Guided active particles

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To account for the possibility of an externally driven taxis in active systems, we develop a model of a guided active drift which relies on the presence of an external guiding field and a vectorial coupling between the mechanical degrees of freedom and a chemical reaction. To characterize the ability of guided active particles to carry cargo, we generalize the notion of Stokes efficiency extending it to the case of stall conditions. To show the generality of the proposed mechanism, we discuss guided electric circuits capable of turning fluctuations into a directed current without a source of voltage.

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I. INTRODUCTION

Self-propelling systems have become a subject of intense interest across several disciplines of physics [1]. The most well-known examples are active Brownian particles (representing motile cells, "walking" grains, etc.) [1–5], and Brownian rachets (representing moving protein machines, synthetic molecular motors, etc.) [6–9].

Less studied are active agents that are softly guided by temporarily and spatially varying, deterministic, or fluctuating external fields as in the cases of chemotaxis [10–12], contact guidance [13–15], and durotaxis [16–18]. For instance, in the phenomenon of contact guidance cells can sense and be steered by the alignment of the fibers in the surrounding matrix. Viewed as self-propelling particles, they would show persistence (directed motion) only along the guiding field whose dynamics may be further coupled to the motion of the particles themselves. Thus, in the case of contact guidance fiber alignment may be strain-induced and therefore affected by the cell motion.

In this paper we introduce a prototypical model of a guided active drift (GAD) which relies on a vectorial coupling between mechanical and chemical degrees of freedom and implies a "strong" violation of detailed balance (DB) as defined below. In the proposed model the chemical subsystem acts as a feedback controller for the mechanical degrees of freedom, and spatial asymmetry derives from an inherently nonequilibrium process involving sensing and adaptation: active forces follow the environment in the same way as one can guide the sail to accommodate the direction of the wind.

The proposed mesoscopic mechanism of chemomechanical coupling leads to the emergence of directed drift with a possibility to carry cargo. It mimics the ability of living organisms to maintain control of their environment through self-regulating, self-powered feedback loops responsible for interconversion of chemical and mechanical energy. At the microscale, it implies the existence of an autonomous, self-sustained system which actively responds to guidance ensuring the targeted performance [19–21].

The paper is organized as follows. In Sec. II we introduce the general three-dimensional (3D) model and derive its analytically transparent one-dimensional (1D) version. In Sec. III we compare the proposed guidance activity mechanism with the existing models. In Sec. IV we analyze the dynamical aspects of the model, including force-velocity relation, anomalous diffusion, and the activity dependence of the decorrelation time. Stochastic thermodynamics of the model is the subject of Sec. V, where we introduce a definition of efficiency extending Stokes efficiency in a way that allows us to access stall conditions. The nontrivial procedure of deriving the overdamped (Smoluchowski) limit for such systems is outlined in Sec. VI, where we also analyze the anomalous behavior exhibited in this limit by thermodynamic quantities. An experimentally feasible circuit analog of the model is discussed in Sec. VII. Our conclusions and some future directions are discussed in Sec. VIII.

II. GUIDED ACTIVE PARTICLES

We propose a mechanism of directional motility that appears at first glance to be purely dissipative because it relies on velocity-dependent forces with strictly positive effective viscous damping coefficient. Consider an inertial dynamics of a particle

$$m\dot{v} = F + f,$$

where m is the mass of the particle, f is an external fixed load, and

$$F = -\hat{\gamma}(v)v$$

is a frictional force with $\hat{\gamma} \geqslant 0$ being a velocity-dependent friction coefficient. At zero temperature this system is dissipative in steady-state conditions with $fv \geqslant 0$. However, as we show below, if one exposes the same particle to a thermal

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reservoir so that

$$m\dot{v} = F + f + \xi, \tag{1}$$

where $\langle \xi \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle \sim \delta(t - t')$, the ensuing system may, for special choices of $\hat{\gamma}(v)$, exhibit "antidissipative" behavior with $f\langle v \rangle \leqslant 0$. In particular, such particle can behave as a Brownian motor with a nonzero drift $\langle v \rangle$ at zero force f [22].

A. 3D model

To expound the above discussion, consider an underdamped Brownian particle in 3D exposed to friction and thermal noise, and assume that its translational dynamics is coupled to a chemical reaction:

$$\begin{aligned} m\dot{\mathbf{v}} &= \mathbf{F}(\mathbf{v}, \zeta) + \mathbf{f} + \boldsymbol{\xi}, \\ \dot{\zeta} &= A(\mathbf{v}, \zeta). \end{aligned} \tag{2}$$

Here m is the mass of the particle, $\mathbf{f}$ is an external load, $\mathbf{F}$ is a frictional or steering force, and A is the driving force acting on the reaction coordinate ζ. The noise is assumed to be Gaussian and white, with $\langle \xi_i(t) \rangle = 0$, and $\langle \xi_i(t)\xi_j(t') \rangle = 2\gamma T \delta_{ij} \delta(t - t')$, where $\gamma > 0$ is the "bare" viscosity coefficient and T is the temperature of the bath (Boltzmann constant is set equal to one).

In an unguided passive system we may write $A = \Delta\mu$ where $\Delta\mu(\zeta)$ is the affinity of the chemical reaction. To simulate guiding, we assume that the fluxes are related to forces through pseudolinear relations [7]

$$\begin{aligned} \mathbf{F} &= -\gamma \mathbf{v} + \lambda(\mathbf{v}/\|\mathbf{v}\|)\Delta\mu, \\ A &= -\lambda(\mathbf{v} \cdot \mathbf{m}) + \Delta\mu, \end{aligned} \tag{3}$$

where the coefficient λ characterizes chemomechanical coupling and $\Delta\mu$ may now depend on both $\mathbf{v}$ and ζ. The unit vector $\mathbf{m}$ introduces a preferred (space and time-dependent) guiding direction; for instance, in the case of chemotaxis, the field $\mathbf{m}(\mathbf{x}, t)$ indicates the local direction of an external concentration gradient. Unless $\mathbf{m} = \mathbf{v}/\|\mathbf{v}\|$, the obtained system is active: the chemical subsystem acts as a feedback controller for the mechanical degrees of freedom, accelerating or slowing the advance of the reaction depending on the relative orientation of the velocity with respect to $\mathbf{m}$.

Note that while chemistry affects dynamics along the direction of motion, the reciprocal effect is controlled by a projection of velocity on a particular direction. In this sense the gradient structure of dissipation is compromised, and, as we show below, such strategy of breaking the DB is fundamentally more efficient than the one relying on the asymmetry of an external potential.

To clarify the physical picture we now compute the "dressed" friction coefficient $\hat{\gamma}(\mathbf{v})$ in the limit where the chemical degree of freedom is fast and can be adiabatically eliminated. To this end we assume the separation of timescales in the sense that $\dot{\zeta} \approx 0$. Then $\mathbf{F} = -\hat{\gamma}(\mathbf{v})\mathbf{v}$ where $\hat{\gamma}(\mathbf{v}) = \gamma[1 - \epsilon\,(\mathbf{m} \cdot \mathbf{v})/(\|\mathbf{v}\|)]$. Here we introduced $\epsilon = \lambda^2/\gamma$, a nondimensional parameter measuring the degree of activity. One can, for instance, think that in response to the measurement of the angle between $\mathbf{m}$ and $\mathbf{v}$ the active system is able to adjust its effective cross section producing the velocity-dependent friction. A more general analysis would not rely on the assumption of fast chemistry and would include measurement-related noise in the chemical dynamics; however, these issues are outside the scope of the present paper.

B. 1D model

To illustrate the nontrivial aspects of the proposed model, it is sufficient to focus on the simplest case when the system is 1D and the vector field $\mathbf{m}$ is time-independent and spatially homogeneous. The ensuing scalar model is described by the equation

$$m\dot{v} = -\hat{\gamma}(v)v + f + \xi, \tag{4}$$

where

$$\hat{\gamma}(v) = \gamma[1 + \epsilon\ \mathrm{sgn}(v)],$$

and sgn is the signum function. The obtained model implies the breakdown of time reversal symmetry (TRS) at the level of the microscopic friction law. Indeed, note that $\hat{\gamma}(v) \neq \hat{\gamma}(-v)$ even though the system is formally dissipative in the sense that $\hat{\gamma}(v) \geqslant 0$ (in the interesting range $|\epsilon| < 1$). If we write

$$-\hat{\gamma}(v) = -\gamma + g(v)/v,$$

where $g(v)$ is the nonlinear contribution to friction, we observe that

$$g(v) \neq -g(-v).$$

This is in contrast with the models respecting the condition $g(v) = -g(-v)$, for instance, the Rayleigh-Helmholtz active particle model [1,3,23,24] and the dry friction model [25–29], where the TRS is not broken at the level of the microscopic friction law and the violation of DB stems from fundamentally different reasons.

III. DEGREE OF NONEQUILIBRIUM

To explain why we associate frictional asymmetry with a "strong" violation of DB, it is instructive to consider a 1D model with general nonlinearity $g(x, v)$, where we now introduce explicitly an additional dependence on the spatial variable to account for the more general case when the system is also exposed to an external potential. The existence of the steady state is guaranteed if we consider a particle moving along a circle, which implies that the function g encodes the underlying spatial periodicity.

A. Active drift

Consider first the case of a free particle and denote by L the spatial period. The dynamics is described by the system of equations $\dot{x} = v$ and $m\dot{v} = -\gamma v + \sqrt{2\gamma T}\xi$. The corresponding Kramers equation is $\partial_t \rho = \mathcal{L}_0^\dagger \rho$ where

$$\mathcal{L}_0 = \frac{\gamma T}{m^2}\partial_v^2 - \frac{\gamma}{m}\partial_v + v\partial_x \tag{5}$$

is the generator and the symbol † stands for transposition. The steady state corresponds to Maxwellian equilibrium with $\rho_{\mathrm{eq}}(x, v) = Z^{-1} \exp[-mv^2/2T]$.

Suppose now that we add the nonlinearity perturbatively,

$$g(x, v) = \varepsilon g_1(x, v) + O(\varepsilon^2),$$

where $\varepsilon \ll 1$. We can then write

$$\mathcal{L} = \mathcal{L}_0 + \frac{\varepsilon}{m} g_1(x, v)\partial_v + O(\varepsilon^2). \tag{6}$$

We now look for a stationary solution of the Kramers equation in the form $\rho_s(x, v) = \lambda(\varepsilon)\rho_{\rm eq}(v) + \varepsilon\rho_1(x, v) + \cdots$, with $\lambda(\varepsilon) = 1 + \varepsilon\lambda_1 + \cdots$, to ensure that the stationary distribution is properly normalized at all orders in ε. Using the stationarity condition, $\mathcal{L}^\dagger \rho_s = 0$, we obtain

$$\begin{aligned} 0 &= \int_{x,v} v\mathcal{L}^\dagger \rho_s(x, v) = \int_{x,v} \rho_s(x, v)\mathcal{L}v \\ &= -\frac{\gamma}{m}\int_{x,v} \rho_s(x, v)v + \frac{\varepsilon}{m}\int_{x,v} \rho_s(x, v)g_1(x, v) + \cdots, \end{aligned} \tag{7}$$

which gives for the stationary velocity

$$\langle v\rangle = \frac{\varepsilon}{\gamma}\int_{x,v} \rho_{\rm eq}(v)g_1(x, v) + O(\varepsilon^2). \tag{8}$$

Here and above we use the notation $\int_{x,v} = \int_0^L dx \int_{-\infty}^{\infty} dv$.

It is now clear from (8) that if $g_1(x, v) \neq -g_1(x, -v)$, the system exhibits nonzero drift velocity as long as $\int g_1(x, v)\, dx \neq 0$. We associate such active drift, which emerges as a $O(\varepsilon)$ effect, with "strong" violation of DB. Instead, if $g_1(x, v) = -g_1(x, -v)$, the drift velocity is zero up to first order in ε: it can then emerge only as a "weak" effect of order $O(\varepsilon^2)$.

B. Violation of detailed balance

We now explain the idea of "strong" violation of DB in more detail. Consider the perturbed system introduced above with the physically meaningful choice

$$g_1(x, v) = g_1(v) - \partial_x U(x),$$

where $U(x)$ is an external potential. To write the corresponding Kramers equation $\partial_t \rho = -\nabla \cdot \mathbf{J}$ we introduce the probability current $\mathbf{J} = (J_x, J_v)$. It will be convenient to split $\mathbf{J}$ into a sum of reversible and dissipative contributions $\mathbf{J} = \mathbf{J}_{\rm r} + \mathbf{J}_{\rm d}$, where [30–32]

$$\mathbf{J}_{\rm r} = \left(v\,\rho, \frac{\varepsilon}{m}\left[g_1^e(v) - U'(x)\right]\rho + O(\varepsilon^2)\right) \tag{9}$$

and

$$\mathbf{J}_{\rm d} = \left(0, \frac{1}{m}\left[\varepsilon g_1^o(v) - \gamma v\right]\rho - \frac{\gamma T}{m^2}\partial_v\rho + O(\varepsilon^2)\right). \tag{10}$$

Here we distinguish between the *even* and the *odd* contributions to the nonlinear part of the friction force by defining

$$g_1^{e,o} = [g_1(v) \pm g_1(-v)]/2.$$

The reversible contribution to the current encodes the streaming or *Liouville* term, plus the velocity-dependent forces that are symmetric upon velocity inversion. Instead, the dissipative part describes the effect of the thermal reservoir and of the velocity-dependent forces that are antisymmetric upon velocity inversion.

For the DB condition to be satisfied, we must have $\mathbf{J}_{\rm d} = 0$ in the steady state, which means that $\partial_v \ln\rho_s = (m/\gamma T)[\varepsilon g_1^o(v) - \gamma v]$ up to the terms of order $O(\varepsilon)$. This implies that ρ_s must factorize into the product of a velocity-dependent and a position-dependent functions. In the stationary state we must also have $\nabla \cdot \mathbf{J}_{\rm r} = 0$ or

$$\partial_x \ln\rho_s - \frac{\varepsilon}{T}U' = \frac{\varepsilon}{T}\left[g_1^e - \frac{T\,\partial_v g_1^e}{m\,v}\right] + O(\varepsilon^2). \tag{11}$$

Since the r.h.s. of (11) cannot depend on v due to the factorization mentioned above, one must have $g_1^e = 0$. Moreover, we see from (11) that for systems with $g_1^e = 0$ but $g_1^o \neq 0$ (say, the Rayleigh-Helmholtz model), the DB condition holds to the first order and breaks only at the order $O(\varepsilon^2)$ (i.e., only in the presence of a coupling with an external potential [25,26]). Instead, when $g_1^e \neq 0$ but $g_1^o = 0$, the detailed balance is already broken at the first order in ε without a need for external interactions. This is another demonstration that our model exhibits a stronger breakdown of DB compared to some other active particle models.

IV. DYNAMICS

We now study in detail the dynamics of the analytically tractable model with

$$g(v) = -\epsilon\gamma\,\mathrm{sgn}(v)\,v,$$

which, in particular, implies that

$$g^e(v) = [g(v) + g(-v)]/2 \neq 0.$$

Using dimensionless variables $\tilde v = v\sqrt{m/T}$, $\tilde t = t\gamma/m$, and $\tilde f = (f/\gamma)\sqrt{m/T}$, we rewrite the main dynamic equation (1) in the form

$$\dot{\tilde v} = -[1 + \epsilon\,\mathrm{sgn}(\tilde v)]\tilde v + \tilde f + \tilde\xi, \tag{12}$$

where now $\langle\tilde\xi(\tilde t)\tilde\xi(\tilde t')\rangle = 2\delta(\tilde t - \tilde t')$.

A. Drift

The $\tilde f$ dependence of the steady-state drift velocity $\tilde v_s = \langle\tilde v\rangle$ can be computed explicitly. Indeed, the stationary probability distribution for Eq. (12) takes the form

$$\rho_s(\tilde v; \tilde f, \epsilon) = \begin{cases} Z^{-1}(\tilde f, \epsilon)\exp\left[-(1-\epsilon)\frac{\tilde v^2}{2} + \tilde f\tilde v\right] & \text{if } \tilde v < 0, \\ Z^{-1}(\tilde f, \epsilon)\exp\left[-(1+\epsilon)\frac{\tilde v^2}{2} + \tilde f\tilde v\right] & \text{if } \tilde v > 0, \end{cases} \tag{13}$$

where we defined $Z = Z_+ + Z_-$ with

$$Z_\pm(\tilde f, \epsilon) = \sqrt{\frac{\pi}{2(1\pm\epsilon)}}\exp\left[\frac{\tilde f^2}{2(1\pm\epsilon)}\right]\mathrm{erfc}\left[\mp\frac{\tilde f}{\sqrt{2(1\pm\epsilon)}}\right]. \tag{14}$$

The stationary velocity of the particle $\tilde v_s(\tilde f, \epsilon) = \int_{-\infty}^{\infty} d\tilde v\,\tilde v\,\rho_s(\tilde v; \tilde f, \epsilon)$ can then be calculated explicitly:

$$\tilde v_s(\tilde f, \epsilon) = \frac{\tilde f}{1-\epsilon^2} - \frac{\epsilon\left\{2 + \tilde f\left[Z_+(\tilde f, \epsilon) - Z_-(\tilde f, \epsilon)\right]\right\}}{\left(1-\epsilon^2\right)Z(\tilde f, \epsilon)}. \tag{15}$$

The typical $\tilde v_s(\tilde f)$ curves are illustrated in Fig. 1(a). One can see that in the case $0 < \epsilon < 1$ in addition to the two purely

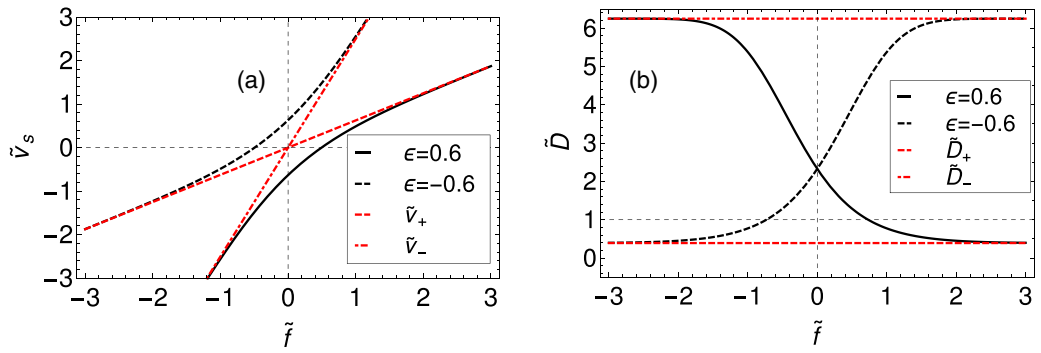

FIG. 1. Stationary response of the system (12): (a) drift velocity and (b) diffusion coefficient. Solid black lines correspond to the case $\epsilon = 0.6$, and solid dashed lines to the symmeric case $\mathbf{m} \to -\mathbf{m}$ when $\epsilon = -0.6$.

dissipative regimes $\tilde{v}_\pm(\tilde{f}) = \tilde{f}/(1 \pm \epsilon)$ reached at $\tilde{f} \to \pm\infty$ the system also exhibits active regimes where $\tilde{f}\tilde{v}_s < 0$, which we can associate with thermal rounding of the $\tilde{v} - \tilde{f}$ curve at a small value of force.

A simple expression can be obtained for the maximal active force at $\tilde{f} = 0$:

$$\tilde{v}_s^{\mathrm{m}}(\epsilon) = \sqrt{\frac{2}{\pi}}\frac{\sqrt{1-\epsilon} - \sqrt{1+\epsilon}}{\sqrt{1-\epsilon^2}}. \tag{16}$$

When $\epsilon \to 0$, we obtain $-\tilde{v}_s^{\mathrm{m}} \sim \epsilon$ or, in dimensional variables, $-v_s^{\mathrm{m}} \sim \epsilon\sqrt{T/m}$. In the presence of cargo, the same scaling can be obtained for the *active* part of the drift

$$v_s^{\mathrm{a}} = v_s - f/\gamma, \tag{17}$$

so that again $-v_s^{\mathrm{a}} \sim \epsilon\sqrt{T/m}$ for small ϵ. This suggests that in the overdamped regime the active behavior emerges only if $\epsilon \sim \sqrt{m}$, which then implies a *double* limit $\epsilon \to 0$ and $m \to 0$. See more about this in Sec. VI.

B. Diffusion

The analytical transparency of the 1D model allows us to also compute the force dependent effective diffusion coefficient

$$\tilde{D} = \lim_{\tilde{t}\to\infty} \langle \tilde{x}^2(\tilde{t})\rangle - \langle \tilde{x}(\tilde{t})\rangle^2/(2\tilde{t}).$$

Indeed, using Green-Kubo relation [33], we can write $\tilde{D} = \int_0^\infty C(\tilde{t})\, d\tilde{t}$, where $C(\tilde{t}) = \langle \tilde{v}(\tilde{t})\tilde{v}(0)\rangle - \tilde{v}_s^2$, is the velocity autocorrelation function. If we now introduce the conditional probability $p(\tilde{v}, \tilde{t}|\tilde{v}_0)$ satisfying

$$\partial_{\tilde{t}} p(\tilde{v}, \tilde{t}|\tilde{v}_0) = \partial_{\tilde{v}}^2 p(\tilde{v}, \tilde{t}|\tilde{v}_0) - \partial_{\tilde{v}}\{[\tilde{f} - \hat{\gamma}(\tilde{v})\tilde{v}]p(\tilde{v}, \tilde{t}|\tilde{v}_0)\}, \tag{18}$$

with initial condition $p(\tilde{v}, \tilde{t} = 0|\tilde{v}_0) = \delta(\tilde{v} - \tilde{v}_0)$, we can write $C(\tilde{t}) = \int_{-\infty}^{\infty} G(\tilde{v}, \tilde{t})\tilde{v}\, d\tilde{v}$, where $G(\tilde{v}, \tilde{t}) = \int_{-\infty}^{\infty} p(\tilde{v}, \tilde{t}|\tilde{v}_0)(\tilde{v}_0 - \tilde{v}_s)\rho_s(\tilde{v}_0)\, d\tilde{v}_0$. The function $G(\tilde{v}, \tilde{t})$ satisfies the equation

$$\partial_{\tilde{t}} G(\tilde{v}, \tilde{t}) = \partial_{\tilde{v}}^2 G(\tilde{v}, \tilde{t}) - \partial_{\tilde{v}}\{[\tilde{f} - \hat{\gamma}(\tilde{v})\tilde{v}]G(\tilde{v}, \tilde{t})\}, \tag{19}$$

with initial condition $G(\tilde{v}, 0) = (\tilde{v} - \tilde{v}_s)\rho_s(\tilde{v})$. It can be solved using the Laplace transform $\hat{G}(\tilde{v}, u) = \int_0^\infty G(\tilde{v}, \tilde{t})e^{-u\tilde{t}}\, d\tilde{t}$. Then, using the Green-Kubo formula, we can write $\tilde{D} = \int_{-\infty}^{\infty} \hat{G}(\tilde{v}, u = 0)\tilde{v}\, d\tilde{v}$, which leads to the final expression:

$$\tilde{D} = \int_{-\infty}^{\infty} \frac{d\tilde{v}}{\rho_s(\tilde{v})}\left[\int_{-\infty}^{\tilde{v}} (\tilde{v}' - \tilde{v}_s)\rho_s(\tilde{v}')\, d\tilde{v}'\right]^2. \tag{20}$$

These results are illustrated in Fig. 1(b). The purely dissipative, large force limits are again different: $\tilde{D}_\pm = 1/(1 \pm \epsilon)^2$. We can also write $\tilde{D}_\pm = \tilde{T}_\pm/\tilde{\gamma}_\pm$ viewing the system as equilibrated with two reservoirs having different temperatures

$$\tilde{T}_\pm = 1/(1 \pm \epsilon)$$

and characterized by different friction coefficients, $\tilde{\gamma}_\pm = 1 \pm \epsilon$. Note that $\tilde{\gamma}_+\tilde{T}_+ = \tilde{\gamma}_-\tilde{T}_- = 1$.

Using this notation we can rewrite (12) in the form

$$\dot{\tilde{v}} = \begin{cases} -\tilde{\gamma}_-\tilde{v} + \tilde{f} + \sqrt{2\tilde{\gamma}_-\tilde{T}_-}\,\xi_- & \tilde{v} < 0, \\ -\tilde{\gamma}_+\tilde{v} + \tilde{f} + \sqrt{2\tilde{\gamma}_+\tilde{T}_+}\,\xi_+ & \tilde{v} > 0, \end{cases} \tag{21}$$

with $\langle \xi_i(\tilde{t})\xi_j(\tilde{t}')\rangle = \delta_{ij}\delta(\tilde{t} - \tilde{t}')$ and $i, j = \pm$. Such a reformulation stresses the fact that guidance in this system can be interpreted as the exposure to two reservoirs with different temperatures $\tilde{T}_\pm$.

C. Persistence and criticality

The representation of the dynamics in terms of two Ornstein-Uhlenbeck processes (21) makes explicit that guidance emerges as the directional dependence of the viscous relaxation time. We now consider the simplest case, $\tilde{f} = 0$, and compute the effective persistence time that emerges from the asymmetry of viscous relaxation.

Persistence is linked to the decorrelation in the orientation of the velocity; the latter can be assessed from the correlation function of the orientation $C(\tilde{t}, \tilde{t}') = \langle \mathrm{sgn}[\tilde{v}(\tilde{t})]\mathrm{sgn}[\tilde{v}(\tilde{t}')]\rangle$. More specifically, we can associate the persistence time with the spectral gap $\tau = -1/\lambda$ where λ is the largest (negative) eigenvalue of the generator $L = \partial_{\tilde{v}}^2 - \tilde{v}\,[1 + \epsilon\,\mathrm{sgn}(\tilde{v})]\,\partial_{\tilde{v}}$. To find τ we need to solve the eigenvalue problem

$$\begin{aligned} g''(\tilde{v}) - \tilde{v}(1+\epsilon)g'(\tilde{v}) &= \lambda g(\tilde{v}), \quad \text{for } \tilde{v} > 0, \\ g''(\tilde{v}) - \tilde{v}(1-\epsilon)g'(\tilde{v}) &= \lambda g(\tilde{v}), \quad \text{for } \tilde{v} < 0, \end{aligned} \tag{22}$$

supplemented by the matching conditions: $g(0^+) = g(0^-)$ and $g'(0^+) = g'(0^-)$.

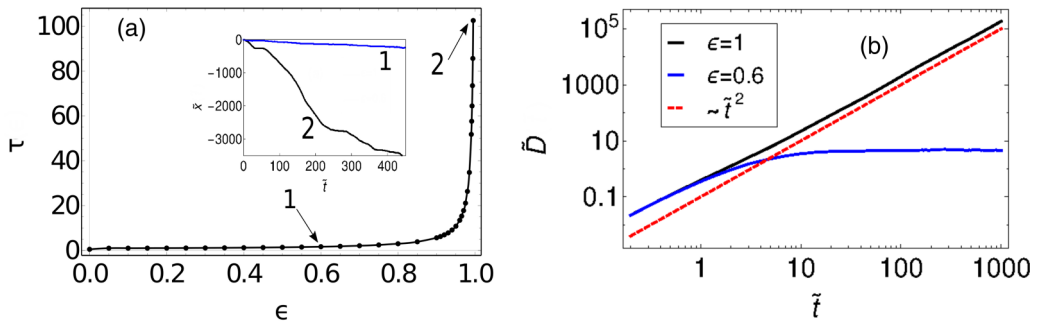

FIG. 2. (a) Persistence time as a function of ϵ for $\tilde{f} = 0$.The inset shows typical stochastic realizations of the trajectory of the particle at $\epsilon = 0.6$ (regime 1), and in the *critical* state, $\epsilon = 1$ (regime 2). (b) "'Finite time" diffusion coefficient in the critical and non critical regimes.

The solution of this problem can be written explicitly in terms of Hermite functions $H_\nu(z)$ [34],

$$g(\tilde{v}) = \begin{cases} A_+ H_{-\lambda/\tilde{\gamma}_+}\left(\tilde{v}\sqrt{\frac{\tilde{\gamma}_+}{2}}\right) \text{ for } \tilde{v} > 0, \\ A_- H_{-\lambda/\tilde{\gamma}_-}\left(-\tilde{v}\sqrt{\frac{\tilde{\gamma}_-}{2}}\right) \text{ for } \tilde{v} < 0, \end{cases} \tag{23}$$

and A_+ and A_- are two constants. Using the continuity conditions we can eliminate A_+ and A_- and obtain the eigenvalue equation, $g'(0^+)/g(0^+) = g'(0^-)/g(0^-)$, or equivalently

$$\frac{\sqrt{\tilde{\gamma}_+}}{B\left(\frac{\lambda}{2\tilde{\gamma}_+}, \frac{1}{2}\right)} + \frac{\sqrt{\tilde{\gamma}_-}}{B\left(\frac{\lambda}{2\tilde{\gamma}_-}, \frac{1}{2}\right)} = 0, \tag{24}$$

where $B(x, y)$ is the β function [35]. To obtain Fig. 2(a) we solved (24) numerically.

For the passive system ($\epsilon = 0$) we have $\tau = 1/2$. In the presence of activity, the spectral gap tends to close as ϵ increases, causing the increase of the decorrelation (persistence) time. In Fig. 2(a) we show the function $\tau(\epsilon)$ for $\tilde{f} = 0$.

The divergence of τ at $\epsilon \to 1^-$ indicates that $(\epsilon, \tilde{f}) = (1, 0)$ corresponds to a dynamic critical point. Note that in the limit $\epsilon \to 1^-$ the effective temperature of the "hot reservoir" $\tilde{T}_-$ diverges and the velocity dynamics in the corresponding direction ($\tilde{v} < 0$) becomes Brownian. As a result both the average drift velocity and the recrossing time (from negative to positive velocity) also diverge and the dynamics becomes critical exhibiting (in average) anomalous unidirectional persistence; see the inset in Fig. 2(a).

To quantify more explicitly the divergence of the persistence time, note that in the limit $\epsilon \to 1^-$, we obtain that $\tilde{\gamma}_+ \to 2$ and $\lambda \to 0$. Then Eq. (24) can be approximately written as $\lambda + 2\sqrt{\tilde{\gamma}_+\tilde{\gamma}_-}/B(\frac{\lambda}{2\tilde{\gamma}_-}, \frac{1}{2}) \approx 0$, or equivalently $\frac{\lambda}{2\tilde{\gamma}_-} B(\frac{\lambda}{2\tilde{\gamma}_-}, \frac{1}{2}) \sim \sqrt{\tilde{\gamma}_+/\tilde{\gamma}_-}$. Since the right-hand side of this equation diverges when $\epsilon \to 1^-$, and $\lambda < 0$, the value of $\frac{\lambda}{2\tilde{\gamma}_-}$ must be close to the largest (negative) pole of the β function, i.e., $\frac{\lambda}{2\tilde{\gamma}_-} \approx -1$. Expanding to the lowest order in the associated Laurent series, we obtain $\frac{\lambda}{2\tilde{\gamma}_-} \sim -1 + \frac{1}{2\sqrt{2}}\sqrt{1-\epsilon}$. We can then write $\lambda = -2(1-\epsilon) + O[(1-\epsilon)^{3/2}]$, or $\tau = -1/\lambda \sim (1-\epsilon)^{-\sigma}$, with critical exponent $\sigma = 1$. Note also that in this limit we observe superdiffusive behavior with $\langle\tilde{x}\rangle \sim -\tilde{t}^{3/2}$, and the anomalous behavior of the "finite time" diffusion coefficient $\tilde{D}(t) = \langle\tilde{x}^2(\tilde{t})\rangle - \langle\tilde{x}(\tilde{t})\rangle^2/(2\tilde{t}) \sim \tilde{t}^2$; see Fig. 2(b).

V. THERMODYNAMICS

We now turn to the stochastic thermodynamics of GAD. It will be convenient to reintroduce dimensional variables and start with a slightly more general 1D model:

$$m\dot{v} = -\gamma v + g_e + f + \xi, \tag{25}$$

where the function $g_e(v)$ is assumed to be even. The goal is to formulate the first and second laws of thermodynamics for the system (25) and to associate an adequate concept of efficiency with the energy transduction process. The latter is assumed to be driven by the external source described by the function g_e and resulting in active transport of the cargo f.

A. Energy balance

The energy balance along a particular trajectory of duration t can be derived by multiplying (25) by v and integrating over time, which gives [36,37]

$$\mathcal{E}_t = \mathcal{U}_t^a - \mathcal{W}_t - \mathcal{Q}_t.$$

Here

$$\mathcal{E}_t = (m/2)[v^2(t) - v^2(0)]$$

is the change in kinetic energy of the particle,

$$\mathcal{U}_t^a = \int_0^t dt' v g_e(v)$$

is the active work performed on the particle by the guiding device,

$$\mathcal{W}_t = -f\int_0^t dt' v$$

is the work of transporting cargo, and

$$\mathcal{Q}_t = \int_0^t dt' v(\gamma v - \xi) \tag{26}$$

is the released heat [36].

The conventional form of the first law of thermodynamics can be obtained if we average the above expressions over the ensemble of possible trajectories (in what follows we denote such averages by italic capital letters) and take time derivatives, for instance, $\dot{E} = (d/dt)\langle\mathcal{E}_t\rangle$. In a stationary state $\dot{E} = 0$ we obtain

$$\dot{U}^{\rm a} = \dot{W} + \dot{Q}, \tag{27}$$

where, for instance, $\dot{W} = -f v_s$.

B. Entropy production

The entropy production along a particular stochastic trajectory can be split into a contribution from the system (particle) and from the reservoir (equilibrium component of the environment) [37]:

$$\mathcal{S}_t = \mathcal{S}_t^s + \mathcal{S}_t^r. \tag{28}$$

To define these entries, consider a trajectory $\{v(t')\}_{t'=0}^t$, starting at the velocity value v_0, which is sampled from the initial probability distribution with the density $p_0(v_0)$. Assume that after time t, the probability density function for v (reflecting the forward dynamics) is $p_t(v)$. Consider also the time-reversed trajectory $\{\hat{v}(t')\}_{t'=0}^t \equiv \{-v(t-t')\}_{t'=0}^t$, whose starting velocity $\hat{v}_0 = -v_t$ is sampled from the probability distribution with the density $p_t(-\hat{v}_0) \equiv p_t(v_t)$.

The next step is to introduce the (functional) probability $\Pi[v|v_0]$ for forward trajectories with initial condition v_0 and its time-reversed version $\hat{\Pi}[\hat{v}|\hat{v}_0]$. Then the stochastic entropy production over duration t can be written in the form [37]

$$\mathcal{S}_t[v] = \ln\frac{p_0(v_0)}{p_t(v_t)} + \ln\frac{\Pi[v|v_0]}{\hat{\Pi}[\hat{v}|\hat{v}_0]}. \tag{29}$$

The first term in (29) can be associated with the entropy change in the system [37],

$$\mathcal{S}_t^s = \ln\frac{p_0(v_0)}{p_t(v_t)};$$

in particular, its ensemble average $\langle\mathcal{S}_t^s\rangle$ is simply the change of the Shannon entropy,

$$S_t^s = \langle\ln[p_0(v_0)/p_t(v_t)]\rangle = \int p_0\ln p_0 - \int p_t\ln p_t.$$

The second term in Eq. (29) accounts for entropy production in the reservoir

$$\mathcal{S}_t^r = \ln\frac{\Pi[v|v_0]}{\hat{\Pi}[\hat{v}|\hat{v}_0]}. \tag{30}$$

The conditional path probability in (30) can be written as

$$\Pi[v|v_0] = \mathcal{N}\exp\{-\mathcal{A}[v]\},$$

where $\mathcal{N}$ is an unimportant normalization factor [37]. Here $\mathcal{A}$ is the dynamic action $\mathcal{A}$ associated with (25) (see for, instance, Ref. [32]):

$$\mathcal{A}[v] = \frac{1}{2m}\int_0^t dt'\partial_v g_e(v) + \frac{1}{4\gamma T}\int_0^t dt'\big[m\dot{v} + \gamma v - g_e(v) - f\big]^2. \tag{31}$$

Similarly, for the reversed trajectory $\{\hat{v}(t')\}_{t'=0}^t = \{-v(t-t')\}_{t'=0}^t$ we can write

$$\mathcal{A}[\hat{v}] = \mathcal{A}[v] - \frac{1}{m}\int_0^t dt'\partial_v g_e(v) - \frac{1}{T}\int_0^t dt'\, v[m\dot{v} - g_e(v) - f]. \tag{32}$$

Note that

$$\mathcal{A}[\hat{v}] = \mathcal{A}[v] - \frac{1}{m}\int_0^t dt'\partial_v g_e(v) + \frac{\mathcal{Q}_t}{T},$$

where $\mathcal{Q}_t[v]$ was defined in (26).

We can now write

$$\mathcal{S}_t^r = \mathcal{A}[\hat{v}] - \mathcal{A}[v] = \frac{\mathcal{Q}_t}{T} - \mathcal{S}_t^{\rm a}, \tag{33}$$

where

$$\mathcal{S}_t^{\rm a} = m^{-1}\int_0^t dt'\partial_v g_e(v)$$

is the active contribution which has previously appeared in the literature in the context of feedback cooling as the "entropy-pumping" term describing information exchange [38–40].

To summarize, the total stochastic entropy production takes the form

$$\mathcal{S}_t = \mathcal{S}_t^s + \frac{\mathcal{Q}_t}{T} - \mathcal{S}_t^{\rm a}. \tag{34}$$

If we average this expression over the ensemble of trajectories assuming stationary conditions, take the time derivative with respect to t, and use the fact that $\dot{S}^s = 0$, we obtain the second law of thermodynamics in the form

$$\dot{S} = \frac{\dot{Q}}{T} - \dot{S}^{\rm a} \geqslant 0. \tag{35}$$

The inequality in Eq. (35) can be justified if we note that

$$\dot{S} = \frac{1}{T}\int v[g_e(v)+f]\rho_s(v)\,dv - \frac{m}{T}\int v\big\langle\dot{v}(t)\delta[v-v(t)]\big\rangle_s\,dv - \frac{1}{m}\int\partial_v g_e(v)\rho_s(v)\,dv. \tag{36}$$

The notation $\langle\ldots\rangle_s$ is used to stress that the average is taken over stationary dynamics. Grouping the first and the last integrals we write

$$\dot{S} = -\frac{m}{\gamma T}\int\big[g_e(v)+f\big]J_d(v) - \frac{m}{T}\int v\big\langle\dot{v}(t)\delta[v-v(t)]\big\rangle_s\,dv, \tag{37}$$

where $J_d(v) = -m^{-1}[\gamma v + (\gamma T\, m^{-1})\partial_v]\rho_s(v)$ is the dissipative part of the stationary probability current. From the stationary Fokker-Planck equation for this system we obtain

$$\frac{\gamma T}{m}\partial_v\rho_s(v) - \big[g_e(v)+f-\gamma v\big]\rho_s(v) = -mJ_d(v) - [g_e(v)+f]\rho_s(v) = 0 \quad\Rightarrow\quad g_e(v)+f = -\frac{mJ_d(v)}{\rho_s(v)}. \tag{38}$$

We can then write

$$\dot{S} = \frac{m^2}{\gamma T}\int\frac{J_d^2(v)}{\rho_s(v)}\,dv - \frac{m}{T}\int v\big\langle\dot{v}(t)\delta[v-v(t)]\big\rangle_s\,dv. \tag{39}$$

The second integral in (39) vanishes since

$$\big\langle\dot{v}(t)\delta[v-v(t)]\big\rangle_s = -\partial_t\big\langle\Theta[v-v(t)]\big\rangle_s = -\int_{-\infty}^v\partial_t\big\langle\delta[v'-v(t)]\big\rangle_s\,dv' = -\int_{-\infty}^v\partial_t\rho_s(v')\,dv' \equiv 0, \tag{40}$$

which allows us to write

$$\dot{S} = \frac{m^2}{\gamma T}\int \frac{J_d^2(v)}{\rho_s(v)}\,dv \geqslant 0. \tag{41}$$

C. Efficiency

To assess the efficiency of GAD we first introduce the injection rate of the Helmholtz free energy

$$\dot{F}^{\rm a} = \dot{U}^{\rm a} - T\dot{S}^{\rm a}.$$

Then the inequality (35) can be rewritten as

$$T\dot{S} = \dot{F}^{\rm a} - \dot{W} \geqslant 0,$$

which suggests the following definition of the thermodynamic efficiency [41,42]:

$$\eta_T = \dot{W}/\dot{F}^{\rm a} \leqslant 1. \tag{42}$$

This definition, however, accounts neither for the capacity of an active particle to self-propel at zero force nor for its ability to generate force in stall conditions: in both limits the machine works (either by achieving persistent unidirectional displacement or equally persistent localization) with apparently zero efficiency.

A known way to resolve the first of these issues is to consider the Stokes efficiency [43],

$$\eta_S = (\dot{W} + \gamma v_s^2)/\dot{F}^{\rm a},$$

which, however, still vanishes in stall conditions. In other words, it cannot be used to assess the force generation efficiency of an active system.

To fix this problem we now introduce a definition of "active" efficiency

$$\eta_{\rm a} = \dot{W}^{\rm a}/\dot{G}^{\rm a}, \tag{43}$$

where in the denominator we replaced the rate of change of the active *Helmholtz* free energy $\dot{F}^{\rm a}$ by the more natural (in the presence of a cargo) rate of change of the active *Gibbs* free energy

$$\dot{G}^{\rm a} = \dot{F}^{\rm a} - f v_s^{\rm a},$$

where $f v_s^{\rm a} < 0$. In the numerator we replaced the thermodynamic work $\dot{W} = -f v_s$, entering the definition of the thermodynamical efficiency η_T, and $\dot{W}^S = -f v_s + \gamma v_s^2$, entering the definition of Stokes efficiency η_S, with the term,

$$\dot{W}^{\rm a} = \gamma v_s^{\rm a2},$$

where $v_s^{\rm a}$ is given by (17). We observe that $\dot{W}^{\rm a} = \dot{W} + \gamma {v_s}^2 - f v_s + f^2/\gamma = \dot{W}^S - f v_s + f^2/\gamma$.

The chosen expression for the functional power $\dot{W}^{\rm a}$ can be interpreted as the "necessary" dissipated work needed, for instance, to self-propel against frictional forces, to hold the load against gravity or to stretch a spring, and, most importantly, to carry a load. Rewriting it as $\dot{W}^{\rm a} = \gamma(v_s - f/\gamma)^2$ we see that it can be also universally interpreted as the apparent work against frictional forces in a reference frame that "moves" at the effective velocity f/γ.

A more illuminating interpretation of the active efficiency $\eta_{\rm a}$ can be obtained if we observe that the (squared) total active force generated by the guiding device is $\langle g_e(v)^2\rangle_s = \gamma\dot{F}^{\rm a} - \gamma f v_s^{\rm a}$, while only an amount $\langle g_e(v)\rangle_s^2 = (\gamma v_s - f)^2 = \gamma^2 (v_s^{\rm a})^2$ is functional. Then our efficiency can be seen to quantify active force generation:

$$\eta_{\rm a} = \langle g_e(v)\rangle_s^2/\langle g_e(v)^2\rangle_s. \tag{44}$$

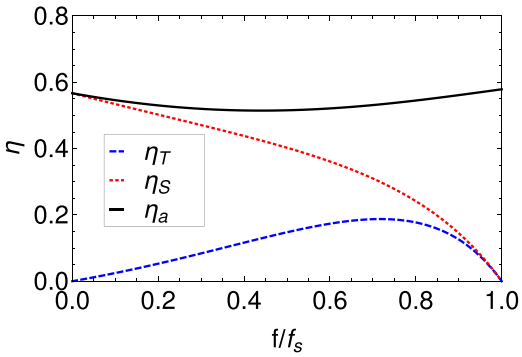

FIG. 3. Typical force dependence of the thermodynamic efficiency η_T, Stokes efficiency η_S, and our efficiency $\eta_{\rm a}$ for the GAP model (12) with $\epsilon = 0.9$; f is normalized by the stall force f_s.

Finally, we point out that the definition (43) is different from the recently introduced notion of chemical efficiency, which also allows one to account for stall force conditions [44]. A comparison of all three efficiencies η_T, η_S, and $\eta_{\rm a}$ for our system is presented in Fig. 3.

VI. OVERDAMPED LIMIT

We recall that active drift in our system survives in the overdamped (Smoluchovski) limit with $m \to 0$, only when we simultaneously weaken the activity so that $\epsilon \sim -v_{\rm a}^*\sqrt{\pi m/2T}$. More precisely, only in this double limit does the active velocity $v_s^{\rm a} \to v_{\rm a}^*$ not vanish. The overdamped limit is of particular importance for applications at the cellular level where inertial terms are usually neglected. The theoretical challenge stems from the fact that if we set directly $m = 0$ in our original equation (1) we obtain an ill-defined problem.

To explain the difficulty, consider more general overdamped stochastic differential equations of the form

$$\phi(\dot{x}) = \xi(t), \tag{45}$$

where $\xi(t)$ is the standard white noise. If the function ϕ is nonlinear, the mathematical nature of the ensuing problem is obscure. However, one can assign a well-defined meaning to the solutions of the regularized problem

$$m\ddot{x} + \phi(\dot{x}) = \xi(t). \tag{46}$$

It is then natural to introduce the *inertial* solutions of (45) as $m \to 0$ limits of the solutions of (46). Some of the the challenges associated with such an interpretation are discussed below.

A. Dynamics

Consider our special case (4) and define formally an auxiliary stochastic process

$$y(t) = x(t) + m\varphi[v(t)],$$

where the function $h(v) = \partial_v \varphi(v)$ satisfies

$$\frac{\gamma T}{m}\partial_v h(v) - \hat{\gamma}(v) v h(v) = v_s^{\rm m} - v. \tag{47}$$

Here $v_s^{\rm m}$ is the maximal active velocity (the average velocity at zero force introduced in Sec. IV).

Looking for the bounded solution of the equation (47) on the whole axis we obtain

$$h(v) = \frac{m}{\gamma T}\, e^{m\hat{\gamma}(v)v^2/2\gamma T} \int_{-\infty}^{v} e^{-m\hat{\gamma}(v')v'^2/2\gamma T} \left(v_s^{\rm m} - v'\right) dv'. \tag{48}$$

To show that $h(v)$ is uniformly bounded, consider first the case $-\sqrt{T/m} \leqslant v \leqslant 0$. If we introduce a variable $v' = z\sqrt{T/m}$ we can use the explicit form of $\hat{\gamma}(v)$ to rewrite (48) in the form

$$h(v) = \frac{1}{\gamma}\sqrt{\frac{m}{T}}\, v_s^{\rm m}\, e^{m(1-\epsilon)v^2/2T} \int_{-\infty}^{v\sqrt{m/T}} e^{-(1-\epsilon)z^2/2}\, dz + 1/[\gamma(1-\epsilon)]. \tag{49}$$

It is not difficult to show that in this interval of velocities, $h(v)$ converges to $1/\gamma[1-\epsilon(m=0)]$ when m tends to zero (provided $v_s^{\rm m}$ stays bounded, which takes place for $\epsilon \sim \sqrt{m}$) and the convergence is uniform in v.

For $v < -\sqrt{T/m}$ we can write

$$\begin{aligned} h(v) - \frac{1}{\gamma(1-\epsilon)} &= -\frac{v_s^{\rm m}}{\gamma(1-\epsilon)v} - \frac{1}{\gamma}\sqrt{\frac{m}{T}}\, v_s^{\rm m}\, e^{m(1-\epsilon)v^2/2T} \\ &\quad \times \int_{-\infty}^{v\sqrt{m/T}} e^{-(1-\epsilon)z^2/2}\, \frac{1}{(1-\epsilon)z^2}\, dz, \end{aligned} \tag{50}$$

which in this range of v is uniformly bounded in absolute value by a constant of order $\sqrt{m}$. Therefore also in this interval we obtain uniform convergence of $h(v)$ to $1/\gamma$. A similar argument holds for $v > 0$, with $h(v)$ converging to $1/\gamma[1+\epsilon(m=0)] = 1/\gamma$.

Now, recall that the function φ is defined up to a constant, so, for instance, we can choose

$$\varphi(v) = \int_0^v h(v')\, dv'.$$

Note also that the absolute value of φ grows at most linearly in $|v|$ and this growth is uniform in m (when m tends to zero). In particular $m\,\varphi(v)$ tends to zero with probability one when m tends to zero.

After these preparations, we can use the Itô formula to write

$$\begin{aligned} \dot{y} &= \dot{x} + m\,\partial_v\varphi(v)\dot{v} + \frac{\gamma T}{m}\partial_v^2\varphi(v) \\ &= \partial_v\varphi(v)\big[f + \sqrt{2\gamma T}\,\eta(t)\big] + v_s^{\rm m}, \end{aligned} \tag{51}$$

where in the last step we used the fact that $\partial_v\varphi(v) = h(v)$ together with Eq. (47). There is still the factor $\partial_v\varphi(v)$ here which depends on v, but in the limit $m \to 0$ with $\epsilon \sim \sqrt{m}$ we have $v_s^{\rm m} \to v_{\rm a}^*$ and $\lim_{m\to 0}\partial_v\varphi(v) \equiv \lim_{m\to 0} h(v) = 1/\gamma$ uniformly; the uniform convergence is important since fluctuations in v diverge as $\sqrt{T/m}$. At the end we obtain for the process y the limiting equation $\dot{y} = f/\gamma + v_{\rm a}^* + \sqrt{2T/\gamma}\,\eta$. If we now recall that for $m \to 0$, $y(t) = x(t) + m\varphi(v) \to x(t)$ and $m\varphi(v) \to 0$ with probability one, we obtain the limiting equation for $x(t)$:

$$\dot{x} = \frac{f}{\gamma} + v_{\rm a}^* + \sqrt{\frac{2T}{\gamma}}\,\xi. \tag{52}$$

Observe the emergence in (52) of the active drift described by the term $v_{\rm a}^*$ without any modifications in the diffusion coefficient. While models like (52) containing either externally prescribed active force or active velocity are often postulated phenomenologically in the study of Brownian motors [45], the implied "weak" limits miss some important physical effects. For instance, since they underrepresent velocity fluctuations (of order $\sim\sqrt{T/m}$) they are known to distort the stochastic thermodynamics of the system [46–51]; see below.

B. Thermodynamics

We now proceed to show that in the overdamped limit, $(\epsilon, m) \to (0,0)$ with $\epsilon \sim \sqrt{m}$, the expressions for the thermodynamic observables for the system described by (4) may contain nontrivial corrections comparing to their analogs computed directly from the overdamped dynamics described by (52).

From energy balance (27) we obtain

$$\begin{aligned} \dot{Q} = \dot{U}^{\rm a} - \dot{W} &= \int v[g_e(v) + f]\rho_s(v)\, dv \\ &= \int v\left[\frac{\gamma T}{m}\partial_v\rho_s(v) + \gamma v\rho_s(v)\right] dv \\ &= -\frac{\gamma T}{m} + \gamma\langle v^2\rangle_s, \end{aligned} \tag{53}$$

where we used the stationary Fokker-Planck equation (38). Using the identity $\frac{dv_s}{df} = \frac{m}{\gamma T}\langle[v - v_s]^2\rangle_s$ we further obtain $\langle v^2\rangle_s = v_s^2 + \frac{\gamma T}{m}\frac{dv_s}{df}$, which allows us to rewrite (53) in the form

$$\dot{Q} = \gamma v_s^2 + \frac{\gamma T}{m}\left(\gamma\frac{dv_s}{df} - 1\right). \tag{54}$$

Now, in the overdamped limit, $v_s \to v_{\rm a}^* + f/\gamma$, we can write $\dot{Q} = \dot{Q}_{\rm o} + \dot{Q}_h$, where the "overdamped" term

$$\dot{Q}_{\rm o} = \gamma v_s^2 \equiv \frac{1}{\gamma}(f + \gamma v_{\rm a}^*)^2$$

describes the heat release (heat dissipation) rate in the overdamped dynamics, while the remaining term

$$\dot{Q}_h = \lim_{m\to 0}\frac{\gamma T}{m}\left(\gamma\frac{dv_s}{df} - 1\right) \tag{55}$$

is the "hidden" heat dissipation rate.

We point out that the limit in (55) is nontrivial because the relation $v_s \to v_{\rm a}^* + f/\gamma$ implies that $\gamma(dv_s/df) - 1 \to 0$, while $\gamma T/m \to \infty$. A more careful analysis gives the asymptotics

$$\gamma\frac{dv_s}{df} = 1 - \frac{\epsilon f}{\gamma}\sqrt{\frac{2m}{\pi T}} + \left(\frac{3}{2} - \frac{2}{\pi}\right)\epsilon^2 + \cdots, \tag{56}$$

which yields

$$\gamma\frac{dv_s}{df} = 1 + \frac{m}{\gamma T} f v_a^* + \frac{m}{T}\left(\frac{3\pi}{4} - 1\right)(v_a^*)^2 + O(m^2), \quad (57)$$

where we used the scaling $\epsilon \sim -v_a^*\sqrt{\pi m/2T}$. The expression for the "hidden" heat release now can be written explicitly:

$$\dot{Q}_h = \left(\frac{3\pi}{4} - 1\right)\gamma(v_a^*)^2 + f v_a^*. \quad (58)$$

Next, we compute the limit value of the active work rate. From the overdamped dynamics one simply has $\dot{U}_o^a = \gamma v_s v_a^* = \gamma(v_a^*)^2 + f v_a^*$. Instead, the true active work rate is

$$\dot{U}^a = \dot{Q} + \dot{W} \equiv \dot{U}_o^a + \dot{U}_h^a, \quad (59)$$

where the "hidden" contribution reads

$$\dot{U}_h^a = \dot{Q}_h = \left(\frac{3\pi}{4} - 1\right)\gamma(v_a^*)^2 + f v_a^*. \quad (60)$$

Note that the "hidden" active work rate exactly matches the "hidden" heat dissipation rate. This is, of course, a consequence of the energy balance, since the passive work rate does not exhibit any "hidden" contributions.

Finally, we can use Eq. (41) and the last equality in (38) to write an equivalent expression for the entropy production rate

$$\dot{S} = \frac{1}{\gamma T}\int [g_e(v) + f]^2 \rho_s(v)\, dv = \frac{\langle g_e(v)^2\rangle_s}{\gamma T} + \frac{(2\gamma v_s - f)f}{\gamma T}, \quad (61)$$

where we expanded the square and used the equation of motion (25) to write $\langle g_e(v)\rangle_s = \gamma v_s - f$. In the overdamped limit $v_s \to v_a^* + f/\gamma$, so we can write

$$\dot{S} \to \lim_{(\epsilon,m)\to(0,0)}\left[\frac{\langle g_e(v)^2\rangle_s}{\gamma T}\right] + \frac{(2\gamma v_a^* + f)f}{\gamma T}, \quad (62)$$

where the double limit is taken along the path $\epsilon = -v_a^*\sqrt{\pi m/2T}$. Completing the square in the second fraction in (62), and noting that $\dot{S}_o = \dot{Q}_o/T = (\gamma T)^{-1}(f + \gamma v_a^*)^2$ [52], we obtain the expression for the "hidden" entropy production

$$\dot{S}_h = \lim_{(\epsilon,m)\to(0,0)}\left[\frac{\langle g_e(v)^2\rangle_s}{\gamma T}\right] - \frac{\gamma(v_a^*)^2}{T}. \quad (63)$$

To compute the remaining limit we use the explicit form $g_e(v) = -\gamma\epsilon\,\mathrm{sgn}(v)v \equiv -\gamma\epsilon|v|$ to rewrite $\langle g_e(v)^2\rangle_s = \gamma^2\epsilon^2\langle v^2\rangle_s$. In view of

$$\gamma^2\epsilon^2\langle v^2\rangle_s \equiv \frac{\gamma^2(v_a^*)^2\pi m}{2T}v_s^2 + \frac{\gamma^3(v_a^*)^2\pi}{2}\frac{dv_s}{df} \quad (64)$$

and the fact that $v_s \to v_a^* + f/\gamma$ and $\partial_f v_s \to 1/\gamma$, we can write

$$\langle g_e(v)^2\rangle_s \to \frac{\gamma^2(v_a^*)^2\pi}{2}. \quad (65)$$

Finally, substituting (65) into (63), we get the result

$$\dot{S}_h = \left(\frac{\pi}{2} - 1\right)\frac{\gamma(v_a^*)^2}{T}. \quad (66)$$

We can now identify the active contribution to the entropy production rate. If we recall that in the overdamped limit $\dot{S}_o^a = 0$, we obtain that the whole active contribution

$$\dot{S}^a \equiv \dot{S}_h^a = \frac{\dot{Q}_h}{T} - \dot{S}_h = \frac{\pi\gamma(v_a^*)^2}{4T} + \frac{v_a^*}{T} \quad (67)$$

is "hidden."

To summarize, (52) can at most yield a lower bound of the actual entropy production $\dot{S}$ and is even misleading in predicting the active work $\dot{U}^a$. The latter is an important observation in view of a recent discovery of a link between the fluctuations of the active work and the transition between phases of different motility in active matter [53,54].

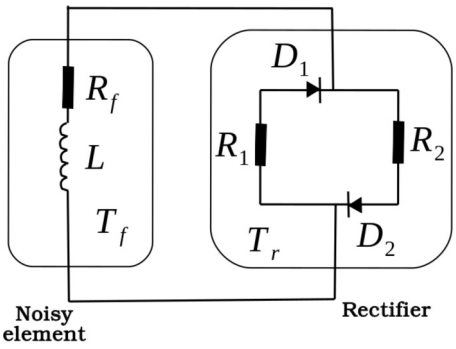

FIG. 4. Electric circuit imitating the behavior of the system (12) with $f = 0$ when $T_r \ll T_f$.

VII. ELECTRIC ANALOGY

To show that the proposed mechanism is not an abstraction and that it can be implemented experimentally, we briefly discuss a simple realization of the system (12) in the form of an electric circuit; see Fig. 4. The "noisy element" of the circuit contains an electric resistance R_f and an ideal inductance L, in thermal contact with a bath at temperature T_f. The "rectifier" is made of two parallel branches, each containing a resistor R_i and an ideal diode D_i in series ($i = 1, 2$), and is in thermal contact with another bath with temperature $T_r \ll T_f$. This inequality is necessary to ensure that electrical fluctuations are essential only in resistor R_f. The "rectifier" plays the role of the guiding mechanism alternating the effective resistance depending on the direction of the current generated by the noisy element.

From Kirchoff second law, the sum of all voltage drops in the main circuit add to zero:

$$V_L + V_f + V_n + V_r = 0, \quad (68)$$

where $V_L = L(dI/dt)$ is the inductive voltage, $V_f = IR_f$ is the voltage drop in R_f, V_n is the noise voltage induced by thermal fluctuations (which, given the condition $T_r \ll T_f$ can be associated with R_f only), and V_r is the total voltage drop in the rectifier. We can then write

$$L\frac{dI}{dt} = -R_f I - V_r + \sqrt{2R_f T_f}\,\xi. \quad (69)$$

To account for the voltage drop in the rectifier, we adopt a sign convention for the electric current: it is positive when it circulates clockwise, and negative when the circulation is counterclockwise. Given that the diodes are considered ideal,

we have

$$V_r = \Theta(I)R_2 I + [1 - \Theta(I)]R_1 I, \tag{70}$$

where $\Theta(\bullet)$ denotes the Heaviside step function with $\Theta(0) = 1/2$. Then we can write $\Theta(I) = [1 + \mathrm{sgn}(I)]/2$, which leads to the equivalent result:

$$V_r = \left[\frac{R_2 + R_1}{2} + \frac{R_2 - R_1}{2}\mathrm{sgn}(I)\right] I. \tag{71}$$

We then obtain

$$L\frac{dI}{dt} = -\left[R_f + \frac{R_2 + R_1}{2} + \frac{R_2 - R_1}{2}\mathrm{sgn}(I)\right] I + \sqrt{2R_f T_f}\xi, \tag{72}$$

which can be now rewritten as

$$L\dot{I} = -R_e[1 + \epsilon\,\mathrm{sgn}(I)]I + \sqrt{2R_e T_e}\xi. \tag{73}$$

The effective parameters are $R_e = R_f + (R_1 + R_2)/2$, $T_e = 2R_f T_f/(2R_f + R_1 + R_2)$ and $\epsilon = (R_2 - R_1)/(2R_f + R_1 + R_2)$ (note that $R_f T_f = R_e T_e$). As the analogy between (12) in the absence of load and (73) is complete, the circuit in Fig. 4 should be able to generate a directed current by rectifying thermal fluctuations; the guiding is then ensured by the device maintaining the temperature difference between the "fluctuator" and the "rectifier."

VIII. CONCLUSIONS

We presented an explicitly solvable model of an externally guided active particle which exploits a "strong" mechanism of DB breaking to achieve directional drift. This model appears naturally if one makes the simplest assumptions about a coupling between mechanical degrees of freedom and a chemical reaction, involving a vectorial guiding and scalar fueling. Our model is simple enough as to be treated mostly analytically. We rigorously analyzed the overdamped limit of our model, finding an emergent slow dynamics that has been phenomenologically postulated in previous studies of Brownian motors. We also computed the hidden contributions to all the relevant thermodynamic observables in that limit. One of the most important results of our study is the definition of efficiency extending the idea of Stokes efficiency to stall conditions.

There are many interesting directions along which this work can be extended. The first natural step is to allow the guiding vector **m** to fluctuate in space and time. Such a situation may be relevant to study chemotaxis from a microscopic perspective. Then studying in detail the full chemical dynamics (i.e., relaxing the assumption of fast chemistry) in the presence of imperfect sensing may help to build bridges between the stochastic thermodynamics of feedback-controlled systems and chemotaxis. Further developments should include the study of collective dynamics involving many interacting guided active particles and the development of the corresponding continuum theory.

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