<table>
<thead>
<tr>
<th>Title</th>
<th>Simple mechanosense and response of cilia motion reveal the intrinsic habits of ciliates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author(s)</td>
<td>Ohmura, Takuya; Nishigami, Yukinori; Taniguchi, Atsushi; Nonaka, Shigenori; Manabe, Junichi; Ishikawa, Takuji; Ichikawa, Masatoshi</td>
</tr>
<tr>
<td>Citation</td>
<td>Proceedings of the National Academy of Sciences of the United States of America (2018), 115(13): 3231-3236</td>
</tr>
<tr>
<td>Issue Date</td>
<td>2018-03-27</td>
</tr>
<tr>
<td>URL</td>
<td><a href="http://hdl.handle.net/2433/230282">http://hdl.handle.net/2433/230282</a></td>
</tr>
<tr>
<td>Rights</td>
<td>Copyright © 2018 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).</td>
</tr>
<tr>
<td>Type</td>
<td>Journal Article</td>
</tr>
<tr>
<td>Textversion</td>
<td>publisher</td>
</tr>
</tbody>
</table>

Kyoto University
Simple mechanosense and response of cilia motion reveal the intrinsic habits of ciliates

Takuya Ohmura1, Yukinori Nishigami2, Atsushi Taniguchi1, Shigenori Nonaka3, Junichi Manabe2, Takiji Ishikawa2, and Masatoshi Ichikawa4,5

1Department of Physics, Kyoto University, Sakyo, Kyoto 606-8502, Japan; 2Laboratory for Spatiotemporal Regulations, National Institute for Basic Biology, Okazaki 444-8585, Japan; and 3Graduate School of Engineering, Tohoku University, Aoba, Sendai 980-8579, Japan

Edited by David A. Weitz, Harvard University, Cambridge, MA, and approved February 20, 2018 (received for review October 19, 2017)

An important habit of ciliates, namely, their behavioral preference for walls, is revealed through experiments and hydrodynamic simulations. A simple mechanical response of individual ciliary beating (i.e., the beating is stalled by the cillum contacting a wall) can solely determine the sliding motion of the ciliate along the wall and result in a wall-prefering behavior. Considering ciliate ethology, this mechanosensing system is likely an advantage in the single cell’s ability to locate nutrition. In other words, ciliates can skillfully use both the sliding motion to feed on a surface and the traveling motion in bulk water to locate new surfaces according to the single “swimming” mission.

Microorganisms play crucial roles in ecosystems and are essential to life on Earth (1–5). Eukaryotic unicellular microorganisms (i.e., protists) are dominant microorganisms in aquatic ecosystems (6–10). One class of protists, ciliates, exhibits a rapid translational swimming motion. Ciliates have a large number of hairlike organelles, termed cilia, that beat around the whole body to induce thrust force. While the remarkable activity of ciliates is usually measured from the observation on this side wall was 13.2° on average, the travel speed on the side wall (Fig. 1B and Movie S2). The steady swimming angle measured from the observation on this side wall was 13.2° on average (Fig. 1C) and was distributed below 40.0°. The travel speed in bulk water (up to 100 μm from the bottom wall) was 281.4 μm·s−1 on average, the travel speed on the MPC-coated glass was 138.2 μm·s−1 and the travel speed on the uncoated glass plate was 64.9 μm·s−1 (Fig. 1D). The travel speeds on the MPC-coated glass bottom walls were 49.1% as fast as those in bulk water, while those

Significance

Single-celled microorganisms are important in ecosystems, and their behaviors impact the Earth’s environments. To survive in harsh environments, these organisms frequently act as though exercising discretion. How do they achieve such intelligent behaviors? In this work, we focused on the accumulation of ciliates on solid/fluid interfaces, where they can obtain sufficient nutrients and a stable environment. This phenomenon is not described in the standard hydrodynamics of microswimmers. Our experiment and simulation revealed that simple principles, the anisotropic shape of the cell and the mechanosensing nature of cilia, induce the accumulation of ciliates on solid/fluid interfaces. The contribution of our work is that a simple response of the cellular apparatus and fluid dynamics explain the apparently clever behavior of ciliates.

Author contributions: T.I. and M.I. designed research; T.O. and Y.N. performed research; A.T., S.N., I.M., and T.I. contributed new reagents/analytic tools; T.O. and Y.N. analyzed data; and T.O., Y.N., and M.I. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

1T.O. and Y.N. contributed equally to this work.

2To whom correspondence should be addressed. Email: ichi@scphys.kyoto-u.ac.jp.

This article contains supporting information online at www.pnas.org/cgi/doi/10.1073/pnas.1718294115/DCSupplemental.
on the uncoated glass were 23.1% as fast as those in bulk water. These results confirm the interesting features of *T. pyriformis* on the wall; namely, *T. pyriformis* prefers a surface where it is not fixed but can slide. In this paper, “sliding” is defined as the observed motion adjacent to the wall. Considering the function of the MPC coat used to prevent the adhesion of proteins and biomacromolecules, the adhesive interaction strength between the substrate and the cilia was relatively inhibited on the coated surface. In addition, the sliding motions were observed on the antiadhesive glass for longer than on the normal glass. Thus, the adhesive bond pinning the cilia during long-duration beating is not the immediate cause of the sliding phenomenon. In other words, the pressure generated by other factors toward the wall should be investigated.

To examine the contributions and interactions of cilia and the wall according to their hydrodynamics, we visualized microscopic motion and flow fields around the single cells. Fig. 2A and Movie S3 show bright-field images of a single *T. pyriformis* from a 28° depression angle between the bottom glass plate and the cell. The surface of the bottom plate was identified based on the horizon between the direct image and the reflected virtual image. The estimated distances between the cell body and the wall were ~3 μm, which is almost equal to the natural cilium length of *T. pyriformis*. The distances and motions of the cell reveal that *T. pyriformis* swam by contacting the wall only with its cilia. This observation was confirmed by fluorescent live cell imaging using the same perspective as in Fig. 2B and Movie S4, in which the cilia contacting the wall almost stopped beating (Fig. 2B, Bottom), whereas other intact cilia (e.g., those on the opposite side of the cell) continued beating (Fig. 2B, Top). Stopping of the cilia beating on the wall side of the cell was also noted in phase-contrast observations from the bottom view. Fig. 2C shows numerous stopped cilia at the face of the bottom wall, where vertically standing cilia are visualized as black dots (indicated by red circles) in phase-contrast imaging (Movie S5). The beating speeds of the stopped cilia were estimated as 1/10th of those on the bulk side (Fig. 2D). Since the stopping of individual cilia occurred transiently with an average duration of 0.16 s at the single-cilium level, it is appropriate to refer to this phenomenon as a beating stall. In fact, the motion of probe beads indicated that the cilia in the upper and lateral areas of the cell paddled normally, whereas cilia at the bottom hardly paddled, as shown in the intensity and direction maps (Fig. 2E and F). These experimental results indicate that the force generation was disturbed due to the presence of stalled cilia between the cell and the wall only. This phenomenon contributes to the sliding motion. Next, we incorporated the stalled phenomenon of cilium into a hydrodynamic cilium model to reveal the direct mechanism of the sliding motion of *T. pyriformis* on the wall.

Squirmer models have been used as mathematical models of swimming microswimmers (24–26, 35–41). We prescribe the mean shear stress generated by the beating flagella as acting tangentially. This model can approximate ciliary swimming by selecting a parameter to be neutral (i.e., the neutral swimmer). The details of the numerical setup are presented in Materials and Methods and Fig. S3. We simulate this model using the boundary element method to introduce the boundary condition mimicking the experimental results, where the “stop beating area” (SBA) is defined as the area beside a wall to reproduce the cilia that stop near the wall (Fig. 3A). The SBA range can be optimized to represent the stall ratio observed in the experiments. The parameter setup is shown in Fig. 3B. The boundary in this simulation did not contain lateral friction, which indicates that the boundary condition approximately represented the MPC-coated glass plate in the experiment.

First, we checked the motion of the model swimmers near the nonslip boundary wall without SBA (Fig. 4A and B and Movies S6 and S7). Both spherical and ellipsoidal swimmers oriented their swimming direction against the wall, as observed in previous numerical and mathematical works (25, 26, 28). The spherical swimmer is a neutral swimmer, and the ellipsoidal swimmer mimics *T. pyriformis*’s shape. Without the SBA, neither swimmer exhibited a stable sliding mode on the wall, and both swam away from the wall under any initial conditions (Fig. S3). These behaviors are also shown in the graphs in Fig. 5E and F, with α = 0.0, where the swimmer gradually oriented its direction near the wall. However, no stagnated or stable angle beside the wall was noted. Indeed, swimmers landing on the nonslip wall with the SBA did not take off. The range of the SBA was α = 0.3, and the wall was located at z = −2. Notably, the spherical swimmer in the simulation with the SBA stopped on the wall (Fig. 4C and Movie S8), whereas the ellipsoidal swimmer swam and slid adjacent to the wall (Fig. 4D and Movie S9). The latter is a qualitative representation of the sliding motion on the wall observed in the experiments. The trajectories and swimming angles of the swimmers with the SBA are shown in Fig. S4. The swimming angle of the spherical swimmer became perpendicular to the wall, and the translational (x direction) motion stopped (Fig. S4A). The swimming angle of the ellipsoidal swimmer converged to a certain angle and, after colliding, continued to slide on the wall (Fig. S4B). The terminal angle of the ellipsoidal swimmer was 11.9°, while that of the
spherical swimmer was 90.0°. The terminal angle in the ellipsoidal model was close to the experimental value of 13.2° at $a = 0.3$, confirming the experimental result shown in Fig. 1C. The terminal angles are not dependent on the initial entry angles $\theta_0$ at $a = 0.0$ to 0.50, as noted in the supplementary graphs (Figs. S6 and S7, respectively). Summarizing the simulation results, the ellipsoidal swimmer slid on the wall at $a > 0.20$ and the terminal swimming angle varied as a function of $a$. In contrast, the spherical swimmer tended to have an angle of 90.0°. The adjacent motions of the swimmers were bifurcated by certain thresholds: 0.05 < $a$ < 0.10 for the spherical swimmer and 0.20 < $a$ < 0.25 for the ellipsoidal swimmer.

**Discussion**

We discuss the applicability of the model in terms of a qualitative comparison between the experimental and simulated behaviors. The actual body of *T. pyriformis* has an oral apparatus and a pear shape, which correspond to an anterior-posterior asymmetry and rotational asymmetry in the locomotive direction axis. Although the present simulation did not generate angular momentum along the axis, in the experiments, *T. pyriformis* did not exhibit rotational motion during its sliding motion. Therefore, the effects of asymmetry due to the oral apparatus are negligible for qualitative comparison in the present work. The anterior-posterior asymmetry of the shape requires more detailed study, but the present ellipsoidal shape can represent the experimental results semiquantitatively. Therefore, the crucial factor impacting the sliding motion must be the disruption of the spherical-ellipsoidal symmetry. In practical comparisons, the ellipsoidal swimmer slid on the wall in a manner similar to the behavior observed experimentally.

**Fig. 3.** Schematic illustrations of the simulation, indicating the geometries of the SBA and parameters. (A) Beating thrust forces (reaction force due to cilia strokes) along the surface driving the swimmer. We defined the SBA as the gray area on the bottom wall shown in the figure. If the surface is included within the SBA, the beating thrust force vanishes. (B) Parameter setup of the simulation. The shape of the force swimmer was determined by the ratio of the main axis length $L_1$ defined by the propelling direction to the waistline diameter $L_2$. The parameters were set as $L_1 = 2$ and $L_2 = 1$ or 2. $L_1 / L_2 = 1$ corresponded to a spherical shape, and $L_1 / L_2 = 2$ corresponded to an ellipsoidal shape. The SBA range was the defined length $a$. The initial angle was $\theta_0$, and the initial height was fixed at $h_0 = 2.0$. 

Ohmura et al.  
PNAS Latest Articles | 3 of 6
that is, the terminal swimming angles of the cell body were close to each other: 13.2° (nose-down, experiment) and 11.9° (nose-down, numerical calculation for the ellipsoidal swimmer at $a = 0.3$), where the ratio of the projected area of cilia stopping at $a = 0.3$ was almost the same as that estimated by the experiment. In addition, the match between the swimming speeds of the experiments and the simulations was achieved. The speed-reducing ratios of the sliding speed on the wall $V_w$ over the speed in the bulk $V_b$ were $V_w/V_b = 0.49$ (experiment, on the MPC-coated glass) and $V_w/V_b = 0.55$ (simulation), which indicated that the boundary condition on the MPC-coated glass possibly had little lateral friction, inhibited the adhesion between cilia and the substrate, and was quantitatively represented by simulation with no lateral friction. In contrast, the ratio on the uncoated glass in the experiment was $V_w/V_b = 0.23$, and the difference must result from lateral friction. In addition, the force that the respective cilium experienced from the wall was at least 1.87 pN according to a comparison between the results of the experiment (~30 cilia stalled) and the simulation (56.2 pN was applied). In any event, the surface sliding phenomena of *T. pyriformis* accompanied by the stopping of ciliary beating were observed. According to the above-mentioned features, our simulation qualitatively reproduced actual ciliate swimming near the wall. Thus, the disruption of spherical-ellipsoidal symmetry and the cessation of ciliary beating near the wall are critical factors for ciliates swimming adjacent to a wall.

Since head-tail polar swimming direction(s) with angular velocity contribute primarily to determining whether a swimmer stops, slides, or departs from the wall, any torque balance that influences the swimmer and develops angular velocity should be considered. The causes of this torque are categorized into three factors: hydrodynamic interaction, stopping of beating, and wall repulsion (Fig. 6). If the swimmer approaches the wall from the top left, the hydrodynamic interaction from the wall has a nose-up torque, and asymmetrical propelling force due to the stoppage of beating acts as a nose-down torque. Both torques act on both spherical and ellipsoidal swimmers. In contrast, wall repulsion gives rotational torque not to the spherical swimmer but to the ellipsoidal swimmer. Under this simplified scheme, the spherical swimmer touching the wall is given total torque from two factors without a balance point; thus, the swimming direction is downward when $a > 0.2$ and to the top right when $a < 0.15$ (Fig. S7). These values correspond to stop and departure, respectively. However, the torque from the wall repulsion additionally acts on the ellipsoidal swimmer, affecting the total torque with a stationary fixed point of a certain angle $\theta_{m1} = -90.0° < \theta_{m1} < 0.0°$. Thus, the ellipsoidal swimmer could slide on the wall, and the adjacent swimmer was stable at a certain angle (Fig. 5 and Fig. S6).

Finally, we discuss the biological relevance and applicability of the present results through comparison with other species. One well-studied ciliate, *Paramecium caudatum*, usually exhibits a back-and-forth motion against the uncoated wall (Movie S1), which is caused by a mechanosensing system at the anterior region of the cell (14). However, with the MPC-coated glass, *P. caudatum* also showed sliding motion for a long time (Movie S12), as did *T. pyriformis*, which would arise from the same dynamics. Ciliates are known to exist at air/fluid and solid/liquid interfaces in nature because these interfaces provide biofilm scaffolds composed of diatoms, algae, bacteria, polysaccharides, and proteins (42–45). These components are favorite foods for ciliates (3, 9, 10). In the case of the water/air interface (WAI), Ferracci et al. (20) determined that *Tetrahymena* is also trapped at the WAI. However, the trapped cells did not stop their ciliary beating. This finding indicates that the cell does not have an SBA at the WAI, and the mechanisms of entrapment at the WAI will differ from those at the water/wall interface presented here. Adapting these facts to our results, the coupling of the mechanical and hydrodynamical responses allows ciliates to easily remain on solid interfaces, which is one of their preferred environments. This is a discovery of the ethology of ciliates accompanied by the mechanism coupling cilia motion and swimming behavior, and the finding also suggests why many ciliates have evolved ellipsoidal shapes. Spherical ciliates have a disadvantage in finding nutrients when sliding on surfaces. In the experiments, when *T. pyriformis* slid on a wall, its oral apparatus was located at the most appropriate position (i.e., close to the wall) (Fig. 24). As for the
Fluorescence and Bright-Field Observations of *T. pyriformis* at a Low Angle. To acquire low-angle fluorescence images of *T. pyriformis* attached to the glass surface, observations were performed as described previously (50). In brief, a light-sheet, which was used as an excitation light, was generated by a line-scanning laser beam (FV10-LS559; Olympus) (Fig. S1 A and B) using a confocal laser-scanning microscope (FV1000; Olympus). An sCMOS camera (ORCA-Flash4.0) with an optical axis orthogonal to the plane of the excitation light was used for image acquisition. A cover glass was set at an angle of 28° to the optical axis (Fig. S1C). After the chamber unit was filled with observation solution, *T. pyriformis* was stained for 10 min in observation solution containing 10 μg/mL CellMask Orange plasma membrane stain (Molecular Probes) and washed three times with observation solution. The organism was then added to the chamber unit, and the cells on the glass were observed through a bandpass filter (BA570-625HQ; Olympus). In bright-field observation, a halogen lamp (LS-P52; Olympus) was used as the light source (Fig. S1D).

**Particle Image Velocimetry Analysis.** The flow velocity field and speed intensity around the cell body (Fig. 2 E and F) were obtained using an open-source MATLAB code (PIVlab) (51). The raw movie was recorded at 2,000 fps (Movie S10), and the snapshots at a 1.5-ms interval were used for particle image velocimetry (PIV) analysis.

**Three Surfaces in Our Numerical Model.** In this calculation, there are three defined boundaries: body surface, stress surface, and cilia surface (Fig. S3B). The body surface is rigid and has a nonslip boundary condition. The shape is spherical or prolate ellipsoidal. An actual ciliate is anisotropic in shape, as in the prolate ellipsoidal. The diameter of the spherical surface is 2.0. The major and minor lengths of the ellipsoidal surface are 2.0 and 1.0, respectively. The cilia surface is located outside the body surface. The length of the cilia in this model is fixed at 0.1, which is estimated from the actual cells. The stress surface is defined to reproduce the stress force of ciliary beating per unit area. Usually, the squirmer model is given by a velocity field on the surface, but we used a thrust stress force instead of a velocity field to precisely reproduce the actual beating (Fig. S3A). The stress surface is located between the body surface and the cilia surface (Fig. S3D). We used a boundary element method for numerical calculation (21). All surfaces are discretized by 162 material points far from the boundary and 2,562 material points near the boundary. The length unit is normalized by the radius of the spherical swimmer (i.e., 1.0).

**Numerical Methods.** We derived a numerical method assuming \( x = (x, y, z) \) as an observation point and \( y \) as a source point. Assuming the surface traction acting on the cell surface \( q(y) \) and the thrust force per unit area \( F(x) \), the flow field is given by a boundary integral equation (52):}

\[
 u(x) = u_x(x) - \int_{\partial B(x)} \left( \begin{array}{c} j_x \delta_s \delta_y \delta_z \left( \begin{array}{c} q(y) \delta_s \delta_y \delta_z \end{array} y \right) \right) - \int_{\partial B(x)} F(y) \delta_s \delta_y \delta_z (y),
\]

where \( \delta_s \) and \( \delta_y \) are the body surface and the stress surface, respectively. \( j_x(x, y) = 1/(\delta_{sx}/\delta_y + r_t/r_z) \) represents the single-layer potentials of Green’s function, which is the second-order tensor called the Oseen tensor, and \( u_x(x) \) expresses the external flow field. In this paper, \( u_x(x) \) is defined as zero.

Next, the flow field on the body surface \( u_b(x) \) is determined using the velocity of the mass \( U \) and the turning angular velocity \( \Omega \) considering the nonslip boundary condition. The kinetic velocity on the body surface is described as follows:

\[
 u_b(x) = U + \Omega \times (y - X_0).
\]

Here, the external force \( F \) and torque \( T \) are decided as boundary conditions:

\[
 F = \int q(y) \delta_s \delta_y \delta_z (y) = \int F(y) \delta_s \delta_y \delta_z (y),
\]

\[
 T = \int q(y) \delta_s \delta_y \delta_z (y) \times (y - X_0) \delta_s \delta_y \delta_z (y).
\]

By solving the simultaneous Eqs. 1-4, \( U, \Omega, \) and \( q(x) \) can be derived. Once the translational and angular velocities are obtained, the material points are updated by a fourth-order Adams-Bashforth method. The time step was set to \( \Delta t = 1.0 \times 10^{-4} \). The swimming speed at infinity \( U \) and the viscosity \( \mu \) were fixed to \( U = \mu = 1.0 \). Fig. S3C shows the streamlines of this model. The swimmer has a dipole-like velocity potential, which is the property of a neutral swimmer.

**Wall Interactions.** Assuming that a wall is a rigid, nonslip boundary, the swimmer experiences forces and torques from the wall. First, we considered the hydrodynamic interactions with the wall. The hydrodynamic interactions

**Materials and Methods**

**Preparation of Tetrahymena pyriformis.** *T. pyriformis* was kindly gifted by Osamu Numata, University of Tsukuba, Tsukuba, Japan. The cells were cultured in growth medium [1.2% (wt/vol) Bacto Proteose Peptone (Becton, Dickinson and Company), 0.6% (wt/vol) Patec (Kyokuto), and 0.2% (wt/vol) Bacto Yeast Extract (Becton, Dickinson and Company)] at room temperature (20-25 °C) with aeration (e-AIR6000WB; GEX). Serial transfer of the cells was performed twice per week. Before observation, the cells in midlog phase were washed three times with observation solution (10 mM 3-(N-morpholino)propanesulfonic acid/Tris (pH 7.2), 1 mM KCl, 1 mM NaCl, and 1 mM CaCl2) (49) and equilibrated with observation solution for more than 1 h before observation.

**Bright- and Dark-Field Observations of *T. pyriformis* at Perpendicular and Parallel Angles.** To prevent nonspecific binding between the cells and the surface of the cover glasses, the cover glasses (thickness no. 1, 30 × 40 mm; Matsunami) were coated with MPC polymer (Lipidure-CM5206; NOF Corporation). Specifically, MPC polymer was dissolved in ethanol to a final concentration of 0.5% (wt/vol), and 20 μL of MPC polymer solution was placed on the cover glass. To dry the coating solution, the glass was left at room temperature for more than 2 h. The observation solution containing *T. pyriformis* was deposited between MPC-coated cover glasses with a spacer (a silicone sheet (thickness of 400 μm) with a square hole (side length of 10 mm)). *T. pyriformis* was observed and recorded by using bright-field and dark-field inverted microscopy (Eclipse Ti; Nikon) with an sCMOS camera (ORCA-Flash4.0, Hamamatsu). To observe side views of *T. pyriformis* in a bright field, the cover glasses (thickness no. 1; Matsunami) were substituted for silicone spacers, and *T. pyriformis* on the glass spacers was observed using the methods described above.

**Fig. 6.** Schematic illustrations of torques for a spherical swimmer (Top) and ellipsoidal swimmer (Bottom) approaching a wall from the left side. (A) Hydrodynamic interactions caused by the wall apply nose-up torques. (B) Stopping the cilia beating inside the SBA affects the total propelling force around the bodies, leading to asymmetry and nose-down torques. (C) Mechanical repulsion from the wall. The spherical swimmer experienced no torque, whereas the ellipsoidal swimmer experienced nose-up torque.
next, we considered the repulsion from the rigid wall. When the swimmer is approaching the wall, the swimmer sometimes overlaps the wall. Therefore, the repulsion force and torque from the collision are added to Eqs. 3 and 4:

\[
F_{\text{rep}} = \int F'_{\text{rep}}(y) \, dS(y),
\]

\[
T_{\text{rep}} = \int F'_{\text{rep}}(y) \times (\gamma' - \gamma) \, dS(y),
\]

where \(F'_{\text{rep}}(y)\) is expressed as the repulsion force between the cilia and the wall per unit area. To reproduce the interaction between the cilia and the wall, we assume that the cilia are linear springs and \(F'_{\text{rep}}(y) = k(y)\gamma(y)\), where \(\gamma(y)\) is the shrinking length of the cilia, \(k\) is the spring constant, and \(\gamma\) is the area of cilia touching the wall. We do not consider friction with the wall in this calculation. Therefore, the repulsion force has only a \(y\) component.

Finally, we introduced a boundary condition. To reproduce the stopping of the cilia near the wall, we defined the SBA as the gray area on the bottom wall shown in Fig. 3A. The ciliary beating inside the SBA stops, thus, the thrust force \(F(y)\) near the wall vanishes. We define length \(l\) as the parameter of the SBA range in Fig. 3B. When the ellipsoidal swimmer touched the bottom wall at a swimming angle of 11.9°, the ratio of the projected area of cilia stopping at \(a = 0.34\) was 69.9%, which almost corresponds to the value estimated by the experiment.

ACKNOWLEDGMENTS. We thank Prof. Osamu Numata and Dr. Kentaro Nakano (University of Tsukuba) for the gift of \(P. pyriformis\). This work was supported by Grant 17-503 of the NIBB Collaborative Research Program. Paramecium cells used in this study were provided by the Symbiosis Laboratory at Yamaguchi University with support, in part, from the National Bio-Resource Project of the Japan Agency for Medical Research and Development. This work was supported by Grant-in-Aid for Scientific Research (C) 16K05585 from JSPS. The authors are grateful to the MAV Mathematik- und Naturwissenschaftliches Haus at the University of Cambridge for hosting them during the preparation of this manuscript.