
Supplementary information

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enhances bacterial motility**

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Supplementary Information

The colloidal nature of complex fluids enhances bacterial motility

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1 Quantitative similarities of bacterial swimming in dilute colloidal suspensions and in dilute polymer solutions

Our experiments have shown that all the reported swimming behaviors of flagellated bacteria in dilute colloidal suspensions are *quantitatively* similar to those in dilute polymer solutions. These features are summarized below:

- (i) The non-monotonic trend of the swimming speed of bacteria with the increasing concentration of colloids (or equivalently the increasing concentration of polymer) (Fig. 1c);
- (ii) The correlation between the swimming speed of bacteria and the size of colloids (or equivalently the size of polymer coils) (Fig. 2);

(iii) The nearly linear anticorrelation between the wobble angle of bacteria and the swimming speed of bacteria (Fig. 3b);

(iv) The decrease of the rotational diffusivity of bacteria with the increasing concentration of colloids (or equivalently the increasing concentration of polymer) (Extended Data Fig. 2a);

(v) The rotational diffusivity of bacteria is nearly independent of the size of colloids (or equivalently the size of polymer coils) (Extended Data Fig. 2a);

(vi) The increase of the run time of bacteria with the concentration of colloids (or equivalently the concentration of polymer) (Extended Data Fig. 2b);

(vii) The increase of the tumble time of bacteria with the concentration of colloids (or equivalently the concentration of polymer) (Extended Data Fig. 2c).

The quantitative similarities of these different bacterial swimming behaviors strongly suggest that a common underlying mechanism dictates bacterial swimming in both dilute colloidal suspensions and dilute polymer solutions.

2 Bacterial motility enhancement

2.1 Boundary induced torque (BIT) on bacteria

Since the characteristic size and swimming speed of bacteria are $1\text{ }\mu\text{m}$ and $10\text{ }\mu\text{m/s}$ in water respectively, the corresponding Reynolds number (Re) of bacterial swimming is small on the order of 10^{-5} . Therefore, bacterial flow can be well approximated as a creeping flow dictated by the linear Stokes equation. In the creeping flow limit, we consider a single bacterium swims with a velocity $\mathbf{V}_b$ next to a spherical colloid of radius R . $\mathbf{V}_b$ is the velocity of the bacterium tangential to its helical trajectory in 3D. The swimming speed of the bacterium measured in experiments V is the projection of $\mathbf{V}_b$ along the helical axis of the bacterial helical trajectory (Extended Data Fig. 4a). $\mathbf{V} = \mathbf{V}_b$ when the wobble angle $\theta = 0$. While V is a strong function of θ , we assume the magnitude of $\mathbf{V}_b$, V_b , is a constant independent of θ . Strictly speaking, we should use the component of the bacterial tangential velocity along the direction of its flagellar bundle $V_b^f = \mathbf{V}_b \cdot (-\mathbf{i}_f)$, where $\mathbf{i}_f$ is the unit vector along the direction of the bacterial flagellar bundle. The difference does not affect the calculation of the boundary-induced torque below. Thus, to simplify our discussion, we treat V_b as the magnitude of the bacterial tangential velocity in this section. We shall discuss the fine difference between V_b and V_b^f within the model of bacterial wobbling, where we will also justify why V_b^f is constant independent of the

wobble angle (see Sec. 3.4.4).

To reduce mathematical difficulty, we take two approximations, which do not significantly affect the numerical accuracy of our calculation. First, since the lubrication interaction between the bacterium and the colloid decays quickly with increasing bacterium-colloid distance d , we consider only the situation, where d has reached the minimum and the component of $\mathbf{V}_b$ along the position vector $\mathbf{r}$ pointing from the hydrodynamic center of the bacterial body to the center of colloid is zero. Correspondingly, we define $\mathbf{V}_b$ along the z direction, normal to the position vector $\mathbf{r}$ along the y direction. Second, since the aspect ratio of bacterial body is less than 3, the effect of the shape of bacterial body is small in the creeping flow. Thus, we approximate the bacterial body as a sphere with a radius r_b .

The linearity of the creeping flow dictates the following relation between the velocity and the effective force:

$$\begin{pmatrix} \mathbf{F}_1 \\ \mathbf{F}_2 \\ \boldsymbol{\tau}_1 \\ \boldsymbol{\tau}_2 \end{pmatrix} = \mu \begin{pmatrix} A_{11} & A_{12} & \tilde{B}_{11} & \tilde{B}_{12} \\ A_{21} & A_{22} & \tilde{B}_{21} & \tilde{B}_{22} \\ B_{11} & B_{12} & C_{11} & C_{12} \\ B_{21} & B_{22} & C_{21} & C_{22} \end{pmatrix} \begin{pmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \boldsymbol{\omega}_1 \\ \boldsymbol{\omega}_2 \end{pmatrix}, \quad (1)$$

where $\mathbf{F}_1$ and $\boldsymbol{\tau}_1 = (\tau_1^x, \tau_1^y, \tau_1^z)$ are the force and torque on the bacterium, respectively. $\mathbf{u}_1 = (u_1^x, u_1^y, u_1^z)$ and $\boldsymbol{\omega}_1 = (\omega_1^x, \omega_1^y, \omega_1^z)$ are the linear and angular velocity of the bacterium in the lab frame. $\mathbf{F}_2$ and $\boldsymbol{\tau}_2$ are the force and torque on the colloid. $\mathbf{u}_2 = (u_2^x, u_2^y, u_2^z)$ and $\boldsymbol{\omega}_2 = (\omega_2^x, \omega_2^y, \omega_2^z)$ are the linear and angular velocity of the colloid in the lab frame. μ is the viscosity of the buffer. The resistance matrix in equation (1) has been calculated previously in the limit when $(r_b, R) \gg d$ using the lubrication theory [1]. The boundary-induced torque on the bacterial body is given by

$$\boldsymbol{\tau}_1 = \mu (B_{11}\mathbf{u}_1 + B_{12}\mathbf{u}_2 + C_{11}\boldsymbol{\omega}_1 + C_{12}\boldsymbol{\omega}_2), \quad (2)$$

where

$$B_{11} = \begin{pmatrix} 0 & 0 & -Y_{11}^B \\ 0 & 0 & 0 \\ Y_{11}^B & 0 & 0 \end{pmatrix} \quad \text{and} \quad B_{12} = \begin{pmatrix} 0 & 0 & -Y_{12}^B \\ 0 & 0 & 0 \\ Y_{12}^B & 0 & 0 \end{pmatrix}, \quad (3)$$

and

$$C_{11} = \begin{pmatrix} Y_{11}^C & 0 & 0 \\ 0 & X_{11}^C & 0 \\ 0 & 0 & Y_{11}^C \end{pmatrix} \quad \text{and} \quad C_{12} = \begin{pmatrix} Y_{12}^C & 0 & 0 \\ 0 & X_{12}^C & 0 \\ 0 & 0 & Y_{12}^C \end{pmatrix}. \quad (4)$$

Thus, the x component of the torque that changes the wobbling of bacterium is

$$\tau_1^x = \mu \left(-Y_{11}^B u_1^z - Y_{12}^B u_2^z + Y_{11}^C \omega_1^x + Y_{12}^C \omega_2^x \right). \quad (5)$$

Similarly, the x component of the torque on the colloid is

$$\tau_2^x = \mu \left(-Y_{21}^B u_1^z - Y_{22}^B u_2^z + Y_{21}^C \omega_1^x + Y_{22}^C \omega_2^x \right). \quad (6)$$

Here,

$$\begin{aligned} Y_{11}^B &= \frac{4\pi}{5} \frac{\gamma(4+\gamma)}{(1+\gamma)^2} r_b^2 \ln \xi, \\ Y_{12}^B &= -Y_{11}^B, \\ Y_{21}^B &= -\frac{4\pi\gamma^2(4\gamma+1)}{5(1+\gamma)^2} r_b^2 \ln \xi \\ Y_{22}^B &= -Y_{21}^B, \\ Y_{11}^C &= -\frac{16\pi}{5} \frac{\gamma}{(1+\gamma)} r_b^3 \ln \xi, \\ Y_{22}^C &= \gamma^2 Y_{11}^C, \\ Y_{12}^C &= -\frac{4\pi}{5} \frac{\gamma^2}{1+\gamma} r_b^3 \ln \xi, \\ Y_{21}^C &= Y_{12}^C, \end{aligned} \quad (7)$$

where $\gamma \equiv R/r_b$ is the size ratio of the colloid and the bacterium and $\xi \equiv 2d/(r_b + R)$ is the scaled surface-to-surface distance between the bacterial body and the colloid. Numerically, we choose $d \approx 50$ nm based on experimental observation [2]. Thus, the lubrication approximation applies when $R > 50$ nm or $\gamma > 0.05$.

In our model of bacterial wobbling discussed in Sec. 3 below, the angular velocity of bacterial body is confined within the y - z plane (see Extended Data Fig. 4b and discussion in Sec. 3.4.4). Thus, $\omega_1^x = 0$. The torque-free condition

on the colloid further requires

$$\omega_2^x = \frac{Y_{21}^B(u_1^z - u_2^z)}{Y_{22}^C} \quad (8)$$

from equation (6). Inserting equation (8) in equation (5), we finally have the boundary-induced torque on the bacterium

$$\tau_1^x = \frac{\pi}{5} \mu r_b^2 V_b \frac{\gamma(17+8\gamma)}{(1+\gamma)^2} \ln \frac{r_b(1+\gamma)}{2d}, \quad (9)$$

where we take the relative velocity between the bacterium and the colloid as $(u_1^z - u_2^z) \approx V_b$. Equation (9) is the equation (1) of the main text.

2.2 Size-dependent motility enhancement

The boundary induced torque is balanced by the restoring torque of the bacterial body τ_r , which arises due to the deviation of the wobble angle of bacterial body θ away from its equilibrium wobble angle $\theta_0 = 45.1^\circ$ in water without colloids. We assume the flagellar hook is linearly elastic with a bending stiffness K . Thus,

$$\tau_r = -K(\theta - \theta_0). \quad (10)$$

The balance of equation (9) and (10) then leads to

$$-K(\theta - \theta_0) = \frac{\pi}{5} \mu r_b^2 V_b \frac{\gamma(17+8\gamma)}{(1+\gamma)^2} \ln \frac{r_b(1+\gamma)}{2d}, \quad (11)$$

which gives the relation between the wobble angle θ and the size ratio γ , $\theta(\gamma)$.

To further convert the relation $\theta(\gamma)$ to $V(\gamma)$, we take the empirical linear relation between θ and the average swimming speed V : $\theta = a_1 - b_1 V$ from the direct fitting of the experimental data (the dashed line in Fig. 3b), where $a_1 = 1.25$ rad and $b_1 = 3.61 \times 10^4$ rad/s/m. Equation (11) is converted to

$$\frac{V}{V_0} = 1 + \frac{\pi}{5} \frac{C}{K} \frac{\mu r_b^2}{b_1} \frac{\gamma(17+8\gamma)}{(1+\gamma)^2} \ln \frac{r_b(1+\gamma)}{2d}, \quad (12)$$

where we have used the condition $\theta_0 = a_1 - b_1 V_0$ with $V_0 = 13$ $\mu\text{m/s}$ the average swimming speed of bacteria in water. In addition, we write $V_b = C V_0$ with C a proportional constant. V_b is linearly proportional to V_0 as required by the linearity of the creeping flow. The lower bound of C is set by the maximum

velocity of bacteria observed in experiments when the wobble angle is smallest around $\theta = 25^\circ$. Thus, $C > 1.8$. Equation (12) shows an excellent agreement with experiments with the fitting parameter $K/C = 2.68 \times 10^{-19}$ N·m (the black solid line in Fig. 2).

When the wobble angle θ reaches zero, equation (11) becomes

$$K\theta_0 = \frac{\pi}{5} \mu r_b^2 C V_0 \frac{\gamma(17 + 8\gamma)}{(1 + \gamma)^2} \ln \frac{r_b(1 + \gamma)}{2d}. \quad (13)$$

Solving equation (13) using the fitting value of K/C yields the size of particles that completely suppresses bacterial wobbling $\gamma = 2.22$. Since $V = V_b$ when the wobble angle reduces to zero, we have $C = 2.67$ after inserting $\gamma = 2.22$ back into equation (12). As a result, $K = 7.16 \times 10^{-19}$ N·m, agreeing well with the bending stiffness of the flagellar hook on the order of 5×10^{-19} N·m obtained from direct measurements with optical tweezers [3]. Hence, the simple hydrodynamic calculation presented here provides a parameter-free description of the motility enhancement of bacteria.

Note that the bending stiffness of the hook is about two to three orders of magnitude smaller than that of the flagellar filament [4, 5]. A single flagellum (including the flagellar filament and the hook) behaves like springs in series. Under an external torque, the component with the larger compliance would suffer the most bending. The total bending stiffness of the flagellum, K_t , can be estimated as $1/K_t = 1/K + 1/K_f$, where K and K_f are the bending stiffness of the hook and the flagellar filament, respectively. Since $K \ll K_f$, $K_t \approx K$. As a flagellar bundle is typically consistent of three or four individual flagellum, each with its own hook, we may further approximate the configuration of a flagellar bundle as springs in parallel. Hence, the bending stiffness of the flagellar bundle would be $K_b = nK_t \approx nK$, where $n = 3$ or 4 is the number of flagella in the bundle. As our model provides only an order of magnitude estimate of the bending stiffness of the flagellar bundle, the order one factor n would not affect the conclusion of our calculation.

The calculation based on the BIT is simple and generic, independent of the detailed kinematics of bacterial locomotion. In particular, we assume the BIT is balanced by the deviation of the bacterial wobbling angle θ from its equilibrium angle θ_0 . As we shall show next in the model of bacterial wobbling, the BIT directly modifies the misaligned angle between the axis of the bacterial body and the axis of its flagellar bundle, α (Extended Data Fig. 4b and Extended

Data Fig. 6b), which in turn changes the wobble angle θ . Nevertheless, since bacterial swimming speed V is also nearly linearly anti-correlated with α (Extended Data Fig. 4d inset), the above calculation does not change when we replace θ with α (and θ_0 with α_0) in equations (10) and (11) (see Sec. 3.4.4). We also achieve a quantitative description of bacterial motility enhancement observed in experiments with a quantitatively similar flagellar bending stiffness $K = 8.5 \times 10^{-19}$ N·m and $C = 2.09$ (the red dashed line in Fig. 2).

3 Model of bacterial wobbling

3.1 Background

It has long been known that the swimming trajectory of flagellated bacteria such as *E. coli* is helical in 3D, which manifests as the wobbling of bacterial body in the 2D projection of optical microscopy (Extended Data Fig. 4a) [6, 7, 8]. Several mechanisms have been proposed for explaining the origin of bacterial wobbling. First, the shape of bacterial body may not be perfectly axially symmetric, which leads to the misalignment between the axis of the flagellar bundle and the axis of the bacterial body. The misalignment leads to an unbalanced torque, giving rise to 3D helical trajectories and therefore bacterial wobbling. Second, the flagellar bundle may traverse a non-integral number of wavelengths that leaves a residual unbalanced transverse force on flagella. Bacterial body has to rotate in the opposite direction to balance this transverse force, which leads to a high-frequency wobbling at the rate of flagellar rotation. While the first mechanism is intrinsic to bacteria and unlikely to be affected by the presence of colloids, the second mechanism results in weak high-frequency wobbling [9], irrelevant to the large-amplitude low-frequency wobbling observed in our experiments. The third and the most widely circulated mechanism of bacterial wobbling argues that bacterial flagella generally do not bundle at the pole along the symmetric axis of the bacterial body. The thrust of the off-axial flagellar bundle exerts a net torque on the body, resulting in the extra rotation of the body in addition to its usual counter-rotation induced by the rotary flagellar motor. As a result, the angular velocity of the bacterial body does not align with its translational velocity, resulting in 3D helical trajectories and bacterial wobbling.

Hyon *et al.* constructed a minimal model based on the third mechanism [6]. By setting the orientation of the flagellar bundle with respect to the bacterial

body and discretizing the surface of the body and bundle, they numerically solved the rotation and translation of the bacterium using a boundary element method. Specifically, they assumed that the velocity at the surface point $\mathbf{r}_\alpha$ of the bacterium follows

$$\mathbf{v}(\mathbf{r}_\alpha) = \mathbf{V}_b + \boldsymbol{\Omega} \times \mathbf{r}'_\alpha + \delta \dot{\mathbf{r}}_\alpha, \quad (14)$$

where $\mathbf{V}_b$ is the translation velocity of the hydrodynamic center of resistance of the bacterial body, $\boldsymbol{\Omega}$ is the overall angular velocity of the body, and $\mathbf{r}'_\alpha$ is the relative position measured from the hydrodynamic center of the bacterial body. $\delta \dot{\mathbf{r}}_\alpha$ specifies the rotation of the flagellar bundle relative to the bacterial body at a controlled angular frequency. Although the numerical results successfully demonstrated the existence of bacterial wobbling, the model on bacteria with a single flagellar bundle failed to reproduce helical trajectories of large pitches ($> 4 \mu\text{m}$), which are frequently observed in experiments. Large-pitch trajectories could be generated by introducing multiple flagellar bundles in the model. However, although *B. subtilis* swimming with two flagellar bundles has been reported, experiments on *E. coli* only reported swimming with a single flagellar bundle [7, 10]. Multiple flagella or flagellar bundles lead to tumbling, instead of swimming.

Qu and Breuer has calculated the motility enhancement based on the off-axial configuration of a single bacterial bundle using a simplified scalar model in a recent study [11]. The speed enhancement in the model arises because of the change of the drag coefficients of bacterial body of different orientations. The model predicts less than 8% speed enhancement when the wobbling angle decreases over the full range from 90° down to 0° . In comparison, our experiments show 80% speed enhancement with the decrease of the wobble angle over a much smaller range from 45° to 25° . The calculation suggests that the ellipsoidal shape of bacterial body and the change of the drag coefficients due to different body orientations contribute little to the motility enhancement. The finding agrees with the general expectation of the creeping flow, where the effect of shape anisotropy is greatly mitigated due to the dominant effect of viscosity. Thus, for simplicity, we shall approximate the bacterial body as a sphere in our calculation below. Due to the large discrepancy between the model prediction and experiments, Qu and Breuer concluded that the reduction of wobbling is not the origin of the motility enhancement.

Nevertheless, both previous experiments on bacterial swimming in polymer

solutions and our experiments on bacterial swimming in colloidal suspensions showed that the decrease of wobbling angles is nearly linearly correlated with the increase of bacterial swimming speeds (Fig. 3b). Such a strong anticorrelation emerges not only at the average level but also at the level of individual bacteria, where an individual bacterium that has a larger wobble angle also exhibits a slower swimming speed, independent of whether the bacterium is in pure buffer or in suspensions (Extended Data Fig. 3a). In addition, a single bacterium shows simultaneously the increase of swimming speed and the decrease of the wobble angle when the bacterium swims next to a colloid (Supplementary Video). These observations together strongly suggest the causal relation between bacterial swimming and wobbling. Hence, the discrepancy between the existing wobbling models and the experimental observations on both the large-pitch trajectories and the strong motility enhancement suggests that our current understanding of the mechanism of bacterial wobbling is still incomplete. Here, we propose a new model of bacterial wobbling, which not only quantitatively explains the strong anticorrelation between bacterial wobbling angles and swimming speeds, but also produces large-pitch wobbling trajectories with a single flagellar bundle matching experimental observations. In addition, a symmetry breaking mechanism naturally arises from the model, which explains why the presence of colloids or polymer coils preferentially reduces bacterial wobbling. In the next section, we shall set up our model first.

3.2 Model description

Driven by the rotary flagellar motor, the bacterial body and the flagellar bundle rotate at angular velocities $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$, respectively (Extended Data Fig. 4b). $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$ are generally not colinear and form an angle α . We define a Cartesian coordinate, so that $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$ are in the y - z plane. $\boldsymbol{\omega}_t$ is along the negative z direction, whereas the two components of $\boldsymbol{\omega}_b$ are along the positive z direction and the negative y direction, respectively. Due to the misalignment of $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$, the bacterium must also rotate as a whole as a rigid body with an angular velocity $\boldsymbol{\omega}_{cm}$ in order to balance the torque. $\boldsymbol{\omega}_{cm}$ should be in the same plane as $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$. We name the plane formed by $\boldsymbol{\omega}_{cm}$, $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$ as the ω plane below. Together, the velocity of the surface point $\mathbf{r}$ of the body can be written as

$$\mathbf{v}_b(\mathbf{r}) = \mathbf{V}_b + \boldsymbol{\omega}_b \times (\mathbf{r} - \mathbf{r}_b) + \boldsymbol{\omega}_{cm} \times (\mathbf{r} - \mathbf{r}_b), \quad (15)$$

whereas the velocity of the surface point $\mathbf{r}$ of the flagellar bundle can be written as

$$\mathbf{v}_t(\mathbf{r}) = \mathbf{V}_b + \boldsymbol{\omega}_t \times (\mathbf{r} - \mathbf{r}_t) + \boldsymbol{\omega}_{cm} \times (\mathbf{r} - \mathbf{r}_b). \quad (16)$$

Here, $\mathbf{r}_b$ is the hydrodynamic center of resistance of the body and $\mathbf{r}_t$ is the hydrodynamic center of resistance of the flagellar bundle.

It is worth comparing our model with the minimal model proposed by Hyon and co-workers [6]. In the minimal model, the body rotation is represented by an overall angular velocity, which combines the rotation from the flagellar motor and the rotation induced by the thrust of the off-axial flagellar bundle, $\boldsymbol{\Omega} = \boldsymbol{\omega}_b + \boldsymbol{\omega}_{cm}$ (equation (14)). The rotation of the flagellar bundle specified by $\delta \dot{\mathbf{r}}_\alpha$ is then defined with respect to the overall body rotation $\boldsymbol{\Omega}$. In contrast, we distinguish the two different body rotations and their independent effects on the flagellar motion in our model. Although the self-rotation of the bacterial body $\boldsymbol{\omega}_b$ does correlate with the flagellar rotation $\boldsymbol{\omega}_t$ via a kinematic condition of the flagellar hook as we shall discuss momentarily, it does not dictate the flagellar rotation via a rigid-body-like rotation $\boldsymbol{\omega}_b \times (\mathbf{r} - \mathbf{r}_b)$ in our model. Instead, the flagellar bundle rotates only with the rigid-body part of the body rotation through $\boldsymbol{\omega}_{cm} \times (\mathbf{r} - \mathbf{r}_b)$ in our model (equation (16)). With the separation of $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_{cm}$, the axis of the helical bacterial trajectory should align with $\boldsymbol{\omega}_{cm}$, instead of the overall angular velocity $\boldsymbol{\Omega}$. Since a large part of the flagellar torque induced by $\boldsymbol{\omega}_t$ is balanced by the body self-rotation $\boldsymbol{\omega}_b$, the rigid-body rotation $\boldsymbol{\omega}_{cm}$ is significantly smaller than the overall angular velocity $\boldsymbol{\Omega}$ at a given motor torque. As the pitch of helical trajectories is given by $P \sim 1/\omega_{cm}$ (or $\sim 1/\Omega$ in the minimal model [6]), the pitch predicted by our model is much larger than that predicted by the minimal model, leading to better quantitative agreement with experiments (see Sec. 3.4 below). The extra degree of freedom introduced by the separation of $\boldsymbol{\Omega}$ into the two parts can be fixed by a kinematic condition. The detailed balance equation will be given below (equation (31)).

Instead of numerical solutions obtained previously in the minimal model, we aim to analytically solve the helical trajectory of bacteria of our model. Several standard approximations have been adapted to reduce the mathematical complexity. Boundary element calculation is only used to obtain the coefficients of resistance matrices. We also conduct a numerical simulation on the interaction between a wobbling bacterium and a colloid to demonstrate the symmetry breaking mechanism discussed in Sec. 3.4.5. In the next section, we shall first describe the detailed calculation of our model.

3.3 Calculation

Ignoring the hydrodynamic coupling between the bacterial body and the flagellar bundle [12, 13], we can calculate the force and torque on the bacterial body with respect to $\mathbf{r}_b$ as

$$\begin{pmatrix} \mathbf{F}_b \\ \boldsymbol{\tau}_b \end{pmatrix} = \begin{pmatrix} \xi_{TT}^b & 0 \\ 0 & \xi_{RR}^b \end{pmatrix} \begin{pmatrix} \mathbf{V}_b \\ \boldsymbol{\omega}_b + \boldsymbol{\omega}_{cm} \end{pmatrix}. \quad (17)$$

Similarly, the force and torque on the flagellar bundle with respect to $\mathbf{r}_t$ can be calculated as

$$\begin{pmatrix} \mathbf{F}'_t \\ \boldsymbol{\tau}'_t \end{pmatrix} = \begin{pmatrix} \xi_{TT}^t & \xi_{TR}^t \\ \xi_{RT}^t & \xi_{RR}^t \end{pmatrix} \begin{pmatrix} \mathbf{V}'_t \\ \boldsymbol{\omega}'_t + \boldsymbol{\omega}'_{cm} \end{pmatrix}. \quad (18)$$

Here, we use $'$ to indicate variables defined with respect to $\mathbf{r}_t$, whereas variables without $'$ are defined with respect to $\mathbf{r}_b$. While forces and angular velocities are independent of the choice of the reference point, torques and linear velocities depend on which reference point ($\mathbf{r}_b$ or $\mathbf{r}_t$) is used. Particularly, $\mathbf{F}'_t = \mathbf{F}_t$, $\boldsymbol{\omega}'_t = \boldsymbol{\omega}_t$ and $\boldsymbol{\omega}'_{cm} = \boldsymbol{\omega}_{cm}$, whereas $\boldsymbol{\tau}_t = \boldsymbol{\tau}'_t + (\mathbf{r}_t - \mathbf{r}_b) \times \mathbf{F}_t$. The rigid-body rotation further dictates

$$\mathbf{V}'_t = \mathbf{V}_b + \boldsymbol{\omega}_{cm} \times (\mathbf{r}_t - \mathbf{r}_b). \quad (19)$$

Different reference points are chosen in order to simplify the forms of the resistance matrices of the body and the flagellar bundle. In the present representation, the resistance matrices of the flagellar bundle have the simplest form:

$$\xi_{TT}^t = \mu \begin{pmatrix} a & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & b \end{pmatrix}, \quad \xi_{RR}^t = \mu \begin{pmatrix} c & 0 & 0 \\ 0 & c & 0 \\ 0 & 0 & d \end{pmatrix},$$

and

$$\xi_{TR}^t = (\xi_{RT}^t)^T = \mu \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & e \end{pmatrix}, \quad (20)$$

where $a = 13.9 \text{ } \mu\text{m}$, $b = 11.9 \text{ } \mu\text{m}$, $c = 86.5 \text{ } \mu\text{m}^3$, $d = 3.65 \text{ } \mu\text{m}^3$ and $e = 1.2 \text{ } \mu\text{m}^2$. $\mu = 1 \text{ mPa}\cdot\text{s}$ is the buffer viscosity. The forms of the matrices arise from the symmetry of the flagellar bundle. The sign of e in ξ_{TR}^t is determined by the chirality and the direction of the flagellar rotation. We obtain the values of the coefficients by numerically calculating the drag force and torque on a model

flagellar bundle of controlled linear and angular velocities using the method of Stokeslets, where the helical bundle has a radius $0.4 \mu\text{m}$ and two pitches of pitch length $2.0 \mu\text{m}$. The thickness of the flagellar bundle is $0.04 \mu\text{m}$. The resistance matrices of the bacterial body are

$$\xi_{TT}^b = \mu \begin{pmatrix} A & 0 & 0 \\ 0 & A & 0 \\ 0 & 0 & A \end{pmatrix} \quad \text{and} \quad \xi_{RR}^b = \mu \begin{pmatrix} B & 0 & 0 \\ 0 & B & 0 \\ 0 & 0 & B \end{pmatrix}, \quad (21)$$

where $A = 6\pi r_b$ and $B = 8\pi r_b^3$. Here, we approximate the body as a sphere with a radius of $r_b = 0.7 \mu\text{m}$. The aspect ratio of the body is small, which has a weak hydrodynamic effect in the creeping flow. As shown in the previous study [11], the effect of the shape of bacterial body on the speed enhancement is negligible. We have tested different bacterial geometries by changing the size of bacterial body and the shape of flagellar bundle within a biologically relevant range. The key predictions of our model including the size-dependence motility enhancement (Fig. 2) and the anti-correlation between wobble angle and swimming speed (Fig. 3) are robust and do not qualitatively change.

The force-free condition and the torque-free condition can be written as

$$\mathbf{F}_b = -\mathbf{F}_t = -\mathbf{F}'_t \quad (22)$$

and

$$\boldsymbol{\tau}_b = -\boldsymbol{\tau}_t = -\boldsymbol{\tau}'_t - (\mathbf{r}_t - \mathbf{r}_b) \times \mathbf{F}_t, \quad (23)$$

respectively. If we define $\mathbf{R} \equiv \mathbf{r}_t - \mathbf{r}_b = (R_x, R_y, R_z)$ and

$$\mathcal{R} \equiv \begin{pmatrix} 0 & -R_z & R_y \\ R_z & 0 & -R_x \\ -R_y & R_x & 0 \end{pmatrix}, \quad (24)$$

then

$$(\mathbf{r}_t - \mathbf{r}_b) \times \mathbf{X} = \mathcal{R} \cdot \mathbf{X}, \quad (25)$$

where $\mathbf{X}$ is an arbitrary vector. Since $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$ define the y - z plane, $R_x = 0$ in our calculation.

From the force-free condition (equations (22)) in combination with equations (17), (18) and (19) as well as the resistance matrices equation (20) and

(21), we have

$$\begin{pmatrix} A+a & 0 & 0 \\ 0 & A+a & 0 \\ 0 & 0 & A+b \end{pmatrix} \cdot \mathbf{V}_b - \begin{pmatrix} a & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & b \end{pmatrix} \cdot \mathcal{R} \cdot \boldsymbol{\omega}_{cm} = - \begin{pmatrix} 0 \\ 0 \\ e\omega_t \end{pmatrix}. \quad (26)$$

Here, we take the approximation $|\boldsymbol{\omega}_{cm}| \ll |\boldsymbol{\omega}_t|$ in the derivation, which we shall check later for consistence. Note that $\boldsymbol{\omega}_t = \omega_t \mathbf{i}_z$, where $\mathbf{i}_z$ is the unit vector along the z direction and $\omega_t < 0$. Similarly, using the torque-free condition (equation (23)), we have

$$\begin{pmatrix} A & 0 & 0 \\ 0 & A & 0 \\ 0 & 0 & A \end{pmatrix} \cdot \mathcal{R} \cdot \mathbf{V}_b - \begin{pmatrix} B+c & 0 & 0 \\ 0 & B+c & 0 \\ 0 & 0 & B+d \end{pmatrix} \cdot \boldsymbol{\omega}_{cm} = \begin{pmatrix} 0 \\ -B\omega_b \sin \alpha \\ eV_b^z + d\omega_t + B\omega_b \cos \alpha \end{pmatrix}, \quad (27)$$

where $\mathbf{V}_b = (V_b^x, V_b^y, V_b^z)$ and $\boldsymbol{\omega}_b = (0, -\omega_b \sin \alpha, \omega_b \cos \alpha)$ based on the definition of our coordinate system. The vector equations (26) and (27) can be solved for $\mathbf{V}_b$ and $\boldsymbol{\omega}_{cm}$ in the following order:

$$\begin{aligned} \omega_{cm}^x &= - \left(\frac{AR_y}{A+b} \right) (e\omega_t) \left[B+c + \frac{Ab}{A+b} R_y^2 + \frac{Aa}{A+a} R_z^2 \right]^{-1}, \\ V_b^y &= \frac{aR_z}{A+a} \omega_{cm}^x, \\ V_b^z &= - \frac{e\omega_t + bR_y \omega_{cm}^x}{A+b}, \\ \omega_{cm}^z &= \frac{\frac{Aa}{A+a} R_y R_z B \omega_b \sin \alpha - (eV_b^z + eR_y \omega_{cm}^x + d\omega_t + B\omega_b \cos \alpha) \left(B+c + \frac{Aa}{A+a} R_z^2 \right)}{\left(B+c + \frac{Aa}{A+a} R_z^2 \right) \left(B+d + \frac{Aa}{A+a} R_y^2 \right) - \left(\frac{Aa}{A+a} R_y R_z \right)^2}, \\ \omega_{cm}^y &= \frac{B\omega_b \sin \alpha \left(B+d + \frac{Aa}{A+a} R_y^2 \right) - \frac{Aa}{A+a} R_y R_z (eV_b^z + eR_y \omega_{cm}^x + d\omega_t + B\omega_b \cos \alpha)}{\left(B+c + \frac{Aa}{A+a} R_z^2 \right) \left(B+d + \frac{Aa}{A+a} R_y^2 \right) - \left(\frac{Aa}{A+a} R_y R_z \right)^2}, \\ V_b^x &= \frac{a}{A+a} (R_y \omega_{cm}^z - R_z \omega_{cm}^y). \end{aligned} \quad (28)$$

To reduce the mathematical complexity and reveal the key physics contained in equation (28), we take the following approximation on the configuration of the flagellar bundle. Since the linear size of bacterial body is much smaller than that of bacterial flagella, we approximate $|R_y|/|R_z| \ll 1$ in our calculation, which gives $|R_y| \ll |R_z| \sim \mathcal{O}(1) \mu\text{m}$. In other words, we assume that the

hydrodynamic center of the flagellar bundle is underneath the hydrodynamic center of the bacterial body. In this configuration, $R_y \approx 0$ and $R_z = -(r_b + l/2) \approx -2.5 \text{ } \mu\text{m}$, where r_b is the radius of the bacterial body and l is the length of the flagellar bundle. Under the approximation, equation (28) is greatly simplified,

$$\begin{aligned}
\omega_{cm}^x &= 0, \\
V_b^y &= 0, \\
V_b^z &= -\frac{e\omega_t}{A+b}, \\
\omega_{cm}^z &= -\frac{eV_b^z + d\omega_t + B\omega_b \cos \alpha}{B+d}, \\
\omega_{cm}^y &= \frac{B\omega_b \sin \alpha}{B+c + \frac{Aa}{A+a}R_z^2}, \\
V_b^x &= -\frac{a}{A+a}R_z\omega_{cm}^y.
\end{aligned} \tag{29}$$

To proceed further, we need to specify the relation between ω_b and ω_t . The flagellar hook connecting the body and the flagella is generally considered as a universal joint [7, 14, 15]. However, for the simplest realization of a universal joint, the rotational speed of the flagella would vary periodically with the rotation angle of the rotary motor, even when the motor rotates at a constant speed [16]. To simplify the problem, we assume that the projection of ω_b along the flagellum axis is proportional to ω_t , a relation that is consistent with a universal joint without the angle-dependent term,

$$\frac{\omega_b \cos \alpha}{\omega_t} = C. \tag{30}$$

This hypothesis agrees with the relation proposed in [15], which further determines the constant C via the torque balance along the flagellum axis of tethered bacteria,

$$\frac{\omega_b \cos \alpha}{\omega_t} = -\frac{d}{B}. \tag{31}$$

With Eq. (29) and the balance equation (31), the wobble angle of bacteria can be finally calculated as

$$\theta = \beta - \alpha. \tag{32}$$

Here, β is the angle of ω_{cm} with respect to the negative z direction (Extended

Data Fig. 4b), which is given as

$$\beta = \arctan\left(-\frac{\omega_{cm}^y}{\omega_{cm}^z}\right) = \arctan\left\{\frac{(A+a)(A+b)(B+d)d\tan\alpha}{[(A+a)(B+c)+AaR_z^2]e^2}\right\}. \quad (33)$$

The swimming speed of bacteria along the axis of the helical trajectory can be also calculated as

$$V = \frac{|\mathbf{V}_b \cdot \boldsymbol{\omega}_{cm}|}{|\boldsymbol{\omega}_{cm}|} = V_b^z \cos\beta = -\frac{C_1}{\sqrt{C_2}}\omega_t, \quad (34)$$

where

$$C_1 = \frac{e^3}{(A+b)^2(B+d)}$$

and

$$C_2 = \frac{\omega_{cm}^2}{\omega_t^2} = \left[\frac{(A+a)d\tan\alpha}{(A+a)(B+c)+AaR_z^2}\right]^2 + \left[\frac{e^2}{(A+b)(B+d)}\right]^2. \quad (35)$$

Note that V is the swimming speed of bacteria actually measured in experiments.

Lastly, the pitch of the wobbling trajectories can be calculated as

$$P = \frac{2\pi}{|\boldsymbol{\omega}_{cm}|}V = 2\pi\frac{C_1}{C_2}. \quad (36)$$

The radius of the wobbling trajectories can be calculated as

$$R_w = \frac{V_\perp}{|\boldsymbol{\omega}_{cm}|} = \frac{\sqrt{C_2C_3 - C_1^2}}{C_2}, \quad (37)$$

where $V_\perp = \sqrt{V_b^2 - V^2}$ and

$$C_3 = \left[\frac{adR_z\tan\alpha}{(B+c)(A+a)+AaR_z^2}\right]^2 + \left(\frac{e}{A+b}\right)^2. \quad (38)$$

Several points regarding the angular velocity of the flagellar bundle ω_t are worth of comments. First, the wobble angle θ , the pitch P and the radius R_w of bacterial trajectories are all independent of ω_t . The swimming speed V is linearly proportional to ω_t as dictated by the linearity of the creeping flow. If we assume the output torque of the flagellar motor is constant [13], the decrease of ω_t is less than 7% in our model when the wobble angle increases from 20° to 45° covering the range of the wobble angle observed in our experiments. Hence,

we can approximate ω_t as a constant, independent of the wobble angle. The constant ω_t is then canceled, when we compute the normalized velocity V/V_0 . Thus, when compared with experiments on V/V_0 , none of our model predictions depend on ω_t . Second, $|\boldsymbol{\omega}_{cm}|/|\boldsymbol{\omega}_t| < 0.012$ over the experimental range of the wobble angle, justifying our approximation in deriving equation (26). Lastly, we can fix the value of ω_t by matching the swimming speed of bacteria at the wobble angle of $\theta = 44.5^\circ$, i.e., the maximum wobble of the model (see Sec. 3.4.1 below), with the measured bacterial swimming speed in buffer at $\theta = 45^\circ$, $V_0 = 13 \mu\text{m/s}$. We obtain $\omega_t = 568.2 \text{ s}^{-1}$, which gives the rotational frequency of the flagellar bundle $f_t = \omega_t/(2\pi) = 90.4 \text{ Hz}$, agreeing well with the literature value on the order of 100 Hz [10]. This agreement validates the bacterial geometry and the coefficients of the resistance matrices used in our model.

3.4 Results and discussion

Without any free parameters, our model leads to several nontrivial predictions, quantitatively matching experiments.

3.4.1 Maximum wobble angle

First, we examine the relation between the misaligned angle α formed by $\boldsymbol{\omega}_b$ and $\boldsymbol{\omega}_t$ and the wobble angle θ (Extended Data Fig. 4c). Interestingly, $\theta(\alpha)$ is non-monotonic exhibiting a maximum wobble angle $\theta_{max} = 44.5^\circ$. The result provides a natural explanation on the existence of the maximum average wobble angle $\theta_0 = 45.1^\circ \pm 0.5^\circ$ observed for bacteria in pure buffer (Fig. 3a). θ_{max} is reached when $\alpha_{max} = 22.8^\circ$.

3.4.2 Anticorrelation between swimming speed and wobble angle

Equations (32) and (34) together form a parametric representation of the relation between the swimming speed $V(\alpha)$ and the wobble angle of bacteria $\theta(\alpha)$. Figure 3b and Extended Data Figure 4d compare our theoretical prediction with the experimental observation with and without normalizing the wobble angle, respectively. The quantitative agreement between our model and experiments unambiguously demonstrates the causal link between bacterial swimming speeds and wobble angles. Our model reveals the origin of the strong correlation between the two important swimming features of bacterial swimming.

3.4.3 Pitch and radius of wobbling trajectories

Furthermore, our model also predicts wobbling helical trajectories with large pitches for bacteria with a single flagellar bundle, which cannot be produced from the minimal model of bacterial wobbling [6]. Quantitatively, we find that the pitch P decreases with the wobble angle θ (Extended Data Fig. 5a). A limiting pitch of $\sim 65 \mu\text{m}$ is reached when the wobble angle approaches zero. Note that although the pitch is geometrically ill-defined for straight trajectories, equation (36) is still valid in this limit and provides the limiting pitch as $\mathbf{V}_b$ and $\boldsymbol{\omega}_{cm}$ approaching a colinear direction. In comparison, the limiting pitch of the minimal model is less than $4 \mu\text{m}$ for bacteria with a single flagellar bundle, which is much smaller than that observed in experiments [6]. To evaluate the probability distribution of the pitch of bacterial helical trajectories in buffer, we assume that the misaligned angle α follows a Gaussian distribution with a mean $\langle\alpha\rangle$ and a standard deviation σ_α , which reflects the natural cell-to-cell variation. $\langle\alpha\rangle$ can be determined from $\theta(\langle\alpha\rangle) = 44.5^\circ$ for bacteria swimming in buffer without colloids, whereas σ_α is fixed by the average standard deviation of θ from experimental measurements. $\langle\alpha\rangle = \alpha_{max} = 22.8^\circ$ and $\sigma_\alpha \approx 0.5\alpha_{max}$. Our model quantitatively predicts the experimentally measured probability distribution of the pitch of helical trajectories (Extended Data Fig. 5b).

Despite of the large pitches, the radius of wobbling trajectories R_w remains small in our model, consistent with the results of the minimal model and experiments [6]. R_w is non-monotonic with increasing θ (Extended Data Fig. 5a). A maximum wobbling radius $R_{w,max} = 5.2 \mu\text{m}$ is reached at $\theta = 35.5^\circ$ in our model. In comparison, the maximum wobbling radius from the minimal model is $R_{w,max} = 4.25 \mu\text{m}$. Experimental measurements show that most bacteria have small R_w , where the peak of the probability distribution of R_w is around $0.5 \mu\text{m}$ on the order of the width of bacteria (Fig. 2b of Ref. [6]).

3.4.4 Size-dependence of motility enhancement

We now incorporate the generic calculation of the boundary-induced torque (BIT) in Sec. 2 within the framework of our wobbling model. By combining the BIT calculation and the wobbling model, we quantitatively predict the size-dependent motility enhancement without recourse to the empirical fitting of $V(\theta)$.

First, colloids that can most effectively modify the wobble angle of a bacterium should be within in the ω plane (the y - z plane) outside the helical cylin-

der (Extended Data Fig. 6b). Thus, the component of the bacterial velocity determining the BIT should also be in the y - z plane. Because $V_b^y = 0$, this component is V_b^z . In other words, the relevant velocity for the BIT calculation is the component of the tangential velocity of the bacterium $\mathbf{V}_b$ projected along the direction of its flagellar bundle, i.e., $V_b^z = V_b^f$ as defined in Sec. 2.1. Note that $V_b^z = V_b = V$ when $\theta = 0$. Thus, our calculation in Sec. 2.1 does not change when replacing V_b with V_b^z . Since $V_b^z = -e\omega_t/(A + b)$ (equation (29)) and ω_t is approximately constant, V_b^z is constant independent of the wobble angle, justifying our assumption on the constant V_b^f in Sec. 2.1.

Second, because both ω_{cm}^x and ω_b^x are zero, the angular velocity of the bacterium normal to the ω plane must be zero. Thus, $\omega_1^x = 0$, agreeing with our assumption taken in deriving equation (9).

Lastly, the BIT directly reduces the misaligned angle α (Extended Data Fig. 6b), which in turn reduces the wobble angle θ . Thus, we need to modify the torque balance equation (equation (11)) by replacing θ with α and θ_0 with α_0

$$-K(\alpha - \alpha_0) = \frac{\pi}{5}\mu r_b^2 V_b \frac{\gamma(17 + 8\gamma)}{(1 + \gamma)^2} \ln \frac{r_b(1 + \gamma)}{2d}, \quad (39)$$

where $\alpha_0 \approx 23^\circ$ is the equilibrium misaligned angle in buffer. Equation (39) can be solved to reach $\gamma(\alpha)$, whereas equation (34) of the wobbling model further predicts $V(\alpha)$ (Extended Data Fig. 4d inset). Together, $V(\alpha)$ and $\gamma(\alpha)$ form a parametric representation of the size-dependent motility enhancement $V(\gamma)$, which quantitatively agrees with experiments (the red dashed line in Fig. 2). The bending stiffness $K = 8.5 \times 10^{-19}$ N·m with $C = 2.09$ is obtained, quantitatively similar to that obtained based on the empirical fitting with $K = 7.16 \times 10^{-19}$ N·m.

3.4.5 Symmetry breaking mechanism

Without considering detailed bacterium-colloid interactions, it is natural to assume that colloids or polymer coils in a dilute solution randomly distribute around a bacterium. Hence, the hydrodynamic interaction between the bacterium and particles discussed in Sec. 2.1 would promote and suppress bacterial wobbling with equal probabilities. Why does the interaction preferentially suppress the bacterial wobbling and enhance its motility? Here, we propose a symmetry breaking mechanism based on our model of bacterial wobbling, which explains why the encounter of a bacterium with a colloid likely decreases, in-

stead of increasing, the wobble angle of the bacterium. Two physical factors are needed for the symmetry breaking: (i) the unique 3D configuration of wobbling bacteria and (ii) the depletion of colloids from bacterial helical trajectories. We shall explain the two factors in turn.

- *Bacterial configuration in 3D.* To visualize the 3D configuration of a swimming bacterium with respect to its wobbling helical trajectory, we determine the position of the axis of the helical wobbling trajectory with respect to the ω plane, i.e., the plane formed by ω_b , ω_t and ω_{cm} . We denote the points on the helical axis as $\mathbf{r}_0$. By definition, we have

$$\mathbf{V}_\perp = \omega_{cm} \times (\mathbf{r}_b - \mathbf{r}_0), \quad (40)$$

where $\mathbf{V}_\perp = (V_b^x, V_b^z \sin \beta \cos \beta, V_b^z \sin^2 \beta)$ is the component of bacterial velocity $\mathbf{V}_b$ normal to the direction of ω_{cm} . Defining $(\mathbf{r}_b - \mathbf{r}_0) = (x, y, z)$, equation (40) gives

$$x = \frac{V_b^z \sin \beta \cos \beta}{\omega_{cm}^z}, \quad (41)$$

$$-\omega_{cm}^z y + \omega_{cm}^y z = V_b^x. \quad (42)$$

Since $V_b^z > 0$ and $\omega_{cm}^z < 0$, $x < 0$ from equation (41). Thus, the x component of $(\mathbf{r}_0 - \mathbf{r}_b)$ is positive. The helical axis must be in front of the ω plane in the positive x direction in the coordinate system defined in Extended Data Fig. 4b. To pin the position of the helical axis, we can simply calculate the coordinates of two points on the axis from equations (41) and (42):

$$\begin{pmatrix} x_1 \\ y_1 \\ z_1 \end{pmatrix} = \begin{pmatrix} V_b^z \sin \beta \cos \beta / \omega_{cm}^z \\ -V_b^x / \omega_{cm}^z \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} x_2 \\ y_2 \\ z_2 \end{pmatrix} = \begin{pmatrix} V_b^z \sin \beta \cos \beta / \omega_{cm}^z \\ 0 \\ V_b^x / \omega_{cm}^y \end{pmatrix}. \quad (43)$$

The line goes through the two points is parallel to ω_{cm} as expected.

Furthermore, we also have

$$(\omega_b \times \omega_t) \cdot \mathbf{V}_b = |\omega_b| |\omega_t| V_b^x > 0, \quad (44)$$

where we have used $V_b^x > 0$. Equation (44) shows that the vector spanned by the orientations of the bacterial body ω_b and the flagellar bundle ω_t forms an acute angle with the direction of the bacterial velocity.

Information provided by equations (43) and (44) is sufficient for us to draw the 3D configuration of the bacterium with respect to its helical trajectory (Extended Data Fig. 6a and b). The trajectory of the bacterium is a left-handed helix, which encloses a cylindrical space of radius R_w , which we shall refer to as the helical cylinder below. The helical cylinder naturally divides the originally uniform space into two regions: the inner region within the cylinder (the gray area in Extended Data Fig. 6a and b) and the outer region in the rest of the space. Importantly, the angle formed by ω_b and ω_t always faces towards the inner region. In other words, the bacterium clamps onto the helical cylinder.

- *Depletion of colloids from the cylindrical space enclosed by bacterial helical trajectories.* Next, we shall show that the long-range hydrodynamic flow induced by the swimming of the bacterium effectively depletes colloids in the inner region of the helical trajectory in front of the bacterium. As a result, the short-range lubrication interaction that leads to the boundary-induced torque (BIT) considered in Sec. 2 arises dominantly between the bacterium and colloids in the outer region at the side of the bacterium. The effect, in combination with the special bacterial configuration around the helical cylinder discussed above, breaks the symmetrical role of colloids and results in the reduction of wobbling.

It has been well established that the far-field flow field of swimming *E. coli* can be described as a pusher-type dipolar flow, where the flow moves away from the head and the tail of the bacterium and comes in towards the side of the bacterium (see e.g. Fig. 1 of [17]). As the radius of the helical cylinder R_w is small on the order of the width of bacteria, the time-average flow induced by a wobbling bacterium can still be accurately approximated by the dipolar flow. For small colloids, the motion of the colloids follows the local flow field of the bacterium. Thus, colloids in front of the bacterium in the inner region are advected away by the long-range dipolar flow and are depleted in the inner region. For large colloids that are almost immobile in the flow field of the bacterium, the hydrodynamic interaction between the bacterium and colloids will deflect the trajectory of the bacterium, so that the bacterium deviates from the colloids to avoid the direct collision onto the surface of colloids. In other words, large colloids reorient the bacterium before the bacterium touches the colloids. This can be clearly illustrated if we switch from the lab reference frame to the frame of the bacterium, where the center of the bacterial body sits at the origin and the orientation of the axis of the bacterial body is invariant. In the bacterium frame, the large colloids in front of the bacterium move away from the bacterium, similar to the case of small colloids. In fact, given the small

R_w , it is geometrically impossible for a large colloid to sit inside the inner region of the helical trajectory when the bacterium pass by the colloid. For colloids of intermediate sizes between the two limits, both colloids and the bacterium change their trajectories as they approach each other. The net effect again leads to the depletion the colloids in the inner region.

To verify the above picture, we directly simulate the pair dynamics of a wobbling bacterium and a colloid with hydrodynamic interactions. The detail of the simulation method can be found in Ref. [18]. The numerical results first show that free colloids of small and intermediate sizes that are initially within the inner region when the bacterium is far away are advected out to the outer region as the bacterium approaches the colloids (the top and middle rows of Extended Data Fig. 7). Moreover, we also perform simulations with a colloid of radius $1.5\text{ }\mu\text{m}$ pinned in the lab frame, mimicking our experiments with optical tweezers. Our simulations again show that the trajectory of the bacterium deviates from its original path as the bacterium approaches the immobile colloid. As a result, the colloid moves from the inner region to the outer region of bacterial helical trajectory *in the reference frame of the bacterium*, regardless the initial position of the colloid (the bottom row of Extended Data Fig. 7). Taken together, our simulations with colloids of different sizes directly verify the physical argument argued above. Wobbling bacteria effectively deplete colloids within the inner region of their helical trajectories, regardless the size of colloids or whether colloids are free or pinned. Note that although Extended Data Fig. 7 shows multiple trajectories of colloids with different initial positions in each plot, the scattering of only one single colloid by the bacterium is considered in each simulation run. The change of the swimming speed of bacteria during the bacterium-colloid scattering due to the long-range hydrodynamic interaction is less than a few percent and therefore negligible.

- *Symmetry breaking mechanism.* We have now established two crucial factors for the symmetry breaking. (i) Wobbling bacteria face towards the inner region of the helical trajectory and clamp onto the helical cylinder (Extended Data Fig. 6). (ii) Colloids are depleted from the inner region by the long-range hydrodynamic flow (Extended Data Fig. 7). The short-range lubrication interaction that results in the BIT arises from the interaction between bacteria and colloids in the outer region at the side of bacteria. Based on these two factors, it is straightforward to see from the geometry that the lubrication interaction between the bacterium and the outer colloids should always reduce the misaligned angle α and, therefore, suppresses the wobble angle θ (Extended Data Fig. 6b).

Specifically, the hydrodynamic interaction between bacteria and colloids that perturbs the uniform distribution of colloids around bacteria is long-ranged in nature. In contrast, the hydrodynamic interaction that induces the BIT on bacteria is the short-range lubrication interaction (see Sec. 2), which decays quickly with the distance between colloids and bacteria. Such a lubrication interaction only occurs when a colloid is very close to a bacterium next to the outer surface of the helical cylinder. As the opening between ω_b and ω_t (the angle $\pi - \alpha$ in Extended Data Fig. 6b) faces towards to the inner region of the helical cylinder away from the neighboring colloid outside the cylinder, the lubrication interaction between the bacterium and the colloid induces a torque on the bacterial body pointing into the paper of Extended Data Fig. 6b, which reduces the misaligned angle α and therefore the wobble angle θ . A colloid on the far side of the cylinder at a distance at least $2w$ away from the bacterium exerts a much weaker lubrication force on the bacterial body and therefore does not strongly affect the wobble angle. When the bacterium rotates 180° to the far side of the cylinder, the colloid on the far side now becomes the neighboring colloid. However, since ω_b and ω_t also rotate with the trajectory and the opening between ω_b and ω_t now faces away from the colloid after the rotation, the colloid again reduces the wobble angle. Therefore, as long as colloids are depleted from the inner region of the helical cylinder, which is enforced by the long-range hydrodynamic interaction, colloids always reduce the wobble angle and increase swimming speed. In short, the long-range hydrodynamic interaction perturbs the uniform distribution of free colloids around bacteria (but does not change bacterial speed), whereas the short-range lubrication interaction induces the BIT on bacterial body and reduces the wobbling angle of bacteria. This separation of the hydrodynamic interaction into the far-field long-range contribution and the near-field short-range lubrication contribution has been used in the study of the dynamics of colloidal suspensions [19] and in the study of bacterium-colloid interaction [20].

Thus, the unique wobbling dynamics, in combination with the hydrodynamic flow of swimming bacteria, breaks the translational symmetry of the random distribution colloidal suspensions around bacteria and results in the suppression of bacterial wobbling and the enhancement of bacterial motility.

This symmetry breaking mechanism qualitatively explains the sharp drop of the probability distribution of bacterial wobble angles near zero wobble angle in 4% colloidal suspensions (Extended Data Fig. 3b). As the wobble angle of bacteria approaches zero, bacteria swim in straighter lines. The radius of

the helical cylinder shrinks to zero correspondingly. While bacteria with large wobble angles interact only with colloids in the near side of the helical cylinder close to their body due to the short-range nature of the lubrication interaction (Extended Data Fig. 6b), bacteria with nearly zero wobble angle can interact both with colloids on the near side of the cylinder that reduce wobbling and with colloids on the far side of the cylinder that enhance wobbling. Thus, a colloid is equally likely to enhance or reduce the wobble angle of bacteria in this limit. The average effect of colloids on reducing wobbling vanishes as the wobble angle of bacteria approaches zero. Therefore, with increasing volume fraction of colloidal suspensions, the position of the peak of the probability distribution of bacterial wobble angles shifts towards smaller angles. However, the probability of finding bacteria without wobbling remains small, independent of whether there are colloids or not. As a result, the probability distribution drops sharply near zero wobble angle at high enough colloidal volume fractions (Extended Data Fig. 3b).

- *Interaction time.* Lastly, we may further estimate the interaction time between colloids and bacteria. Based on the simple dimensional analysis, the time scale for the interaction between a colloid and a bacterium should be $t_b = D/V$, where D is the diameter of the colloid and V is the swimming speed of the bacterium. A dimensionless time is needed in order to determine whether t_b is long or not for the rise of the BIT. Since the bacterium interacts with many colloids to maintain its steady-state wobble angle, t_b should be compared with the mean free flight time of the bacterium t_f , during which the bacterium swims freely without interacting with any colloids. Without the BIT, the wobble angle of the bacterium relaxes back to its equilibrium value during the free flight. t_f can be easily estimated geometrically as $t_f = \frac{2}{3} \frac{D}{V} \left(\frac{D}{2r_b + D} \right)^2 \frac{1}{\phi}$. Here, $2r_b$ is the width of bacteria and ϕ is the volume fraction of colloids. Hence, the dimensionless interaction time is given as

$$\frac{t_b}{t_f} = \frac{3}{2} \phi \left(\frac{2r_b}{D} + 1 \right)^2. \quad (45)$$

At a fixed ϕ , the relative interaction time becomes longer for smaller colloids. Although the absolute interaction time decreases for small colloids, the frequency of close encounters between bacteria and colloids increases. Even for large colloids of the order of the size of bacteria, $t_b/t_f \sim \mathcal{O}(1)$ when $\phi = \phi_{max} \approx 5\%$. The discussion above is solely based on the dimensional analysis and does not

consider the influence of the dipolar flow of bacteria on colloids. Under the dipolar flow, colloids in the front of bacteria are depleted and pushed away from bacteria, whereas colloids on the side of bacteria are pulled towards bacteria, which extends the time period of the close encounter between bacteria and colloids in a configuration favorable for wobbling reduction.

3.5 Conclusion

Without fitting parameters, our simple model of bacterial wobbling quantitatively predicts the key features of bacterial swimming. Specifically, the model shows the quantitative relations between the swimming speed V , the wobble angle θ , the pitch P and the radius R_w of wobbling trajectories, matching experimental measurements. In addition, the model provides a symmetry breaking mechanism explaining the dominant effect of colloids in suppressing bacterial wobbling. In combination with our calculation of the boundary-induced torque that applies for both colloids and polymer coils, the model gives a quantitative description of the motility enhancement of flagellated bacteria in dilute colloidal and polymeric fluids. Taken together, our experimental and theoretical results demonstrate that the colloidal nature of complex fluids plays the leading role in bacterial motility enhancement. To the best of our knowledge, none of the existing theories on bacterial motility enhancement can predict the 80% speed enhancement using physically relevant parameters. As such, our study solves two long-standing problems of bacterial locomotion at the same time, i.e., the origin of bacterial motility enhancement in complex fluids and the mechanism of bacterial wobbling in simple Newtonian fluids.

Finally, our current study is complementary to the extensive research in recent years on the enhanced diffusion of colloidal tracers in active bath of microswimmers [21, 22, 23, 24, 25]. Instead of probing the influence of bacterial swimming on the motion of colloids, we show here that the presence of low-concentration colloids can in turn profoundly modify the swimming behaviors of bacteria.

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