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Reinterpreting the basic theorem of flagellar hydrodynamics

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Abstract. Lorentz [1] pioneered the representation of flows at very low Reynolds number by a surface distribution of stokeslets – whose strengths, nowadays, are computed by surface-velocity collocations. That method is here compared with a representation widely used in flagellar hydrodynamics, by a curvilinear distribution of stokeslets and dipoles along the flagellar centreline; with the velocity of each cross-section expressed as a centreline value of the combined fields of singularities beyond a certain cutoff distance. The latter is also a good representation, and offers moreover some computational advantages. This paper establishes the equivalence of the two representations, and identifies those properties of Stokes flows which make both the dipoles and the cutoff essential to that equivalence.

1. Introduction

One important aspect of the great paper by H.A. Lorentz [1] celebrated in this volume is his demonstration that every flow at very low Reynolds number is a superposition of elementary flow fields – now called stokeslet fields – defined in terms of the total force (pressure and viscous force) with which each point on the solid boundary acts on the fluid. The whole flow field, in short, is a surface distribution of stokeslet fields.

In many applications this result yields a highly convenient method for computing flows at very low Reynolds number associated with specified movements of a solid surface. It is simply necessary to determine that surface distribution of force whose corresponding flow field coincides on the surface with those specified movements.

Nevertheless in one key application an alternative method has been found fruitful. This is the study of flows generated by movements of the flagella of microorganisms. Owing to their characteristic ratios of length to diameter of order 10^2 , any representation of the flow field in terms of a distribution of stokeslets over the boundary of each cross-section would tend to require that the flow field be resolved on the inconveniently small scale of a flagellar diameter.

Workers in this field have preferred therefore to adopt a different approach, founded on what I shall here call "the basic theorem of flagellar hydrodynamics"; that is, the theorem stated on p.194 of my 1975 John von Neumann Lecture "Flagellar Hydrodynamics" [2]. It represents the flow, not by a surface distribution, but simply by a curvilinear distribution of elementary flow fields along the centreline of the flagellum. Each such elementary flow field does moreover include a stokeslet, defined in terms of the force exerted on the fluid by unit length of flagellum; nonetheless, the curvilinear distribution incorporates two new features absent from the surface distribution:

(a) the stokeslet is accompanied by a hydrodynamic dipole, of strength proportional to the stokeslet strength resolved onto the plane normal to the centreline; while
(b) each cross-section of the flagellum moves as a whole with a velocity which, besides including a term proportion to the local dipole strength, includes also the centreline

value of the linear combination of all stokeslet fields associated with cross-sections more distant than a cutoff value δ, given as a certain multiple of the flagellar radius.

Such a cutoff δ is indeed much needed, since the velocity associated with a curvilinear distribution of stokeslet fields would become infinite (like ln δ) if δ were allowed to vanish.

A brief recapitulation (with some historical notes) of the theorem's statement and proof, given in section 2, emphasizes above all its good accuracy: the error varies only linearly – rather than logarithmically as in some alternative formulations – with the ratio of flagellar radius to length-scale. Accordingly, the theorem offers a satisfactorily precise, yet numerically convenient, approach to flagellar hydrodynamics (see, for example, Higdon [3]–[4]), through the determination of that curvilinear distribution of stokeslet strengths which generates a given curvilinear distribution of velocities of flagellar cross-sections.

The existing proof (section 2) of the basic theorem has an essentially ad hoc character. Nevertheless it seems appropriate, in a volume celebrating that paper of Lorentz [1] which established a quite general representation of any flow at very low Reynolds number as the linear superposition of a surface distribution of stokeslet fields, to consider whether this result might make possible a reinterpretation of the basic theorem.

Such a reinterpretation is given below in sections 3 and 4. Here, respectively, each of the features (a) and (b) characteristic of the curvilinear distribution of elementary flow fields appearing in the basic theorem is reinterpreted in terms of the equivalent surface distribution of stokeslet fields.

To this end, it is first shown that the total force (pressure and viscous force) with which each elementary area of flagellar surface acts on the fluid is to a good approximation uniform over any cross-section. This at first sight surprising result is closely parallel to the well known result (Batchelor [5], p.233) for motion of a sphere at very low Reynolds number. It means that the force exerted by a flagellar cross-section is distributed uniformly over its surface.

It follows that the Lorentz distribution of stokeslet fields is a surface distribution whose vector strength per unit area is uniform over a cross-section. Thus the basic theorem, on elementary flow fields distributed along the centreline subject to the two special features (a) and (b), needs to be reinterpreted by comparison with the occurrence at each cross-section of stokeslet fields uniformly distributed around its perimeter. Briefly, this allows the following interpretations of those special features:

(a) arises because the Laplace operator applied to a stokeslet field yields a dipole field, while moreover any difference between a nearly linear distribution of elementary flow fields and an associated nearly cylindrical distribution uniform over a cross-section can be related to the action of such a Laplace operator; while

(b) arises because the uniform ring of stokeslet fields distributed around a given cross-section of radius a is found to produce at every point on the surface of a different cross-section a specific finite velocity, which indeed coincides with the centreline velocity associated with stokeslets distributed along the centreline beyond a cutoff distance δ.

Here moreover the ratio δ/a is found to take the same value ($0.5e^{1/2} = 0.824$) as in the basic theorem.

Even though, for clear reasons of convenience, the basic theorem will probably continue to be used widely in flagellar hydrodynamics, I believe that confidence in its use may be reinforced by the above reinterpretation in terms of the important results of Lorentz [1].

2. Mathematical aspects of the basic theorem

Flagellar hydrodynamics is devoted to movements of microorganisms in fluid at Reynolds numbers so small that all effects of inertia (whether on the fluid or on the microorganism) are completely negligible. It means that both the resultant, and the moment, of all forces acting on the microorganism are zero at each instant. Also, the fluid satisfies the equations

$$\mu \nabla^2 \mathbf{u} = \nabla p \quad \text{and} \quad \nabla \cdot \mathbf{u} = 0 \ (\text{so that } \nabla^2 p = 0) \tag{1}$$

appropriate to motions without inertia.

The fundamental singular solution of these equations, representing the effect of a concentrated external force $\mathbf{F}$ acting at a single point of the fluid, is the stokeslet field

$$\mathbf{u} = \frac{r^2\mathbf{F}+(\mathbf{F}\cdot\mathbf{r})\mathbf{r}}{8\pi\mu r^3}, \quad p = \frac{\mathbf{F}\cdot\mathbf{r}}{4\pi r^3}, \tag{2}$$

where $\mathbf{r}$ stands for vector displacement from the point of application of the force. (Thus this field satisfies Eqs. (1) with an additional term $\mathbf{F}\delta(\mathbf{r})$ on the left-hand side of the first equation.) Here, the expression for p as the potential of a dipole field (with $(-\mathbf{F})$ as the dipole strength) confirms the statement in section 1 that the Laplacian $\nabla^2\mathbf{u}$ (which by (1) is $\mu^{-1}\nabla p$) is a velocity field of dipole type.

Some special problems arise (see below) from the remarkable inverse-first-power dependence (2) of the velocity field on r (the distance from the point of application of the force). However, the classical paradox that, in unbounded fluid, such a velocity field has infinite energy disappears completely in any application to swimming microorganisms. Because the total force on the organism is zero (see above), its total reaction on the water must be zero; thus, the flow field is a combination of (i) stokeslet fields associated with flagellar thrust and (ii) stokeslet fields associated with an equal and opposite resistance to movement of the cell-body. Because the vector sum of all the stokeslet strengths is zero, the inverse-first-power terms in the combined far fields must cancel; accordingly, the kinetic energy of the fluid takes a sensible finite value (without any modified theory based on the Oseen equation having to be introduced).

As explained in section 1, the basic theorem (see below) of flagellar hydrodynamics expresses in a convenient form the relationship between two curvilinear distributions; that is, between how a flagellum's velocity of movement and the force which it exerts are distributed along its length.

THEOREM. If $\mathbf{f}(s)$ is the force per unit length with which a flagellum of small radius a acts on a fluid, where the variable s signifies distance measured along the centreline of the flagellum from some given cross-section, then the resulting fluid motion can be represented by a distribution of stokeslets along the centreline of strength $\mathbf{f}(s)$ per unit length, accompanied by dipoles of strength

$$-\frac{a^2\mathbf{f}_n(s)}{4\mu} \tag{3}$$

per unit length; here, $\mathbf{f}_n(s)$ is the vector normal to the centreline obtained by resolving $\mathbf{f}(s)$ onto the plane normal to the centreline. The fluid velocity field $\mathbf{u}$ closely matches flagellar movements $\mathbf{w}$ such that the whole cross-section where $s = s_0$ moves with velocity

$$\mathbf{w}(s_0) = \frac{\mathbf{f}_n(s_0)}{4\pi\mu} + \int_{r_0>\delta} \frac{r_0^2\mathbf{f}(s) + [\mathbf{f}(s)\cdot\mathbf{r}_0]\,\mathbf{r}_0}{8\pi\mu r_0^3} ds, \tag{4}$$

where $\delta = 0.5ae^{1/2} = 0.824a$ and $\mathbf{r}_0$ is the position vector of the point s_0 on the centreline relative to the point s.

NOTES ON THE THEOREM. The general idea of the basic theorem (and of its proof) was given in special cases, and fruitfully applied, by Hancock [6]. Some similar results were given in very general cases by Batchelor [7] and Cox [8], who used a series expansion in integer powers of a parameter $\epsilon = [\ln(2\ell/a)]^{-1}$, where ℓ is a flagellar length scale. Retention of one or two terms in such an expansion involves errors whose magnitude depends on the natural logarithm of $2\ell/a$ (which, for example, may only be 4.6 for $2\ell/a = 100$). The word "closely" is used in the above theorem to indicate [2] that, by contrast, the error in Eq. (4) tends to zero linearly (rather than logarithmically) as $a/\ell \to 0$. All practical use of that equation demands, of course, some form of inversion of the relationship to derive the force distribution $\mathbf{f}(s)$ in terms of the flagellar velocity distribution $\mathbf{w}(s)$. Eq. (4) makes this computationally feasible because it relates those two distributions as functions of just a single variable s, representing position on the centreline, with variations in every direction at right angles to the centreline eliminated.

NOTES ON THE PROOF. The idea of the proof is, first, to pick a distance q which is a large multiple of the radius a but a small fraction of a flagellar wavelength; and, then, to show that stokeslets whose distance r_0 from the cross-section $s = s_0$ is less than q produce, together with their associated dipoles (3), a velocity on the cross-section's surface given closely by Eq. (4) with the integral limited to $\delta < r_0 < q$. After that, the proof is readily concluded by recognizing that the fields (2) of all the other stokeslets (those with $r_0 > q$) generate at the centre of the cross-section $s = s_0$ a velocity given by the integral in (4) limited to $r_0 > q$; while, moreover, all of them are far enough away to justify neglecting both (i) any differences between values at the cross-section's centre and on its surface and (ii) the inverse-cube velocity fields of their accompanying dipole distributions (3).

CORE OF THE PROOF. In the proof's core, velocity contributions from singularities within $r_0 < q$ are calculated for a simplified case – such that, in this region, the flagellum is effectively cylindrical while any departures of $\mathbf{f}(s)$ from its value at $s = s_0$ are negligible. Then the proof's final section assesses the errors arising from those two simplifications.

In conveniently chosen coordinates, with x measured along the axis of the cylinder from an origin at the centre of the cross-section $s = s_0$, the contribution from the tangential component f_x of the uniform distribution (f_x, f_y, f_z) of stokeslet strength is determined first. Since no dipole distribution (3) accompanies this tangential component, the velocity fields (2) of the distributed stokeslets combine to give

$$\int_{-q}^{q} \frac{f_x}{8\pi\mu}\left(\frac{1}{r} + \frac{(x-X)(x-X)}{r^3}, \frac{(x-X)y}{r^3}, \frac{(x-X)z}{r^3}\right) \mathrm{d}X, \tag{5}$$

where

$$r = \left[(x-X)^2 + y^2 + z^2\right]^{1/2} \tag{6}$$

represents distance from a stokeslet at $(X, 0, 0)$.

But the theorem is purely concerned with velocities on the surface of the cross-section $s = s_0$, where the above choice of coordinates yields

$$x = 0,\ y^2 + z^2 = a^2;\ \text{ so that } r = (X^2 + a^2)^{1/2}. \tag{7}$$

Evidently, where $x = 0$, the y- and z-components of the velocity field (5) are zero (being integrals of odd functions of X). At the same time, the x-component can be evaluated, through an integration by parts in its second term, as

$$\frac{f_x}{8\pi\mu}\left(2\int_{-q}^{q}\frac{\mathrm{d}X}{r} - \left[\frac{X}{r}\right]_{-q}^{q}\right) = \frac{f_x}{8\pi\mu}\left[4\sinh^{-1}\left(\frac{q}{a}\right) - \frac{2q}{(q^2+a^2)^{1/2}}\right]. \tag{8}$$

With an error of order $(a/q)^2$, this expression can be written as

$$\frac{f_x}{8\pi\mu}\left(4\ln\frac{2q}{a} - 2\right) = \frac{f_x}{8\pi\mu}\left(4\ln\frac{q}{\delta}\right) \tag{9}$$

with $\delta = 0.5ae^{1/2}$. This in turn is the same as

$$\int_{\delta<r_0<q}\frac{f_x}{8\pi\mu}\frac{2\mathrm{d}s}{r_0}; \tag{10}$$

that is, as the contribution to the x-component of (4) from the f_x-component of $f(s)$ in $r_0 < q$ (where, in the present coordinates, $\mathrm{d}s = \mathrm{d}X$ and $r_0 = |X|$).

Furthermore, the velocity field generated by the y-component f_y of the stokeslet distribution, with its accompanying dipole distribution $-a^2 f_y/4\mu$, is

$$\int_{-q}^{q}\frac{f_y}{8\pi\mu}\left[\left(\frac{(x-X)\,y,\ r^2+y^2,\ yz}{r^3}\right) + \tfrac{1}{2}a^2\left(\frac{-3(x-X)y,\ \ r^2-3y^2,\ -3yz}{r^5}\right)\right]\mathrm{d}X. \tag{11}$$

This is easily evaluated on the cross-sectional surface (7) because, with quantities of order $(a/q)^2$ again neglected,

$$\int_{-q}^{q}\frac{\mathrm{d}X}{r^3} = \tfrac{3}{2}a^2\int_{-q}^{q}\frac{\mathrm{d}X}{r^5} \tag{12}$$

(both sides taking the value $2/a^2$), so that the terms in y, y^2 and yz that vary around the cross-section cancel out. Accordingly, the only nonzero component of (11) is its y-component

$$\frac{f_y}{8\pi\mu}\left(\int_{-q}^{q}\frac{\mathrm{d}X}{r} + \tfrac{1}{2}a^2\int_{-q}^{q}\frac{\mathrm{d}X}{r^3}\right) = \frac{f_y}{8\pi\mu}\left(2\ln\frac{2q}{a}+1\right), \tag{13}$$

which by comparison with (9) can be written

$$\frac{f_y}{4\pi\mu} + \frac{f_y}{8\pi\mu}\left(2\ln\frac{q}{\delta}\right); \tag{14}$$

that is, as the contribution to the y-component of (4) from the f_y-component of $f(s)$ in $r_0 < q$. The proof for the f_z-component proceeds exactly as for the f_y-component.

ASSESSMENT OF ERROR. It remains to assess the errors which may have arisen through those two simplifications that were adopted in the core of the proof; namely, the assumptions of uniform stokeslet distribution and zero centreline curvature in $r_0 < q$. We show that, if the radius a is much less than other lengths in the problem, then the error varies linearly (rather than, say, logarithmically) with that ratio of lengths.

For example, if points on the centreline have coordinates $(X, \kappa X^2, 0)$, corresponding to a curvature κ in the plane $z = 0$, then y must be replaced in (5) and (6) by $y - \kappa X^2$. On the cross-section $x = 0$, $y^2 + z^2 = a^2$ this, to a first approximation in κ, makes

$$r = \left[X^2 + (y - \kappa X^2)^2 + z^2\right]^{1/2} \doteq \left[(1 - \kappa y)^2 X^2 + a^2\right]^{1/2}, \tag{15}$$

exactly as if X were replaced by $(1 - \kappa y)X$. In short, there are relative errors of order κa in the constancy of the velocity distributions (10) and (14) all around the cross-section; that is, errors varying linearly with the ratio of the radius a of the flagellum to the radius of curvature of its centreline.

Again, the effect of nonuniformity in stokeslet distribution may be test by inserting a factor $(1 + \xi X)$ within the integrals (5) or (11) to allow for the effect of a component of stokeslet strength varying at a relative rate per unit length alone the centreline. The result is to change (5) by an amount

$$(0,\ \xi y,\ \xi z)\frac{f_x}{8\pi\mu}\left(-2\ln\frac{2q}{a} + 2\right) \tag{16}$$

representing a relative error of order ξa varying linearly with the ratio of a to the length scale ξ^{-1} of variation of stokeslet strength. The same order of magnitude error is produced in (11), and it may be concluded that a close approximation to the velocity distribution (14) is produced all over the cross-section $s = s_0$, as stated in the basic theorem.

3. Spherical and circular means for Stokes flows.

The last two sections of this paper reinterpret, respectively, those two features of the basic theorem that were designated (a) and (b) in section 1. Firstly, then, the presence of dipoles is discussed.

There is an inherent relationship between any Lorentz representation of a flow at very low Reynolds number by means of a surface distribution of stokeslets and alternative representations through centrally located stokeslet/dipole combinations. This relationship is already present in Stokes's classical motion of fluid generated when a sphere of radius a acts on it with force $\mathbf{F}$. (Here, $\mathbf{F} = 6\pi\mu a\mathbf{U}$, where $\mathbf{U}$ is the sphere's resulting velocity.) As mentioned in section 1, the total force (pressure and viscous force) with which each unit of the sphere's surface area acts on the fluid takes a uniform value (Batchelor [5], p.233). This can be written $\mathbf{F}/4\pi a^2$ (overall force divided by overall area) and so the Lorentz representation of the flow is as a uniform distribution of stokeslets of strength $\mathbf{F}/4\pi a^2$ per unit area over the surface of the sphere.

Now, because the stokeslet field (2) depends only on the vector displacement $\mathbf{r}$, which signifies the position of a field point P relative to the stokeslet's position, the velocity at P due to stokeslets of total strength $\mathbf{F}$ distributed uniformly over a sphere of radius a centred on O is identical with the average velocity over a sphere of radius a centred on P due to just one stokeslet of strength $\mathbf{F}$ concentrated at O. This average velocity is often called a spherical mean.

A familiar result for a solution of Laplace's equation is that its mean value over any sphere is equal to its value at the centre. But for a velocity field satisfying Eqs. (1) it is not $\mathbf{u}$ but its

Laplacian $\nabla^2\mathbf{u}$ which (itself) satisfies Laplace's equation. The spherical mean $\mathbf{S}(a)$ of such a velocity field $\mathbf{u}$ over a sphere of radius a is equal, not to the value of $\mathbf{u}$ at the centre P, but to the value of

$$\mathbf{u}+\frac{1}{6}a^2\nabla^2\mathbf{u} \tag{17}$$

at P. (This slightly less familiar result is proved by using the divergence theorem to express $4\pi a^2 d\mathbf{S}/da$ as the volume integral of $\nabla^2\mathbf{u}$ over the sphere's interior; which in turn is equal to the sphere's volume $(4\pi a^3/3)$ times the central value of $\nabla^2\mathbf{u}$ since all of its spherical means coincide with that central value.)

Moreover, Eqs. (1) and (2) show how, when a stokeslet of strength $\mathbf{F}$ has $\mathbf{u}$ as its field, $\nabla^2\mathbf{u}$ is the field associated with a dipole of strength $(-\mathbf{F}/\mu)$. Accordingly, expression (17) is just that combination of the stokelet with a dipole of strength $(-a^2\mathbf{F}/6\mu)$ which appears in the classical motion of Stokes – here reinterpreted in terms of Lorentz's surface distribution of stokeslets.

The result analogous to (17) for a two-dimensional velocity field $\mathbf{u}(y, z)$ satisfying Eqs. (1) is that the circular mean $\mathbf{C}(a)$ of $\mathbf{u}$, taken around any circle of radius a in the (y, z) plane, is equal to the value of

$$\mathbf{u}+\frac{1}{4}a^2\nabla^2\mathbf{u} \tag{18}$$

at its centre P. (Here, the result emerges when the divergence theorem is used to express $2\pi a d\mathbf{C}/da$ as the area integral of $\nabla^2\mathbf{u}$ over the circle's interior; which is the circle's area πa^2 times that central value with which all circular means of the harmonic function $\nabla^2\mathbf{u}$ coincide.)

Such a locally two-dimensional field is generated by those stokeslets normal to the flagellar centreline whose strengths are designated in the basic theorem as $\mathbf{f}_n(s)$ per unit length. Now, if it can be shown that (as stated in section 1) the force with which a section of flagellum acts on the fluid is distributed uniformly around its perimeter, then also the Lorentz distribution of normal stokeslets is similarly uniform. Therefore its velocity field at P is identical to the circular mean $\mathbf{C}(a)$ around a circle centred on P for the field $\mathbf{u}$ of a line distribution of stokeslets concentrated along the x-axis. Eq. (18) for $\mathbf{C}(a)$, alongside a continued identification of the Laplacian $\nabla^2\mathbf{u}$ of the field of a stokeslet of strength $\mathbf{F}$ with the field of a dipole of strength $(-\mathbf{F}/\mu)$, would then give a complete explanation of the result (3) that normal stokeslets of strength $\mathbf{f}_n(s)$ per unit length are accompanied by dipoles of strength $(-a^2\mathbf{f}_n(s)/4\mu)$ per unit length.

This plausible elucidation of the result (3) rests on the supposition that any normal force $\mathbf{f}_n(s)$ with which unit length of flagellum acts on the fluid is distributed uniformly around its surface. Section 3 is now concluded with a direct verification of this uniformity for the velocity field (11) associated with a force f_y in the y-direction.

Briefly, the velocity field (11) in the plane $x = 0$ has its x-component zero (as the integral of an odd function of X) and its y-component and z-components equal to

$$u_y = \frac{f_y}{8\pi\mu}\left[2\ln\frac{2q}{(y^2+z^2)^{1/2}}+\frac{2y^2}{y^2+z^2}-a^2\frac{y^2-z^2}{(y^2+z^2)^2}\right] \tag{19}$$

$$u_z = \frac{f_y}{8\pi\mu}\left[\frac{2yz}{y^2+z^2}-a^2\frac{2yz}{(y^2+z^2)^2}\right]; \tag{20}$$

from which the associated distribution of pressure p is derived, by Eq. (1), as

$$p = \frac{f_y}{2\pi} \frac{y}{y^2 + z^2} \, . \tag{21}$$

Next, the (compressive) stress distributions

$$p_{yy} = p - 2\mu \frac{\partial u_y}{\partial y}, \quad p_{yz} = -\mu \left(\frac{\partial u_y}{\partial z} + \frac{\partial u_z}{\partial y} \right), \quad p_{zz} = p - 2\mu \frac{\partial u_z}{\partial z} \tag{22}$$

can be calculated, and their values on the surface (7) of the cross-section obtained as

$$p_{yy} = \frac{f_y}{2\pi a^4}(y^3 + 3yz^2), \; p_{yz} = \frac{f_y}{2\pi a^4}(z^3 - y^2 z), \; p_{zz} = \frac{f_y}{2\pi a^4}(y^3 - yz^2); \tag{23}$$

from which it follows that the force per unit area with which the flagellum acts on the fluid has y- and z-components

$$\frac{yp_{yy} + zp_{yz}}{a} = \frac{f_y}{2\pi a} \frac{(y^2 + z^2)^2}{a^4} = \frac{f_y}{2\pi a} \quad \text{and} \quad \frac{yp_{yz} + zp_{zz}}{a} = 0. \tag{24}$$

These take, as previously stated, uniform values (equal, of course, to force per unit length divided by cross-section circumference). A similar check may be made for the f_z-component of force, completing the elucidation of feature (a) of the basic theorem in terms of the Lorentz distribution.

4. Stokeslet rings and their three-dimensional fields

Its other feature (b) is related to that cutoff δ which the inverse-first-power behaviour of a stokeslet field (2) makes necessary if effects on the flagellar surface of a curvilinear distribution of stokeslets along the flagellar centreline are to be represented (as in the theorem) by corresponding effects on the centreline itself. It turns out that an identical cutoff is needed when effects of the Lorentz distribution of stokeslets around the flagellar surface are to be similarly represented.

It has just been shown that, at each cross-section, the "ring of stokeslets" around the perimeter is of uniform strength, even for stokeslet components normal to the centreline (the corresponding result is sufficiently obvious by symmetry – as well as analytically immediate from (5) – for components parallel to the centreline). This section is concerned with inverse-first-power terms in three-dimensional fields associated with distributions of such azimuthally uniform stokeslet rings.

As in section 3, we use the fact that a stokeslet field (2) depends only on the relative position $\mathbf{r}$ between field point and stokeslet. Accordingly, terms in r^{-1} in expressions (8) and (11) for the velocity field on the surface due to a distribution of stokeslets along the centreline have a "reciprocal" property: they are identical to terms in r^{-1} in the velocity field on the centreline due to a distribution of stokeslet rings of the same strength per unit length. On the other hand, these r^{-1} terms in that velocity field must take their centreline values at all points inside or on the flagellar surface; simply because, as cylindrically symmetrical potentials satisfying Laplace's equation throughout the interior of the flagellar surface, they are constrained to remain constant. In particular, the surface values of these terms in r^{-1} associated with stokeslet rings coincide with centreline values; which themselves, as just remarked, coincide with surface values due to a distribution of stokeslets along the centreline. Therefore, both distributions share the same cutoff value δ.

This simple argument without the need for any calculation is supported, of course, by a detailed analysis where, in expressions (8) and (11), there is a substitution of each term

$$\int_{-q}^{q} \frac{\mathrm{d}X}{(X^2+a^2)^{1/2}} \quad \text{by} \quad \int_0^{2\pi}\int_{-q}^{q} \frac{\mathrm{d}X}{\left[X^2+4a^2\sin^2(\theta/2)\right]^{1/2}}\,\mathrm{d}\theta \tag{25}$$

to represent the effect of stokeslet rings. Here, $2a\sin(\theta/2)$ is the length of the chord joining points on a circular cross-section which subtend an angle θ at the centre. With an error of order $(a/q)^2$, both terms in (25) take the same value $2\ln(2q/a)$, as follows from the standard integral result (itself derived by comparing the results of alternative substitutions $\theta = \pi - \theta_1$ and $\theta = 2\theta_2$)

$$\int_0^{\pi} \ln\left[2\sin(\theta/2)\right]\mathrm{d}\theta = 0. \tag{26}$$

It may be noted that even though the inner integral in (25) becomes infinite for $\theta = 0$ (where field point and stokeslet are at the same azimuthal position) the stokeslet ring as a whole has no corresponding singularity because the integral (26) converges. Its actual value of zero, moreover, confirms the previously given reinterpretation of the theorem's feature (b) in terms of those distributions of stokeslet rings which are suggested by the pioneering work of Lorentz [1].

5. Conclusion

The basic theorem, offering a computationally convenient representation of the flow field of a waving flagellum by a curvilinear distribution of singularities along the flagellar centreline – with two special features, that (a) the singularities include dipoles as well as stokeslets and that (b) centreline values of velocity fields are determined by singularities beyond a certain cutoff distance – was stated and proved in section 2. Then it was reinterpreted in sections 3 and 4, covering features (a) and (b) respectively, and shown to be fully compatible with the Lorentz representation by a surface distribution of stokeslets.

Both special features arise because a stokeslet field depends only on the relative position of singularity and field point. Accordingly, (a) the Lorentz field is effectively a circular mean of a curvilinear distribution of stokeslet fields, and thus equates to a stokeslet/dipole distribution as in the theorem; while, moreover, (b) the Lorentz distribution of stokeslet rings has values of inverse-first-power terms in its field on the flagellar surface which, by standard properties of harmonic functions, coincide with any interior value, including that centreline value which necessarily has the same cutoff distance as the surface field of a centreline distribution of stokeslets.

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