

Wall Torque Controls Propulsion of Curved Microstructures in Bacterial Baths

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The persistent dynamics of active particles makes them explore extended portions of an obstacle's boundary during collisions. From impact to escape, the net applied forces depend on the curvature of the wall and increase in the presence of concave features. Here we systematically investigate the forces exerted by swimming bacteria on microfabricated structures, where the radii of curvature can be varied parametrically. We find that these microsails are propelled with a speed that scales linearly with curvature and is directed from concave to convex side along the axis of symmetry. By solving the collision problem for microswimmers subject to aligning torques at the wall, we show that, despite bacteria rapidly aligning with the surface plane, the resulting force law reduces to that of spherical active particles, with the wall-induced reorientation rate effectively replacing rotational diffusion.

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What is the mechanical action exerted by active particles on a suspended passive object is a problem that has attracted enormous interest both because of fundamental issues related to the generalization of the concept of pressure in nonequilibrium systems [1–4] and because of obvious applications to the transport of colloidal cargos [5–8]. The two issues are evidently interconnected, as the emergence of a net propulsion on a passive tracer necessitates a pressure distribution that, unlike in equilibrium conditions, is not homogeneous along the object's contour. This can be achieved by unbalancing the activity around the object [9] or, more often, by giving it an asymmetrical shape that results in the preferential accumulation of active particles in concave regions that act as propulsion hot spots [7,10–13]. This latter geometric rectification is particularly efficient at high densities where jammed pockets of particles can cooperatively participate to propulsion through polar alignment induced by anisotropic interactions, such as in elongated swimmers [8,11,14]. However, interparticle interactions are not a necessary ingredient; asymmetric shapes can still lead to unbalanced pressure in the regime of noninteracting active particles. In this dilute regime, collisions of individual particles lead to the exploration of extended portions of the boundary with an overall mechanical action that depends on global characteristics of the wall contour, such as curvature. This has been extensively studied both theoretically and

numerically for active Brownian particles, i.e., self-propelled spherical objects with diffusive rotational dynamics that are typically unaffected by interactions with walls. When confined by flat solid walls, these particles exert a mechanical pressure that can be derived from bulk properties by means of an equation of state, as for fluids in thermal equilibrium [1–3]. In the presence of curved boundaries, the equation of state breaks down and the pressure may exhibit a strong dependence on curvature [4,15–19]. Numerical simulations demonstrate that even minimally curved objects can display directed motion due to a difference in active pressure between their concave and convex sides, resulting in net propulsion that grows linearly with the curvature [18,20,21]. However, it remains uncertain how relevant the predictions made with spherical particles and ignoring the effects of alignment on the walls are for real systems. Indeed, the propulsion of active particles often relies on anisotropies in their surrounding environment, which are inevitably perturbed by nearby boundaries. As a result, even spherical active particles can exhibit reorientation near walls [22–26]. For swimming microorganisms, reorientation at the wall is even stronger due to anisotropic shape and flagellar dynamics [27–29]. Accounting for torque interactions with walls is then essential to understand and predict rectification phenomena in experimentally relevant situations. Here we study the mechanical action of swimming bacteria on microfabricated objects with a precise and systematically varied radius of curvature. Despite the strong alignment effects on the walls, we recover the active Brownian particles prediction of a linear dependence on the curvature of the net force, albeit for completely different reasons. We account for this trend by developing a deterministic model based solely on steric interactions between bacteria and walls,

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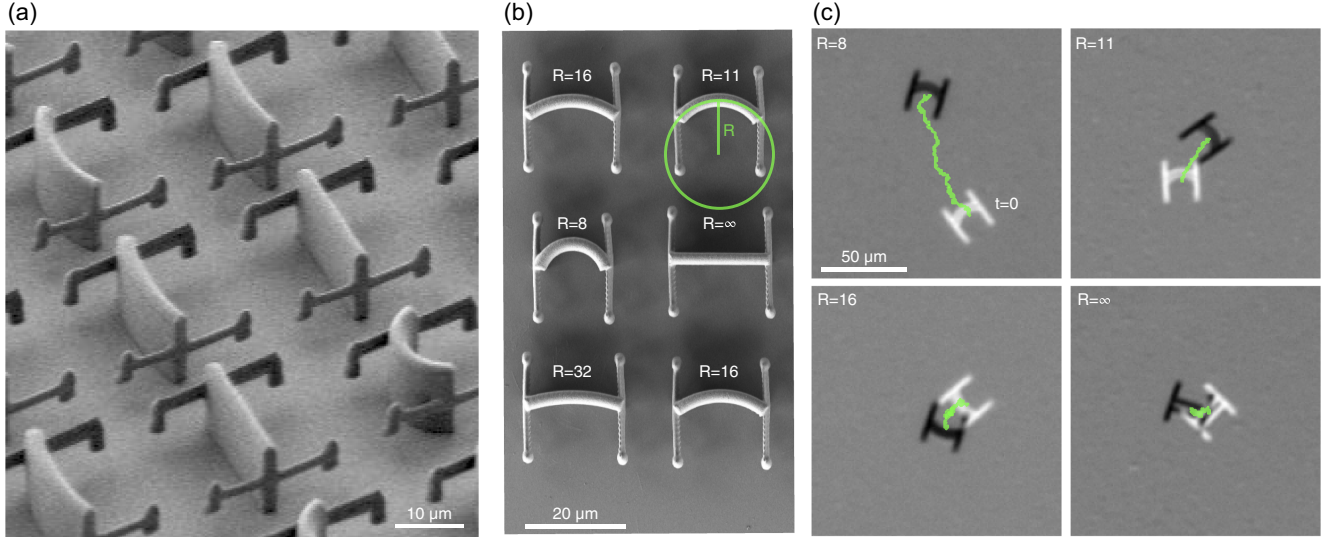


FIG. 1. Design and dynamics of microsails in a bacterial bath. (a),(b) SEM images of SU-8 microsails with varying curvatures: (a) side view and (b) top view. (c) Postprocessed bright-field images showing the initial (white) and final (black) positions of the microsails, with the trajectory highlighted in green.

enabling us to predict the forward impulse exerted by a single cell during a collision event and revealing connections with idealized active systems.

Results—We used two-photon polymerization to fabricate microstructures from SU-8 photoresist [13,30] that have the shape of a systematically curved wall. A scanning electron microscope (SEM) image of the fabricated structures are shown in Figs. 1(a) and 1(b). These microsails have a fixed arch length of 20 μm , height of 12 μm , wall thickness of 2 μm , and five different radii of curvature $R = [\infty, 32, 16, 11, 8]$ μm . The microsails are kept vertical by H-shaped supports at the two extremes. The experiment is performed by adding the microsails and 5 μL of *Escherichia coli* bacteria to an open chamber with a glass bottom filled with 1 mL of water and Tween 20 (0.02%), (final bacterial optical density OD = 0.035). The microsails are coated with bovine serum albumin to prevent adhesion to both the glass substrate and the surrounding bacteria [31]. The large volume and the high density of the microsails keep them fully sedimented on the bottom cover glass, but without sticking. For all experiments, we used a smooth-swimming *E. coli* strain, in which cell reorientation arises solely from rotational diffusion or collisions with boundaries. Further details on the bacteria strain, micro-sail fabrication, and sample preparation are provided in the Methods section in Supplemental Material [32]. The density of bacteria is kept low to avoid polar ordering and trapping of bacteria inside the concave regions of the micro-sail. We estimated a bacterial surface density of $\sigma \approx 0.006$ cells/ μm^2 , and a mean bacterial speed of $v_b = 30 \pm 5$ $\mu\text{m/s}$, measured by differential dynamic microscopy applied to bright-field recordings acquired using a 10 $\times$ objective [9,37].

The micro-sail dynamics are recorded for 7 min at 2 frames/s in bright field on an inverted microscope equipped with a 4 $\times$ objective. We can extract their positions and orientations using a custom tracking algorithm based on template matching [7]. In Fig. 1(c), we show a sample trajectory of microsails with different radii of curvature. In Supplemental Material, we provide a video of micro-sail dynamics for low (Video 1) and high magnification (Video 2) [32]. The propulsion of the curved microsails can be quantified by the longitudinal displacement $s_{\parallel}(t) = \int_0^t \mathbf{v}(t') \cdot \hat{\mathbf{e}}_{\parallel}(t') dt'$ where $\mathbf{v}(t')$ is the instantaneous velocity at time t' and $\hat{\mathbf{e}}_{\parallel}(t)$ is the main axis of symmetry of the structure pointing from the convex to the concave side of the wall. As an example, in Fig. 2(a) we show the longitudinal mean displacement $\langle \Delta s_{\parallel}(t) \rangle$ of five individual microsails with different curvatures. As curvature $k = 1/R$ increases, microsails exhibit a growing net longitudinal displacement. This behavior is also reflected in the longitudinal mean square displacement [$\text{MSD}_{\parallel} = \langle \Delta s_{\parallel}^2(t) \rangle$], which exhibits ballistic growth at long times, but flattens at short times because of uncorrelated tracking errors [Fig. 2(b)]. Because of the left-right symmetry of the micro-sail, we expect the transverse force exerted by the bacteria to average to zero. Indeed, we observe only small transverse mean displacements $\langle \Delta s_{\perp}(t) \rangle$ along $\hat{\mathbf{e}}_{\perp}$ for all curvatures [Fig. 2(a)], and the transverse mean square displacement, $\text{MSD}_{\perp} = \langle \Delta s_{\perp}^2(t) \rangle$, exhibits a diffusive regime [Fig. 2(b)].

From the mean displacement, we can directly extract the net propulsion speed in each direction, using the equation

$$\langle s_{\alpha} \rangle = V_{\alpha}(k)t. \quad (1)$$

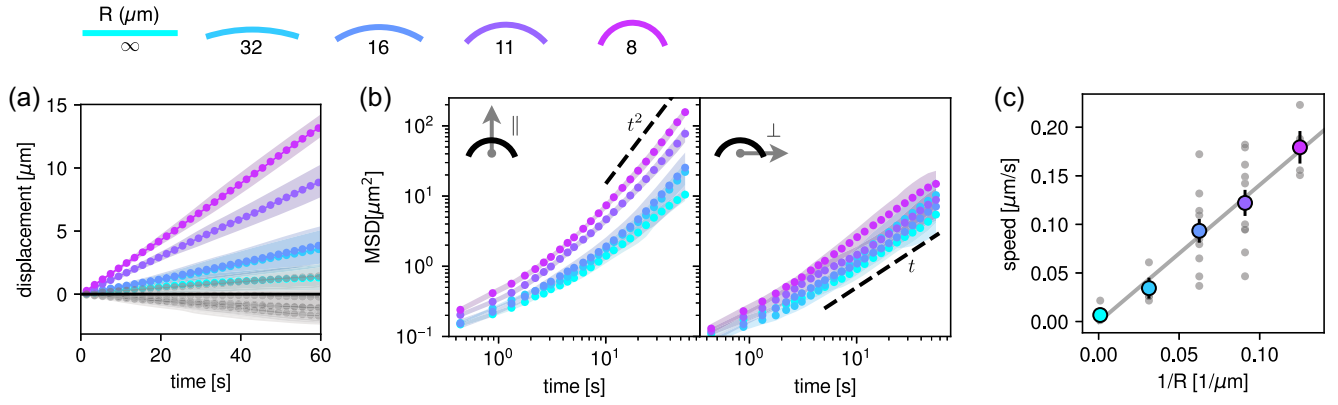


FIG. 2. Microsail propulsion. For five microsaills with varying curvatures, we report (a) mean displacement along the longitudinal (colored markers) and perpendicular (gray markers) directions; (b) the MSD along the longitudinal (left) and perpendicular (right) directions. Standard errors are shown as shaded areas around the data points and are calculated using Flyvbjerg and Petersen’s block-averaging method with a 60 s block size [38]. (c) The average propulsion velocity along the longitudinal direction increases linearly with microsaill curvature. Each gray dot corresponds to the velocity extracted from the mean displacement of an individual microsaill (30 in total), while black dots indicate the mean values with standard error bars.

By extracting the net speed $V_\alpha(k)$ for 30 different microsaills, we find that the average propulsion speed in the longitudinal direction $V_\parallel$ increases linearly with curvature, reaching a maximum value of $V_\parallel \approx 0.20 \mu\text{m/s}$ for the microsaill with the highest curvature, Fig. 2(c). As expected, the extracted transverse speeds $V_\perp$ are very small compared with those along the main axis and show no linear dependence on curvature; see Supplemental Material, Fig. 2(a) [32]. Regarding the angular speed V_z , we find that it is nonzero and consistently clockwise (when viewed from above the substrate). However, it does not exhibit any clear dependence on the curvature (see Supplemental Material, Figs. 2(b)–2(d) [32]). The small angular and transverse speeds may be related to the chiral nature of bacterial baths near solid surfaces, where *E. coli* cells tend to move in circles [39].

We now introduce a minimal collision model that only considers self-propulsion, elongated shape, and steric interactions between bacteria and walls. Following the derivation in Supplemental Material, Sec. II [32], we find that a cell swimming at speed v_0 toward the wall slows down upon collision and subsequently slides along the wall tangent with a speed v ,

$$v = v_0 \cos \theta, \quad (2)$$

where θ is the angle between the bacterial propulsion direction and the surface tangent, Fig. 3(a). Right after contact, the normal reaction from the wall will produce alignment with angular speed

$$\dot{\theta} = -\alpha \cos \theta \sin \theta, \quad (3)$$

where α characterizes the torque induced by the interaction with the wall [32] and also represents the typical rate at

which the bacterium reorients upon encountering a flat surface [27]. At each moment during sliding, the cell will exert a normal force on the wall given by

$$N = \gamma \sqrt{v_0^2 - v^2}, \quad (4)$$

where γ is the translational drag of a full cell. In this context, the normal force exerted by a single cell on a curved surface can be estimated solely from the kinematic quantities v_0 and v , which are readily obtained from cell tracking data. This force can thus be found from the initial and instantaneous velocity without knowing the θ angle, which can be challenging to measure accurately in the vicinity of the microsaill due to the wobbling of the cell. For the whole duration of a collision event, the cell will transfer a forward impulse I to the microsaill given by $I \simeq \int_0^\tau N(t) dt$, where $t = 0$ and τ are the initial and final time of collision (residence time). We assume that the curvatures are small enough that the normal force N is always approximately aligned with the microsaill axis $\hat{\mathbf{e}}_\parallel$.

At low Reynolds numbers, the impulse of a force translates to a displacement once it is divided by the viscous drag of the object receiving it. Based on the discussion above, we can estimate the mean forward impulse transferred by a cell to a microsaill during a collision event by tracking fluorescent bacteria colliding with microsaills of variable curvature and fixed to the substrate glass. Figure 3(b) shows the tracked trajectory of many individual *E. coli* cells during a single recording of 30 s with a $60\times$ objective, see Video 3 in Supplemental Material [32]. As an illustrative example, Figs. 3(c) and 3(d) show the dynamics of individual bacteria upon colliding with surfaces of three different radii of curvatures ($R = -8, 0, 8 \mu\text{m}$). In the case of a surface with zero or

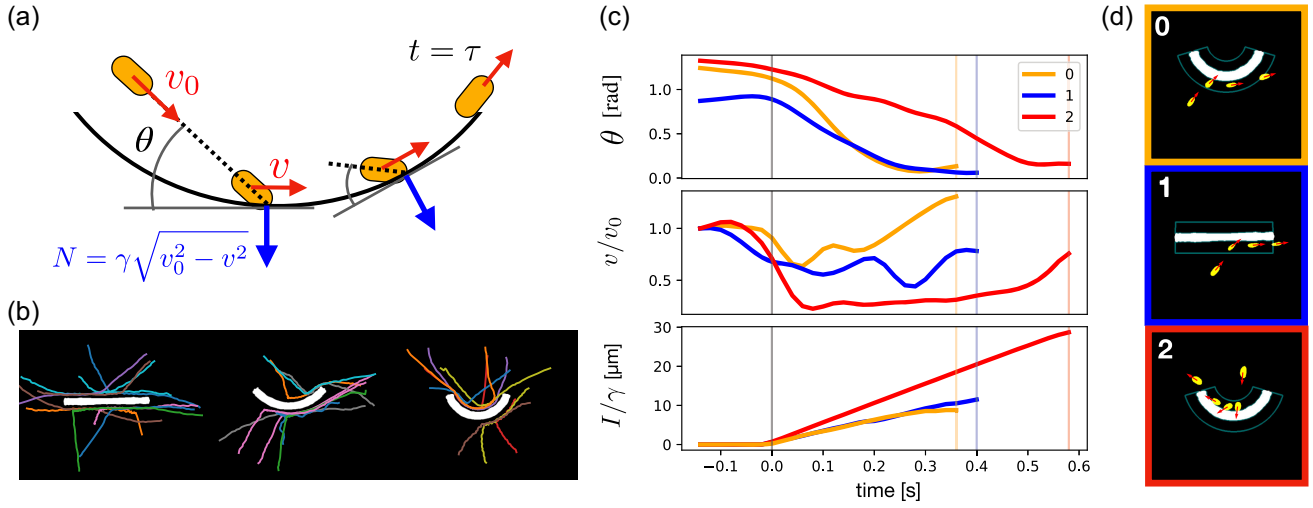


FIG. 3. Measuring the force exerted by bacteria on microsails through trajectory analysis. (a) Schematic of a bacterium's trajectory along a curved surface. (b) Experimental trajectories of bacteria interacting with fixed microsails recorded during a 30-s data acquisition. (c) The angle θ between the direction of bacterial propulsion and the surface tangent, normalized velocity, and impulse $[I(t) = \int_0^t f(t')dt']$ for three bacteria colliding with microsails of negative, flat, and positive curvature. The vertical gray line marks the moment of collision, while the colored lines indicate when the bacteria detach from the microsail. (d) Trajectories of the three bacteria, with their orientation indicated by red arrows.

negative curvature, the bacterium reorients to align with the surface ($\theta \approx 0$) and then either leaves the wall ($k < 0$) or moves nearly parallel to it at its original speed, exerting minimal force ($k = 0$). Conversely, for surfaces with positive curvature, the bacteria take longer to align, and after that, resulting in a continuous application of force throughout their time on the surface, which leads to a greater total impulse being applied. From the set of bacterial trajectories, we compute the average impulse exerted by a bacterium that increases with the curvature, Fig. 4(a). Notably, the net forward impulse on a microsail,

calculated as $\Delta I(k) = I(k) - I(-k)$, shows a linear increase with curvature, aligning with experimental observations of moving microsails, Fig. 4(b). For the calculation of $\Delta I(k)$, we assume that the number of bacteria impacting the microsails do not depend on the curvature. We then proceed to calculate the forward impulse on a microsail based on simulations of the angular dynamics of θ , as described in Eq. (3). The effect of surface curvature is introduced as an additional term [40], leading to

$$\dot{\theta} = -\alpha \cos \theta \sin \theta + v_0 k \cos \theta. \quad (5)$$

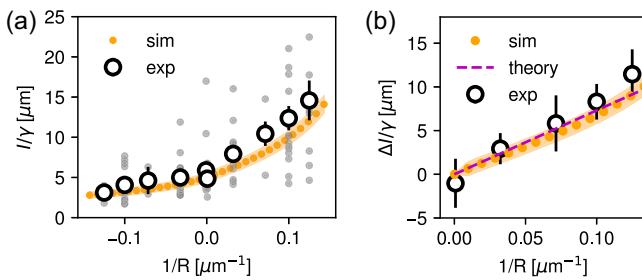


FIG. 4. Net impulse on microsails increases linearly with curvature: experiments and model predictions. (a) Total impulse exerted by a single bacterium as a function of surface curvature. Gray circles represent data from individual bacterial trajectories, while white markers show the average. Error bars indicate standard error. (b) The net impulse on fixed microsails, $\Delta I(k) = I(k) - I(-k)$, increases linearly with curvature. Error bars represent propagation errors. For both panels, simulations are shown as orange markers with shadowed area representing standard error. Dashed magenta line represents the predicted net impulse from Eq. (8).

Here, $v_0 \cos \theta$ represents the bacterium's velocity parallel to the surface, and $k = 1/R$ is the curvature. In the equation above, we excluded hydrodynamic interactions with the wall that are responsible for hydrodynamic trapping by convex walls with radius of curvature larger than $R^* \approx 50 \mu\text{m}$ [40]. By direct Euler integration, we numerically calculated the dynamics of θ for bacteria colliding with a curved boundary of arc length $l = 20 \mu\text{m}$ and for various initial angle θ_0 and impact position. Additional details on the simulation methods can be found in Sec. III of Supplemental Material [32]. Each simulated trajectory stops when the bacterium leaves the surface (at time τ), which happens in two situations: (i) when the cell reaches the end of the curved wall; (ii) for negative curvatures, when the bacteria are aligned tangential to the surface, i.e., $\theta = 0$. The simulated angular dynamics are illustrated in Supplemental Material, Fig. 3 [32]. We use parameters obtained from experiments: $v_0 \approx 30 \pm 5 \mu\text{m/s}$ and $\alpha \approx 8 \pm 2 \text{ s}^{-1}$ extracted from experimental trajectories for the case

of zero curvature ($R = \infty$), see Supplemental Material, Fig. 4 [32]. We then calculate the transmitted impulse applied to the boundary as $I/\gamma = \int_0^\tau v_0 \sin \theta dt$, for all incident angles θ_0 and impact positions, and average the result. The resulting impulses are shown as a function of the curvature and superimposed to experimental data, Fig. 4(a). The simulation predicts a net impulse $\Delta I(k) = I(k) - I(-k)$ that is also in good agreement with the experiments with fixed structures and is a linear function of the curvature, Fig. 4(b), thus validating our results with mobile structures again.

Discussion—The impulse generated by each bacterium can be analytically derived from Eq. (5) (Supplemental Material, Sec. IV [32]),

$$\frac{I(k)}{\gamma v_0} = \frac{v_0 k}{\alpha} \tau(k) + \frac{1}{2\alpha} \log \left[\frac{1 + \sin \theta_0}{1 - \sin \theta_0} \frac{1 - \sin \theta_1}{1 + \sin \theta_1} \right]. \quad (6)$$

The second term represents the total impulse transferred by a cell to a flat surface during reorientation from initial angle θ_0 and final angle θ_1 . For positive curvatures, cells reorient to reach a final stationary angle $\bar{\theta} = \arcsin(v_0 k / \alpha)$ corresponding to the stationary solution ($\dot{\theta} = 0$) of Eq. (5). The first term can be thus interpreted as the impulse transferred by a cell sliding at the stationary angle $\bar{\theta}$ for the entire residence time τ . For negative curvatures, cells reorient to reach $\theta = 0$ and then leave the surface. The first term has no clear physical interpretation in this case and accounts for a faster reorientation dynamics due to the negative second term in Eq. (5). The total net impulse on the micro-sail, defined as $\Delta I = I(k) - I(-k)$, can be thus written as

$$\frac{\Delta I(k)}{\gamma v_0} = \frac{v_0 k}{\alpha} \left[\tau(k) + \tau(-k) - \frac{1}{\alpha} \right] + O(v_0 k / \alpha)^3. \quad (7)$$

This expression predicts a linear relationship between propulsion and curvature, provided the sum of the residence times $[\tau(k) + \tau(-k)]$ is only weakly dependent on k . Both measured and simulated residence times exhibit a strong dependence on curvature [Supplemental Material, Fig. 5(a), Sec. V [32]]. However, this curvature dependence is largely suppressed in the combined quantity $\tau(k) + \tau(-k)$, which shows only a weak variation. Thus, assuming $\tau(k) + \tau(-k)$ is approximately constant, we can estimate it as $2\tau(0)$, which is significantly easier to compute (see Supplemental Material, Sec. VI [32]). Solving the flat-surface dynamics, we find $[\tau(k) + \tau(-k) - (1/\alpha)] \approx l/v_0$, leading to an expression for the net impulse on the micro-sail,

$$\frac{\Delta I(k)}{\gamma} \simeq \frac{v_0 l}{\alpha} k. \quad (8)$$

Figure 4(b) compares the predicted net impulse—computed using the previously measured parameters—with the

experimental and simulation data, showing good agreement. However, the cellular parameters in Eq. (8) are averaged over a broad distribution of bacterial cell sizes, which nontrivially affect swimming speed [41], drag, and torque interactions with the wall as captured by the parameter α [32]. This variability is difficult to incorporate and may partly explain the small discrepancies between theory and experiment. We can then estimate the average force experienced by a micro-sail by assuming that the average rate of bacterial collisions with the tracer is $\sigma l v_0 / \pi$, where σ is the surface density of bacteria, l is the tracer's effective cross section, and we assume isotropic distribution of swimming speeds. Under this assumption, the average force is given by

$$F \simeq \frac{\sigma l^2 \gamma v_0^2}{\pi \alpha} k. \quad (9)$$

This expression is remarkably similar to the one obtained for spherical active Brownian particles (ABPs) [18], despite the fact that the reorientation dynamics is completely different. While ABPs typically align their propulsion axis with the surface normal [16,18], elongated swimmers, such as bacteria, rapidly align to the surface tangent due to strong wall-induced torques [42,43]. Nevertheless, in the limit of small curvature, the force for ABPs reduces to $F_{\text{ABP}} \simeq (\sigma l^2 \gamma v_0^2 / 2D_r) k$, where the rotational diffusion D_r effectively replaces the wall reorientation rate α appearing in Eq. (9). In summary, our findings provide a robust experimental foundation for extending previous theoretical analyses of active pressure on curved boundaries to more realistic scenarios that include torque interactions at the wall. This reveals a general expression for the net force that applies broadly to both idealized and realistic active systems. While our model accurately captures the dynamics of pushers such as *E. coli*, wall collision dynamics can differ significantly for other microorganisms [44,45], highlighting the need for future research to test the general validity of our results. From a more applied perspective, these results may inform the design of passive structures that harness bacterial thrust in biohybrid microrobotics [7,46].

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Data availability—The data that support the findings of this Letter are openly available [47].

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