Gravitaxis of asymmetric self-propelled colloidal particles

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Many motile microorganisms adjust their swimming motion relative to the gravitational field and thus counteract sedimentation to the ground. This gravitactic behaviour is often the result of an inhomogeneous mass distribution, which aligns the microorganism similar to a buoy. However, it has been suggested that gravitaxis can also result from a geometric fore–rear asymmetry, typical for many self-propelling organisms. Despite several attempts, no conclusive evidence for such an asymmetry-induced gravitactic motion exists. Here, we study the motion of asymmetric self-propelled colloidal particles which have a homogeneous mass density and a well-defined shape. In experiments and by theoretical modelling, we demonstrate that a shape anisotropy alone is sufficient to induce gravitactic motion with either preferential upward or downward swimming. In addition, also trochoid-like trajectories transversal to the direction of gravity are observed.
Gravitaxis (known historically as geotaxis) describes the response of motile microorganisms to an external gravitational field and has been studied for several decades. In particular, negative gravitaxis, that is, a swimming motion opposed to a gravitational force $F_G$, is frequently observed for flagellates and ciliates such as *Chlamydomonas* or *Paramecium*. Since this ability enables microorganisms to counteract sedimentation, gravitaxis extends the range of their habitat and allows them to optimize their position in environments with spatial gradients. In case of photosynthetic habitat and allows them to optimize their position in environments with spatial gradients. To achieve a gravitactic motion, in general, a stable orientation of the microorganism relative to the gravitational field is required. While in some organisms such an alignment is likely to be dominated by an active physiological mechanism, its origin in other systems is still controversially discussed. It has been suggested that gravitaxis can also result from purely passive effects like, for example, an inhomogeneous mass density within the organism (bottom heaviness), which would lead to an alignment similar to that of a buoy in the ocean. (We use the term ‘gravitaxis’, which is not uniformly defined in the literature, also in the context of passive alignment effects.) Under such conditions, the organism’s alignment should be the same regardless whether it sediments downward or upward in a hypo- or hyperdensity medium, respectively, as indeed observed for pleuronectid larvae. However, corresponding experiments with immobilized *Paramecium* and gastrula larvae showed an alignment reversal for opposite sedimentation directions. This suggests another mechanical alignment mechanism that is caused by the organism’s fore–rear asymmetry.

To explore the role of shape asymmetry on the gravitactic behaviour and to avoid the presence of additional physiological mechanisms, in our experiments, we study the motion of colloidal micron-sized swimmers with asymmetric shapes in a gravitational field. The self-propulsion mechanism is based on diffusiophoresis, where a local chemical gradient is induced in the solvent around the microswimmer. It has been shown that the corresponding type of motion is similar to that of biological microorganisms. On the basis of our experimental and theoretical results, we demonstrate that a shape anisotropy alone is sufficient to induce gravitactic motion with either upward or downward swimming. In addition to straight trajectories, more complex swimming patterns are observed, where the swimmers perform a trochoid-like (that is, a generalized cycloid-like) motion transversal to the direction of gravity.

**Results**

**Experiments.** For our experiments we use asymmetric L-shaped microswimmers with arm lengths of 9 and 6 μm, respectively, and 3 μm thickness that are obtained by soft lithography (see Methods for details). To induce a self-diffusiophoretic motion, the particles are covered with a thin Au coating on the front side of the short arm, which leads to local heating on laser illumination with intensity $I$ (see Fig. 1d). When such particles are suspended in a binary mixture of water and 2,6-lutidine at critical composition, this heating causes a local demixing of the solvent that results in an intensity-dependent phoretic propulsion in the direction normal to the plane of the metal cap. To restrict the particle’s motion to two spatial dimensions, we use a sample cell with a height of 7 μm. Further details are provided in Methods. Variation of the gravitational force is achieved by mounting the sample cell on a microscope, which can be inclined by an angle $\alpha$ relative to the horizontal plane (see Fig. 1b).

**Passive sedimentation.** Figure 1a shows the measured orientation distribution $p(\phi)$ of a sedimenting passive L-shaped particle for $I = 0$ in a thin sample cell that was tilted by $\alpha = 10.67^\circ$ relative to the horizontal plane. The data show a clear maximum at the orientation angle $\phi = -34^\circ$, that is, the swimmer aligns slightly turned relative to the direction of gravity as schematically illustrated in Fig. 1b. A typical trajectory for such a sedimenting particle is plotted in Fig. 1c1. To estimate the effect of the Au layer on the particle orientation, we also performed sedimentation experiments for non-coated particles and did not find measurable deviations. This suggests that the alignment cannot be attributed to an inhomogeneous mass distribution. The observed alignment with the shorter arm at the bottom

![Figure 1](https://example.com/figure1.png)

**Figure 1 | Characterization of the experimental setup.** (a) Measured probability distribution $p(\phi)$ of the orientation $\phi$ of a passive L-shaped particle during sedimentation for an inclination angle $\alpha = 10.67^\circ$ (see sketch in b). (c) Experimental trajectories for the same inclination angle and increasing illumination intensity: (1) $I = 0$, (2–5) $0.6 \mu W \mu m^{-2} < I < 4.8 \mu W \mu m^{-2}$, (6) $I > 4.8 \mu W \mu m^{-2}$. All trajectories start at the origin of the graph (red bullet). The particle positions after 1 min each are marked by yellow diamonds (passive straight downward trajectory), orange squares (straight upward trajectories), green bullets (active tilted straight downward trajectory), and blue triangles (trochoid-like trajectory). (d) Geometrical sketch of an ideal L-shaped particle (the Au coating is indicated by the yellow line) with dimensions $a = 9 \mu m$ and $b = 3 \mu m$ and coordinates $x_{CM} = -2.25 \mu m$ and $y_{CM} = 3.75 \mu m$ of the centre of mass (CM) (with the origin of coordinates in the bottom right corner of the particle and when the Au coating is neglected).
(see Fig. 1b) is characteristic for sedimenting objects with homogeneous mass distribution and a fore–rear asymmetry\(^1\). This can easily be understood by considering an asymmetric dumbbell formed by two spheres with identical mass density but different radii \(R_1\) and \(R_2 > R_1\). The sedimentation speed of a single sphere with radius \(R\) due to gravitational and viscous forces is \(v \propto R^2\). Therefore, if hydrodynamic interactions between the spheres are ignored, the dumbbell experiences a viscous torque resulting in an alignment where the bigger sphere is below the smaller one\(^1\).

In Fig. 1c, we show the particle’s centre-of-mass motion in the \(x\)-\(y\) plane as a consequence of the self-propulsion acting normally to the Au coating (see Fig. 1d). When the self-propulsion is sufficiently high to overcome sedimentation, the particle performs a rather rectilinear motion in upward direction, that is, against gravity (negative gravitaxis\(^1\), see Fig. 1c.2–4). With increasing self-propulsion, that is, light intensity, the angle between the trajectory and the \(y\) axis increases until it exceeds 90°. For even higher intensities, interestingly, the particle performs an effective downward motion again (see Fig. 1c,5). It should be mentioned that in case of the above straight trajectories, the particle’s orientation \(\phi\) remains stable (apart from slight fluctuations) and shows a monotonic dependence on the illumination intensity (as will be discussed in more detail further below). Finally, for strong self-propulsion corresponding to high light intensity, the microswimmer performs a trochoid-like motion (see Fig. 1c,6).

To obtain a theoretical understanding of gravitaxis of asymmetric microswimmers, we first study the sedimentation of passive particles in a viscous solvent\(^29\) based on the Langevin equations

\[
\dot{r} = \beta \mathbf{D}_r \mathbf{F}_G + \zeta_r, \\
\dot{\phi} = \beta \mathbf{D}_\phi \mathbf{F}_G + \zeta_\phi,
\]

(1)

for the time-dependent centre-of-mass position \(\mathbf{r}(t) = (x(t), y(t))\) and orientation \(\phi(t)\) of a particle. Here, the gravitational force \(\mathbf{F}_G\), the translational short-time diffusion tensor \(\mathbf{D}_r\), the translational–rotational coupling vector \(\mathbf{D}_\phi\), the inverse effective thermal energy \(\beta = 1/(k_B T)\) and the Brownian noise terms \(\zeta_r\) and \(\zeta_\phi\) are involved (see Methods for details).

Neglecting the stochastic contributions in equation (1), one obtains the stable long-time particle orientation angle

\[
\phi_\infty \equiv \phi(t \to \infty) = - \arctan \left( \frac{D_c^\parallel}{D_c^\perp} \right),
\]

(2)

which only depends on the two coupling coefficients \(D_c^\parallel\) and \(D_c^\perp\) determined by the particle’s geometry.

**Swimming patterns under gravity.** Extending equation (1) to also account for the active motion of an asymmetric microswimmer yields (see Methods for a hydrodynamic derivation)

\[
\dot{r} = (P^*/b)(\mathbf{D}_r \mathbf{u}_r + \mathbf{D}_c \mathbf{u}_c) + \beta \mathbf{D}_r \mathbf{F}_G + \zeta_r,
\]

\[
\dot{\phi} = (P^*/b)(\ell \mathbf{D}_r + \mathbf{D}_c \cdot \mathbf{u}_c) + \beta \mathbf{D}_c \cdot \mathbf{F}_G + \zeta_\phi,
\]

(3)

(4)

where the dimensionless number \(P^*\) is the strength of the self-propulsion, \(b\) is a characteristic length of the L-shaped particle (see Fig. 1d), \(\ell\) denotes an effective lever arm (see Fig. 1d), and \(D_r\) is the rotational diffusion coefficient of the particle. As shown in Methods, one can view \(F = |F| = P^*/(b\ell)\) and \(M = |M| = F/\ell\) as an effective force (in \(\mathbf{u}_c\)-direction) and an effective torque (perpendicular to the L-shaped particle), respectively, describing the self-propulsion of the particle (see Fig. 1d). This concept is in line with other theoretical work that has been presented recently\(^30–33\). The above equations of motion are fully compatible with the fact that, apart from gravity, a self-propelled swimmer is force-free and torque-free (see Methods).

The self-propulsion strength \(P^*\) is obtained from the experiment by measuring the particle velocity (see Methods for details). The rotational motion of the microswimmer depends on the detailed asymmetry of the particle shape and is characterized by the effective lever arm \(\ell\) relative to the centre-of-mass position as the reference point (see Fig. 1d). Note that the choice of the reference point also changes the translational and coupling elements of the diffusion tensor. If the reference point does not coincide with the centre of mass of the particle, in the presence of a gravitational force an additional torque has to be considered in equation (4). In line with our experiments (see Fig. 1c), the noise-free asymptotic solutions of equations (3) and (4) are either straight (upward or downward) trajectories or periodic swimming paths. Up to a threshold value of \(P^*\), the effective torque originating from the self-propulsion (first term on the right-hand side of equation (4)) can be compensated by the gravitational torque (second term \(\beta \mathbf{D}_c \cdot \mathbf{F}_G\) on the right-hand side of equation (4)) so that there is no net rotation and the trajectories are straight. In this case, after a transient regime the particle orientation converges to

\[
\phi_\infty = - \arctan \left( \frac{D_c^\parallel}{D_c^\perp} \right) + \arcsin \left( - \frac{P^*}{\beta b F_G} \frac{D_c^\parallel + \ell \mathbf{D}_r}{\sqrt{\ell^2 + D_c^\parallel^2}} \right),
\]

(5)

with the magnitude of the gravitational force \(F_G = |\mathbf{F}_G|\). Obviously, \(\phi_\infty\) is a superposition of the passive case (first term on the right-hand side, cf. equation (2)) with a correction due to self-propulsion (second term on the right-hand side). The theoretical prediction given by equation (5) is visualized in Fig. 2 by the solid line, which is fitted to the experimental data (symbols) by using \(D_c^\parallel\) as fit parameter.

The restoring torque caused by gravity depends on the orientation of the particle and becomes maximal at the critical angle \(\phi_{crit} = \arctan(D_c^\parallel/D_c^\perp) - \pi\). According to equation (5), this...
corresponds to a critical self-propulsion strength

\[ P^{*}_{\text{crit}} = \beta b mg \sin \alpha \frac{\sqrt{D_{\perp}^{\perp} + D_{\parallel}^{\parallel}}}{D_{\perp} - \ell D_{R}} \]  

with the particle’s buoyant mass \( m \) and the gravity acceleration of earth \( g \approx 9.81 \text{ m s}^{-2} \). When \( P^* \) exceeds this critical value for a given inclination angle of the setup, the effective torque originating from the non-central drive can no longer be compensated by the restoring torque due to gravity (see equation (4)) so that \( \phi \neq 0 \) and a periodic motion occurs.

To apply our theory to the experiments, we use the values of the various parameters as shown in Table 1. All data are obtained from our measurements as described in Methods.

**Dynamical state diagram.** Depending on the self-propulsion strength \( P^* \) and the substrate inclination angle \( \alpha \), different types of motion occur (see Fig. 3a). (For clarity, we neglected the noise in Fig. 3, but we checked that noise changes the trajectories only marginally.) For very small values of \( P^* \), the particle performs straight downward swimming. The theoretical calculations reveal two regimes where on top of the downward motion either a small drift to the left or to the right is superimposed. For zero self-propulsion, this additional lateral drift originates from the difference \( D_{\perp} - D_{\parallel} \), between the translational diffusion coefficients, which is characteristic for non-spherical particles. Further increasing \( P^* \) results in negative gravitaxis, that is, straight upward swimming. Here, the vertical component of the self-propulsion counteracting gravity exceeds the strength of the gravitational force. For even higher \( P^* \), the velocity-dependent torque exerted on the particle further increases and leads to trajectories that are tilted more and more until a re-entrance to a straight downward motion with a drift to the right is observed. For the highest values of \( P^* \), the particle performs a trochoid-like motion. The critical self-propulsion \( P^{*}_{\text{crit}} \) for the transition from straight to trochoid-like motion as obtained analytically from equation (6) is indicated by a thick black line in Fig. 3a.

Indeed, the experimentally observed types of motion taken from Fig. 1c correspond to those in the theoretical state diagram. This is shown in Fig. 3b where we plotted the experimental data for \( \alpha = 10.67^\circ \) as a function of the self-propulsion strength \( P^* \). Apart from small deviations due to thermal fluctuations, quantitative agreement between experiment and theory is obtained.

**Discussion**

Our model allows to derive general criteria for the existence of negative gravitaxis, which are applicable to arbitrary particle shapes. For a continuous upward motion, first, the self-propulsion \( P^* \) trivially has to be strong enough to overcome gravity. Secondly, the net rotation of the particle must vanish, which is the case for \( P^* \leq P^{*}_{\text{crit}} \) (see equation (6)). Otherwise, for example, trochoid-like trajectories are observed. As shown in the state diagrams in Figs 3 and 4, the motional behaviour depends
sensitively on several parameters such as the strength of the self-propulsion and the length of the effective lever arm. This may also provide an explanation why gravitaxis is only observed for particular microorganisms as, for example, *Chlamydomonas reinhardtii* and why the gravitactic behaviour is subjected to large variations within a single population.7

In our experiments, the particles had an almost homogeneous mass distribution to reveal pure shape-induced gravitaxis. For real biological systems, gravitaxis is a combination of the shape-induced mechanism studied here and bottom heaviness resulting from an inhomogeneous mass distribution. In particular for eukaryotic cells, small mass inhomogeneities due to the nucleus or organella are rather likely. Bottom heaviness can straightforwardly be included in our modelling by an additional torque contribution and would support negative gravitaxis. Even for microorganisms with axial symmetry but fore–rear asymmetry1 like *Paramecium*, both the associated shape-dependent hydrodynamic friction and bottom heaviness contribute to gravitaxis so that the particle shape matters also in this special case.

In conclusion, our theory and experiments demonstrate that the presence of a gravitational field leads to straight downward and upward motion (gravitaxis) and also to trochoid-like trajectories of asymmetric self-propelled colloidal particles. On the basis of a set of Langevin equations, one can predict from the shape of a microswimmer, its mass distribution, and the geometry of the self-propulsion mechanism whether negative gravitaxis can occur. Although our study does not rule out additional physiological mechanisms for gravitaxis3,4,5, our results suggest that a swimming motion of biological microswimmers opposed to gravity can be entirely caused by a fore–rear asymmetry, that is, passive effects11. Such passive alignment mechanisms may also be useful in situations where directed motion of autonomous self-propelled objects is required as, for example, in applications where they serve as microshuttles for directed cargo delivery. Furthermore, their different response to a gravitational field could be utilized to sort microswimmers with respect to their shape and activity33.

**Methods**

**Experimental details.** Asymmetric L-shaped microswimmers were fabricated from photore sist SU-8 by photolithography. A 3-μm thick layer of SU-8 is spin coated onto a silicon wafer, soft baked for 80 s at 95 °C and then exposed to ultraviolet light through a photomask. After a postexposure bake at 95 °C for 140 s, the entire wafer with the attached particles is covered by a several-nm-thick Au coating. During this process, the substrate is aligned by a specific angle relative to the evaporation source. Depending on the chosen angle, the Au coating can selectively be applied to specific regions of the front sides of the short arms of the particles. Afterwards, the particles are released from the substrate by an ultrasonic treatment and suspended in a binary mixture of water and 2,6-lutidine at critical composition (28.6 mass percent of lutidine) that is kept several degrees below its lower critical point *Tc* = 34.1 °C. Time-dependent particle positions and orientations were acquired by video microscopy at a frame rate of 7.5 fps and stored for further analysis.

**Langevin equations for a sedimenting passive particle.** The Langevin equations for the centre-of-mass position *r*(t) and orientation ϕ(t) of an arbitrarily shaped passive particle that sediments under the gravitational force *F*₉ = (0, −mg sin α) are given by equation (1). The key quantities are the translational short-time diffusion tensor *D*ₜ = *D*₀ *u*ᵣ + *D*ₜ*: (*a*ᵣ + *u*ᵣ + *u*ₐ + *u*ₐ) + *D*₂ *u*ᵣ + *u*ₐ with ⊙ denoting the dyadic product and the translational–rotational coupling vector *D*ₗ = *D*ₗ*: *u*ᵣ + *D*ₗ*: *u*ₐ with the centre-of-mass position as reference point. The orientation vectors *u*ᵣ = (cos ϕ, sin ϕ) and *u*ₐ = (−sin ϕ, cos ϕ) are fixed in the body frame of the particle. (Notice that equation (1) could equivalently be written with friction coefficients instead of diffusion coefficients18.) In this article, we use the given representation since the diffusion coefficients can directly be obtained from our experiments. Finally, ϕ₀(t) and ϕ₁(t) are Gaussian noise terms of zero mean and variances (ϕ₀(t) ⊙ ϕ₀(t)) = 2 *D*₀ *D*₀, (ϕ₀(t) ⊙ ϕ₁(t)) = 2 *D*₀ *D*₁, and (ϕ₁(t) ⊙ ϕ₁(t)) = 2 *D*₁ *D*₁. Within this formalism, the specific particle shape enters via the translational diffusion coefficients *D*₀, *D*₁, and *D*₂, the rotational diffusion coefficients *D*₀, *D*₁, and the coupling coefficients *D*ₗ *D*ₗ and *D*ₗ *D*₁. The theory is adapted to describe the movement of a rigid L-shaped particle in three-dimensional Stokes flow as sketched in Fig. 5. A key assumption is that the width 2z of the arms of the particle is much smaller than the total arc length *L* ≈ a + 2b of the particle, where *a* and 2b are its arm lengths. Though *z* = 1.5 μm is only one order of magnitude smaller than *L* ≈ 15 μm in the experiments, the slenderness approximation ε ≪ 1 offers valuable fundamental insight into the effects of self-propulsion and gravity on the particle’s motion, as examined below.

The centreline position *x*(s) of the slender L-shaped particle is described by a parameter *s* with −2b ≤ s ≤ a:

\[
x(s) = r - r_{CM} + \begin{cases} \mathbf{a}_u, & \text{if } 0 < s \leq a, \\ \mathbf{a}_s, & \text{if } -2b \leq s \leq 0. \end{cases}
\]

Here, *r* is the centre-of-mass position of the particle, *a*₁ and *b* are unit vectors defining the particle’s frame of reference and *r*₂₃₄ = (a₁*a₂ + 4p*a₃)/(2L) is a vector from the point where the two arms meet at right angles to the
centre of mass (CM) (see Fig. 5). The fluid velocity on the particle surface is approximated by $\mathbf{x} + v_x(z)$, where $v_x(z)$ is a prescribed slip velocity averaged over the intersection line of the particle surface and the plane through the point $z$ adjacent to the centreline. Motivated by the slip flow generated near the Au coating in the experiments, we set $v_x = -V_x \mathbf{u}_x$ along the shorter arm ($-2b \leq z \leq 0$) and no slip (that is, $v_x = 0$) along the other arm. According to the leading-order terms in slender-body theory, the fluid velocity is related to the local force per unit length $f(z)$ on the particle surface and given by

$$\mathbf{x} + v_x = (\mathbf{1} + \mathbf{x}' \otimes \mathbf{x}') f$$

(8)

with the constant $c = \log(L(c))/({\Delta n})$, the identity matrix $\mathbf{1}$, the vector $\mathbf{x}' = \mathbf{0}$ or $\mathbf{3}$ that is locally tangent to the centreline and the dyadic product $\otimes$. The force density $f$ satisfies the integral constraints that the net force on the particle is the gravitational force,

$$\mathbf{F}_g = \int_{-2b}^{0} f \, dz,$$

(9)

and that the net torque relative to the centre of mass of the particle vanishes,

$$\mathbf{e}_z \cdot \int_{-2b}^{0} (-\mathbf{r}_{CM} + x'x') f \, dz$$

$$= \left\{ \begin{array}{ll} \mathbf{1} + \mathbf{u}_1 \otimes \mathbf{u}_1 - \mathbf{f} & \text{if } -2b \leq z \leq 0, \\ \mathbf{1} + \mathbf{u}_1 \otimes \mathbf{u}_1 + \mathbf{f} & \text{if } 0 < z \leq a, \end{array} \right.$$  

(10)

where $\mathbf{e}_z$ is the unit vector parallel to the $z$ axis. Thus, in the absence of gravity, the self-propelled particle is force-free and torque-free as required.

We differentiate equation (7) with respect to time and insert it into equation (8). This leads to

$$\dot{\mathbf{r}} + v_x = \frac{\phi}{c} \left( a^2 \mathbf{u}_1 \otimes \mathbf{u}_1 + 4b^2 \mathbf{u}_1 \right)$$

$$= \left\{ \begin{array}{ll} \mathbf{1} + \mathbf{u}_1 \otimes \mathbf{u}_1 - \mathbf{f} & \text{if } -2b \leq z \leq 0, \\ \mathbf{1} + \mathbf{u}_1 \otimes \mathbf{u}_1 + \mathbf{f} & \text{if } 0 < z \leq a, \end{array} \right.$$  

(11)

The $\mathbf{u}_1$ and $\mathbf{u}_1$ components of equation (11) are given by

$$\mathbf{u}_1 \cdot (\dot{\mathbf{r}} + v_x) + 2\frac{\phi}{c} = \left\{ \begin{array}{ll} 2\mathbf{c}_1 \cdot \mathbf{f} & \text{if } -2b \leq z \leq 0, \\ \mathbf{c}_1 \cdot \mathbf{f} + \phi & \text{if } 0 < z \leq a, \end{array} \right.$$  

(12)

and

$$\mathbf{u}_1 \cdot (\dot{\mathbf{r}} + v_x) + 2\frac{\phi}{c} = \left\{ \begin{array}{ll} \mathbf{c}_1 \cdot \mathbf{f} - \phi & \text{if } -2b \leq z \leq 0, \\ 2\mathbf{c}_1 \cdot \mathbf{f} & \text{if } 0 < z \leq a. \end{array} \right.$$  

(13)

After integrating equations (12) and (13) over $z$ from $-2b$ to $0$ and separately from $0$ to $a$, the unknown $\mathbf{f}$ can be eliminated using equations (9) and (10). This results in the system of ordinary differential equations

$$\dot{\mathbf{u}}_1 + \frac{\phi}{c} \left( \begin{array}{c} 2(a+b) \\ 0 \\ -a^2b/L \end{array} \right) = \left( \begin{array}{c} 0 \\ a+4b \\ -2ab^2/L \end{array} \right) \mathbf{u}_1 + \dot{\mathbf{r}}$$

(14)

with the constant $A = (8L^2 - 6ab(a^2 + 8b^2 - 6b^2(a + 16b^4))/(12L^2)$. It is important to note that the matrix $H$ is identical to the grand resistance matrix (also called ‘hydrodynamic friction tensor’) for a passive particle (see further below). Since equation (14) is given in the particle’s frame of reference, we next transform it to the laboratory frame by means of the rotation matrix

$$\mathbf{M}(\phi) = \begin{pmatrix} \cos \phi & -\sin \phi & 0 \\ \sin \phi & \cos \phi & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

(15)

As obtained from the hydrodynamic derivation, the generalized diffusion tensor

$$\mathbf{D} = \frac{1}{16} \mathbf{H}^{-1} = \begin{pmatrix} D_1 & D_2 & D_3 \\ D_2 & D_1 & D_3 \\ D_3 & D_3 & D_1 \end{pmatrix},$$

(16)

where $\beta = 1/(k_BT)$ is the inverse effective thermal energy, is determined by the parameters

$$D_1 = \frac{2a^2b^3 K}{L^2},$$

(17)

$$D_2 = \frac{2a^2b^3 K}{L^2},$$

(18)

$$D_3 = \frac{2a^2b^3 K}{L^2},$$

(19)

$$D_1 = \frac{2a^2b^3 K}{L^2},$$

(20)

$$D_2 = \frac{2a^2b^3 K}{L^2},$$

(21)

$$D_3 = \frac{2a^2b^3 K}{L^2},$$

(22)

with the constant $K = \frac{c}{L} \left( \frac{2(a+b)(a+4b)A}{-a^2b/L} \right)^{-1}$. For the comparison of the self-propelled particle with fluid slip $v_s = -V_x \mathbf{u}_x$ along the shorter arm is identical to the motion of a passive particle driven by a net external force $F = F_u = (2bV_a/c)\mathbf{u}_1$ and torque $M_{ext} = -(a+4b)F = -/E$ with the effective self-propulsion force $F = 2bV_a/E$ and the effective lever arm $\ell = -ab/L$. (Note that while the equations of motion of a self-propelled particle and an externally driven passive particle are the same in this case, the flow and pressure fields generated by the particles are different).

Consequently, the concept of effective forces and torques, where formally external (‘effective’) forces and torques that move with the self-propelled particle are used to model its self-propulsion, is justified and can be applied to facilitate the understanding of the dynamics of self-propelled particles.

Analysis of the experimental trajectories. For the interpretation of the experimental results in the context of the theoretical model, it is necessary to determine the self-propulsion strength $P^*$ for the various observed trajectories. This is achieved by means of the relation

$$P^* = \frac{v_o - \beta FC_u (D_1 - D_3)}{D_3} \sin \phi \cos \phi,$$

(29)

which is obtained from equation (3). It provides $P^*$ as a function of the measured centre-of-mass velocity $v_o$ in a direction. On the other hand, the gravitational force $F_G = mg$ size is easily adjustable inclination angle $\phi$ of the experimental setup.

**Determination of the experimental parameters.** For the comparison of the theory with our measurements, specific values of a number of parameters have to
be determined. These are the various diffusion and coupling coefficients, the effective lever arm and the buoyant mass of the particles. The translational and rotational diffusion coefficients \(D_T = 7.2 \times 10^{-7} \) μm² s⁻¹ and \(D_R = 8.1 \times 10^{-3} \) μm² s⁻¹ and \(D_b = 6.2 \times 10^{-4} \) s⁻¹ are obtained experimentally from short-time correlations of the particle trajectories for zero gravity. Since \(D_T\) is negligible compared with \(\tilde{D}_T\) and \(\tilde{D}_R\), we set \(\tilde{D}_T = 0\). The relation between the two coupling coefficients \(\tilde{D}_R\) and \(\tilde{D}_R\) is determined from sedimentation experiments with passive L-particles. The peak position \(\phi = 34°\) of the measured probability distribution \(P(\phi)\) (see arrow in Fig. 1a) implies \(\tilde{D}_R = 0.67D_T\) via equation (2). The only remaining open parameter is the absolute value of the coupling coefficient \(\tilde{D}_R\), which is used as fit parameter in Fig. 2. Best agreement of the experimental data with the theoretical prediction (see equation (3)) is achieved for \(\tilde{D}_R = 5.7 \times 10^{-5} \) μm² s⁻¹. The diffusion coefficients have also been calculated numerically by solving the Stokes equation and good agreement with the experimental values has been found. The influence of the substrate has been investigated for zero gravity. Since the effective self-propulsion force acting vertically on the centre of the front side of the short arm (see Fig. 1d), the buoyant mass \(m = 2.5 \times 10^{-14} \) kg is obtained by measuring the sedimentation velocity of passive particles.

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Author contributions

B.H., F.K., R.W., H.L. and C.B. designed the research, analysed the data and wrote the paper; B.H. and R.W. carried out the analytical calculations and the simulations; F.K. performed the experiments; D.T. provided the hydrodynamic derivation in the Methods section.

Additional information

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