Propulsion of microorganisms by a helical flagellum

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Contributed by Harry L. Swinney, November 28, 2012 (sent for review September 16, 2012)

The swimming of a bacterium or a biomimetic nanobot driven by a rotating helical flagellum is often interpreted using the resistive force theory developed by Gray and Hancock and by Lighthill, but this theory has not been tested for a range of physically relevant parameters. We test resistive force theory in experiments on macroscopic swimmers in a fluid that is highly viscous so the Reynolds number is small compared to unity, just as for swimming microorganisms. The measurements are made for the range of helical wavelengths \( \lambda \), radii \( R \), and lengths \( L \) relevant to bacterial flagella. The experiments determine thrust, torque, and drag, thus providing a complete description of swimming driven by a rotating helix at low Reynolds number. Complementary numerical simulations are conducted using the resistive force theories, the slender body theories of Lighthill and Johnson, and the regularized Stokeslet method. The experimental results differ qualitatively and quantitatively from the predictions of resistive force theory. The difference is especially large for \( \lambda < 6 \pi R \) and/or \( L > 3 \lambda \), parameter ranges common for bacteria. In contrast, the predictions of Stokeslet and slender body analyses agree with the laboratory measurements within the experimental uncertainty (a few percent) for all \( \lambda, R \), and \( L \). We present code implementing the slender body, regularized Stokeslet, and resistive force theories; thus readers can readily compute force, torque, and drag for any bacterium or nanobot driven by a rotating helical flagellum.

hydrodynamic interaction | motility

Gray and Hancock (1955) (1) and Lighthill (1976) (2) developed resistive force theory to describe swimming at low Reynolds number. The theory is used to interpret propulsion by a planar wave in sperm (3), small worms (4), Chlamydomonas reinhardti (5), and swimmers in a granular material (6); however, rather than using the drag coefficients given by ref. 1 or ref. 2, the coefficients are usually adjusted to fit the observations. The theory is also used to describe bacterial propulsion by a rotating helical flagellum (5, 7–12) and nanobots (13–16). The algebraic expressions relating forces and torques to a helical flagellum’s axial velocity and rotation rate (1, 2) are convenient to use but have not been tested for a wide range of helical parameters. The experiments reported here test resistive force theory for helical flagella. Also, we compare the laboratory observations to the predictions of slender body theory (2, 17) and regularized Stokeslet theory (18).

A helical bacterial flagellum can be modeled as a rigid rotating helix (19) with radius \( R \), pitch \( \lambda \), length \( L \), pitch angle \( \theta \), contour length \( \Lambda = L / \cos \theta \), and filament radius \( a \) (Fig. 1). The pitch is typically in the range \( 2 \pi R < \lambda < 11 \pi R \) and the length is in the range \( 3 \lambda < L < 11 \lambda \), as illustrated by the examples in Table 1 (10, 20–23).

For a microorganism driven by a helical flagellum rotating about its axis, the Reynolds number \( Re \) is typically \( 10^{-4} \text{–} 10^{-2} \), where \( Re = \rho \Omega R^2 / \mu \) (\( \Omega \) is the rotation rate; \( \mu \), the dynamic viscosity; and \( \rho \), the fluid density). At low Reynolds number a rotating flagellum exerts an axial thrust \( \tau \) and torque \( \tau \) related to the flagellum’s axial velocity \( U \) and rotation rate \( \Omega \) by (24, 25)

\[
\begin{bmatrix}
\tau \\
\tau
\end{bmatrix}
= \begin{bmatrix}
A_{11} & A_{12} \\
A_{12} & A_{22}
\end{bmatrix}
\begin{bmatrix}
U \\
\Omega
\end{bmatrix}.
\]

The symmetric 2 \( \times \) 2 propulsive matrix in Eq. 1 depends only on the geometry of the flagellum. The elements of the propulsive matrix can be determined by measuring the axial thrust \( F \) and torque \( T \) for a rotating nontranslating flagellum and the axial drag \( D \) on a translating nonrotating flagellum: \( D = A_{11} F / \Omega, F = A_{12} \Omega, \) and \( T = A_{22} \Omega \).

Other researchers have compared experimental measurements to resistive force theory and found that it does not accurately describe the swimming of model spirochetes (i.e., super helices) (26, 27) and swimming Escherichia coli (9, 28). The present work specifically examines swimming driven by a rigid helix in a Newtonian fluid (29) and compares laboratory measurements with predictions of various models for a wide range of helical parameters.

We measure thrust \( F \), torque \( T \), and drag \( D \) for model helical flagella that are macroscopic (\( R = 6.5 \text{mm} \)) but swim in a highly viscous fluid so \( Re \approx 10^{-3} \). The length, pitch, and radii of the laboratory helices are varied to cover the range relevant to microorganisms and nanobots. The laboratory results are compared to the predictions of resistive force theory (1, 2) and to results from our numerical simulations of the slender body theory of Lighthill (2) and Johnson (17) and the regularized Stokeslet method of Cortez et al. (18).

Results

Comparison of Experiment and Resistive Force Theory. Our measurements of thrust, torque, and drag for flagella with different pitch are presented in Fig. 2. The results presented are dimensionless; for reference, the actual values for \( \lambda = 9 \pi R \) are \( F = 80 \text{ mNm}, T = 6.0 \text{ mNm}, \) and \( D = 66 \text{ mN} \). We also measured thrust, torque, and drag as a function of helix length (for fixed pitch and filament radius), as shown in Fig. 3.

The measurements in Figs. 2 and 3 depart both qualitatively and quantitatively from the resistive force theory predictions of Gray and Hancock (1) and Lighthill (2), who obtained the force and torque on a flagellum by integrating the local forces on each small segment (Fig. 1,Inset). Gray and Hancock’s expressions for the drag coefficients in the directions normal and tangential to the segment differ from the coefficients obtained by Lighthill; both sets of expressions are given in Methods. For both approaches the predictions for thrust and drag differ significantly from the measurements, especially for flagellae with small pitch (\( \lambda < 10 \pi R \), Fig. 2) and/or large length (\( L > 2 \lambda \), Fig. 3). On the other hand, Lighthill’s predictions for torque agree fairly well with the measurements as a function of both helix pitch (Fig. 2) and helix length (Fig. 3), whereas the Gray and Hancock predictions for torque are smaller than the measured values.

Resistive force theory fails because it neglects hydrodynamic interactions between flows induced by different parts of a flagellum; these interactions are long-ranged at low Reynolds number. As \( \lambda \) decreases, the separation of filament segments in a helical

Author contributions: B.R., H.L.S., and H.P.Z. designed research; B.R., C.-H.C., B.L., and H.P.Z. performed research; B.L. and H.P.Z. contributed new reagents/analytic tools; B.R., C.-H.C., H.L.S., and H.P.Z. analyzed data; and B.R., B.L., and H.P.Z. wrote the paper.

The authors declare no conflict of interest.

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See Author Summary on page 1574 (volume 110, number 5).

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1219831110/-/DCSupplemental.
flagellum decreases, leading to stronger hydrodynamic interactions. In the limit $\lambda \to 0$, a helix becomes a cylinder that produces zero thrust. The failure of resistive force theory due to hydrodynamic interactions when helices have small pitch has been reported previously (26, 27) but not quantified. Neglect of hydrodynamic interactions also leads to the failure of resistive force theory to describe the observed length dependence shown in Fig. 3, as discussed in the next section.

**Comparison of Experiment with Stokeslet and Slender Body Theories.**

Stokeslet and slender body theories both rely on the linearity of the Stokes equations for low Reynolds number flow. The solution at a spatial location $r$ for the fluid velocity and pressure fields, $u(\mathbf{r})$ and $p(\mathbf{r})$, resulting from a point force at the origin, $\delta(\mathbf{r})$, is given by a “Stokeslet” (30)

$$u(\mathbf{r}) = \mathbf{f} \cdot \mathbf{J}(\mathbf{r}) \quad \text{and} \quad p(\mathbf{r}) = \frac{\mathbf{f} \cdot \mathbf{r}}{4\pi |\mathbf{r}|^3},$$

where $\mathbf{J}(\mathbf{r})$ is the Oseen tensor,

$$\mathbf{J}(\mathbf{r}) \equiv \frac{1}{8\pi \mu} \left( \frac{\mathbf{I}}{|\mathbf{r}|} + \frac{\mathbf{r}\mathbf{r}^T}{|\mathbf{r}|^3} \right).$$

The response to a continuous force distribution from an immersed body can be found by superposing Stokeslets (31). Thus, forces on a flagellum and the resultant flow field can be found by discretizing a flagellum’s surface and assigning a Stokeslet to represent the fluid response to each surface element, as shown schematically in Fig. 4. The total force on the flagellum is found by integrating over the Stokeslets.

We compute the propulsive matrix elements using a technique developed by Cortez et al. (18), who used a “regularized” Stokeslet, which is an approximate point force, $\delta(\mathbf{r})$, where the radial cutoff function $\gamma_{\lambda}(\mathbf{r})$ avoids singular, nonintegrable kernels in numerical simulations (Methods). We also compute the propulsive matrix, using the slender body theory approximation to describe flagellar swimming, as developed by Lighthill (2) and Johnson (17). Slender body theory uses Lorentz’s (31) result that the far field fluid response to a moving sphere can be represented by a Stokeslet and a source dipole (doublet) of the same strength at the center of the sphere. In this approach Stokeslets and doublets are arranged along the axis of the flagellum, and the force per unit length on a flagellum is obtained by inverting the integral equation, relating the velocity of the flagellum’s center line and the strength of the Stokeslets and doublets.

Numerical simulations using the regularized Stokeslet method (18) and the Lighthill (2) and Johnson (17) formulations of the slender body theory are described in Methods, and a Matlab version of the code (Code S1 in SI Numerical Simulations) can be used to reproduce the data presented in Figs. 2 and 3. As can be seen in Figs. 2 and 3, the results from both slender body theory
and the regularized Stokeslet method agree well with the laboratory observations; the difference is within the experimental uncertainty. The agreement between measurements and calculations for the flagella suggests that the stationary motor housing, unlike with a moving cell body (9), does not interact strongly with the flagellum.

**Long Flagella.** By expanding Lighthill’s slender body expressions (Methods), we obtain scaling relationships for thrust, torque, and drag in the limit $L \to \infty$,

$$F = \left(\frac{a_2}{a_1 a_4}\right) \frac{L}{\ln(L/R)} \Omega$$  \hspace{1cm} [4]

$$T = \left(\frac{1}{a_4}\right) L \Omega$$  \hspace{1cm} [5]

$$D = \left(\frac{1}{a_1}\right) \frac{L}{\ln(L/R)} U,$$  \hspace{1cm} [6]

where the constants $a_1$–$a_4$ depend on the flagellum geometry (expressions are given in Methods).

The logarithmic factor in the expressions for thrust and drag in the long length limit is absent in resistive force theory, but is necessary to obtain the length dependence behavior we found. The predictions of the asymptotic analysis agree within a few percent with both the Lighthill and Johnson versions of slender body theory for $L/\lambda > 1000$ ($\lambda = 2.42 R$). In the limit $L \to \infty$, slender body theory and resistive force theory predict the same functional dependence, but the proportionality coefficient for resistive force theory is different from that for slender body theory. Further, our thrust and drag data in the biologically relevant regime $L/R < 30$ are consistent with $L/\ln(L/R)$ scaling within the experimental uncertainty.

**Dependence on Filament Radius.** We use the slender body theory and regularized Stokeslet method simulations to examine the dependence of force, torque, and drag on filament radius, which was fixed in our experiments at $a/R = 0.063$. The filament radius results from slender body theory and the regularized Stokeslet method agree well for radii relevant to bacterial filaments ($a/R < 0.07$), as shown in Fig. 5. For larger $a/R$ values, not relevant to bacteria but possibly relevant to some nanobots, the Stokeslet simulations predict torque values somewhat larger than predicted by slender body theory. The results in Fig. 5, like those in Figs. 2 and 3, can be generated using code provided as Code S1 in SI Numerical Simulations.

**Discussion**

Our experiments reveal that resistive force theory fails to provide an accurate description of low Reynolds number swimmers driven by a rotating helical flagellum for helices with $\lambda < 6R$ and/or $L > 3\lambda$, which is the range relevant to bacteria. The measured values of thrust, torque, and drag differ significantly from the predictions of resistive force theory with either Gray and Hancock’s (1) or Lighthill’s (2) drag coefficients (Figs. 2 and 3). The measurements were made for values of helical pitch $\lambda$ and length $L$ that include the ranges relevant to bacteria.

Hancock (30) pioneered the analysis of swimming microorganisms more than a half century ago. His “slender body model” yielded predictions in terms of integrals that could not be nu-

![Figure 3](https://www.pnas.org/doi/10.1073/pnas.1219831110)

**Fig. 3.** Thrust, torque, and drag for helical flagella as a function of length for flagella with the same filament radius $a = R/16$ and pitch $\lambda = 2.42 R$: experiment (solid black circles), regularized Stokeslet theory (solid black lines), slender body theory of Lighthill (2) (solid blue lines), resistive force theory of Gray and Hancock (1) (green lines), and resistive force theory of Lighthill (2) (dashed blue lines). The regularized Stokeslet theory and slender body theory results are very similar so the curves can be difficult to distinguish; results from the slender body theory of Johnson (17) are essentially the same and so are not plotted.

![Figure 4](https://www.pnas.org/doi/10.1073/pnas.1219831110)

**Fig. 4.** Regularized Stokeslet method of Cortez et al. (18) discretizes the surface of the flagellum and represents each surface element by a regularized Stokeslet, which approximates a Stokeslet but avoids using delta function singularities. Slender body theory represents a flagellum using Stokeslets and doublets arranged along the helical centerline; the combination of a Stokeslet plus dipole approximates the fluid response to a flagellum segment. In the simulations, the distance between cross sections is smaller than their separation in the drawing, and there are 12 regularized Stokeslets per cross section rather than 6 as drawn (Methods).
Efficient of viscosity, \(1.00 \times 10^{-6}\) kg m\(^{-1}\) s\(^{-1}\)/°C and thermal expansion coefficient, \(9.4 \times 10^{-4}\) °C. We measured the oil temperature using a calibrated thermostir (Barnant Model 600-1075 LogThermistor/Datalogger).

Model flagella were constructed from initially straight pieces of type 304 stainless steel welding wire with radius 0.397 mm. The wire was wrapped around aluminum mandrels with helical V-shaped grooves of varying pitches on rods with radius 6.4 mm and lengths of either 152.5 or 305.3 mm. In measurements of the dependence on pitch, the helical radius was \(R = 6.3 \pm 0.4\) mm, the length was \(L = 130 \pm 5\) mm, and pitch was varied in the range 2.2 \(\leq \lambda \leq 15.3\) K. In measurements of the dependence on length, the radius was \(R = 6.6 \pm 0.2\) mm, the pitch was \(\lambda = 2.42R \pm 0.02R\), and the length was varied in the range 3.3 \(\leq L \leq 11.2\) K. Measurements were made with each flagellum’s axis about 250 mm from the tank walls to minimize boundary effects. The ends of a flagellum were kept at least 100 mm from the wall boundaries and from the free surface. To examine possible changes of the radius and wavelength of the wire helices under load, we analyzed videos for different rotation rates and for different rotation directions, and the change in wavelength and radius was smaller than the measurement uncertainty.

**Thrust Measurements.** A block of acrylic (89 mm \(\times\) 38 mm \(\times\) 35 mm) housed a reversible variable-speed motor (Pololu 298:1 Micro Metal Gear Motor) that rotated a flagellum immersed in the silicone oil (Fig. 6A). A stainless steel shaft adapter extended through the bearing, connecting the motor shaft inside the body to the flagellum outside of the body.

To measure the thrust generated by a rotating flagellum, the swimmer was attached to a load cell (Omega LCL-227G), using a 9.5-mm diameter vertical rod extending from a structure above the tank. This vertical rod was fitted into two ball bearings (VXB 6.38 \(\times\) 78/732 Full Ceramic Miniature Ball Bearing) to constrain the swimmer’s movement to one direction. The distance from the bearings’ center of rotation to the center of an attached flagellum was 125 mm. The load cell was at the top of the vertical rod, 25.4 mm above the bearings’ center of rotation. With this arrangement, the force acting on the load cell is about 10 times larger than generated thrust, thereby increasing the measurement sensitivity. The load cell had a maximum deflection of 1.27 mm for a full-scale load (2.23 N); therefore, the swimmer could rotate at most 3° at the bottom end of the vertical rod.

The load cell was connected to an amplifier/driver (Omega DP258 E-A 1/8 DIN Process Panel meter and Controller) and its output fed into a digital data acquisition board (National Instruments NIDAQ 6008 USB) that also provided motor speed control (Pololu TrxEx Jr Dual Motor Controller DMC02A). We recorded videos of the flagellum during each 200-s-long recording of load cell data. Flagellum rotation rates were determined by analyzing the movie with a Matlab Power Spectral Density function. The composite spectrum produced by averaging the 10\(^{th}\) spectra from the region of the image containing the flagellum had a peak (more than three orders of magnitude above the noise level) corresponding to the flagellum rotation rate (\(\pm 0.50 Hz\)). For each flagellum, we measured the force for clockwise (CW) and counterclockwise (CCW) rotation for six or seven rotation speeds in each direction; the results from CW and CCW rotation differed typically by 2%. We fitted the data for each rotation direction to a line, and the average slope of these two lines yielded the force per unit frequency for the flagellum (Fig. 7A).

**Torque Measurements.** The torque required to rotate a flagellum was measured with a torque sensor (Magnova MLY Torque Transducer, maximum torque, \(\leq 25\) mNm; manufacturer’s stated accuracy, \(\pm 1\%\) of full scale). For torque measurements, the flagellum was mounted to a straight vertical rod using the 6.35-mm diameter adapter (Fig. 6B). The stepper motor used to rotate the flagellum gave precise control of rotation rate so no frequency analysis was required. Again, multiple measurements at different rotation speeds were made and fit to a line, giving the torque per unit frequency in each direction; these values were averaged. There is also a background offset in this measurement. The torque created by rotating the rod and adapter alone was subtracted from the value measured when a flagellum was attached. Fig. 7B shows that the background value for these data was about 30% of the total signal; the final torque value has an uncertainty of 4%.

**Drag Measurements.** The drag on a flagellum was measured by translating the undulating swimmers horizontally, as illustrated in Fig. 6C. The flagellum was mounted on a 9.5-mm diameter vertical rod that had a 6.35-mm diameter adapter mounted perpendicular to the vertical rod into which the flagellum was mounted. The rod, shaft adapter, and flagellum assembly were pulled through the fluid for 70 mm, and the drag was measured with the same load cell as for thrust measurements. Six or seven measurements were made at different translation velocities in both the flagellum-first and
Fig. 7 shows typical data used to determine thrust, torque, and drag. The data are linear with respect to the rotation rate or velocity, depending on the measurement. Despite large background values for the rod and adapter holding the flagellum, the values of torque and drag determined from the linear fit have uncertainties typically less than 5%.

Numerical Simulations
A program titled Helical Swimming Simulator, provided here as Code S1 in SI Numerical Simulations, calculates thrust, torque, and drag for any helical flagellum, using the regularized Stokeslet method, Lighthill’s formulation of slender body theory, or Johnson’s version of slender body theory; resistive force theory results are also provided for comparison. (To permit updates, the code, entitled “Helical Swimming Simulator,” is also provided on the Matlab File Exchange, www.mathworks.com/matlabcentral/fileexchange/.) The program takes as input the parameters for a helical flagellum: radius $R$, pitch $\lambda$, length $L$, filament radius $a$, velocity $U$, and rotation rate $\Omega$. The helical radius $R$ is used as the unit of length; thrust, torque, and drag are made dimensionless by dividing by $\mu QR^2$, $\mu QR^3$, and $\mu UR$, respectively. The following describes the methods used for each type of calculation.

Resistive Force Theory. Resistive force theory obtains the total force and torque for motion of a flagellum by integrating the local forces on each small segment (Fig. 1, Inset). The local forces are calculated using drag coefficients per unit length in the directions normal and tangential to the segment, $C_n$ and $C_t$, respectively. Resistive force theory predicts that the thrust, torque, and drag on a flagellum are given by

$$F = (\Omega R)(C_n - C_t)\sin \theta \cos \theta \frac{L}{\cos \theta}$$

$$T = (\Omega R^2)(C_n \cos^2 \theta + C_t \sin^2 \theta)\frac{L}{\cos \theta}$$

$$D = U(C_n \sin^2 \theta + C_t \cos^2 \theta)\frac{L}{\cos \theta}$$

Two sets of drag coefficients are commonly used in the literature, those by Gray and Hancock (1) and those by Lighthill (2); both are based on slender body theory, assuming that the effect of each small filament segment is only locally important. Gray and Hancock’s drag coefficients are

$$C_n = \frac{2\pi \mu}{\ln \frac{2a}{a - 1/2}}$$

$$C_t = \frac{4\pi \mu}{\ln \frac{2a}{a + 1/2}}$$

and Lighthill’s are

$$C_n = \frac{2\pi \mu}{\ln \frac{0.18r}{a \cos \theta}}$$

$$C_t = \frac{4\pi \mu}{\ln \frac{0.18r}{a \cos \theta + 1/2}}$$

These drag coefficients are used in Eqs. 7–9 for comparison with experiments. See Figs. 2 and 3.

Regularized Stokeslet Method. Stokeslet theory includes Dirac delta functions, which are difficult to evaluate computationally. Therefore, Cortez et al. (18) use an approximate delta function, a radially symmetric cutoff function $\phi_\epsilon(r)$ given by

$$\phi_\epsilon(r) = \frac{15\pi^4}{8\pi (r^2 + \epsilon^2)^{7/2}}$$

where $r = |r|$ and $\epsilon$ is assumed to be small. This regularization parameter prevents nonintegrable kernels, but also has a physical meaning representing surface area over which the force is distributed. Over 97% of the weight of Eq. 12 is within a radius of one $\epsilon$.

For $N$ regularized point forces $f_{\phi_\epsilon}(r_n)$ at locations $r_n$ on the surface of a body in motion, the fluid velocity at any point $r$ is

$$u_r(r) = \frac{1}{8\pi \mu} \sum_{n=1}^{N} \sum_{i=1}^{3} S_{ij}(r - r_n)f_{n,i}A_n,$$

where $A_n$ are quadrature weights, and the regularized Green’s function $S_{ij}(r)$ is

$$S_{ij}(r) = \frac{\delta_{ij}(r^2 + 2\epsilon^2) + r_i r_j}{(r^2 + \epsilon^2)^{3/2}}$$

The regularized Green’s function $S_{ij}$ depends only on the geometry of the object in motion and the regularization parameter $\epsilon$. Evaluating Eq. 13 at each of the $N$ regularized Stokeslets gives a linear relation between the velocities and the forces exerted at these points. For a helical flagellum, we discretize the surface with cross sections along its length and use 12 regularized Stokeslets on the perimeter of each circular cross section. We separate adjacent cross sections by a distance equal to one-half of the filament perimeter.
We solved Eq. 13 numerically for point forces fi for boundary conditions specified by u. Using the computed fi, we determined the dependence of the thrust, torque, and drag on wavelength, length, and filament radius, using the methods of both Cortez et al. (18) and Gonzalez (32) with the same grid resolution in both studies, Δs = a/2 (i.e., 12 Stokeslets per cross section). There was less than 0.5% difference between the two methods providing ε/Δs = 1/2 in the regularized Stokeslet simulations. This close correspondence provides further support for our choice of ε.

Other recent studies such as ref. 34 used ε/Δs = 7/12 because it gave results very similar to slender body theory calculations, whereas ref. 35 used ε/Δs = 1/3 because it seemed to give the best convergence as a function of grid spacing to the analytic solution for the flow past an ellipsoid. We find that for our geometry ε/Δs = 1/2 gives results that are the most similar to both slender body theory and to the Gonzalez method, as well as to the experimental data.

Lighthill Slender Body Theory. Slender body theory represents a flagellum with an arrangement of Stokeslets and doublets along the flagellum’s centerline. Because dipolar fields fall off as r−2,

radius. We choose a regularization parameter ε to be half of the grid spacing so adjacent regularized Stokeslets do not overlap extensively. Fig. 8 shows the effect of varying ε and varying grid spacing in simulations of thrust, torque, and drag for a flagellum similar to those in the experiments. Using a value of ε/Δs = 1/2, we obtain values for F, T, and D that are nearly the same for all three grid resolutions. Increasing the grid resolution from Δs = a/2 to Δs = a/3 changes the values by less than 1%, providing ε/Δs = 1/2. However, the values change by about 1.5% for a 20% change in ε.

Because the regularized Stokeslet method results depend on the choice of ε, we also simulated flagellar propulsion, using a new boundary integral method developed by Gonzalez (32) for solving solid body Stokes flow problems. This numerical method also discretizes the flagellum surface and assigns Stokeslets to represent each surface element, and it includes a parallel offset parameter, which is the distance by which a parallel virtual surface is offset from the flagellum. The flow is solved using a single-layer potential on the parallel surface and a related double-layer potential on the flagellum. The two potentials have a unique solution that depends on the no-slip boundary condition of the flagellum. The solution gives the strength of the Stokeslets at the surface and thus the fluid stresses on the flagellum. The advantage of this formulation is that Gonzalez shows the results are independent of the choice of parallel offset parameter and so its choice is based on ease of solvability (32, 33).

Fig. 7. (A) Thrust measurements for a flagellum with R = 6.6 mm, a = R/16, L = 20R, λ = 6.5R: slope for forward rotation = 243.3 ± 0.8 mN/Hz; slope for reverse rotation = 239.9 ± 5.4 mN/Hz; average slope = 242.6 ± 5.5 mN/Hz (2.3% uncertainty). (B) Torque measurements: slope for helix + shaft = 16.8 ± 0.2 mNm/Hz; reverse slope = 16.0 ± 0.2 mNm/Hz; average slope = 16.4 ± 0.3 mNm/Hz; slope for shaft alone = 5.3 ± 0.2 mNm/Hz; reverse slope = 5.1 ± 0.1 mNm/Hz; average slope = 5.2 ± 0.2 mNm/Hz. The resultant net torque is 11.2 ± 0.4 mNm/Hz (3.6% uncertainty). (C) Drag measurements: slope for helix + downrod = 91.6 ± 0.4 N s−1 m−1; slope for downrod alone = 272.6 ± 0.3 N s−1 m−1. The difference is the net torque = 19.0 ± 0.5 N s−1 m−1 (2.6% uncertainty).

Fig. 8. Thrust, torque, and drag from regularized Stokeslet method simulations using different values of the regularization parameter ε and for different grid resolution for a helix with pitch λ = 6R, length L = 20R, and a/R = 1/16. Data are scaled by the value with ε/Δs = 1/2 and Δs = a/2 (12 regularized Stokeslets per cross section), the values used in our analysis. The red curves are simulations using Δs = a (6 regularized Stokeslets per cross section), and the green curves are results from simulations with Δs = a/3 (18 regularized Stokeslets per cross section). Different wavelengths have similar dependence on ε; thrust is more sensitive to its variation. However, near ε = Δs/2 the values change slowly when ε is either increased or decreased.

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where Stokeslets fall off as \( r^{-1} \). Lighthill (2) reasoned there should be some intermediate distance \( q \) from any given point on the flagellum where only dipoles within \( a \ll q \ll \lambda \) are important in determining the flow at that point, although all of the Stokeslets on the centerline must be considered because they are longer ranged. He showed that the sum of the near- and far-field solutions for the induced fluid flow on a given segment could be made independent of \( q \) by the choice of dipoles of the form (36, 37)

\[
-\frac{a^2 f_1(s)}{4\mu}, \tag{15}
\]

where \( f_1(s) \) is the component of the Stokeslet strength \( f \) in the plane perpendicular to the flagellum’s centerline at a location \( s \) along the centerline of the flagellum (2). This combination of a Stokeslet plus a dipole determines the flow induced by each element of the flagellum. Lighthill showed that the local velocity of a segment of the helix located at \( s \) is related to the force per unit length (i.e., Stokeslet strength) along the filament \( f(s) \) by

\[
\mathbf{u}(s) = \frac{f_1(s)}{4\pi\mu} + \int_{|\mathbf{r}_0(s,x)| > \delta} f(s') \cdot \mathbf{J}(\mathbf{r}_0) d\mathbf{s}', \tag{16}
\]

where \( \delta = \sqrt{\lambda^2 / 2} / 2 \) is the “natural cutoff” (2), \( \mathbf{r}_0 \) is the position vector from the point \( s \) on the centerline relative to the point \( s' \), and \( \mathbf{J} \) is defined by Eq. 3.

We evaluate Eq. 16 using the rectangular rule of numerical integration to calculate the thrust, torque, and drag for flagella with the same parameters as in the experiments. Our numerical scheme, similar to the method used in ref. 29, uses the helical phase \( \phi \equiv k s \cos \theta \), where \( k = 2\pi / \lambda \), to parameterize spatial locations

\[
\mathbf{r}(\phi) = R(\phi \cot \theta, \cos \phi, \sin \phi), \tag{17}
\]

so Eq. 16 becomes

\[
\begin{align*}
\mathbf{u}_n &= \frac{(1 - i\mathbf{t}_n + D_n) \cdot \mathbf{f}_m}{4\pi\mu} + \frac{R\Delta \phi \csc \theta}{8\pi\mu} \sum_{m=1}^N \frac{\mathbf{r}_{nm} \cdot \mathbf{r}_{nm}}{r_{nm}} \cdot \mathbf{f}_m \\
&+ \mathcal{O}(\Delta \phi), \tag{18}
\end{align*}
\]

where \( n,m = 1, 2, \ldots, N \), \( r_{nm} = \mathbf{r}(\phi_m) - \mathbf{r}(\phi_n) \) is the position vector between spatial locations, \( \mathbf{t}_n = (\cos \theta, -\sin \theta \sin \phi_n, \sin \theta \cos \phi_n) \) is the tangential unit vector at \( \mathbf{r}_n \), and \( \Delta \phi \) is the mesh size of the helical phase. Note that the integral in Eq. 16 is separated into two terms in Eq. 18. The first part of the integral is represented by the tensor \( D_n \), which is the integral from the lower bound (natural cutoff) to the size of the grid spacing. \( D_n \) is solved explicitly because this portion of the integral is below the grid resolution and would otherwise be unresolved. The remainder of the integral appears as the second term in Eq. 18.

We now work in a frame rotated with the helical phase to derive expressions for the velocity components \( \mathbf{u}_n \) that are invariant along the helix. We use these invariant velocity components to create a linear mapping between the velocity and force per unit length, which can be evaluated for a specified helical geometry, helical axial velocity \( U \), and rotation rate \( \Omega \) to give the thrust, torque, and drag.

The tensor \( D_n \) is symmetric and is the contribution of the helical segment centered at \( \mathbf{r} \), located at a distance between the cutoff length \( \delta \) and the grid size away from \( \mathbf{r}_n \); i.e., \( |\mathbf{r} - \mathbf{r}_n| \in (\delta, \delta') \), where

\[
\delta' = \frac{1}{2} R \Delta \phi \csc \theta \tag{19}
\]

and \( D_n \) is the expansion of the following integral to the lowest order of the grid size \( \Delta \phi \),

\[
D_n = \frac{1}{2} \int_{|\mathbf{r} - \mathbf{r}_n| \in (\delta, \delta')} ds(\phi) \left( \frac{\mathbf{r} - \mathbf{r}_n}{|\mathbf{r} - \mathbf{r}_n|^3} \cdot \mathcal{A} \mathbf{z}(\phi - \phi_n) \right), \tag{20}
\]

where \( \mathcal{A} \mathbf{z} \), the rotation operator along the axial direction, can be expressed as

\[
\mathcal{A} \mathbf{z}(\phi) = \begin{pmatrix}
\cos \phi & -\sin \phi & 0 \\
\sin \phi & \cos \phi & 0 \\
0 & 0 & 1
\end{pmatrix}. \tag{21}
\]

For simplicity, we introduce new velocity and force density vectors as

\[
\mathbf{u}_n' = \mathcal{A} \mathbf{z}(-\phi_n) \cdot \mathbf{u}_n, \quad \mathbf{f}_n' = \mathcal{A} \mathbf{z}(-\phi_n) \cdot \mathbf{f}_n \tag{22}
\]

so that \( \mathbf{u}_n' \) is invariant along the helical filament. For a rigid helix that rotates at rate \( \Omega \) and translates at speed \( U \) along its axial direction, we have

\[
\mathbf{u}_n' = (0, \Omega R, U)^T \tag{23}
\]

and

\[
\sum_n \mathbf{f}_n' R \Delta \phi \csc \theta = \begin{pmatrix} 0 \frac{R}{U} F_x \end{pmatrix}^T. \tag{24}
\]

Lighthill’s slender body theory can thus be formulated as

\[
\mathbf{u}_n' = \frac{(1 - i\mathbf{t}_n + D_n') \cdot \mathbf{f}_n'}{4\pi\mu} + \frac{R\Delta \phi \csc \theta}{8\pi\mu} \sum_{m=1}^N \frac{\mathcal{A} \mathbf{z}(\phi_m - \phi_n) + \mathcal{A} \mathbf{z}(-\phi_n) \cdot \mathbf{r}_{nm} \cdot \mathcal{A} \mathbf{z}(-\phi_n) \cdot \mathbf{f}_m}{r_{nm}} \tag{25}
\]

where \( \mathbf{t}' \), \( D_n' \) are now invariant along the helical filament,

\[
\mathbf{t}' = (0, \sin \theta, \cos \theta) \tag{26}
\]

and

\[
D_n' = \int_{k \delta \cos \theta} d\phi \mathbf{f} \begin{pmatrix} 1 & 0 & 0 \\
0 & \sin^2 \theta & \sin \theta \cos \theta \\
0 & \sin \theta \cos \theta & \cos^2 \theta
\end{pmatrix} \tag{27}
\]

\[
= \mathbf{f} \begin{pmatrix} \delta' \sin \theta \\
\delta' \cos \theta \\
\delta'
\end{pmatrix} (1 + i\mathbf{t}'). \tag{27}
\]

Therefore, the linear mapping between the velocity \( \mathbf{u}' \) and force density \( \mathbf{f}' \) is given by

\[
\begin{pmatrix}
\mathbf{u}_n' \\
\mathbf{u}_z' \\
\cdots \\
\mathbf{u}_N'
\end{pmatrix} = \mathbf{G} \begin{pmatrix}
\mathbf{f}_1' \\
\mathbf{f}_z' \\
\cdots \\
\mathbf{f}_N'
\end{pmatrix}. \tag{28}
\]
For prescribed motion of a rigid helix, e.g., \( \mathbf{u}_t = \mathbf{u}_0 = (0, \Omega R, U)^T \), we have
\[
\begin{pmatrix}
  f_1 \\
  f_2 \\
  \vdots \\
  f_N
\end{pmatrix} = \begin{pmatrix}
  -1 \\
  \vdots \\
  \vdots
\end{pmatrix} \begin{pmatrix}
  u_0 \\
  \vdots \\
  \vdots
\end{pmatrix}.
\]  \[\tag{29}\]

The net axial hydrodynamic force \( F_t \) and the net torque \( T \) are thus given by
\[
\begin{pmatrix}
  0 \\
  T/R \\
  F_t
\end{pmatrix}^T = \sum_{i=1}^N \mathbf{f}_i \Delta \phi \csc \theta,
\]  \[\tag{30}\]
allowing us to calculate the thrust, torque, and drag for any helical flagellum.

**Johnson Slender Body Theory.** Johnson (17) created a formulation of slender body theory to model the end effects ignored by Lighthill. The primary difference between the two formulations is that Johnson’s slender body is a long slender prolate spheroid that terminates smoothly. Johnson’s slender body theory gives the following equations for the velocity of a point on a helical flagellum in terms of local and nonlocal velocity terms,
\[
\mathbf{u}(r) = \mathbf{u}_{local}(r) + \mathbf{u}_{nonlocal}(r)
\]  \[\tag{31}\]
with
\[
\mathbf{u}_{local}(r) = \frac{1}{8\pi \mu} \left[ -\ln \left( x^2 e \right) \left( \mathbf{I} + \mathbf{t}(r) \right)(r) + 2 \left( \mathbf{I} - \mathbf{t}(r) \right)(r) \right] \mathbf{f}(0),
\]  \[\tag{32}\]
and
\[
\mathbf{u}_{nonlocal}(r) = \int \mathbf{I}(r' - r) \cdot \mathbf{f}(r') \, dr' - \frac{1}{8\pi \mu} \int \frac{\mathbf{I} + \mathbf{t}(r') \mathbf{t}(r')}{|s - s'|} \mathbf{f}(r') \, dr',
\]  \[\tag{33}\]
where \( \kappa = a/\Lambda \) and \( \Lambda \) is the contour length as defined in Fig. 1. The radius of the cross section vanishes at either end of the slender body and is given by \( a(s) = a \sqrt{1 - 4s^2/\Lambda^2} \), where \( s \in [-\Lambda/2, \Lambda/2] \). The filament radius has an average value of \( a \Lambda/4 \); therefore in our Johnson slender body theory calculations we set the filament radius to be \( 4/\pi \) times the radius used in the experiments and other simulations.

We again use the rectangular rule of integration and the same rotational mapping Eqs. 21–24 to numerically evaluate Eq. 31 to obtain
\[
\mathbf{u}_t = \frac{1}{8\pi \mu} \left[ -\ln \left( x^2 e \right) \left( \mathbf{I} + \mathbf{t}(r) \right) + 2 \left( \mathbf{I} - \mathbf{t}(r) \right) \right] \mathbf{f}(0),
\]  \[\tag{32}\]
and
\[
\mathbf{u}_{nonlocal}(r) = \int \mathbf{I}(r' - r) \cdot \mathbf{f}(r') \, dr' - \frac{1}{8\pi \mu} \int \frac{\mathbf{I} + \mathbf{t}(r') \mathbf{t}(r')}{|s - s'|} \mathbf{f}(r') \, dr',
\]  \[\tag{33}\]
where
\[
K = \frac{1}{2} \left[ \sum_{n \neq 0} \mathbf{f}_m \right] + \ln \left( x^2 e \right).
\]  \[\tag{36}\]
This discretized formulation is very similar to the Lighthill version (Eq. 25), except that the constant \( \ln(\delta / \delta) \) in the \( D_i \) term in Eq. 27 is replaced by \( -K \). The net force is solved using the same numerical strategy as used for the Lighthill formulation, giving force, torque, and drag.

**Asymptotic Theory for a Long Flagellum**

In this section we expand Lighthill’s slender body theory to understand the length dependence shown in Fig. 3. Consider a flagellum parameterized by \( s \) as in Eq. 16 with a length \( L \gg R \) and \( L \gg \lambda \). For a sufficiently long helix, end effects are minimal so each segment is essentially the same. Therefore, the force per unit length can be written \( \mathbf{f}(s) \approx f_x \mathbf{x} \sin \phi + f_z \mathbf{z} \cos \phi \), where \( f_x \) is the force per unit length in the \( x \) direction and \( f_z \) is the tangential force per unit length perpendicular to the \( x \) direction. The tangential force per unit length has components in the \( y \) and \( z \) directions, depending on the segment’s helical phase \( \phi \equiv ks \cos \theta \), where \( k = 2\pi/\lambda \). The associated velocity of the helical filament is \( \mathbf{u}(s) = (U, -\Omega R \sin \phi, \Omega R \cos \phi) \) so the velocity formulation from Lighthill’s slender body theory gives, for the \( x \) direction and tangential velocities, respectively,
\[
U = \frac{f_x \sin \phi - f_z \cos \phi}{4\pi \mu} \sin \theta
\] 
\[
\int \csc \theta \, d\phi \left( f_x + f_z \sin \phi \cot \theta + f_z \phi^2 \cot \phi \right)
\] 
\[
\frac{4\pi \mu^3}{k \delta \cos \theta}
\]  \[\tag{37}\]
\[
\Omega = \frac{(-f_x \sin \theta + f_\Omega \cos \theta) \cos \theta}{4\pi\mu}
\]
\[
+ \int \frac{\csc \theta d\phi}{\phi} \left( \frac{f_\Omega \cos \phi + f_x \sin \phi \cot \theta}{4\pi\mu\xi} + \frac{f_x \sin^2 \phi + f_x \sin \phi \cot \theta}{4\pi\mu \xi^3} \right) \cdot
\]

where \( \xi(\phi, \theta) = \sqrt{4 \sin^2(\phi/2) + \theta^2 \cot^2 \theta} \), which means \( \phi \to \infty \) as \( \theta \to \infty \) (i.e., \( \frac{R}{L} \gg R, \lambda \)).

One can rewrite Eqs. 37 and 38 as

\[
U = \frac{f_x}{4\pi\mu} \sin \theta - (\tau_1/R) \cos \theta \sin \theta
\]
\[
+ \int \frac{\csc \theta d\phi}{\phi} \left( \frac{f_x}{4\pi\mu\xi} + \frac{(\tau_1/R) \sin \phi \sin \phi \cot \theta + f_x \theta^2 \cot^2 \theta}{4\pi\mu \xi^3} \right)
\]
\[
= \frac{f_x}{4\pi\mu} \left[ \sin^2 \theta + \int \csc \theta d\phi \left( \frac{\sin \phi \sin \phi \cot \theta}{\xi} \right) \right]
\]
\[
+ \frac{\tau_1}{4\pi\mu R} \left[ -\cos \theta \sin \phi + \int \csc \theta d\phi \left( \frac{\sin \phi \sin \phi \cot \theta}{\xi^3} \right) \right]
\]

showing these scalings are accurate.

where

\[
a_1 = \lim_{\phi \to \infty} \frac{1}{4\pi\mu \ln(L/R)} \left[ \sin^2 \theta + \int \csc \theta d\phi \left( \frac{\sin \phi \cot \theta}{\xi^3} \right) \right]
\]

[43]

\[
a_2 = \lim_{\phi \to \infty} \frac{1}{4\pi\mu R} \left[ -\sin \theta \cos \phi + \int \csc \theta d\phi \left( \frac{\sin \phi \sin \phi \cot \theta}{\xi^3} \right) \right]
\]

[44]

\[
a_3 = a_2
\]

[45]

\[
a_4 = \lim_{\phi \to \infty} \frac{1}{4\pi\mu R} \left[ \cos^2 \theta + \int \csc \theta d\phi \left( \frac{\cos \phi}{\xi^3} \right) \right]
\]

[46]

Expressing \( \tau \) and \( \tau \) in terms of \( \tau \) and \( \Omega \) as \( L \to \infty \), we have for the force and torque from Eq. 1

\[
\tau = A_{12} U + A_{22} \Omega
\]

[47]

\[
\tau = A_{12} U + A_{22} \Omega,
\]

[48]

where \( A_{11} = (\sec \theta/a_1)L/\ln(L/R), \ A_{12} = -[a_2 \sec \theta/(a_1 a_4)]L/\ln(L/R), \) and \( A_{22} = \sec \theta/a_4 L \).

Using Eqs. 47 and 48 and Eqs. 43–46, one can obtain the following scaling relationships for thrust, torque, and drag in the limit that \( L \to \infty \),

\[
F = -a_2 \sec \theta \frac{L}{a_1 a_4} \ln(L/R) \Omega
\]

[49]

\[
T = \frac{\sec \theta}{a_4} \frac{L \Omega}{L/R} U
\]

[50]

\[
D = \frac{\sec \theta}{a_4} \frac{L}{\ln(L/R)U}
\]

[51]

as given in Eqs. 4–6.

We rescale our slender body theory results and plot them in Fig. 9 along with the asymptotic predictions of our theory, showing these scalings are accurate.

ACKNOWLEDGMENTS. We acknowledge Oscar Gonzalez for his advice and for providing a numerical implementation of his boundary integral method. H.P.L. acknowledges financial support of the National Natural Science Foundation of China through Grant 11104179. H.L.S. acknowledges the support of the Sid W. Richardson Foundation.

Supporting Information

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SI Numerical Simulations

A Matlab program is provided. It calculates thrust, torque, and drag for any helical flagellum, using the regularized Stokeslet method, Lighthill’s formulation of slender body theory, or Johnson’s version of slender body theory; resistive force theory results are also provided for comparison. Source files of this program have been deposited on [http://202.121.182.14:8080/faculty/hpzhang/RodenbornPNAS.html](http://202.121.182.14:8080/faculty/hpzhang/RodenbornPNAS.html), [http://chaos.utexas.edu/people/faculty/harry-l-swinney/propulsion-by-a-helical-flagellum](http://chaos.utexas.edu/people/faculty/harry-l-swinney/propulsion-by-a-helical-flagellum), and on the Matlab File Exchange under the title “Helical Swimming Simulator.” Instructions to use this program can be found on the same web pages.