Optimal Shapes of Surface Slip Driven Self-Propelled Microswimmers

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We study the efficiency of self-propelled swimmers at low Reynolds numbers, assuming that the local energetic cost of maintaining a propulsive surface slip velocity is proportional to the square of that velocity. We determine numerically the optimal shape of a swimmer such that the total power is minimal while maintaining the volume and the swimming speed. The resulting shape depends strongly on the allowed maximum curvature. When sufficient curvature is allowed the optimal swimmer exhibits two protrusions along the symmetry axis. The results show that prolate swimmers such as *Paramecium* have an efficiency that is ~20% higher than that of a spherical body, whereas some microorganisms have shapes that allow even higher efficiency.

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Many microorganisms use cilia or flagella for their propulsion. Flagella usually have a length that is comparable with the size of the organism, but cilia are much shorter and appear in large numbers, typically some thousands. Because they are short in comparison with the body of the swimmer, one can separate the length scale of ciliary beating from that of the fluid flow around the swimmer [1–3]. In this way the ciliary layer on the surface is replaced by an active surface slip velocity [4–6]. In other words, the relative fluid velocity close to the surface is not zero, but has a constant value determined by the action of cilia. The fluid itself is described by the Stokes equation.

Besides natural swimmers, a number of artificial swimmers have been proposed and also fabricated recently. While some of them use shape changes (often magnetically actuated) for propulsion [7], there are also a number of chemiphoretic swimmers [8–10], which can be well described with the surface slip formalism [5].

The search for the strokes that allow swimmers to maintain a certain speed with minimum dissipation has drawn considerable attention in recent years. Solved problems include the optimal stroke pattern of Purcell's three link swimmer [11], of an ideal elastic flagellum [12], of driven surface anchored filaments [13], of a shape-changing body [14], of a two-sphere and a three-sphere swimmer [15], of a spherical squirmer [16], and of *Chlamydomonas*' flagella [17].

We have recently numerically determined the optimal beating patterns of individual cilia, as well as densely covered infinite ciliated surfaces [3]. The resulting patterns have remarkable resemblance with many cilia found in nature. The stroke consists of a fast, stretched working stroke and a slower sweeping recovery stroke. The phases of cilia form metachronal waves. We have also shown how the ciliary efficiency is related to the swimming efficiency of a ciliated swimmer, which we assumed to be spherical. By comparing the theoretical optimum with an efficiency estimate for *Paramecium* we found them to differ by no more than a factor of 2, indicating that microorganisms have evolved for efficient swimming. This is in contrast with the opinion that swimming efficiency is not a major issue at the microscopic scale [18]. In fact, it has been shown experimentally that *Paramecium* uses more than half of its energy for swimming [19].

In this Letter we will go one step further and determine the optimal shape of the swimmer. For bodies driven by an external force, the shape with minimum drag was determined several decades ago by Pironneau [20]. It has the form of a rugby ball with an angle of 120° at both ends and a drag coefficient that is 0.954 times that of the sphere with the same volume [21]. So the gain from shape optimization of 4.5% is rather modest. We will show that it can be much bigger in the case of self-propelled swimmers.

The problem is formulated as follows. We are looking for the shape of the swimmer that is able to maintain a swimming speed u with minimum dissipation, while having a fixed volume V and a minimum allowed curvature radius $r_{\min}$. We will see later why it is important to restrict the maximum curvature. We have previously shown that the surface density of the power needed to generate a velocity v above the ciliary layer is given as

$$\frac{dP}{dS} = \frac{v^2}{\pi^2 \epsilon_c} = \frac{\eta}{\pi^2 L \epsilon_c'} v^2, \tag{1}$$

where η is the fluid viscosity, L is the length of the cilia, and ϵ_c' is the dimensionless collective efficiency, which can achieve a maximum value of ~0.016 [3]. Apart from the prefactors, the equation is easy to understand. If the fluid has the velocity v at a height L above the surface, but velocity 0 at the surface, the dissipated power per unit area is $\eta v^2/L$ in the case of uniform shear. Of course, any realistic propulsion mechanism has a significantly higher dissipation. For cilia it is at least 5 times higher. This equation also reveals that longer cilia are generally more efficient, but there are other limitations such as the bending moment and the power a cilium can generate.

We therefore have to minimize the integral $\oint v^2 dS$ for a constant swimming speed u and volume V. As there is no benefit in breaking the axial symmetry of the body shape we restrict ourselves to bodies that are axisymmetric around the direction of motion. The surface velocity v also has to be axisymmetric.

We parametrize the shape of the axisymmetric swimmer as $\rho(s)$ and $z(s)$. Then the volume of the body is

$$V = \int_{z_{\min}}^{z_{\max}} \pi \rho^2 dz. \tag{2}$$

We describe the fluid using finite boundary elements, specifically a method of regularized Stokeslets [22], adapted for axisymmetric bodies. The idea of regularized Stokeslets is to represent the force a body exerts on the surrounding fluid as a collection of highly localized forces distributed along its surface. In the axisymmetric case we replace the localized forces with N symmetric rings, as shown in Fig. 1. We denote the radius and position of the ith ring as ρ_i and z_i. The axial and radial components of the force density on the same ring are $f_{z,i}$ and $f_{\rho,i}$. The fluid velocity due to this force distribution, evaluated at point $(\rho_i, 0, z_i)$ is

$$\begin{aligned}\mathbf{v}_i = \frac{1}{8\pi\eta}\sum_{j=1}^{N}\int_0^{2\pi} & S^{\epsilon}(\rho_i \hat{e}_x + (z_i - z_j)\hat{e}_z - \rho_j \hat{e}_\rho(\phi)) \\ & \times [f_{\rho,j}\hat{e}_\rho(\phi) + f_{z,j}\hat{e}_z]\rho_j d\phi \end{aligned} \tag{3}$$

with $\hat{e}_\rho(\phi) = \hat{e}_x \cos\phi + \hat{e}_y \sin\phi$. S^ϵ is the tensor of a regularized Stokeslet

$$S^{\epsilon}_{\alpha\beta}(\mathbf{r}) = \frac{\delta_{\alpha\beta}(r^2 + 2\epsilon^2) + r_\alpha r_\beta}{(r^2 + \epsilon^2)^{3/2}}. \tag{4}$$

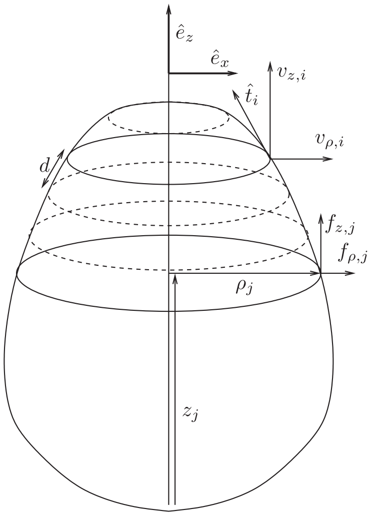

FIG. 1. We parametrize the axisymmetric body as N rings, each at height z_i with radius ρ_i. The fluid velocity at each ring has the radial component $v_{\rho,i}$ and the axial component $v_{z,i}$.

ϵ is a regularization parameter which does not influence the result if the mesh is sufficiently dense. In our calculation we used $\epsilon = 0.1d$ where d denotes the distance between two adjacent rings. An analytical solution for all components of the integral in Eq. (3) is given in Supplemental Material [23]. It can be written in matrix form as

$$v_{\alpha,i} = \sum_{\beta\in\{\rho,z\}}\sum_{j=1}^{N} M_{\alpha,i;\beta,j}F_{\beta,j}, \tag{5}$$

where the index α represents the ρ or z component and i runs over all rings in the parametrization. We also introduced the forces $F_{z,i} = 2\pi\rho_i f_{z,i}$ and $F_{\rho,i} = 2\pi\rho_i f_{\rho,i}$ in a way that keeps the mobility matrix M symmetric. We next denote the tangent vector on the surface at point i as $\hat{t}_i$. The total speed of the fluid at that point is then the sum of the tangential surface slip velocity and the swimming velocity u:

$$v_{\alpha,i} = \hat{t}_{\alpha,i}v_{t,i} + u\delta_{\alpha,z}. \tag{6}$$

Combining these two equations gives

$$F_{\alpha,i} = \sum_{\beta\in\{\rho,z\}}\sum_{j=1}^{N}(M^{-1})_{\alpha,i;\beta,j}\hat{t}_{\beta,j}v_{t,j} + u\sum_{j=1}^{N}(M^{-1})_{\alpha,i;z,j}. \tag{7}$$

The force balance condition on the swimmer, $\sum_{i=1}^{N} F_{z,i} = 0$, finally allows us to express the swimming velocity u with the local surface slip velocities $v_{t,i}$:

$$u = -\frac{\sum_{\beta\in\{\rho,z\}}\sum_{i,j=1}^{N}(M^{-1})_{z,i;\beta,j}\hat{t}_{\beta,j}v_{t,j}}{\sum_{i,j=1}^{N}(M^{-1})_{z,i;z,j}} =: -\sum_{j=1}^{N} A_j v_{t,j} \tag{8}$$

Likewise, the dissipation can be written as $P = \sum_{j=1}^{N} B_j v_{t,j}^2$ with

$$B_j = \frac{1}{\pi^2 \epsilon_c} 2\pi\rho_j d. \tag{9}$$

Minimization of P while keeping u constant can be performed using Lagrange multipliers, $(\partial P/\partial v_{t,i}) - \lambda(\partial u/\partial v_{t,i}) = 0$, leading to

$$v_{t,i} = -\frac{\lambda A_i}{2B_i} = -u\frac{A_i/B_i}{\sum_{j=1}^{N} A_j^2/B_j}. \tag{10}$$

For a given shape of the swimmer, this equation gives us the optimal distribution of surface velocities to achieve the swimming speed u with minimal dissipation. The dissipation itself follows as

$$P = u^2\left(\sum_{i=1}^{N}\frac{A_i^2}{B_i}\right)^{-1}. \tag{11}$$

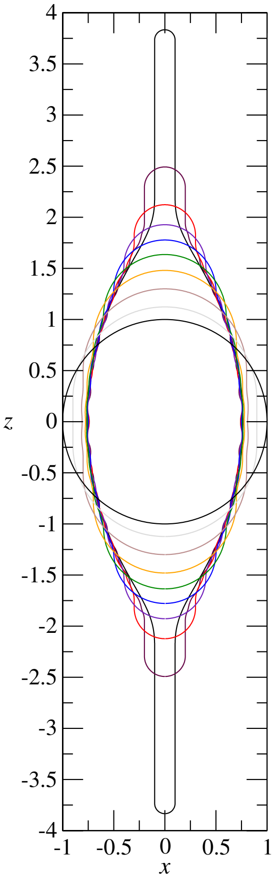

FIG. 2 (color online). Optimal shapes of bodies with minimum radius of curvature $\hat{r}_{\text{min}} = 0.1, \ldots, 1$.

For a spherical swimmer, the velocity distribution and the dissipated power can be easily calculated analytically [3]:

$$v_t = \frac{3}{2} u \sin\theta \qquad P_{\text{sphere}} = \frac{6R^2}{\pi\epsilon_c} u^2 \tag{12}$$

In the following we normalize the power relative to the result for a sphere with the same volume ($R = \sqrt[3]{3V/4\pi}$)

$$\hat{P} = \frac{P}{P_{\text{sphere}}}. \tag{13}$$

We also use a dimensionless value of the minimum curvature radius, $\hat{r}_{\text{min}} = r_{\text{min}}/R$.

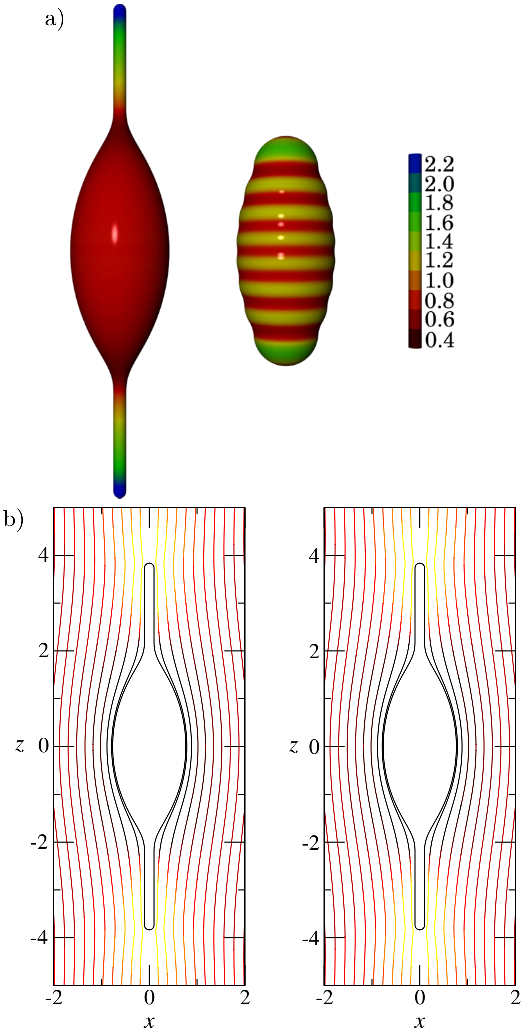

FIG. 3 (color online). (a) Color coded tangential propulsion velocity v_t/u of the optimal optimal swimmer for $\hat{r}_{\text{min}} = 0.1$ (left) and $\hat{r}_{\text{min}} = 0.5$ (right). (b) Streamlines of the same two swimmers in a body-fixed frame.

In order to obtain the optimal shape, we numerically optimized the coordinates ρ_i and z_i while keeping the distances between the rings fixed. We performed the optimization by means of the sequential quadratic programming method using the Numerical Algorithms Group routine E04WDF. The results for several radii of curvature are shown in Fig. 2. The data are calculated with $N = 3201$ rings, of which 2×100 were subject to optimization and the remaining were interpolated as piecewise Euler spirals (clothoid segments). The distribution of the propulsion velocities v_t for two solutions is shown in Fig. 3(a). For the optimal shape we can also determine the flow streamlines, which are shown in Fig. 3(b) for two values of $\hat{r}_{\text{min}}$.

Most interestingly, for $\hat{r}_{\text{min}} \lesssim 0.2$ the optimal shape exhibits two protrusions along the symmetry axis. They bring the benefit of exerting a force on the fluid at a distant point where the flow is less perturbed. In the limit $\hat{r}_{\text{min}} \longrightarrow 0$ the central part becomes increasingly passive and eventually assumes the shape of Pironneau's minimum drag body [20]. Another curious feature is the appearance of small ripples on the surface for values of $0.1 \lesssim \hat{r}_{\text{min}} \lesssim 0.8$. Having a higher driving speed at the crest of a ripple and lower in the trough slightly increases the efficiency. But the difference is extremely small—if we include a small penalty on curvature in the optimization to eliminate the ripples, the dissipation increases by no more than 0.5%. So the effect is completely irrelevant for microorganisms. We discuss the ripples in more detail in Supplemental Material [23].

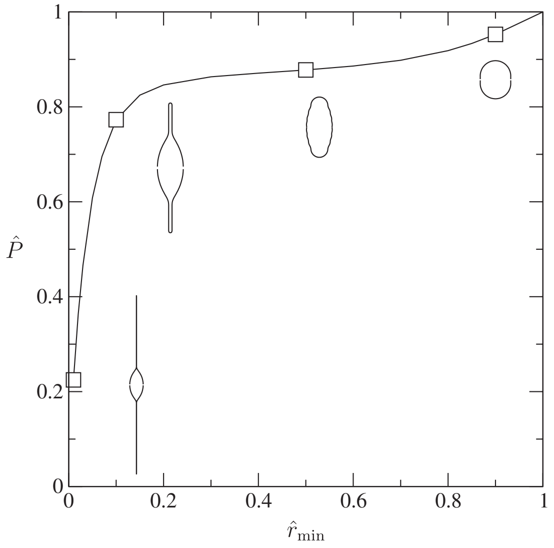

FIG. 4. Optimal normalized dissipation $\hat{P}$ (dissipated power, divided by the value for a sphere of the same volume) as a function of the minimum curvature radius $\hat{r}_{\min} = 0.1, \ldots, 1$. Optimal shapes are shown as insets at four points.

Figure 4 shows the dissipation as a function of the minimum radius of curvature $\hat{r}_{\min}$. For $\hat{r}_{\min} = 1$ the swimmer is spherical and we have $\hat{P} = 1$ by definition. Then $\hat{P}$ reaches a plateau around 0.85 for a wide range of prolate swimmers. When we allow sufficient curvature, $\hat{r}_{\min} \lesssim 0.2$, the optimal swimmer obtains thin protrusions at both ends and $\hat{P}$ can be reduced indefinitely. However, with the real ciliated swimmer in mind, the situation is more complex. Strictly speaking Eq. (1) loses its validity if the protrusions are too thin in comparison with the ciliary length L. We can incorporate this limitation into the model by requesting $r_{\min} > L$. Because the propulsion efficiency is inversely proportional to the length [Eq. (1)], making the cilia shorter would actually worsen the overall efficiency.

We have shown that with a moderate curvature a surface-propelled swimmer can increase its swimming efficiency by about 20% relative to a sphere. Ciliated microorganisms make wide use of it, as the majority of them has a strongly elongated shape. But it is much more surprising that the efficiency can be further increased by growing two protrusions along the symmetry axis. Although there are certainly other limitations on the body shape, there are still a number of microorganisms that have at least one such ciliated protrusion. Remarkable examples include, e.g., *Litonotus* and *Amphileptus* [24,25], which are shown in Fig. 5. We therefore conclude that not only do the cilia beat in a way that is very close to the theoretical optimum [3], but the body shape of many microorganisms also assumes a form that enables efficient propulsion.

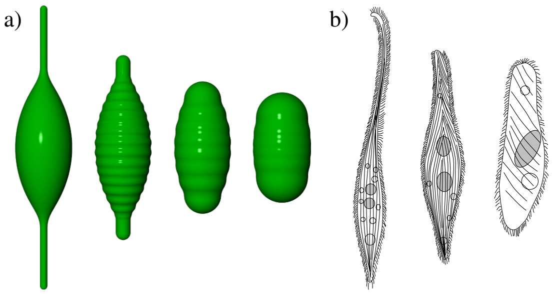

FIG. 5 (color online). (a) Three-dimensional shapes of optimal swimmers for $\hat{r}_{\min} = 0.1$, 0.2, 0.5, and 0.7. (b) Some ciliated protozoa: *Litonotus cygnus*, *Amphileptus pleurosigma* (drawn after Ref. [24]) and *Paramecium caudatum*.

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[1] M. J. Lighthill, Commun. Pure Appl. Math. **5**, 109 (1952).
[2] J. Blake, J. Biomech. **6**, 133 (1973).
[3] N. Osterman and A. Vilfan, Proc. Natl. Acad. Sci. U.S.A. **108**, 15727 (2011).
[4] J. L. Anderson, Annu. Rev. Fluid Mech. **21**, 61 (1989).
[5] F. Jülicher and J. Prost, Eur. Phys. J. E **29**, 27 (2009).
[6] B. Sabass and U. Seifert, J. Chem. Phys. **136**, 064508 (2012).
[7] R. Dreyfus, J. Baudry, M. L. Roper, M. Fermigier, H. A. Stone, and J. Bibette, Nature (London) **437**, 862 (2005).
[8] R. Golestanian, T. B. Liverpool, and A. Ajdari, Phys. Rev. Lett. **94**, 220801 (2005).
[9] W. F. Paxton, S. Sundararajan, T. E. Mallouk, and A. Sen, Angew. Chem., Int. Ed. **45**, 5420 (2006).
[10] A. Walther and A. H. E. Müller, Soft Matter **4**, 663 (2008).
[11] D. Tam and A. E. Hosoi, Phys. Rev. Lett. **98**, 068105 (2007).
[12] S. E. Spagnolie and E. Lauga, Phys. Fluids **22**, 031901 (2010).
[13] Y. W. Kim and R. R. Netz, Phys. Rev. Lett. **96**, 158101 (2006).
[14] J. E. Avron, O. Gat, and O. Kenneth, Phys. Rev. Lett. **93**, 186001 (2004).
[15] F. Alouges, A. DeSimone, and A. Lefebvre, Eur. Phys. J. E **28**, 279 (2009).
[16] S. Michelin and E. Lauga, Phys. Fluids **22**, 111901 (2010).
[17] D. Tam and A. E. Hosoi, Proc. Natl. Acad. Sci. U.S.A. **108**, 1001 (2011).
[18] E. M. Purcell, Am. J. Phys. **45**, 3 (1977).
[19] Y. Katsu-Kimura, F. Nakaya, S. A. Baba, and Y. Mogami, J. Exp. Biol. **212**, 1819 (2009).
[20] O. Pironneau, J. Fluid Mech. **59**, 117 (1973).

[21] J.-M. Bourot, J. Fluid Mech. **65**, 513 (1974).
[22] R. Cortez, L. Fauci, and A. Medovikov, Phys. Fluids **17**, 031504 (2005).
[23] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.109.128105 for a derivation of mobility matrix elements and a discussion of surface ripples.
[24] W. Foissner, Hydrobiologia **119**, 193 (1984).
[25] M. Sleigh, *Protozoa and Other Protists* (Cambridge University Press, Cambridge, England, 1991).