

Confinement-Induced Motion of Ciliates

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The time dynamics of flagellar and ciliary beating is often neglected in theories of microswimmers, with the most common models prescribing a time-constant actuation of the surrounding fluid. By explicitly introducing a metachronal wave, coarse-grained to a sinusoidal surface slip velocity, we show that a spatial resonance between the metachronal wave and the corrugation of a confining cylindrical channel enables a ciliate to swim even when it cannot move forward in a bulk fluid. Using lubrication theory, we reduce the problem to the Adler equation that reveals an oscillatory and steady swimming regime. Interestingly, a ciliate can even reverse its swimming direction in a corrugated channel compared to the bulk fluid.

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It is widely known that bodies undergoing a reciprocal motion cannot propel in bulk fluids at low Reynolds numbers [1]. Thus, microorganisms need to rely on structures such as flagella [2] or cilia [3] that beat in a nonreciprocal fashion [1,4]. Because of the challenge of fully capturing the dynamics of each flagellum or cilium, theoretical descriptions of microswimmers typically rely on a coarse graining. Examples include the specification of an effective surface slip velocity in the well-known squirmer model [5–10] or a truncated multipolar expansion for the swimmer-generated flow fields [7,11–14]. Such models have been successful in shedding light on the behavior of microswimmers in complex environments, including swimmer suspensions [15–20], also under confinement by flat [9,21–29] or curved [30–36] walls, as well as porous [37,38] and deformable [39] materials.

However, nearly all of the cited theoretical work focuses on the time-averaged actuation of the fluid by the flagellar or ciliary beat, i.e., prescribes slip velocity profiles and multipolar expansion coefficients that are constant in time. While such descriptions may capture the dynamics of microswimming on long timescales, they fail to describe the dynamics on the timescale of the beating period [40–43]. In this Letter, we show that accounting for the time dynamics of ciliary beating is crucial to understanding the motion of ciliates in spatially inhomogeneous confinement. In particular, their ability to move forward is heavily affected by a spatiotemporal resonance between the fluid

forcing coming from the ciliary beating pattern and the modulated environment.

In our studies, we use both lattice-Boltzmann simulations and a theoretical analysis based on the lubrication approximation. The latter is a versatile tool and has been used extensively in different contexts such as biological flows [44–47], fluid-mediated interactions [48–51], chemically active [52–56] or charged [57,58] flows, as well as droplets and films [59–62].

In the following, we demonstrate how a sinusoidal metachronal wave coarse-grained to a surface slip velocity that spatially resonates with the corrugation of a confining channel enables ciliates to swim, even when they cannot move forward in a bulk fluid. In particular, we reduce the swimming dynamics to the Adler equation that shows an oscillatory and a steady regime.

Specifically, we aim to investigate the motion of a ciliate in a cylindrical channel aligned with the x axis [63] and whose local radius $R(x)$ varies according to

$$R(x) = R_c + R_0 + R_1 \cos(k_w x). \quad (1)$$

Here, R_c is the radius of the ciliate, R_0 is the spatially averaged distance between the ciliate and the channel wall, R_1 is the amplitude of the corrugation, and k_w is its wave number [see Fig. 1(a)]. The ciliate is modeled as a cylinder whose length L_c is much larger than the wavelength $\lambda_w = 2\pi/k_w$ and so can be considered effectively infinite in length. Ciliates are covered by a carpet of beating cilia, which move fluid along the ciliate surface and thereby propel the microorganism forward. Because variations in height of the ciliary layer are typically much smaller than R_c [64], we coarse-grain the operation of this layer into an effective slip velocity tangential to the surface of the ciliate,

$$\mathbf{v}(x, r = R_c, t) = [v_p(t) + v_c(x, t)]\mathbf{e}_x, \quad (2)$$

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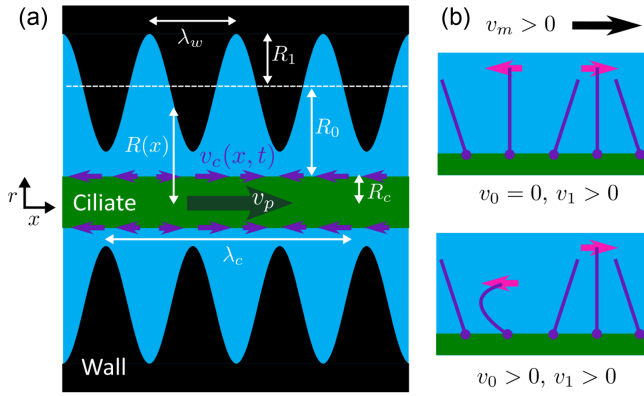


FIG. 1. (a) Schematic of a long ciliate (green cylinder) that swims in a cylindrical channel with corrugated walls, which are depicted in black while the surrounding fluid is drawn in blue. The cilia are coarse-grained to an effective slip velocity v_c , represented by purple arrows on the surface of the ciliate, while the ciliate moves with velocity v_p . (b) Schematics of a reciprocal (above) and nonreciprocal (below) ciliary beat pattern. Pink arrows indicate the direction of motion of the single cilia. The metachronal wave travels from left to right with speed $v_m > 0$. For a sufficiently sparse ciliary carpet, the net fluid flow of the reciprocal beat pattern is negligible.

Here, $\mathbf{v}(x, r, t)$ is the velocity of the fluid constrained between the ciliate and the corrugated channel wall, $v_p(t)$ is the swimming velocity of the ciliate, which needs to be determined, and the slip velocity $v_c(x, t)$ encodes the ciliary beating. Contrary to previous work, we do not take the velocity $v_c(x, t)$ to be constant in time, as we aim to capture the time-varying actuation by the ciliary layer and its effect on the surrounding fluid. Indeed, cilia beat in a periodic fashion with period T_c and their motions often split into a power and recovery stroke [3,65] [see Fig. 1(b)] that are nonreciprocal, enabling net swimming and motion of fluid.

Typically, neighboring cilia beat with a phase lag and thereby form a metachronal wave [66–69] with a wavelength λ_c much smaller than the size L_c of the ciliate [64]. To capture these features, we propose for the slip velocity at the surface of the ciliate,

$$v_c(x, t) = v_0 + v_1 \cos\{k_c[x - x_p(t)] - \omega t\}, \quad (3)$$

where v_0 is the time-averaged velocity imposed by the ciliary layer, and v_1 is the amplitude of the metachronal wave. Here, $v_0 \neq 0$ indicates that the ciliary carpet induces a net fluid transport across the surface of the ciliate. Such a transport may result from nonreciprocal power and recovery strokes or even from reciprocally beating cilia that are packed densely enough so that hydrodynamic interactions lead to net fluid flow [70]. Furthermore, $k_c = 2\pi/\lambda_c$ is the wave number of the metachronal wave and $\omega = 2\pi/T_c$ is the ciliary frequency. As a result, the metachronal wave travels with a speed $v_m = \omega/k_c$ in the body-fixed frame of

the ciliate. The origin of this frame of reference moves with velocity $v_p(t)$ along the x direction and is located at position $x_p(t) = \int_0^t v_p(t') dt'$.

Now, the main task is to determine the swimming velocity of the ciliate, $v_p(t)$. At low Reynolds numbers, the fluid obeys Stokes' equations and the incompressibility condition, $\nabla P(\mathbf{r}, t) = \mu \Delta \mathbf{v}(\mathbf{r}, t)$ and $\nabla \cdot \mathbf{v}(\mathbf{r}, t) = 0$, where μ is the dynamic viscosity and $P(\mathbf{r}, t)$ is the pressure. No-slip boundary conditions apply at the surface of the channel, $\mathbf{v}[x, r = R(x), t] = 0$. The ciliate swims in an otherwise quiescent fluid such that no external pressure gradient is applied, and moves force-free, meaning without an applied external force, $\oint_S \boldsymbol{\sigma}(\mathbf{r}, t) \cdot \mathbf{n}(\mathbf{r}, t) dS = \mathbf{0}$, where S is the surface of the ciliate, $\boldsymbol{\sigma}(\mathbf{r}, t)$ is the Newtonian stress tensor, $\boldsymbol{\sigma}(\mathbf{r}, t) = -P(\mathbf{r}, t)\mathbf{I} + \mu[\nabla \otimes \mathbf{v}(\mathbf{r}, t) + (\nabla \otimes \mathbf{v})^T(\mathbf{r}, t)]$, and $\mathbf{n}(\mathbf{r}, t)$ is the outer normal.

Lubrication theory and linearization—We solve the above equations by employing the lubrication approximation [71], whereby the velocity field is taken to vary much more rapidly in the radial direction than in the x direction. Such an assumption is true if the characteristic lengths in the radial direction (R_0, R_1) are much smaller than the characteristic lengths along the x axis (λ_w, λ_c). Ultimately, we arrive at the following equation for the time evolution of $x_p(t)$:

$$\dot{x}_p(t) = -\langle \mathcal{G}(x) v_c(x, t) \rangle, \quad (4)$$

where the angle brackets indicate an average over x , and the local mobility coefficient $\mathcal{G}(x)$ only depends on the shape of the channel wall and the radius of the ciliate (see Supplemental Material Sec. I [72]). In particular, $\langle \mathcal{G}(x) \rangle = 1$. Since $v_c(x, t)$ is a sinusoid [Eq. (3)], one immediately obtains

$$\dot{x}_p(t) = \begin{cases} -v_0 - v_1 \frac{\mathcal{G}_n}{2} \cos[k_c x_p(t) + \omega t] & \text{if } \lambda_c = \lambda_w/n \\ -v_0 & \text{if } \lambda_c \neq \lambda_w/n, \end{cases} \quad (5)$$

where n is a natural number and $\mathcal{G}_n$ are the respective Fourier coefficients of $\mathcal{G}(x)$. In the limits of small curvature of the ciliate body ($R_0/R_c \ll 1$) and shallow corrugation ($R_1/R_0 \ll 1$), a linearization with respect to these parameters shows that only the Fourier coefficient for $n = 1$ is nonzero, becoming $\mathcal{G}_1 = 2R_1/R_0$. Clearly, in the case where the spatiotemporal dynamics of the ciliary carpet is discarded ($v_1 = 0$), the channel is flat ($R_1 = 0$), or the wavelengths of the metachronal wave and the corrugation do not match ($\lambda_c \neq \lambda_w/n$), the ciliate swims with a velocity $v_p = -v_0$, as it would when placed in bulk fluid. However, if none of the three previous conditions are met, a resonance between the local hydrodynamic resistance (resulting from the corrugated wall profile) and the fluid forcing (resulting from the metachronal wave) generates the

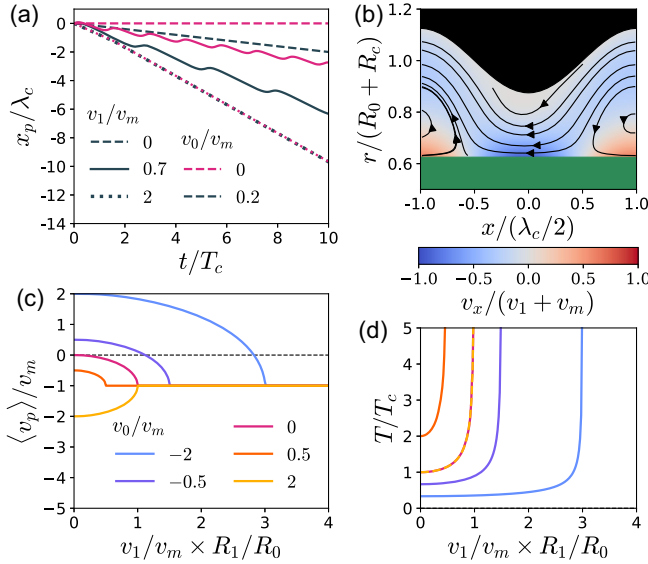


FIG. 2. Resonance between confinement and metachronal wave. (a) Position x_p of the ciliate plotted vs time for different values of v_0/v_m and v_1/v_m with $\mathcal{G}_n = 2$. Colors indicate value of v_0/v_m and line types indicate v_1/v_m . (b) Snapshot of the fluid flow for $v_0 = 0$, $R_0/R_c = 3/5$, $R_1/R_0 = 1/3$, $R_0/\lambda_c = 3/20$, $v_1/v_m = 3.6$, taken at $t/T_c = 3.78$. The fluid streamlines are shown in black and the color indicates the flow-velocity component v_x . In this moment, the ciliate moves to the left. (c) Time-averaged ciliate velocity $\langle v_p \rangle$ and (d) period of oscillatory motion T plotted vs the amplitude of ciliary slip velocity, v_1/v_m , times the amplitude of channel corrugation, R_1/R_0 , for several values of v_0/v_m . In all panels $\lambda_c = \lambda_w$.

extra term in Eq. (5). The effect on the trajectory of the ciliate can be seen by numerically solving Eq. (5), the results of which we show in Fig. 2(a). When $v_1/v_m = 0.7$ (full lines), where v_m is the metachronal-wave speed, the ciliate swims with an overall drift and superimposed oscillations.

Remarkably, such a drift occurs even when the ciliary carpet does not generate net fluid transport along its surface [$v_0 = 0$, magenta lines in Fig. 2(a)]. An organism with $v_0 = 0$ cannot propel itself in a bulk fluid, but it is able to when placed in a corrugated channel of appropriate wavelength. The cause is an imbalance between the net propulsion generated by the power stroke and the recovery stroke. While both generate the same slip velocity (in magnitude), they are performed in regions of different film thickness, where the generated flow experiences different effective hydrodynamic resistances [see Fig. 2(b)]. The result is directed motion even when the time-and-space-averaged slip velocity is zero. Every pair of forward and backward beating cilia can be thought of as two people playing tug of war. Even if they are equally strong, the pair will still move if one person stands on dry concrete and the other on slippery mud. Thus, motion is enabled by a variation in the friction profile, which occurs on a length scale comparable to the rope's length. Depending on the

phase difference between the corrugated wall and the velocity profile on the surface of the ciliate, the ciliate swims either with or against the metachronal wave. What enables net propulsion (rather than oscillation about a certain position) is the fact that the metachronal wave has a given direction. Because the velocity of the metachronal wave in the laboratory frame is the sum of the velocities of the ciliate velocity and of the metachronal wave, configurations of the flow leading to swimming against the wave persist longer than configurations that lead to swimming with the wave. As such, the ciliate spends more time swimming against the metachronal wave than with it, as can be seen in Supplemental Video 1 [72].

For high enough values of v_1 , the trajectory is no longer oscillatory, but instead becomes steady, in the direction opposite to the metachronal wave, and exactly at its speed [see Fig. 2(a)]. Thus, no matter how strongly the ciliary carpet may push, the ciliate is constrained to swim with the metachronal phase speed v_m . In this regime, the slip velocity profile becomes stationary in the laboratory frame of reference, as can be seen in Supplemental Video 2 [72]. Thus, the phase difference between the channel corrugation and the slip velocity profile is constant, and no further acceleration is possible.

One can indeed rationalize the two observed dynamical regimes by introducing the nondimensional coordinate in the frame of reference moving with the metachronal wave, $\xi = k_c x_p(t) + \omega t + \pi/2$. Rescaling time by ω^{-1} , Eq. (5) for $\lambda_c = \lambda_w/n$ can be cast in the form of the well-known Adler equation [73–75],

$$\dot{\xi} = a - b \sin \xi \quad \text{with} \quad a = 1 - \frac{v_0}{v_m} \quad \text{and} \quad b = \frac{v_1 \mathcal{G}_n}{v_m 2}, \quad (6)$$

which indeed shows a dynamical transition for

$$\left| \frac{a}{b} \right| = \left| \left(1 - \frac{v_0}{v_m} \right) / \left(\frac{v_1 \mathcal{G}_n}{v_m 2} \right) \right| = 1. \quad (7)$$

It is now possible to infer the time-averaged velocity of the ciliate, $\langle v_p \rangle$ [73,75]. In the phase-locked regime ($|a/b| < 1$), one obtains $\langle v_p \rangle = -v_m$, while the oscillatory regime ($|a/b| > 1$) yields

$$\frac{\langle v_p \rangle}{v_m} = \left(1 - \frac{v_0}{v_m} \right) \sqrt{1 - \left(\frac{\frac{v_1 \mathcal{G}_n}{v_m 2}}{1 - \frac{v_0}{v_m}} \right)^2} - 1. \quad (8)$$

As mentioned earlier, in the linearized limit, $\mathcal{G}_n = 2R_1/R_0 \delta_{1n}$, where δ_{ij} is the Kronecker symbol. So, in Fig. 2(c), we plot the time-averaged ciliate velocity vs $v_1/v_m \times R_1/R_0$ for different v_0/v_m and $\lambda_c = \lambda_w$. For increasing $v_1 R_1$, the ciliate velocity approaches that of the metachronal wave. Depending on v_0 , $\langle v_p \rangle$ either decreases or increases toward $-v_m$. In fact, the ciliate even

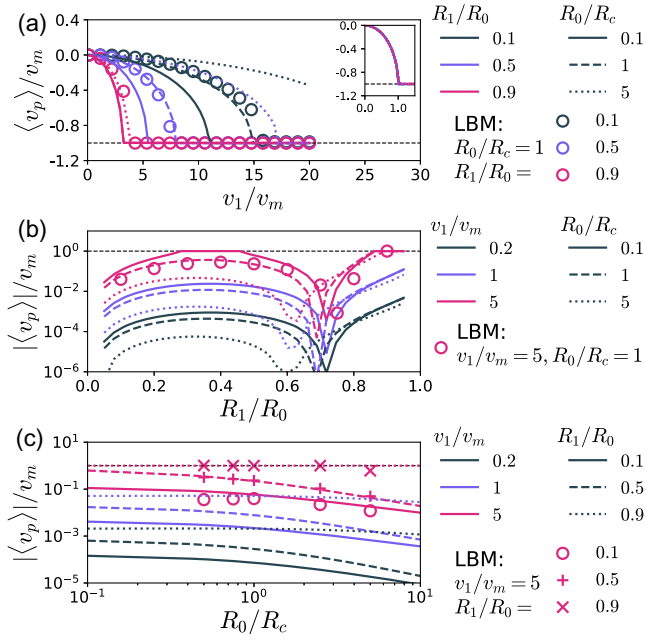


FIG. 3. Confinement-induced motion. Time-averaged ciliate velocity $\langle v_p \rangle$ as function of (a) ciliary wave amplitude v_1/v_m , (b) corrugation amplitude R_1/R_0 , and (c) ciliate curvature R_0/R_c for $\lambda_c/\lambda_w = 1$, $R_0/\lambda_c = 1/4$, and $v_0 = 0$. The two varied parameters of the curves are indicated in the legends by color and line style, respectively. Colored symbols show results from lattice-Boltzmann simulations. Inset in (a): master curve $\langle v_p \rangle / v_m = \sqrt{1 - v_1^2/v_*^2} - 1$ with $v_* = 2v_m/\mathcal{G}_1$. In (b),(c) the magnitude $|\langle v_p \rangle|$ is plotted. Colors indicate values of R_1/R_0 in (a) and v_1/v_m in (b),(c), while line types indicate values of R_0/R_c in (a),(b), and R_1/R_0 in (c).

reverses direction with respect to the bulk fluid if $v_0/v_m < 0$ and $v_1/v_m \times R_1/R_0 > \sqrt{a^2 - 1}$. Thus, an anti-plectic ciliate, which swims in the same direction as the metachronal wave in the bulk fluid (e.g., *Paramecium* [76]), may become a symplectic swimmer that moves opposite to the metachronal wave (e.g., *Opalina* [77]) in a sufficiently corrugated channel.

The period of the oscillatory motion, T , can also be obtained analytically [73,75],

$$T = \frac{T_c}{\sqrt{\left(\frac{v_0}{v_m} - 1\right)^2 - \left(\frac{v_1}{v_m} \frac{\mathcal{G}_n}{2}\right)^2}}. \quad (9)$$

It diverges at the transition from the oscillatory to the phase-locked regime, and takes values both below and above T_c , as shown in Fig. 2(d).

Full lubrication theory and lattice-Boltzmann simulations—In the full theory, the Fourier coefficients $\mathcal{G}_n$, and thereby $\langle v_p \rangle$, have a nontrivial dependence on R_1 and R_c , which we now explore. We also support our

findings with lattice-Boltzmann simulations [78]. In the following, we shall focus on the motion of ciliates with $v_0 = 0$ since this case provides the clearest and physically most interesting manifestation of the interplay between corrugation and slip velocity.

First, in Fig. 3(a) we again observe the expected transition from the oscillatory to the phase-locked regime with $\langle v_p \rangle = -v_m$ for increasing wave amplitude v_1 . As deduced from Eq. (8), all curves collapse on a master curve of the form $\langle v_p \rangle / v_m = \sqrt{1 - v_1^2/v_*^2} - 1$ with the critical wave amplitude $v_* = 2v_m/\mathcal{G}_1$ separating the two dynamical regimes from each other [see inset of Fig. 3(a)]. In Fig. 3(b), the swimming velocity shows two local maxima for increasing corrugation R_1/R_0 . The maximum at $R_1/R_0 \approx 1$ corresponds to the limiting case where fluid transport through the bottlenecks and along the entire ciliate is greatly suppressed such that the velocity field instead resembles an array of vortices. Swimming in such a channel geometry is not due to fluid transport from fore to aft, but due to an effective grip between the ciliate and the channel wall mediated by the enclosed pockets of fluid. Surprisingly, between the two local maxima, a strong dip in $|\langle v_p \rangle|$ occurs at R_1/R_0 , the value of which is mainly determined by R_0/R_c . In fact, the instantaneous ciliate velocity becomes zero as well due to a root of the function $\mathcal{G}_1(R_1/R_0)$ (see Supplemental Material Sec. II [72]). No matter the phase shift between the wall corrugation and the metachronal wave, the cilia beatings in the fore and aft directions compensate each other. The dip in $v_p(t)$ arises when the system transitions between two flow morphologies. For R_1/R_0 below R_1^*/R_0 , the velocity field reveals a fluid layer that spans the entire modulated channel and flows in the same direction as the ciliate [blue-shaded region in Fig. 2(b)]. In the opposite case (e.g., $R_1/R_0 = 0.8$), the size of this layer is greatly reduced, and the flow is dominated instead by large vortices within the pockets. At $R_1/R_0 = R_1^*/R_0$, the two flow types cancel each other and $\langle v_p \rangle$ drops to zero. More details can be found in Supplemental Material together with illustrative Videos 4–6 [72]. Finally, Fig. 3(c) demonstrates that with increasing ciliate curvature R_0/R_c , the swimming velocity decreases. Thus, ciliates with negligible curvature ($R_0/R_c \rightarrow 0$) swim fastest. The presented curves are directly supported by lattice-Boltzmann simulations, as the symbols in Figs. 3(a)–3(c) show.

Now, we relax the condition $\lambda_c = \lambda_w$ and show in Fig. 4(a) that net swimming is also possible for the higher harmonics, $\lambda_w/\lambda_c = n$, as predicted by Eq. (5). The swimming velocity decreases with this ratio once the phase-locked regime with $v_p/v_m = -1$ is no longer reached.

Finally, we relax the limit of a very long ciliate, which allows swimming motion only at the metachronal wavelengths $\lambda_c = \lambda_w/n$. To demonstrate the corrugation-enabled motion also for finite ciliates, we perform lattice-Boltzmann simulations for ciliates shaped like spherocylinders with

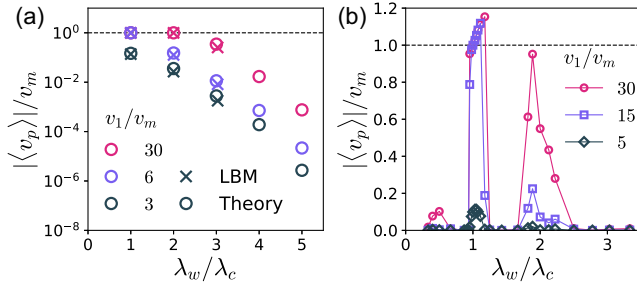


FIG. 4. Resonance for finite ciliates. Time-averaged ciliate velocity $\langle v_p \rangle$ vs the ratio λ_w / λ_c for various v_1 / v_m . (a) Finite ciliate with length $L_c / \lambda_w \gg 1$. (b) Results from lattice-Boltzmann simulations for a finite, spherocylindrical ciliate with length $L_c / \lambda_c = 3.2$ and $d / L_c = 0.25$, where d is the surface-to-surface distance between the ciliate and its periodic image. For both panels, $R_0 / R_c = 3/5$ and $R_1 / R_0 = 1/3$. For panel (a), $R_0 / \lambda_c = 1/10$, and (b) $R_0 / \lambda_w = 3/20$.

no-slip boundary conditions on the spherical half-caps, with a total length $L_c / \lambda_c = 3.2$ (Supplemental Video 3 [72]), as well as for ellipsoidal-shaped ciliates (Supplemental Videos 7 and 8 [72]). We again observe oscillatory trajectories with net drift for relevant lengths $R_0 / \lambda_c = R_0 / \lambda_w = 1$, where lubrication theory is no longer valid.

As expected, peaks in the time-averaged propulsion velocity exist around the integer ratios λ_w / λ_c but now they have a finite width [see Fig. 4(b)]. Further interesting features are visible: motion is also possible for $\lambda_w / \lambda_c < 1$, a time-averaged speed larger than v_m occurs, and the peak for $\lambda_w / \lambda_c = 3$ is suppressed. However, a more thorough investigation of the influence of L_c / λ_c on the propulsion speed is beyond the scope of this Letter. As a final test, our results remain valid when expanding our model to include a metachronal wave, which propagates oblique to the x axis. In such a case, the dynamical regimes we describe in this Letter appear when the channel shows indentations in the azimuthal direction that corkscrew along the x axis, similar to the internal surface of a rifle's barrel (Supplemental Material Sec. III and Supplemental Video 9 [72]).

Using lubrication theory and lattice-Boltzmann simulations, we show that the explicit time dynamics of metachronal waves enables ciliates to swim in a corrugated channel, even if they do not move, on average, in a bulk fluid. This is due to a resonance between the local hydrodynamic resistance, arising from a spatially varying radius of the channel, and the active flows generated by a sinusoidal metachronal wave. We rationalize our findings via the Adler equation that describes the transition from the oscillatory to the steady swimming regime. The mean swimming velocity can even reverse compared to the bulk fluid.

This reversal of direction of motion may be used to fabricate a filter or chromatograph, which blocks the passage of a microorganism with a metachronal wave

matching the channel corrugation, but allows other microorganisms to pass. Estimates for *Paramecium* and a mutant show that the slow down and even reversal of the swimming velocity in a corrugated channel may be observable (see End Matter). Despite motivating our model via ciliated microorganisms, our work provides a deeper understanding of how swimmers with a spatiotemporal fluid forcing at their surface behave in a corrugated channel, regardless of the nature of this forcing. The mechanism described in this Letter is in fact general enough that we expect it to also apply to other living beings, which propel via a metachronal wave of forcing, such as the gait displayed by centipedes [79], millipedes [80], or cockroaches [81]. For these terrestrial creatures, a modulated ground friction profile can play a role analogous to the spatially nonuniform channel radius. We further emphasize the applicability of our results to artificial swimmers or walkers that employ, e.g., magnetically actuated ciliary carpets [82] for which parameters like v_1 / v_0 can be tuned. The mechanism described in this Letter thus opens a new avenue for environment-sensitive motility and environment-mediated control of robots moving in confinement.

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Data availability—The data for the current publication are available on Zenodo [83].

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End Matter

Experimental predictions—Despite the scarcity of experimental data for most ciliates (particularly with respect to the metachronal parameters λ_c , ω , and the velocity amplitude v_1), we are able to predict the corrugation needed to reverse the direction of motion of *Paramecium*. The parameters R_c , L_c , v_0 , λ_c , and ω [64] are approximately known, and the parameter v_1/v_0 may be estimated as $v_1/v_0 \approx 3$ upon comparison with the cilia covering other organisms such as *Tetrahymena* [84] and *Plenaria* [85]. We predict that with an estimated swimming velocity of $\approx 784 \mu\text{m/s}$ [76] (in a microchannel without corrugation), a *Paramecium* in a corrugated channel of average radius $\approx 57 \mu\text{m}$ ($R_0/R_c = 1$ [64]) will invert direction when $R_1/R_0 \gtrsim 0.96$. The effect of the

corrugation is, however, already seen when $R_1/R_0 = 0.9$, for which the swimming velocity is $\approx 65\%$ of the value in the bulk fluid.

A more amenable case is that of a *Paramecium* mutant showing a deformed ciliary beat, which leads to a smaller swimming speed of $\approx 196 \mu\text{m}$ [76]. Assuming that only the average actuation of the fluid and not the beat amplitude is affected, yields $v_1/v_0 \approx 12$, and an inversion of the swimming direction when $R_1/R_0 \gtrsim 0.875$. Furthermore, we predict a velocity $\approx 65\%$ of the bulk-fluid value for $R_1/R_0 \approx 0.35$ and $R_1/R_0 \approx 0.825$.

All these numbers show that the slow down and even reversal of the swimming velocity in a corrugated channel should be observable in an experiment.