantee the vanishing of (6.6) on a specified circle. The heuristic argument of Saffman (1976) is inconsistent.

6.3. *Comparison with Liron & Blake (1981) and Jeffrey & Onishi (1981)*

Strictly speaking, (4.8) and (5.7) have been derived for $\lambda \ll 1$ with $1-\beta$ fixed. Clearly, both expressions break down when $1-\beta$ becomes comparable to λ: in that limit the particle may no longer be considered to be remote from the boundary. We emphasise, however, that (4.8) and (5.7) remain valid provided

$$\lambda \ll 1 - \beta \ll 1. \tag{6.8}$$

With $1-\beta$ small, the particle is close to the boundary on the membrane scale, whereby the boundary appears straight. With $\lambda \ll 1-\beta$, the particle separation from the wall is still large compared with its size. In that limit, (4.8) and (5.7) reduce to

$$F_\parallel = \frac{4\pi}{\ln\frac{2(1-\beta)}{\lambda} - 1}, \quad F_\perp = \frac{4\pi}{\ln\frac{2(1-\beta)}{\lambda}}, \tag{6.9}$$

respectively.

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We note that $\lambda/(1-\beta)$ represents the ratio – say ϵ – of the particle radius to the distance between the particle centre and the boundary. Approximations (6.9) thus read

$$F_{\parallel} = \frac{4\pi}{\ln\frac{2}{\epsilon} - 1}, \qquad F_{\perp} = \frac{4\pi}{\ln\frac{2}{\epsilon}}. \tag{6.10}$$

Making use of the known expressions for a Stokeslet near a straight wall (Liron & Blake 1981), it may be verified that these are indeed the drag expressions appropriate for a disk of radius ϵh at a distance h from a straight wall, in the limit $\epsilon \to 0$. Note that the membrane radius $\mathcal{R}$ completely disappeared from (6.10); this is consistent with its absence from the force scale used in the non-dimensionalisation process.

More generally, the drag expressions for the particle–wall geometry have been obtained by Jeffrey & Onishi (1981) for arbitrary ϵ. In the present notation,

$$F_{\parallel} = \frac{4\pi}{\ln\frac{1+(1-\epsilon^2)^{1/2}}{\epsilon} - (1-\epsilon^2)^{1/2}}, \qquad F_{\perp} = \frac{4\pi}{\ln\frac{1+(1-\epsilon^2)^{1/2}}{\epsilon}}. \tag{6.11}$$

It follows that (6.10) constitute overlapping expressions for the drag approximations in the small-particle limit ($\lambda \ll 1$, β fixed), as given by (4.8) and (5.7), and the drag approximations in the near-boundary limit ($\lambda \ll 1$, $\lambda/(1-\beta)$ fixed), as given by (6.11). By adding the two approximations and subtracting the overlapping expressions (6.10), we obtain the uniform approximations:

$$F_{\parallel} = \frac{4\pi}{\ln\frac{1-\beta^2}{\lambda} - 1} + \frac{4\pi}{\ln\frac{1-\beta+((1-\beta)^2-\lambda^2)^{1/2}}{\lambda} - \frac{((1-\beta)^2-\lambda^2)^{1/2}}{1-\beta}} - \frac{4\pi}{\ln\frac{2(1-\beta)}{\lambda} - 1}, \tag{6.12}$$

$$F_{\perp} = \frac{4\pi}{\ln\frac{1-\beta^2}{\lambda} - 1 + \beta^2} + \frac{4\pi}{\ln\frac{1-\beta+((1-\beta)^2-\lambda^2)^{1/2}}{\lambda}} - \frac{4\pi}{\ln\frac{2(1-\beta)}{\lambda}}. \tag{6.13}$$

These provide leading-order approximations for $\lambda \ll 1$ for the entire range of β values.

6.4. *Diffusivities*

In many situations interest lies in the diffusivity of the membrane-trapped particle. The theory of Brownian motion (Einstein 1956; Landau & Lifshitz 1987) provides the diffusivity tensor as the product of kT with the mobility tensor, k being the Boltzmann constant and T the absolute temperature.

In the general eccentric case, the translational mobility tensor is not necessarily anisotropic. Symmetry arguments, however, restrict it to the form

$$\frac{1}{\mu_s}\left[\hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}}\, M_{\parallel} + (\mathsf{I}_2 - \hat{\boldsymbol{\imath}}\hat{\boldsymbol{\imath}})M_{\perp}\right]. \tag{6.14}$$

Comparing with (2.2), it is tempting to write

$$M_{\parallel} = 1/F_{\parallel}, \qquad M_{\perp} = 1/F_{\perp}. \tag{6.15}$$

Justification of (6.15), however, requires some care due to hydrodynamic coupling between translation and rotation.

The hydrodynamic calculation in the paper addressed a resistance problem associated with the translation of a particle with a specified velocity. In addition to the hydrodynamic drag, the translation gives rise to a hydrodynamic torque. Dimensional and symmetry arguments (Happel & Brenner 1965) necessitate that the torque is of the form

$$\mu_s \lambda \mathcal{R} \mathcal{U} C(\beta, \lambda)\, \hat{\boldsymbol{\imath}} \times \hat{\boldsymbol{e}}. \tag{6.16}$$

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Here C is a dimensionless function of β and λ (which clearly vanishes for $\beta = 0$).

Consider now the comparable resistance problem associated with the rotation of the particle with angular velocity $\Omega \hat{\boldsymbol{k}}$. The particle experiences a hydrodynamic torque, say $-\mu_s \lambda^2 \mathcal{R}^2 \Omega G(\beta, \lambda) \hat{\boldsymbol{k}}$. In addition, it experiences a force of the form

$$\mu_s \lambda \mathcal{R} \Omega \tilde{C}(\beta, \lambda)\, \hat{\boldsymbol{j}}. \tag{6.17}$$

It follows from symmetry properties of the coupling tensor (Happel & Brenner 1965) that $\tilde{C} = C$.

In general, the grand mobility tensor is obtained by inverting the grand resistance tensor (Kim & Karrila 2005). For $\beta = 0$, where the coupling coefficient C vanishes, (6.14) is the inverse of (2.2); relations (6.15) then readily follow. In the general eccentric case, however, the translational mobility coefficients $M_\parallel$ and $M_\perp$ depend not only upon $F_\parallel$ and $F_\perp$, but also upon C and G. Our claim is that the latter dependence disappears as $\lambda \to 0$.

To show that, we consider the rotation problem. Unlike the translation problem, there is no Stokes paradox: the problem of 2-D rotation is well posed, with the Rotlet flow decaying like $1/r$. (At leading order, then, $G = 4\pi$.) With that decay rate, it is evident that C is of order λ. In the leading-order approximation, the hydrodynamic coupling does not affect the mobility. At that order, then, relations (6.15) hold.

The distinction between resistance and mobility calculations was not addressed by Saffman (1976). Indeed, the membrane geometry is isotropic in the concentric case, as well as in the original unbounded problem considered by Saffman (1976). The solution of the translational drag problem then immediately provides the associated mobility.

7. Concluding remarks

The three-dimensional problem of sphere diffusion inside a spherical cavity, motivated by transport processes within a cell, has received significant attention in the fluids community (Aponte-Rivera & Zia 2016). In this paper, we have considered the 2-D analogue. Motivated by Saffman's calculation, we have analysed the translation of a circular disk in a viscous membrane which is bounded by a circular boundary, considering the general eccentric case. Symmetry arguments reduce the problem to the calculation of two drag coefficients, corresponding to radial and transverse motion. Both coefficients depend upon two geometric parameters, the particle–membrane eccentricity and the ratio of particle size to membrane size. We have focused upon the asymptotic limit where the latter ratio is small. Analysing this singular limit using matched asymptotic expansions has provided closed-form approximations for the radial and transverse coefficients. When degenerated to the concentric case, our results reveal an oversight in Saffman's drag approximation. The flaw in Saffman's argument has been discussed in detail.

The predictions of the zero-thickness membrane model employed herein immediately apply to a more realistic membrane model of an anisotropic viscous sheet of finite thickness, say h, provided the surface viscosity μ_s is interpreted as product of h with the in-plane sheet viscosity. The disk then corresponds to a sheet-trapped cylinder, also of thickness h. In fact, the underlying premise of large Boussinesq number (i.e. negligible bulk stresses) implies that the latter assumption of a cylindrical shape may be relaxed, allowing the particle to protrude into the adjacent liquid.

We emphasise that our asymptotic calculation, being aimed at a leading-order approximation for the hydrodynamic drag, does not provide 'finite-size' corrections. Indeed, these are tantamount to algebraically small errors. Superficially, this may appear surprising: in three dimensions, incorporation of the boundary effects on the

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hydrodynamic drag is only required if one seeks to calculate these corrections (which are $O(\lambda)$, due to the decay rate associated with a Stokeslet). Recall, however, that the problem of a particle in an unbounded domain is well-posed in three dimensions. In the present 2-D problem, accounting for the boundary is necessary for obtaining the leading-order approximation for the drag (in the Fraenkel interpretation).

As explained by Saffman (1976), the 2-D analysis of a bounded membrane is applicable when the membrane size $\mathcal{R}$ is small compared with the Saffman–Delbrück distance, provided by the ratio of the membrane viscosity to the bulk viscosity. The present analysis illustrates what may be the simplest problem where a 2-D Stokes-flow description is adequate. A related scenario, studied by Henle & Levine (2010), is that of a (spherical or cylindrical) membrane that 'closes on itself'. The 2-D Stokes-flow problem becomes well-posed in an infinite membrane when the particle of interest is forced to move relative to a fixed bed of immobilised particles – a standard model of plasma membranes (Bussell, Koch & Hammer 1995; Dodd *et al.* 1995). Another set-up where the 2-D Stokes-flow problem is well-posed in an infinite membrane, studied recently by Yariv & Peng (2024), is that of the mutual interaction between a particle pair. In all these distinct configurations, the hydrodynamic drag on a membrane-trapped particle exhibits a logarithmic dependence upon the ratio of particle size to the appropriate 'cut-off' distance – say membrane size, Brinkman screening length or particle–pair separation. This dependence stems from the fundamental form of 2-D Stokes flow about a single particle which experiences a net hydrodynamic force.

Declaration of interests. The authors report no conflict of interest.

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