Optimal Power Extraction from Active Particles with Hidden States

Luca Cocconi,1,2,* Jacob Knight,2 and Connor Roberts2

1The Francis Crick Institute, London NW1 1AT, United Kingdom
2Department of Mathematics, Imperial College London, South Kensington, London SW7 2BZ, United Kingdom

(Received 18 January 2023; revised 23 May 2023; accepted 12 October 2023; published 1 November 2023)

We identify generic protocols achieving optimal power extraction from a single active particle subject to continuous feedback control under the assumption that its spatial trajectory, but not its instantaneous self-propulsion force, is accessible to direct observation. Our Bayesian approach draws on the Onsager-Machlup path integral formalism and is exemplified in the cases of free run-and-tumble and active Ornstein-Uhlenbeck dynamics in one dimension. Such optimal protocols extract positive work even in models characterized by time-symmetric positional trajectories and thus vanishing informational entropy production rates. We argue that the theoretical bounds derived in this work are those against which the performance of realistic active matter engines should be compared.

DOI: 10.1103/PhysRevLett.131.188301

Macroscopic living creatures such as horses and oxen have been utilized by humans for millennia to do useful work. A question of current theoretical and practical interest is the extent to which energy can be efficiently harvested from microscopically active systems [1–6], whose motion is subject to non-negligible noise. The efficiency of existing many-particle microscopic active matter engines, such as turbines driven by the persistent motion of E. coli bacteria in solution [7–9], is heavily limited by the difficulty of rectifying the incoherent motion of collections of individual swimmers with weak alignment interactions in the bulk. Even under idealized conditions, where individual active particles can be manipulated independently, strict upper bounds on extractable power are not well understood, particularly when only a subset of the observables characterizing active motion are accessible to direct observation [10–12]. Here, we present a generic framework for the power extraction from a single active particle under continuous feedback control with the assumption that the instantaneous net velocity, \( \dot{x}(t) \), but not the fluctuating contribution originating from the self-propulsion, \( w(t) \), is observable. This is typically the case for realistic active matter engines [1,7]. Our Bayesian approach, which draws on the Onsager-Machlup path integral formalism [13], applies to a generic stochastic self-propulsion process and is illustrated in the cases of free run-and-tumble (RnT) [14] and active Ornstein-Uhlenbeck (AOU) [15] dynamics in one dimension.

Both models are characterized by time-symmetric positional trajectories (Supplemental Material, Sec. SI [16]) and thus vanishing informational entropy production rates (iEPR) [24,25], defined as the Kullback-Leibler divergence [26] per unit time of the ensemble of forward and their time-reversed counterparts [27,28].

In the Markovian case, where all degrees of freedom are observable, the iEPR is proportional to the thermodynamic dissipation and thus provides a (loose) upper bound to the extractable power. This relation fails to apply in the presence of hidden states [12,29,30]. Indeed, we show that positive average power extraction remains possible even for vanishing iEPR upon Bayesian inference of the hidden state (cf. [31], where it is argued that vanishing local iEPR implies zero extractable work). Measurement-driven protocols of the type we discuss in the following incur a thermodynamic maintenance cost [32,33], but are not constrained by Landauer’s principle in the same way as equilibrium information engines [6,34].

Definition of the optimal protocol.—Consider the overdamped Langevin equation for a generic active particle \( x(t) = w(t) + \gamma^{-1} F_{\text{ext}}(t) + \sqrt{2D_x} \xi(t) \), where \( \xi(t) \) is a white noise of unit covariance with associated diffusivity \( D_x \) and \( \gamma \) denotes the viscosity. We henceforth work in units whereby \( \gamma = 1 \). Here, \( w(t) \) is a stochastic self-propulsion velocity, which for the time being we take to be measurable by an external observer tasked with controlling the applied force \( F_{\text{ext}}(t) \). In practice, \( F_{\text{ext}}(t) \) could be implemented using an optical trap [34] or, for a charged active colloid [35], through an external electric field of time-varying magnitude and direction. Positive average work is readily extracted by applying an \( F_{\text{ext}}(t) \) smaller than and opposite to the particle’s self-propulsion [1,7,36]. Over a
duration $T$ this generates a noise-averaged total work by the particle against the known external force

$$
E_{\xi}[W_{\text{ext}}(F_{\text{ext}})] = - \int_0^T dt E_{\xi}[\dot{x}(t)]
$$

$$
= - \int_0^T dt F_{\text{ext}}(t)[w(t) + F_{\text{ext}}(t)],
$$

which constitutes the key observable of a hypothetical experiment. Above and henceforth, $E_{\phi}[\cdot]$ is used to denote an average with respect to the steady-state distribution of the random variable $\phi$. We will subsequently refer to $F_{\text{ext}}(t)$ as “the protocol.” The integrand of Eq. (1), corresponding to the instantaneous power output, can be maximized at each time $t$ by applying the protocol $F_{\text{ext}}(t) = -w(t)/2$. The corresponding steady-state average power output is

$$
\lim_{T \to \infty} \frac{E_{\xi}[W_{\text{tot}}(F_{\text{ext}})]}{T} = \frac{\tilde{\nu}^2}{4} + \frac{E_w[(w(t) - \tilde{\nu})^2]}{4},
$$

where $\tilde{\nu} \equiv E_w[w(t)]$ and we have invoked ergodicity to convert time averages to ensemble averages. The average power is smaller than the thermodynamic dissipation at $F_{\text{ext}} = 0$, given by $D_1 S_1 = E_w[w^2(t)]$ [37,38], demonstrating that the entropy production rate $S_1$ provides only a loose upper bound to the extractable power at low Reynolds number, due to the unavoidability of viscous effects when $\dot{x}(t) \neq 0$. We will henceforth refer to protocols $F_{\text{ext}}(t)$ achieving the maximum average power output allowed under a particular set of constraints as optimal.

Consider now the case where the underlying dynamics of the active particle (in the form of the full set of governing equations) are known but the instantaneous self-propulsion velocity $w(t)$ is not accessible to direct observation, i.e., it is a hidden variable. Naïvely, this suggests positive work extraction is unattainable since there is no immediate indication of which direction and magnitude should be chosen for $F_{\text{ext}}(t)$. However, since $w(t)$ can still be partially inferred from the history of $x(t)$, positive work can be extracted during transient periods of persistent motion. To see this, let $P(v(T) = \nu|\{x\}_0^T)$ denote the posterior probability density that the instantaneous self-propulsion velocity of the active particle at current time $T$ equals $v$ given a particular spatial trajectory $\{x\}_0^T$ has been observed. The expected work extracted during a time window of duration $T$ can be expressed as the following functional of the generic protocol $F_{\text{ext}}(t)$,

$$
E_{\xi,w}[W_{\text{ext}}(F_{\text{ext}})] = - \int_0^T dt \int_{-\infty}^{\infty} dv P(v|\{x\}_0^T)F_{\text{ext}}(t)[v + F_{\text{ext}}(t)].
$$

The optimal protocol $F_{\text{ext}}^*(t)$ is obtained from

$$
\delta E_{\xi,w}[W_{\text{ext}}(F_{\text{ext}})]/\delta F_{\text{ext}} = 0,
$$

FIG. 1. Optimal power extraction from an active particle (here visualized as a bacterium) with hidden self-propulsion velocity is achieved by subjecting the latter to continuous feedback control, whereby the magnitude and direction of the protocol $F_{\text{ext}}(t)$ are modulated according to the inferred self-propulsion velocity.

$$
F_{\text{ext}}^*(T) = -\frac{1}{2} \int_{-\infty}^{\infty} dv P(v|\{x\}_0^T)v = \frac{E_w[w(T)|\{x\}_0^T]}{2},
$$

cf. Eq. (2). In the following, we take $\tilde{\nu} = 0$ to focus on the nontrivial term appearing on the right-hand side of Eq. (5). Figure 1 schematizes the feedback control described above.

**Warm-up: The run-and-tumble particle.—**We have reduced the problem of identifying the optimal protocol to the evaluation of the posterior expectation $E_{\xi,w}[w(T)|\{x\}_0^T]$, Eq. (4). Now we proceed to show how this can be done for the case of RnT motion in one dimension, $\dot{x}(t) = \nu(T) + F_{\text{ext}}(t) + \sqrt{2D_1}\xi(t)$, whose binary internal self-propulsion mode $w(t)$ constitutes the simplest example of a state-space amenable to nontrivial coarse graining.

In particular, let $w(t) \in \{-1, 1\}$ be a dimensionless dichotomous noise with symmetric transition rate $\alpha$. We seek the posterior probability that the particle is a right self-propeller, $w(T) = +1$, given its positional trajectory up to the current time $T$, which we denote $P_+(T) = \mathbb{P}[w(T) = +1|\{x\}_0^T]$ for compactness. The complementary probability is denoted $P_-(T) = \mathbb{P}[w(T) = -1|\{x\}_0^T]$. Defining the
confidence parameter \( Q\{\{x\}_0^T\} = \log(P_+(T)/P_-(T)) \) and using \( P_+(T) + P_-(T) = 1 \), we can write

\[
P_+(T) = \frac{e^Q}{1+e^Q} = \frac{1+e^{Q-1}}{2(1+e^{Q-1})}.
\]

Equation (6) reduces to the prior probability \( P(w = \pm 1) = 1/2 \) when \( Q = 0 \). To calculate \( P_+(T) \) via \( Q \) we thus need to find an expression for the ratio of the conditional path probabilities. To do so, we first invoke Bayes’ theorem,

\[
P[w(T) = \pm 1|\{x\}_0^T] = \frac{\mathbb{P}\{\{x\}_0^T|w(T) = \pm 1\} \mathbb{P}[\{x\}_0^T]}{2\mathbb{P}[\{x\}_0^T]},
\]

where we have used \( \mathbb{P}[w(T) = \pm 1] = 1/2 \). We can equivalently write

\[
Q\{\{x\}_0^T\} = \log \frac{\mathbb{P}[\{x\}_0^T|w(T) = +1]}{\mathbb{P}[\{x\}_0^T|w(T) = -1]},
\]

reminiscent of a stochastic entropy [28]. We now introduce the notation for the average with respect to the distribution of \( w(t) \) path probabilities conditioned on a particular final value \( w(T) \),

\[
\mathbb{e}(v) \equiv \int \mathcal{D}w \cdot \mathbb{P}[\{w(t)\}_0^T|w(T) = v],
\]

which allows us to express the path probabilities in Eq. (8) as

\[
\mathbb{P}[\{x\}_0^T|w(T) = +1] = \mathbb{P}[\{x\}_0^T|\{w\}_0^T]_{(+1)},
\]

\[
\mathbb{P}[\{x\}_0^T|w(T) = -1] = \mathbb{P}[\{x\}_0^T|\{w\}_0^T]_{(-1)}.
\]

Finally, we invoke the Onsager-Machlup path integral form [13] of the conditional path probability in the Stratonovich discretization

\[
\mathbb{P}[\{x\}_0^T|\{w\}_0^T] \propto \exp \left( -\frac{1}{4D_x} \int_0^T dt (\dot{x}_c(t) - \nu w(t))^2 \right),
\]

where \( \dot{x}_c = \dot{x} - F_{\text{ext}} \) denotes the velocity in the reference frame where the externally imposed drift is subtracted away. Substituting Eq. (11) into Eq. (10), combining the resulting expressions with Eq. (8), and canceling common \( w(t) \)-independent factors appearing in the numerator and denominator, we eventually arrive at

\[
Q\{\{x\}_0^T\} = \log \frac{\exp \left( \frac{\nu}{2D_x} \int_0^T dt \dot{x}_c(t) w(t) \right)_{(+1)}}{\exp \left( \frac{\nu}{2D_x} \int_0^T dt \dot{x}_c(t) w(t) \right)_{(-1)}},
\]

where we have also used \( w^2(t) = 1 \) for all \( t \in [0, T] \). To make further progress we exploit the identity between the logarithm of a moment-generating function and its cumulant-generating function [39,40], as well as the parity of the cumulants (see Supplemental Material, Sec. SII [16]). This leads to

\[
Q\{\{x\}_0^T\} = \sum_{\kappa=0}^{\infty} \frac{P_{\text{e}}^{\kappa}}{2\kappa-1} \mathbb{E}[\{z\}_0^T]_{(+1)c},
\]

with Péclet number \( P_{\text{e}} = \nu^2/(D_c \alpha) \) and

\[
\mathbb{E}[\{z\}_0^T] = \int_0^T dt_1 \ldots dt_n \prod_{i=1}^n \left( \frac{\dot{x}_c(t_i) \alpha}{\nu} \right) w(t_i),
\]

where the superscript \( c \) in expectations, e.g., \( z^{(c)} \), denotes the corresponding cumulant. Substituting Eq. (13) into Eq. (6), combined with Eq. (4), returns the optimal protocol.

Computing the right-hand side of Eq. (13) is unfeasible in general. However, \( Q\{\{x\}_0^T\} \) can be computed analytically in the low-Péclet asymptotic regime. To leading order in \( P_{\text{e}} \ll 1 \), only the first cumulant \( \mathbb{E}[\{z\}_0^T]_{(+1)c} \) is required, which in turn draws on \( w(t)_{(+1)c} = w(t)_{(+1)} \) = \( \exp[-2\alpha(T-t)] \), Supplemental Material, Sec. SII [16], whence we find

\[
Q\{\{x\}_0^T\} = P_{\text{e}} \int_0^T dt \left( \frac{\dot{x}_c(t)}{\nu} \right) e^{-2\alpha(T-t)} + O(P_{\text{e}}^3).
\]

In order to conveniently apply the optimal protocol under continuous feedback control, we can differentiate Eq. (15) with respect to \( T \) and use the Leibniz integration rule [assuming \( \dot{x}_c(t) = 0 \) for \( t < 0 \)] to obtain a differential equation for the time evolution of \( Q \), i.e.,

\[
\dot{Q}(T) = \nu \dot{x}_c(T)/D_x - 2\alpha Q(T).
\]

Remarkably, upon substituting for \( \dot{x}_c \) and rescaling time by the switching rate, \( T' = \alpha T \), the Langevin equation for \( Q(T') \) reads like that of a RnT particle in a harmonic potential with self-propulsion speed and diffusivity both equal to the Péclet number, i.e.,

\[
\frac{dQ(T')}{dT'} = P_{\text{e}} w(T') - 2Q(T') + \sqrt{2P_{\text{e}} \xi(T')}.
\]

We now proceed to make the connection with the rate of work extraction. First of all, we have by combining Eqs. (4) and (6) that the optimal protocol is given to leading order in \( Q \sim P_{\text{e}} \) by \( F_{\text{opt}}^{\kappa}(T) = -\left( \nu^2/4Q + O(Q^2) \right) \). When the optimal protocol is applied at all times, the resulting noise-averaged power output, Eq. (5), is given by

\[
\mathbb{E}_\xi[\dot{w}_{\text{RnT}}(F_{\text{opt}}^{\kappa}(t))] = \nu^2 Q^2(T)/16 + O(P_{\text{e}}^2).
\]

Taking a further expectation with respect to the dichotomous noise \( w(t) \) and exploiting the mapping of the Q dynamics onto those of a RnT particle in a harmonic potential, Eq. (16), whence

\[
\mathbb{E}_\xi[Q^2] = (1 + P_{\text{e}}^4)/2P_{\text{e}}^2 \ [14],
\]

we eventually arrive at
which constitutes a tight upper bound to the average extractable power from a RnT particle with hidden self-propulsion velocity in the low-Pe regime. Higher moments of the fluctuating power output under \(F_{\text{ext}}^*\) can be computed similarly, see Supplemental Material, Sec. SIII [16].

A boundary-update protocol.—We further introduce an independent approach to computing the posterior probability \(P_v(T)\) in real time. This novel “boundary-update” protocol, described in full detail in Supplemental Material Sec. SVI [16], both saturates the bound (17) and is conjectured to achieve optimality for all Pe. It draws on the conditional splitting probabilities of the RnT process, which, to the best of our knowledge, we compute here for the first time. These are the probabilities that a particle initialized at \(x_0 \in [-(L/2), L/2]\) in a given statistical superposition of internal states exits said interval through either the left or right boundary in either a left or right self-propulsion state. Knowledge of the splitting statistics is used in combination with Bayes’ theorem to update the posterior distribution of the internal state \(w(t)\) each time the particle is observed to undergo a net displacement larger than \(L/2\) in the reference frame where the deterministic drift is subtracted away, \(\dot{x}_c = x - F_{\text{ext}}\). In the limit \(L \to 0\), the posterior updating frequency diverges and we conjecture that optimal inference is achieved. Figure 2 shows application of the boundary-update approach indeed produces an average power output matching the bounds Eqs. (17) and (2) in the low- and high-Pe limits, respectively.

\[
E_{\xi, w} [\dot{W}_{\text{RnT}} (F_{\text{ext}}^*)] = \frac{L^2 \text{Pe}}{4} + \mathcal{O}(\text{Pe}^2), \tag{17}
\]

...
The form of Eq. (22) matches the RnT result, Eq. (15), except for the appearance of a term depending on the second-order cumulant \( \omega^2(t) \), which was absent in the RnT case due to the norm of the self-propulsion velocity being constant. The correlation functions of the hidden state \( w(t) \) in Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

In Supplemental Material, Sec. SIV [16], we apply the Onsager-Machlup formalism to the AOU process (as defined in Supplemental Material, Sec. SIV [16]), allowing us to explore the high-Pe asymptote. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

In Supplemental Material, Sec. SIV [16], we apply the Onsager-Machlup formalism to the AOU process (as defined in Supplemental Material, Sec. SIV [16]), allowing us to explore the high-Pe asymptote. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

In Supplemental Material, Sec. SIV [16], we apply the Onsager-Machlup formalism to the AOU process (as defined in Supplemental Material, Sec. SIV [16]), allowing us to explore the high-Pe asymptote. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

In Supplemental Material, Sec. SIV [16], we apply the Onsager-Machlup formalism to the AOU process (as defined in Supplemental Material, Sec. SIV [16]), allowing us to explore the high-Pe asymptote. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.

Langevin dynamics: High-Pe asymptotics.—When the dynamics of \( w(t) \) are described by a Langevin process, Eq. (18) also allows us to explore the high-Pe asymptote through a saddle-point expansion. For the particular case of the AOU process (as defined in Supplemental Material, Sec. SIV [16]), we can write, using the Onsager-Machlup formalism, the form of Eq. (22) can be reconstructed from observable trajectories (see Supplemental Material, Sec. SIV [16]), allowing us to relax \( a \) posteriori the requirement that the equations governing the dynamics of \( w(t) \) be known, and to extract work even in this case.
Conclusion.—We have identified generic continuous feedback protocols achieving maximum average power extraction from active particles with a (zero-mean) hidden self-propulsion state. These optimal protocols can be written in closed form in the asymptotes $\text{Pe} \ll 1$ and $\text{Pe} \gg 1$, and provide upper bounds to the average extractable work by any such protocol (cf. [6]), e.g., Eqs. (17), (23), and (31). These bounds are those against which the performance of autonomous active matter engines, which typically do not have access to the self-propulsion states of the individual constituent particles [1,2], should be compared. Furthermore, our “boundary-update” approach enables work extraction in experimental settings where real-time particle tracking is unfeasible, since only the detection of first-passage events is required for its implementation.

The optimal protocol is generally non-Markovian. However, this difficulty can be circumvented at $\text{Pe} \ll 1$ by embedding the dynamics in a higher dimensional phase space [42], e.g., via the auxiliary dynamics in Eq. (16). Analogously to equilibrium information engines [6,34], the thermodynamic cost of operating the feedback control can be identified with the increase in the total entropy production rate upon expanding the phase space to include such auxiliary variables [17]. In an idealized situation where the operating temperature of the measurement device is arbitrary, and can thus be chosen to be arbitrarily small, the associated dissipation is negligible [34]. The unique utility of information engines operating on active particles arises from their nonvanishing efficiency even when the measurement device and the particle are coupled to the same heat bath [6]. Future work will characterize the efficiency of the optimal protocols in this case.

The authors thank Gunnar Pruessner, Farid Kaveh, Henry Alston, and Zigan Zhen for useful discussions, and Yuning Chen for contributing to the schematic in Fig. 1. L. C. acknowledges support from the Francis Crick Institute, which receives its core funding from Cancer Research UK, the UK Medical Research Council, and the Wellcome Trust (FC001317). J. K. and C. R. acknowledge support from the Engineering and Physical Sciences Research Council (Grants No. 2620369 and No. 2478322, respectively).

.canvas-fade

PHYSICAL REVIEW LETTERS 131, 188301 (2023)

1. L. C. acknowledges support from the Francis Crick Institute, which receives its core funding from Cancer Research UK, the UK Medical Research Council, and the Wellcome Trust (FC001317). J. K. and C. R. acknowledge support from the Engineering and Physical Sciences Research Council (Grants No. 2620369 and No. 2478322, respectively).

1*luca.cocconi@ds.mpg.de

Present address: Max Planck Institute for Dynamics and Self-Organization (MPIDS), 37077 Göttingen, Germany.

[1] P. Pietzonka, É. Fodor, C. Lohrmann, M. E. Cates, and U. Seifert, Autonomous engines driven by active matter: Energetics and design principles, Phys. Rev. X 9, 041032 (2019).

[2] I. A. Martínez, É. Roldán, L. Dinis, and R. A. Rica, Colloidal heat engines: A review, Soft Matter 13, 22 (2017).

[3] I. A. Martínez, É. Roldán, L. Dinis, D. Petrov, J. M. Parrondo, and R. A. Rica, Brownian Carnot engine, Nat. Phys. 12, 67 (2016).

[4] T. Speck, Efficiency of isothermal active matter engines: Strong driving beats weak driving, Phys. Rev. E 105, L012601 (2022).

[5] A.-K. Pumm, W. Engelen, E. Kopperger, J. Isensee, M. Vogt, V. Kozina, M. Kube, M. N. Honemann, E. Bertosin, M. Langecker et al., A DNA origami rotary ratchet motor, Nature (London) 607, 492 (2022).

[6] P. Malgaretti and H. Stark, Szilard engines and information-based work extraction for active systems, Phys. Rev. Lett. 129, 228005 (2022).

[7] R. Di Leonardo, L. Angelani, D. Dell’Arciprete, G. Ruocco, V. Iebba, S. Schippa, M. P. Conte, F. Mecarini, F. De Angelis, and E. Di Fabrizio, Bacterial ratchet motors, Proc. Natl. Acad. Sci. U.S.A. 107, 9541 (2010).

[8] S. P. Thampi, A. Doostmohammadi, T. N. Shendruk, R. Golestanian, and J. M. Yeomans, Active micromachines: Microfluidics powered by mesoscale turbulence, Sci. Adv. 2, e1501854 (2016).

[9] W. Pönisch and V. Zaburdaev, A pili-driven bacterial turbine, Front. Phys. 10, 875687 (2022).

[10] Z. Zhen and G. Pruessner, Optimal ratchet potentials for run-and-tumble particles, arXiv:2204.04070.

[11] F. Berger, T. Schmiedl, and U. Seifert, Optimal potentials for temperature ratchets, Phys. Rev. E 79, 031118 (2009).

[12] M. Esposito, Stochastic thermodynamics under coarse graining, Phys. Rev. E 85, 041125 (2012).

[13] L. Onsager and S. Machlup, Fluctuations and irreversible processes, Phys. Rev. 91, 1505 (1953).

[14] R. García-Millan and G. Pruessner, Run-and-tumble motion in a harmonic potential: Field theory and entropy production, J. Stat. Mech. (2021) 063203.

[15] D. Martin, J. O’Byrne, M. E. Cates, É. Fodor, C. Nardini, J. Tailleur, and F. van Wijland, Statistical mechanics of active Ornstein-Uhlenbeck particles, Phys. Rev. E 103, 032607 (2021).

[16] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.131.188301 for detailed derivations and further discussion, which includes Refs. [17–23].

[17] S. A. Loos and S. H. Klapp, Irreversibility, heat and information flows induced by non-reciprocal interactions, New J. Phys. 22, 123051 (2020).

[18] J. R. Medeiros and S. M. D. Queirós, Effective temperatures for single particle system under dichotomous noise, J. Stat. Mech.: Theory Exp. 2021, 063205 (2021).

[19] A. Celani, S. Bo, R. Eichhorn, and E. Aurell, Anomalous thermodynamics at the microscale, Phys. Rev. Lett. 109, 260603 (2012).

[20] C. W. Gardiner et al., Handbook of Stochastic Methods (Springer, Berlin, 1985), Vol. 3.

[21] H. C. Andrews, F. Billingsley, J. Fiasconaro, B. Frieden, R. Read, J. Shanks, and S. Treitel, Picture Processing and Digital Filtering (Springer Science & Business Media, New York, 2013), Vol. 6.

[22] K. Malakar, V. Jemseena, A. Kundu, K. V. Kumar, S. Sabhapandit, S. N. Majumdar, S. Redner, and A. Dhar, Steady state, relaxation and first-passage properties of a
run-and-tumble particle in one-dimension, J. Stat. Mech. (2018) 043215.

[23] N. G. Van Kampen, *Stochastic Processes in Physics and Chemistry* (Elsevier, New York, 1992), Vol. 1.

[24] É. Fodor, R. L. Jack, and M. E. Cates, Irreversibility and biased ensembles in active matter: Insights from stochastic thermodynamics, Annu. Rev. Condens. Matter Phys. 13, 215 (2022).

[25] T. Markovich, É. Fodor, E. Tjhung, and M. E. Cates, Thermodynamics of active field theories: Energetic cost of coupling to reservoirs, Phys. Rev. X 11, 021057 (2021).

[26] S. Kullback and R. A. Leibler, On information and sufficiency, Ann. Math. Stat. 22, 79 (1951).

[27] P. Gaspard, Time-reversed dynamical entropy and irreversibility in Markovian random processes, J. Stat. Phys. 117, 599 (2004).

[28] É. Roldán, I. Neri, M. Dörpinghaus, H. Meyr, and F. Jülicher, Decision making in the arrow of time, Phys. Rev. Lett. 115, 250602 (2015).

[29] L. Cocconi, G. Salbreux, and G. Pruessner, Scaling of entropy production under coarse graining in active disordered media, Phys. Rev. E 105, L042601 (2022).

[30] Q. Yu, D. Zhang, and Y. Tu, Inverse power law scaling of energy dissipation rate in nonequilibrium reaction networks, Phys. Rev. Lett. 126, 080601 (2021).

[31] S. Ro, B. Guo, A. Shih, T. V. Phan, R. H. Austin, D. Levine, P. M. Chaikin, and S. Martiniani, Model-free measurement of local entropy production and extractable work in active matter, Phys. Rev. Lett. 129, 220601 (2022).

[32] H. Leff and A. F. Rex, *Maxwell’s Demon 2 Entropy, Classical and Quantum Information, Computing* (CRC Press, Boca Raton, 2002).

[33] T. E. Ouldridge, R. A. Brittain, and P. R. t. Wolde, The power of being explicit: Demystifying work, heat, and free energy in the physics of computation, in *The Energetics of Computing in Life and Machines*, edited by D. H. Wolpert (SFI Press, Santa Fe, New Mexico, 2018).

[34] T. K. Saha, J. Ehrich, M. Gavrilo, S. Still, D. A. Sivak, and J. Bechhoefer, Information engine in a nonequilibrium bath, Phys. Rev. Lett. 131, 057101 (2022).

[35] M. Sandoval, R. Velasco, and J. Jiménez-Aquino, Magnetic field effect on charged brownian swimmers, Physica (Amsterdam) 442A, 321 (2016).

[36] C. Roberts and Z. Zhen, Run-and-tumble motion in a linear ratchet potential: Analytic solution, power extraction, and first-passage properties, Phys. Rev. E 108, 014139 (2023).

[37] U. Seifert, Stochastic thermodynamics, fluctuation theorems and molecular machines, Rep. Prog. Phys. 75, 126001 (2012).

[38] L. Cocconi, R. Garcia-Millan, Z. Zhen, B. Buturca, and G. Pruessner, Entropy production in exactly solvable systems, Entropy 22, 1252 (2020).

[39] M. Le Bellac, *Quantum and Statistical Field Theory* (Clarendon Press, New York, 1991).

[40] M. Bothe, L. Cocconi, Z. Zhen, and G. Pruessner, Particle entity in the Doi-Peliti and response field formalisms, J. Phys. 56, 175002 (2023).

[41] L. Caprini, A. R. Sprenger, H. Löwen, and R. Wittmann, The parental active model: A unifying stochastic description of self-propulsion, J. Chem. Phys. 156, 071102 (2022).

[42] S. A. Loos and S. H. Klapp, Fokker-Planck equations for time-delayed systems via Markovian embedding, J. Stat. Phys. 177, 95 (2019).