







## Minimal design of a synthetic cilium

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We study a slender filament beating in a viscous fluid with novel curvature-dependent bending stiffness. Our numerical and experimental investigations reveal that such differential stiffness can sustain planar bending waves far along flexible filaments, in stark contrast to the uniform-stiffness case which requires more sophisticated control. In particular, we establish basal actuation as a viable, parsimonious mechanism for generating high-amplitude planar bending waves. Moreover, the resulting beat patterns closely resemble the power-and-recovery strokes of propulsive biological filaments such as cilia, suggesting extensive applications in robotic and engineered systems.

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**Introduction.** The cilium is a complex, highly conserved organelle found in diverse organisms where it contributes to a host of important functions, including flow manipulation and self-propulsion of microorganisms [1,2]. Inspired by these natural capabilities, there has been significant interest and progress in the field in fabricating micro or even nanoscopic devices that can also be used to enable fluid pumping, swimming, particle mixing, and manipulation. Synthetic systems are currently unable to match the versatility of biological cilia, which has driven the development of sophisticated artificial control mechanisms. Magnetic actuation has become the favored strategy to precisely engineer realistic beat patterns in ensembles of artificial cilia, though many other methods have been employed, including pneumatic, electrochemical, and optical actuation [3,4]. Rather than devise increasingly sophisticated modalities of control, we consider an alternative approach: Is it possible to engineer the material properties of a filament to produce realistic, cilia-like beat patterns using only a simple control mechanism?

To explore this idea, we revisit a seminal study of the fluid-structure interactions of a swimming mammalian

spermatozoan, Fig. 1(a), from the 1950s. Here Machin contrasted two popular competing hypotheses of the time [7]: (1) the filament is driven from the base (at its interface with the cell body) but is otherwise passive, and (2) it is driven by active elements along its length. Through a theoretical analysis of an idealized Euler elastica in the absence of inertia, Machin concluded that passive, proximally driven filaments were incapable of reproducing large-amplitude bending waves that are characteristic of eukaryotic cilia and flagella [2,8,9]. In particular, Machin noted that, depending on parameters, one of two things occurred: (1) the amplitude of bending waves decayed rapidly along the flagellum, so that distal amplitudes were effectively negligible (Figs. 3 F–J of Ref. [7]) or (2) bending only occurred with long wavelength, with fewer than approximately 1.5 wavelengths being present along the flagellum (Figs. 3 A–E of Ref. [7]).

Machin's study refuted the first of the two hypotheses for flagellar beating, a result later confirmed by experiments that culminated in the identification of spatially distributed dynein as the molecular motors responsible for force generation inside these filaments [10–12]. As these filaments are remarkably conserved across eukaryotes (Refs. [1,11,13,14] and Fig. 1), it is now well established that ciliary beating is universally driven by distributed activity rather than localized actuation. Indeed, cilia completely isolated from the cell body continue to beat in the presence of ATP [15–17]. Hence, proximal actuation has been duly passed over as a driver of motility in eukaryotic systems. This notably contrasts with flagellated bacteria and archaea, which self-propel using a rotary motor that generates basal torque to spin a helical flagellum [18,19].

Thus, the prospect of driving cilia-like beating patterns in elastic filaments via basal actuation alone would appear

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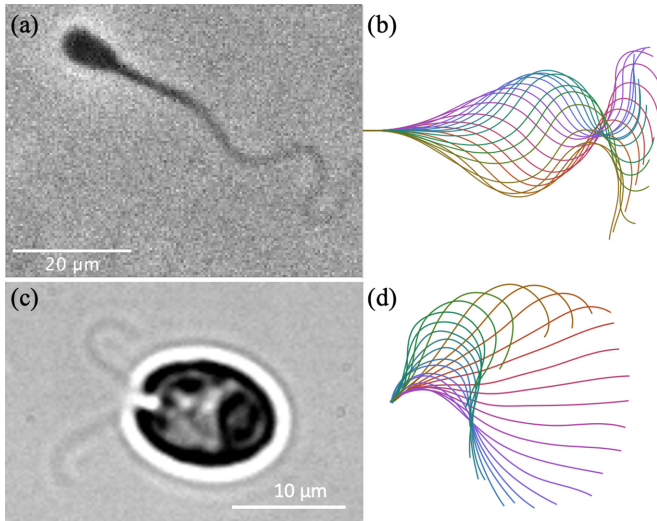


FIG. 1. Examples of flagellar actuation in biological microswimmers. Beating flagella of (a) a bovine spermatozoon and (c) *Chlamydomonas reinhardtii* display large amplitude bending at their distal ends. [(b) and (d)] Traces of the waveforms, color coded in time, highlight the symmetric beat pattern for the sperm cell and marked asymmetry in *Chlamydomonas* between the power and recovery strokes. Images (a) and (b) as well as (c) and (d) are reproduced with permission from Walker *et al.* [5] and Wan and Goldstein [6], respectively.

to be unrealistic. However, while the material properties of biological cilia and flagella are restricted by developmental or evolutionary constraints, engineered synthetic filaments may be designed with more freedom [3,20–22]. This raises a simple question: By modifying the mechanical properties of a filament, can the conclusions of Machin’s analysis be sidestepped? Can we produce realistic bending waves in engineered passive filaments for low-Reynolds number propulsion using only basal actuation? If so, then this simple mechanism would facilitate the development of markedly simple synthetic systems without intricate mechanisms of distributed driving or control. In turn, these may be designed to exploit asymmetric ciliary beating either for propulsion, such as in multi-ciliated swimmers like *Chlamydomonas*, or for flow generation, as observed in epithelial cilia. This strategy is analogous to implementing directional compliance in robotic appendages modelled on the limbs of insects [23], the undulatory motion of snakes [24] or magnetic metamaterials [25–27], which can greatly reduce the costs of gait computation.

Seeking to embody novel functionality within simple synthetic systems, we combine theoretical study with an engineered physical system. In this Letter we establish how sustained, cilialike beating patterns can be driven by basal actuation alone in appropriately designed filaments.

*Machin’s low-amplitude model.* To motivate our eventual design principle, we consider (following Ref. [7]) the propagation of bending waves along an elastic filament in a fluid using the dimensionless small-amplitude beam equation

$$\frac{\partial y}{\partial t} = -\frac{\partial^2}{\partial x^2} \left( E \frac{\partial^2 y}{\partial x^2} \right) \quad (1)$$

with boundary conditions

$$y(0, t) = 0, \quad \frac{\partial y}{\partial x}(0, t) = A \sin t, \quad (2a)$$

$$\frac{\partial^2 y}{\partial x^2}(1, t) = 0, \quad \frac{\partial^3 y}{\partial x^3}(1, t) = 0. \quad (2b)$$

This system corresponds to a filament with displacement  $y$  driven by rotation about a hinge at  $x = 0$ , with moment-free and shear-free conditions at the tip  $x = 1$ . Throughout, we use dimensionless quantities such that  $E$  captures the ratio of bending resistance to drag, the driving oscillations occur at unit frequency, and the filament is of unit length. Balancing terms in Eq. (1) gives rise to a natural dimensionless lengthscale  $l \propto \sqrt[4]{E}$ , over which planar elastic waves decay exponentially.

Many studies have generalized Machin’s model, going beyond the small-amplitude limit and into three dimensions [28–31], or have considered hydrodynamic and basal synchronization of several flagella [32,33], follower force actuation [34] or nonuniform, spatially varying stiffness [35,36]. Here we seek an alternative generalization and incorporate state dependence into the stiffness, setting  $E = E(\frac{\partial^2 y}{\partial x^2})$  to depend on the local linearized curvature. For simplicity, we consider  $E$  to be piecewise constant, so that

$$E(\kappa) = \begin{cases} E_L & \text{if } \kappa > 0 \\ E_R & \text{if } \kappa \leq 0 \end{cases} \quad (3)$$

for unequal constants  $E_L > E_R > 0$  and curvature  $\kappa \in \mathbb{R}$ . Solving Eq. (1) is now somewhat involved, but we can estimate the appropriate decay lengthscale by considering a further simplification.

Suppose that, instantaneously, the filament is divided into two equal regions of positive and negative curvature, similarly to a sinusoid over a single period. Up to constants and over a fixed timescale, the appropriate decay lengthscale in the region of positive curvature is  $l_L = \sqrt[4]{E_L}$ ; in the region of negative curvature, the decay lengthscale is  $l_R = \sqrt[4]{E_R}$ . Note  $l_L > l_R$ . Hence, the amplitude of planar bending waves after passing through both regions experiences decay scaling with  $\exp(-\frac{1}{2}[1/l_L + 1/l_R])$ , as opposed to either of  $\exp(-1/l_L)$  and  $\exp(-1/l_R)$ . Hence, there is an effective decay lengthscale of  $2(1/l_L + 1/l_R)^{-1}$  in the filament, equal to the harmonic mean of the two individual lengthscales of decay. Notably, this is at least as large as the smallest lengthscale  $l_R$  and approaches  $2l_R$  as  $E_L \rightarrow \infty$ . Intuitively, this latter case corresponds to a filament that is extremely hard to bend in one direction, while being relatively compliant in the other.

This reasoning readily generalizes to filaments where a proportion  $\alpha \in (0, 1)$  is bent such that  $E = E_R$ . In this case, the effective lengthscale is  $([1 - \alpha]/l_L + \alpha/l_R)^{-1}$ , which approaches  $l_R/\alpha > l_R$  as  $E_L \rightarrow \infty$ . While clearly  $\alpha$  should not be considered to be a fixed quantity in a dynamic filament, this back-of-the-envelope scaling analysis suggests that state-dependent bending stiffness could greatly enhance the effective decay length, with filaments thereby being able to transmit bending waves far along their lengths. Importantly, this mechanism unifies desirable properties of both high and low stiffness regimes: Bending waves can be of high curvature (associated with the lower bending stiffness) and also

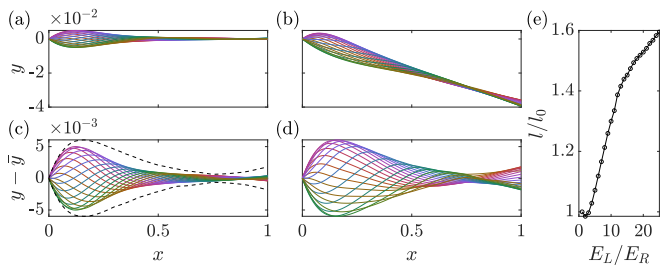


FIG. 2. Differential stiffness and small-amplitude beating. [(a) and (b)] Computed solutions of the small-amplitude beam equation over time with (a)  $E_L = E_R = 10^{-4}$  and (b)  $E_L = 10^{-3}$ ,  $E_R = 10^{-4}$ . [(c) and (d)] Deviation from the average configuration  $\bar{y}$ , highlighting increased amplitude with differential filament stiffness. The envelope of (d) is overlaid on (c) as black dashed curves. (e) Estimated decay lengthscale  $l$  as a function of differential stiffness, relative to the lengthscale  $l_0$  in the equal-stiffness case. Here  $A = 0.1$ .

propagate far along the filament (associated with the higher bending stiffness). Thus, filaments with differential stiffness are qualitatively different to their constant-stiffness counterparts.

To examine these idealized arguments thoroughly, a numerical study of filaments with differential bending stiffness is presented in Fig. 2, computed using FEniCS [37], wherein the state-dependent stiffness is taken to vary smoothly (but rapidly) between  $E_L$  and  $E_R$  (detailed in the Supplemental Material [38]). We encourage readers to explore this system for themselves via a browser-based VisualPDE simulation [39,40]. The contrast between a uniform filament [Figs. 2(a)] and a filament with state-dependent stiffness [Figs. 2(b)] is marked, with the latter being highly asymmetric. The amplitude of distal motion is significantly greater in Fig. 2(b) than in Fig. 2(a), visible in the mean-centered plots of Figs. 2(c) and 2(d). This enhancement of both the distal amplitude and the apparent decay lengthscale agree qualitatively with the scaling analysis. This is further supported by numerical estimation of the decay lengthscale as a function of the degree of differential stiffness [Fig. 2(e)], described in the Supplemental Material [38]. Thus, at least in the small-amplitude regime, state-dependent stiffness is a plausible mechanism for propagating planar bending waves along filaments.

**Large-amplitude bending.** To investigate beyond the small-amplitude regime, we adopt a geometrically nonlinear framework [41,42]. The analog of Eq. (1) in the geometrically nonlinear regime is

$$E \frac{\partial \theta}{\partial s} + \int_s^1 [\mathbf{x}(\tilde{s}) - \mathbf{x}(s)] \times \mathbf{f}(\tilde{s}) d\tilde{s} = 0, \quad (4)$$

written in terms of the tangent angle  $\theta$  (measured relative to a fixed axis), position  $\mathbf{x} = (x, y)$ , and hydrodynamic drag  $\mathbf{f}$ , each functions of arclength  $s \in [0, 1]$  and dimensionless. The derivation of this integral equation and the underlying assumptions are described in detail by Moreau *et al.* [41], recounted in part in the Supplemental Material [38]. In the nonlinear regime, curvature is  $\kappa = \frac{\partial \theta}{\partial s}$ , so that  $E = E(\kappa)$ . Solving this integrodifferential equation numerically (as described in the Supplemental Material [38]) allows us to test

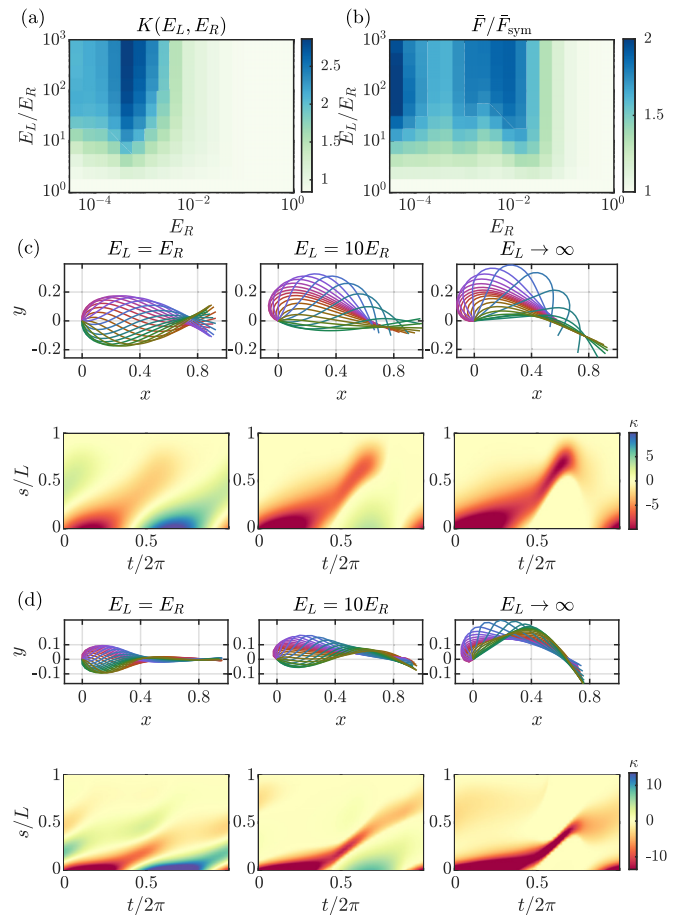


FIG. 3. Effects of differential stiffness in the geometrically nonlinear regime ( $A = \pi/2$ ), obtained from numerical solution of Eq. (4). [(a) and (b)] Relative increase in (a) maximal curvature and (b) average force at the pinned end, for a range of stiffnesses  $E_R$  and differential stiffnesses  $E_L/E_R$ . Example waveforms are shown below for (c) medium stiffness ( $E_R = 1.6 \times 10^{-3}$ ) and (d) low stiffness ( $E_R = 1 \times 10^{-4}$ ). [(c) and (d)] Example beating patterns (rotated in the beating plane to align horizontally) and associated curvature kymographs for filaments of (c) medium stiffness ( $E_R = 1.6 \times 10^{-3}$ ) and (d) low stiffness ( $E_R = 1 \times 10^{-4}$ ). From left to right: Symmetric beating ( $E_L = E_R$ ), resembling the classical solution of Fig. 2; an intermediate case ( $E_L/E_R = 10$ ), matching that studied in the small-amplitude regime; and a highly asymmetric “locking” case ( $E_L/E_R = 10^3$ ), effectively forbidding negative curvatures.

the predictions of the linear theory well beyond its regime of validity. In the following, we set  $A = \pi/2$ .

In this general regime, a quantitative measure of the effects of stiffness is the relative increase in maximum curvature over one beating period, averaged over the flagellum, defined for given  $E_L$  and  $E_R$  as

$$K(E_L, E_R) = \int_0^1 \frac{\max_t |\kappa_{E_L, E_R}(s, t)|}{\max_t |\kappa_{E_R, E_R}(s, t)|} ds, \quad (5)$$

where the maximum over  $t$  is computed over one time period in the limiting periodic regime. Naturally,  $\kappa_{E_L, E_R}(s, t)$  and  $\kappa_{E_R, E_R}(s, t)$  refer to the curvature for the asymmetric and symmetric filaments, respectively.



This quantity is presented in Fig. 3(a), plotted as a function of  $E_R$  and the differential stiffness  $E_L/E_R$ , demonstrating that differential stiffness can greatly enhance the curvatures attained by a filament during a beating period. The relative increase is threefold around  $E_R \approx 1 \times 10^{-3}$ .

To confirm that the increase in average curvature is localized towards the distal end of the filament, we also determined the maximum value  $K_{\max}$  and its argument  $s_{\max}$  over  $s \in [0, 1]$  of the integrand in Eq. (5), indicating where the qualitative change between uniform and differential stiffness is the greatest. For any value of  $E_L$  and  $E_R$ ,  $s_{\max}$  takes values between 0.5 and 0.8, confirming the trend in Fig. 3. Around  $E_R \approx 1 \times 10^{-3}$ , the corresponding value of  $K_{\max}$  goes up to 6, further highlighting the capacity of differential stiffness to transport and even amplify curvature for large beating amplitudes.

Machin identified (in the small-amplitude limit) that exponential decay significantly hinders planar wave propagation towards the distal end when the filament length exceeds five times the characteristic lengthscale  $\sqrt[4]{E_R}$ . Surprisingly, the parameter regime in which we see maximal curvature increase due to differential stiffness approximately corresponds to this case. Moreover, the curvature increase remains markedly high even when considering very small  $E_R$  ( $< 10^{-4}$ , representing a filament more than 10 times longer than the relaxation lengthscale), for which the effect of proximal actuation with uniform stiffness is virtually negligible at the distal end.

Figure 3(b) displays the magnitude  $\bar{F}$  of the pinning force, exerted on the point of attachment at the proximal end, averaged over one beating period and normalized by the time-averaged force without differential stiffness,  $\bar{F}_{\text{sym}}$ . As should be expected, maintaining a prescribed actuation while increasing filament stiffness for positive curvature comes at the cost of increasing the average pinning force. However, this relative increase remains smaller than the relative curvature enhancement through most values of  $E_R$  and  $E_L$ , indicating that differential stiffness constitutes an efficient way of increasing curvature according to this measure. For all values of  $E_L/E_R$ , the relative force  $\bar{F}/\bar{F}_{\text{sym}}$  has a local minimum with respect to  $E_R$  for  $E_R \approx 1.6 \times 10^{-3}$ . Simultaneously,  $K(E_L, E_R)$  is approximately maximal, so that the ratio between  $K(E_L, E_R)$  and  $\bar{F}/\bar{F}_{\text{sym}}$  is also approximately maximal. This value of  $E_R$  appears to be optimal for enhanced curvature generation with differential stiffness.

Figures 3(c) and 3(d) illustrate filament beats in the large amplitude regime for various degrees of differential stiffness. In the left column, we take  $E_L = E_R$  and reproduce the symmetric, short-lengthscale beating predicted by Machin's low-amplitude analysis for differing baseline stiffness  $E_R$ . In the subsequent columns, increasing degrees of differential stiffness yield larger amplitude deviations at the distal end of the filament while also allowing for high-curvature planar bending waves to propagate. These beats are further represented in the plots of signed curvature  $\kappa$  beneath the beating patterns, from which the high curvatures of the asymmetric regimes are evident. The spatial extent of bending waves is also clearly visible, with differential stiffness giving rise to far-reaching bending. Moreover, in the case  $E_R \approx 1.6 \times 10^{-3}$  [Fig. 3(c)], the resulting beat patterns begin to resemble the *power-and-recovery strokes* typical of most cilia, including

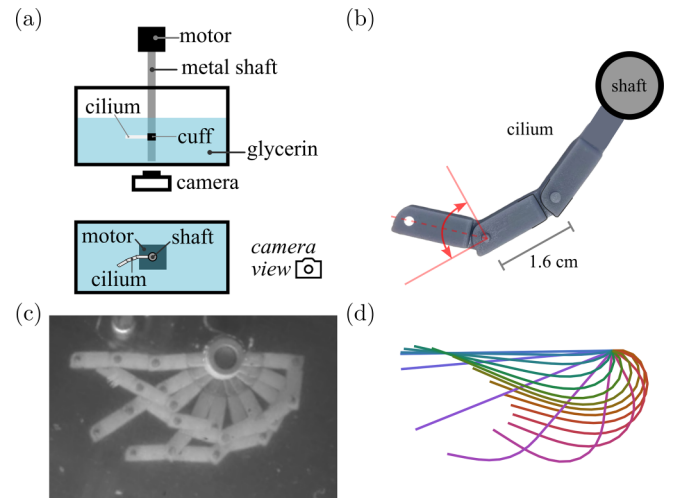


FIG. 4. Experimental realization of differential stiffness in a bioinspired macroscale robotic cilium (Supplemental Video 1). Motion is driven only by actuating the base of the filament. (a) Diagram of the experimental setup, not to scale. The cilium is placed in a tank of glycerin and imaged from below. The cilium is connected to the driving motor by a vertical metal shaft. (b) Detail of the locking mechanism. The links are designed so that each link can rotate freely only within the  $90^\circ$  angle indicated in red. (c) Snapshots of the robotic filament overlaid in time compared to (d) a simulated waveforms, with  $A = \pi/2$ ,  $E_R = 2 \times 10^{-3}$ ,  $E_L \gg E_R$  highlighting marked agreement between the synthetic and *in silico* systems.

*Chlamydomonas* [Fig. 1(d)], other protists [43–45], and vertebrate respiratory cilia [46].

Thus, even beyond the small-amplitude regime, differential stiffness presents itself as an effective mechanism for enhancing elastic planar wave propagation.

*Engineering ciliarylike beating.* Given the striking resemblance of the simulated beat of Fig. 3(c) with those seen in certain biological specimens, we now ask if we can realize biomimetic beating in practice using only basal actuation and differential stiffness. To explore this, we built a macroscopic robotic realization of a basally actuated filament, schematized in Fig. 4(a). The continuum limit is difficult to implement in practice, so our robotic filament comprises a finite number of links connected by custom hinges that are designed to qualitatively mimic differential stiffness [20].

These hinges, illustrated in Fig. 4(b), are asymmetric in shape, so they only admit bending in one direction, similarly to the “locking” limit  $E_L \gg E_R$  explored above. Each of the three links is 1.6 cm long, with a 1.2 cm basal attachment, so that the total length of the filament from its rotation point is 6 cm. The locking hinges are designed to reproduce the most extreme case of differential stiffness in the limit of  $E_L \gg E_R$  [as seen in Fig. 3(c)]. Notably, these hinges are simple to customize and produce.

The filament is driven at the base by a XL430-W250 dynamixel motor, which rotates through  $180^\circ$  at an angular velocity of  $5^\circ\text{s}^{-1}$ . To remain in the low-Reynolds regime, the filament is placed in a tank of glycerin, which has density of  $1.26 \times 10^3 \text{ kg m}^{-3}$  and viscosity 1.4 Pa s. The oscillatory Reynolds number  $\rho f L^2 / \eta = 0.3$ . Visual inspection of

the beating filament confirmed that inertial coasting was negligible. The tank measures 60 cm by 32 cm, with depth 18 cm. The filament is positioned far from walls to minimize boundary interactions. Imaging was performed at 1 Hz using a Logitech webcam. The cilia were resin printed using an Anycubic Photon Mono X, in Anycubic resin, and density matched to the glycerin.

Prescribing a basal amplitude  $A = \pi/2$ , the beat pattern of the robotic filament is showcased in Fig. 4(c). Even without elasticity, the power and recovery strokes are clearly distinguished, with experimental waveforms closely resembling the cilialike beating observed in our nonlinear simulations [Fig. 4(d)]. Further analysis, including a maximum intensity projection of the full video (Supplemental video 1, 12 beat cycles in total), shows that small tracer particles in the fluid move a net distance of approximately 0.1 cm per beat cycle, evidencing net pumping of fluid by this artificial cilium. (See the Supplemental Material for details.) A full and faithful model of the robotic system and a complete parameter analysis will be explored in future study.

*Summary and conclusions.* Through a combination of experiments and theory, we have demonstrated that enhanced wave propagation can be achieved with marked simplicity, realizing cilialike beats in engineered filaments using basal actuation alone, contrasting for instance with distributed magnetic actuation in recent similar designs of robots with structural asymmetric stiffness [25,27]. By incorporating a curvature-dependent stiffness we pragmatically generate biologically realistic planar waveforms using only a simple modality of control. This highlights and establishes the ready potential for simple, parsimonious synthetic systems to reproduce this well studied, broadly applicable, and widely conserved biological phenomenon. More generally, it paves the way for avenues of multidisciplinary enquiry into the motility and actuation of synthetic systems at the microscale.

It is well known that mammalian sperm flagella have a spatially heterogeneous bending stiffness with higher proximal stiffness [47,48]. This is potentially analogous to the larger initial link in the macroscale robotic cilium depicted in Fig. 4(b), which prevents proximal bending, and the functional impact of time-independent axisymmetric heterogeneity has been explored in a number of studies [49,50]. However, biological cilia also possess numerous protein complexes positioned along axonemal microtubule arrays that could harbor *dynamic* structural heterogeneities that do not possess axisymmetry, contributing to an effective state-dependent stiffness [51–54]. The potential for dynamic tuning of apparent and state dependent bending stiffness in these structures has not been previously considered. Nonetheless, the dynamic modulation of these asymmetries in live cells, e.g., by phosphorylation, could contribute to the generation of distinct beat patterns on the same structure, noting that flagellar stiffness changes with the level of ATP [55–57], which in turn has been associated with the extent of phosphorylation of outer dynein arm-linked proteins [58]. In particular, to achieve control systems for microscale movement, cells must exploit the mechanical or physical intelligence of their bodies, which could be realized, at least in part, through state-dependent bending stiffness of their cilia.

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