Thermodynamic uncertainty relation of interacting oscillators in synchrony

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The thermodynamic uncertainty relation sets the minimal bound of the cost-precision tradeoff relation for dissipative processes. Examining the dynamics of an internally coupled system that is driven by a constant thermodynamic force, we, however, find that the tradeoff relation of a subsystem is not constrained by the minimal bound of conventional uncertainty relation. We made our point explicit by using an exactly solvable model of interacting oscillators. As the number (N) of interacting oscillators increases, the uncertainty bound of individual oscillators is reduced to $2k_BT/N$ upon full synchronization under strong coupling. The cost-precision tradeoff for interacting subsystems is particularly relevant for subcellular processes where interactions among multiple energy-expending components lead to emergence of collective dynamics.

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I. INTRODUCTION

Orders that emerge in life are maintained via exchanges of energy, matter, and information with the environment [1,2]. The recent advances in stochastic thermodynamics [3–5] underscores the interplay between energy, information, and their tradeoffs in small systems out of equilibrium, epitomized by diverse biological processes [6–15]. To maintain a dissipative process at nonequilibrium steady states (NESS), free energy consumption (or heat dissipation), $q(\tau)$, is bound to the precision of time-integrated output observable, $\theta(\tau)$, that characterizes the process [8,9]. The thermodynamic uncertainty relation (TUR) concisely recapitulates this tradeoff relation and specifies its minimal bound [16],

$$\mathcal{Q} \equiv \langle q(\tau)\rangle \frac{\langle \delta\theta(\tau)^2\rangle}{\langle \theta(\tau)\rangle^2} \geqslant \mathcal{Q}_{\min} = 2k_BT, \tag{1}$$

where k_B is the Boltzmann constant, T is temperature, and $\langle\cdots\rangle$ represents an average over an ensemble of many realizations.

Since the TUR was conjectured, general proofs and extension of the relation have been put forward from entirely different perspectives [17–21], which have greatly enriched our understanding of the dynamical processes in nonequilibrium. Further, analyses of experimental data exploiting the idea of TUR shine new light on problems associated with biological physics [22]. It is remarkable that the thermodynamic consideration alone can provide a novel understanding into the design principle of molecular machines in an isothermal condition [22,23]. Nonetheless, currently the focus of TUR is on the energetic cost for the operation of a single enzyme and molecular motor, or for a system consisting of multiple energy-consuming modules as a whole. In practice, measurement of energetic cost can be made on a subsystem that interacts with other modules of the whole system; that is, calculation of uncertainty measure $\mathcal{Q}$ can be made for the subsystem. For example, in biological cells, it is often recognized that the individual energy-consuming modules are not in strict isolation, but are coupled with others, displaying collective or cooperative dynamics [24–27].

Studying the cost-precision tradeoffs for internally coupled systems driven by a constant thermodynamic force, one could choose θ_i, an output observable to monitor the time evolution of the ith subsystem, and also measure q_i, the energetic cost to operate the ith subsystem. The uncertainty measure for the subsystem $\mathcal{Q}^{\rm sub} = \mathcal{Q}(q_i, \theta_i)$, which probes the tradeoff between cost q_i and squared relative error in the observable θ_i, $\langle\delta\theta_i^2\rangle/\langle\theta_i\rangle^2$ could, in practice, be a more relevant measure to explore in studying subcellular processes than $\mathcal{Q}(q, \theta_i)$, which considers the energetic cost of operating the whole system $q = \sum_i q_i$.

In this study, we explore the cost-precision tradeoff relation of a subsystem that is energetically coupled with the remaining part of the system as well as its thermal bath of temperature T. To this end, we investigate a concrete example, a system of interacting oscillators under thermal fluctuations (Fig. 1). When individual oscillators are noninteracting and independent from each other, the TUR still holds regardless of which output variable is probed and which part of cost is included for the calculation of uncertainty measure. We, however, show that when the dynamics of interacting oscillators are synchronized, the individual oscillator can achieve, with the same amount of energetic cost, a higher phase precision than the bound dictated by the conventional TUR.

This paper is organized as follows. In Sec. II, we introduce our model of interacting oscillators under thermal fluctuations and present the results of TUR for subsystems using numerical simulations. We explain the results from numerical simulations in light of the analytical solution of the model at limiting cases in Sec. III. We extend our conclusion on TUR to N coupled oscillators in Sec. IV and examine TUR for general collective dynamics in Sec. V. Finally, we discuss our finding in Sec. VI.

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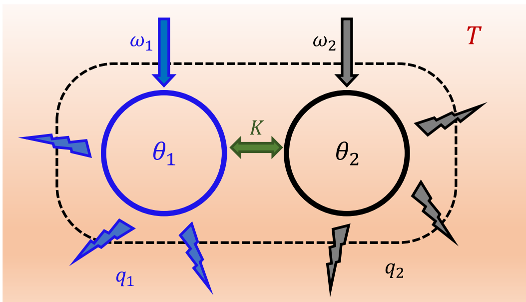

FIG. 1. Two interacting oscillators embedded in a thermal reservoir at temperature T. The motion of each oscillator, described by the phase variable $\theta_{1,2}$, is powered by the inherent frequency $\omega_{1,2}$, corresponding to the nonconservative driving force. The parameter K characterizes the interaction strength between the oscillators, which elicits the synchronization of the phases. The heat dissipated from each oscillator is denoted by $q_{1,2}$.

II. MODEL

As our model system, we adopted the noisy Stuart-Landau oscillator that has recently been used to discuss the tradeoff between the energetic cost and the precision of phase variable [8]. First, the single noisy Stuart-Landau oscillator, in the absence of amplitude-phase coupling, indeed meets the minimal bound $\mathcal{Q}_{\min} = 2k_BT$ (see Appendix A). Next, to study the effect of coupling between two oscillators on the uncertainty relation, we consider the phase dynamics of noisy coupled oscillators [28]:

$$\frac{d\theta_1}{dt} = \omega_1 + \frac{K}{2}\sin(\theta_2 - \theta_1) + \eta_1,$$
$$\frac{d\theta_2}{dt} = \omega_2 + \frac{K}{2}\sin(\theta_1 - \theta_2) + \eta_2, \tag{2}$$

where $\omega_{1,2}$ are the intrinsic frequencies of the two oscillators, K is the coupling strength, and $\eta_{1,2}$ are thermal noises that satisfy $\langle\eta_i(t)\rangle = 0$ and $\langle\eta_i(t)\eta_j(s)\rangle = 2D\delta_{ij}\delta(t-s)$. Here, the noise represents the effect of the thermal bath, whose strength satisfies the Einstein relation, $D = \mu k_BT$. If $\omega_i \ll K$ and $\sqrt{D}$, a condition corresponding to the XY model, strong interaction between the oscillators or large noise suppress the regular oscillation [29]. To impose the NESS condition without phase locking, we mainly consider the parameter range: $|\omega_i| > |K| \gg \sqrt{D}$. Mapped on a Langevin equation, $\dot{\theta}_i = \mu F_i + \eta_i$, where μ is the motility coefficient, which we set to $\mu = 1$ for convenience. The force term F_i of the model is divided into the dissipative (ω_i) and conservative forces [$f_{ji} = (K/2)\sin(\theta_j - \theta_i)$]. Two points are of note: (i) the dissipative forces corresponding to ω_1 and ω_2 are the source of driving; (ii) $f_{12} + f_{21} = 0$ so that the net contribution of the conservative force to the whole system is zero. When the steady state is reached, the heat generated from the oscillator is calculated using [4]

$$q_i(\tau) = \int_0^\tau dt\, F_i(t) \circ \frac{d\theta_i}{dt}, \tag{3}$$

where the notation $\circ$ indicates that the integral was taken in the Stratonovich sense. Note that Eq. (3) amounts to calculating heat dissipated for time interval τ from the hydrodynamic friction experienced by the oscillator with the surrounding solvent molecules in the bath. To examine the uncertainty relation of this system, we calculate the following three quantities:

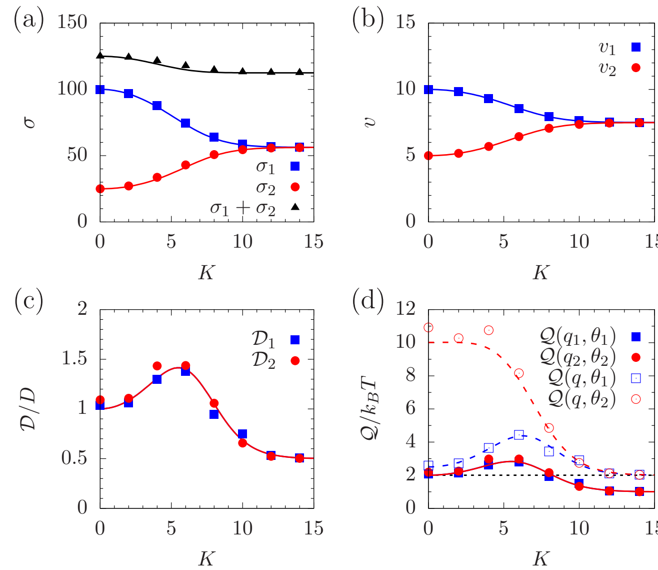

FIG. 2. Thermodynamic uncertainty relations for two coupled oscillators. (a) Heat dissipation rates of two oscillators (blue squares and red circles) and their total heat dissipation rate (black triangles). The two oscillators have intrinsic frequencies of $\omega_1 = 10$ and $\omega_2 = 5$, respectively, and the noise strength is set to $D = 1$. (b) Mean phase velocities of two oscillators. (c) Relative diffusion constants that represent phase fluctuations. (d) The uncertainty measures for the cost-precision tradeoffs calculated for the total systems [$\mathcal{Q}(q, \theta_i)$] and subsystems [$\mathcal{Q}(q_i, \theta_i)$]. The dotted black line represents the usual minimal bound of TUR, $2k_BT$. To compute σ, v, and $\mathcal{D}$, an ensemble of 10^3 realizations of stochastic process are used. The lines depict analytical expressions of σ, v, $\mathcal{D}$, and $\mathcal{Q}$ (see Appendix B).

$$\sigma_i = \lim_{\tau\to\infty} \frac{\langle q_i(\tau)\rangle}{\tau},$$
$$v_i = \lim_{\tau\to\infty} \frac{\langle \theta_i(\tau)\rangle}{\tau},$$
$$\mathcal{D}_i = \lim_{\tau\to\infty} \frac{\langle \delta\theta_i(\tau)^2\rangle}{2\tau}, \tag{4}$$

where σ_i, v_i, and $\mathcal{D}_i$ are the mean heat dissipation rate, mean phase velocity, and effective diffusion constant of the ith oscillator, respectively. Integrating Eq. (2) numerically, we obtain the three quantities as a function of coupling strength K. The two interacting oscillator model is, in fact, exactly solvable (see Appendix A); thus, the results from the numerics (data points in Fig. 2) can also be compared with the analytical expressions (lines in Fig. 2) with no tuning parameter. A few points are worth noting:

(i) In the absence of coupling, the energetic cost to operate each oscillator σ_1 and σ_2 depends on each of the driving frequency ω_1 and ω_2. However, upon synchronization at large K, which slows down the oscillator 1, speeds up the oscillator 2, and converges the mean phase velocities of the two oscillators (v_1 and v_2) [Fig. 2(b)], the amount of cost σ_1 and σ_2 becomes identical [Fig. 2(a)]. Remarkably, the total

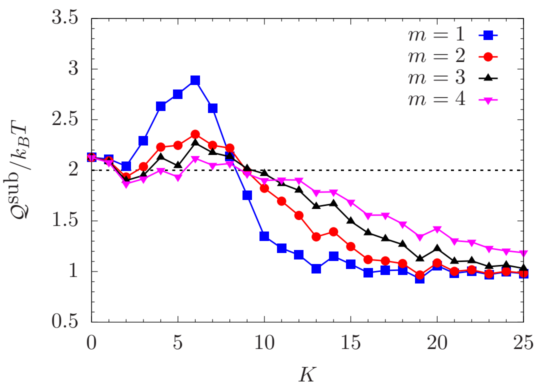

FIG. 3. Thermodynamic uncertainty relation for interaction strengths of the form of $K\sin[m(\theta_j-\theta_i)]$. $\mathcal{Q}^{\rm sub}/k_BT$ for various $m\in\{1,2,3,4\}$ for two coupled oscillators ($N=2$) with intrinsic frequencies, $\omega_1=10$ and $\omega_2=5$. The noise strength is set to $D=1$. To compute the cost-precision tradeoff, we took an average over an ensemble of 10^3 realizations.

energetic cost $\sigma_1+\sigma_2$ to operate the two oscillators under synchronization is smaller than that under small K [30]. This means that more work is required for operating disordered oscillators than ordered oscillators in synchrony.

(ii) In the absence of coupling ($K=0$), the diffusivity of phase variable is determined by the noise strength of the thermal bath ($\mathcal{D}_i=D$). Weak coupling (small K) elicits additional fluctuations in the phase variable [see Eq. (2)], which gives rise to an increase in the diffusivity ($\mathcal{D}_i>D$). Stronger couplings (large K) engendering the phase synchronization reduce the phase fluctuation below the thermal noise strength ($\mathcal{D}_i\to D/2$). The effective diffusivity $\mathcal{D}_i$ is maximized at $K\approx|\omega_1-\omega_2|$ [Fig. 2(c)].

(iii) Combining the three quantities, we evaluate the cost-precision tradeoffs: $\mathcal{Q}(q,\theta_i)=(\sum_j\sigma_j)(2\mathcal{D}_i)/v_i^2$ for the whole system and $\mathcal{Q}(q_i,\theta_i)=\sigma_i(2\mathcal{D}_i)/v_i^2$ for the subsystems. In the absence of coupling ($K=0$), the subsystems behave independently from each other. The uncertainty measure calculated for the heat dissipation and phase fluctuations of a subsystem attains the minimal bound $\mathcal{Q}(q_i,\theta_i)=2k_BT$. The uncertainty measure accounting for the whole heat dissipation is always greater than the minimal bound of the conventional TUR, i.e., $\mathcal{Q}(q,\theta_i)\geqslant 2k_BT$ [Fig. 2(d)] [16]. In marked contrast, once the subsystems are synchronized under strong coupling ($K\gg|\omega_1-\omega_2|$), the minimal bound of the uncertainty measure is reduced to $\mathcal{Q}(q_i,\theta_i)=k_BT$. This implies that without demanding extra thermodynamic cost the interacting oscillators under constant thermodynamic driving can attain a higher precision in the phase variable via synchronization. In the presence of synergetic interactions between the components of the system, the bound of cost-precision tradeoff relation germane to the subsystem can be smaller than $2k_BT$, the conventional bound of TUR. This is the principal finding of this study.

We also numerically confirmed that the conclusion still holds for the higher-order odd trigonometric interactions, $\sin[m(\theta_j-\theta_i)]$ (Fig. 3). This implies that our finding is generalized into interacting oscillators with a general periodic coupling with odd parity, which can be decomposed to a Fourier series in terms of odd harmonics.

III. ANALYSIS

The problem of two coupled oscillators is exactly solvable. Analyses at limiting cases allow us to gain a better understanding of the tradeoff relation of interacting subsystems. A joint probability density $P(\theta_1,\theta_2,t)$ for the noisy coupled oscillators obeys the Fokker-Planck equation, $\partial_tP=-\partial_{\theta_1}J_1-\partial_{\theta_2}J_2$, where $J_i=F_iP-D\partial P/\partial\theta_i$ is a probability current. The steady-state condition $\partial P/\partial t=0$ defines the steady-state current J_i^{ss}. For a given J_i^{ss}, which allows us to calculate $v_i=\int_0^{2\pi}d\theta_1\int_0^{2\pi}d\theta_2J_i^{ss}$ and $\sigma_i=\int_0^{2\pi}d\theta_1\int_0^{2\pi}d\theta_2F_iJ_i^{ss}$. The steady-state current for each oscillator J_i^{ss} is conveniently calculated by using an orthogonal coordinate, $\phi_1=\theta_1+\theta_2$ and $\phi_2=\theta_1-\theta_2$. From Eq. (2), the time evolutions of the orthogonal coordinates are given as

$$\frac{d\phi_1}{dt}=2\bar{\omega}+\xi_1 \tag{5}$$

$$\frac{d\phi_2}{dt}=\Delta\omega-K\sin\phi_2+\xi_2, \tag{6}$$

where $2\bar{\omega}\equiv\omega_1+\omega_2$ and $\Delta\omega\equiv\omega_1-\omega_2$ and $\langle\xi_i(t)\rangle=0$ and $\langle\xi_i(t)\xi_j(s)\rangle=4D\delta_{ij}\delta(t-s)$. Note that Eqs. (5) and (6) are isomorphic to the Brownian motion in tilted periodic potentials, which have recently been used to study the TUR [31], where $\mathcal{Q}$ was shown nonmonotonic with the tilt and its minimal bound was attained at both weak and strong tilt limits. The present result of nonmonotonic dependence of $\mathcal{Q}$ with varying K, demonstrated in Fig. 2(d), is realized in the large tilt limit where the force terms, $2\bar{\omega}$ and $\Delta\omega-K\sin\phi_2$, in Eqs. (5) and (6) are greater than the thermal noise.

Equation (5) straightforwardly leads to $\langle\delta\phi_1(\tau)^2\rangle=4D\tau$. The phase fluctuation $\langle\delta\phi_2(\tau)^2\rangle=4D_{\rm eff}\tau$ under the tilted period potential $V(\phi_2)=-K\cos\phi_2-\Delta\omega\times\phi_2$ is explicitly calculated using [32]

$$\frac{D_{\rm eff}}{D}=\frac{\int_0^{2\pi}d\phi_2I_\mp(\phi_2)I_+(\phi_2)I_-(\phi_2)}{\left[\int_0^{2\pi}d\phi_2I_\mp(\phi_2)\right]^3}, \tag{7}$$

where $I_+(\phi_2)=\exp[V(\phi_2)/2D]\int_{\phi_2-2\pi}^{\phi_2}d\psi\exp[-V(\psi)/2D]$ and $I_-(\phi_2)=\exp[-V(\phi_2)/2D]\int_{\phi_2}^{\phi_2+2\pi}d\psi\exp[V(\psi)/2D]$. The orthogonality condition $\langle\delta\phi_1\delta\phi_2\rangle=0$ leads to $\langle\delta\theta_1^2\rangle=\langle\delta\theta_2^2\rangle=(\langle\delta\phi_1^2\rangle+\langle\delta\phi_2^2\rangle)/4$; thus the phase fluctuations of each oscillator are straightforwardly related to the diffusion constants obtained for the two orthogonal coordinates as

$$\langle\delta\theta_i(\tau)^2\rangle=2\mathcal{D}_i\tau=(D+D_{\rm eff})\tau. \tag{8}$$

In the large K limit, the oscillators are synchronized with a negligible phase difference ($\phi_2=\theta_1-\theta_2\approx0$), which linearizes Eq. (6) to $d\phi_2/dt=\Delta\omega-K\phi_2+\xi_2$. The variance of ϕ_2 from its formal solution is

$$\langle\delta\phi_2(\tau)^2\rangle=\frac{2D}{|K|}[1-\exp(-2|K|\tau)]. \tag{9}$$

Thus, $\langle\delta\phi_2^2\rangle=0$ for $K\gg\Delta\omega$, and $\langle\delta\phi_2^2\rangle=4D\tau$ for $K\to0$.

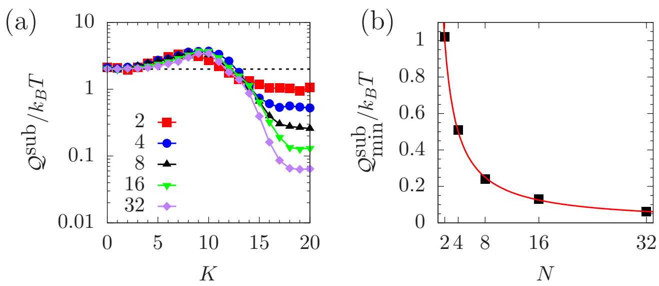

FIG. 4. Thermodynamic uncertainty relations for subsystems of interacting oscillators. (a) $\mathcal{Q}^{\rm sub}/k_BT$ for various numbers ($N = 2, 4, 8, 16, 32$) of oscillators as a function of interaction strength K. Plotted are $\mathcal{Q}^{\rm sub}/k_BT$ averaged over N oscillators. Individual oscillators have intrinsic frequencies sampled from a normal distribution $\mathcal{N}(\bar{\omega}, \Delta\omega)$ with a mean $\bar{\omega} = 10$ and a standard deviation $\Delta\omega = 5$. The noise strength is set to $D = 1$. (b) The minimal bound of $\mathcal{Q}^{\rm sub}$ for large $K \gg \Delta\omega$ ($\mathcal{Q}^{\rm sub}_{\rm min}$) for varying N (data point) is obtained from the simulations of N-oscillator system. The red line depicts $2/N$.

Next, at the two limiting cases of $K \to 0$ and $K \gg \Delta\omega$, the rate of heat dissipation is the square of the mean phase velocity ($\sigma_i = v_i^2$): (i) For weak coupling limit ($K \to 0$), the two oscillators behave independently from each other and oscillate with their own phase velocities $v_i = \omega_i$, which leads to

$$\sigma_i = \omega_i^2; \tag{10}$$

(ii) For strong coupling limit ($K \gg \Delta\omega$), the motion of oscillators is synchronized with the phase velocity of $v_1 = v_2 = (\omega_1 + \omega_2)/2$, which gives rise to the heat dissipation of

$$\sigma_1 = \sigma_2 = \frac{(\omega_1 + \omega_2)^2}{4}. \tag{11}$$

Finally, combining v_i, $\mathcal{D}_i$, and σ_i to calculate $\mathcal{Q}(q_i, \theta_i) = \sigma_i(2\mathcal{D}_i)/v_i^2$, we confirm $\mathcal{Q}(q_i, \theta_i) = 2k_BT$ under weak coupling (small K), whereas $\mathcal{Q}(q_i, \theta_i) = k_BT$ under strong coupling (large K). Note that the reduced minimal bound of cost-precision tradeoff uncertainty measure $\mathcal{Q}(q_i, \theta_i)$ under strong coupling is mainly caused by the reduction in phase fluctuations rather than the changes in heat dissipation or phase velocity (see Fig. 2).

IV. THERMODYNAMIC LIMIT

We generalize Eq. (2) into N-coupled oscillators and explore how the bound of cost-precision relation for subsystems changes with N.

$$\frac{d\theta_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=1}^{N}\sin(\theta_j - \theta_i) + \eta_i, \tag{12}$$

where we assume the driving frequency for the ith oscillator ω_i sampled from a Gaussian distribution with a mean $\bar{\omega}$ and a standard deviation $\Delta\omega$. The numerically calculated $\mathcal{Q}(q_i, \theta_i)$ for the N-interacting oscillators confirms that the bound of TUR for subsystems is lowered by $1/N$ upon full synchronization (Fig. 4). From the numerics, we find that the minimal bound of the uncertainty measure $\mathcal{Q}^{\rm sub}$ for the individual oscillators for large K in the N-interacting system inversely scales with N as

$$\mathcal{Q}^{\rm sub} = \langle q_i(\tau)\rangle \frac{\langle\delta\theta_i(\tau)^2\rangle}{\langle\theta_i(\tau)\rangle^2} \geqslant \mathcal{Q}^{\rm sub}_{\rm min} = \frac{2k_BT}{N}. \tag{13}$$

This finding can be rationalized with ease considering the following argument. In the limit of full synchronization, $\theta_i \approx \theta_j$; hence Eq. (12) can be approximated as $d\theta_i/dt = \omega_i + \sum_j M_{ij}\theta_j + \eta_i$ with the interaction matrix

$$\mathbf{M} = \begin{bmatrix} -K & \frac{K}{N} & \frac{K}{N} & \cdots & \frac{K}{N} \\ \frac{K}{N} & -K & \frac{K}{N} & \cdots & \frac{K}{N} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{K}{N} & \frac{K}{N} & \frac{K}{N} & \cdots & -K \end{bmatrix}. \tag{14}$$

$\mathbf{M}$ has one zero eigenvalue ($\lambda_1 = 0$) with corresponding eigenvector $\phi_1 = \theta_1 + \theta_2 + \ldots + \theta_N$. The other $(N-1)$ eigenvalues are all negative with corresponding eigenvectors, $\phi_i = \theta_1 - \theta_i$ for $i \in \{2, 3, \ldots, N\}$. Then, using $\theta_1 = (\phi_1 + \phi_2 + \ldots + \phi_N)/N$, one can obtain

$$\langle\delta\theta_1(\tau)^2\rangle = \frac{\sum_{i=1}^{N}\langle\delta\phi_i(\tau)^2\rangle}{N^2} \approx \frac{\langle\delta\phi_1(\tau)^2\rangle}{N^2} = \frac{2D\tau}{N}, \tag{15}$$

where we have used $\langle\delta\phi_i^2\rangle \to 0$ for $i \neq 1$ at steady states ($\tau \to \infty$) because their eigenvalues are negative. Furthermore, in the limit of phase synchrony ($\phi_i = \theta_1 - \theta_i \approx 0$), the phase fluctuations are equivalent $\langle\delta\theta_i^2\rangle = \langle\delta\theta_1^2\rangle$ for all i. Since the phase synchrony leads to $\langle q_i\rangle/\tau = \langle\theta_i\rangle^2$, every subsystem achieves the reduced lower bound $\mathcal{Q}^{\rm sub}_{\rm min} = 2k_BT/N$ with the reduced phase fluctuation in Eq. (15).

V. COLLECTIVE DYNAMICS

We note that the in-phase synchrony of interacting oscillators is not a prerequisite for the condition of reduced minimal bound, $\mathcal{Q}^{\rm sub}_{\rm min} \leqslant \mathcal{Q}_{\rm min} (= 2k_BT)$. Although we considered only the positive interaction ($K > 0$) in Eq. (12), the sign of the interaction can be negative ($K < 0$) or a mixture of positive ($K_i = K_+ > 0$) and negative ($K_i = K_- < 0$) depending on the oscillator index i [33]. When two repulsive oscillators with negative interaction strengths are in out-of-phase synchrony [Fig. 5(a)], or when three repulsive oscillators repel each other, forming a splay state [Fig. 5(b)], each oscillator can have an uncertainty bound smaller than $2k_BT$. Furthermore, we confirm the main finding of this study, i.e., the minimal bound of subsystem TUR is less than $2k_BT$ even when both signs of coupling are present in the system forming two clusters, called a cluster state [Fig. 5(c)].

VI. DISCUSSION

Whereas the TUR sets a minimal bound ($\mathcal{Q}_{\rm min} = 2k_BT$) to the energy cost to operate an entire system for a given precision in the output observable, many experimental measurements are often made by focusing on the dynamic process of subsystems. For a system of interacting oscillators, we demonstrated that when the coupling between the oscillators is strong enough to elicit a full synchronization, individual oscillators could achieve a higher phase precision with a reduced net energetic cost.

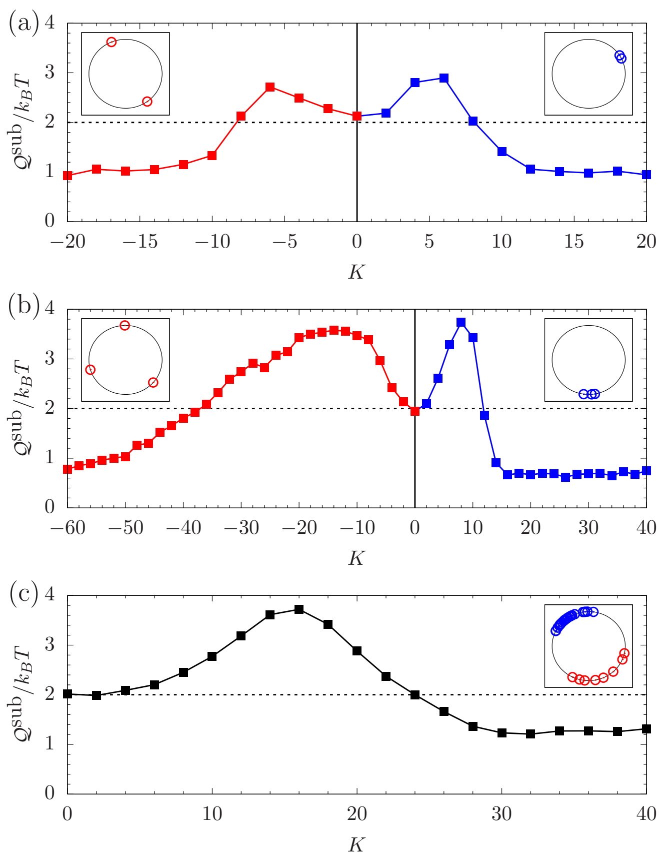

FIG. 5. Subsystem cost-precision tradeoffs for various collective dynamics. (a) Two coupled oscillators ($N = 2$) with intrinsic frequencies $\omega_1 = 10$ and $\omega_2 = 5$ under attractive ($K > 0$) and repulsive ($K < 0$) interactions. (b) Three coupled oscillators ($N = 3$) with intrinsic frequencies $\omega_1 = 15$, $\omega_2 = 10$, and $\omega_3 = 5$ under attractive and repulsive interactions. (c) Thirty-two coupled oscillators ($N = 32$) whose intrinsic frequencies are sampled from a normal distribution $\mathcal{N}(\bar{\omega}, \Delta\omega)$ with a mean $\bar{\omega} = 10$ and a standard deviation $\Delta\omega = 5$. Among them, 24 oscillators ("conformists") have attractive coupling strengths ($K_+ = K$), whereas eight oscillators ("contrarians") have negative coupling strengths ($K_- = -K/2$). The noise strength is set to $D = 1$. To compute the tradeoff, an ensemble of 10^3 realizations of stochastic process are used. Insets represent phase snapshots of attractive oscillators (blue circles) and repulsive oscillators (red circles) at strong coupling regimes.

Our findings on the minimal bound of TUR for subsystems at two extreme interaction strengths ($K = 0$ and $K \to \infty$) are easily rationalized as follows. For $K = 0$, each subsystem is effectively isolated and operates independently from each other, which leads to $\mathcal{Q}^{\rm sub}_{\rm min} = 2k_BT$. At another extreme case when every subsystem operates identically due to strong coupling ($K \to \infty$), the phase dynamics of a subsystem will be characterized with the same precision $\langle\delta\theta_i^2\rangle/\langle\theta_i\rangle^2$, regardless of the oscillator index i, and $q = \sum_i^N q_i = Nq_i$. This gives rise to $\mathcal{Q}^{\rm sub} = \mathcal{Q}(q_i, \theta_i) = \mathcal{Q}(q, \theta_i)/N$ with $\mathcal{Q} \geqslant \mathcal{Q}_{\rm min} = 2k_BT$, and hence we obtain $\mathcal{Q}^{\rm sub}_{\rm min} = 2k_BT/N$. Physically, this is observed because the phase precision of the individual oscillator is benefited by the interaction with other oscillators without incurring extra energetic cost. Over the range of intermediate K, however, $\mathcal{Q}^{\rm sub}$ is maximized at a critical coupling strength K_c. The peak of $\mathcal{Q}^{\rm sub}$ originates from the large fluctuation (diffusivity) of an observable θ_i at K_c, due to extra noise emanating from interaction with the phase θ_j of neighboring oscillators as well as from the thermal noise. Given the dynamics $d\theta_i/dt = \omega_i + K/N\sum_j \sin(\theta_j - \theta_i) + \eta_i$, the role played by the coupling term $[\sin(\theta_j - \theta_i)]$ is twofold: (i) synchronizing the phases of oscillators by reducing their differences; (ii) transferring phase fluctuations from neighboring oscillators. At small $K < K_c$, as the coupling strength K increases, the noise transfer becomes amplified. However, at large $K > K_c$, the first contribution becomes more dominant, which reduces the phase fluctuation.

We note that there is a recent study pointing out that a system represented by stochastic clocks driven by a periodic external protocol can achieve arbitrary precision at arbitrarily low cost [9]. Our scenario that the precision increased by the mutual interaction between subsystems under constant thermodynamic force has not been considered before; yet is quite relevant to experimental situations encountered in subcellular systems [34]. Here, the mutual interaction modeled with sine functions, which leads to the synchronization, is conservative in nature that the net force exchanged between subsystems is compensated to be zero. In general, any periodic coupling with odd parity contributes to a higher phase precision as long as the coupling is sufficiently strong.

The synchronization between interacting oscillators not only reduces total energetic cost to operate the whole system [30], but also enhances the efficiency of power transfer between oscillators [35]. The key finding underscored in this study, the reduction of the bound of cost-precision tradeoff for subsystems through synchronization, sheds light on the design principle underlying biological systems. Cooperative cargo transport by multiple motors [25], force generation by the coordination among muscle proteins [24], and synchronization of bacterial flagellar motors via hydrodynamic coupling [36–38] are the seminal examples that the whole system comprised of multiple energy-expending modules improves the precision of biological function by means of synchronization.

To conclude, our generalized uncertainty relation offers a valuable insight into the tradeoff principle underlying biological processes that have many interacting components. It would also be of great interest to survey the diverse forms of collective dynamics [39] from the perspective of TUR.

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APPENDIX A: THERMODYNAMIC UNCERTAINTY RELATION FOR A STUART-LANDAU OSCILLATOR

Here, we derive the thermodynamic uncertainty relation between heat dissipation and phase precision for a Stuart-

Landau oscillator [8]:

$$\frac{dz}{dt} = (R^2 + i\omega + i\alpha|z|^2 - |z|^2)z, \tag{A1}$$

where the complex variable $z = r\exp(i\theta)$ includes amplitude r and phase θ. The converging amplitude R, intrinsic frequency ω, and amplitude-phase coupling α are all positive definite. The corresponding amplitude and phase dynamics under noisy environment are

$$\frac{dr}{dt} = R^2 r - r^3 + \eta_r \tag{A2}$$

$$\frac{d\theta}{dt} = \omega + \alpha r^2 + \eta_\theta, \tag{A3}$$

where $\langle\eta_r(t)\rangle = \langle\eta_\theta(t)\rangle = 0$, $\langle\eta_r(t)\eta_r(s)\rangle = 2D\delta(t-s)$, and $\langle\eta_\theta(t)\eta_\theta(s)\rangle = (2D/R^2)\delta(t-s)$. The amplitude of the nonlinear oscillator (r) converges to R. Then, the phase can be clearly defined without ambiguity only for the small amplitude fluctuation, $\langle\delta r^2\rangle \equiv \langle(r-R)^2\rangle \ll R^2$. Expansion of the above equations around $r = R + \delta r$ gives

$$\frac{d\delta r}{dt} = -2R^2\delta r + \eta_r \tag{A4}$$

$$\frac{d\theta}{dt} = \omega + \alpha R^2 + 2\alpha R\delta r + \eta_\theta. \tag{A5}$$

Then, one can obtain $\lim_{\tau\to\infty}\langle\delta r(\tau)^2\rangle = D/(2R^2)$, and the condition $\langle\delta r^2\rangle \ll R^2$ is translated as $2R^4 \gg D$. Similarly, the phase fluctuation after one period τ is calculated as

$$\begin{aligned}\langle\delta\theta(\tau)^2\rangle &= \frac{2D\tau}{R^2} + (2\alpha R)^2\int_0^\tau dt_1\int_0^\tau dt_2\langle\delta r(t_1)\delta r(t_2)\rangle\\ &= \frac{2D\tau}{R^2}(1+\alpha^2R^2).\end{aligned} \tag{A6}$$

Then, the dimensionless phase fluctuation is determined as

$$\frac{\langle\delta\theta(\tau)^2\rangle}{\langle\theta(\tau)\rangle^2} = \frac{D\tau}{2\pi^2R^2}(1+\alpha^2R^2). \tag{A7}$$

Next, we compute the heat dissipated from the Stuart-Landau oscillator. The probability density of amplitude and phase $P(r,\theta,t)$ evolves according to the Fokker-Planck equation:

$$\begin{aligned}\frac{\partial P}{\partial t} &= -\frac{1}{r}\frac{\partial}{\partial r}\left[(R^2r - r^3)rP - rD\frac{\partial P}{\partial r}\right]\\ &\quad - \frac{\partial}{\partial\theta}\left[(\omega+\alpha r^2)P - \frac{D}{r^2}\frac{\partial^2 P}{\partial\theta^2}\right]\\ &= -\frac{1}{r}\frac{\partial J_r}{\partial r} - \frac{\partial J_\theta}{\partial\theta}.\end{aligned} \tag{A8}$$

The steady-state probability density $P^{ss}(r,\theta)$ depends only on the amplitude r:

$$P^{ss}(r) = Z\exp\left[-\frac{r^4 - 2R^2r^2}{4D}\right] \tag{A9}$$

with a normalization constant Z to satisfy $2\pi\int_0^\infty rP^{ss}(r)dr = 1$. Using $P^{ss}(r)$, one can obtain the probability current for amplitude and phase, $J_r^{ss} = 0$ and $J_\theta^{ss} = \omega_{\rm eff}(r)P^{ss}$, respectively, with $\omega_{\rm eff}(r) = \omega + \alpha r^2$. The mean heat dissipation rate is obtained as

$$\sigma = \int_0^{2\pi} d\theta\int_0^\infty rdr\frac{\left(rJ_\theta^{ss}\right)^2}{P^{ss}} = \left\langle r^2\omega_{\rm eff}^2\right\rangle. \tag{A10}$$

Thus, the heat dissipated over a time period τ ($\approx 2\pi/\langle\omega_{\rm eff}\rangle$ for $\delta r^2 \ll R^2$) is

$$\begin{aligned}q(\tau) = \tau\sigma &\approx \frac{2\pi\left\langle r^2\omega_{\rm eff}^2\right\rangle}{\langle\omega_{\rm eff}\rangle}\\ &\approx 2\pi R^2\omega\left(1 + \frac{\alpha R^2}{\omega} + \frac{2\alpha^2D}{\omega(\omega+\alpha R^2)} + \frac{4\alpha D}{R^2\omega}\right)\\ &\approx 2\pi R^2\omega\left(1 + \frac{2\alpha^2D}{\omega^2} + \frac{4\alpha D}{R^2\omega}\right)\\ &\approx 2\pi R^2\omega,\end{aligned} \tag{A11}$$

where the first line was analytically solved by using Eq. (A10), and expanded under the conditions of small amplitude fluctuation ($2R^4 \gg D$) and phase dynamics ($\omega \gg \alpha R^2$) [8], which implies that the intrinsic factor ω should be much greater than the amplitude coupling factor αR^2 in $\omega_{\rm eff} = \omega + \alpha r^2$. Then, from the two conditions, it follows that $2R^2\omega \gg \alpha D$ and $2\omega^2 \gg \alpha^2 D$. The last line in Eq. (A11) follows from these two inequalities. Finally, the cost-precision tradeoff can be evaluated using the heat dissipation [Eq. (A11)] and the phase fluctuation [Eq. (A7)]:

$$\begin{aligned}\mathcal{Q} &\equiv q(\tau)\frac{\langle\delta\theta(\tau)^2\rangle}{\langle\theta(\tau)\rangle^2}\\ &= 2\pi R^2\omega\frac{D2\pi/\langle\omega_{\rm eff}\rangle}{2\pi^2R^2}(1+\alpha^2R^2)\\ &\approx 2k_BT(1+\alpha^2R^2) \geqslant 2k_BT,\end{aligned} \tag{A12}$$

where we have used $\langle\omega_{\rm eff}\rangle/\omega = \langle 1 + \alpha r^2/\omega\rangle \approx 1$ under the condition of $\omega \gg \alpha R^2$, and the Einstein relation $D = \mu k_BT$ with $\mu = 1$. Therefore, the uncertainty relation achieves the minimal bound $\mathcal{Q}_{\rm min} = 2k_BT$, when the amplitude coupling for phase dynamics is absent ($\alpha = 0$). Reference [8] has already studied in detail the heat dissipation and phase fluctuation of the noisy Stuart-Landau oscillator, and this study corroborates the minimal bound of their tradeoff. The pure phase dynamics of the noisy Kuramoto model without coupling,

$$\frac{d\theta}{dt} = \omega + \eta, \tag{A13}$$

is the basis for this study.

APPENDIX B: PHASE VELOCITY AND HEAT DISSIPATION OF COUPLED OSCILLATORS

Using the probability density $P(\theta_1,\theta_2,t)$ for phases of two coupled oscillators, one can derive the mean phase velocity and mean heat dissipation rate at nonequilibrium steady state [30]. We consider the transformed probability density $P(\theta_1,\theta_2,t) = P(\phi_2,t)/2\pi$ for the orthogonal coordinate, $\phi_1 = \theta_1 + \theta_2$ and $\phi_2 = \theta_1 - \theta_2$. The probability density function follows the Fokker-Planck equation:

$$\frac{\partial P(\phi_2,t)}{\partial t} = -\frac{\partial}{\partial\phi_2}\left[\Delta\omega - K\sin\phi_2 - 2D\frac{\partial}{\partial\phi_2}\right]P(\phi_2,t). \tag{B1}$$

Its steady-state solution is given as

$$P^{ss}(\phi_2) = \frac{1}{Z}\exp\left[-\frac{V(\phi_2)}{2D}\right]\int_{\phi_2}^{\phi_2+2\pi} d\psi \exp\left[\frac{V(\psi)}{2D}\right], \tag{B2}$$

where $V(\phi_2) = -K\cos\phi_2 - \Delta\omega\phi_2$ is an effective potential, and Z is a normalization constant to satisfy $\int_0^{2\pi} d\phi_2 P^{ss}(\phi_2) = 1$:

$$Z = \int_0^{2\pi} d\phi_2 \int_{\phi_2}^{\phi_2+2\pi} d\psi \exp\left[\frac{V(\psi)-V(\phi_2)}{2D}\right]. \tag{B3}$$

Then, using the steady state probability density P^{ss}, one can define the steady-state current as

$$\begin{aligned} J_i^{ss}(\phi_2) &= \left[F_i - D\frac{\partial}{\partial\theta_i}\right]P^{ss}(\theta_1,\theta_2) \\ &= \left[F_i - D\left(\frac{\partial\phi_1}{\partial\theta_i}\frac{\partial}{\partial\phi_1} + \frac{\partial\phi_2}{\partial\theta_i}\frac{\partial}{\partial\phi_2}\right)\right]P^{ss}(\phi_1,\phi_2) \\ &= \left[F_i + \frac{1}{2}\frac{\partial\phi_2}{\partial\theta_i}\frac{\partial V(\phi_2)}{\partial\phi_2}\right]\frac{P^{ss}(\phi_2)}{2\pi} \\ &\quad + \frac{D}{2\pi Z}\frac{\partial\phi_2}{\partial\theta_i}\left[1 - \exp\left(-\frac{\Delta\omega\pi}{D}\right)\right]. \end{aligned} \tag{B4}$$

Here the subscript i in J_i^{ss} denotes the index of the ith oscillator. The steady-state current for each oscillator is

$$J_1^{ss} = \frac{\omega_1+\omega_2}{4\pi}P^{ss}(\phi_2) + \frac{D}{2\pi Z}\left[1 - \exp\left(-\frac{\Delta\omega\pi}{D}\right)\right], \tag{B5}$$

$$J_2^{ss} = \frac{\omega_1+\omega_2}{4\pi}P^{ss}(\phi_2) - \frac{D}{2\pi Z}\left[1 - \exp\left(-\frac{\Delta\omega\pi}{D}\right)\right]. \tag{B6}$$

Given the steady-state current, one can obtain the mean phase velocity

$$\begin{aligned} v_i &= \int_0^{2\pi} d\theta_1 \int_0^{2\pi} d\theta_2 J_i^{ss}(\theta_1,\theta_2) \\ &= 2\pi\int_0^{2\pi} d\phi_2 J_i^{ss}(\phi_2). \end{aligned} \tag{B7}$$

The mean phase velocity for each oscillator is

$$\begin{aligned} v_1 &= \frac{\omega_1+\omega_2}{2} + \frac{2\pi D}{Z}\left[1 - \exp\left(-\frac{\Delta\omega\pi}{D}\right)\right], \\ v_2 &= \frac{\omega_1+\omega_2}{2} - \frac{2\pi D}{Z}\left[1 - \exp\left(-\frac{\Delta\omega\pi}{D}\right)\right]. \end{aligned} \tag{B8}$$

For $K \to 0$, $v_i \to \omega_i$, whereas for the large K limit, $v_1 = v_2 = (\omega_1+\omega_2)/2$. Next, using the steady-state current, one can also obtain the heat dissipation rate,

$$\begin{aligned} \sigma_i &= \int_0^{2\pi} d\theta_1 \int_0^{2\pi} d\theta_2 F_i(\theta_1,\theta_2) J_i^{ss}(\theta_1,\theta_2) \\ &= 2\pi\int_0^{2\pi} d\phi_2 F_i(\phi_2) J_i^{ss}(\phi_2). \end{aligned} \tag{B9}$$

The mean heat dissipation rate for each oscillator is

$$\begin{aligned} \sigma_1 &= \omega_1 v_1 - \frac{(\omega_1+\omega_2)K}{4}\langle\sin\phi_2\rangle, \\ \sigma_2 &= \omega_2 v_2 + \frac{(\omega_1+\omega_2)K}{4}\langle\sin\phi_2\rangle, \end{aligned} \tag{B10}$$

where $\langle\sin\phi_2\rangle \equiv 2\pi\int_0^{2\pi} d\phi_2 \sin\phi_2 P^{ss}(\phi_2)$. At the large K limit, $\langle\sin\phi_2\rangle = (\omega_1-\omega_2)/K$; and hence the two synchronized oscillators have the same heat dissipation rate $\sigma_1 = \sigma_2 = (\omega_1+\omega_2)^2/4$. On the other hand, in the limit of $K \to 0$, $\sigma_i = \omega_i^2$.

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