On Optimizing Energetic Cost of Noise Reduction in Systems with Negative Feedback

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Many biological functions require the dynamics to be necessarily driven out-of-equilibrium. In contrast, in various contexts, a nonequilibrium dynamics at fast timescales can be described by an effective equilibrium dynamics at a slower timescale. In this work we study the two different aspects (i) the energy-efficiency trade-off for a specific nonequilibrium linear dynamics of two variables with feedback, and (ii) the cost of effective parameters given by the “hidden” dissipation and entropy production rate in the effective equilibrium limit of the dynamics. To meaningfully discuss the trade-off between the energy consumption and the efficiency of the desired function a one-to-one mapping between function(s) and energy input is required. The function considered is the variance. A one-to-one mapping between is obtained by calculating the minimum variance achieved under the constraint of fixed entropy production rate and vice-versa. We find that this minimum variance (entropy production rate) is a monotonically decreasing (increasing) function of the given entropy production rate (variance). When there is a timescale separation, in the effective equilibrium limit, the cost of the effective potential and temperature is the associated “hidden” entropy production rate which depends on the parameters of the fast variables and can be optimized the same way as the full nonequilibrium dynamics.

I. INTRODUCTION

Adaptation, kinetic proofreading, and motor transport are some examples of processes in biological systems that are necessarily out-of-equilibrium, hence, it requires a finite rate of energy input \[1\,2\]. Does an increase in the energy input lead to an increase in the efficiency of the desired function(s) in such systems? In adaptation dynamics, the trade-off between adaptation error, energy input, and the timescales has been shown to exist \[3–6\]. Similar relations for circuits with negative feedback have also been proposed \[7–8\]. In kinetic proofreading the relation between discrimination efficiency, time, and energy consumption has been established \[9,10\]. The directed motion of motor proteins necessarily consumes energy \[11\]. The cell’s efficiency to estimate the concentration of ligand improved with an increase in energy consumption. \[12–15\]. However, in a recent study, it has been shown that for some of the above-mentioned cases an increase in energy dissipation may lead to a decrease in function efficiency \[16\].

Through an example of a linear model of negative feedback, we show that a meaningful discussion of the trade-off requires a one-to-one mapping between the function(s) and the energy dissipation. To obtain a one-to-one mapping a well-defined optimization problem needs to be posed. This is done by first optimizing the function for given energy input and then studying this optimum as the value of the energy input is changed.

A contrasting situation to the process which needs to be necessarily out-of-equilibrium to perform a task is posed by the processes which, at timescales of interest, can be successfully modeled using equilibrium processes. The underlying processes at faster timescales, however, can be nonequilibrium and hence energy-consuming. Such an effective equilibrium description of a nonequilibrium process obtained by integrating out the fast degrees-of-freedom has been studied in various contexts in active matter \[17–20\]. The resulting effective equilibrium is described by the remaining slow variables with effective parameters that retain some memory of the integrated out fast variables. The steady-state entropy production rate (EPR) and heat dissipation rate (HDR) is zero, however, the limiting value of the EPR obtained from the full dynamics, in general, may be nonzero. This difference in EPR and HDR has been referred to as “hidden” EPR (HEPR) and “hidden” HDR (HHDR) \[21–27\]. The HHDR and HEPR can be thought of as the cost of generating effective parameters.

In this work, we study the two different aspects, (i) the energy-efficiency trade-off for a specific nonequilibrium model, and (ii) the cost of effective parameters given by the “hidden” dissipation and entropy production rate in the coarse-grained theory. We consider a linear nonequilibrium dynamics of two variables \((x, y)\) with and without feedback. The dynamics is nonequilibrium due to the non-conservative forces acting of the two variables and they are driven by fluctuations from two different temperature baths. Of particular interest is the case of negative feedback which is relevant for various biological circuits, for instance, as a mechanism to reduce noise \[28–30\], homeostasis \[31\], and adaptation \[8\]. In this work, the function considered for analyzing the efficiency is the noise reduction, i.e., the variance of the variables \(x\), and the associated cost is given by the HDR and EPR. When there is a timescale separation between the two variables, an effective equilibrium limit is obtained by integrating out the fast variable \((y)\). To compare with different models we take the mobility and the temperature of the fast variable to scale differently.

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The main results are that in the presence of feedback the variance of $x$ and the EPR can be tuned independently. A one-to-one mapping between the function and the cost is obtained by calculating the minimum variance that can be achieved for a given EPR and vice-versa. We find that this minimum variance (EPR) is a monotonically decreasing (increasing) function of the given EPR (variance) given by Eq. 12. This shows that, in this example, there is a clear trade-off between the variance of $y$ and $y$ is made explicitly by $\tau \epsilon$ dynamics is linear noise approximation. In this limit the stochastic driving is due to a fluctuating potential and an effective temperature, the associated cost is the HEPR which depends upon the parameters of the fast variables and can be optimized the same way as the full nonequilibrium dynamics.

In the following, we first discuss the feed-forward case and then processed to the dynamics with feedback.

II. PARTICLE DRIVEN BY AN ORNSTEIN-UHLENBECK PROCESS

We first consider a feedforward dynamics where $x$ is driven by $y$ but $y$ is independent of $x$. The dynamics is taken to be linear which can be thought of as an expansion of a nonlinear dynamics around a steady state in linear noise approximation. In this limit the stochatic dynamics is

$$\dot{x} = -\mu_1 (x - \alpha y) + \sqrt{2\lambda_1 \mu_1} \xi_i (t), \quad (1)$$
$$\dot{y} = -\frac{\mu_0}{\tau} y + \frac{1}{\tau \epsilon} \sqrt{2\lambda_0 \mu_0} \xi_0 (t), \quad (2)$$

where $\xi_i (t)$ and $\xi_1 (t)$ are Gaussian white noise of zero mean and unit variance $\langle \xi_i (t) \xi_j (t') \rangle = \delta_{ij} \delta(t - t')$, where $i, j \in 0, 1$. The separation of timescale between $x$ and $y$ is made explicitly by $\tau$. In general, the correlation time of $y$ and its variance may scale differently with $\tau$, this difference in scaling is captured by $\epsilon$: the mobility scales as $\tau^{-1}$ and the fluctuation scales as $\tau^{1-2\epsilon}$. From Eq. 2 the correlation function $\langle y(t) y(t') \rangle = \tau^{1-2\epsilon} \lambda_0 \mu_0 \exp(-\tau(t-t')/\mu_0)$. The two choices of $\epsilon$ commonly used in literature are $\epsilon = 1/2$ and $\epsilon = 1$. In ref. 21 where the stochastic driving is due to a fluctuating potential the dynamics under fast switching corresponds to the Langevin Eq. 1 and 2 with $\omega = \lambda_0 / \mu_0$ and the timescale separation is due to the coupling to $\lambda_0$ through $y$. Without explicit timescale separation this EPR has been obtained in various other contexts [21, 27, 36, 37].

Effective equilibrium limit: In the limit $\tau \rightarrow 0$ and $\epsilon \leq 1$ (for $\epsilon > 1$ the adiabatic limit does not exist) the two-variable nonequilibrium dynamics reduces to the following effective equilibrium dynamics:

$$\dot{x} = -\mu_1 x + \sqrt{2\lambda_0 \mu_1} \xi, \quad (9)$$

where the effective temperature is

$$\frac{\lambda_0 \mu_0}{\lambda_1} = \left\{ \begin{array}{ll} 1, & \epsilon < 1, \\ \frac{1}{1 + \frac{\mu_0 \alpha^2 \lambda_0}{\mu_1 \lambda_1}}, & \epsilon = 1. \end{array} \right. \quad (10)$$

From Eq. 4 the mean $\langle x \rangle = 0$. The steady state variance of $x$ is given by

$$\langle x^2 \rangle_{ff} = \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \tilde{C}_{xx} (\omega), \quad (4)$$

where the tilde denotes the Fourier defined as $\tilde{\phi}(\omega) = \int_{-\infty}^{\infty} dt e^{i\omega t} \phi(t)$. The subscript "ff" denoting feedforward dynamics. Obtaining the correlation spectrum from Eq. 12 and using Eq. 4 the steady state variance of $x$ is given by

$$\langle x^2 \rangle_{ff} = \lambda_1 + \frac{\mu_1 \alpha^2 \lambda_0 \tau^{2-2\epsilon}}{\mu_0 + \mu_1 \tau}, \quad (5)$$

where the first term is the variance is the direct contribution due to fluctuation source $\lambda_1$ and the second is due to the coupling to $\lambda_0$ through $y$.

The linear response function for a small force $\delta f_p$ is defined as 33

$$\langle x - \langle x \rangle \rangle_{\delta f} = \int \chi_x (t - t') \delta f_p (t') dt', \quad (6)$$

where the averages are over the perturbed dynamics. Eq. 1 and Eq. 2 give $\chi_x = 1/(i\omega + \mu_1)$. From the response and correlation function the heat dissipation rate can be obtained using the Harada-Sasa relation with zero mean velocity, which reads as 34 35

$$h_x = \frac{1}{\mu_1} \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \left( \omega^2 \tilde{C}_{xx} (\omega) - 2\omega \lambda_1 \chi_x'' (\omega) \right), \quad (7)$$

where we have used the relation $\tilde{C}_{uv} = \omega^2 \tilde{C}_{xx}$ and $\chi'' = \omega \chi''$. Note that we have used $\lambda_1$ as the temperature of the heat bath connected to $x$. In case $\lambda_1$ includes thermal contributions then the corresponding fast degrees-of-freedom need to be included to obtain correct EPR and HDR. Since there is no feedback of $x$ on $y$ the HDR corresponding to variable $y$ is zero.

The EPR $\sigma = h_x / \lambda_1$ using Eq. 7 is

$$\sigma = \frac{\lambda_0 \mu_0}{\lambda_1} \frac{\alpha^2 \tau^{1-2\epsilon}}{\lambda_1 (\mu_0 + \mu_1 \tau)}. \quad (8)$$

Without explicit timescale separation this EPR has been obtained in various other contexts [21, 27, 36, 37].

Effective equilibrium limit: In the limit $\tau \rightarrow 0$ and $\epsilon \leq 1$ (for $\epsilon > 1$ the adiabatic limit does not exist) the two-variable nonequilibrium dynamics reduces to the following effective equilibrium dynamics:

$$\dot{x} = -\mu_1 x + \sqrt{2\lambda_0 \mu_1} \xi, \quad (9)$$

where the effective temperature is

$$\frac{\lambda_0 \mu_0}{\lambda_1} = \left\{ \begin{array}{ll} 1, & \epsilon < 1, \\ \frac{1}{1 + \frac{\mu_0 \alpha^2 \lambda_0}{\mu_1 \lambda_1}}, & \epsilon = 1. \end{array} \right. \quad (10)$$
The variance \( \langle x^2 \rangle_H = \lambda_{\text{eff}} \). The EPR corresponding to Eq.\[9\] is zero, however, \( \Delta \sigma = \lim_{\tau \to 0} \sigma \neq 0 \), where \( \Delta \sigma \) is the HEPR given by

\[
\frac{\Delta \sigma}{\mu_1} = \left\{ \begin{array}{ll}
0 & \epsilon < 1/2, \\
\lambda_0 \alpha^2 / \lambda_1 & \epsilon = 1/2, \\
\infty & \epsilon > 1/2.
\end{array} \right.
\] (11)

We see that \( \Delta \sigma \) is finite only for \( \epsilon \leq 1/2 \). Consistent with \[21\] we get finite EPR for \( \epsilon = 1/2 \), which depends on the parameters of the fast variable even though effective dynamics in Eq.\[5\] does not. For \( \epsilon > 1/2 \) faster degrees of freedom like inertial relaxation needs to be included, this introduces a high frequency cut-off leading to a finite EPR \[27\].

Fluctuation and dissipation rate: From Eq.\[5\] and Eq.\[8\] we get a one-to-one mapping between the variance of \( x \) and entropy produced over the timescale \( \tau / \mu_0 \) which reads as

\[
\frac{\langle x^2 \rangle_H}{\lambda_1} = 1 + \frac{\tau}{\mu_0} \sigma.
\] (12)

For a given timescale increase in EPR leads to increase in the fluctuation.

III. WITH FEEDBACK

We now consider the dynamics with feedback. As before, the dynamics is linearized around the steady state of the non-linear dynamics. The stochastic dynamics we consider is

\[
\dot{x} = -\mu_1 (x - \alpha y) + \sqrt{2\lambda_1 \mu_1} \xi_1(t),
\] (13)

\[
\tau \dot{y} = -\mu_0 (y - kx) + \tau^1 - \epsilon \sqrt{2\lambda_0 \mu_0} \xi_0(t),
\] (14)

where, same as before, \( \xi_1(t) \) and \( \xi_0(t) \) are Gaussian white noise of zero mean and unit variance, \( \alpha \) and \( k \) are the feedback parameters, and the separation of timescale between the variables is made explicit through \( \tau \) and \( \epsilon \). The dynamics is stable for \( k \alpha < 1 \). Fig. \[1\](a) shows the stable regions and the schematic of the feedback in \( k \) and \( \alpha \) parameter space. For \( k \alpha > 0 \) the feedback is positive and for \( k \alpha < 0 \) the feedback is negative.

In various biological contexts, negative feedback is a mechanism to reduce the variance. Since negative feedback is necessarily out-of-equilibrium, in this work, the function considered for energy-efficiency trade-off is the variance of \( x \).

The steady state variance of \( x \) after substituting correlation spectrum obtained Eq.\[13\]-\[14\] in Eq.\[3\] and integrating is

\[
\langle x^2 \rangle_{H'} = \frac{\lambda_1 \mu_1 \tau}{\mu_0 + \mu_1 \tau} + \frac{\mu_0 \lambda_1 + \alpha^2 \tau^2 - 2\epsilon x \lambda_0 \mu_1}{(1 - k \alpha)(\mu_0 + \mu_1 \tau)}.
\] (15)

The HDR corresponding to variable \( x \) is given by Eq.\[7\] which upon substituting correlation and response functions obtained from Eq.\[13\]-\[14\] and integrating gives

\[
h_x^f = \frac{\mu_0 \mu_1}{\mu_0 + \mu_1 \tau} \left( \tau^{1 - 2\epsilon} \lambda_0 \alpha^2 - k \alpha \lambda_1 \right).
\] (16)

The first term in the bracket is the heat dissipation rate in bath \( \lambda_1 \) due to the driving by bath \( \lambda_0 \) and the second term is the dissipation due to feedback.

In contrast to feedforward case, the HDR corresponding to the variable \( y \) is now nonzero. Taking the effective temperature corresponding to \( y \) as \( \tau^{1 - 2\epsilon} \lambda_0 \), the HDR of \( y \) using Harada-Sasa relation is given by

\[
h_y = \frac{\tau}{\mu_0} \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \left( \omega^2 C_{gg}(\omega) - 2\omega \lambda_0 \tau^{1 - 2\epsilon} \tilde{\tilde{\chi}}_{y}(\omega) \right).
\] (17)

Upon substituting the correlation and the response function obtained from Eq.\[13\]-\[14\] in Eq.\[17\] and integrating we get

\[
h_y^f = \frac{\mu_0 \mu_1}{\mu_0 + \mu_1 \tau} \left( \lambda_1 k^2 - k \alpha \lambda_0 \tau^{1 - 2\epsilon} \right).
\] (18)

Similar to \( x \), the first term in the bracket is the dissipation rate due to the driving from the bath \( \lambda_1 \) and the second term is due to the feedback. The total HDR \( h^f = h_x^f + h_y^f \), which upon substitution gives

\[
h^f = \left( 1 - \frac{k}{\alpha} \right) h_x^f,
\] (19)

and the total EPR is given by

\[
\sigma^f = \frac{h_x^f}{\lambda_1} + \frac{h_y^f}{\lambda_0 \tau^{1 - 2\epsilon}},
\] (20)

which upon substituting Eq.\[16\] and Eq.\[18\] gives

\[
\sigma^f = \frac{\tau^{2\epsilon - 1} \mu_0 \mu_1 \lambda_1 k - \tau^{1 - 2\epsilon} \lambda_0 \alpha \lambda_1 \alpha^2}{\lambda_1 \lambda_0 (\mu_0 + \mu_1 \tau)}.
\] (21)

As we did for the feedforward case, we first look at the limit \( \tau \to 0 \). We then analyze the relationship between EPR and variance of \( x \).
A. Effective equilibrium limit

Similar to feedforward case, in the limit \( \tau \to 0 \) and \( \varepsilon \leq 1 \) we get the following effective one-variable dynamics:

\[
\dot{x} = \mu_1 (1 - k \alpha) x + \sqrt{\lambda_{\text{eff}} \mu_1 \xi},
\]

where \( \lambda_{\text{eff}} \) is given by Eq. [10]. The effect of feedback is apparent in the stiffness of the harmonic potential along with the effective temperature. The steady state variance of \( x \) from Eq. [22] is

\[
\lim_{\tau \to 0} \langle x^2 \rangle_{\text{fb}} = \frac{\lambda_{\text{eff}}}{(1 - k \alpha)}. \tag{23}
\]

The EPR corresponding to Eq. [22] is zero, however, \( \Delta \sigma = \lim_{\tau \to 0} \sigma_{\text{fb}} \neq 0 \), where \( \Delta \sigma \) is the “hidden” EPR obtained from Eq. [21] is given by

\[
\Delta \sigma \over \mu_1 = \left\{ \begin{array}{ll}
\infty & \varepsilon \neq 1/2, \\
\frac{\lambda_1 k - \lambda_0 \lambda_0 \alpha^2}{\lambda_1 \lambda_0} & \varepsilon = 1/2.
\end{array} \right. \tag{24}
\]

In the following, we focus on the physically relevant case of \( \varepsilon = 1/2 \). Unlike the feedforward case, the variance in the effective theory depends upon the parameters of the integrated out variable. We see that for a given timescale \( \mu_1 \) there is no one-to-one mapping between the EPR and the variance. For a given EPR the variance can be tuned by changing the feedback parameters. However, a one-to-one mapping is obtained when the question is set as a well-defined optimization problem. What is the minimum value of variance for a given entropy production rate and timescale? For a given value of \( S^* = \Delta \sigma / \mu_1 \) the variance has a minimum as function of \( k \) and \( \alpha \) by

\[
\Lambda^* = \frac{4}{4 + S^*}, \tag{25}
\]

where \( \Lambda^* = \min\left(\langle x^2 \rangle_{\text{fb}} / \lambda_1 \right) \). Thus we see that for given effective temperature \( \lambda_1 \) and \( \lambda_0 \) there is a one-to-one mapping between the minimum of the variance and \( \Delta \sigma / \mu_1 \). Specifically, \( \min\left(\langle x^2 \rangle_{\text{fb}}\right) \) is a monotonically decreasing function of the EPR. Inverting Eq. [25] gives the relation between the minimum EPR required for a given variance \( \Lambda^* \) as \( S^* = 4 \left(1/\Lambda^* - 1\right) \). When \( \Lambda^* > 1 \) the \( S^* = 0 \). For \( \lambda < 1 \) there is a minimum HEPR required. The dissipation in the medium is given by the total heat dissipation rate by \( \tau \to 0 \) limit in Eq. [19]. The minimum dissipation defined as \( H^* = \min\left(\lim_{\tau \to 0} h_{\text{fb}} / \mu_1 \lambda_1 \right) \) required for a given variance \( \Lambda^* \) is

\[
H^* = \frac{(1 + \sqrt{r})^2}{4} S^*, \tag{26}
\]

thus we see that the dissipation depends on the temperature of the fast variable. We now analyze the same for the full dynamics.

B. Fluctuation and the Dissipation rate

To analyze the general case, where there is no timescale separation, we set \( \tau = 1 \). Using the definition \( r \equiv \lambda_0 / \lambda_1 \) and \( d \equiv \mu_1 / \lambda_0 \) Eq. [15] reads

\[
\frac{\langle x^2 \rangle_{\text{fb}}}{\lambda_1} = \frac{(1 + d) + d \alpha (\alpha r - k)}{(1 - k \alpha)(1 + d)}. \tag{27}
\]

It can be shown that the variance \( \langle x^2 \rangle_{\text{fb}} \) is a monotonically increasing function of \( r, k \) and a monotonically decreasing function of \( d \); the variance is non-monotonic in \( \alpha \) and has a minimum for \( \alpha = 1 - \sqrt{(k^2 + d r)/2 k^2 d r} \). Fig. [1(b)] show the effect of feedback on the variance. As well established, negative feedback leads to reduced variance, i.e., \( \langle x^2 \rangle_{\text{fb}} < \langle x^2 \rangle_{\text{ff}} \). Moreover, in a sub-region of the negative feedback parameter space (shown in green) between the line \( \alpha \lambda_0 \mu_1 = -k \lambda_1 \mu_0 \) and \( r = 0 \), \( \langle x^2 \rangle_{\text{fb}} < \lambda_1 \). In the stable regions of the first and third quadrant the feedback is positive \( (k \alpha > 0) \) and the fluctuation is larger than that without feedback, i.e., \( \langle x^2 \rangle_{\text{fb}} > \langle x^2 \rangle_{\text{ff}} \). The EPR in Eq. [21] for \( \tau = 1 \) reduces to

\[
\frac{\sigma_{\text{fb}}^2}{\mu_1} = \frac{(k - r \alpha)^2}{r(1 + d)}. \tag{28}
\]

The minimum value of EPR is \( \sigma^2_{\text{fb}} = 0 \) for \( \alpha \lambda_0 = k \lambda_1 \), for this value the fluctuation dissipation relation is satisfied, hence, the dynamics can be mapped to the following
effective equilibrium model
\[ \dot{x} = -\mu_1 (x - \alpha y) + \sqrt{2\lambda_1 \mu_1 \xi_1(t)}, \] (29)
\[ \dot{y} = -\mu (ry - \alpha x) + \sqrt{2\lambda_1 \mu_\alpha(t)}, \] (30)
where \( \mu = \mu_0 \frac{\lambda_0}{\lambda_1} \). This mapping is not unique, equivalent models are obtained by scaling of the mobility and the effective temperature. The total heat dissipation rate is given by
\[ \frac{h^{\text{th}}}{\mu_1 \lambda_1} = \frac{(\alpha - k)(\alpha - k)}{(1 + d)}. \] (31)

Energy-efficiency trade-off: Does increase in entropy production rate lead to a decrease in the variance? It is clear form Eq. 28 and Eq. 27 that there is no one-to-one mapping between the two. Fig. 2, which shows the fluctuation and the EPR along different sections of the parameter space. Along the line \( \alpha \lambda_1 \mu_0 = -k \lambda_0 \mu_1 \) for which the fluctuation is constant \( \langle x^2 \rangle_{\text{th}} = \lambda_1 \) and the EPR changes with minimum for \( k = \alpha = 0 \). Contrary can be observed along the line \( \lambda_0 \alpha = k \lambda_1 \) along with the EPR is zero and the fluctuation changes with minimum at \( k = \alpha \) shown in Fig. 2(b). In general, we can find regimes where the fluctuation decrease with an increase in EPR as well as fluctuation increase with an increase in EPR (Fig. 2 d, e).

As discussed in the effective-equilibrium limit, there is a one-to-one mapping between the minimum variance for a given EPR and timescale and vice-versa. We calculate the minimum energy dissipation required to attain a fluctuation. For \( \min(\langle x^2 \rangle_{\text{th}}) > \lambda_1 \) the minimum EPR required is zero. For \( \min(\langle x^2 \rangle_{\text{th}}) < \lambda_1 \) a finite EPR is required that is given by
\[ S^* = 4\Lambda^*(1 - \Lambda^*) \frac{(1 + d)}{(1 + d) \Lambda^* - d^2}. \] (32)

where \( S^* = \sigma / \mu_1 \) and is independent of \( r \), for \( d \to 0 \) this reduces to the one-variable limit in Eq. 25. The minimum fluctuation for a given EPR is obtained by inverting this equation. Fig. 3 shows that the minimum variance is a monotonically decreasing function of the entropy production rate. This shows that in this particular case more dissipation is required to gain a function. The minimum fluctuation obtained for zero EPR is \( \lambda_1 \), \( \lim_{x \to 0} \min(\langle x^2 \rangle_{\text{th}}) = \lambda_1 \) and \( \lim_{x \to \infty} \min(\langle x^2 \rangle_{\text{th}}) = d \lambda_1 / (1 + d) \).

We emphasize that here we have taken the constraint to be the EPR, the dissipation in the two temperature baths is given by the total heat. For \( r = 1 \) this is given by \( H^* = \lambda_1 S^* \). When \( r \neq 1 \) the minimum dissipation can be obtained by minimizing Eq. 31 for a given variance.

C. Conservative vs. Non-Conservative Coupling

The dynamics given by Eq. 13 and Eq. 14 is out-of-equilibrium due to the non-conservative coupling between

\[ x \text{ and } y \text{ and that due to the difference of the effective temperature of the two baths } (\lambda_1 \neq \lambda_0). \] The dynamics when the coupling is conservative is of the form
\[ \dot{x} = \mu_1 d_x \Phi(x, y) + \sqrt{\lambda_1 \mu_1 \xi_1(t)}, \] (33)
\[ \dot{y} = \mu_0 d_y \Phi(x, y) + \frac{1}{r} \sqrt{\lambda_0 \mu_0 \xi_0(t)}. \] (34)

For \( \lambda_1 = \lambda_0 \), the steady state is given by the Boltzmann distribution \( P(x, y) \propto e^{-\beta \Phi(x, y)} \) and the EPR is zero. For \( \lambda_1 \neq \lambda_0 \) there is finite EPR and HDR at steady state, however, the total heat flow must be zero the heat flows from the “hotter” to the “colder” path [38, 39]. For Eq. 13 and Eq. 14 the coupling is conservative only when \( k = \alpha \) for which \( \Phi = x^2 / 2 + y^2 / 2 + k xy \). In this case \( h^th_x + h^th_y = 0 \). When the coupling is non-conservative \( (k \neq \alpha) \) the total heat flow is nonzero. This implies that there are variables that are not included explicitly in the dynamics but implicit through the non-conservative coupling which acts as an energy source.

Fig. 3 shows the sign of heat flow. The total heat \( h^th_x + h^th_y = 0 \) when the coupling is conservation \( (k = \alpha) \) and when the dynamics can be mapped to an effective equilibrium dynamics \( (\lambda_0 \alpha = k \lambda_1) \). In the region between these two lines \( h < 0 \) (shown in green), i.e, there is a net heat flow of the system. In the rest of the parameter space, there is net heat flow into the system.

A physical example of non-conservative coupling is hydrodynamic interaction in the presence of nonequilibrium fluctuations [40, 42] and effective interaction between chemically interacting particles [43]. Generally, the models analyzed in signaling and gene networks are effective and include non-conservative coupling.

IV. DISCUSSION

In summary, we consider two interacting particles \( x \) and \( y \) that are driven out-of-equilibrium by non-conservative forces and connected to different temperature baths. We calculate the steady state variance of \( x \),
heat dissipation, and entropy production rate when the coupling between the particles is feedforward and when there is feedback.

An effective one-particle description is obtained when there is a separation of timescales between the dynamics of the two particles. In this limit, the parameters of the slow variable $x$ depend upon its coupling with the integrated out fast variable $y$. For the feedforward case, the effective parameter is the effective temperature. In the presence of feedback, the effective theory is described by an effective potential along with the effective temperature. The “hidden” entropy production rate for the two cases with and without feedback depends upon the relative scaling of the temperature $\lambda_0$, the mobility $\mu_0$ of the fast variable $y$, and the feedback parameters. The HEPR is the cost associated with the effective parameters in the coarse-grained equilibrium theory. When there is feedback is negative large stiffness of the effective potential (smaller variance) requires larger HHDR and HEPR.

In absence of the timescale separation, the variance of $x$, the EPR, and the HDR depends on the ratio of the timescales $(d = \mu_1/\mu_0)$. The lower bound on the variance is set at $d/(1 + d)$. Negative feedback is always out-of-equilibrium and for suitable values of the parameter, it leads to a reduction of variance in comparison to the independent dynamics.

Does an increase in energy dissipation always lead to improve in function (variance of $x$)? We find that for a given timescale the relation between EPR and variance could be very heterogeneous. For instance, the EPR can be changed without affecting the variance and vice-versa or even opposite trends can be observed. A similar observation has been made in ref. [10] which contradicts the results in ref. [3] where the later shows a trade-off between speed-energy-error and the former shows that the efficiency does not always improve with an increase in energy. In this paper, we argue that the trade-off problem in these studies is ill-posed since there is no one-to-one mapping possible between function(s) and energy consumption without setting up a well-defined optimization problem. This will become even more obvious for a higher dimensional problem involving more variables and parameters.

A one-to-one mapping between the energy dissipation and efficiency is obtained by minimizing the dissipation as a function of variance or vice-versa. We find that there is a minimum entropy production rate required to decrease the variance below its value in absence of feedback and this minimum value increases with a decrease in the variance. Thus for the case of a reduction of fluctuation by negative feedback the more the energy input the lower the variance that can be attained. However, it is far from clear that any function which requires the dynamics to be necessarily out-of-equilibrium will lead to such energy-efficiency relation. A more general analysis in a higher dimension will be a useful future direction to explore.

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