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The translational and rotational drag on a cylinder moving in a membrane

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The translational and rotational drag coefficients for a cylinder undergoing uniform translational and rotational motion in a model lipid bilayer membrane is calculated from the appropriate linearized Navier–Stokes equations. The calculation serves as a model for the lateral and rotational diffusion of membrane-bound particles and can be used to infer the 'microviscosity' of the membrane from the measured diffusion coefficients. The drag coefficients are obtained exactly using dual integral equation techniques. The region of validity of an earlier asymptotic solution obtained by Saffman (1976) is elucidated.

1. Introduction

The lateral and rotational motion of lipids and proteins in biological membranes plays a crucial role in many life processes. For example, the clustering of membrane-bound protein receptors directly mediates many immunological and hormonal responses (Catt & Dufau 1977). The use of fluorescent probes and NMR techniques enables the measurement of diffusion coefficients of these membrane-bound particles to be made (Edidin 1974). Using the Einstein relations

$$\lambda = kT/D$$

the drag coefficients λ_T and λ_R can be computed from the measured translational and rotational diffusion coefficients D_T and D_R. Biophysicists have variously used two- and three-dimensional Stokes-law expressions for λ_T and λ_R to extract information about particle size and the local membrane viscosity ('microviscosity'). These order-of-magnitude calculations have revealed microviscosities of the order of 1–10 P when the lipid material should have a bulk viscosity of $\sim 0{\cdot}3$ P. This discrepancy has given rise in the literature to considerable speculation and confusion (Saffman & Delbrück 1975). This is compounded by the possible existence of long-time tails in the velocity autocorrelation function in two dimensions, which has led to the conjecture that there is no hydrodynamics in two dimensions and that the concept of a two-dimensional viscosity is inadmissible (Berne & Forster 1971).

Even if one ignores this work, the drag on a translating particle in two-dimensional hydrodynamics is essentially nonlinear in the velocity (Batchelor 1967). The existence of nonlinear drag forces would then invalidate the Einstein relation and render meaningless the inference of the drag coefficient from diffusion coefficients. The nonlinearity of the drag force in two-dimensional hydrodynamics has its origin in the inability of the linearized Navier–Stokes equations to simultaneously satisfy the boundary conditions imposed on the flow field of the system at the particle surface and at infinity.

The important point, as developed by Saffman (1976), is that in the real world a two-dimensional membrane system is surrounded by a three-dimensional fluid medium – the inside and outside of the cellular structure that the membrane bounds. The two-dimensional motion of a membrane-bound particle induces flow fields in the surrounding medium which exert reaction forces on the membrane. As explained later, these forces provide a body force on the membrane and so permit a solution to the linearized Navier–Stokes equations in the membrane which can satisfy all the boundary conditions simultaneously. In this essentially three-dimensional system, there is therefore a linear term in the hydrodynamic drag on a translating membrane-bound particle. Further, in a diffusion experiment the velocity is so small that the nonlinear terms in the Navier–Stokes equations can be totally neglected.

The most striking feature of Saffman's analysis was his finding that the translational drag on a membrane-bound object is not well described by a linear Stokes-law expression. He showed that the translational drag problem was a singular perturbation problem and that the drag coefficient depends nonlinearly on the particle dimensions and membrane viscosity. This singular behaviour is a function of the two-dimensional nature of the membrane as a hydrodynamic system.

It is therefore of paramount importance to compute the drag coefficient for some canonical problems to understand the intricate relationship of membrane viscosity, external medium viscosity and particle size imposed by the constraints of membrane-bound motions. Saffman (1976) has calculated the leading-order behaviour of the translational and rotational drag coefficients of membrane-bound cylindrical objects valid for large membrane viscosities. The purpose of the present work is to extend that analysis to intermediate values of membrane viscosity and to elucidate the region of validity of the limiting asymptotic forms. The original problem as posed by Saffman generates dual integral equation sets which are amenable to exact solution as outlined below.

2. Formulation of the translation problem

We wish to calculate the drag force acting on a cylinder of radius a and height h constrained to move laterally with constant velocity $\mathbf{U} = U\hat{\mathbf{x}}$ in a membrane of viscosity η, bounded above and below by fluids of viscosity μ_1 and μ_2 respectively (see figure 1). The membrane film has thickness h and its properties will be described more fully below. In this section, we set up a boundary-value problem, the solution of which describes the flow fields inside and outside the membrane and we evaluate the drag force on the cylinder in terms of these flow fields.

(a) *The exterior flow field*

In the region $z > 0$, the velocity field $\mathbf{u}(r, \phi, z)$ (where (r, ϕ, z) are the usual cylindrical polar co-ordinates with ϕ measured from the $\hat{\mathbf{x}}$ direction) satisfies

$$\mu_1 \nabla^2 \mathbf{u} - \nabla p = 0, \quad \nabla . \mathbf{u} = 0, \tag{2.1), (2.2}$$

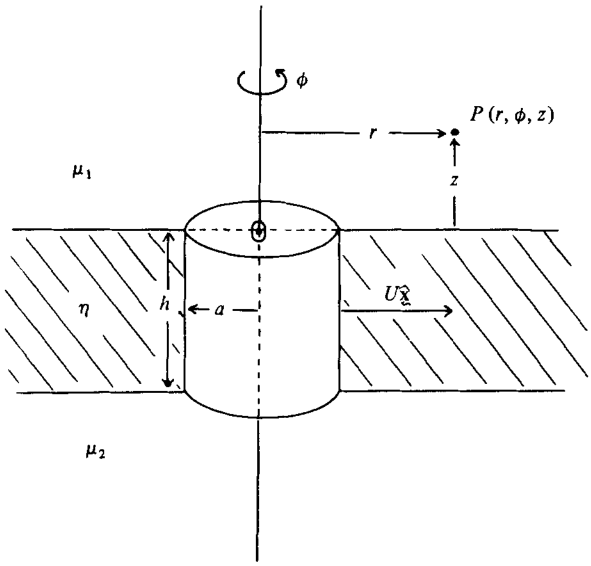

FIGURE 1. Model membrane system comprising a cylindrical object of radius a embedded in a film of thickness h and viscosity η. The half-spaces $z > 0$ and $z < -h$ are filled with fluids of viscosities μ_1 and μ_2 respectively. The system is characterized by the dimensionless constant

$$\epsilon = \left(\frac{a}{h}\right)\left(\frac{\mu_1+\mu_2}{\eta}\right).$$

the usual equations for the slow motion of an incompressible fluid. The fluid is at rest at infinity, i.e.

$$\lim_{(r^2+z^2)^{\frac{1}{2}}\to\infty} \begin{Bmatrix} \mathbf{u}(r,\phi,z) \\ p(r,\phi,z) \end{Bmatrix} = 0. \tag{2.3}$$

The boundary conditions on the plane are

$$\mathbf{u}(r,\phi,0) = \mathbf{U} \quad (0 < r < a), \tag{2.4}$$

$$u_z(r,\phi,0) = 0 \quad (0 < r < \infty). \tag{2.5}$$

Following Saffman (1976), a solution exists of the form

$$u_r(r,\phi,z) = \tfrac{1}{2}U\cos\phi[S(r,z)+D(r,z)], \tag{2.6}$$

$$u_\phi(r,\phi,z) = \tfrac{1}{2}U\sin\phi[S(r,z)-D(r,z)], \tag{2.7}$$

$$u_z(r,\phi,z) = \tfrac{1}{2}U\cos\phi[zP(r,z)], \tag{2.8}$$

$$p(r,\phi,z) = \mu_1 U\cos\phi[P(r,z)], \tag{2.9}$$

where

$$S(r,z) = \int_0^\infty dk\, J_2(kr)\left[s(k) - \frac{zk}{2}(s(k)-d(k))\right]e^{-kz}, \tag{2.10}$$

$$D(r,z) = \int_0^\infty dk\, J_0(kr)\left[d(k) + \frac{zk}{2}(s(k)-d(k))\right]e^{-kz}, \tag{2.11}$$

$$P(r,z) = -\int_0^\infty dk\, k J_1(kr)\,[s(k)-d(k)]\,e^{-kz}. \tag{2.12}$$

The boundary condition (2.5) is automatically satisfied and (2.4) becomes

$$\left.\begin{aligned}\int_0^\infty dk\, J_0(kr)\, d(k) &= 2, \qquad (2.13)\\ \int_0^\infty dk\, J_2(kr)\, s(k) &= 0, \qquad (2.14)\end{aligned}\right\} \quad r < a.$$

These integral equations constitute the first two of a set of four simultaneous dual-integral equations to be solved for the unknown functions $s(k)$ and $d(k)$. The other two are derived by considering the flow field in the membrane.

(b) *The membrane flow fields*

The membrane $(-h < z < 0)$ cannot, because of its molecular nature, be considered as a simple fluid film. To maintain the integrity of the membrane, composed as it is of inextensible long-chain hydrocarbons, we must require that all velocities within it can have no z variation. This fact, coupled with the adoption of the 'stick' boundary condition at $z = 0$ and $z = -h$, implies that, throughout the membrane, the velocity field $\mathbf{u}^{\mathrm{M}}$ is given by

$$\mathbf{u}^{\mathrm{M}}(r, \phi, z) = \mathbf{u}(r, \phi, 0) \quad (0 > z > -h, \quad r > a) \tag{2.15}$$

where $\mathbf{u}(r, \phi, 0)$ is the exterior flow field evaluated at $z = 0$. The exterior flow field $\mathbf{u}(z \geqslant 0)$ exerts a traction $\mathbf{F}_1$ on the membrane, where

$$\mathbf{F}_1(r, \phi) = \hat{\mathbf{z}} \cdot \boldsymbol{\sigma}(r, \phi, z)|_{z=0} \tag{2.16}$$

and $\boldsymbol{\sigma}$ is the stress tensor in the exterior flow field. Evaluating $\boldsymbol{\sigma}$ from its definition in terms of the exterior flow field, we have that

$$F_{1z} = 0, \quad F_{1r} = \mu_1 \frac{\partial u_r}{\partial z}\bigg|_{z=0}, \quad F_{1\phi} = \mu_1 \frac{\partial u_\phi}{\partial z}\bigg|_{z=0}. \tag{2.17}$$

If the membrane interior behaved as a simple liquid, it would be sufficient to balance $\mathbf{F}_1$ with the surface traction exerted by the membrane flow field on the half-space $z > 0$. This traction is zero, however, since no z variation in $\mathbf{u}^{\mathrm{M}}$ is permitted. The force which the membrane exerts on the half-space $z > 0$ has its origin in the mechanical stresses set up in the membrane to prevent this z variation. Such forces are not in the scope of the present paper and need not concern us further since we may regard this force balance at $z = 0$ to occur automatically. The pressure $\mathbf{F}_1$ must then be regarded as a body force $\mathbf{F}_1/h$ per unit volume of the membrane in so far as it determines the flow fields in the membrane. When the pressure $\mathbf{F}_2$ exerted by the lower half-space $(z < -h)$ is added, the Navier–Stokes equation for the membrane flow field is

$$\eta \nabla^2 \mathbf{u}^{\mathrm{M}} - \nabla p^{\mathrm{M}} + (\mathbf{F}_1 + \mathbf{F}_2)/h = 0. \tag{2.18}$$

The assumption of incompressibility of the membrane, viz.

$$\nabla \cdot \mathbf{u}^{\mathrm{M}} = 0, \tag{2.19}$$

yields a subsidiary condition on the solution. Inserting (2.15) into (2.19) and using the general solution (2.6)–(2.12), we obtain a third integral equation for the unknown functions $s(k)$, $d(k)$, viz.

$$\int_0^\infty dk\, k\, J_1(kr)\, (s(k) - d(k)) = 0 \quad (r > a). \tag{2.20}$$

The fourth integral equation is obtained by taking the curl of (2.18) to eliminate the membrane pressure p^{M}. Again using (2.15) and (2.6)–(2.12), we obtain, after a little algebra,

$$\int_0^\infty dk\, k^2\left(k+\frac{\epsilon}{a}\right) J_1(kr)\,(s(k)+d(k)) = 0 \quad (r > a), \tag{2.21}$$

where

$$\epsilon = \left(\frac{a}{h}\right)\left(\frac{\mu_1+\mu_2}{\eta}\right). \tag{2.22}$$

Equations (2.13), (2.14), (2.20), (2.21) constitute a set of simultaneous dual integral equations for the functions $s(k)$ and $d(k)$. Since they are of non-standard type (see Sneddon 1966), we should first see what information we require of the functions $s(k)$ and $d(k)$. We are concerned here with the calculation of the drag force on the cylinder and we require from $s(k)$ and $d(k)$ only such information as is necessary to determine this force.

(c) *The drag force on the cylinder*

The force per unit area on the curved wall of the cylinder is given by

$$\mathbf{f} = \hat{\mathbf{r}}\,.\,\boldsymbol{\sigma}^{\mathrm{M}}\big|_{r=a}, \tag{2.23}$$

where $\boldsymbol{\sigma}^{\mathrm{M}}$ is the hydrodynamic stress tensor in the membrane. The relevant components are

$$\sigma_{rz}^{\mathrm{M}} = 0, \tag{2.24}$$

$$\sigma_{rr}^{\mathrm{M}} = -p^{\mathrm{M}} + 2\eta\frac{\partial u_r^{\mathrm{M}}}{\partial r}, \tag{2.25}$$

$$\sigma_{r\phi}^{\mathrm{M}} = \eta\left[\frac{1}{r}\frac{\partial u_r^{\mathrm{M}}}{\partial \phi}+\frac{\partial u_\phi^{\mathrm{M}}}{\partial r}-\frac{u_\phi^{\mathrm{M}}}{r}\right]. \tag{2.26}$$

To obtain an expression for the membrane pressure p^{M}, we use the symmetry of the problem to write

$$p^{\mathrm{M}}(r,\phi,z) = \eta U P^{\mathrm{M}}(r)\cos\phi \tag{2.27}$$

and, substituting this form into the $\hat{\boldsymbol{\phi}}$ component of the membrane Navier–Stokes equation (2.18), we obtain

$$P^{\mathrm{M}}(r) = \frac{1}{2}\int_0^\infty dk\left(k+\frac{\epsilon}{a}\right)\{kr\,J_2(kr)\,(s(k)+d(k)) - J_1(kr)\,(3d(k)-s(k))\} \tag{2.28}$$

with the help of (2.6)–(2.12).

The total force $\mathbf{F}_{\mathrm{w}}$ on the cylindrical walls is therefore

$$\mathbf{F}_{\mathrm{w}} = ha\int_0^{2\pi} d\phi\,[\sigma_{rr}^{\mathrm{M}}\hat{\mathbf{r}}+\sigma_{r\phi}^{\mathrm{M}}\hat{\boldsymbol{\phi}}]_{r\to a^+}. \tag{2.29}$$

With the aid of (2.6)–(2.12) and (2.25), (2.26), we may perform the ϕ integration to obtain

$$\mathbf{F}_{\mathrm{w}} = -\frac{\pi}{2}\eta ha\,\mathbf{U}\int_0^\infty dk\left\{\left(k+\frac{\epsilon}{a}\right)kr\,J_2(kr)\,(s(k)+d(k)) - \frac{\epsilon}{a}J_1(kr)\,(3d(k)-s(k))\right\}\bigg|_{r\to a^+}. \tag{2.30}$$

In a similar fashion, it is straightforward to show that the force $\mathbf{F}_{\mathrm{T}}$ exerted on the top of the cylinder is

$$\mathbf{F}_{\mathrm{T}} = -\frac{\pi}{2}\mu_1 a\mathbf{U}\int_0^\infty dk\,J_1(kr)\,(3d(k)-s(k))\bigg|_{r\to a^-}. \tag{2.31}$$

The total drag force on the cylinder is

$$\mathbf{F}_\mathrm{D} = \mathbf{F}_\mathrm{w} + \mathbf{F}_\mathrm{T} + \mathbf{F}_\mathrm{B} \tag{2.32}$$

$$= -\lambda_\mathrm{T}\mathbf{U} \tag{2.33}$$

where $\mathbf{F}_\mathrm{B}$ is the drag on the bottom of the cylinder and

$$\lambda_\mathrm{T} = \frac{\pi}{2}\eta h \int_0^\infty dk\{(ka+\epsilon)\,ka^+ J_2(ka^+)\,(s(k)+d(k)) - \epsilon J_1(ka^+)\,(3d(k)-s(k)) + \epsilon J_1(ka^-)\,(3d(k)-s(k))\}, \tag{2.34}$$

where we have adopted the notation that

$$\int_0^\infty dk f(k, a^\pm) = \lim_{r\to a^\pm}\int_0^\infty dk f(k,r). \tag{2.35}$$

It is because of a possible jump discontinuity in the integral

$$\int_0^\infty dk\, J_1(kr)\,(3d(k)-s(k))$$

at $r = a$ that we have not cancelled the last two terms of (2.34). We introduce the notation

$$\Delta\int_0^\infty dk f(k,r) = \lim_{r\to a^+}\int_0^\infty dk f(k,r) - \lim_{r\to a^-}\int_0^\infty dk f(k,r)$$

and write the drag coefficient as

$$\lambda_\mathrm{T} = \frac{\pi\eta h}{2}\left[\int_0^\infty dk\,(ka+\epsilon)\,(ka)\,J_2(ka^+)\,(s(k)+d(k)) - \epsilon\Delta\int_0^\infty dk\,J_1(kr)\,(3d(k)-s(k))\right]. \tag{2.36}$$

3. Solution

The set of simultaneous dual integral equations (2.13), (2.14), (2.20), (2.21) are not in the standard form (Sneddon 1966). They can, however, be reduced to a single integral equation which can be solved to yield the relevant information needed to calculate λ_T via (2.36).

We introduce the scaled variables

$$x = \frac{r}{a}, \quad u = ak \tag{3.1}$$

and define new functions $s'(u)$ and $d'(u)$ by

$$s(k) = us'(u), \quad d(k) = ud'(u). \tag{3.2}$$

In the notation of Sneddon (1966), the dual integral equations become

$$\left.\begin{aligned} S_{1,0}s'(x) &= 0, \\ S_{0,0}d'(x) &= 2a, \end{aligned}\right\}\quad x < 1; \qquad \begin{cases}(3.3)\\(3.4)\end{cases}$$

$$\left.\begin{aligned} S_{1,-1}s'(x) &= S_{1,-1}d'(x), \\ \epsilon S_{\frac{3}{2},-2}(s'+d')(x) &= -\frac{2}{x}S_{2,-3}(s'+d')(x), \end{aligned}\right\}\quad x > 1; \qquad \begin{matrix}(3.5)\\(3.6)\end{matrix}$$

where the modified Hankel transform operator $S_{\eta,\alpha}$ is defined by

$$S_{\eta,\alpha} f(x) = 2^{\alpha} x^{-\alpha} \int_0^\infty dt\, t^{1-\alpha} J_{2\eta+\alpha}(xt) f(t). \tag{3.7}$$

To proceed we define a function $Q(x)$ for all x by

$$Q(x) = S_{0,0} d'(x). \tag{3.8}$$

From (3.4), we have
$$Q(x) = 2a \quad (x < 1). \tag{3.9}$$

Application of the inverse operator (Sneddon 1966)

$$S_{\eta,\alpha}^{-1} = S_{\eta+\alpha,-\alpha} \quad (2\eta + \alpha \geqslant -\tfrac{1}{2}) \tag{3.10}$$

to (3.8) yields
$$d'(u) = S_{0,0} Q(u). \tag{3.11}$$

We have $d'(u)$ defined in terms of the function $Q(x)$. We now proceed to determine $s'(u)$. Substituting (3.11) in (3.5), we have

$$S_{1,-1} s'(x) = K_{1,-1} Q(x) \quad (x > 1), \tag{3.12}$$

where we use the result
$$S_{\eta,\alpha} S_{\eta+\alpha,\beta} = K_{\eta,\alpha+\beta}. \tag{3.13}$$

The properties of the Erdélyi–Kober operators $K_{\eta,\alpha}$ and $I_{\eta,\alpha}$ are to be found in Sneddon (1966). When a particular property is required for our present purposes, it will be quoted without comment and a full discussion of it can be found in Sneddon's book.

Application of the operator $I_{1,-1}$ to (3.3) yields

$$S_{1,-1} s'(x) = 0 \quad (x < 1) \tag{3.14}$$

where we make use of the equation

$$I_{\eta+\alpha,\beta} S_{\eta,\alpha} = S_{\eta,\alpha+\beta}. \tag{3.15}$$

Equations (3.12) and (3.14) constitute a single integral equation for $s'(u)$

$$S_{1,-1} s'(x) = \begin{cases} 0 & (x < 1), \\ K_{1,-1} Q(x) & (x > 1). \end{cases} \tag{3.16}$$

Application of the inverse operator $S_{0,1}$ yields the desired expression

$$s'(u) = S_{0,1} \left\{ \begin{matrix} 0, & x < 1 \\ K_{1,-1} Q(x), & x > 1 \end{matrix} \right\} (u). \tag{3.17}$$

Consider the function $\chi(x)$ defined by

$$\chi(x) = K_{1,-1} Q(x) \tag{3.18}$$

for all x. We employ the result that

$$K_{1,-1} f(x) = -\frac{x}{2} \frac{df(x)}{dx}. \tag{3.19}$$

Since $Q(x)$ is constant for $x < 1$ (equation (3.9)) we see that

$$\chi(x) = 0 \quad (x < 1). \tag{3.20}$$

If the function $Q(x)$ has a jump discontinuity at $x = 1$, we define

$$\Delta Q = \lim_{\delta\to 0^+} \{Q(1+\delta) - Q(1-\delta)\}. \tag{3.21}$$

The operator $K_{1,-1}$ applied to $Q(x)$ at $x = 1$ will therefore produce a term $-\frac{1}{2}\Delta Q\delta(x-1)$ in $\chi(x)$. It follows immediately that

$$K_{1,-1}Q(x) + \frac{\Delta Q}{2}\delta(x-1) = \begin{cases} 0 & (x<1), \\ K_{1,-1}Q(x) & (x>1). \end{cases} \tag{3.22}$$

Equation (3.17) becomes

$$s'(u) = S_{0,0}Q(u) + \Delta Q\frac{J_1(u)}{u}, \tag{3.23}$$

where we use the results

$$S_{\eta,\alpha}K_{\eta+\alpha,\beta} = S_{\eta,\alpha+\beta} \tag{3.24}$$

and

$$S_{\eta,\alpha}\{\delta(x-1)\}(u) = 2^{\alpha}u^{-\alpha}J_{2\eta+\alpha}(u). \tag{3.25}$$

We have, therefore,

$$s'(u) = d'(u) + \Delta Q\,\frac{J_1(u)}{u}. \tag{3.26}$$

The result of Saffman (1976), *viz.*

$$s'(u) = d'(u) \tag{3.27}$$

(in our notation), will follow only if ΔQ is zero. As we shall show, this is indeed the case.

To proceed, we define a function $\psi(u)$ by

$$d'(u) = \frac{4}{\pi}\left(a + \frac{\Delta Q}{4}\right)\psi(u) - \frac{\Delta Q}{2}\frac{J_1(u)}{u}. \tag{3.28}$$

It follows from (3.26) that

$$s'(u) = \frac{4}{\pi}\left(a + \frac{\Delta Q}{4}\right)\psi(u) + \frac{\Delta Q}{2}\frac{J_1(u)}{u} \tag{3.29}$$

and

$$s'(u) + d'(u) = \frac{8}{\pi}\left(a + \frac{\Delta Q}{4}\right)\psi(u). \tag{3.30}$$

Thus $s'(u)$ and $d'(u)$ are determined once $\psi(u)$ is known. We now obtain a single integral equation for the function $\psi(u)$. Substituting (3.28) into (3.4), we obtain

$$S_{0,0}\psi(x) = \tfrac{1}{2}\pi \quad (x<1) \tag{3.31}$$

with the aid of the definition (3.7) and the result (Abramowitz & Stegun 1965)

$$\int_0^\infty du\, J_\mu(au)J_{\mu-1}(bu) = \begin{cases} \dfrac{1}{b}\left(\dfrac{b}{a}\right)^{\mu}, & 0<b<a, \\ \dfrac{1}{2b}, & 0<b=a, \\ 0, & b>a>0. \end{cases} \tag{3.32}$$

Substituting (3.29) into (3.3), a similar manipulation yields

$$S_{1,0}\psi(x) = 0 \quad (x<1). \tag{3.33}$$

Substituting (3.30) into (3.6) yields

$$\epsilon S_{\frac{3}{2},-2}\psi(x) = -\frac{2}{x}S_{2,-3}\psi(x) \quad (x>1). \tag{3.34}$$

We choose to solve (3.31) and (3.34) as a single pair of dual integral equations whose solution must also satisfy (3.33) as a subsidiary condition. A straightforward application of the Erdélyi–Kober operators together with (3.10) yields the solution of the dual integral equation pair

$$\psi(u) = S_{-\frac{1}{2},\frac{1}{2}}\left\{\begin{matrix} \dfrac{\pi^{\frac{1}{2}}}{2}, & x < 1 \\ \dfrac{-2}{\epsilon x} S_{\frac{1}{2},-\frac{1}{2}}\psi(x), & x > 1 \end{matrix}\right\}(u). \tag{3.35}$$

It is easily demonstrated that (3.35) satisfies (3.33) by direct substitution. Using the definition of the $S_{\eta,\alpha}$ operator, a little algebra enables us to write (3.35) in a more conventional form, viz.

$$u(u+\epsilon)\psi(u) = \frac{\epsilon \sin u}{u} + \frac{1}{\pi}\int_0^\infty dz\, z^2\psi(z)\left\{\frac{\sin(u+z)}{u+z} + \frac{\sin(u-z)}{u-z}\right\}. \tag{3.36}$$

It is interesting to note that the reduction of the problem to the solution of (3.36) has implicitly assumed that ϵ is non-zero. That this is so can be seen by sending ϵ to zero in the original equation (3.34). The techniques used above to obtain equation (3.36) cannot be applied to the resultant pair of dual integral equations. We are dealing, therefore, with a singular perturbation problem in the classical sense.

Before we proceed with the solution of (3.36) let us prove Saffman's 'conjecture' that

$$\Delta Q = 0.$$

From (3.8), we have that

$$Q(1^+) = \frac{4}{\pi}\left(a + \frac{\Delta Q}{4}\right)\int_0^\infty du\, uJ_0(1^+u)\,\psi(u) \tag{3.37}$$

and

$$Q(1^-) = \frac{4}{\pi}\left(a + \frac{\Delta Q}{4}\right)\int_0^\infty du\, uJ_0(1^-u)\,\psi(u) - \frac{\Delta Q}{2}, \tag{3.38}$$

where we have substituted (3.28) for $d'(u)$ and used the result (3.32). Subtracting,

$$\Delta Q = \frac{8}{\pi}\left(a + \frac{\Delta Q}{4}\right)\Delta\int_0^\infty du\, uJ_0(ux)\,\psi(u), \tag{3.39}$$

where we modify our previous convention, *viz.*

$$\Delta\int du\, f(u,x) = \lim_{\delta\to 0^+}\left\{\int du\, f(u, 1+\delta) - \int du\, f(u, 1-\delta)\right\}. \tag{3.40}$$

The function

$$\int_0^\infty du\, u\psi(u)\, J_\mu(xu)$$

can be shown to be a continuous function of x for $\mu \geqslant 0$, i.e.

$$\Delta\int_0^\infty du\, u\psi(u)\, J_\mu(xu) = 0. \tag{3.41}$$

Briefly, from Lebesgue's dominated convergence theorem (Apostol 1974), it follows that it is sufficient, in this particular case, to require that

$$\int_0^\infty du\, u|\psi(u)|$$

exists for continuity of the integral across $x = 1$. It is straightforward to show the existence of

$$\int_0^\infty du\, u\,|\psi(u)|$$

from the integral equation (3.36) for $\psi(u)$ (see Hughes 1980 for details). From (3.41) and (3.39), it follows that ΔQ is zero. Equations (3.28) and (3.29) become, therefore,

$$d'(u) = s'(u) = \frac{4a}{\pi}\psi(u). \tag{3.42}$$

Using these results, the drag coefficient λ_T, given by (2.36), can be written in the form

$$\lambda_{\mathrm{T}} = 4\pi(\mu_1+\mu_2)\,a\Lambda_{\mathrm{T}}(\epsilon), \tag{3.43}$$

where

$$\Lambda_{\mathrm{T}}(\epsilon) = \frac{1}{\pi\epsilon}\int_0^\infty du\, u^2(u+\epsilon)\,J_2(u1^+)\,\psi(u) \tag{3.44}$$

is the reduced drag coefficient. Using the expansion (Abramowitz & Stegun 1965)

$$\frac{\sin\,(u^2+v^2-2uv\cos\theta)^{\frac{1}{2}}}{(u^2+v^2-2uv\cos\theta)^{\frac{1}{2}}} = \sum_{m=0}^{\infty}(2m+1)j_m(u)j_m(v)\,P_n(\cos\theta), \tag{3.45}$$

the integral equation (3.36) can be written as

$$u(u+\epsilon)\,\psi(u) = \epsilon j_0(u) + \frac{2}{\pi}\sum_{m=0}^{\infty}(4m+1)\,\psi_m j_{2m}(u), \tag{3.46}$$

where we define

$$\psi_m = \int_0^\infty du\, u^2\psi(u)\,j_{2m}(u). \tag{3.47}$$

Multiplying (3.46) by $uJ_2(u1^+)$ and integrating over u, we obtain

$$\Lambda_{\mathrm{T}}(\epsilon) = \frac{2}{\pi}\left(1+\frac{2}{\pi}\frac{\psi_0}{\epsilon}\right), \tag{3.48}$$

where we make use of the result

$$\int_0^\infty du\, uj_{2m}(u)\,J_2(u1^+) = 2\delta_{m,0} \tag{3.49}$$

which follows from the Weber–Schafheitlin integral (Abramowitz & Stegun 1965).

Therefore, the reduced drag coefficient $\Lambda_{\mathrm{T}}(\epsilon)$ can be obtained directly from a knowledge of the coefficient ψ_0 defined by (3.47). The coefficients ψ_m can be obtained from the equation (3.46) by multiplying by $uj_{2l}(u)/(u+\epsilon)$ and integrating over u. We obtain the infinite set of equations

$$\frac{\delta_{l,0}}{\epsilon\Lambda_{\mathrm{T}}(\epsilon)} = \int_0^\infty \frac{du\, j_{2l}(u)}{u+\epsilon}\left\{j_0(u)+\frac{4}{\pi^2\epsilon\Lambda_{\mathrm{T}}(\epsilon)}\sum_{m=1}^{\infty}(4m+1)\,\psi_m(\epsilon)j_{2m}(u)\right\} \quad (l = 0,1,2,\ldots), \tag{3.50}$$

using the result (Watson 1944)

$$\int_0^\infty du\, j_{2l}(u)\,j_{2m}(u) = \frac{\pi}{2}\frac{\delta_{l,m}}{4m+1}. \tag{3.51}$$

It proves convenient to define new coefficients $\chi_m(\epsilon)$ by

$$\psi_m(\epsilon) = \frac{\pi^2 \epsilon \Lambda_T(\epsilon)}{4(4m+1)}\{(-1)^m (4m+1)[P_{2m}(0)]^2 + \epsilon \chi_m(\epsilon)\} \quad (m = 1, 2, \dots), \tag{3.52}$$

where $P_\nu(x)$ is the Legendre function of degree ν. From (3.50), we obtain from the $l = 0$ equation

$$\frac{1}{\epsilon \Lambda_T(\epsilon)} = T(\epsilon) + \epsilon \sum_{m=1}^{\infty} t_m(\epsilon)\, \chi_m(\epsilon), \tag{3.53}$$

where
$$T(\epsilon) = \int_0^\infty du \frac{j_0(u)\, J_0(u)}{u+\epsilon} \tag{3.54}$$

and
$$t_m(\epsilon) = \int_0^\infty du \frac{j_0(u)\, j_{2m}(u)}{u+\epsilon}. \tag{3.55}$$

For $l > 0$, we obtain, from (3.50) and (3.52)

$$\int_0^\infty du \frac{j_{2l}(u)}{u+\epsilon}\left\{J_0(u) + \epsilon \sum_{m=1}^{\infty} \chi_m(\epsilon) j_{2m}(u)\right\} = 0 \quad (l = 1, 2, \dots). \tag{3.56}$$

In deriving (3.53) and (3.56) we use the result (Abramowitz & Stegun 1965)

$$J_0(u(1-x^2)^{\frac{1}{2}}) = \sum_{m=0}^{\infty} (-1)^m (4m+1)\, P_{2m}(0)\, P_{2m}(x) j_{2m}(u). \tag{3.57}$$

To simplify (3.56), we multiply the $(l-1)$th equation by $-\epsilon^2/(4l+1)(4l-1)$, the lth equation by $1 - 2\epsilon^2/(4l+3)(4l-1) - \epsilon^2/(4l+1)(4l+3)$ and the $(l+1)$th equation by $-\epsilon^2/(4l+1)(4l+3)$ and add to obtain the result

$$\sum_{m=1}^{\infty} (t'_{lm} - \epsilon t''_{lm})\, \chi_m(\epsilon) = T'_l - \frac{\delta_{l,1}}{15 \Lambda_T(\epsilon)} \quad (l = 1, 2, \dots), \tag{3.58}$$

where (Watson 1944)

$$t'_{l,m} = \int_0^\infty \frac{du}{u} j_{2l}(u) j_{2m}(u) \tag{3.59}$$

$$= \frac{(-1)^{l+m+1}}{2(4(l-m^2)-1)\,(m+l)\,(m+l+1)}, \tag{3.60}$$

$$t''_{l,m} = \int_0^\infty \frac{du}{u^2} j_{2l}(u) j_{2m}(u)$$

$$= \frac{\pi}{2}\left\{\frac{\delta_{m,l-1}}{(4l-3)(4l-1)(4l+1)} + \frac{2\delta_{m,l}}{(4l-1)(4l+1)(4l+3)} + \frac{\delta_{m,l+1}}{(4l+1)(4l+3)(4l+5)}\right\} \tag{3.61}$$

and
$$T'_l = \int_0^\infty \frac{du}{u^2} j_{2l}(u)\, J_0(u) \tag{3.62}$$

$$= \left(\frac{3(-1)^{l+1}}{32}\right)\left[\frac{\Gamma(l-\frac{1}{2})}{\Gamma(l+2)}\right]^2 \tag{3.63}$$

are special cases of the Weber–Schafheitlin integral.

In deriving (3.58), we use the result

$$\frac{-\epsilon^2 j_{2l-2}(u)}{(4l+1)(4l-1)}+\left[1-\frac{2\epsilon^2}{(4l-1)(4l+3)}\right]j_{2l}(u)-\frac{\epsilon^2 j_{2l+2}(u)}{(4l+1)(4l+3)}=\left[\frac{u^2-\epsilon^2}{u^2}\right]j_{2l}(u) \quad (3.64)$$

which follows from the recurrence relation

$$j_{n-1}(u)+j_{n+1}(u)=\frac{2n+1}{u}j_n(u) \quad (3.65)$$

for the spherical Bessel functions (Abramowitz & Stegun 1965).

The solution of (3.58) is therefore

$$\chi_m(\epsilon)=\chi_m^{(1)}(\epsilon)-\frac{1}{15\Lambda_{\mathrm{T}}(\epsilon)}\chi_m^{(2)}(\epsilon) \quad (3.66)$$

where the $\chi_m^{(i)}$ $(i=1,2)$ are the solutions of

$$\sum_{m=1}^{\infty}(t'_{l,m}-\epsilon t''_{l,m})\chi_m^{(i)}=\begin{cases}T'_l & (i=1),\\ \delta_{l,1} & (i=2),\end{cases} \quad (3.67)$$

and where

$$\Lambda_{\mathrm{T}}(\epsilon)=\frac{1+\frac{\epsilon^2}{15}\sum_{m=1}^{\infty}t_m(\epsilon)\chi_m^{(2)}(\epsilon)}{\epsilon\left(T(\epsilon)+\epsilon\sum_{m=1}^{\infty}t_m(\epsilon)\chi_m^{(1)}(\epsilon)\right)}. \quad (3.68)$$

The equation (3.58) is one of many possible matrix equations that may be derived from the original integral equation (3.36), e.g. see Hughes (1980). The present scheme was adopted due to the simplicity of the matrix elements involved and the facility with which asymptotic results may be derived from it. Thus equations (3.66)–(3.68) provide a simple numerical scheme for the solution of the translational drag problem. In appendix A we derive ascending expansions of the functions $T(\epsilon)$ and $t_m(\epsilon)$ needed in the computation. However, before proceeding with the calculation of the numerical result, we derive the asymptotic behaviour of $\Lambda_{\mathrm{T}}(\epsilon)$ for small ϵ.

4. Asymptotic behaviour of $\Lambda_{\mathrm{T}}(\epsilon)$

We see (from appendix A) that

$$T(\epsilon)=\ln(2/\epsilon)-\gamma+\tfrac{3}{8}\pi\epsilon-\tfrac{5}{12}\epsilon^2\ln(2/\epsilon)+O(\epsilon^2). \quad (4.1)$$

It follows, from (3.53) and (3.58), that

$$\Lambda_{\mathrm{T}}(\epsilon)\sim\frac{1}{\epsilon\ln(2/\epsilon)} \quad (4.2)$$

for small ϵ, and that the $\chi_m(0)$ are finite. Therefore, we may write

$$\chi_m=\chi_m(0)-\tfrac{1}{15}(t'^{-1})_{ml}\,\epsilon\ln(2/\epsilon)+O(\epsilon), \quad (4.3)$$

where, from (3.58),

$$\chi_m(0)=\sum_{n=1}^{\infty}(t'^{-1})_{mn}T'_n \quad (4.4)$$

and $\mathbf{t}'^{-1}$ is the inverse of the matrix $\mathbf{t}'$ defined in (3.59).

It follows that we may write, from (3.53),

$$\Lambda_{\mathrm{T}}(\epsilon)=\frac{1}{\epsilon[\ln(2/\epsilon)-\gamma+\epsilon B-C\epsilon^2\ln(2/\epsilon)+O(\epsilon^2)]}, \quad (4.5)$$

where
$$B = \frac{3\pi}{8} + \sum_{m,\,n=1}^{\infty} t_m(0)\,(t'^{-1})_{mn}\,T'_n \tag{4.6}$$

and
$$C = \tfrac{5}{12} + \frac{1}{15}\sum_{m=1}^{\infty} t_m(0)\,(t'^{-1})_{ml}. \tag{4.7}$$

In appendix B, we show that the inverse matrix $\mathbf{t}'^{-1}$ is given by

$$(t'^{-1})_{mn} = (-1)^{m+n}\,(4m+1)\,(4n+1)\,P_{2n}(0)\int_0^1 \frac{dx}{x}\,(1-x^2)\frac{dP_{2m}(x)}{dx}\frac{dP_{2n}(x)}{dx}. \tag{4.8}$$

To evaluate the constants B and C we consider the sum

$$C_n = \sum_{m=1}^{\infty} t_m(0)\,(t'^{-1})_{m,n}. \tag{4.9}$$

From the definitions (3.55) and (4.8) and the result (A 15), we have

$$\begin{aligned} C_n &= (-1)^n\,(4n+1)\,P_{2n}(0)\int_0^1 dx\,(1-x^2)^{\frac{1}{2}}\frac{dP_{2n}(x)}{dx}\int_0^\infty du\,j_0(u)\,J_1(u(1-x^2)^{\frac{1}{2}}) \\ &= (-1)^n\,(4n+1)\,P_{2n}(0)\int_0^1 dx\,(1-x)\frac{dP_{2n}}{dx}, \end{aligned} \tag{4.10}$$

where (Abramowitz & Stegun 1965)

$$\int_0^\infty du\,j_0(u)\,J_1(u(1-x^2)^{\frac{1}{2}}) = \frac{(1-x^2)^{\frac{1}{2}}}{1+x}. \tag{4.11}$$

Integrating (4.10) by parts, we obtain

$$C_n = (-1)^{n+1}\,(4n+1)\,(P_{2n}(0))^2. \tag{4.12}$$

Therefore, from (4.7)
$$C = \tfrac{1}{2}. \tag{4.13}$$

Using (4.12) and the definition (3.62) of the T'_n, equation (4.6) becomes

$$B = \frac{3\pi}{8} - \int_0^\infty \frac{du}{u^2}\,J_0(u)\,(J_0(u) - j_0(u)) \tag{4.14}$$

with the aid of (3.57). By expanding $j_0(u)$ in an infinite series of Bessel functions $J_n(u)$ and integrating terms by term using the Weber–Schafheitlin integral, the integral in (4.14) can be evaluated to yield

$$B = 4/\pi. \tag{4.15}$$

Therefore, for small ϵ,

$$\Lambda_{\mathrm{T}}(\epsilon) = \left[\epsilon\left(\ln(2/\epsilon) - \gamma + \frac{4}{\pi}\epsilon - \tfrac{1}{2}\epsilon^2\ln(2/\epsilon) + O(\epsilon^2)\right)\right]^{-1}. \tag{4.16}$$

This may be compared with the expression obtained by Saffman (1976) by a perturbation-theoretic method, *viz.*

$$\Lambda_{\mathrm{T}}(\epsilon) \sim [\epsilon(\ln(2/\epsilon) - \gamma)]^{-1}. \tag{4.17}$$

Unlike Saffman's form, equation (4.16) does not possess a singularity and decays monotonically as ϵ increases.

The asymptotic form of $\Lambda_T(\epsilon)$ for large ϵ is interesting. By noting that the leading-order asymptotic expressions for $T(\epsilon)$ and $t_m(\epsilon)$ are given by

$$T(\epsilon) \sim \frac{\pi}{2\epsilon} + \dots, \tag{4.18}$$

$$t_m(\epsilon) \sim \frac{\pi}{2\epsilon}\delta_{m,0} + \dots, \tag{4.19}$$

it follows, from (3.53) and (3.56), that

$$\chi_m(\epsilon) = O\left(\frac{1}{\epsilon}\right), \quad \Lambda_T(\epsilon) \sim \frac{2}{\pi} \qquad (4.20), (4.21)$$

for ϵ large.

One might expect that, in the limit $\epsilon \to \infty$, the problem would reduce to the drag on an infinitely thin disk moving in the plane of the disk. In which case, we should have obtained (Happel & Brenner 1965)

$$\lim_{\epsilon \to \infty} \Lambda_T(\epsilon) = \frac{4}{3\pi}. \tag{4.22}$$

The discrepancy between (4.21) and (3.22) is further evidence of the singular nature of the translational problem in that even in the limit that the membrane becomes infinitely thin, it continues to influence the flow fields in the surrounding infinite fluid media.

5. The rotational problem

In this section, we set up and solve the boundary-value problem for a membrane-bound cylinder in uniform rotational motion with angular velocity $\mathbf{\Omega} = \Omega\hat{\mathbf{z}}$. We wish to derive the retarding torque exerted by the surrounding media on the rotating cylinder.

In the region $z > 0$ the appropriate solution of the Navier–Stokes equations (2.1) and (2.2) subject to the boundary condition (2.3) takes the form

$$u_r(r,\phi,z) = -\frac{1}{2}\int_0^\infty dk\, J_1(kr)\, P(k)\left(\frac{1}{k} - z\right) e^{-kz}, \tag{5.1}$$

$$u_\phi(r,\phi,z) = \frac{4\Omega a^2}{\pi}\int_0^\infty dk\, J_1(kr)\, \Phi(k)\, e^{-kz}, \tag{5.2}$$

$$u_z(r,\phi,z) = \frac{z}{2}\int_0^\infty dk\, J_0(kr)\, P(k)\, e^{-kz}, \tag{5.3}$$

$$p(r,\phi,z) = \mu_1\int_0^\infty dk\, J_0(kr)\, P(k)\, e^{-kz}. \tag{5.4}$$

The boundary conditions on the $z = 0$ plane are

$$\mathbf{u}(r,\phi,0) = \mathbf{\Omega} \times \mathbf{r} \quad (r < a), \tag{5.5}$$

$$u_z(r,\phi,0) = 0 \quad (0 < r < \infty). \tag{5.6}$$

It follows immediately that

$$\int_0^\infty dk\, J_1(kr)\frac{P(k)}{k} = 0 \quad (0 < r < a), \tag{5.7}$$

$$\int_0^\infty dk\, J_1(kr)\,\Phi(k) = \frac{\pi r}{4a^2} \quad (0 < r < a). \tag{5.8}$$

These equations are the first two of four integral equations that the unknown functions $P(k)$ and $\Phi(k)$ must satisfy. The other pair of equations arise from consideration of the membrane flow field.

As before the stick boundary condition at $z = 0$ and $z = -h$ together with the z invariance of the membrane velocity field require that the membrane velocity field is given by $u(r, \phi, 0)$.

The ϕ component of the membrane Navier–Stokes equation (2.18) with the aid of (5.1)–(5.4) reduces to the integral equation

$$\int_0^\infty dk\, k\left(k+\frac{\epsilon}{a}\right) J_1(kr)\,\Phi(k) = 0 \quad (r > a). \tag{5.9}$$

The incompressibility of the membrane (equation (2.19)) yields the integral equation

$$\int_0^\infty dk\, J_0(kr)\, P(k) = 0 \quad (a < r < \infty). \tag{5.10}$$

Equations (5.7) and (5.10) constitute a pair of dual integral equations for $P(k)$. Since these equations lack an inhomogeneous term, it follows that

$$P(k) = 0 \tag{5.11}$$

is an acceptable solution. Equations (5.8) and (5.9) constitute a pair of dual integral equations for $\Phi(k)$. In terms of the reduced variables x and u given by (3.1), the dual integral set can be written as

$$\left.\begin{aligned} &\int_0^\infty du\, J_1(xu)\,\phi(u) = \tfrac{1}{4}\pi x && (x < 1),\\ &\int_0^\infty du\, u(u+\epsilon)\, J_1(xu)\,\phi(u) = 0 && (x > 1) \end{aligned}\right\} \tag{5.12}$$

with

$$\phi(u) = \Phi(k). \tag{5.13}$$

Before solving this equation set, we need an expression for the torque exerted on the cylinder surface. The torque $\mathbf{L}$ is given by

$$\mathbf{L} = \int dS\, \mathbf{r}\times\hat{\mathbf{n}}.\boldsymbol{\sigma}, \tag{5.14}$$

where the integral is over the cylinder surface, $\hat{\mathbf{n}}$ being the unit normal and $\mathbf{r}$ the vector distance of a point on the surface normal to the cylinder axis. Evaluating the non-zero components $\sigma_{z\phi}$ and $\sigma_{r\phi}$ of the stress tensor with the aid of (5.2), we obtain, from (5.14),

$$\mathbf{L} = -\lambda_{\mathrm{R}}\boldsymbol{\Omega}, \tag{5.15}$$

where the rotational drag coefficient λ_R is given by

$$\lambda_R = 4\pi(\mu_1+\mu_2)\,a^3\,\Lambda_R(\epsilon), \tag{5.16}$$

where
$$\Lambda_R(\epsilon) = \frac{2}{\pi\epsilon}\left(\int_0^\infty du\,(u+\epsilon)\,J_2(u1^+)\,\phi(u) - \epsilon\Delta\int_0^\infty du\,J_2(ux)\,\phi(u)\right). \tag{5.17}$$

The second term in (5.17) is the jump in the integral across $x = 1$ in the notation (3.40).

To solve (5.12), we use the notation of Sneddon (1966) to write the integral equations as

$$\left.\begin{aligned} S_{0,1}\phi(x) &= \frac{\pi}{2} && (x<1),\\ S_{\frac{1}{2},0}\phi(x) &= -\frac{2}{\epsilon x}S_{1,-1}\phi(x) && (x>1).\end{aligned}\right\} \tag{5.18}$$

The solution of this equation set is (Sneddon 1966)

$$\phi(u) = S_{\frac{1}{2},-\frac{1}{2}}\left\{\begin{array}{ll}\pi^{\frac{1}{2}} & (x<1),\\ -\dfrac{2}{\epsilon x}S_{\frac{1}{2},-\frac{1}{2}}\phi(x) & (x>1).\end{array}\right\} \tag{5.19}$$

More conventionally, (5.19) may be written as the integral equation

$$(u+\epsilon)\,\phi(u) = \epsilon j_1(u) + \frac{1}{\pi}\int_0^\infty dz\,z\,\phi(z)\,[j_0(u-z) - j_0(u+z)]. \tag{5.20}$$

Using the expansion (3.45), the solution of (5.20) can be written as

$$(u+\epsilon)\,\phi(u) = \frac{\pi}{6}\sum_{m=0}^{\infty}\phi_m(\epsilon)\,j_{2m+1}(u), \tag{5.21}$$

where the coefficients $\phi_m(\epsilon)$ are defined as

$$\phi_m(\epsilon) = \frac{6\epsilon}{\pi}\,\delta_{m,0} + \frac{12}{\pi^2}(4m+3)\int_0^\infty dz\,z\,\phi(z)\,j_{2m+1}(z) \quad (m = 0,1,2,\ldots). \tag{5.22}$$

It follows from (5.20), by an argument identical to that of § 3, that

$$\Delta\int_0^\infty du\,J_2(ux)\,\phi(u) = 0, \tag{5.23}$$

so that the reduced rotational drag coefficient $\Lambda_R(\epsilon)$ can then be written as

$$\Lambda_R(\epsilon) = \frac{2}{\pi\epsilon}\int_0^\infty du\,(u+\epsilon)\,J_2(u1^+)\,\phi(u). \tag{5.24}$$

Multiplying (5.21) by $J_2(ul^+)$ and integrating over u, we obtain the result

$$\Lambda_R(\epsilon) = \frac{2}{9\epsilon}\phi_0(\epsilon) \tag{5.25}$$

with the aid of the Weber–Schafheitlin integral (Abramowitz & Stegun 1965). As in the translational problem, we need only to calculate the coefficient $\phi_0(\epsilon)$ in order to compute $\Lambda_R(\epsilon)$.

A suitable scheme for computing $\Lambda_R(\epsilon)$ can be derived as follows. Multiplying (5.21) by $uj_{2l+1}(u)/(u+\epsilon)$ and integrating over u, we obtain the set of simultaneous equations

$$\sum_{m=0}^{\infty}\phi_m(\epsilon)\int_0^\infty du\,\frac{j_{2l+1}(u)\,j_{2m+1}(u)}{u+\epsilon} = \delta_{l,0} \quad (l = 0,1,2,\ldots). \tag{5.26}$$

We define the new coefficients

$$\Phi_m(\epsilon) = \phi_m(\epsilon)/\phi_0(\epsilon) \quad (m = 1, 2, \ldots). \tag{5.27}$$

Then, the $l = 0$ equation of (5.26) can be written

$$\frac{2}{9\epsilon\Lambda_{\mathrm{R}}(\epsilon)} = r_0(\epsilon) + \sum_{m=1}^{\infty} \Phi_m(\epsilon)\, r_m(\epsilon), \tag{5.28}$$

where

$$r_m(\epsilon) = \int_0^\infty du\, \frac{j_{2m+1}(u)\, j_1(u)}{u+\epsilon} \quad (m = 0, 1, 2, \ldots). \tag{5.29}$$

For l non-zero, the remaining equations of (5.26) can be written

$$\sum_{m=1}^{\infty} \left(\int_0^\infty du\, \frac{j_{2l+1}(u)\, j_{2m+1}(u)}{u+\epsilon} \right) \Phi_m(\epsilon) = -r_l(\epsilon) \quad (l = 1, 2, \ldots). \tag{5.30}$$

The matrix elements of this simultaneous equation set can be simplified (as in the translational problem) by multiplying the $(l-1)$th equation by $-\epsilon^2/(4l+1)(4l+3)$ and the lth equation by $1-2\epsilon^2/(4l+1)(4l+5)$ and the $(l+1)$th equation by $-\epsilon^2/(4l+3)(4l+5)$ and adding to obtain

$$\sum_{m=1}^{\infty} (R_{l,m} - \epsilon R'_{l,m})\, \Phi_m(\epsilon) = -R_{0,l} + \epsilon R'_{0,l} - \frac{2\epsilon\delta_{l,1}}{315\Lambda_{\mathrm{R}}(\epsilon)} \quad (l = 1, 2, 3, \ldots), \tag{5.31}$$

where

$$R_{l,m} = \int_0^\infty du\, \frac{j_{2l+1}(u)\, j_{2m+1}(u)}{u} = \frac{(-1)^{m+l+1}}{2[4(m-l)^2-1]\,(l+m+1)\,(l+m+2)} \quad (l, m = 0, 1, 2, \ldots) \tag{5.32}$$

and

$$\begin{aligned} R'_{l,m} &= \int_0^\infty \frac{du}{u^2}\, j_{2l+1}(u)\, j_{2m+1}(u) \\ &= \frac{\pi\delta_{l,m-1}}{2(4m+3)\,(4m+1)\,(4m-1)} + \frac{\pi\delta_{l,m}}{(4m+5)\,(4m+3)\,(4m+1)} \\ &\quad + \frac{\pi\delta_{l,m+1}}{2(4m+7)\,(4m+5)\,(4m+3)} \quad (l, m = 0, 1, 2, \ldots). \end{aligned} \tag{5.33}$$

The solution of (5.31) is therefore

$$\Phi_m(\epsilon) = \Phi_m^{(1)}(\epsilon) - \frac{2\epsilon}{315\Lambda_{\mathrm{R}}(\epsilon)}\, \Phi_m^{(2)}(\epsilon), \tag{5.34}$$

where the $\Phi_m^{(i)}$ are the solutions of

$$\sum_{m=1}^{\infty} (R_{l,m} - \epsilon R'_{l,m})\, \Phi_m^{(i)} = \begin{cases} -R_{0,l} + \epsilon R'_{0,l} & (i = 1), \\ \delta_{l,1} & (i = 2). \end{cases} \tag{5.35}$$

The rotational drag coefficient $\Lambda_{\mathrm{R}}(\epsilon)$ is, from (5.28),

$$\Lambda_{\mathrm{R}}(\epsilon) = \frac{2}{9\epsilon} \left(\frac{1 + \dfrac{\epsilon^2}{35} \sum\limits_{m=1}^{\infty} r_m(\epsilon)\, \Phi_m^{(2)}(\epsilon)}{r_0(\epsilon) + \sum\limits_{m=1}^{\infty} r_m(\epsilon)\, \Phi_m^{(1)}(\epsilon)} \right). \tag{5.36}$$

Equations (5.35) and (5.36) provide a suitable numerical scheme for the exact numerical computation of $\Lambda_R(\epsilon)$. Ascending expansions of the functions suitable for their numerical evaluation are given in appendix A.

6. Asymptotic behaviour of $\Lambda_R(\epsilon)$

To derive the asymptotic form of $\Lambda_R(\epsilon)$ we return to equation (5.26). At $\epsilon = 0$, this set of equations reduces to

$$\sum_{m=0}^{\infty} R_{l,m}\phi_m(0) = \delta_{l,0} \quad (l = 0, 1, \ldots). \tag{6.1}$$

We make use of the result (see appendix B) that the inverse of the infinite matrix whose elements are $R_{l,m}$ is given by

$$(R^{-1})_{l,m} = (-1)^{m+l}(4l+3)(4m+3)\frac{dP_{2l+1}(0)}{dx}\frac{dP_{2m+1}(0)}{dx}\int_0^1 \frac{dx}{x} P_{2l+1}(x) P_{2m+1}(x), \tag{6.2}$$

where
$$\frac{dP_{2l+1}(0)}{dx} = \frac{(-1)^m 2\Gamma(l+\frac{3}{2})}{\pi^{\frac{1}{2}}\Gamma(l+1)} \tag{6.3}$$

(Abramowitz & Stegun 1965). Applying this inverse matrix to (6.1), we obtain

$$\phi_m(0) = (R^{-1})_{m,0} \tag{6.4}$$

$$= \frac{3(-1)^m(4m+3)(m+\frac{1}{2})}{\pi(m+1)}\left(\frac{\Gamma(m+\frac{1}{2})}{\Gamma(m+1)}\right)^2, \tag{6.5}$$

using the results (Abramowitz & Stegun 1965)

$$P_1(x) = x, \tag{6.5}$$

$$\int_0^1 dx\, P_{2m+1}(x) = \frac{\pi^{\frac{1}{2}}}{2\Gamma(\frac{1}{2}-m)\Gamma(m+2)}. \tag{6.6}$$

In particular
$$\phi_0(0) = \tfrac{9}{2}. \tag{6.7}$$

If we write
$$\phi_m(\epsilon) = \phi_m(0) + \epsilon\Delta\phi_m(\epsilon) \tag{6.8}$$

then (5.26) can be written as

$$\sum_{m=0}^{\infty}\left(\int_0^{\infty} du \frac{j_{2l+1}(u)\, j_{2m+1}(u)}{u+\epsilon}\right)\Delta\phi_m(\epsilon) = 3\int_0^{\infty} du \frac{j_{2l+1}(u)\, J_1(u)}{u(u+\epsilon)} \quad (l = 0, 1, 2, \ldots) \tag{6.9}$$

with the aid of (6.2) and (6.4). At $\epsilon = 0$ equation (6.9) reduces to

$$\sum_{m=0}^{\infty} R_{lm}\Delta\phi_m(0) = 3\int_0^{\infty} du \frac{j_{2l+1}(u)\, J_1(u)}{u^2}. \tag{6.10}$$

Applying the inverse matrix to (6.10), we obtain

$$\Delta\phi_m(0) = 3\sum_{l=0}^{\infty} R_{ml}^{-1}\int_0^{\infty} du \frac{j_{2l+1}(u)\, J_1(u)}{u^2} \tag{6.11}$$

$$= 3(4m+3)(-1)^m\frac{dP_{2m+1}(0)}{dx}\int_0^{\infty}\frac{du}{u}J_1(u)\int_0^1 dx\, P_{2m+1}(x)\, J_0[u(1-x^2)^{\frac{1}{2}}] \tag{6.12}$$

with the aid of (6.2) and (B 6). In particular, for $m = 0$ we have

$$\Delta\phi_0(0) = 9\int_0^\infty \int_0^\infty \frac{du}{u} J_1(u) \int_0^1 dx\, x\, J_0[u(1-x^2)^{\frac{1}{2}}] \tag{6.13}$$

$$= 9\int_0^\infty du \left(\frac{J_1(u)}{u}\right)^2 \tag{6.14}$$

$$= \frac{4}{3\pi} \tag{6.15}$$

from Watson (1944).

From (5.25), we have then, for small ϵ,

$$\Lambda_R(\epsilon) = \frac{1}{\epsilon} + \frac{8}{3\pi} + O(\epsilon). \tag{6.16}$$

The leading term is that obtained by Saffman (1976). The accuracy of these asymptotic forms will be tested in the next section.

Finally, we derive the large-ϵ form of $\Lambda_R(\epsilon)$. For ϵ large, we have that

$$\int_0^\infty du \frac{j_{2l+1}(u)\, j_{2m+1}(u)}{u+\epsilon} \sim \frac{1}{\epsilon}\int_0^\infty du\, j_{2l+1}(u)\, j_{2m+1}(u) \sim \frac{\pi\delta_{l,m}}{2\epsilon(4l+3)} \tag{6.17}$$

(Abramowitz & Stegun 1965). Thus, for large ϵ, (5.26) reduces to

$$\phi_0(\epsilon) \sim \frac{6\epsilon}{\pi} \tag{6.18}$$

so that

$$\Lambda_R(\epsilon) \sim \frac{4}{3\pi}. \tag{6.19}$$

This result is in agreement with the rotational drag coefficient for an infinitely thin disk (Happel & Brenner 1965).

7. Results and discussion

The numerical computation of $\Lambda_T(\epsilon)$ proceeds as follows: For a given value of ϵ, we evaluate $T(\epsilon)$ and $t_m(\epsilon)$ ($m = 1, 2, \ldots$) using the expansions derived in appendix A. Then, by truncating equation (3.67) to yield a finite set of simultaneous equations, we can solve to obtain the two solutions $\chi_m^{(i)}(\epsilon)$ ($i = 1, 2$). The translational drag coefficient is calculated from (3.68).

It is found that the neglect of all coefficients $\chi_m(\epsilon)$ above $\chi_{50}(\epsilon)$ produces negligible error in $\chi_T(\epsilon)$. In figure 2 we plot the curve $\Lambda_T(\epsilon)$ obtained by this procedure and compare it with the asymptotic results of Saffman (4.17) and the present work (4.16). We note that Saffman's result is an excellent approximation to the exact solution for $\epsilon < 0{\cdot}1$ whereas the result (4.16) extends the agreement to $\epsilon < 1$.

The calculation of $\Lambda_R(\epsilon)$ parallels that for Λ_T. We evaluate $r_m(\epsilon)$ using the expansions given in appendix A and $R_{l,m}(\epsilon)$ and $R'_{l,m}(\epsilon)$ using equations (5.32) and (5.33). Equations (5.35) may be truncated, with negligible error, at about Φ_{50} and so yield $\Phi_m^{(i)}$. $\Lambda_R(\epsilon)$ then follows from equation (5.36).

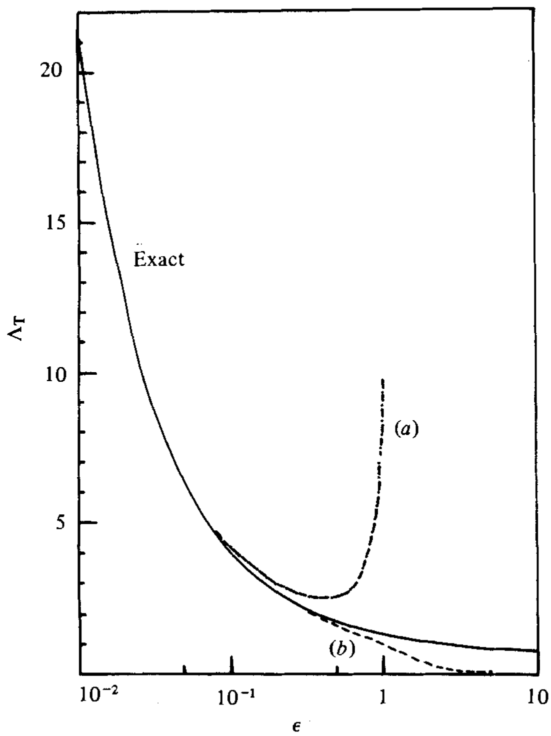

FIGURE 2.

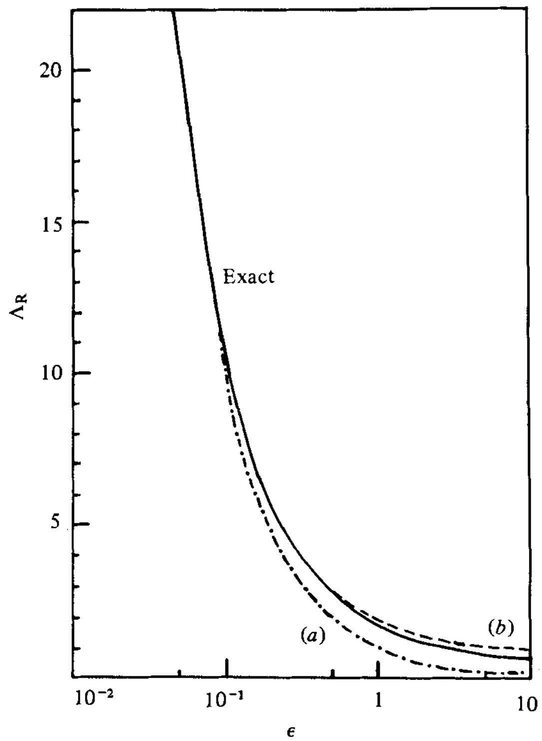

FIGURE 3.

FIGURE 2. The reduced translational drag coefficient $\Lambda_T(\epsilon)$ defined by equation (3.43) as a function of ϵ. The continuous line is the exact numerical calculation and the dotted lines are (*a*) the asymptotic result of Saffman (1976) (equation (4.17)) and (*b*) the asymptotic result of the present work (equation (4.16)).

FIGURE 3. The dimensionless rotational drag coefficient $\Lambda_R(\epsilon)$ defined by (5.16) as a function of ϵ. The continuous line is the exact numerical result. The dotted lines are the asymptotic results of (*a*) Saffman (1976) and (*b*) the present work (equation (6.16)).

Figure 3 displays the resultant curve for $\Lambda_R(\epsilon)$; the asymptotic results of the present study (6.16) and of Saffman are also shown. Again Saffman's result is good for $\epsilon < 0{\cdot}1$ while equation (6.16) is acceptable for $\epsilon < 1$.

A quantity of interest in diffusion studies is the ratio of diffusion coefficients

$$\frac{D_T}{D_R} = a^2 \frac{\Lambda_R(\epsilon)}{\Lambda_T(\epsilon)}. \tag{7.1}$$

We see that the simultaneous measurement of D_T and D_R enables the values of ϵ to be obtained unambiguously from (7.1) (with an appropriate choice of the radius a). Subsequent use of the individual measurements of D_T and D_R lead to the inference of both $\mu_1+\mu_2$ and η. It should be noted that in real membranes the exterior viscosities in the vicinity of the membrane are by no means well determined. For small ϵ, equations (4.16) and (6.16) yield

$$\frac{D_T}{a^2 D_R} = \frac{1+\dfrac{8}{3\pi}\epsilon + O(\epsilon^2)}{\epsilon^2 \ln(2/\epsilon) - \gamma + \dfrac{4}{\pi}\epsilon - \frac{1}{2}\epsilon^2 \ln(2/\epsilon) + O(\epsilon^2)}. \tag{7.2}$$

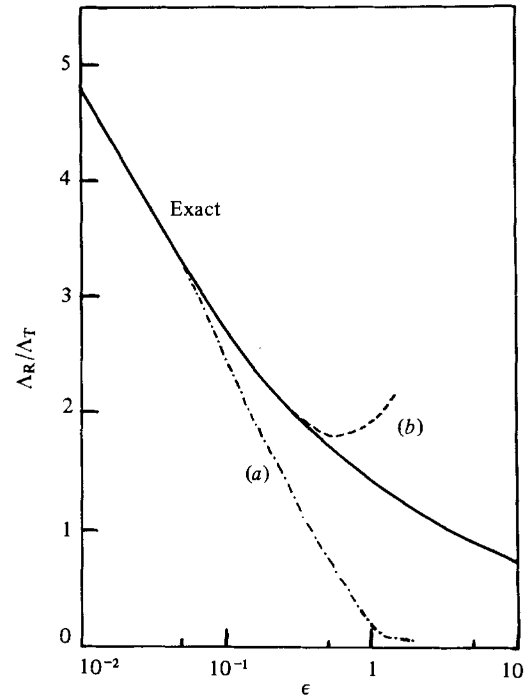

FIGURE 4. The ratio $D_T/a^2D_R = \Lambda_R/\Lambda_T$ as a function of ϵ. The continuous line is the exact numerical result and the dotted lines are the asymptotic results of (*a*) Saffman (1976) and (*b*) the present work (equations (4.16) and (6.16)).

In figure 4 we plot the ratio D_T/a^2D_R as a function of ϵ obtained from the exact numerical solution of the problem and compare it with the asymptotic form (7.2). For $\epsilon < 0{\cdot}4$ the two results are in good agreement.

The implication of this and Saffman's study is that the unusually low diffusion coefficients measured in experimental membrane studies may have their origin *not* only in a large membrane viscosity, but also in the interplay of geometry (i.e. the ratio a/h) and the viscosity of the external medium facilitated by the inextensibility of the membrane lipids.

We point out finally that failure of reasonable values of a, h, μ and η *simultaneously* to predict measured D_T and D_R will indicate inapplicability of the present model to membrane systems. In particular we do not expect membrane-bound proteins to be flush with the membrane interface, as shown in figure 1, but rather to protrude into the external media. Neglect of the ends is only permissible if the experimental results indicate that ϵ is small when the dominant contribution to the drag comes from the cylinder walls.

The authors would like to acknowledge Professor P. G. Saffman for his most constructive comments on an earlier version of this work.

Appendix A

We develop here an expansion of the $t_m(\epsilon)$ functions which arise in the solution of the integral equation (3.36). We have, from the definition (3.55),

$$t_m(\epsilon) = \int_0^\infty du\, u^{-1}\left[1+\frac{\epsilon}{u}\right]^{-1} j_0(u) j_{2m}(u). \tag{A 1}$$

The integral in (A 1) is in the classic form of a Mellin transform convolution and, taking the Mellin transform of (A 1), we obtain (Erdélyi 1954)

$$\mathscr{M}(t_m(\epsilon);\, \epsilon \to s) = \frac{\pi}{\sin \pi s}\int_0^\infty du\, u^{s-1} j_0(u) j_{2m}(u) \quad (0 < \operatorname{Re} s < 1) \tag{A 2}$$

$$= \frac{\pi^2}{8}\frac{2^s}{\sin \pi s}\frac{\Gamma(2-s)\,\Gamma(m+\frac{1}{2}s)}{\Gamma(2+m-\frac{1}{2}s)\,\Gamma(\frac{1}{2}(3-s)-m)\,\Gamma(\frac{1}{2}(3-s)+m)}. \tag{A 3}$$

The inverse transform is

$$t_m(\epsilon) = \frac{1}{2\pi i}\int_{c-i\infty}^{c+i\infty} ds\, \epsilon^{-s}\mathscr{M}(t_m(\epsilon);\, \epsilon \to s) \quad (0 < c = \operatorname{Re} s < 1). \tag{A 4}$$

Closing this contour to the left and evaluating the residues at the poles of the integrand generates the ascending expansion in ϵ, which will be suitable for evaluating $t_m(\epsilon)$ provided ϵ is not too large. We obtain

$$t_m(\epsilon) = t_m^{(1)}(\epsilon) + t_m^{(2)}(\epsilon) + t_m^{(3)}(\epsilon), \tag{A 5}$$

where

$$t_m^{(1)}(\epsilon) = \frac{\pi^2}{8}\sum_{n=0}^{\infty}\frac{(-1)^{m-n}\,\Gamma(2n+3)\,(\frac{1}{2}\epsilon)^{2n+1}}{\Gamma(n+2-m)\,\Gamma(n+2+m)\,\Gamma(n+\frac{3}{2}-m)\,\Gamma(n+\frac{5}{2}+m)}, \tag{A 6}$$

$$t_m^{(2)}(\epsilon) = \frac{\pi}{8}\sum_{n=0}^{m-1}\frac{\Gamma(2n+2)\,\Gamma(m-n)\,(\frac{1}{2}\epsilon)^{2n}}{\Gamma(\frac{3}{2}-m+n)\,\Gamma(\frac{3}{2}+m+n)\,\Gamma(2+m+n)} \quad (m-1 \geqslant 0), \tag{A 7}$$

$$t_m^{(3)}(\epsilon) = \frac{\pi}{4}\sum_{n=0}^{\infty}(-1)^n\,[\ln(2/\epsilon) - \psi(2+2m+2n) + \tfrac{1}{2}\psi(n+1) + \tfrac{1}{2}\psi(\tfrac{3}{2}+n) + \tfrac{1}{2}\psi(\tfrac{3}{2}+2m+n)$$
$$+ \tfrac{1}{2}\psi(2+2m+n)]\,\frac{\Gamma(2+2m+2n)\,(\frac{1}{2}\epsilon)^{2m+2n}}{\Gamma(n+1)\,\Gamma(\frac{3}{2}+n)\,\Gamma(\frac{3}{2}+2m+n)\,\Gamma(2+2m+n)}. \tag{A 8}$$

We note that $\lim_{\epsilon\to 0} t_m(\epsilon)$ is finite (for $m > 0$).

The $T(\epsilon)$ function given by

$$T(\epsilon) = \int_0^\infty du\,\frac{j_0(u)\,J_0(u)}{u+\epsilon} \tag{A 9}$$

can be evaluated in an identical fashion. In this case

$$\mathscr{M}\{T(\epsilon);\, \epsilon \to s\} = \frac{\pi^{\frac{3}{2}}2^s\,\Gamma(\frac{1}{2}s)\,\Gamma(\frac{3}{2}-s)}{4\sin \pi s\,\Gamma^2(\frac{3}{2}-\frac{1}{2}s)\,\Gamma(1-\frac{1}{2}s)} \quad (0 < \operatorname{Re} s < 1). \tag{A 10}$$

Closing the inversion contour to the left and evaluating the residues at the poles of the integrand, we obtain

$$T(\epsilon) = T^{(1)}(\epsilon) + T^{(2)}(\epsilon), \tag{A 11}$$

where

$$T^{(1)}(\epsilon) = \frac{\pi^{\frac{3}{2}}}{4} \sum_{n=0}^{\infty} \frac{(\frac{1}{2}\epsilon)^{2n+1} (-1)^n \Gamma(\frac{5}{2}+2n)}{\Gamma^2(n+\frac{3}{2})\,\Gamma^2(n+2)}. \tag{A 12}$$

$$T^{(2)}(\epsilon) = \frac{\pi^{\frac{1}{2}}}{2} \sum_{n=0}^{\infty} \frac{(-1)^n (\frac{1}{2}\epsilon)^{2n}\,\Gamma(2n+\frac{3}{2})}{\Gamma^2(n+1)\,\Gamma^2(n+\frac{3}{2})} \{\ln(2\epsilon) - \psi(2n+\tfrac{3}{2}) + \psi(n+1) + \psi(n+\tfrac{3}{2})\}. \tag{A 13}$$

The expansions for $t_m(\epsilon)$ and $T(\epsilon)$ are convergent for all ϵ; however, for practical computation we are restricted to $\epsilon < 10$. For larger values of ϵ, one may, of course, derive descending expansions for $t_m(\epsilon)$ and $T(\epsilon)$ from their contour integrals by closing to the right. However, such large values of ϵ are of no physical interest.

The ascending expansion of the $r_m(\epsilon)$ functions defined by (5.29) are obtained in an identical manner and only the result will be reported, *viz.*

$$r_m(\epsilon) = r_m^{(1)}(\epsilon) + r_m^{(2)}(\epsilon) + r_m^{(3)}(\epsilon), \tag{A 14}$$

where

$$r_m^{(1)}(\epsilon) = -\frac{\pi}{8} \sum_{\substack{n=0\,(m\neq 0)\\ =1\,(m=0)}}^{\infty} \frac{(\frac{1}{2}\epsilon)^{2m+2n-1}\,\Gamma(\frac{3}{2}-n)\,\Gamma(1+2m+2n)}{\Gamma(1+2m+n)\,\Gamma(1+n)\,\Gamma(2m+n+\frac{5}{2})}, \tag{A 15}$$

$$r_m^{(2)}(\epsilon) = \frac{\pi}{8} \sum_{n=0}^{m} \frac{(\frac{1}{2}\epsilon)^{2n}\,\Gamma(1+m-n)\,\Gamma(2+2n)}{\Gamma(\frac{3}{2}+m+n)\,\Gamma(\frac{3}{2}-m+n)\,\Gamma(3+m+n)}, \tag{A 16}$$

$$\begin{aligned} r_m^{(3)}(\epsilon) = \frac{\pi}{4} \sum_{n=0}^{\infty} & \frac{(-1)^n (\frac{1}{2}\epsilon)^{2m+2n+2}\,\Gamma(4+2m+2n)}{\Gamma(n+1)\,\Gamma(\frac{5}{2}+2m+n)\,\Gamma(\frac{5}{2}+n)\,\Gamma(4+2m+n)} \\ & \times (\ln(2/\epsilon) - \psi(4+2m+2n) + \tfrac{1}{2}\psi(\tfrac{5}{2}+2m+n) + \tfrac{1}{2}\psi(n+1) \\ & + \tfrac{1}{2}\psi(n+\tfrac{5}{2}) + \tfrac{1}{2}\psi(4+2m+n)). \end{aligned} \tag{A 17}$$

Appendix B

We wish to prove here that (4.8) is the inverse of the matrix $\mathbf{t}'$ defined by (3.59). From (4.8) and (3.59) we have that

$$\begin{aligned} (\mathbf{t}'^{-1}.\mathbf{t}')_{ml} = (-1)^m (4m+1) P_{2m}(0) \int_0^1 dx\,(1-x)^{\frac{1}{2}} \frac{dP_{2m}(x)}{dx} \\ \times \int_0^\infty du\, j_{2l}(u)\, J_1(u(1-x^2)^{\frac{1}{2}}), \end{aligned} \tag{B 1}$$

where we have made use of the result

$$\frac{ux}{(1-x^2)^{\frac{1}{2}}} J_1(u(1-x^2)^{\frac{1}{2}}) = \sum_{n=1}^{\infty} (-1)^n (4n+1) P_{2n}(0) \frac{dP_{2n}(x)}{dx} j_{2n}(u) \tag{B 2}$$

which follows directly from a differentiation of (3.57) with respect to x.

Evaluating the u integration by the Weber–Schafheitlin formula, we obtain

$$(\mathbf{t}'^{-1}.\mathbf{t}')_{ml} = \left[\frac{(-1)^{m+l}(4m+1)\,P_{2m}(0)}{2l(2l+1)\,P_{2l}(0)}\right] \int_0^1 dx\,(1-x^2) \frac{dP_{2m}(x)}{dx} \frac{dP_{2l}(x)}{dx}. \tag{B 3}$$

Integrating by parts, and using the result (Abramowitz & Stegun 1965)

$$\frac{d}{dx}\left[(1-x^2)\frac{dP_\nu(x)}{dx}\right] = -\nu(\nu+1)\,P_\nu(x), \tag{B 4}$$

we obtain

$$(\mathbf{t}'^{-1}.\mathbf{t}')_{ml} = \frac{(-1)^{m+l}(4m+1)P_{2m}(0)}{P_{2l}(0)}\int_0^1 dx\, P_{2m}(x)\, P_{2l}(x)$$
$$= \delta_{m,l}, \tag{B 5}$$

which is the desired result.

The proof that (6.2) is the inverse of the matrix $R_{l,m}$ defined by (5.32) follows in a similar manner to the proof above using the results (Watson 1944)

$$ux\, J_0[u(1-x^2)^{\frac{1}{2}}] = \sum_{m=0}^{\infty}(-1)^m(4m+3)\frac{dP_{2m+1}(0)}{dx} j_{2m+1}(u)\, P_{2m+1}(x) \tag{B 6}$$

and
$$\int_0^\infty du\, j_{2l+1}(u)\, J_0[u(1-x^2)^{\frac{1}{2}}] = \frac{\pi^{\frac{1}{2}}}{2}\frac{\Gamma(l+1)}{\Gamma(l+\frac{3}{2})}P_{2l+1}(x) \quad (0 < x < 1), \tag{B 7}$$

and the orthogonality of the odd Legendre polynomials on the range $0 < x < 1$.

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