



Enhancement of bacterial rheotaxis in non-Newtonian fluids

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Many microorganisms exhibit upstream swimming, which is important to many biological processes and can cause contamination of biomedical devices and the infection of organs. This process, called rheotaxis, has been studied extensively in Newtonian fluids. However, most microorganisms thrive in non-Newtonian fluids that contain suspended polymers such as mucus and biofilms. Here, we investigate the rheotactic behavior of *Escherichia coli* near walls in non-Newtonian fluids. Our experiments demonstrate that bacterial upstream swimming is enhanced by an order of magnitude in shear-thinning (ST) polymeric fluids relative to Newtonian fluids. This result is explained by direct numerical simulations, revealing a torque that promotes the alignment of bacteria against the flow. From this analysis, we develop a theoretical model that accurately describes experimental rheotactic data in both Newtonian and ST fluids.

bacterial motility | complex fluids | rheotaxis | shear-thinning

Microorganisms (e.g., bacteria, sperm cells) often find themselves immersed in external flows, like circulatory flows or oceanic turbulence, that significantly affect their swimming behavior (1, 2). The coupling between external and self-generated active flows leads to unusual transport properties (3, 4). In particular, many microswimmers display rheotaxis, which is the ability to reorient against flows and move upstream (5–10) through a mechanical interplay between activity and a guiding external shear flow. Rheotaxis has been observed in sperm cells (11), ciliates (12), flagellated (5, 10, 13, 14) and nonflagellated bacteria (15), and microrobots (8, 16). For bacteria, the ability to resist and overcome adverse flows is a selective advantage for pathogens colonizing environments where liquids are flowing, including the urinary tract, bloodstream, or hospital tubing (14, 17).

Bacterial rheotaxis occurs in bulk flows (18, 19) but upstream swimming is significantly stronger in the vicinity of walls (5, 10, 13, 14). The mechanical response to fluid flow gradients near surfaces results from the interactions of the swimmer with the flow and the wall. Bacteria swimming near a surface experience alignment due to steric and hydrodynamic interactions (20, 21), and are directed toward the wall in clockwise circular trajectories due to hydrodynamic torque (21, 22). The shear flow produces a “weathervane effect” that aligns the flagellum downstream (7, 10, 23). Together, the combined effects of the wall, shear flow, and self-propulsion enable bacteria to swim upstream (5, 10).

Much of our current understanding of rheotaxis derives from Newtonian fluids (5, 24). Many microorganisms, however, inhabit natural environments (from soil to the human body) that contain suspended particles and/or (bio)polymers and often exhibit non-Newtonian behavior such as shear-thinning (ST) viscosity behavior and viscoelasticity (25–27). The non-Newtonian properties of the surrounding fluid influence every aspect of microscale propulsion (26, 27): depending on propulsion mode and fluid properties, it can lead to an increase (28–31) or a decrease (32, 33) in swimming speed and affects the interaction of swimmers with external flows (34) and boundaries (35). Investigating microorganisms swimming upstream in model ST fluids, for example, can provide crucial insight into the pathways of pathogens in the body (36), fertility (25), and food safety (37). Thus, locomotion in complex systems and its interplay with external cues have attracted significant experimental and theoretical attention in recent years (27). However, despite its biomedical significance, little is known about rheotaxis in complex fluids. It has been investigated using theory and numerical simulations (38), but experiments exploring the relationship between non-Newtonian fluid properties and microbial upstream swimming remain scarce. Here, we aim to address this gap in the literature. The current manuscript focuses predominately on ST viscosity effects.

We combine experiments, numerical simulations, and theory to investigate the upstream motion of *Escherichia coli* in Newtonian and polymeric fluids at varying flow

Significance

Positive rheotaxis, swimming against flow currents, is a common trait among microorganisms (e.g., bacteria, protozoa, and sperm cells) and plays an important role in many biological processes (e.g., human reproduction and spread of infections). While much is known about bacterial rheotaxis in Newtonian fluids, our understanding of it in complex fluids (e.g., mucus) remains limited. Here, we show that fluid shear-thinning viscosity behavior significantly enhances the upstream migration of bacteria, enabling contamination at flow rates that are nearly an order of magnitude larger than in water and Newtonian fluids. Our work has important consequences for the study of medical, food, or wastewater contamination, and applications in designing medical devices that could prevent medical infections.

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rates near a surface. Our experiments show that ST viscosity behavior can result in a significant enhancement of upstream swimming, even for dilute solutions. Bacterial trajectories are rectified due to ST effects near walls, which explains the increase in upstream swimming. We develop a simple model for the bacterial orientation and position that captures their average swimming speed upstream and lateral to the imposed flow.

1. Experiments with Non-Newtonian Fluids

We track *E. coli* near a surface in the presence of an external flow, and measure the speed of the bacteria upstream (V_x) and lateral (V_y) directions relative to the flow. We focus our efforts on understanding the effects of ST viscosity behavior on V_x and V_y . Experiments are performed in a microfluidic channel with a controlled external volumetric flow, Q (Fig. 1A and Section 4). The region of interest (ROI) is positioned on the bottom wall in the fully developed flow region, away from the channel's corners to avoid shear-trapping and edge currents effects (39, 40). We use both Newtonian and ST fluids in the channel. For Newtonian fluids, we perform experiments with buffer (water-like viscosity) and Ficoll solutions to control for the effect of enhanced viscosity; these solutions provide a viscosity range from 1 cp to 8 cp. Aqueous solutions of xanthan gum (XG), a semirigid polymer, are used to produce ST fluids; polymer concentrations range from $0.2c^*$ to c^* , where c^* denotes the overlap concentration (SI Appendix). We also experimented with (dilute) solutions of a more flexible polymer, carboxymethyl cellulose (CMC), that produces fluids with a ST viscosity and some elasticity (41, 42).

All fluids are characterized using a stress-controlled rheometer; shear rates ($\dot{\gamma}$) near the surface of the microfluidic channel are obtained using numerical simulations (SI Appendix).

Swimming *E. coli* cells near the bottom wall of the microfluidic chamber are identified, and Lagrangian trajectories are obtained using an in-house tracking method (42) (Fig. 1B). We use cells' trajectories to compute V_x and V_y , as shown in Fig. 2.

1.1. No-Flow Condition. We characterize bacteria swimming behavior under quiescent conditions by measuring the mean swimming speed, V_0 , of the motile bacterial population. We find that, in Newtonian fluids (Ficoll solutions), *E. coli* mean swimming speed decreases monotonically as viscosity increases. For dilute ST fluids, on the other hand, the mean swimming speed of *E. coli* increases with polymer concentration, even as the steady fluid viscosity is also increasing (SI Appendix, Fig. S2). We observe speed enhancement of *E. coli* near walls of up to 50% compared to Newtonian fluids, consistent with previous studies in the bulk (42–44).

Similar to previous results (21, 22), we find that bacteria display the expected clockwise circular trajectories near walls. In ST fluids, however, these circular trajectories become less defined, noisier, and display larger mean curvatures (SI Appendix, Fig. S7). This suggests that ST viscosity behavior affects the swimmer–wall interaction (35, 45).

1.2. Applied Flow Condition: Rheotaxis. Typical *E. coli* trajectories under an applied flow are shown in Fig. 1B for $Q = 20 \mu\text{L/h}$ for Newtonian (buffer solution, Left panel) and ST

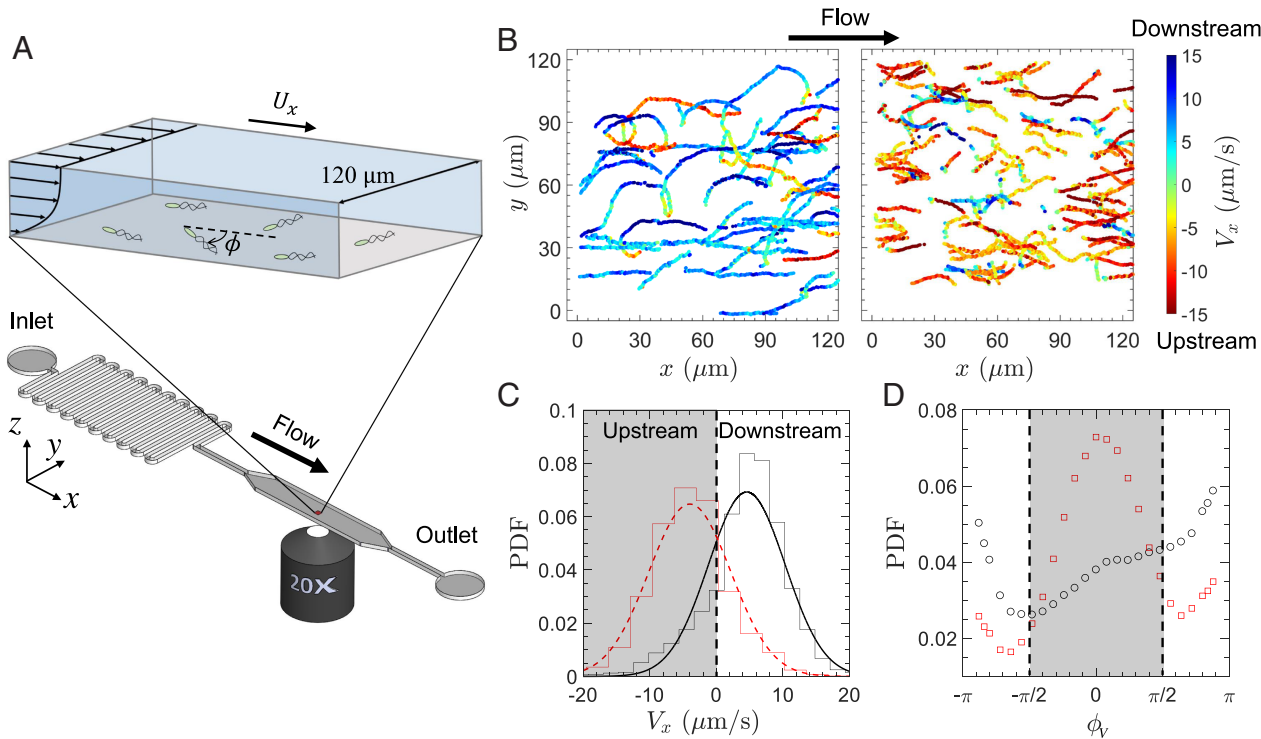


Fig. 1. Experimental set-up and enhanced rheotactic behavior in a ST fluid compared to a Newtonian one at a given flow rate. (A) Microfluidic channel, with a long delay line to minimize fluctuations. The region of interest (ROI, $120 \mu\text{m} \times 120 \mu\text{m}$) is located near the center of the wide part of the channel, away from the vertical walls, and close to the bottom wall. (B) Trajectories of *E. coli* in water (Left) and $c/c^* = 0.6$ of XG (Right), with an applied external flow rate of $20 \mu\text{L/h}$ (top view). The tracks of *E. coli* in XG show a bias in the upstream direction, whereas those in water display fewer swimmers going against the flow. These results suggest that the ST properties of the fluid contribute to bacterial rheotaxis. (C) PDFs of bacterial upstream swimming speed, V_x , for both water (black) and $c/c^* = 0.6$ of XG (red) under an external flow rate of $20 \mu\text{L/h}$. (D) PDFs of the orientation of the bacteria trajectory relative to the flow direction ϕ_V for both water (black) and $c/c^* = 0.6$ of XG (red) under the same external flow rate $Q = 20 \mu\text{L/h}$. Note that ϕ_V is different from the angle ϕ of the bacterium itself with the flow direction because the swimmer also gets advected.

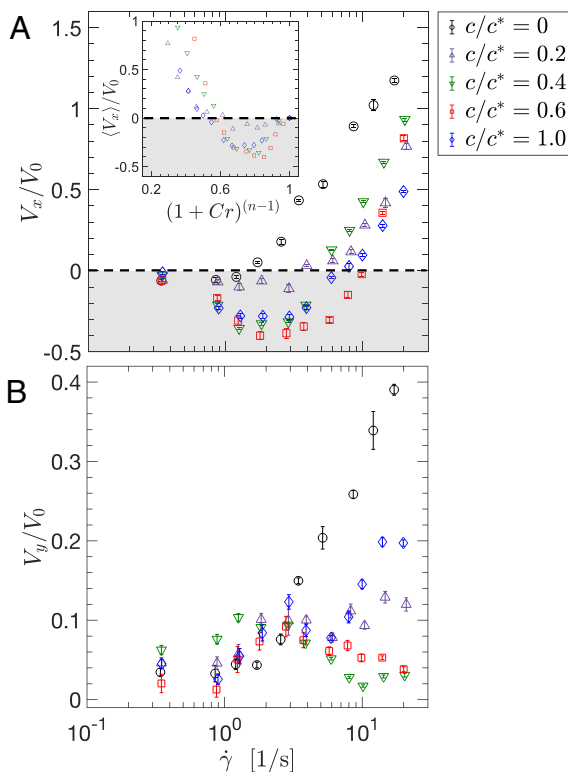


Fig. 2. Average swimming speed of *E. coli* upstream and lateral to the flow direction. (A) Average upstream swimming speed, V_x/V_0 , where V_0 is the mean swimming speed without an external flow ($Q = 0 \mu\text{L/h}$) as a function of shear rate $\dot{\gamma}$. Results are shown for water (black) and XG solutions at $c/c^* = 0.2$ (violet), $c/c^* = 0.4$ (green), $c/c^* = 0.6$ (red), $c/c^* = 1.0$ (blue). The data reveal a substantial enhancement of upstream swimming in XG solutions, which also occurs over a broader range of flow rates. The *Inset* graph shows V_x/V_0 as a function of a normalized shear rate $(1 + Cr)^{n-1}$, where Cr is the Carreau number. (B) Average swimming velocity lateral (perpendicular) to the flow direction, V_y/V_0 , as a function of shear rate, showing a reduction in the net lateral drift V_y in polymer solutions.

(XG $c/c^* = 0.6$, *Right* panel) fluids cases. While most bacteria in the Newtonian fluid (*Left* panel) are dragged downstream (positive x -direction) by the flow, we find significant bacteria upstream motion in the ST fluid (*Right* panel). We quantify these observations by computing the probability density functions (PDFs) of cell swimming speed in the axial direction V_x for Newtonian and ST fluids under the same flow rate (Fig. 1C). The data show that the Newtonian speed distribution is centered at approximately (positive) $6 \mu\text{m/s}$ and displays a downstream bias, while the ST distribution is centered at approximately $-5 \mu\text{m/s}$ with an upstream bias; the ST distribution is also broader than the Newtonian ones. These trends are consistent with the representative trajectories shown in Fig. 1B. The PDFs of *E. coli* orientation relative to the flow direction in Fig. 1D confirm that bacteria in ST fluids show a pronounced alignment with the flow upstream direction (relative to the Newtonian case). We note that the enhancement in (positive) rheotactic behavior observed with the ST fluid (XG solution) is not simply due to an increase in (absolute) fluid viscosity; in fact, increasing the fluid viscosity (with Ficoll) leads to a decrease in bacterial (positive) rheotactic behavior (*SI Appendix, Fig. S4*). Instead, the observed enhancement likely stems from the local viscosity gradients that develop around the bacterium due to ST viscosity behavior. Overall, these results highlight the significant impact of fluid ST properties on the rheotactic behavior of microorganisms. Our results show that ST viscosity behavior enables positive rheotaxis at flow rates beyond the accessible range in Newtonian fluids.

We now investigate bacterial rheotactic behavior as a function of viscosity and polymer concentration. Fig. 2A shows the normalized average upstream swimming speed (V_x/V_0) as a function of shear rate ($\dot{\gamma}$), where V_0 is the bacteria mean speed under quiescent conditions. In a Newtonian fluid (buffer solution), we observe limited rheotaxis at low shear rates $\dot{\gamma} \approx 0.3$ to 2.4 s^{-1} (Fig. 2A, dark circles); as $\dot{\gamma}$ increases, nearly the entire bacteria population gets advected (or dragged) downstream. Notably, any bacterial rheotactic behavior is lost in fluids with higher Newtonian viscosities (Ficoll) (*SI Appendix, Fig. S4*). However, for ST fluids (XG solutions), we find i) more pronounced rheotactic behavior (relative to the Newtonian case) and ii) rheotaxis over a broader range of $\dot{\gamma}$ (from 0.9 to 9 s^{-1}), as shown in Fig. 2A (color noncircle symbols). At sufficiently high shear rates, all bacteria are dragged downstream in both Newtonian and ST cases. Note that similar behavior is found with CMC solutions (*SI Appendix, Fig. S5*), although some differences are found due to the flexible nature of the CMC molecule, which leads to fluid elasticity.

Next, we examine the average swimming speed of bacteria lateral (perpendicular) to the flow direction (V_y) as a function of shear rates $\dot{\gamma}$ (Fig. 2B). Bacteria swimming in viscous fluids near surfaces display clockwise trajectories in quiescent fluids (10, 22). In the presence of flow, this clockwise motion competes with the imposed shear flow, which leads to a lateral drift to the right in the $+y$ -direction, i.e., a positive mean lateral speed, V_y (10, 23). By contrast, for all ST fluids investigated here, we find that the lateral speed V_y (colored markers) decreases relative to the Newtonian case (black markers). We will explore how fluid ST viscosity behavior affects V_y in Section 2.3. Combined with the V_x data (Fig. 2A), this observation indicates that ST viscosity can significantly enhance bacteria alignment with the flow.

Our experimental results show that only a small portion of the population can swim upstream in Newtonian fluids, while the majority is advected downstream even at very low shear rates. However, in ST fluids, a large fraction of the same bacteria population can swim upstream up to the point where the local flow velocity becomes comparable to their swimming speed. That is, bacterial rheotaxis is significantly enhanced (relative to Newtonian fluids) by ST viscosity behavior. What are the main mechanisms governing the observed rheotactic enhancement in non-Newtonian fluids? We will explore this question next using a simple model.

2. Model, Mechanisms, and Discussion

In this section, we develop a model to describe the experimental observation and gain insight into the main mechanism responsible for the enhancement in rheotactic behavior in ST fluids near walls. We focus our efforts on the concentration that leads to the strongest level of rheotaxis, $c = 0.6c^*$. The model is described in more detail in Section 4; only a brief account is provided below.

The main goal of our model is to obtain expressions for the bacteria upstream (V_x) and lateral (V_y) swimming speeds under an applied flow. In this system, V_x and V_y are set by cell orientation with respect to the wall θ and the flow ϕ (see sketch in Fig. 3A; see also Eq. 2 in Section 4). Our model therefore focuses on the mechanisms that govern these angles and the corresponding cell reorientation rates, characterized by the angular frequencies $\Omega_{\theta, \phi}$ (see Eqs. 3–7 in Section 4). Here, we consider both cell hydrodynamic and steric interactions with the wall, as well as cell reorientation due to flow (5) and ST viscosity effects (45).

We model an elongated bacterium that swims forward at a constant speed, V_0 , along its axis. As a first approximation, the

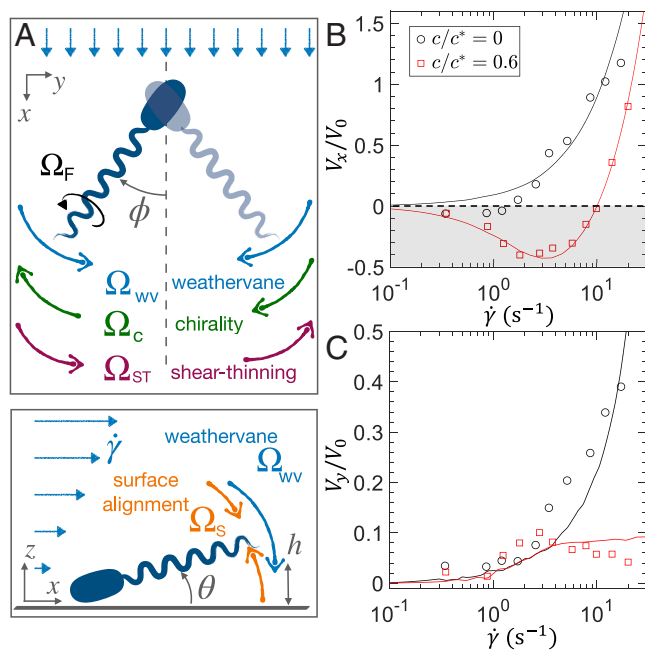


Fig. 3. A minimal model for the orientation of the bacteria captures both the enhanced rheotaxis and the decreased lateral drift in a ST fluid. (A) Reorientation mechanisms for a bacterium at the wall, as listed in the model. In the horizontal plane (Top), the weather-vane effect causes the bacterium to reorient toward the upstream direction. The chirality of the bacterium's flagella induces a drift toward the negative y -direction. However, this effect is counteracted in ST fluids by the rotation-induced drift. In the vertical direction (Bottom), the bacterium tends to swim at an angle in a quiescent fluid. Meanwhile, the weather-vane effect encourages horizontal alignment with the flow. We simulate 50,000 swimmers and calculate their average swimming velocities. (B) *E. coli* average upstream swimming speed, V_x , in Newtonian (water) and a ST fluid (XG), normalized by V_0 , as a function of shear rate $\dot{\gamma}$. Experimental measurements for water and XG at $c/c^* = 0.6$ are shown as black circles and red squares, respectively. Solid lines represent simulations of each fluid, revealing a notable increase in bacterial swimming upstream in the ST fluids across the experimental range of shear rates $\dot{\gamma}$. (C) *E. coli* average (normalized) lateral swimming speed, V_y , in the same fluids. ST properties enhance the alignment of bacteria with the flow. Simulations match the experiments over the entire range of flow rates examined. Specifically, both simulations and experiments reveal a decrease in the lateral drift in the presence of the ST XG solution.

bacterium swims at a fixed height above the wall, h , independent of both fluid type and flow rate (35). We assume that, near the wall where a linear shear flow profile develops, the bacterium is advected (downstream) by the flow at a speed $\dot{\gamma}h$. Thus, both quantities V_0 and h can be extracted from the experimental data (Section 4) at zero (quiescent) and high shear rates, respectively, since $\dot{\gamma}$ is known. We initially set V_0 constant at $10 \mu\text{m s}^{-1}$ and find a swimming height $h \sim 0.9 \mu\text{m}$ that is independent of fluid type. Note that while polymer concentration and fluid viscosity can affect bacteria swimming speed (V_0), our results seem relatively insensitive to the value of V_0 . Furthermore, we do not believe that the observed enhancement in bacterial rheotactic behavior in ST fluids can be ascribed to changes in V_0 . For instance, changes in V_0 do not lead to changes in bacteria alignment with flow.

2.1. No-Flow Condition.

2.1.1. Newtonian fluids. It has been previously shown that, near solid walls, bacteria in viscous fluids preferentially swim parallel to the surface with a small tilt angle $\theta_0 \approx 10^\circ$ (5, 46). This viscous behavior is described in Eq. 3 in Section 4, which depends on θ and a prefactor that corresponds to the alignment strength [obtained from previous works (10, 46)].

As mentioned before, the motion of bacteria such as *E. coli* near walls in Newtonian fluids is clockwise circular (22). This stems from the hydrodynamic interaction of the rotating head and the counterrotating cylinder with the wall (22) (Fig. 4C): in a viscous fluid, a 3D sphere rotating near a no-slip wall translates in the rolling direction. As the translations for the flagellum and the head go in opposite directions, the bacterium is reoriented and turns continuously to the right. We approximate this effect as a constant rotation rate due to chirality, Ω_ϕ^C (see Eq. 4 in Section 4).

2.1.2. ST fluids. For a bacterium near a wall, we do not expect the tilt angle (θ_0) to be modified by ST viscosity behavior due to the absence of lift forces (47). Therefore, we keep $\theta_0 \approx 10^\circ$ (same as the Newtonian case). We do, however, anticipate the curvature of the bacteria trajectories near walls to be modified by local viscosity gradients (SI Appendix, Fig. S7). Indeed, it has been previously shown that the translation of a cylinder rotating above a wall is modified by ST viscosity effects (45). To capture this behavior, we numerically investigate the effect of shear thinning viscosity on the orientation of the bacterium in a quiescent fluid, following ref. 45. For simplicity, we idealize the rotating bacterium as two counterrotating cylinders, as shown at the top of Fig. 4C; ST behavior is modeled using the Carreau–Yasuda equation fitted to our rheology data.

To minimize computation costs, we use finite element numerical simulations (SI Appendix) to compute the respective forces, $|F_+|$ and $|F_-|$, on the upper and lower half of a cylinder rotating above a no-slip wall (Fig. 4 and SI Appendix). In two dimensions (2D), an infinite cylinder rotating in a quiescent Newtonian fluid exhibits zero translation close to a wall (48); thus, our results account only for the ST effect which adds up to the previously described Newtonian chiral reorientation.

In a quiescent ST fluid, strong velocity gradients develop between the wall and the cylinder, creating a relatively low viscosity region. Consequently, the bottom half of the cylinder experiences a lower drag force, F_- , compared to F_+ on the upper half; that is $|F_-| < |F_+|$. Since the cylinder is force-free, the difference in forces leads to a net lateral translation, U , in the direction opposed to rolling, which depends nonmonotonically on the rotation rate, Ω (45) (Fig. 4c, black line). Therefore, we include a counterclockwise ST reorientation, Ω_ϕ^{ST} , that competes with the clockwise rolling effect, Ω_ϕ^C (Fig. 3A); see Eq. 5 in Section 4. Next, we investigate the case in which a flow is applied.

2.2. Applied Flow Condition.

2.2.1. Newtonian fluids. The driving effect of (surface) rheotaxis is the passive upstream reorientation of bacteria by the flow (5, 7, 8); this is the so-called weather-vane effect. Because of the relatively high viscous drag and low flow speed near the wall, the bacterium head acts as an anchor, while its flagellum is allowed to reorient freely. The flagellum is advected by the flow like a weather-vane and tends to align with it: this reorients the bacterium upstream and enables rheotaxis close to walls. This weather-vane effect is described in Eq. 6 in Section 4. The strength of the upstream alignment is obtained from a fit to the Newtonian data. As a result, in a Newtonian fluid, the upstream reorientation of bacteria in a shear flow competes with their tendency to turn clockwise near a surface, leading to a lateral drift to the right in the $+y$ -direction, and positive lateral velocity V_y (Fig. 3C).

2.2.2. ST fluids. How is bacterial rheotaxis modified by ST viscosity effects? We start by developing a force-free simulation to examine the advection of a nonrotating cylinder in an external

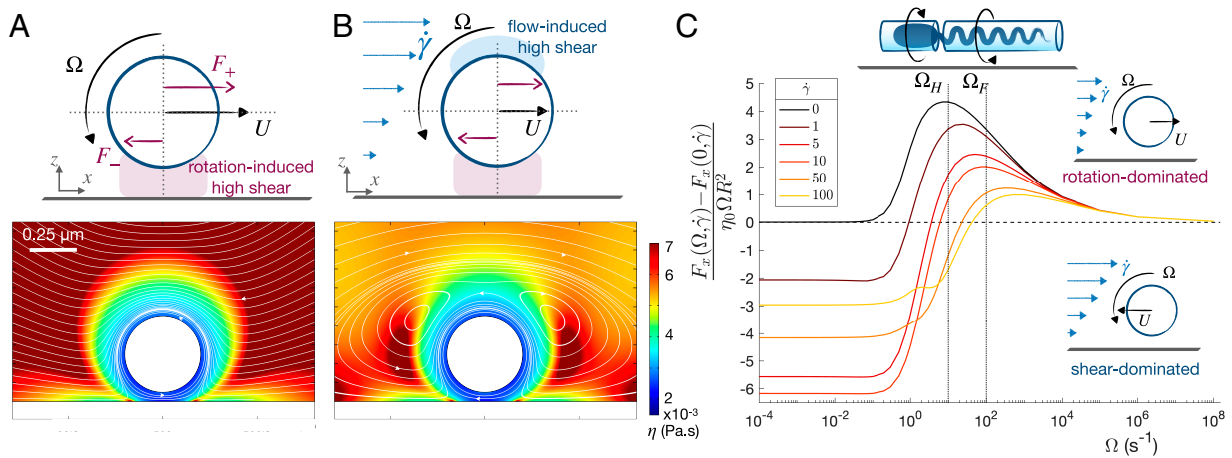


Fig. 4. The coupling between the rotation and translation of a cylinder in a ST fluid above a wall explains the reorientation of a bacterium with counterrotating head and flagellum. (A) Sketch (Top) and simulated local viscosity (Bottom) of a cylinder rotating at a rate Ω near a wall in a ST fluid. Confinement results in higher shear rates and, hence, lower viscosity η on the lower side of the cylinder. As a result, the horizontal component of the force resisting the rotation F_- is lower on the lower half than on the upper half F_+ , consequently the rotation induces a translation to the right U . (B) When adding an external flow, high shears are instead induced on the upper half. The direction of the rotation-induced translation of the cylinder is therefore determined by a competition between these two effects. (C) Difference between the scaled forces on the cylinder with $(F(\Omega, \dot{\gamma}))$ and without rotation $(F(0, \dot{\gamma}))$ at different shear rates. When the shear rate dominates (low Ω), the coupling occurs in the negative direction because the viscosity is overall lower above the cylinder. When rotation dominates (high Ω), the viscosity is lower below, leading to a rotation-induced translation in the positive x -direction. The vertical lines indicate the rotation rates of the bacterium head Ω_H and flagellum Ω_F (sketched).

flow in a ST fluid. Our results hint at very weak effects of the ST fluid on the weathervane effect. Therefore, we treat this effect as independent of fluid type (SI Appendix).

We now extend our finite element simulations to a rotating cylinder in a ST fluid to include an external shear in the x -direction. As noted before, these are 2D simulations, and therefore the flow direction (x -axis) and the cylinder rotation axis (y -axis) are always orthogonal. This 2D scenario corresponds to the case $\phi = \pm\pi/2$. Our ST simulations show that the presence of the wall near the bottom of the cylinder breaks the flow symmetry and creates a region of high shear rates and low viscosity at the top of the cylinder (see Fig. 4B and SI Appendix, Fig. S10). It is now surrounded by two competing high-shear regions with low viscosity, one close to the wall controlled by the rotation and one above the cylinder set by the external flow. We identify the dominant effect (flow or cylinder rotation) by computing the net force acting on the cylinder (F_{cy}) as a function of cylinder rotation rate (Ω) for different values of $+\dot{\gamma}$ in Fig. 4C. For parameters values relevant to *E. coli* rheotaxis, namely the rotation rates of the flagellum ($\Omega_F = 100$ s $^{-1}$) and body ($\Omega_H = 10$ s $^{-1}$) at intermediate shear rates ($\dot{\gamma} < 100$ s $^{-1}$), the translation occurs in the positive x -direction, opposite to rolling.

In our minimal model, we consider a linear decrease of the ST-induced reorientation Ω_ϕ^{ST} with shear rate ($\dot{\gamma}$) as a first approximation. Although the actual decrease is nonlinear, this approximation allows us to formulate a minimal closed-form model. Without flow, the ST reorientation compensates to the chiral one ($\Omega_\phi^{ST} = -\Omega_\phi^C$), in agreement with experiments. This effect then decreases linearly with $\dot{\gamma}$, providing the flow-sensitivity fitting parameter for the ST case in Fig. 3B. We include rotational noise and neglect weaker contributions to the orientation (10) (Section 4). In our model, the only fitting parameters are the strength of the weathervane effect and the ST flow sensitivity (Eq. 7); they are obtained from fits to the experimental data in the Newtonian and ST cases respectively.

2.3. Comparison between Simulations and Experiments. Using our model, we can now obtain time evolution and long-term averages of the upstream (V_x/V_0) and lateral (V_y/V_0) swimming

speeds of our model bacteria. Fig. 3B and C shows a comparison between the experimental (symbols) and numerical (lines) results of V_x/V_0 and V_y/V_0 , respectively, as a function of applied shear rates. We start by noting that, for Newtonian fluids, the model and experiments show no or minimal positive rheotactic behavior (Fig. 3B, black line) across all shear rates, even if there is still a fraction of cells that move against the flow, as shown in Fig. 1C. For ST fluids, the model successfully captures the deviation from the Newtonian case and the nonlinear rheotactic behavior as a function of shear rate (Fig. 3B, red line); the largest bacterial upstream swimming speed can be as large as 40% of its intrinsic swimming speed. We find that, in both experiments and simulations, the cross-over from upstream to downstream swimming occurs at shear rates that are an order of magnitude larger than in the Newtonian case. Similarly, our numerical results recover the bacterial swimming alignment (or lateral speed, V_y/V_0) behavior relatively well for both Newtonian (black line) and ST (red line) cases (Fig. 3C); the simulations also capture the enhanced bacteria alignment with the applied flow in ST fluids (Figs. 1D and 5).

Overall, our numerical model captures the main features of the bacterial rheotactic behavior in Newtonian and ST fluids, including the strong bacteria rheotactic response at low and intermediate shear rates ($\dot{\gamma}$) and the reduction in lateral drift V_y for $\dot{\gamma} > 3$ s $^{-1}$. Results from our model (which includes deterministic reorientation mechanisms and rotational noise) also show that the lateral angle (ϕ) distributions are significantly different in a ST fluid compared to a Newtonian one (Fig. 5). On the other hand, the tilt angle (θ) distributions remain nearly identical for the ST and Newtonian cases (Fig. 5, Inset).

These observations suggest that the dynamics are predominantly planar, or 2D, and that the fluid-dependent curvature of the quiescent trajectories plays a crucial role in the rheotactic behavior. The deterministic competition between reorientation at the surface and the upstream alignment can be described as an Adler equation (49) (SI Appendix, section IIIB). When the flow increases, the dynamics undergo a transition from loopy trajectories dominated by circular swimming to straighter (rheotactic) trajectories with a drift to the right reflecting the bacteria's chirality (10, 23, 50). The transition from loops

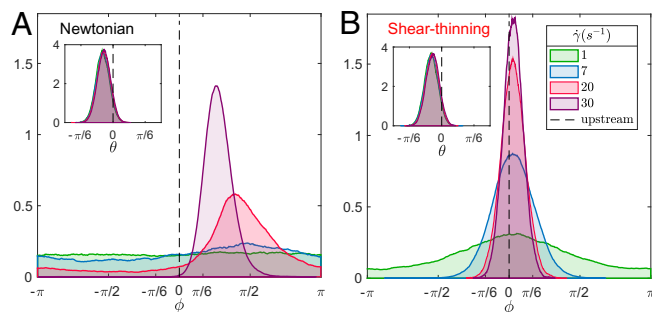


Fig. 5. Distribution of the lateral ϕ angle in our simulations for the Newtonian case (A) compared to the ST one (B) for different shear rates $\dot{\gamma}$. Insets show the tilt angle θ , which depends weakly on the shear rate and fluid rheology. At low shear rates ($\dot{\gamma} = 1 \text{ s}^{-1}$), the ST swimmers respond to the flow while the Newtonian ones are uniformly distributed. At intermediate shear rates, the lateral distribution of ST swimmers shows a sharp peak close to the upstream position ($\phi = 0$), hence allowing for efficient rheotaxis. The alignment of Newtonian swimmers occurs instead at high shear rates ($\dot{\gamma} = 20, 30 \text{ s}^{-1}$) when the external flow is already too strong to allow for upstream swimming.

with a zero or weak average swimming displacement to linear swimming with a net upstream swimming velocity occurs at a critical shear rate, $\dot{\gamma}_c$. This transition shear rate is reached when the weathervane effect compensates for the circular swimming (see Section 4 and [SI Appendix](#) for more details) and scales linearly with the quiescent reorientation rate Ω_C . Decreasing this reorientation and swimming in larger circles or straight, as in a ST fluid, therefore allows for upstream swimming at (much) lower shear rates than in the Newtonian case. For noisy and mostly straight swimmers, as in the ST experiments, the transition is dominated by noise but again occurs for flows that we predict to be an order of magnitude weaker in the ST fluids than in water. Moreover, after this transition, the swimmers in the ST fluid align closely to the upstream direction, while in water (Newtonian), circular swimming causes a strong drift to the right. These combined effects enable rheotaxis at low and intermediate shear rates in a population of *E. coli* in a ST environment. More broadly, we expect rheotaxis to be strongest for swimmers with straight trajectories or small curvature (Fig. 4B and [SI Appendix](#)).

3. Conclusion

We find that ST viscosity significantly affects the rheotactic behavior of *E. coli* near solid surfaces. Relative to Newtonian fluids, ST limits the chirality of the trajectories, which enables a bacteria rheotactic response to an imposed flow at relatively low shear rates; that is, the transition to bacterial rheotactic behavior happens at lower critical shear rates than in typical Newtonian fluids. After the transition, ST effects reduce the bacteria's lateral drift (to the right). Consequently, swimmers have sharper orientation distributions and are better aligned upstream, which ultimately increases their rheotactic ability in ST fluids. Conversely, a relatively large curvature of the trajectories in Newtonian solutions leads to a delay (in terms of $\dot{\gamma}$) in the transition to rheotaxis and to a drift to the right that weakens the upstream alignment. As a result, upstream swimming ($V_x < 0$) does not occur in the model and only marginally in experiments. Importantly, the fluid-dependent chiral rotation rate in a quiescent fluid is identified as a good predictor of swimmer population rheotactic ability, and we expect this finding to hold not only at the population but also at the individual level.

Our results provide a better understanding of the behavior of swimming organisms in complex environments. Our work

has important consequences for the study of medical, food, or wastewater treatment, and applications in designing medical devices that could prevent medical infections. In particular, we identify low curvature or, equivalently, high gyration radii, of bacteria trajectories near a surface in a quiescent fluid as a key predictive parameter of an efficient rheotaxis. As the curvature of the trajectories depends on the rheology of the surrounding fluid, we expect the rheotactic efficiency, and therefore the ability of a population to spread spatially and contaminate their environment, to greatly depend on the properties of the local fluid. Many polymeric solutions exhibit ST behavior, which we have shown here to enhance the rheotactic ability of *E. coli*. The expectation is that other fluid rheological properties such as viscoelasticity, also common in many biological fluids, will also produce nontrivial rheotactic behavior (see for example ref. 51). More broadly, these biological complex fluids often possess a microstructure that responds nonlinearly to applied stresses, giving rise to their non-Newtonian flow behavior. Understanding the interplay between fluid microstructure and the flow fields collectively generated by swimming bacteria (near or away from walls) under flow is an important next step.

4. Materials and Methods

4.1. Experimental Methods.

4.1.1. Microfluidic device. Experiments are performed in a microfluidic channel with dimensions of $900 \mu\text{m}$ width and $100 \mu\text{m}$ depth. The applied external volumetric flow, Q , is controlled through a syringe pump (Harvard Ph.D. 2000) over a range of flow rates $0 \mu\text{L/h} \leq Q \leq 100 \mu\text{L/h}$. A long delay line is incorporated at the start of the microfluidic device to provide high flow resistance and minimize the impact of pump-induced fluctuations and small bubbles as shown in Fig. 1A. Our ROI is located on the bottom wall, away from the corners to avoid the effects of shear-trapping and edge currents (39, 40). When flow is applied, the ROI is situated in the high-shear region of the fully developed flow.

4.1.2. Polymeric fluids. The effects of fluid ST viscosity behavior on bacterial rheotaxis are investigated using two main polymeric fluids. Shear-thinning fluids with negligible levels of elasticity are produced using aqueous solutions of xanthan gum (XG), a semirigid polymer of molecular weight $M_w = 2.0 \times 10^6$ and an overlap concentration $c^* = 290 \text{ ppm}$. To minimize the effects of elasticity we perform experiments with dilute XG solutions ($c/c^* \leq 1$); four formulations are used: $c/c^* = 0.2, c/c^* = 0.4, c/c^* = 0.6$, and $c/c^* = 1.0$. XG solutions show significant ST viscosity behavior ([SI Appendix, Fig. S1](#)). We also experiment with aqueous solutions of carboxymethyl cellulose (CMC), a flexible polymer of molecular weight $M_w = 7.0 \times 10^5$ and an overlap concentration $c^* = 10^4 \text{ ppm}$. Elasticity is minimized by using a relatively low M_w polymer in the dilute regime ($c/c^* = 0.25, c/c^* = 0.5$). Experiments with Newtonian fluids are performed with aqueous buffer solutions with shear viscosity (η) of 1 mPa s . We viscosify the buffer solutions by adding Ficoll ($M_w = 7.0 \times 10^4$, $R_g \approx 4.6 \text{ nm}$) at 10% ($\eta \approx 3 \text{ mPa s}$) and 15% ($\eta \approx 5 \text{ mPa s}$) in concentration by mass ([SI Appendix, Fig. S1](#)). These Ficoll solutions serve as the control case.

4.1.3. Rheology. Fluids are characterized using a stress-controlled rheometer (TA instruments, DHR-3) with a 60 mm cone geometry ([SI Appendix](#)). All rheological experiments are performed within the range of shear rates $\dot{\gamma}$ that the *E. coli* experiences in the microfluidic channel. Viscosity data for the ST fluids (XG solutions) are fitted with the Carreau-Yasuda model (52)

$$\eta(\dot{\gamma}) = \eta_w + (\eta_0 - \eta_w) (1 + \lambda \dot{\gamma})^{n-1}. \quad [1]$$

This empirical model is known to capture the viscosity behavior of polymeric solutions for a wide range of shear rates. We find that the Carreau-Yasuda model provides an adequate description of our fluids for a range of $\dot{\gamma} = 0.5 - 100 \text{ s}^{-1}$. Here, η_0 is the zero-shear ($\dot{\gamma} = 0$) viscosity, $\eta_w = 1 \text{ mPa s}$ is the limit viscosity at high shear rates; here this value is set to the viscosity of the solvent, i.e., water. The time-scale λ and the exponent n characterize respectively the onset ($Cr = \lambda \dot{\gamma} > 1$) and the magnitude of ST effects in the fluid. Note that XG

solutions have values of η_0 over an order of magnitude higher than water (or buffer solution). As expected, Newtonian Ficoll solutions display a constant viscosity in a dynamic setting (SI Appendix, Fig. S1).

4.1.4. Near-wall shear rate. The flow shear rates ($\dot{\gamma}$) near the surface of the microfluidic channel are obtained using simple numerical simulations (COMSOL Multiphysics) for the various fluids and flow rates Q . We obtain the values of $\dot{\gamma}$ for the XG solutions by using the Carreau-Yasuda fits to the rheology data in simulations. That is, for each simulation, we input the flow rate and fluid properties obtained through fitting Eq. 1 to the rheological data. To extract the shear values from the 3D flow profile in the ROI, we calculate the average $\dot{\gamma} = \frac{\partial U_x}{\partial z}$ over a region of $z < 7 \mu\text{m}$.

4.1.5. Cell tracking. We track individual *E. coli* (42) near the bottom wall of the microfluidic chamber in a $120 \mu\text{m} \times 120 \mu\text{m}$ field of view captured by a CCD camera (Sony XCD-SX90, 30 frames per second) and a microscope (Zeiss Z1, $20\times$ objective). We use *E. coli* displacement data to calculate the cells' average swimming speed in both upstream V_x and lateral V_y directions to the flow. Bacteria that move less than one body length over the recording are excluded from the data analysis.

Model. Surface rheotaxis stems from the interplay between self-propulsion, the no-slip wall, and local flow. To understand how ST enables upstream swimming, we investigate how local differences in viscosity stemming from ST affect these interactions. This section provides details on our model for the tilt and lateral orientation angles of the bacteria, θ and ϕ , (Fig. 3A). The vertical tilt angle is $\theta \in [-\pi/2; \pi/2]$, and the lateral angle with respect to the flow direction is $\phi \in [-\pi; \pi]$, so that $\phi = 0$ represents upstream swimming, $\phi > 0$ denotes a drift to the right (i.e., $V_y > 0$), and $\phi < 0$ denotes a drift to the left (i.e., $V_y < 0$). The velocity of the swimming bacterium is then

$$\begin{aligned} V_x &= \dot{\gamma}h - V_0 \cos \phi \cos \theta, \\ V_y &= V_0 \sin \phi \cos \theta. \end{aligned} \quad [2]$$

The average swimming height (h) is extracted from experimental data using the swimmer's speed along the flow direction at large flow rates when $\dot{\gamma}h \gg V_0 \cos \phi \cos \theta$. We find that $h \approx 0.9 \mu\text{m}$, consistent with previous results (46).

Next, we provide minimal expressions for the mechanisms that set the tilt (θ) and lateral angles (ϕ) in a population of swimmers. Each torque that reorients a swimmer near a solid surface induces a rotation speed in θ and ϕ , denoted respectively as Ω_θ and Ω_ϕ . The combination of all the reorientation rates then sets the time evolution of the position of the swimmer as given by the (θ, ϕ) pair.

4.1.6. Wall alignment. The preferred wall alignment rate, Ω_θ^S , is described by the relationship (10),

$$\Omega_\theta^S = -w_s \sin(2(\theta - \theta_0)), \quad [3]$$

where $w_s = 4 \text{ s}^{-1}$ is the magnitude of the reorientation rate and $\theta_0 = 10^\circ$ (10, 46). In the absence of viscoelastic lift force, this preferred angle is expected to be independent of the fluid type.

4.1.7. Circular swimming in Newtonian fluids. We model the chiral interaction of the rotating flagellum and counterrotating head with the wall as a constant rotation rate due to chirality,

$$\Omega_\phi^C = w_C, \quad [4]$$

with $w_C = 1 \text{ s}^{-1}$ for *E. coli* (10).

4.1.8. ST induced reorientation. We estimate the translation induced by the ST behavior of the fluid Ω^{ST} . The swimmer is modeled using a rotating (infinite) cylinder for simplicity, which has been shown to provide useful insights into propulsion mechanisms (35). Numerical simulations are performed using a ST Carreau fluid model fitted to our fluid rheological data to compute the resulting flow and force balance on the cylinder (see SI Appendix for details). The cylinder rotation (above the wall) leads to a dimensionless net horizontal force $F_{cyl} = F_x(\Omega)/(\eta_0 \Omega R^2)$. Previous results (45) show a net cylinder translation in the direction opposite to rolling. Similar results are found here using the methods described in ref. 45, as shown in Fig. 4C.

These results are extended to include flow effects, that is $\dot{\gamma} \neq 0$. We again consider a cylinder of radius R held at a fixed position rotating parallel to a no-slip wall at a rate Ω and include an external flow along the x -direction, with shear rate $+\dot{\gamma}$ (or $-\dot{\gamma}$; see SI Appendix), as sketched in Fig. 4B. Note that forces on a stationary cylinder (with no rotation) due to advection, $F(0, \dot{\gamma})$, are already considered through the weathervane effect (Eq. 6).

We compute the modified horizontal force on the cylinder $F_{cyl} = (F_x(\Omega, \dot{\gamma}) - F_x(\Omega, 0))/(\eta_0 \Omega R^2)$. We find a nonmonotonic relationship between F_{cyl} and Ω , as well as two main regimes: shear- and rotation-dominated. In the shear-dominated regime (relative low values of Ω), resistance to rotation is lower on the upper half of the cylinder than in its lower half, $|F_+| < |F_-|$, and any rotation of the cylinder induces a rolling drift in the $-y$ -direction. Importantly, for parameters values relevant to bacterial rheotaxis, namely the rotation rates of the bacterial flagellum ($\Omega_F = 100 \text{ s}^{-1}$) and head ($\Omega_H = 10 \text{ s}^{-1}$) and intermediate shear rates ($\dot{\gamma} < 100 \text{ s}^{-1}$), the translation occurs in the positive x direction, opposite to rolling, as shown in Fig. 4C.

This new contribution is added to the model using a linear expression for the swimmer rotation rate such that

$$\Omega_\phi^{ST} = -w_{ST} (1 - \alpha \dot{\gamma}/\Omega_F). \quad [5]$$

The best fit to the experiments for the shear thinning effect is $w_{ST} = w_C = 1 \text{ s}^{-1}$, with a sensitivity to the flow $\alpha = 0.35$.

4.1.9. Weathervane effect. We approximate the swimmer reorientation due to the flow gradients at the wall by considering the movement of an object held at a fixed distance $L/2$ of an anchor at the wall and advected by the external linear shear flow (SI Appendix) and add that this effect is only valid when the bacterium points to the wall, $\theta > 0$. We can describe the reorientation rates due to the weathervane effect, Ω_θ^{WV} , in the θ and ϕ directions as

$$\begin{aligned} \Omega_\theta^{WV} &= -\dot{\gamma} w_{WV} (\sin \theta)^2 \cos \phi \mathbf{1}_{\theta > 0}, \\ \Omega_\phi^{WV} &= -\dot{\gamma} w_{WV} \sin \phi \tan \theta \mathbf{1}_{\theta > 0}. \end{aligned} \quad [6]$$

The quantity Ω_ϕ^{WV} scales linearly with $\dot{\gamma}$, as expected for Newtonian fluids.

The effects of ST viscosity behavior on Ω_ϕ^{WV} are not well known, so we investigate them by performing simulations of a 2D cylinder being advected (near a wall) by a shear flow using the Carreau model in COMSOL. The simulations do not show significant differences between the ST and Newtonian cases, particularly for the cylinder speed (SI Appendix). Therefore, we set $w_{WV} = 0.24$ for all fluids investigated here; the w_{WV} value is obtained by fitting the simulations from Eq. 7 to the Newtonian experimental results.

4.1.10. Noise. One could consider other contributions in our models such as a chiral interaction with the bulk flow and Jeffery orbits (5, 10). Chiral interaction between the flagella and the bulk flow can, by themselves, lead to rheotaxis (6, 53), but at the considered flow rate, they are small compared to wall-mediated ones. Jeffery orbits lead to a small oscillatory component in the trajectories (10), and they are not affected by shear thinning (54). Thus, we neglect these two components.

Finally, we include rotational noise in our model through a Langevin equation adapted to our angular coordinates (55), with strength $D_r = 0.057 \text{ s}^{-1}$ (56). The flow-dependent reorientation rates of the bacterium are

$$\begin{aligned} \dot{\theta} &= \Omega_\theta^S + \Omega_\theta^{WV}(\dot{\gamma}) + D_r \tan \theta + \sqrt{2D_r} d\xi_\theta, \\ \dot{\phi} &= \Omega_\phi^C + \Omega_\phi^{WV}(\dot{\gamma}) + \Omega_\phi^{ST}(\dot{\gamma}) + \frac{\sqrt{2D_r}}{\cos \theta} d\xi_\phi. \end{aligned} \quad [7]$$

where ξ_θ and ξ_ϕ are uncorrelated Gaussian white noises.

4.1.11. Model integration. We use the above equations to obtain the dynamics (and values) of θ and ϕ for the experimental range of shear rates, $\dot{\gamma}$. Similarly, we use Eq. 2 (and distributions of θ and ϕ) to obtain the average long-term velocities of the swimming bacteria as a function of $\dot{\gamma}$. Note that the only fitting parameters in our model are w_{WV} for the Newtonian case and w_{ST} and α for the ST case. For the cases shown in Fig. 3 B and C, $w_{WV} = 0.24$, $w_{ST} = 1 \text{ s}^{-1}$, and

$\alpha = 0.35$. The remaining parameters, namely $\theta_0 = 10^\circ$, $w_s = 4 \text{ s}^{-1}$ and $w_C = 1 \text{ s}^{-1}$, are obtained from the existing literature (10, 46).

The quantitative features of our model, in particular, the predicted velocities (V_x , V_y) and the transition shear rate, are sensitive to the values of the reorientation parameters that we fit to the experiments, namely w_{WW} , w_{ST} and α . Other model components are sensitive to the geometry of individual swimmers, such as the weathervane effect (Ω^{WW}) that is expected to scale as l^2 . Nevertheless, we find that model trends (Fig. 3 B and C) are very robust to population diversity and changes in parameters.

4.1.12. Transition to rheotaxis. The deterministic ($D_r = 0$) critical Adler shear rate $\dot{\gamma}_c$ is reached when the chirality and weathervane rotations cancel each other. For the Newtonian case, $\dot{\gamma}_{c,N} = w_C / (w_{WW} \sin \theta_0)$. From the parameters of our model $\dot{\gamma}_{c,N} \approx 24 \text{ s}^{-1}$. After the transition, the swimmers are oriented with a deterministic lateral drift $\phi = \arcsin(\dot{\gamma}_{c,N} / \dot{\gamma})$ (see SI Appendix for the analytical analysis). In the stochastic case ($D_r > 0$), the noise results in a progressive rather than sharp transition, with a broad distribution of ϕ (50) (Fig. 5A). Increasing $\dot{\gamma}$ beyond the transition range ($\dot{\gamma} > 25 \text{ s}^{-1}$) progressively allows the weathervane effect Ω^{WW} to overcome the constant chiral reorientation Ω^C . For high $\dot{\gamma}$ above the experimental range, the distribution of ϕ narrows and tends to lower values, reflecting a strong upstream alignment of the swimmers. The flow at this point is too high to allow for a net upstream displacement.

In a ST fluid, the chiral rotation above the surface is hindered by ST-induced reorientation. The deterministic Adler transition occurs for $\dot{\gamma}_{c,ST} = (w_C - w_{ST}) / (w_{WW} \sin \theta_0) \rightarrow 0$, that is, as soon as the shear flow is turned on. In the stochastic case with rotational diffusion, since $|w_C - w_{ST}| < D_r$, noise controls both the quiescent trajectories and the transition to the biased

rheotactic behavior. For low shear rates ($\dot{\gamma} < 1 \text{ s}^{-1}$), rotational diffusion overcomes the weathervane effect and the distribution of ϕ is broad despite a small upstream bias. As the flow increases, the weathervane effect becomes prominent and encourages visible upstream alignment as early as $\dot{\gamma} = 1 \text{ s}^{-1}$. Consequently, the ϕ distributions are much sharper and closer to direct upstream swimming ($\phi = 0$) (Fig. 5B), although a weak bias to the right remains (see Figs. 3C and 5B and SI Appendix). The swimmers can now efficiently move upstream, as observed experimentally and predicted in our simulations (Fig. 3B).

Data, Materials, and Software Availability. All study data are included in the article and/or SI Appendix.

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