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Propulsion of Microorganisms by Surface Distortions

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Swimming strategies of microorganisms must conform to the principles of self-propulsion at low Reynolds numbers. Here we relate the translational and rotational speeds to the surface motions of a swimmer and, for spheres, make evident novel constraints on mechanisms for propulsion. The results are applied to a cyanobacterium, an organism whose motile mechanism is unknown, by considering incompressible streaming of the cell surface and oscillatory, tangential surface deformations. Finally, swimming efficiency using tangential motions is related to the surface velocities and a bound on the efficiency is obtained. [S0031-9007(96)01605-5]

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Swimming microorganisms live in an environment where viscous forces control their movements [1,2]. Motion is produced by a cyclic distortion of the body shape [3,4], e.g., by the coordinated use of cilia or flagella [5,6]. The swimming speed depends on the details of such motions and is constrained such that geometrically reversible surface deformations produce no net displacement of the cell body [5,7].

One topic of scientific interest is to relate an organism's swimming speed to the surface velocity which is prescribed by a particular cyclic deformation [4,8,9]. Traditional approaches to this problem involve obtaining the general solution to the governing differential equations of low Reynolds number flows, imposing the boundary conditions for the particular surface motion of interest, and then calculating the swimming speed. In fact, as is shown below, there is a direct relationship between the swimming speed and the surface motions, which does not entail developing the detailed flow field. Furthermore, in certain cases, the swimming speed may be easily calculated from this relationship. An upper bound on the efficiency of the swimming stroke may also be established.

We begin our analysis with the equations for incompressible fluid motion in the low Reynolds number limit,

$$-\nabla p + \mu \nabla^2 \mathbf{u} = \mathbf{0} = \nabla \cdot \boldsymbol{\sigma} \quad \text{and} \quad \nabla \cdot \mathbf{u} = 0 \,, \tag{1}$$

where $\mathbf{u}$ and p are the fluid velocity and pressure, respectively, and $\boldsymbol{\sigma}$ is the stress tensor. The lack of explicit time dependence in the equations requires that a self-propelled object must execute, in shape space, a cyclic deformation which does not retrace its path [4], and so reciprocal motions are not allowed.

We next utilize the reciprocal theorem from low Reynolds number hydrodynamics [10] in order to relate the surface motions to the swimming speed. We are interested in the solution to Eq. (1) for self-propelled swimming microorganisms. Let $(\mathbf{u}, \boldsymbol{\sigma})$ be the velocity and stress fields that are the solution to (1) such that there is no net force or torque on the swimming body. Also, let $(\hat{\mathbf{u}}, \hat{\boldsymbol{\sigma}})$ be the solution to (1) for translation of the same shaped object at a velocity $\hat{\mathbf{U}}(t)$ when acted upon by an external force $\hat{\mathbf{F}}(t)$. The reciprocal theorem states that the solution $(\mathbf{u}, \boldsymbol{\sigma})$ and $(\hat{\mathbf{u}}, \hat{\boldsymbol{\sigma}})$ are related by

$$\int_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u} \, dS = \int_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma} \cdot \hat{\mathbf{u}} \, dS \,, \tag{2}$$

where $S(t)$ is the instantaneous boundary of the swimming object, $\mathbf{n}$ is the unit outward normal to S, $\mathbf{n} \cdot \boldsymbol{\sigma}$ is the stress the fluid exerts on the surface, and the velocities $\mathbf{u}$ and $\hat{\mathbf{u}}$ decay far from S. Since $\hat{\mathbf{u}} = \hat{\mathbf{U}}$ on S and the swimming object is force-free, the right-hand side of (2) vanishes. The surface velocity for the self-propelled swimmer is then decomposed into a translational velocity $\mathbf{U}(t)$ and a disturbance motion $\mathbf{u}'$, which typically varies over the surface. Equation (2) then simplifies to

$$\hat{\mathbf{F}}(t) \cdot \mathbf{U}(t) = -\int_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}' \, dS \,. \tag{3}$$

Equation (3) relates the instantaneous swimming speed to the instantaneous surface velocity for any shape of self-propelled organism.

In particular, for a sphere of radius a, the surface stress is $\mathbf{n} \cdot \hat{\boldsymbol{\sigma}} = -\frac{3\mu}{2a} \hat{\mathbf{U}}$ and the Stokes drag force is $\hat{\mathbf{F}} = -6\pi\mu a \hat{\mathbf{U}}$ so that (3) reduces to

$$\mathbf{U}(t) = -\frac{1}{4\pi a^2} \int_S \mathbf{u}' \, dS \,. \tag{4}$$

For many cyclic deformations, $\mathbf{u}'$ is time dependent. The mean translational velocity corresponds to the time average of Eq. (4).

For an arbitrarily shaped, torque-free swimmer that rotates with angular velocity $\boldsymbol{\Omega}(t)$ (without translation) owing to a suitable cyclic deformation of the surface, the analog of (3) is

$$\hat{\mathbf{L}} \cdot \mathbf{\Omega} = -\int_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}' dS \,, \tag{5}$$

where $\hat{\mathbf{L}}$ is the hydrodynamic torque that acts on the rigid object when it rotates with angular velocity $\hat{\mathbf{\Omega}}$. For a rigidly rotating sphere $\hat{\mathbf{L}} = -8\pi\mu a^3 \hat{\mathbf{\Omega}}$ and $\mathbf{n} \cdot \hat{\boldsymbol{\sigma}} = -3\mu \hat{\mathbf{\Omega}} \wedge \mathbf{n}$ from which it follows that the angular velocity of a spherical swimmer due to surface deformation obeys

$$\mathbf{\Omega}(t) = -\frac{3}{8\pi a^3} \int_S \mathbf{n} \wedge \mathbf{u}' dS \,. \tag{6}$$

We note that both (4) and (6) were arrived at recently using a perturbation expansion approach to the swimming problem for the special case of small amplitude oscillations of a spherical object [11,12]. The derivation presented here shows that analogous results, (3) and (5), are valid for arbitrarily shaped swimmers. Equations (4) and (6), which apply to spherical swimmers, hold for finite amplitude surface deformations. Simultaneous translation and rotation are studied simply by adding Eqs. (3) and (5).

Using Eq. (4) particular mechanisms for swimming motility may be explored. Here we discuss swimming cyanobacteria [13] with the understanding that our results apply equally well to other species. As cyanobacteria have no external appendages, the cell body (approximately a spheroid with aspect ratio about 2) must itself generate thrust. Also, no observable shape changes accompany translation. Pitta and Berg [14] exclude the possibility of self-electrophoresis and raise the possibility of a bulk streaming of the cell surface. Here we model the cyanobacterium as a sphere and note that an incompressible (i.e., divergence-free) surface velocity field on a sphere can be written as the curl of a potential function which has but a radial component. The surface integral of such a surface flow is identically zero, and hence according to (4) the swimming speed is zero. Thus, incompressible, tangential surface deformations are not propulsive, which rules out simple tangential streaming of the cell surface as a possible swimming mechanism.

The remaining mechanism for cyanobacteria's motility is a cyclic, nonreciprocal, and compressible surface distortion, i.e., a traveling wave. Blake [9] originally considered this type of problem for the case of ciliated microorganisms by supposing that the waving tips of the cilia serve as an effective compressible surface. Cyanobacteria [13], though lacking cilia, might be covered with a motor protein which is capable of similar wavelike motions. For instance, in terms of spherical surface coordinates (ϕ, θ), suppose that a material point ϕ_m on the compressible surface moves in a small amplitude sinusoidal fashion [9]: $\phi_m = \phi + \epsilon \cos(n\phi - \omega t)$, which corresponds to a traveling wave moving from the pole at $\phi = 0$ toward $\phi = \pi$ ($\epsilon \ll 1$). Substituting this surface motion into (4), performing the surface integral accurate to $O(\epsilon^2)$, and time averaging gives the result

$$\langle \mathbf{U} \rangle = -\frac{\pi}{8} \epsilon^2 n \omega a \mathbf{e}_z \,, \tag{7}$$

where $\langle \cdot \rangle$ denote the time average and $\mathbf{e}_z$ is the direction from which ϕ is measured. Swimming speeds are about $10a\ \mathrm{s}^{-1}$, so assuming $\epsilon = 1/20$ and $n = 5$–10 yields that the assumed surface motions have frequencies $\omega = O(10^2\text{–}10^3)\ \mathrm{s}^{-1}$. This result [Eq. (7)] was also arrived at recently by using a traditional approach [15]. Note that the equations for low Reynolds number motions may be utilized to analyze periodic surface motions provided $\omega a^2/\nu \ll 1$, which is satisfied for 1 μm radius objects oscillating in water with the frequencies mentioned above.

To assess the plausibility of a mechanism for motility, it is not enough to know that the mechanism generates reasonable swimming speeds; the swimming mechanism should also be energetically efficient. Several authors have introduced definitions of efficiency for characterizing swimming strokes [3,4,9]. For simplicity we follow Lighthill's original definition [3], which is consistent with other definitions in that the same optimum swimming strokes are predicted (see Shapere and Wilczek [4]). In particular, we will draw some conclusions about the efficiency of tangential swimming motions, again using integral identities to bypass detailed calculations.

Any expression for efficiency requires the power $\mathcal{P}$ expended in the swimming stroke. The work done by an arbitrarily shaped swimming organism is dissipated viscously in the fluid and so

$$\mathcal{P} = -\int_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma} \cdot \mathbf{u} dS = 2\mu \int_{V(t)} \mathbf{E} : \mathbf{E} dV \,, \tag{8}$$

where $\mathbf{E}$ is the rate-of-strain tensor and $V(t)$ is the fluid volume surrounding the swimmer. Substituting the kinematic identity: $2\mathbf{E}{:}\mathbf{E} = \boldsymbol{\omega}^2 + 2(\nabla\mathbf{u}){:}(\nabla\mathbf{u})$ and using the divergence theorem, we find

$$\mathcal{P} = \mu \int_{V(t)} \boldsymbol{\omega}^2 dV - 2\mu \int_{S(t)} \mathbf{n} \cdot (\mathbf{u} \cdot \nabla\mathbf{u}) dS \,. \tag{9}$$

This result has two consequences. First, for two objects that translate at the same mean speed, more energy is dissipated by the object which produces the larger amount of vorticity. Therefore, an axisymmetric object that rotates as its swims is less efficient than the nonrotating swimmer [4]. Second, for organisms that move using purely tangential surface motions ($\mathbf{u}'$), the surface integral in (9) may be simplified to involve only the surface velocity (rather than gradients), which leads to

$$\mathcal{P} = \mu \int_{V(t)} \boldsymbol{\omega}^2 dV + 2\mu \int_{S(t)} \mathbf{u}'^2 \kappa_s dS \,, \tag{10}$$

where κ_s denotes the curvature of the surface measured along the direction of the surface flow [16]. In the particular case of spherical shapes translating with axisymmetric surface motions, $\kappa_s = 1/a$.

The Lighthill definition [3] of efficiency η_L of swimming spheres is $6\pi\mu a\langle U\rangle^2/\langle\mathcal{P}\rangle$. The swimming speed and power are known from above in terms of surface integrals of the velocity, and so (4) and (10) lead to the bound

$$\eta_L \leq \frac{3}{4}\left[\frac{\langle\int_S \mathbf{u}' dS\rangle^2}{4\pi a^2\langle\int_S \mathbf{u}'^2 dS\rangle}\right]. \tag{11}$$

Hence, knowledge of the surface velocities alone may be used to set an upper bound for the efficiency of a tangential swimming motion of a sphere. The term in brackets may be shown (using a version of the triangle inequality) to be bounded from above by unity, and so according to the Lighthill definition the swimming efficiency is $\eta_L < 3/4$; the Lighthill definition is proved to satisfy the criterion that the efficiency is less than unity.

For the small amplitude, sinusoidal tangential surface motions considered above, (11) leads to a bound on the efficiency $\eta_L < \frac{3\pi^2}{128}\epsilon^2 n^2$. However, on physical grounds $\mathcal{P} = O(n)$, and so we expect $\eta_L = O(n)$. Using Eq. (8) and details provided by Blake [9], we have calculated the efficiency numerically, and the results may be approximated by $\eta_L \approx \frac{3\pi^2}{128}\epsilon^2 n$ $(n \geq 2)$; this formula is only 2% different from the numerical calculations for $n \geq 10$ and within 33% for $n = 2$. The upper bound on efficiency for small amplitude motions becomes progressively worse as n increases. For the values of ϵ and n considered previously ($\epsilon = 1/20$ and $n = 10$), the efficiency is about 0.5%. For comparison, the hydrodynamic efficiency of a bacterial flagellum is about 2% [7]. We note that the hydrodynamic efficiency is in a real sense the upper bound on the overall mechanism for motility: the mechanism that transduces the organism's potential energy into mechanical work will have less than unit efficiency, and the overall efficiency of the swimming mechanism is the product of the energy transduction efficiency and the hydrodynamic efficiency.

In summary, Eqs. (3) and (5) provide a procedure for calculating swimming speeds for arbitrary swimming shapes and surface deformations. Spherical shapes, representative of many microorganisms, lead to Eqs. (4) and (6), which are particularly appealing and straightforward to apply. Equation (4) imposes a constraint on potential swimming mechanisms: incompressible, tangential surface motions are not propulsive. Furthermore, compressible surface motions lead to a simple result for the average swimming speed [Eq. (7)]. For more general situations, to calculate swimming speeds it is only necessary to calculate the Stokes drag force and torque and the surface stresses on the intermediate shapes within a cycle and perform the integral prescribed in Eqs. (3) and (5). Numerical methods may be applied to solve this more general problem. Finally, for tangential surface distortions, knowledge of the surface velocity field alone sets an upper limit to the swimming efficiency. Numerical methods are needed to calculate the power and efficiency of more complicated motions. Our results demonstrate that tangential travelling surface waves are a plausible mechanism for the swimming of spherical shapes as they predict both reasonable translational speeds and efficiencies.

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