Asymmetric bistability of chiral particle orientation in viscous shear flows

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The migration of helical particles in viscous shear flows plays a crucial role in chiral particle sorting. Attaching a nonchiral head to a helical particle leads to a rheotactic torque inducing particle reorientation. This phenomenon is responsible for bacterial rheotaxis observed for flagellated bacteria as *Escherichia coli* in shear flows. Here, we use a high-resolution microprinting technique to fabricate microparticles with controlled and tunable chiral shape consisting of a spherical head and helical tails of various pitch and handedness. By observing the fully time-resolved dynamics of these microparticles in microfluidic channel flow, we gain valuable insights into chirality-induced orientation dynamics. Our experimental model system allows us to examine the effects of particle elongation, chirality, and head heaviness for different flow rates on the orientation dynamics, while minimizing the influence of Brownian noise. Through our model experiments, we demonstrate the existence of asymmetric bistability of the particle orientation perpendicular to the flow direction. We quantitatively explain the particle equilibrium orientations as a function of particle properties, initial conditions and flow rates, as well as the time-dependence of the reorientation dynamics through a theoretical model. The model parameters are determined using boundary element simulations, and excellent agreement with experiments is obtained without any adjustable parameters. Our findings lead to a better understanding of chiral particle transport and bacterial rheotaxis and might allow the development of targeted delivery applications.

In nature, chirality occurs in a vast number of situations, often in the form of helical structures. At the nano and micron scale, chirality can be encoded in the helical shape of relatively rigid objects, as, for example, DNA strands (1), cholesteric crystals (2), microorganisms such as spirochetes (3) or bacteria flagella (4). It also occurs dynamically, for example, in the beating patterns of cilia in the lungs (5), the helical beating of the tails of sperm cells (6, 7), or of flagella of microalgae such as *Chlamydomonas* or *Volvox* (8). Natural and artificial microswimmers rely on the symmetry breaking induced by the chiral nature of flagella or microfabricated helices for self-propulsion at small scales (9–11).

Chirality also induces symmetry breaking in the transport properties of helical particles in interaction with viscous flows. Passive drift is observed for helical particles in shear flows (12–17) in addition to the well-known Jeffery orbits of elongated objects. When a nonchiral head is added, a rheotactic torque results, leading to a symmetry-breaking reorientation of the object (18, 19) perpendicular to the flow direction. For a microswimmer, these orientation dynamics lead to swimming into preferred directions so-called rheotaxis (18–20).

So far, experimental evidence of the abovementioned phenomena has exclusively been obtained using biological systems (12, 18–20). Despite their importance, their inherent complexity prevents isolating experimentally the role of specific particle properties on the observed phenomena. In addition, Brownian noise often masks the effect of chirality (18, 19).

Recent developments in microfabrication methods give access to remarkable control of particle properties at the micrometer scale (21). In particular, 3D microprinting methods allow for the fabrication of well-controlled rigid (21) or soft (22) structures, that can be functionalized chemically (23) or through metal coatings (11, 24, 25).

Here, we leverage these methods to overcome the limitations of biological systems and to design an experimental model system giving full control of particle shape, in a size range where Brownian noise can be neglected (26). We 3D print with submicron resolution rigid microparticles consisting of a microhelix attached to a slightly more dense spherical head. They mimic the shape of flagellated bacteria without considering low Reynolds number flow | fluid–structure interactions | microfluidics | chirality

Significance

To propel themselves, many biological microswimmers rely on symmetry breaking induced by the chiral nature of their helical flagella. Additionally, flagellar chirality leads to complex transport phenomena, as bacterial rheotaxis. Comprehending these observations in biological systems is challenging as their complexity masks the role of specific particle properties. To overcome this limitation, we exploit recent advances in microprinting to fabricate “passive bacteria” comprising a helical tail attached to a spherical body. Leveraging the precise control of particle geometry, we unravel their complex oscillatory orientation dynamics in shear flow, including increasing or decreasing amplitudes and final orientations perpendicular to the flow direction. The understanding gained opens possibilities to control bacterial transport or to design chiral microrobots for biomedical applications.
other complex properties such as activity while imitating potential bottom-heavyness (here head heaviness) of microorganisms (27, 28) or artificial microrobots (11).

We investigate the orientation dynamics of these particles in viscous shear flows close to the bottom surface of a microfluidic channel. Direct observations under a microscope reveal the full time-resolved orientation dynamics of individual helical particles under flow (Fig. 1 A and B), in contrast to previous observations mostly limited to statistical information (12, 18, 19). We systematically vary the pitch of the microhelices (Fig. 1C) and as such the importance of chirality-induced reorientation effects. We develop a theoretical model which captures the experimental observations quantitatively without using any free fit parameters.

**Particle Design and Fabrication**

Chiral microparticles consisting of a spherical “head” and a helical “tail” are fabricated using a high-resolution 3D microprinter (Nanoscribe) based on a 2-photon direct writing technique. Both “tail” are fabricated using a high-resolution 3D microprinter Chiral microparticles consisting of a spherical “head” and a helical particles have diameter (Nanoscribe) based on a 2-photon direct writing technique. Both

**Experimental Observations**

Fig. 1A shows snapshots of typical dynamics of a left-handed ($\chi = -1$) microparticle under flow at flow rate $Q = 30$ nl/s for a particle of pitch $p = 5$ μm. The first row depicts one full cycle of the observed fast oscillation dynamics of $\psi(t)$, reminiscent of Jeffery orbits of elongated nonchiral neutrally buoyant particles (29). Note that a Jeffery orbit corresponds to an oscillation in three dimensions, and as such, also the out-of-plane angle $\theta(t)$ undergoes periodic oscillations. These can be estimated from the snapshots but are less visible compared to the $\psi(t)$ dynamics that we will discuss in the following. At the time scale of a single oscillation ($\sim 1$ s), the sign of $\psi(t)$ does not change. Here, $\psi(t)$ is always positive, with the head pointing in the $y$ direction, and the particle oscillates around $\psi = \pi/2$ at a certain amplitude, as shown in the first row of Fig. 1A. However, the orientation dynamics changes at longer time scales, as demonstrated in the second row for an initial orientation $\psi_0 < 0$. It shows the slow evolution of the orientation angle $\psi$, depicting a snapshot at maximum amplitude every 5 oscillation periods. The particle starts oriented in the $-y$ direction; then, the orientation of the head switches (“flips”) to the other side ($\psi > 0$) and eventually stabilize at $\psi^* = \pi/2$ (Movie S2). In contrast, when we perform the same set of experiments with right-handed particles ($\chi = 1$), flipping now occurs for initial orientations $\psi_0 > 0$ which stabilize after flipping at $\psi^* = -\pi/2$, as demonstrated in Fig. 1B and Movie S5.
Fig. 2. Typical dynamics of orientation angle ψ(t) for left- (A–C) and right-handed (D–F) particles with pitch p = 5 μm for different initial conditions at flow rate Q = 30 nl/s (colored curves) showing stabilization toward ±π/2 (Movies S1–S6). The dynamics is quantitatively captured by a theoretical model Eqs. 1 and 2, (black curves). Model shear rates have been adjusted to match experimental oscillation frequencies and are in the range \( \dot{\gamma} = 27 \pm 1.5 \text{ s}^{-1} \), within ±5% from independently determined experimental shear rates. Insets: Experimental phase space trajectories (ψ, |θ|) with time color-coded (from blue to red).

Fig. 2 depicts quantitative measurements of ψ(t) for left- and right-handed particles for the same conditions as in Fig. 1 (Q = 30 nl/s, p = 5 μm) now varying the initial orientations \( \psi_0 \). Different dynamics can be observed for identical handedness as a function of the initial orientation, as shown in the Top row for left-handed particles (\( \chi = -1 \)). When the initial \( \psi_0 \) is positive, the particle oscillates around \( \pi/2 \) and the oscillation amplitude decreases with time until the particle stabilizes at \( \psi^* = \pi/2 \) (Fig. 2A and Movie S1). When the initial \( \psi_0 \) is negative and the particle oscillates with a sufficiently large amplitude, an increase in amplitude is observed until the particle flips to the other side and stabilizes again at \( \psi^* = \pi/2 \) (Fig. 2B and Movie S2) similarly to what is shown in Fig. 1A. However, for negative \( \psi_0 \) and sufficiently small oscillation amplitudes the particle does not flip to the other side, but the oscillation amplitude decreases with time and the particle is stabilized at \( \psi^* = -\pi/2 \), as shown in Fig. 2C and Movie S3. We thus observe bistability with final particle orientation at \( \psi_1^* = \pi/2 \) or \( \psi_2^* = -\pi/2 \), depending on the initial orientation \( \psi_0 \). This bistability is asymmetric, as particles with \( \psi_0 < 0 \) can flip to the other side, whereas particles with \( \psi_0 > 0 \) never flip but are always stabilized at \( \psi_1^* = \pi/2 \). We denote the equilibrium position that can also be reached through flipping by \( \psi_1^* \) and the other equilibrium position by \( \psi_2^* \). The dynamics are classified as stabilizing at the more stable orientation \( \psi_2^* \) without flipping (green) or with flipping (red) and stabilizing at the less stable orientation \( \psi_2^* \) (blue).

To demonstrate that this asymmetry stems from the particle chirality, we perform experiments also for right-handed particles (\( \chi = +1 \)). Indeed, we observe exactly the opposite dynamics. While right-handed particles again stabilize either at \( \psi^* = \pi/2 \) (Fig. 2F and Movie S6) or at \( \psi^* = -\pi/2 \) (Fig. 2D and E and Movies S4 and S5), flipping now only occurs for initial orientations \( \psi_0 > 0 \) (Fig. 2E). We can thus write the equilibrium positions in a compact form as \( \psi_1^* = -\chi \pi/2 \) and \( \psi_2^* = \chi \pi/2 \).

A more direct comparison with classical Jeffery dynamics becomes possible when considering the angular phase space dynamics as shown in the insets of Fig. 2. The theoretically measured dynamics (ψ(\( \dot{\epsilon} \)), \( \theta(\dot{\epsilon}) \)) reveal the coupling between in-plane and out-of-plane oscillations. Large amplitudes in ψ also correspond to large amplitudes in \( \theta \), with the maximum amplitude in ψ for \( \theta = 0 \), corresponding to particles aligned with the surface, and the maximum amplitudes for \( \theta \) to \( \psi = \pm \pi/2 \). A decrease in amplitude of ψ and a stabilization toward \( \pm \pi/2 \) also corresponds to a decrease in amplitude of \( \theta \) toward zero and thus particle alignment with the surface. At short times, the dynamics reiterates Jeffery-like oscillatory dynamics; however, damping and flips are observed at longer times. This is evidently in contrast to classical Jeffery orbits where oscillation amplitudes are constant and \( \psi(t) \) is either positive or negative for the entire length of the trajectory (30).

We note that in some cases, after the particle orientation reaches a stable orientation, it assumes a “kick” which restarts the oscillation process at small amplitude, as depicted in Fig. 2F at starting time \( t \approx 18 \text{ s} \). We attribute such disruptions to imperfections, such as small impurities in the channel wall.

Model

To understand the observed particle dynamics, we develop a theoretical model, assuming a constant shear rate \( \dot{\gamma} \) experienced by the particles moving close to the bottom wall, and neglecting hydrodynamic particle–wall interactions and the \( z \)-dependent shear rate (31) (see Discussion below). Then, the dynamic equations for the orientation angles \( \psi \) and \( \theta \) can be written as

\[
\frac{d\psi}{dt} = \dot{\gamma} (1 + a^{-2})^{-1} \sin \psi \tan \theta - \chi \dot{\gamma} v \cos \psi \cos 2\theta / \cos \theta, \tag{1}
\]

\[
\frac{d\theta}{dt} = \frac{1}{2} \dot{\gamma} (1 - (a^2 - 1)(a^2 + 1)^{-1}) \cos 2\theta \cos \psi - \chi \dot{\gamma} v \sin \psi \sin \theta - \Omega_H \cos \theta H(\theta), \tag{2}
\]

including three contributions: The first terms in Eqs. 1 and 2 describe Jeffery oscillation dynamics of elongated particles with effective aspect ratio \( a \) in shear flows (29). The second terms describe chirality-induced reorientation of particles of handedness \( \chi \) and dimensionless “chiral strength” \( v \) depending on the shape of the helix and the size of the spherical head (19, 20). This term rotates particles consisting of a nonchiral head and a chiral tail, such as bacteria, toward the positive or negative vorticity direction of the flow, depending on the chirality of the tail (19, 20). The strength of the chiral reorientation rate is a product of the shear rate and chiral strength, \( \Omega_C = \dot{\gamma} v \). Indeed, it has previously been shown that this chirality-induced reorientation leads to lateral drift of swimming bacteria in shear flows although direct experimental validation on individual trajectories has not been achieved yet (18–20). The third term in Eq. 2 reflects that the head of the particle is heavier than the
helical tail and is the only term not proportional to \( \dot{\gamma} \). This “head-heavy” torque rotates particles toward head-down orientations. In our simplified model, it only depends on \( \theta \), and a constant head-heavy strength \( \Omega_H \) which depends on particle shape and linearly on the density difference \( \Delta \rho = \rho - \rho_f \). It vanishes when the particle head (almost) touches the wall; hence, sedimentation is suppressed. This we capture roughly with the Heaviside function \( \Theta(\theta) = 1 \) for \( \theta > 0 \) and 0 otherwise, meaning that this torque is suppressed when the particle points toward the wall (\( \theta < 0 \)); see also SI Appendix, Text and Fig. S4.

To determine numerical values for the particle properties \( a \), \( \nu \), and \( \Omega_H \), we use the boundary element method (BEM) with a triangulated mesh for the surface of the particles immersed in a simple shear flow (Materials and Methods (32-34)). We perform two independent sets of BEM simulations. First, we determine the particle aspect ratios \( a \) and the chiral strengths \( \nu \) for all the different experimental chiral particle shapes by considering neutrally buoyant right-handed particles \( (\Omega_H = 0, \chi = +1) \) in simple shear flow. To determine \( \nu \) and \( a \), we place the particle aligned with the flow (\( \psi = 0, \theta = 0 \)) at a given shear rate and measure the instantaneous angular velocities for different orientations along the particle axis, i.e., different phase angles where the helix is anchored to the head. By averaging over these orientations, we can immediately determine \( \nu \) and \( a \) from Eqs. 1 and 2.

Second, \( \Omega_H \) is determined by a different set of BEM simulations. We put a particle with a heavy head of the experimentally measured density \( \rho \) which is initially aligned perpendicular to the direction of gravity \( (\theta_0 = \pi/2) \) in a quiescent fluid \( (\dot{\gamma} = 0) \) of the experimentally measured density \( \rho_f \). We then measure the angular velocity due to head heaviness and directly obtain \( \Omega_H \) from Eq. 2.

The values of \( \nu \), \( a \), and \( \Omega_H \) obtained from the BEM simulations for particles of different pitch \( p \) are plotted in Fig. 3. \( \Omega_H \) and \( a \) are comparable for all helix shapes, i.e., \( a \in \{2.8, 3.2\} \) and \( \Omega_H \in \{0.084, 0.098\} \) s\(^{-1}\). Note, \( a \) is somewhat smaller than expected from naive estimates \( a_0 = (L + D)/D \in \{3.5, 4\} \). In contrast, \( \nu \) increases significantly with helix pitch \( p \) from \( \nu = 0.003 \) (\( p = 5 \) \( \mu \)m) to \( \nu = 0.02 \) (\( p = 25 \) \( \mu \)m). Hence, tuning the pitch allows to adjust the chiral strength of the particle, while leaving the effective aspect ratio and head heaviness approximately unaffected.

The parameters \( \nu \) and \( a \) are defined and determined in simple shear flow, while our experimental Poiseuille flow is characterized by nonconstant and wall-bounded shear. To verify the simple shear approximation, we also determine effective values of \( \nu \) and \( a \) in Poiseuille flow, both with and without the presence of bounding walls using BEM. Indeed, we show that the effect of the quadratic Poiseuille flow profile on \( \nu \) and \( a \) is very small. The effect of hydrodynamic interactions with the wall slows down the Jeffery-like reorientation close to the wall, as expected (31), but only has a small effect on the chiral reorientation (SI Appendix, Text and Fig. S6).

The shear rates \( \dot{\gamma} \) experienced by oscillating particles are estimated by two independent methods from the experimental data. First, from the experimentally measured particle velocities \( \nu_p(t) \) at a given flow rate \( Q \), we can estimate the particle position \( x \) and eventually the local shear rate. Second, we determine the oscillation frequencies from the maxima of the power spectrum of the experimental orientation dynamics \( \psi(t) \). The results from both methods consistently show that \( \dot{\gamma} \) can be calculated from the flow rate \( Q \) as \( \dot{\gamma} \approx 0.9Q \) nl\(^{-1} \) (Materials and Methods).

Altogether, we end up with a theoretical model, Eqs. 1 and 2, without free parameters and which can, after numerical integration to obtain \( \psi(t) \) and \( \theta(t) \), be directly compared to the experiments. The model reproduces the experimental trajectories \( \psi(t) \) extremely well; see Fig. 2 (black curves), including oscillation frequencies, amplitude modulations, flipping behavior, and stable positions.

**Discussion**

Combining experimental and theoretical results, we can now analyze the different particle dynamics and their origins in detail. Fig. 4A depicts trajectories in orientation phase space from the theoretical model Eqs. 1 and 2, where \( \theta \) is represented as a function of \( \chi \psi \) to collapse the results for different handedness onto one graph. The different dynamics stabilizing at \( \psi_C^+ \) without and with flipping (red and green) and stabilizing at \( \psi_C^- \) (blue) are indicated using the same color code as in Fig. 2. The results agree qualitatively with the experimental observations shown in the insets of Fig. 2. Reaching either of the two stable orientations depends on the initial condition, and a separatrix (black curve) divides the two stable regions in phase space. We will demonstrate below that the separatrix and the size of the stable regions depend on the ratio of \( \Omega_C \) (= \( \nu \dot{\gamma} \)) and \( \Omega_H \). For constant \( \Omega_H \), the larger \( \nu \dot{\gamma} \), the smaller is the region of initial \( \psi_0 \) values, which approach the less stable position \( \psi_C^- \).

In Fig. 4C, we summarize the experimental results for different chiral strength \( \nu \), handedness \( \chi \), and shear rate \( \dot{\gamma} \) as a function of initial condition \( \chi \psi_0 \) and the product \( \nu \dot{\gamma} \). Again, we classify the results as a function of the three types of trajectories using the same color code as in Fig. 2 and in Fig. 4A. Here, \( \Omega_H \) is kept approximately constant, while \( \dot{\gamma} \) and \( \nu \) are modified independently.

Since in the experiments the initial angle \( \theta_0 \approx 0 \), solely the value of the initial angle \( \psi_0 \) determines the final stable position, bounded by the two \( \psi \)-values of the separatrix at \( \theta = 0 \) (black dots in Fig. 4A). Fig. 4C shows these separatrix values as black dots for many different combinations of \( \nu \) and \( \dot{\gamma} \) values and for constant \( \Omega_H = 0.09 \) s\(^{-1}\). Indeed, they only depend on the product \( \nu \dot{\gamma} \) and the region to reach \( \psi_C^- \) decreases with increasing \( \nu \dot{\gamma} \).

We observe that the theoretically predicted separatrix is in good agreement with experimental results, and our findings unambiguously demonstrate an asymmetric, handedness-dependent bistability of chiral head-heavy particles in flow.

To further show the robustness of our model and the necessity of reorientation contributions from both head heaviness and particle chirality to observe asymmetric bistability, we experimentally and numerically “knock out” each of these contributions separately.

When head heaviness is ignored in the simulations (\( \Omega_H = 0 \)), Fig. 4B, the chiral reorientation rate \( \Omega_C \) alone determines the rise and decay of the amplitudes. All particles will stabilize at

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**Fig. 3.** Parameters obtained from BEM simulations for particles of different pitch \( p \). (A) Chiral strength \( \chi \). (B) Effective particle aspect ratio \( a \). (C) Head-heavy reorientation strength \( \Omega_H \).
In the experiments, we produce particles with two opposite chiralities, leading to effectively nonchiral bistability shown in Fig. 4A and C. Reorientation due to head heaviness is responsible for bistability and reorientation due to chirality for the asymmetry. The asymmetry of the $\psi-\theta$ phase-space for the two different handedness ($\chi = \pm 1$) can be captured by the same phase space when plotted in an $\chi\psi-\theta$ phase space, as in Fig. 4A and C. For a random initial condition, it is more likely to end up at the stable position $\psi_1^* = -\chi \pi/2$, which can also be reached through flipping (red trajectories in Fig. 4A), compared to the less probable stable position $\psi_2^* = \chi \pi/2$.

**Decay Rates**

The particle geometry also determines the timescales to reach the final stable orientations. Fig. 5 shows the decay of the oscillation amplitudes $|\psi|_t$ (after potential flip) from $\pi$ toward the stable orientation at $\pi/2$ for different flow rate $Q$ (or $\dot{\gamma}$) and particle pitch $p$ (or $\nu$). Results from our model are shown in Fig. 5A (dashed curves). Starting from large amplitudes, the initial decay is faster for larger $\dot{\gamma}$ and stronger $\nu$, meaning larger $p$ and $Q$, influencing the times $t^*$ when $|\psi(t)|$ has decayed to the stable value $\pi/2$. For smaller angles, the decay is dominated by head heaviness and is independent of $\nu$ and $\dot{\gamma}$. Indeed in Fig. 5B, when plotted against $t - t^*$, constant slopes can be identified. Removing the effect of head heaviness ($\Omega_H = 0$), dotted curves in Fig. 5A does not influence the initial decay but slows down the approach to the stable position (Fig. 4B). For large amplitudes, the decay is fully given by chirality-induced reorientation and the amplitude decay collapses when plotted against the rescaled time $t/\nu$; see Fig. 5C, with $|\psi(t)| \approx \pi - t/\nu/2$ (red dotted line). In the absence of head heaviness, the amplitude decay collapses to a universal curve (black dotted curve in Fig. 5C).
obtain quantitative agreement between model and experiments in particular for large amplitudes. This is demonstrated in Fig. 5D for different flow rates Q and fixed particle shape (pitch p = 15 μm) and in Fig. 5E for different particle pitch p at fixed flow rate Q = 30 nl/s. Here, we have plotted the experimental amplitudes along with the theoretical curves (dashed lines), in very good quantitative agreement. Fig. 5F and G show the respective plots using rescaled time tν, and indeed, the experimental data collapse well for large amplitudes, in agreement with the theoretical model. As can be seen in Fig. 5F and G, experimental results sometimes start to deviate toward slower decays at small angles and even approach the limit of no head heaviness (black dotted lines). We attribute this to a reduction of the importance of head heaviness due to fluctuating decrease of the experimental density difference. This is particularly pronounced for large t or ν, where chirality-induced reorientation is strong (SI Appendix, Figs. S7–S9).

Conclusions

Through a combination of highly resolved experiments and a theoretical model, we have demonstrated asymmetric bistable orientation dynamics of chiral microparticles in shear flows. The interplay between particle elongation, chirality, and head heaviness is fully captured by an analytical model without adjustable parameters, independently determined from BEM simulations. Our results constitute the first direct experimental observation and quantitative comparison of individual helical particle orientation dynamics. The findings of our work will be helpful to better understand dynamics in more complex biological systems and to design artificial microrobots or targeted delivery applications.

Materials and Methods

Particle Printing. The particles are fabricated with a two-photon lithography microprinter by Nanoscribe, using the Dip-in operational mode with the IP-Dip photoresist (Nanoscribe). The helix is printed at the smallest available resolution, with its cross-section given by the convolution of one voxel (grain of rice shape with 1 μm in height and less than 140 nm in diameter) and helix radius 5 μm. The spherical body is also printed with the same radius, either as a full sphere by multiple layers (slicing distance set to 50 nm to smooth the step between the layers), or as a spherical shell of 1 μm thickness. In the case of the shell, the sphere is open on the side of the helix with a circular cut with radius 2 μm, in.
this way, the unpolymerized resin can be washed away during the development and it can be substituted with the desired fluid. The particles are printed on an array configuration with the axis of the helix parallel to the quartz glass substrate (SI Appendix, Fig. S1), and at a small vertical distance from the substrate so that the helix cross-section is fully resolved (distance of the centerline of the helix from the substrate between 0.4 and 0.7 μm). The sample is left at rest for at least 24 h after the printing, in order for it to gain stiffness and better sustain the development processes. For developing the particles, the sample is put 20 to 30 min in PGMEA (Propylene Glycol Methyl Ether Acetate, from Sigma). To avoid capillary forces which could deform and destroy the helices, the sample is then put for a few seconds into distilled water, then 2 min in isopropanol, and again in water. The outcome particle can be considered rigid under our experimental flow conditions. After the development, the sample is stored in water with a small amount of sodium hypochlorite and BSA at concentration 0.1%, to avoid bacteria growth and particles stickiness.

**Particle Density.** To measure the density of the head, we print the spherical body alone, full or hollow and without helix, to perform sedimentation tests. The individual spherical particle (or spherical shell) is let sinking inside a PDMS chamber in 50% glycerol with no flow, and its position along the sedimentation axis is recorded by continuously adjusting it relative to the focal plane, using a motorized stage, for a distance of around 300 μm. The sphere settling velocity is then used to calculate the particle density by balancing the gravitational force and the buoyancy with the drag given by the Stokes’ law. The measured density of the polymerized material, estimated by the sedimentation of printed spheres, appears to fall in the interval known in the literature, which is between 1.190 and 1.370 g/cm³ (35), but it appears to be also dependent on the exact printing procedure. We measure for the full sphere a density of 1.26 g/cm³, while the density of the helix alone is systematically smaller (estimated to be around 1.20 g/cm³ by repeated sedimentation experiments at increasing fluid density). This unavoidable density inhomogeneity is also confirmed by the fact that the whole particle given by a full sphere and the helix in bulk 50% glycerol is observed falling parallel to gravity with the helix pointing upward. The hollow sphere geometry, instead, provides a better mass distribution, with an average density of the sphere typically from 3% to 6% smaller than the full printed version, much closer to the one of the helix alone.

**Microfluidic Device.** The experimental channel consists of a rectangular PDMS shallow channel, built with standard soft-lithographic techniques, with nominal dimensions 500 μm in width and 100 μm in height (measured 516 μm × 96 μm). The channel is connected from one side to a syringe pump, while the other side is in direct communication to a large pool where the sample with the particles is located. The pool is open on the surface in a way that the experimenter has access to the sample from above, and the particles can be individually manipulated and transported to the entrance of the channel. The manipulation is performed using a thin capillary, with nozzle size ≲ 8 μm, whose position is controlled by a micromanipulator (Eppendorf) connected to a 3 mL plastic syringe. A flow can be manually imposed through the nozzle in both directions, and it is used for grabbing the particle from the sample, by imposing a negative pressure, and releasing it at the entrance of the channel, with positive pressure. The capillary nozzle is functionalized with 2% BSA for 30 min before use in order to avoid other nonspecific capillary–particle interactions. The PDMS channel is sealed to a cover glass coated with a thin layer of PDMS in a way that PDMS also covers the bottom wall, which is in contact with the particle during the experiment. The channel is also treated before use with 3% BSA. This facilitates the experiment with the particle in the vicinity of the wall avoiding any wall-particle interaction apart from steric interaction.

The particle is usually placed at the entrance of the channel, in the vicinity of the bottom wall and sufficiently far away from the lateral walls. The device is placed under a microscope (Zeiss Axios Observer), on a MS-2000 automated stage (ASI), which allows to follow the particle along the whole length of the channel. The capillary has access to the entrance of the channel on the side of the pool, and it can be also used to change, to some extent, the particle initial orientation ψ₀.

**The Fluid and Flow Control.** We use polytungstate solution (PTS) at concentration of 2.7 g/L of salt dissolved in 10 mL of water to match approximately the density of the helical structure, while the spherical head remains typically denser. The corresponding viscosity is η = 1.17 mPas. At this concentration, evaporation from the open pool induces variations in the fluid density and viscosity that has been measured to be limited below 5%. The device is placed inside a transparent box which is open on one side for the particle manipulation, to minimize the solvent loss. The flow is provided by a Hamilton glass 500 μL syringe and controlled by a Nemesys syringe pump. The flow is switched on after the particle has deposited to the bottom wall of the channel, and it is switched off before the particle exits the channel. A typical experiment uses the same particles over many runs, by reversing the flow several times.

**Image Acquisition and Image Processing.** The particle in the channel is visualized through a 20X-long working distance objective with fluorescence microscopy using a high-efficiency filter (BP 430/60, BP 550/100 Zeiss), and images are taken with a Hamamatsu Orca-flash 4.0LT camera, working at 10 or 20 Hz and synchronized with the dumping of the stage position, so that also the particle translation can be completely reconstructed. After a median filtering, the location of the center of mass of the sphere is located either by setting a threshold for the case of the full sphere or by circle detection for low-intensity spherical spheres. Then, the treatment proceeds at the level of the helix: Its shape, especially at the tip, is reconstructed by a maximum filter, and the image is binarized. The helix orientation is found by considering the maximum overlap between the helix and a rotating rectangle pinned at the center of the sphere and with width similar to the helix. The helix projected length Lp is also extrapolated fixing a threshold on the profile of integrated intensity over the rectangle along the correct orientation and rescaling this value by using a measurement of a known projected length.

The absolute value of the out-of-plane angle |ψ| can then be estimated from the projected length Lp, the helix length L, and the helix/sphere diameter D, such that |ψ| = arccos((Lp − D)/L).

**Estimation of Local Shear Rate.** First, ˙γ has been determined from the experimentally measured particle velocities vρ (t). When we neglect hydrodynamic-particle–wall interactions and the flow curvature, we can assume to first approximation that the particles simply follow the flow velocity vρ (y, z) in the rectangular channel. For a given channel geometry and applied flow rate Q, the fluid flow vρ (y, z) in the channel can be calculated, with vmax the velocity in the center of the channel (36). Since our particles are sufficiently far away from the side walls, the flow profile can be approximated as planar Poiseuille flow, vρ (z) = (4/π2) vmax (h − 2z) h with h = 96 μm. Measuring the particle velocity and comparing to the flow profile can then be used to extract the particle position z in the channel and eventually the z-dependent shear rates ˙γ (y, z) = dvρ/dz of the particles; see SI Appendix, Text and Fig. S3.

Second, we determine ˙γ of oscillating particles by calculating the angular frequencies ωm of the maxima of the Fourier transform of ψ(t). Using ωm and the particle aspect ratios a determined from BEM simulations, we use the relation known from Jeffery dynamics, ˙γ = a ωm (a + a−1). The determined shear rates ˙γ for different flow rates Q and for different oscillating head heavy particles of different pitch are shown in SI Appendix, Fig. S2. The linear relation ˙γ = 0.90 nl−1 indeed fits the data well, in agreement with the previously described method.

**Boundary Element Method (BEM).** For the BEM simulations, the surface of the spheres and the helical tails are discretized into a triangular mesh with triangle length ~ 0.075 D (SI Appendix, Fig. S5). Similar triangular discretizations have previously been used to model flagellated bacteria, see, e.g., refs. 37–39. The flow velocity at a given position x can be obtained by the boundary integral formulation:

\[ v_i(x) = v^\infty(x) - \frac{1}{8\pi \eta} \sum_{n} N_2 \sum_{j} G_j(x, y_n) q_j(y_n) dS_n, \]

where v^\infty is the background flow, υ is the viscosity, N2 is the number of mesh triangles, G is the Oseen tensor, q is the viscous traction acting at a surface.
position $y_n$ and $d_n$ is the triangle area. By solving Eq. 3 together with the constraint of force- and torque-free conditions in a matrix form (32, 33), the translational and rotational velocities of the particle can be obtained.

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

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