Self-Starting Micromotors in a Bacterial Bath

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Micromotors pushed by biological entities, such as motile bacteria, constitute a fascinating way to convert chemical energy into mechanical work at the micrometer scale. Here we show, by using numerical simulations, that a properly designed asymmetric object can be spontaneously set into the desired motion when immersed in a chaotic bacterial bath. Our findings open the way to conceive new hybrid microdevices exploiting the mechanical power production of bacterial organisms. Moreover, the system provides an example of how, in contrast with equilibrium thermal baths, the irreversible chaotic motion of active particles can be rectified by asymmetric environments.

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Ensembles of animate organisms behave in a very rich and surprising way if compared to inanimate objects, such as atoms or molecules in a liquid. Everyone has been amazed by the cooperative motion of birds in a flock, fish in a school, or wildebeests in a herd [1,2]. Also at the micrometer scale elementary living organisms, like bacterial cells, show an extraordinary variety of behavior, such as collective motion [3–6], complex chemical-mediated motility or chemotaxis [7], spatiotemporal patterns [8], self-organized structures [9], and biofilms formation [10]. An important peculiarity of animate organisms is the fact that they can be self-propelled, using a variety of different mechanisms for this purpose [11]. Motile cilia and turned flagella are two examples of evolutionary tricks adopted by living organisms to accomplish the hard task of swimming at a low Reynolds number [12]. One can think about such ensembles of organisms as open systems, with a net incoming flux of energy (provided by nutrients) stored and converted into mechanical motion by irreversible processes happening inside the cell body. The resulting dynamics breaks time inversion symmetry so that asymmetric environments can result in directed motions which, in equilibrated Hamiltonian systems, would be forbidden by detailed balance [13,14]. A natural question then arises: is it possible to rectify such a nonequilibrium dynamics to propel microdevices?

Biological molecular motors constitute a fascinating mechanism to generate motion at the nanoscale [15,16]. When larger, micron sized, structures need propulsion, the preassembled motor units found in unicellular motile organism may offer several advantages over isolated proteins. In a recent experiment [17,18] bacterial driven micromotors have been assembled by biochemically attaching motile bacteria to a microrotary motor. Such procedures require the construction of narrow tracks to induce a unidirectional binding of bacterial cells onto the moving rotor with a consequent increased complexity in designs and limited number of working bacteria.

Here we numerically show that a properly designed asymmetric motor immersed in a chaotic bacterial bath can be spontaneously set into the desired motion. Our numerical findings suggest the possibility to construct new opportunely shaped microdevices able to exploit the propelling power of motile bacteria.

Spinning a bundle of helical flagella, bacteria such as *E. coli* may swim along their body axis with speeds of order 10 body lengths per second [19]. Decorrelation of velocity may occur via four different mechanisms: tumbling, Brownian motion, mechanical interactions, and hydrodynamic interactions. The first mechanism is a spontaneous tumble produced by a temporary reversal in the spinning direction of the flagellar motor [20]. Brownian motion can also be effective in producing diffusion of orientation and hence of propelling direction. Interactions with other bacteria can be mechanical, by direct contact, or hydrodynamic, via flow currents produced by the swimming motions. Trying to mimic the behavior of an elongated *E. coli* cell with a minimal model, we only retain the two most effective mechanisms, which are tumbling and mechanical interactions. Hydrodynamic interactions, occurring only through dipole or higher order multipoles, turn out to be effective only over short distances where mechanical interactions between elongated bodies are much more effective in reorienting the bacteria. We directly checked that including hydrodynamic interactions has a negligible effect on the mean squared displacement and on its crossover from ballistic to diffusive regimes.

Each cell is represented by an instantaneous position $\mathbf{r}_i$ and an orientation $\hat{\mathbf{e}}_i$ pointing in the free swimming direction. The elongated hard body of the cells (length l and thickness a) is modeled by the sum of p short-range repulsive potentials centered at equally spaced locations along the cell axis $\mathbf{r}_i^\beta = \mathbf{r}_i + d^\beta \hat{\mathbf{e}}_i$ with $\beta = 1,\ p$ and $d^\beta = (l-a)(2\beta - p - 1)/(2p-2)$. The neighboring cells will then act on the ith cell with a system of forces $\mathbf{F}_i^\beta$ applied at $\mathbf{r}_i^\beta$:

$$\mathbf{F}_i^{\beta} = \sum_{j\neq i,\gamma} \mathbf{f}(\mathbf{r}_i^{\beta} - \mathbf{r}_j^{\gamma}), \tag{1}$$

$$\mathbf{f}(\mathbf{r}) = \frac{A\mathbf{r}}{r^{n+2}}. \tag{2}$$

To such intercellular forces we added intracellular forces consisting of a constant linear propelling force f_0 (directing along $\hat{\mathbf{e}}_i$) which is only active in the *running* state and a random torque $\mathbf{T}_r$ which switches on during the *tumbling* state. The probability per unit time to switch in a tumbling state is constant and such as to give an average free run length of 10 cell lengths [19]. Introducing the state variable θ_i which is 0 in the running state and 1 during a tumbling event, the net forces and torques acting on the ith cell read

$$\mathbf{F}_i = f_0\hat{\mathbf{e}}_i(1-\theta_i) + \sum_{\beta}\mathbf{F}_i^{\beta}, \tag{3}$$

$$\mathbf{T}_i = \mathbf{T}_r\theta_i + \hat{\mathbf{e}}_i \times \sum_{\beta} d^{\beta}\mathbf{F}_i^{\beta}. \tag{4}$$

For the subsequent motion the rigid cell body is modeled as a prolate spheroid of aspect ratio $\alpha = a/l$. Therefore the center of mass and the angular velocities are [21]

$$\mathbf{V}_i = \mathbf{M}_i \cdot \mathbf{F}_i, \tag{5}$$

$$\mathbf{\Omega}_i = \mathbf{K}_i \cdot \mathbf{T}_i, \tag{6}$$

where

$$\mathbf{M}_i = m_{\parallel}\hat{\mathbf{e}}_i\hat{\mathbf{e}}_i + m_{\perp}(\mathbb{1} - \hat{\mathbf{e}}_i\hat{\mathbf{e}}_i), \tag{7}$$

$$\mathbf{K}_i = k_{\parallel}\hat{\mathbf{e}}_i\hat{\mathbf{e}}_i + k_{\perp}(\mathbb{1} - \hat{\mathbf{e}}_i\hat{\mathbf{e}}_i). \tag{8}$$

We choose the force coefficient A in such a way that two bacteria facing head to head on the same line would be in equilibrium at a distance $a = \alpha l$:

$$A/a^{n+1} = f_0 \Rightarrow A \simeq f_0 a^{n+1}. \tag{9}$$

We choose l as the unit length, $\tau = l/v_0$ as the unit of time (where $v_0 = m_{\parallel}f_0$ is the free swimming velocity), and $m_{\parallel}$ as the unit of mobility. When not specified, physical quantities will be expressed in reduced units. A planar geometry will be investigated in a box $L \times L$ with periodic boundary conditions. We will specialize to the case of $N = 1092$ bacteria with number density $\rho = N/L^2 = 0.945$, aspect ratio $\alpha = 1/2$, and potential parameters $p = 2$, $n = 12$. Mobility values are $m_{\parallel} = 1$, $m_{\perp} = 0.87$, $k_{\perp} = 4.8$ ($k_{\parallel}$ does not enter into the equation of motion, because $\mathbf{T}_i$ is perpendicular to $\hat{\mathbf{e}}_i$ in the planar geometry). We consider a micromotor immersed in the bacterial bath. The asymmetric micromotor is a gear with a sawtooth profile whose center of mass is kept fixed at the center of the box. The motor is free to rotate around its axis. Each of the p force centers, describing a single bacterium body, interacts with boundary walls through a force of the form in Eq. (2), where $\mathbf{r}$ is a vector perpendicular to the wall connecting the p centers to a point located at a distance $a/2$ behind the wall.

The resulting cell-boundary forces produce further force and torque terms in Eqs. (5) and (6), and a net fluctuating torque on the gear motor, whose angular velocity is then

$$\Omega_g = K_g T_g, \tag{10}$$

where T_g is the torque exerted by bacteria on the gear whose rotational mobility is K_g. We consider a gear with 8 teeth and internal (external) radius $R_{\text{int}} = 5$ ($R_{\text{ext}} = 8$). The gear mobility is estimated as that of a disk [21] of radius 6.5: $K_g = 1.9 \times 10^{-3}$. Equations of motion (5), (6), and (10) are numerically integrated by the Runge-Kutta method [22] for 2×10^5 steps (with time step $\delta t = 10^{-3}$). At $t = 0$ the bacteria are uniformly distributed in the space outside the external disc of radius R_{ext}.

We find that the micromotor starts to move spontaneously under the effects of pushing bacteria. A net unidirectional motion is observed, with a fluctuating angular velocity around a nonzero mean value. In Fig. 1 we show snapshots of the bacterial bath with a rotary micromotor at

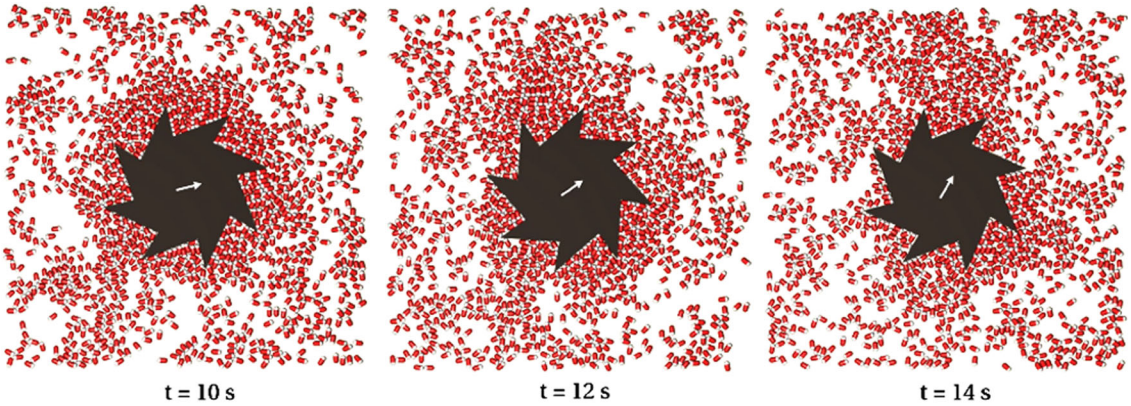

FIG. 1 (color online). Rotary micromotor in a bacterial bath. Snapshots are taken at three different simulation times, $t = 10$, 12, and 14 s. Each bacterium is represented by a spherocylinder (with aspect ratio 1:2) with a white head pointing in the direction of the self-propelling force. The arrow at the center of the gear evidences the counterclockwise rotation at an average angular velocity $\omega_0 \simeq 0.21$ rad/s.

three different times, $t = 10$, 12, and 14 s (physical units are obtained considering realistic values $l = 3$ μm, $v_0 = 30$ μm/s). A densification process close to the device's boundary is evident, in agreement with recent studies on self-propelled cells in confined environments [23,24]. As a result a net rotary counterclockwise motion of the gear during time takes place. The instantaneous angular velocity ω of the motor as a function of time is shown in Fig. 2, where the black line refers to single run, while the red (lighter) line is the average over 100 independent runs. After a short transient clockwise rotation the system reaches a stationary regime with a fluctuating positive (counterclockwise) angular velocity around a nonzero average value $\omega_0 \simeq 0.21$ rad/s, corresponding to 2.0 rpm. The total torque on the device can be estimated around 17 pN μm (assuming $m_{||} = 59$ μm/pN s). The onset of a directed rotation can be understood by analyzing the collision of a single bacterium with the rotor boundary. When a bacterium touches a rotor edge, it will exert a force given by the projection of the propelling force onto the surface normal (arrows in Fig. 3). The same force will act on the bacterium, producing a net torque that will align the cell body along the edge. Depending on the sign of the incident angle measured from the wall normal, the bacterium will then quickly leave the gear back into the solution [Fig. 3(a)] or get stuck at the corner exerting a torque on the rotor [Fig. 3(b)]. The same reasoning applies for both the long and short edges. Most of the collisions, however, will occur on the long edge, contributing a transient negative torque which explains the negative dip in rotor angular velocities observed at short times. It is worth noting that the elongated form of the bacteria is not essential for the observed effect, because the same directed motion of the micromotor also occurs in the presence of "spherical" bacteria, i.e., with aspect ratio $\alpha = 1$. The shape of the motor, instead, plays a crucial role. Indeed, simulations performed with a symmetric gear (with symmetrically shaped teeth) produce on average an immobile motor, whose angular velocity fluctuates around zero (inset in Fig. 2). The asymmetry is then a basic ingredient, as observed in many other thermal ratchet mechanisms discussed so far in the literature [25–27].

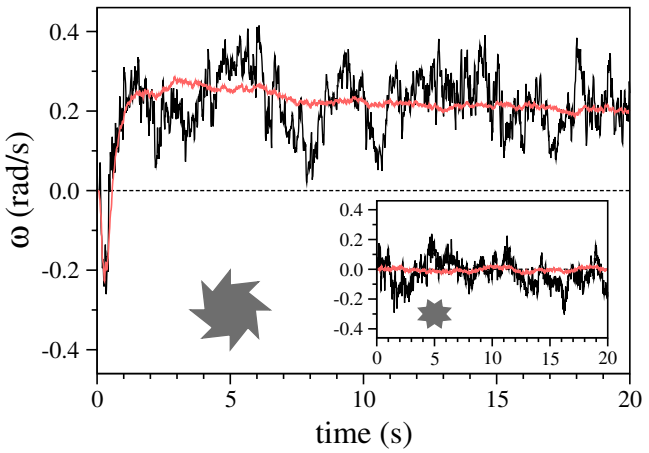

FIG. 2 (color online). Angular velocity ω (in rad/s) of the micromotor as a function of time (in seconds). The black line refers to a single run. The red (lighter) line is the average over 100 independent runs. After a short transient regime (due to initial configuration of bacteria), a fluctuating velocity around a mean value $\omega_0 \simeq 0.21$ rad/s is observed. Inset: same as main plot for a symmetrically shaped micromotor.

Given the above mechanism, one expects that the torque T_g exerted by bacteria would increase as the square of the size R of the rotor as both perimeter (and hence applied forces) and moment arm increase linearly. On the other hand, the rotational mobility of the gear K_g decreases as $1/R^3$, resulting in an average angular velocity decreasing as $1/R$. The maximal work that can be extracted from the bath is obtained when an external reversible system applies an opposing torque equal to $T_g/2$. The extracted mechanical power is then given by $T_g^2 K_g/4$ and increases with R. Therefore in a planar geometry, a two-dimensional array of small gears would perform better, in terms of usable power, than a single big one. The dependence on bacterial concentration is also nontrivial due to the interbacterial interactions that could result in reduced motilities at high packing fractions. We note that, however, the observed directed motion of the rotor is a quite robust effect with respect to the variation of different physical parameters, such as the density of bacteria, their aspect ratio, the shape of the asymmetric rotor, its size, and the boundary conditions (a quantitative discussion on the role of different parameters will appear in a forthcoming paper).

Our main point here is to demonstrate that, in contrast to thermal baths of passive particles, useful work can be extracted from the chaotic motion of a nonequilibrium suspension of active objects. This behavior reminds us of the ratchet effect or Brownian motors [26], in which out-of-equilibrium systems undergo a rectification process in the presence of some asymmetric potential or device. More specifically, in an equilibrated Hamiltonian system, there is

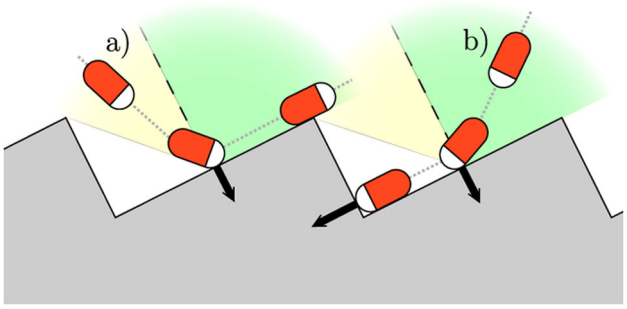

FIG. 3 (color online). Sketch of the collision of a single bacterium with the rotor boundary. Arrows are the forces exerted by the bacterium onto the rotor. (a) Bacteria coming from the left area with respect to the normal leave the gear. (b) Bacteria from the right get stuck at the corner exerting a torque on the rotor.

no entropy production, and time reversal symmetry guarantees that any trajectory has the same probability as its time reversed, so that no systematic directed motion can be observed on average. On the other hand when a self-propelled particle collides into another (or into a boundary), the forces they exchange are not just the repulsion of their rigid bodies—there are also the forces generated by the propelling units. Such forces are directed along the incoming directions of the two particles and therefore would change sign upon time reversal, while particles repulsion would not. Time reversed trajectories are then incompatible with the assumed dynamical laws. From a thermodynamic viewpoint such irreversible dynamics reflects the constant entropy production involved in the chemico-physical processes driving the propelling unit, such as the flagellar rotary motor of *E. coli*. Once time inversion symmetry does not hold, a broken spatial inversion symmetry can result in a spontaneous directed motion.

In conclusion, we have shown that it is possible to conceive opportunely shaped microdevices that can move in a directional way when immersed in a bath of motile microorganisms. In particular, we numerically show that a rotary micromotor, consisting of an asymmetric gear in a bath of *E. coli* bacteria, spontaneously sets into a unidirectional rotational motion at an average speed of a few rpm. Using asymmetrically shaped boundaries, linear translatory motions could be obtained and bacterial driven transport could be achieved by self-assembly of bacteria along the particle's boundary. Remarkably, when coupled to an external reversible device, a net amount of useful energy could be extracted from the chaotic motion of a bacterial bath. Our findings can open the way to new and fascinating applications in the field of hybrid biomicrodevices engineering, and also provide new insight into the more fundamental aspects of nonequilibrium dynamics of active matter.

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