# Stokesian swimming of a prolate spheroid at low Reynolds number 

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#### Abstract

The swimming of a prolate spheroid immersed in a viscous incompressible fluid and performing surface deformations periodically in time is studied on the basis of Stokes' equations of low Reynolds number hydrodynamics. The average over a period of time of the translational and rotational swimming velocity and the rate of dissipation are given by integral expressions of second order in the amplitude of surface deformations. The first order flow velocity and pressure, as functions of prolate spheroidal coordinates, are expressed as sums of basic solutions of Stokes' equations. Sets of superposition coefficients of these solutions which optimize the mean translational swimming speed for given power are derived from an eigenvalue problem. The maximum eigenvalue is a measure of the efficiency of the optimal stroke within the chosen class of motions. The maximum eigenvalue for sets of low multipole order is found to be a strongly increasing function of the aspect ratio of the spheroid.


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## 1. Introduction

The theory of the swimming of micro-organisms in a viscous incompressible fluid is based on the Stokes equations of low Reynolds number hydrodynamics [1]. In this regime inertia plays no role and the effect of swimming can be understood on the basis of purely viscous flow. It was shown by Taylor [2] in the example of the swimming of a planar sheet distorted by a transverse surface wave that the effect is purely kinematic. His calculation to second order in the wave amplitude leads to a swimming velocity which is independent of the viscosity of the fluid. Taylor's analysis was subsequently extended to a squirming sphere by Lighthill [3]. Blake corrected this work and applied it in a spherical envelope approach to ciliary propulsion [4].

The calculations of mean translational swimming velocity and rate of dissipation to second order in the amplitude of surface distortion are complicated, and for simplicity, the analysis for a sphere was restricted to axial strokes. The extension to general strokes was derived only recently [5]. The extension also allows the mean rotational swimming velocity achieved by a general stroke to be calculated.

In the following we consider Stokesian swimming of a prolate spheroid, again to second order in the amplitude of surface distortion. Since arbitrary aspect ratio is allowed, the model provides interesting physical applications. In particular the swimming of Paramecium should be well described by the model.

[^0]Paramecium rotates about its long axis as it swims, so that it is important to consider both the mean translational and rotational swimming velocity. The motion of a prolate spheroid on the basis of active particle theory was studied by Leshansky et al. [6] for a particular mode of steady tangential surface distortion.

The reciprocal theorem [1] is used to derive integral expressions for the mean translational and rotational swimming velocity which are bilinear in the amplitude of surface displacements. We show how these expressions, when written in terms of prolate spheroidal coordinates, can be reduced to one-dimensional integrals over the polar variable. In the process we encounter identities which have been known for a long time in terms of ellipsoidal coordinates [7-9]. The validity of the identities was explained recently by Kim $[10,11]$ on the basis of a symmetry property of the Stokes double-layer operator [12].

In the calculation, the first order flow velocities and pressures are expanded in terms of a basic set of solutions of the steady state Stokes equations. We derive these solutions as functions of prolate spheroidal coordinates. The mean swimming velocities and the mean rate of dissipation become bilinear expressions in terms of the amplitudes of the mode functions involving three matrices corresponding to the chosen representation. As usual, optimization of the translational swimming speed for given power leads to an eigenvalue problem [13-17]. The maximum eigenvalue is a measure of the efficiency of the optimal stroke within the chosen class of motions. In contrast to the case of a sphere, the three matrices cannot be evaluated analytically. We derive numerical results for the maximum eigenvalue for a wide range of aspect ratios, as well as for the corresponding mean rate of rotation.

## 2. Swimming velocity and power

We consider a prolate spheroid of major semi-axis $a$ and minor semi-axis $b$ immersed in a viscous incompressible fluid of shear viscosity $\eta_{s}$. We choose Cartesian coordinates such that the $z$ axis is in the direction of the long axis. At low Reynolds number and on a slow time scale the flow velocity $\boldsymbol{v}(\boldsymbol{r}, t)$ and the pressure $p(\boldsymbol{r}, t)$ satisfy the Stokes equations
$\eta_{s} \nabla^{2} \boldsymbol{v}-\nabla p=0, \quad \nabla \cdot \boldsymbol{v}=0$.
The fluid is set in motion by distortions of the surface which are periodic in time and lead to a time-dependent flow field as well as to a swimming motion of the spheroid. The surface displacement $\boldsymbol{\xi}(\boldsymbol{s}, t)$ is defined as the vector distance
$\xi=s^{\prime}-s$
of a point $\boldsymbol{s}^{\prime}$ on the displaced surface $S(t)$ from the point $\boldsymbol{s}$ on the spheroid with surface $S_{0}$. The fluid velocity $\boldsymbol{v}(\boldsymbol{r}, t)$ in the rest frame is required to satisfy [15]
$\boldsymbol{v}(\boldsymbol{s}+\boldsymbol{\xi}(\boldsymbol{s}, t))=\frac{\partial \boldsymbol{\xi}(\boldsymbol{s}, t)}{\partial t}$,
corresponding to a no-slip boundary condition. The instantaneous translational swimming velocity $\boldsymbol{U}(t)$, the rotational swimming velocity $\boldsymbol{\Omega}(t)$, and the flow pattern $(\boldsymbol{v}, p)$ follow from the condition that no net force or torque is exerted on the fluid. We evaluate these quantities by a perturbation expansion in powers of the displacement $\boldsymbol{\xi}(\boldsymbol{s}, t)$.

To second order in $\xi$ the flow velocity and the swimming velocity take the form [15]

$$
\begin{align*}
& \boldsymbol{v}(\boldsymbol{r}, t)=\boldsymbol{v}_{1}(\boldsymbol{r}, t)+\boldsymbol{v}_{2}(\boldsymbol{r}, t)+\cdots, \\
& \boldsymbol{U}(t)=\boldsymbol{U}_{2}(t)+\cdots . \tag{2.4}
\end{align*}
$$

Both $\boldsymbol{v}_{1}$ and $\boldsymbol{\xi}$ are assumed to vary harmonically with frequency $\omega$, and can be expressed as

$$
\begin{align*}
\boldsymbol{v}_{1}(\boldsymbol{r}, t) & =\boldsymbol{v}_{1 c}(\boldsymbol{r}) \cos \omega t+\boldsymbol{v}_{1 s}(\boldsymbol{r}) \sin \omega t \\
\boldsymbol{\xi}(\boldsymbol{s}, t) & =\boldsymbol{\xi}_{c}(\boldsymbol{s}) \cos \omega t+\boldsymbol{\xi}_{s}(\boldsymbol{s}) \sin \omega t \tag{2.5}
\end{align*}
$$

Expanding the no-slip condition Eq. (2.3) to second order we find for the flow velocity at the surface
$\boldsymbol{u}_{1 S}(\boldsymbol{s}, t)=\left.\boldsymbol{v}_{1}\right|_{S_{0}}=\frac{\partial \boldsymbol{\xi}(\boldsymbol{s}, \boldsymbol{t})}{\partial t}$,
$\boldsymbol{u}_{2 S}(\boldsymbol{s}, t)=\left.\boldsymbol{v}_{2}\right|_{S_{0}}=-\left.\boldsymbol{\xi} \cdot \nabla \boldsymbol{v}_{1}\right|_{S_{0}}$.
In complex notation with $\boldsymbol{v}_{1}=\boldsymbol{v}_{\omega} \exp (-i \omega t)$ the mean second order surface velocity is given by
$\overline{\boldsymbol{u}}_{2 S}(\boldsymbol{s})=-\left.\frac{1}{2} \operatorname{Re}\left(\boldsymbol{\xi}_{\omega}^{*} \cdot \nabla\right) \boldsymbol{v}_{\omega}\right|_{S_{0}}$,
where the overhead bar indicates a time-average over a period $T=2 \pi / \omega$.

The time-averaged second order flow velocity $\overline{\boldsymbol{v}^{(2)}}(\boldsymbol{r})$ and corresponding mean pressure $\overline{\overline{p^{(2)}}}(\boldsymbol{r})$ satisfy the Stokes equations Eq. (2.1) with boundary value $\overline{\boldsymbol{v}^{(2)}}(\boldsymbol{s})=\overline{\boldsymbol{u}}_{2 S}(\boldsymbol{s})$. Moreover the flow tends to $-\overline{\boldsymbol{U}^{(2)}}-\overline{\boldsymbol{\Omega}^{(2)}} \times \boldsymbol{r}$ at infinity and satisfies the condition of vanishing hydrodynamic force and torque. In the laboratory frame this corresponds to the flow $\left(\overline{\boldsymbol{u}^{(2)}}(\boldsymbol{r}), \overline{p^{(2)}}(\boldsymbol{r})\right)$ with
$\overline{\boldsymbol{u}^{(2)}}(\boldsymbol{r})=\overline{\boldsymbol{U}^{(2)}}+\overline{\boldsymbol{\Omega}^{(2)}} \times \boldsymbol{r}+\overline{\boldsymbol{v}^{(2)}}(\boldsymbol{r})$.
As a second flow we consider the solution of the Stokes friction problem for solid body motion of the surface $S_{0}$ with force $\mathcal{F}$ and
torque $\boldsymbol{\mathcal { T }}$ exerted on the fluid. Applying the reciprocal theorem [1] to the pair of flows we find the relation
$\mathcal{F} \cdot \overline{\boldsymbol{U}^{(2)}}+\boldsymbol{\mathcal { T }} \cdot \overline{\boldsymbol{\Omega}^{(2)}}=\int_{S_{0}} \boldsymbol{n} \cdot \boldsymbol{\sigma}_{f r} \cdot \overline{\boldsymbol{u}}_{2 S} d S_{0}$,
where $\boldsymbol{n}$ is the outward normal to the surface $S_{0}$ and $\sigma_{f r}$ is the stress tensor for the Stokes friction problem with translation and rotation.

We consider periodic surface distortions such that the mean translational displacement of the spheroid is in the $z$ direction and the mean rotation is about the $z$ axis. For the second order mean translational swimming velocity $\bar{U}_{2}$ we have
$\bar{U}_{2}=\frac{1}{\mathcal{F}_{z}} \int_{S_{0}} \boldsymbol{n} \cdot \boldsymbol{\sigma}_{T_{z}}(\boldsymbol{s}) \cdot \overline{\boldsymbol{u}}_{2 S}(\boldsymbol{s}) d S_{0}$,
where $\sigma_{T z}(\boldsymbol{s})$ is the stress exerted at the surface $S_{0}$ when the spheroid with no-slip boundary condition is subjected to a force $\mathcal{F}_{z} \boldsymbol{e}_{z}$ in the $z$ direction. Similarly the second order mean rotational swimming velocity $\bar{\Omega}_{2}$ is given by
$\bar{\Omega}_{2}=\frac{1}{\mathcal{T}_{z}} \int_{S_{0}} \boldsymbol{n} \cdot \boldsymbol{\sigma}_{R z}(\boldsymbol{s}) \cdot \overline{\boldsymbol{u}}_{2 S}(\boldsymbol{s}) d S_{0}$,
where $\sigma_{R z}(\boldsymbol{s})$ is the stress exerted at the surface $S_{0}$ when the spheroid with no-slip boundary condition is subjected to a torque $\mathcal{T}_{z} \boldsymbol{e}_{z}$ in the $z$ direction.

To second order the mean rate of dissipation $\overline{\mathscr{D}}_{2}$ is determined entirely by the first order solution. It may be expressed as a surface integral [15]
$\bar{D}_{2}=-\frac{1}{2} \operatorname{Re} \int_{S_{0}} \boldsymbol{v}_{\omega}^{*} \cdot \boldsymbol{\sigma}_{\omega} \cdot \boldsymbol{n} d S_{0}$,
where $\sigma_{\omega}$ is the first order stress tensor, given by
$\boldsymbol{\sigma}_{\omega}=\eta_{s}\left(\nabla \boldsymbol{v}_{\omega}+\left[\nabla \boldsymbol{v}_{\omega}\right]^{T}\right)-p_{\omega} \boldsymbol{I}$.
The mean rate of dissipation equals the power necessary to generate the motion.

## 3. Mode functions

We use spheroidal coordinates $(\xi, \eta, \varphi)$ in which the Cartesian coordinates $(x, y, z)$ are expressed as
$x=c \sqrt{\left(\xi^{2}-1\right)\left(1-\eta^{2}\right)} \cos \varphi$,
$y=c \sqrt{\left(\xi^{2}-1\right)\left(1-\eta^{2}\right)} \sin \varphi$,
$z=-c \xi \eta$,
where $c=\sqrt{a^{2}-b^{2}}$ is the semi-focal distance. The surface of the spheroid corresponds to the value $\xi_{0}$ given by
$a=c \xi_{0}, \quad b=c \sqrt{\xi_{0}^{2}-1}$.
The coordinates vary in the ranges $\xi_{0}<\xi<\infty,-1<\eta<1$, $0<\varphi<2 \pi$. For large $\xi$ the surface $\xi=$ constant becomes spherical and the variable $\eta$ can be identified with $-\cos \theta$, where $\theta$ is the polar angle. The variable $\varphi$ is the azimuthal angle. The coordinates $(\xi, \eta, \varphi)$ are identical to those introduced by Morse and Feshbach [18], except for the minus sign in the last line of Eq. (3.1). Our choice guarantees a right-handed system.

The metric coefficients are given by
$h_{1}=\frac{1}{c} \sqrt{\frac{\xi^{2}-1}{\xi^{2}-\eta^{2}}}, \quad h_{2}=\frac{1}{c} \sqrt{\frac{1-\eta^{2}}{\xi^{2}-\eta^{2}}}$,
$h_{3}=\frac{1}{c} \sqrt{\frac{1}{\left(\xi^{2}-1\right)\left(1-\eta^{2}\right)}}$.

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