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Hydrodynamic interactions are key in thrust-generation of microswimmers with hairy flagella

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Abstract

The important role of flagellates in aquatic microbial food webs is mediated by their flagella that enable them to swim and generate a feeding current. The flagellum in most predatory flagellates is equipped with rigid hairs that reverse the direction of thrust compared to the thrust due to a smooth flagellum. Conventionally, such reversal has been attributed to drag anisotropy of individual hairs, neglecting their hydrodynamic interactions. Here, we show that hydrodynamic interactions are key to thrust-generation and reversal in hairy flagellates, making their hydrodynamics fundamentally different from the slender-body theory governing microswimmers with smooth flagella. Using computational fluid dynamics and model analysis, we demonstrate that long and not too closely spaced hairs and strongly curved flagellar waveforms are optimal for thrust-generation. Our results form a theoretical basis for understanding the diverse flagellar architectures and feeding modes found in predatory flagellates.

Flagella and cilia are ubiquitous in both prokaryotic and eukaryotic organisms. They accomplish different tasks such as locomotion in bacteria, unicellular protists and spermatozoa^{1,2}, feeding and pumping in unicellular and multi-cellular organisms³⁻⁶, and other transport functions in dense ciliary arrays in plankton and mammals⁷⁻⁹. The flagellum is often a smooth, slender organelle and the drag-based propulsion of such 'naked'

flagella is extensively studied and well understood^{10–12}. In many unicellular protists, however, the flagellum is equipped with either a vane¹³, small and thin, non-tubular hairs^{14;15}, or thick and rigid, tubular hairs¹⁶. Little is known about the hydrodynamics of such flagella despite their great significance.

Predatory flagellates are important in the aquatic microbial food webs and in the marine carbon cycle^{3;19–21}, and their survival relies on the feeding flow generated by the flagellum that in most species is equipped with tubular hairs^{22;23}. In hairy flagellates with flagellar wave motion in a two-dimensional plane, the tubular hairs are oriented in the beat plane and perpendicular to the flagellum (Fig. 1a). The hairs cause the thrust to reverse compared with the thrust of a smooth flagellum and to point in the opposite direction of the propagating wave (Fig. 1b). Thus, swimming cells are pulled rather than pushed by the flagellum, and in tethered cells, the flagellum generates a feeding current toward the cell^{17;24;25}. The mechanism of thrust reversal has been ascribed to the drag anisotropy of individual hairs: the presence of hairs on the flagellum effectively increases the tangential drag and decreases the normal drag relative to the flagellum, hence reversing the thrust direction^{26;27}. In these analyses using resistive force theory, the effect of the induced flow generated by the flagellum and the neighboring hairs is neglected, implicitly assuming that hairs are hydrodynamically independent of one another. However, the distance between neighboring hairs is typically much smaller than the length of the hairs, and disregarding hydrodynamic interactions appears unjustified^{26–28}. In this study we use computational fluid dynamics (CFD) to examine hairy flagella, and we demonstrate how the hitherto unexplored interactions dominate the hydrodynamics of thrust-generation and reversal in predatory flagellates.

Thrust in model flagellates with different densities of hairs

We focus on the generic situation in which the flagellum beats in a two-dimensional plane and is equipped with identical and equidistantly spaced hairs that are perpendicular to the flagellum and positioned in the beat plane (Fig. 1c). In most CFD simulations, we use the waveform:

$$\phi(s, t) = A_\phi (1 - \exp\{-s/\delta\}) \sin(2\pi ft - 2\pi s/\lambda_\phi) , \quad (1)$$

where $\phi(s, t)$ is the angle of the tangent of the flagellum with respect to the flagellar axis, s the arc length from the point of attachment on the spherical cell body, A_ϕ the amplitude, λ_ϕ the wavelength, f the beat frequency, and δ the amplitude modulation factor²⁹. Parameters used in Eq. 1 and henceforth are listed in Table S1. The predatory flagellate *Pteridomonas danica* is a representative model organism³, and we use its morphological and kinematic parameters (Methods). Our CFD simulations of *P. danica* predict that the flagellum pulls the cell with the speed $64 \mu\text{m s}^{-1}$ in agreement with observations of freely swimming individuals (SI, Fig. S2), and

Figure 1: **Appearance and function of flagellar hairs.** **a**, Transmission electron micrograph of *Pteridomonas bucheri* with flagellar hairs (tubular mastigonemes). Image by courtesy of Tom Fenchel. **b**, Light micrograph of a tethered individual of *Pteridomonas danica*. The hairy flagellum drives a feeding current (dashed arrows) toward the cell in the opposite direction of the propagating flagellar wave (blue arrow)¹⁷, and the flow goes past the prey-intercepting tentacles extending from the cell (solid black arrows). The hairs on the flagellum are too thin to be visible in light microscopy. Image by courtesy of Sei Suzuki. **c**, Model morphology of *P. danica* with spherical cell (blue), flagellum (green), and hairs (red). The hairs are assumed to be rigid and remain perpendicular to the flagellum, and they are positioned slightly off the beat plane to avoid direct physical interference during the beat (Fig. S2)¹⁸. Scale bars in **a** and **b**: $2\mu\text{m}$.

Figure 2: **Effect of the density of hairs on flow and thrust.** The kinematic parameters in equation (1) are chosen based on the beat analysis of *Pteridomonas danica*, i.e., $f = 50$ Hz, $\lambda_\phi = 10 \mu\text{m}$, $A_\phi = 2\pi/5$, and $\delta = 2 \mu\text{m}$, and the length of the flagellum is $L_f = 12.5 \mu\text{m}$. The length of the hairs is reduced to $l = 0.9 \mu\text{m}$ to avoid physical interference during the beat. **a**, At low density of hairs ($N = 1 \mu\text{m}^{-1}$), the hydrodynamic interactions are weak. **b**, At high density of hairs ($N = 7 \mu\text{m}^{-1}$), as for *P. danica*, the hydrodynamic interactions are dominant. **c**, The time-averaged thrust is approximately the same as the time-averaged thrust due to a flexible, plane sheet with the same beat kinematics when the density of hairs is high.

our calculated time-averaged thrust, $\bar{F}_y = 7$ pN, is consistent with estimates based on the observed flow in tethered individuals²³.

To explore the hydrodynamic interactions we simulate the flow for different densities of hairs, N , i.e., the number of hairs per unit length of the flagellum (Fig. 2a,b). The time-averaged thrust is negative for the smooth flagellum, and the presence of hairs results in thrust-reversal when $N > 1 \mu\text{m}^{-1}$ (Fig. 2c). The thrust increases with the density of hairs, and it saturates when $N > 6 \mu\text{m}^{-1}$, consistent with the observed density of hairs in *P. danica*. The hydrodynamic interactions between the hairs are negligible when they are far apart, and the thrust therefore increases roughly proportional to the number of hairs when the density is low²⁶. However, at higher densities, the hydrodynamic interactions become predominant, and densely spaced hairs generate approximately the same thrust as a flexible, plane sheet (Fig. 2c).

Hair arrays: hydrodynamic interactions and drag anisotropy

At such complete dominance of hydrodynamic interactions, the question is whether the previously suggested anisotropy in the drag of individual hairs can cause thrust reversal^{26;27}. To answer this question, we first consider a segment along the straight part of the hairy flagellum for which resistive force theory predicts that hairs give rise to thrust generation and reversal^{26;27}. We neglect the flagellum itself and assume that hairs along the segment have the same lateral motion. For simplicity, we consider parallel hairs of length l , equidistantly positioned in an array of side length l and moving lengthwise or sideways with speed U cf. Fig. 3a,b. The magnitudes of the normal and the tangential drag on the array approach the asymptotic value of an equivalent square sheet when increasing the density of hairs, thus neutralizing the drag anisotropy of an isolated hair (Fig. 3c). Although the above results are obtained for a specific length of hairs, similar reduction of drag anisotropy is expected for any length of hairs, as long as the hairs are slender, since the induced far field flow primarily depends on the length of the hairs and only weakly on their diameter.

To shed light on the hydrodynamic interactions and their effect on drag anisotropy, we explore the interactions between two parallel hairs (Fig. 3a). The low Reynolds number forces on the second hair $F_t^{(2)}$ and $F_n^{(2)}$ in length and sideways motions, respectively, are proportional to the velocity of the hair relative to the local background flow $U_t^{(2-1)}$ and $U_n^{(2-1)}$ induced by the first hair^{30;31}. We can therefore write:

$$F_t^{(2)} = C_t \mu l \left(U - U_t^{(2-1)} \right), \quad (2)$$

$$F_n^{(2)} = C_n \mu l \left(U - U_n^{(2-1)} \right), \quad (3)$$

where C_t and C_n are the drag coefficients for a single hair in length and sideways motion, respectively (equations 5-11.52 and 5-11.54 in reference³²). As an approximation of the induced velocity past the second hair, consider the velocity in the parallel and the normal direction due to a point force positioned at the center of the first hair and with the same magnitude as the drag on an individual hair¹¹:

$$U_t^{(2-1)} \approx \frac{F_t}{8\pi\mu l} = \frac{C_t U}{8\pi}, \quad (4)$$

$$U_n^{(2-1)} \approx \frac{F_n}{4\pi\mu l} = \frac{C_n U}{4\pi}. \quad (5)$$

Hence, the drag ratio in such a system of two hairs can be approximated:

$$\frac{F_n^{(2)}}{F_t^{(2)}} \approx \frac{C_n \left(1 - \frac{C_n}{4\pi} \right)}{C_t \left(1 - \frac{C_t}{8\pi} \right)} < \frac{C_n}{C_t}. \quad (6)$$

Figure 3: **Hydrodynamic interactions among parallel hairs in translational motion.** Both the length of the hairs and the sideways length of the arrays are $l = 2\mu\text{m}$, and the diameter of the hairs is 20 nm. **a**, The hydrodynamic interactions between two hairs are stronger when they move sideways than when they move lengthwise. **b**, By adding more hairs and increasing their density, N , the flows become similar for the two directions of motion. **c**, The drag on the array in sideways, F_n , and lengthwise, F_t , motion approach the asymptotic value of an equivalent square sheet (top), and the drag anisotropy of the system vanishes (bottom). The theoretical prediction for a single hair is $F_n/F_t = 1.6$ in agreement with the CFD results (blue symbols), and equation (6) predicts $F_n^{(2)}/F_t^{(2)} = 1.4$ for two hairs in agreement with the simulations for $N = 0.5\mu\text{m}^{-1}$.

The approximation is in good agreement with our CFD simulations (Fig. 3c), and the analysis shows that the hydrodynamic interactions reduce the strength of the drag anisotropy because $U_n^{(2-1)} > U_t^{(2-1)}$.

Thrust-generation with sparse and dense hairs

While hydrodynamic interactions neutralize the fundamental anisotropy underlying drag-based propulsion, it brings about another potential mechanism of thrust-generation. Consider the previous array of parallel hairs in the side-wise motion. Upon saturation of the thrust at $N \approx 6 \mu\text{m}^{-1}$, further increasing the density of hairs does not result in more force (Fig. 3c). However, extending the row of hairs, i.e. increasing the sideways length of the array will result in an increased force (Fig. S3). This implies that for a given number of hairs, a net force is produced in a periodic and non-reciprocal fashion, where the sideways length of the array is increased during a “power” stroke and decreased during a “return” stroke. We propose that this mechanism is exploited by the hairy flagellates where the curvature of the flagellum plays a direct and key role by periodically bringing about an anisotropy in the arc length covered by several hairs at either sides of the flagellar crest. This anisotropy in the arc length (analogous to the sideways length of the array) at the two sides, moving in the opposite direction due to the action of the flagellum, results in a net force (thrust).

The proposed mechanism suggests that in a flagellum with dense hairs, the location of thrust generation is shifted from the straight parts to the crests of the passing wave. To illustrate the mechanism, we consider a one quarter wavelength long segment of the flagellum with sparse and dense hairs, respectively. As a simple model that allows us to compare with known expressions from resistive force theory^{26;27}, we use the flagellar kinematics:

$$d(y, t) = A \sin(2\pi ft - 2\pi y/\lambda), \quad (7)$$

where d is the displacement of the material points on the flagellum in the lateral x -direction, y the centerline axis, A the amplitude, and λ the wavelength. In the sparse system, the thrust correlates with the motion of individual hairs, and accordingly, only hairs at the straight part (with a dominant transversal motion) generate thrust, but not the hairs at the crest (with a dominant rotational motion) cf. Fig. 4a,b. In the dense system, on the other hand, the role switches and most of the thrust is generated at the crest (Fig. 4c,d). The resulting $T/4$ phase shift ($T = 1/f$ being the period of the flagellar wave) of the generated thrust due to the hairs from the sparse to the dense system is a signature of the change from drag-based thrust to hydrodynamic interaction based thrust (Fig. 4e). For comparison, consider the time-averaged drag-based thrust generated by a single hair suggested by resistive force theory^{23;26;27}:

Figure 4: **Location of thrust generation on flagella with sparse and dense hairs.** We apply the kinematics in equation (7), and in (a) - (e) we use $f = 27.5 \text{ Hz}$, $\lambda = 12 \mu\text{m}$, $A = 2 \mu\text{m}$, $0 < y < 3 \mu\text{m}$, and $l = 0.9 \mu\text{m}$. (a, b) In the sparse system with 2 hairs ($N = 0.8 \mu\text{m}^{-1}$), the thrust due to the hairs ($\bar{F}_{y,hairs}$, red arrow) is produced at the straight segment of the flagellum. (c, d) In contrast, in the dense system with 24 hairs ($N = 6.8 \mu\text{m}^{-1}$), the thrust is produced at the curved part (dashed arrows show the overall motion of the hairs). e, The thrust in the sparse and the dense system during half of the beat period. f, The generated thrust by hairs as function of the wavelength and with all other parameters as in (a) - (e). The thrust in the sparse system depends only weakly on the wavelength and is described well by the resistive force theory (RFT) model in equation (8), whereas the thrust in the dense system decreases strongly with increasing wavelength (decreasing curvature), and it is significantly overestimated by RFT.

$$\bar{F}_{y,\text{RFT}} = 2(C_n - C_t)\mu l \left(1 - \frac{1}{\sqrt{1 + (2\pi A/\lambda)^2}}\right) \lambda f, \quad (8)$$

where C_t and C_n are the drag coefficients used in equations (2) and (3). The thrust expression is proportional to the difference between C_n and C_t , emphasising the significance of drag anisotropy in drag-based thrust¹². As expected from equations (2) and (3), the resistive force theory model overestimates the generated thrust by the hairs, slightly in the sparse system but significantly in the dense system (Fig. 4f). Importantly, the thrust has a weak dependence on the wavelength for the sparse system, but in contrast in the dense system, it increases significantly by decreasing the wavelength highlighting effect of the curvature of the flagellum (Fig. 4f).

Thrust mechanism and analytical model

Here we present an analytical model that allows us to shed light on the mechanism and key parameter of thrust-generation by flagella with dense hairs ($N > 6\mu\text{m}^{-1}$). We assume that hairs are relatively long ($2l/D_f \gg 1$, where D_f is the diameter of the flagellum), and several hairs, together, effectively function as a sheet cf. Fig. 5a,b. For simplicity of the analytical model, we assume that the amplitude modulation factor, δ , the radius of the flagellum, and the radius of the hairs only affect the thrust weakly. The remaining important parameters are μ , f , λ_ϕ , A_ϕ , L_f , and l . From these dimensional parameters, we can construct two dimensionless parameters. In total, we have the three dimensionless parameters l/λ_ϕ , A_ϕ , and L_f/λ_ϕ , and in our minimal model we can express the thrust:

$$\bar{F}_y = \mu f \lambda_\phi^2 \Phi(l/\lambda_\phi, A_\phi, L_f/\lambda_\phi), \quad (9)$$

where Φ is a dimensionless function. From dimensional analysis it is clear that $\bar{F}_y$ is proportional to μ and f . To determine Φ and develop a mechanistic model, we consider the sinusoidal beat pattern:

$$\phi(s, t) = A_\phi \sin(2\pi f t - 2\pi s/\lambda_\phi). \quad (10)$$

Considering that the thrust is predominantly generated at the crests of the flagellar wave (Fig. 4c, d), we assume that the basic thrust-generating unit spans one quarter of the wavelength and is centered at the crest (Fig. 5c). Each unit consists of two parts on either side of the flagellum where the hairs come close and fan out, respectively. For such unit, the part where the hairs come close moves upwards and creates a negative thrust, whereas the part where the hairs fan out moves downwards and creates a positive thrust. The net thrust, $\bar{F}_{y,\text{unit}}$, is the difference between the two contributions, and we make the low Reynolds number estimate:

$$\bar{F}_{y,\text{unit}} \propto \mu [\theta(r_c + l/2) - \theta(r_c - l/2)] U_{\text{unit}} = \mu \theta l U_{\text{unit}}, \quad (11)$$

Figure 5: **Parameter exploration and analytical thrust model.** **a**, Snapshot of the velocity field for a hairy flagellum with the kinematics in equation (1) and the parameters $f = 50 \text{ Hz}$, $\lambda_\phi = 10 \mu\text{m}$, $A_\phi = 2\pi/5$, $\delta = 2 \mu\text{m}$, $L_f = 12.5 \mu\text{m}$, $l = 0.9 \mu\text{m}$, and $N = 7 \mu\text{m}^{-1}$. **b**, Snapshot of the velocity field produced by an equivalent plane sheet. **c**, Basic thrust unit assuming that the dense system of hairs functions as a sheet (red) on either side of the flagellum (green). **(d - f)**, Dimensionless thrust as function of the dimensionless parameters l/λ_ϕ , A_ϕ , and L_f/λ_ϕ . **d**, Parameters: $\lambda_\phi = 10 \mu\text{m}$, $A_\phi = 2\pi/5$, and $L_f = 12.5 \mu\text{m}$. **e**, Parameters: $\lambda_\phi = 9 \mu\text{m}$, $L_f = 12.5 \mu\text{m}$, and $l = 1.5 \mu\text{m}$. **f**, Parameters: $\lambda_\phi = 10 \mu\text{m}$, $A_\phi = 2\pi/5$, and $l = 0.9 \mu\text{m}$. In all CFD simulations we used $f = 50 \text{ Hz}$ and $N = 8 \mu\text{m}^{-1}$, and the hairs with $l = 1.5 \mu\text{m}$ are slightly off the beat plane to avoid physical interference (Fig. S2a). CFD results (red points) and analytical model in equation (13) with $\alpha = 3.8$ (blue curves).

where U_{unit} is the characteristic speed of the two parts, $\theta(r_c - l/2)$ the characteristic length of the part where the hairs come close (corresponding to the arc length in the middle of the part), and $\theta(r_c + l/2)$ the characteristic length of the part where the hairs fan out (Fig. 5c). Note that $\theta = \sqrt{2}A_\phi$, if the unit spans one quarter of the wavelength. To estimate U_{unit} we use the magnitude of the rotation rate of the hairs at the crests, $\Omega_{\text{unit}} = 2\pi f A_\phi$, since $\partial\phi/\partial t = 2\pi f A_\phi \cos(2\pi ft - 2\pi s/\lambda_\phi)$. Therefore, we obtain that $U_{\text{unit}} = \Omega_{\text{unit}} l/2 = \pi f A_\phi l$. By combining the expressions, we find the estimate:

$$\bar{F}_{y, \text{unit}} = \pi \alpha \mu f A_\phi^2 l^2, \quad (12)$$

where α is a dimensionless shape factor. There are $2L_f/\lambda_\phi$ thrust-generating units along the full length of the flagellum, and the total thrust generated by the hairy flagellum becomes:

$$\bar{F}_{y, \text{sheet}} = \frac{2L_f}{\lambda_\phi} \bar{F}_{y, \text{unit}} = \frac{2\pi \alpha \mu f L_f A_\phi^2 l^2}{\lambda_\phi} = \alpha \mu f L_f \kappa_f A_\phi l^2, \quad (13)$$

where $\kappa_f = 2\pi A_\phi/\lambda_\phi$ is the magnitude of the curvature at the crest. The model gives a reasonable estimate and a consistent functional behaviour of the generated thrust, as compared with the CFD results for the three dimensionless parameters l/λ_ϕ , A_ϕ , and L_f/λ_ϕ (Fig. 5d-f). In the CFD simulations there is also influence of the flagellum itself as well as the cell body (Fig. S5), which are not accounted for in our model. Note that a flagellum with short hairs function like a slender body, in which drag-based thrust is dominant giving rise to a negative thrust (Fig. 5d). However, hydrodynamic interaction-based thrust dominates for longer hairs, as in hairy flagellates with tubular mastigonemes, consistent with the model presented here (Eq. 13).

Perspective

The optimal design of a flagellum with respect to thrust production is suggested by equation (13): The flagellum should be long, curvy, and equipped with long hairs. Indeed, hairy flagella have noticeable shorter wavelengths than naked flagella¹⁷. However, for a planar beat, as in our model organism, hairs longer than the radius of curvature at the crests would physically interfere with each other. One solution is to orient hairs slightly off the beat plane (Fig. S2), but this implies marginally less thrust than if hairs were in the beat plane. This solution is used by flagellates where hairs are oriented at a small angle relative to the beat plane defined by the central pair of axonemal microtubules^{33;34}. A second solution may be bundling of hairs (Fig. S6a)³³, where interference is avoided if hairs become aligned rather than intertwined. Thirdly, the beat of the flagellum itself may not be perfectly planar³³, and many hairy flagellates in fact have complex three-dimensional beat patterns^{3;35}, providing room for longer hairs without interference. Yet another way to increase hydrodynamic interaction based thrust is through terminal branching of the hairs, as found in many species (Fig. S6b)³³, which may

dramatically increase the thrust (Fig. S6d). Finally, the fibrous hairs between the tubular hairs in some species make the hairs further resemble a sheet (Fig. S6b)³³. The diverse flagella designs discussed above can thus all be understood in the context of the mechanism for thrust production suggested here, and they may provide novel ideas for design of artificial swimmers and flow generation in microfluidic devices.

The hydrodynamics of flagella is most often studied in the context of propulsion^{7;11;12}. However, for predatory flagellates, the main consumers of bacteria in the ocean, efficient foraging is likely a much more important component of their fitness than propulsion per se. The presence of hairs on the flagellum is key to foraging in flagellates. Not only does the reversal of the flow increase the capture efficiency of prey arriving in the feeding current²³, the hairs also increase the thrust generation by a factor of 5–10 (Fig. 5d). At low Reynolds number, viscosity impedes predator-prey contact, but the hairy flagellum yields the necessary force and feeding current structure to secure the success and key role of flagellates in the microbial food webs.

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Author contributions

All authors designed the research, proposed the CFD simulations, and wrote the paper. SSA, JHW, and AA developed the theoretical models. TK provided biological advice on the models and interpretation of the results. SSA performed the CFD simulations.

Competing interests

The authors declare no competing interests.

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Methods

Computational fluid dynamics

We use computational fluid dynamics to numerically solve the flow governing equations around the hairy flagellum and cell body. The computational domain is a sphere of diameter $300\text{ }\mu\text{m}$ subtracted by the hairy flagellum and cell body. The domain is discretized on a finite volume mesh and discretized Navier-Stokes equations are solved using commercial software STAR-CCM+ version 15.06.006. Uniform pressure is applied on the spherical outer boundary of the domain, and a no-slip condition on the hairs, the flagellum and the cell body. Using the morphing technique, the computational cells are redistributed corresponding to the motion of the hairy flagellum (Movie S1: *DynamicMesh.avi*) (also see c.f. ^{36–38}). Simulations are conducted for a tethered organism, and the generated thrust is subsequently related to the swimming speed through the resistive matrix of the organisms³⁷. The force is calculated as:

$$\mathbf{F} = \iint_S (\boldsymbol{\sigma} \cdot \mathbf{n}) \, dS, \quad (14)$$

where $\boldsymbol{\sigma}$ is the stress tensor, $\mathbf{n}$ the unit normal vector on the surface S . The generated thrust is the y -component of the force produced by the hairy flagellum, F_y .

Model organism

Pteridomonas danica were isolated from local waters and maintained on a rice grain as substrate for their bacterial prey. Swimming cells were video-recorded through an Olympus IX71 inverted microscope equipped with a UPLSAPO60XO /1.35 oil-immersion objective by a Phantom v210 high-speed digital camera at $1000\text{ frames s}^{-1}$ at a resolution of $5\text{ pixels }\mu\text{m}^{-1}$. The beat pattern is digitized, reconstructed and modeled following the approach given in²⁹, details of which are given in AI, Fig. S1.

The *P. danica* cell is $5\text{ }\mu\text{m}$ in diameter, with a flagellum of length $L_f = 12.5\text{ }\mu\text{m}$ and diameter $D_f = 0.2\text{ }\mu\text{m}$, and a beat frequency of 50 Hz . The flagellum has approximately $13\text{ hairs }\mu\text{m}^{-1}$ in two rows along the flagellum (hence $6.5\text{ hairs }\mu\text{m}^{-1}$ on each side), each of a typical diameter of $D_h = 20\text{ nm}$, and a length $l = 1.5\text{ }\mu\text{m}$ as reported in^{3;27}.

Additional Information

Beat pattern of *Pteridomonas danica*

Details of the analysis and reconstruction of the beat in *Pteridomonas danica* are given in Fig. S1, and parameter used in the CFD and analytical models are listed in table S1.

Symbol	Item	unit
ϕ	angle of the tangent of the flagellum	rad
s	the arclength along the flagellum	μm
t	time	s
A_ϕ	amplitude of the angle	rad
λ_ϕ	wavelength of the angle	μm
f	frequency	s^{-1}
δ	amplitude modulation factor	μm
l	length of hairs	μm
L_f	length of the flagellum	μm
μ	viscosity	Pa s
u	flow velocity	$\mu\text{m s}^{-1}$
N	density of hairs	μm^{-1}
D_h	diameter of hairs	μm
D_f	diameter of the flagellum	μm
d	displacement of the material points on the flagellum	μm
A	amplitude of the displacement	μm
λ	wavelength of the displacement	μm
σ	stress tensor	Pa
F_y	thrust generated by hairy flagellum	pN
$\bar{F}_{y, \text{RFT}}$	thrust prediction of resistive force theory	pN
U	speed of the array of hairs	$\mu\text{m s}^{-1}$
F_t	force (lengthways)	pN
F_n	force (sideways)	pN
U_t	induced velocity (lengthways)	$\mu\text{m s}^{-1}$
U_n	induced velocity (sideways)	$\mu\text{m s}^{-1}$
C_t	drag coefficient (lengthways)	-
C_n	drag coefficient (sideways)	-
l_x	sideway length of the array of hairs	μm
$\bar{F}_{y, \text{unit}}$	thrust generation of the basic thrust unit	pN
θ	angle between the straight edges of the basic thrust unit	rad
U_{unit}	characteristic speed of the unit	$\mu\text{m s}^{-1}$
α	shape factor of the unit	-
Ω_{unit}	rotation rate of the hairs at the crests	rad s^{-1}
r_c	radius of the curvature of the flagellum	μm
$\bar{F}_{y, \text{sheet}}$	thrust generation of the sheet model	pN
D_{cell}	diameter of the cell	μm

Table S1: List of symbols used in the CFD and analytical models.

(a) scale bar 2 μm

(b) Raw tracks

(c) Smoothed tracks

(d) $\phi = \arctan(dx/dy)$ of (c)

(e) Modeled ϕ ($\lambda_\phi = 9 \mu\text{m}$, $A_\phi = 1.25 \text{ rad}$)

(f)

Figure S1: Flagellar beat of *Pteridomonas danica* (a) based on the method in Geyer et al.²⁹. We obtain $\lambda_\phi \simeq 8\text{-}10 \mu\text{m}$, $A_\phi \simeq 1.2\text{-}1.4 \text{ rad}$ ($\delta = 1\text{-}2$). The flagellar¹⁸ beat is reconstructed (f) using $x = x_0 + \int_0^s \cos \phi(s') ds'$, $y = y_0 + \int_0^s \sin \phi(s') ds'$.

Figure S2: CFD model of non-planar hairs and swimming speed in *Pteridomonas danica*. a) To avoid physical interference at the reported³ length of hairs ($l = 1.5 \mu\text{m}$), hairs are oriented slightly off the beat plane. Orientation of hairs along the flagellum is given by $\tilde{\mathbf{r}} = \tilde{\mathbf{n}} + \beta \tilde{\mathbf{b}}$, where $\tilde{\mathbf{n}}$ and $\tilde{\mathbf{b}}$ are normal (in the beat plane) and bi-normal (perpendicular to the beat plane) unit vectors, and $\beta = 0.3 \sin \phi(s)$. b) Percentage of reduction in the generated thrust ($\Delta \bar{F}_{y,\beta} = \frac{\bar{F}_{y,\beta} - \bar{F}_y}{\bar{F}_y} \times 100$) due to hairs oriented off the beat plane (i.e. non-zero and constant β in $\tilde{\mathbf{r}}$) on the generated thrust compared to that of hairs in the beat plane ($\bar{F}_y$). Here $l = 0.9 \mu\text{m}$ to avoid physical interference. c) Averaged flow field over the beat cycle at $l = 1.5 \mu\text{m}$. d) Swimming speed at different value of λ_ϕ : in the observed range of λ_ϕ (dotted lines), there is a good agreement between CFD prediction and observation of the swimming speed. For the case $\delta = 1$, the averaged generated thrust by the flagellum $\bar{F}_y = 6.8 \text{ pN}$, consistent with indirect estimates based on observed flow fields²³, $\sim 7 \text{ pN}$.

Figure S3: The present proposed mechanism of hydrodynamic interaction-based thrust. **a**, $l_x/l = 2$ with 20 hairs, and **b** the equivalent sheet. **c**, due to the strength of hydrodynamic interaction, the total force of several hairs depends on the distance between the hairs i.e. the sideways length of the array (l_x), effectively functioning similar to a sheet for $l_x/l < 5$ (**c**). **d**, in the lack of a drag anisotropy in the straight segments of a hairy flagellum, the curvature of the flagellum plays a direct role in the generated thrust by dynamically regulating the distance between the hairs, and thus the strength of the hydrodynamic interaction at the two sides of the flagellar crest, rotating in the opposite direction (**e**, marked as '1' and '2'), bringing about a net downward thrust. Upon passing through the straight phase (**f**), which now functions as a recovery stroke, the role of the areas '1' and '2' switches in the generated thrust (**g**). Maximum thrust is achieved at a sufficient density of the hairs, as in hairy flagellates, where hairs at the convex part of the crest effectively function similar to a sheet. Dashed arrows show the instantaneous dominant motion of the segment.

Figure S4: Generated thrust by a dense system of Fig. 4 with preserved arc length (inextensible flagellum). In this case, material points on the flagellum have a eight-liked trajectory (a) during the beat cycle, with an upward motion at the straight part of the flagellum and downward motion at the crests. Therefore, the thrust at the straight part is further reduced to negative values (i.e. upward flow), while it is augmented at the crests, and thus shifting further the spatial distribution of the thrust to the sides of the volume swept by the hairy flagellum (b). The mean net thrust values, however, are not significantly affected as compared with extensible dense system of Fig. 4. (e.g. for the above case 12% increase in the magnitude of thrust by hairs ($\bar{F}_{y,hairs} = 0.54$ pN), and 3% decrease by the flagellum ($\bar{F}_{y,flagellum} = -0.31$ pN).)

Figure S5: Effect of the cell size on the thrust of hairy flagellum ($l = 0.9 \mu\text{m}$).

Figure S6: Hair bundling and terminal filaments. a) Hairs in flagellate *Melkoniania moestrupii* are often bundled together. b) In addition, there are thin fibrous hairs in between the thicker tubular hairs as well as terminal filaments (arrow) on individual tubular hairs. Spatial distribution of generated thrust (σ_y) without (c) and with (d) terminal filaments. Here $l = 0.9 \mu\text{m}$, and length of terminal filaments is $l_{tf} = 1.0 \mu\text{m}$ which are positioned at distance $l_0 = 0.8 \mu\text{m}$ on the hairs (measured from the attachment point of the hairs to the flagellum), with an arbitrary orientation of $\tilde{\mathbf{r}} = \tilde{\mathbf{n}} + 11\tilde{\mathbf{b}}$. Addition of the terminal hairs, increases the thrust by 100%. Scale bars in (a) and (b): 1 and $0.2 \mu\text{m}$, respectively. Images courtesy of Robert A. Andersen.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [DynamicMesh.avi](#)