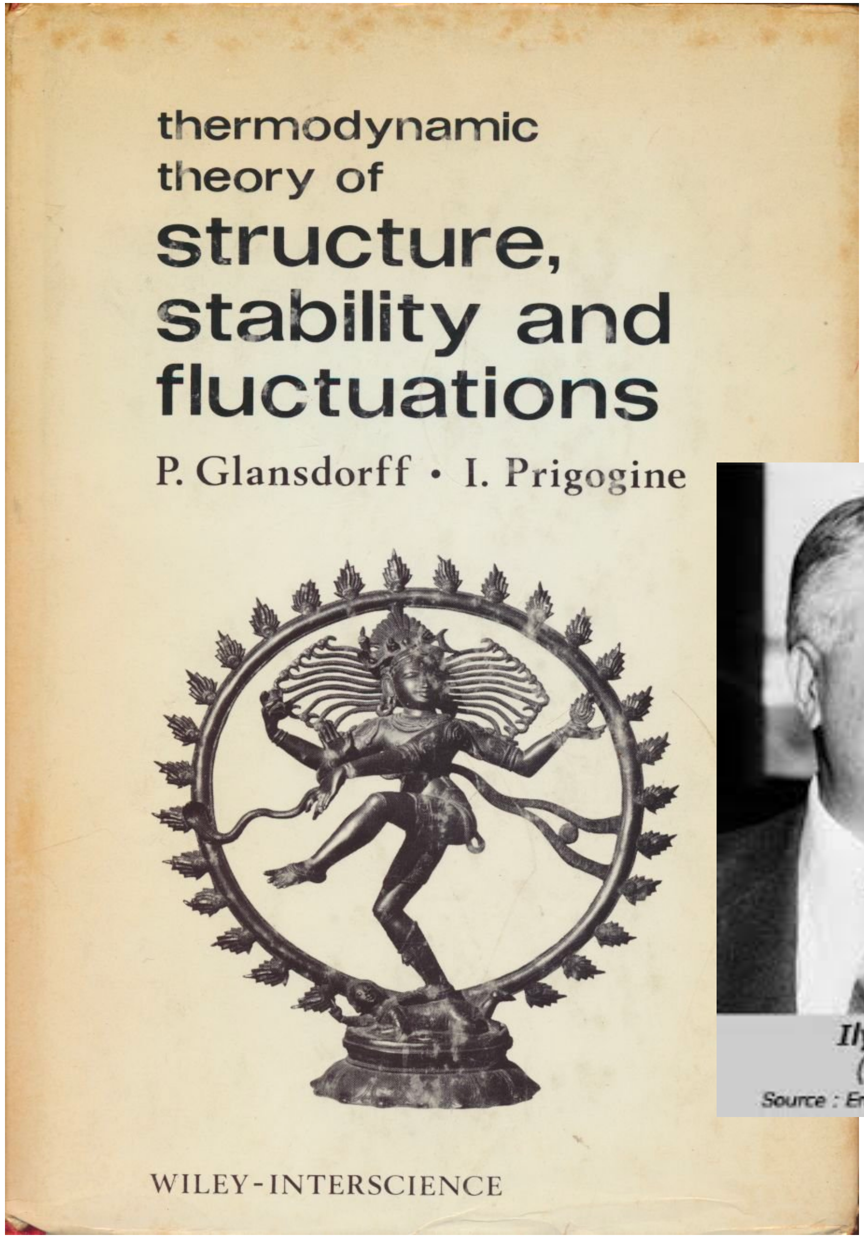
생명현상의 열역학

조정효

(KIAS)

2018 생명물리 여름학교, 7월 10일, 포항

Order under fluctuations



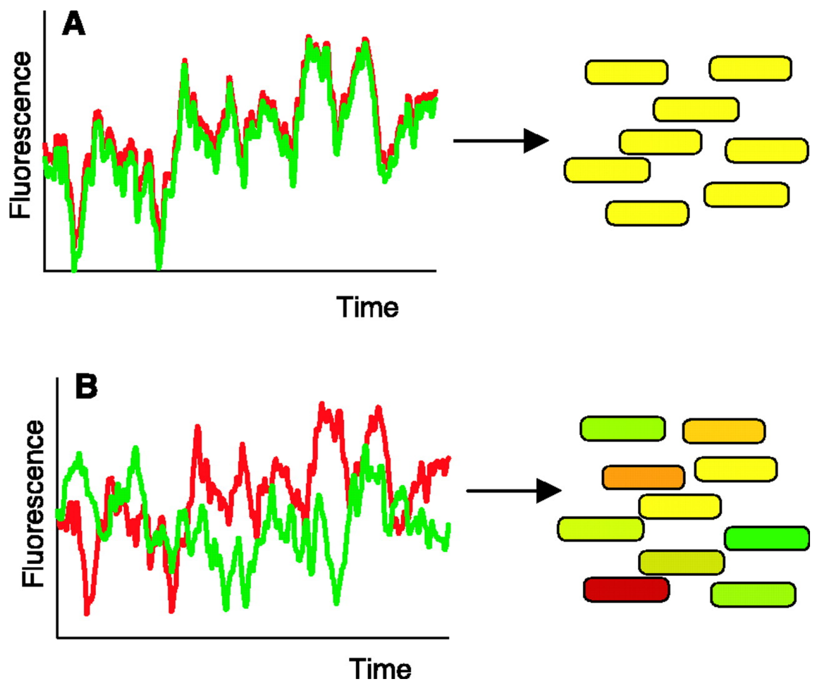
Ilya Prigogine
(1917-2003)
Source : Encyclopedia Britannica online

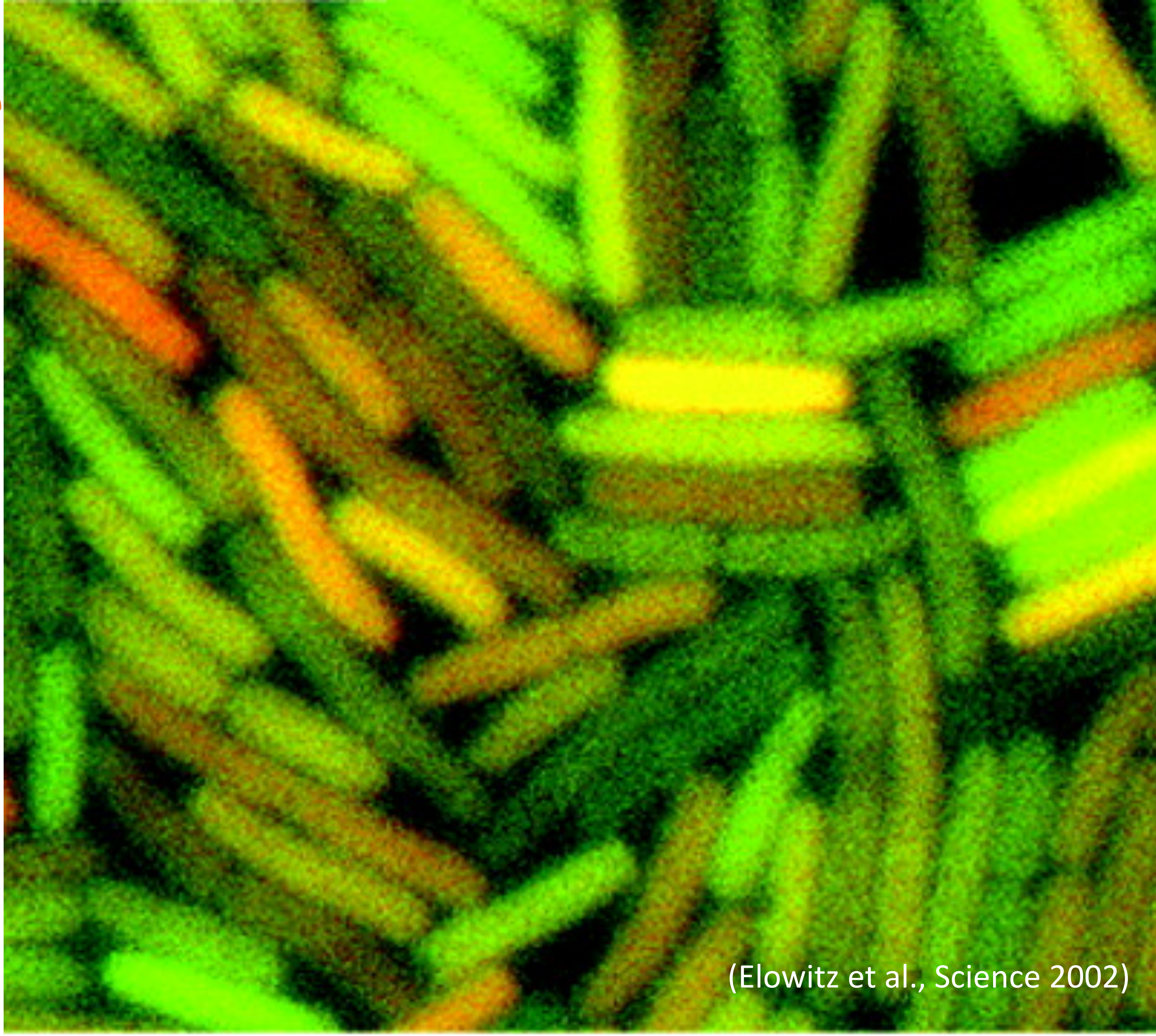
Nature/Nurture/Chance

Dizygotic twins

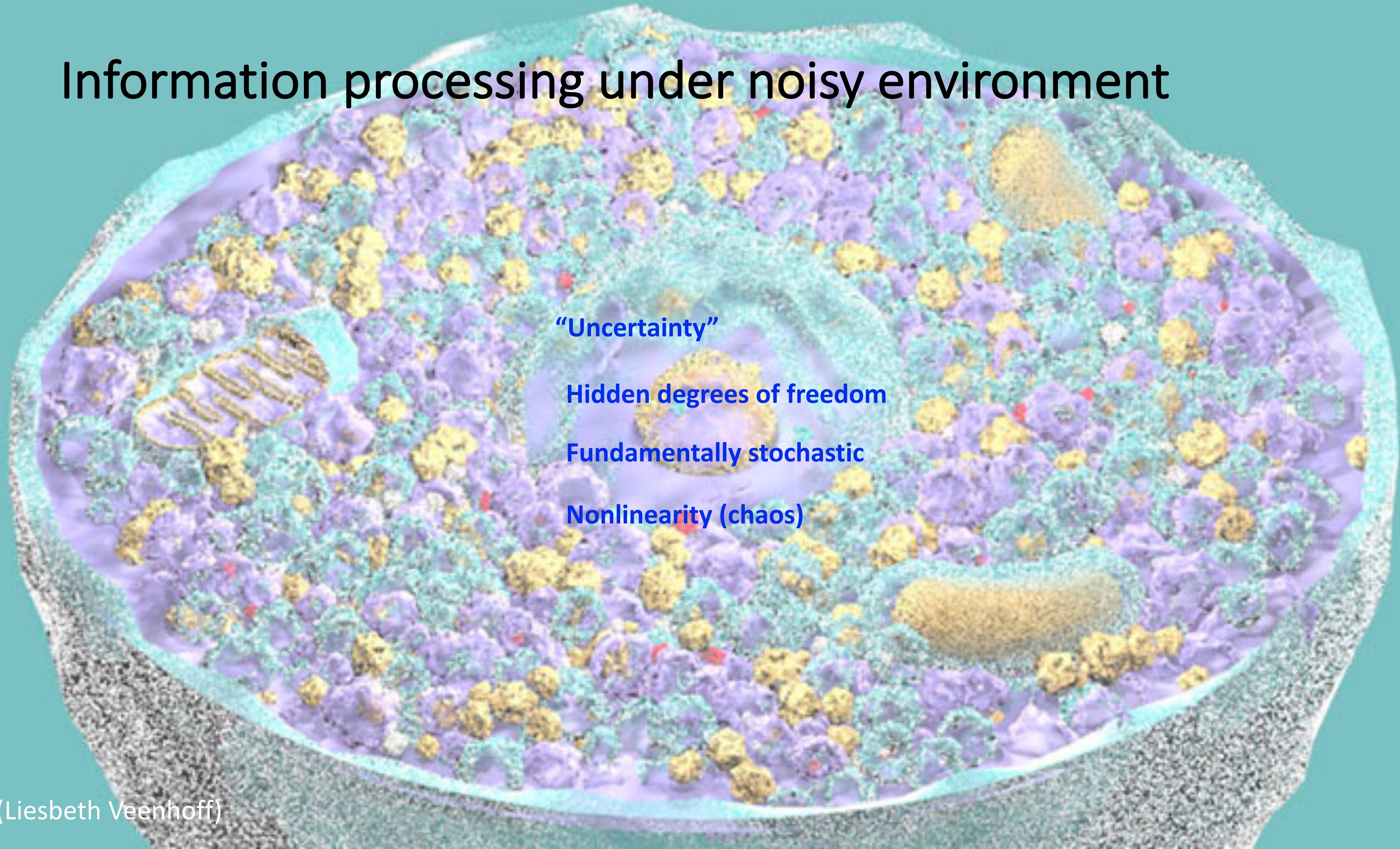
Monozygotic twins

Clonal cells





Information processing under noisy environment



"Uncertainty"

Hidden degrees of freedom

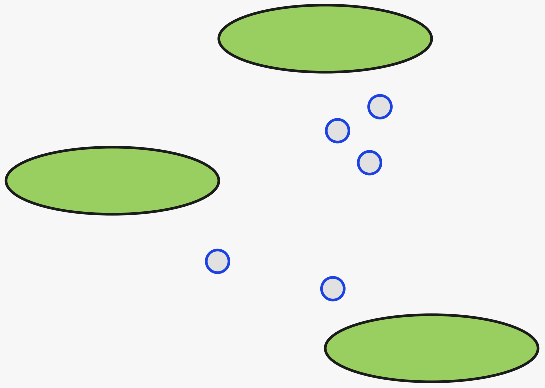
Fundamentally stochastic

Nonlinearity (chaos)

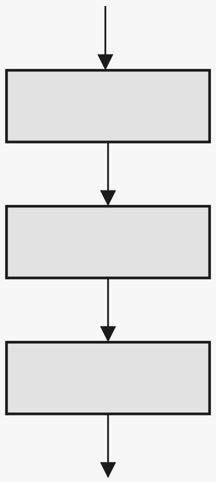
(Liesbeth Veenhoff)

How living systems overcome uncertainty (fluctuations)?

Large number's law



Quorum sensing



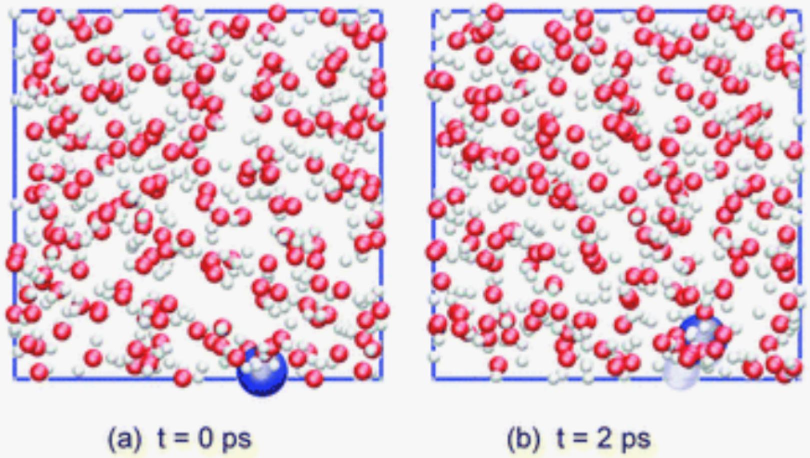
Signal cascade

Time (predictability)

Oscillation

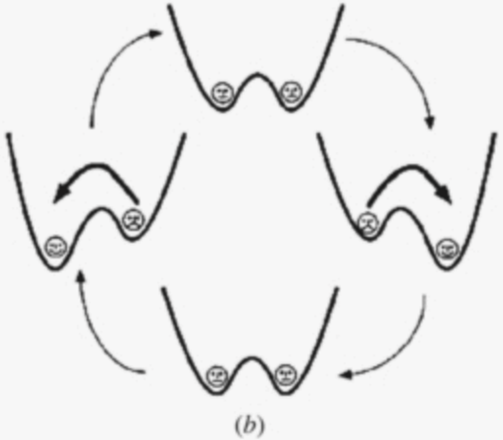
Noise is sometimes useful

Source for energy



Molecular diffusion

(Murdachaew et al., Phys. Chem. Chem. Phys., 2012)



Stochastic resonance

(Yang et al., J. Phys. A, 2009)

Source for evolution

Mutation

50,000 generation of E. coli since 1988
(Richard Lenski)

Non-equilibrium thermodynamics

Jarzynski, Crooks, …

What is life?

Stochastic thermodynamics

Sekimoto, Seifert, …

Information thermodynamics

Ueda, Sagawa, …

THE JOURNAL OF CHEMICAL PHYSICS **139**, 121923 (2013)

Statistical physics of self-replication

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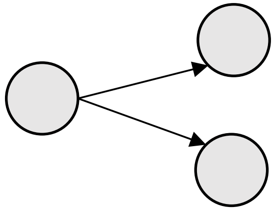
(Received 28 April 2013; accepted 1 August 2013; published online 21 August 2013)

PHYSICAL REVIEW X **6,** 021036 (2016)

Statistical Physics of Adaptation

Nikolay Perunov, Robert A. Marsland, and Jeremy L. England
Department of Physics, Physics of Living Systems Group, Massachusetts Institute of Technology, Floor 6, 400 Tech Square, Cambridge, Massachusetts 02139, USA
(Received 23 December 2014; revised manuscript received 27 March 2016; published 16 June 2016)



Irreversible, entropy-producing, non-equilibrium processes

PHYSICAL REVIEW X **5,** 041039 (2015)

Thermodynamics of Error Correction

Pablo Sartori[1] and Simone Pigolotti[2]
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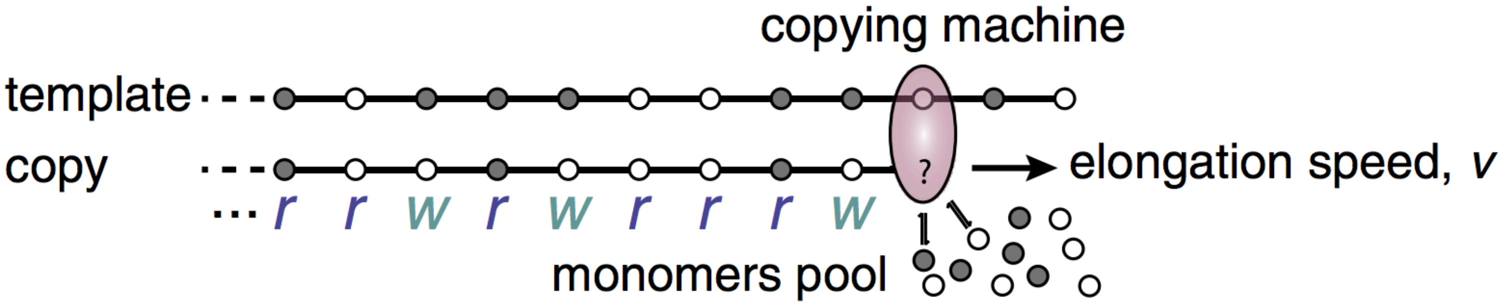
[2]*Departament de Física, Universitat Politècnica de Catalunya, Edifici Gaia, Rambla Sant Nebridi 22, 08222 Terrassa, Barcelona, Spain*
(Received 23 April 2015; revised manuscript received 25 September 2015; published 10 December 2015)



one mistake for every 10^7 nucleotides added

PRL 115, 118102 (2015) PHYSICAL REVIEW LETTERS week ending 11 SEPTEMBER 2015

Free Energy Cost of Reducing Noise while Maintaining a High Sensitivity

Pablo Sartori[1,*] and Yuhai Tu[2]
[1]*Max Planck Institute for the Physics of Complex Systems, Noethnitzer Strasse 38, 01187 Dresden, Germany*
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(Received 27 May 2015; published 8 September 2015)

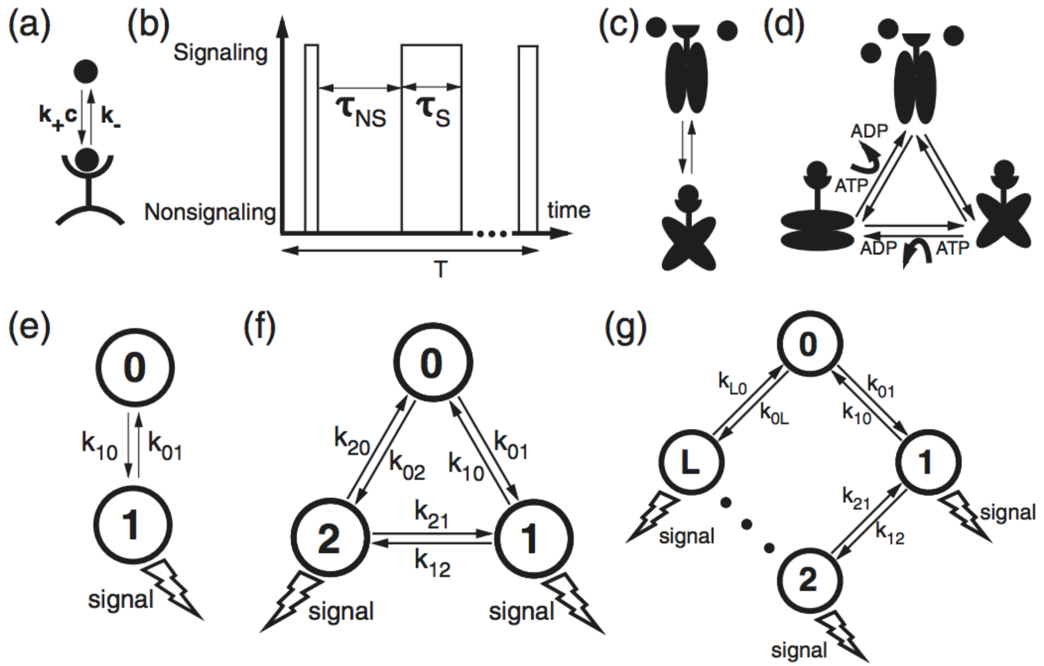
Fluctuation dissipation theorem under equilibrium conditions

Free energy dissipation under non-equilibrium conditions

PRL 113, 148103 (2014) PHYSICAL REVIEW LETTERS week ending 3 OCTOBER 2014

Thermodynamics of Statistical Inference by Cells

Alex H. Lang,[1,*] Charles K. Fisher,[1] Thierry Mora,[2] and Pankaj Mehta[1,†]
[1]Physics Department, Boston University, Boston, Massachusetts 02215, USA
[2]Laboratoire de physique statistique, CNRS, UPMC and École normale supérieure, 75005 Paris, France
(Received 10 June 2014; published 3 October 2014)



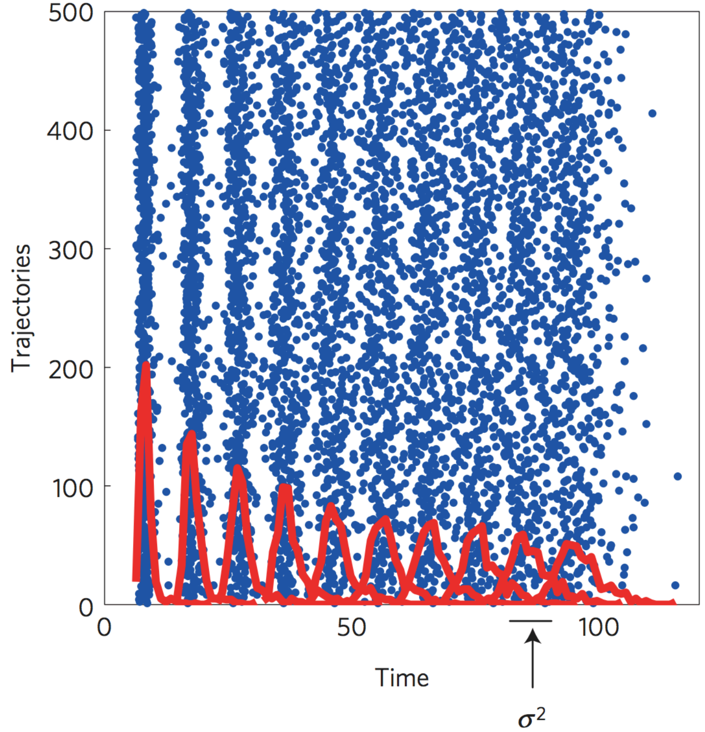
Energetic cost for accurate signaling

ARTICLES
PUBLISHED ONLINE: 27 JULY 2015 | DOI: 10.1038/NPHYS3412

nature physics

The free-energy cost of accurate biochemical oscillations

Yuansheng Cao[1], Hongli Wang[1], Qi Ouyang[1,2]* and Yuhai Tu[3]*



Energetic cost for accurate oscillations

nature COMMUNICATIONS

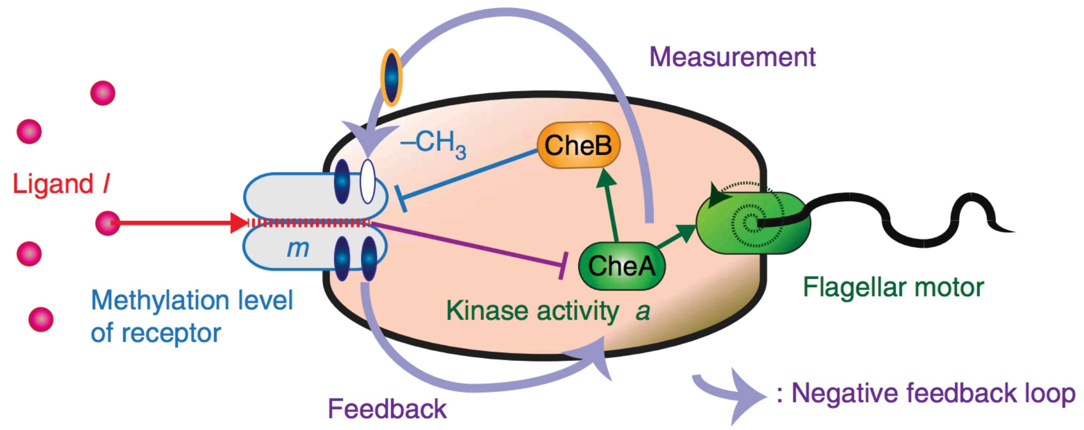
ARTICLE

Received 2 Jul 2014 | Accepted 12 May 2015 | Published 23 Jun 2015

DOI: 10.1038/ncomms8498

Maxwell's demon in biochemical signal transduction with feedback loop

Sosuke Ito[1,†] & Takahiro Sagawa[2,†]



Information entropy

PRL **118,** 010601 (2017) PHYSICAL REVIEW LETTERS week ending 6 JANUARY 2017

Stochastic Thermodynamics of Learning

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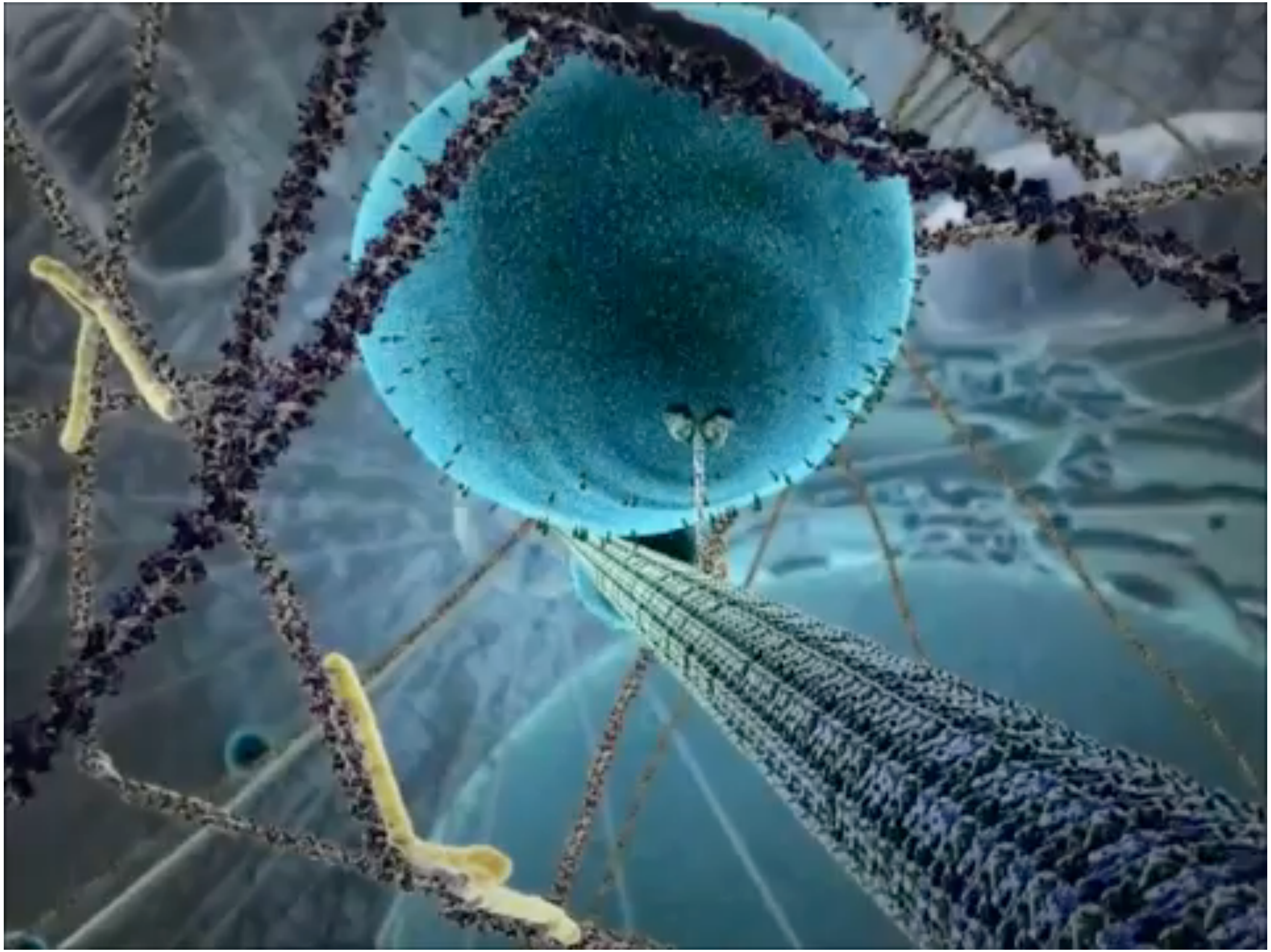
(Received 11 July 2016; revised manuscript received 12 October 2016; published 6 January 2017)

Energetic cost for learning



Dynamics

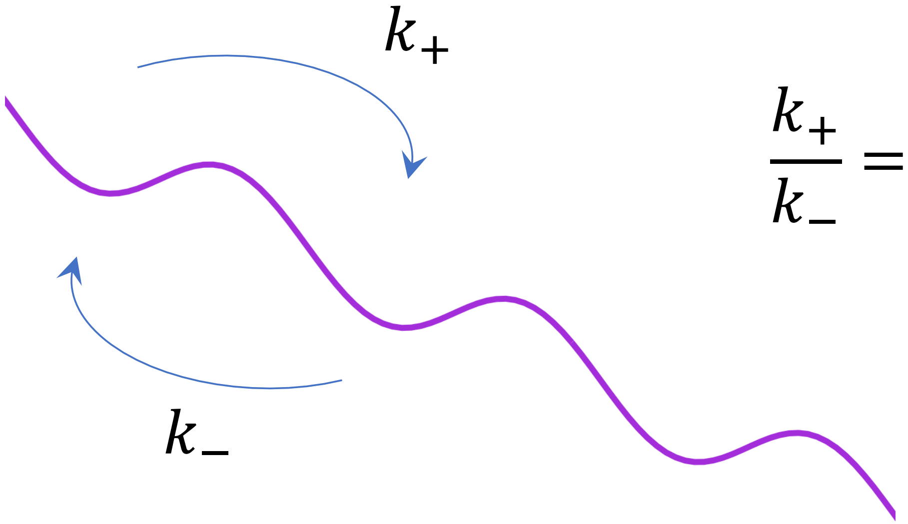
Chemical & mechanical mechanisms

Function (accurate delivery)

Energetic cost?

Youtube

Thermodynamic uncertainty relation (2015)



$$\frac{k_+}{k_-} = \exp\frac{\Delta E}{k_B T}$$

$$\langle X(t)\rangle = (k_+ - k_-)t$$

$$\langle \delta X(t)^2\rangle = (k_+ + k_-)t$$

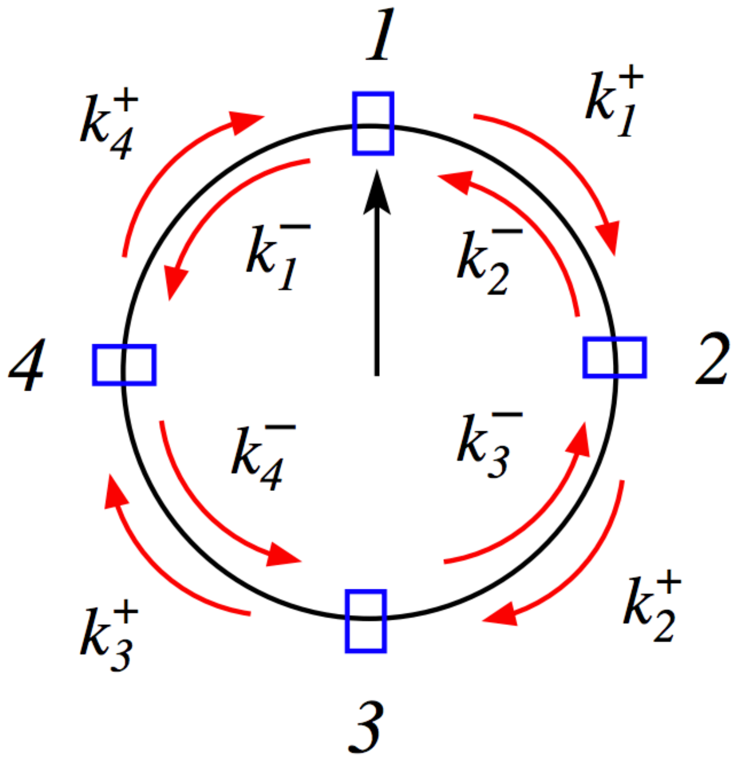
$$\langle q\ (t)\rangle = (k_+ - k_-)t k_B T \log\frac{k_+}{k_-}$$

$$\mathcal{Q} = \langle q\ (t)\rangle \frac{\langle \delta X(t)^2\rangle}{\langle X(t)\rangle^2}$$

$$= k_B T\frac{(k_+ + k_-)}{(k_+ - k_-)}\log\frac{k_+}{k_-} \geq 2k_B T$$

(Barato and Seifert, PRL 2015)

Brownian clock

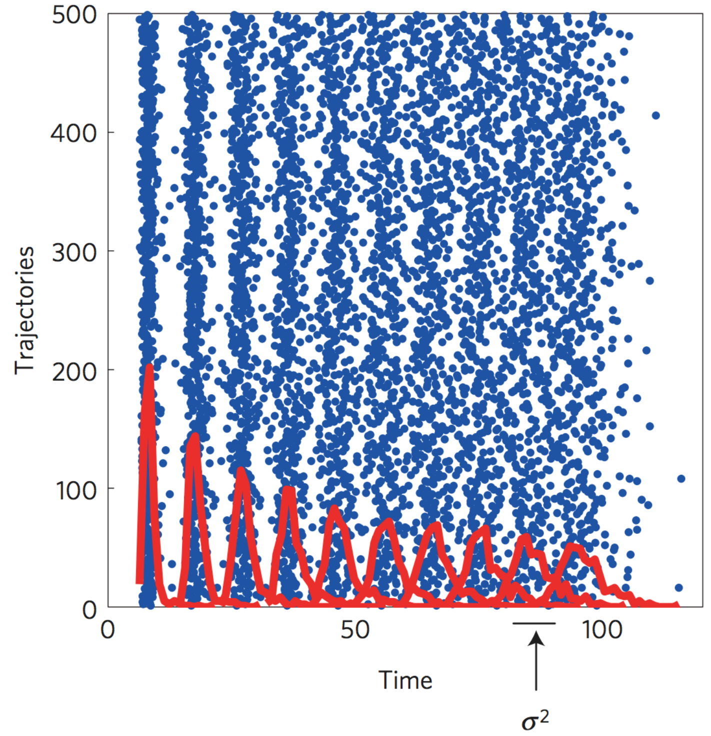


(Barato and Seifert, PRX 2016)

$$k_+ = k_1^+ k_2^+ k_3^+ k_4^+$$

$$k_- = k_1^- k_2^- k_3^- k_4^-$$

$$\mathcal{Q} = \langle q\,(t)\rangle \frac{\langle \delta\theta^2\rangle}{\langle\theta\rangle^2} \geq 2k_B T$$



θ: displacement, time, product number, heat, …

Noisy oscillator

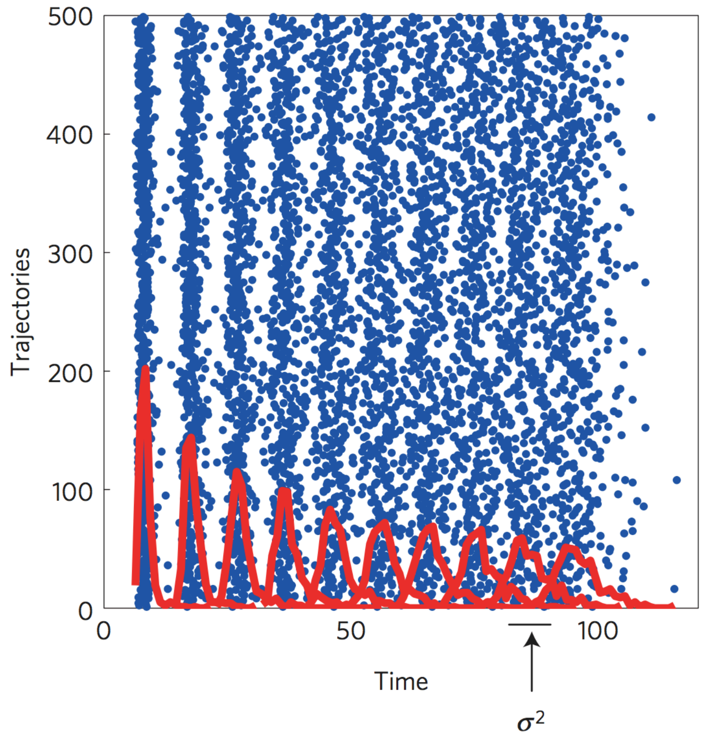
Langevin equation

$$\frac{d\theta}{dt} = \omega + \eta(t)$$

$$\langle \eta(t) \rangle = 0$$

$$\langle \eta(t)\eta(t') \rangle = 2D\delta(t - t')$$

$$D = \mu k_B T$$



$$\langle \theta(t) \rangle = \omega t$$

$$\langle \delta\theta(t)^2 \rangle = 2Dt$$

$$\langle q\ (t) \rangle = \left\langle \int_0^t F(\tau) \circ \frac{d\theta}{d\tau} d\tau \right\rangle = \omega^2 t$$

$$v = \lim_{t\to\infty} \frac{\langle \theta(t) \rangle}{t}$$

$$D = \lim_{t\to\infty} \frac{\langle \delta\theta(t)^2 \rangle}{2t}$$

$$\sigma = \lim_{t\to\infty} \frac{\langle q(t) \rangle}{t}$$

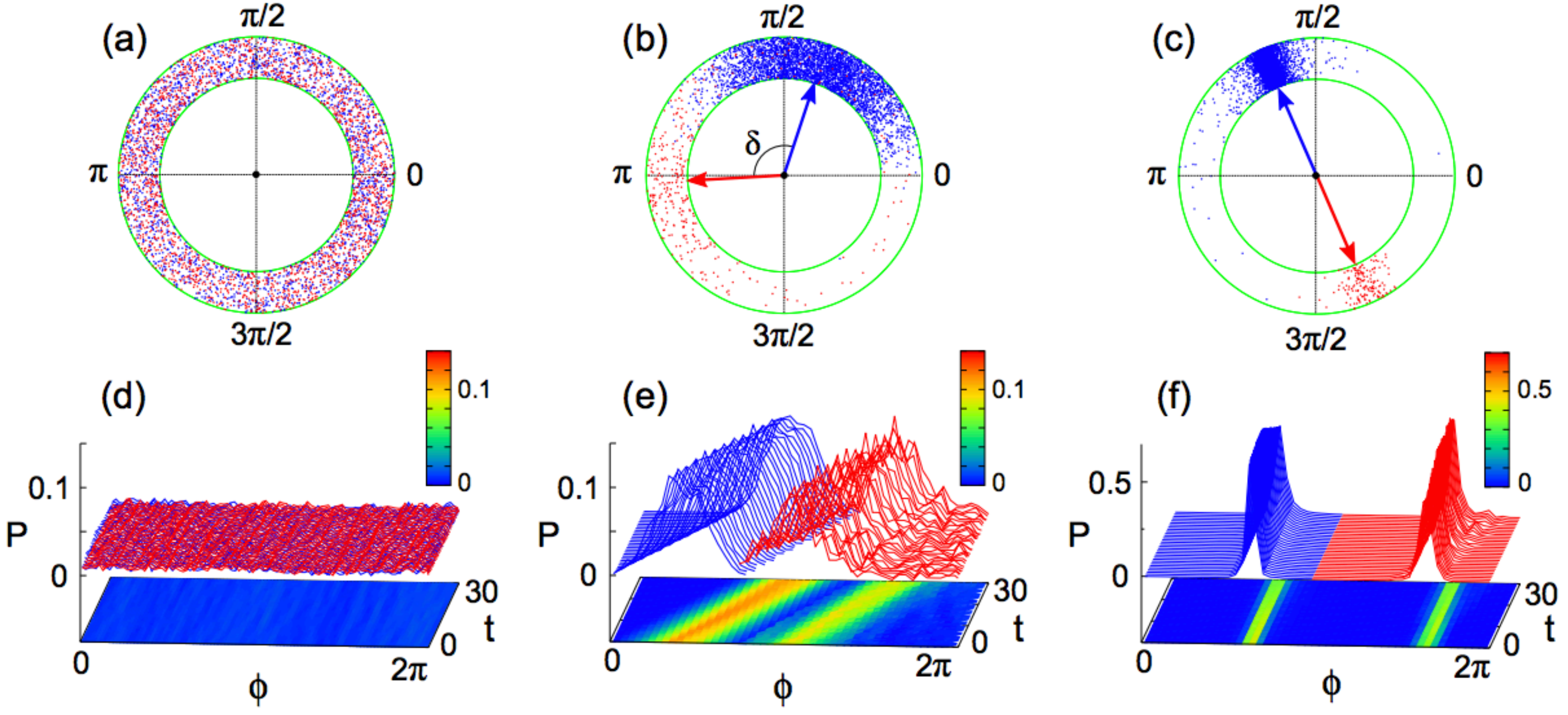
$$\mathcal{Q} = \langle q\ (t) \rangle \frac{\langle \delta\theta(t)^2 \rangle}{\langle \theta(t) \rangle^2} = \sigma \frac{2D}{v^2} = 2k_B T$$

Interacting oscillators

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

Kuramoto model

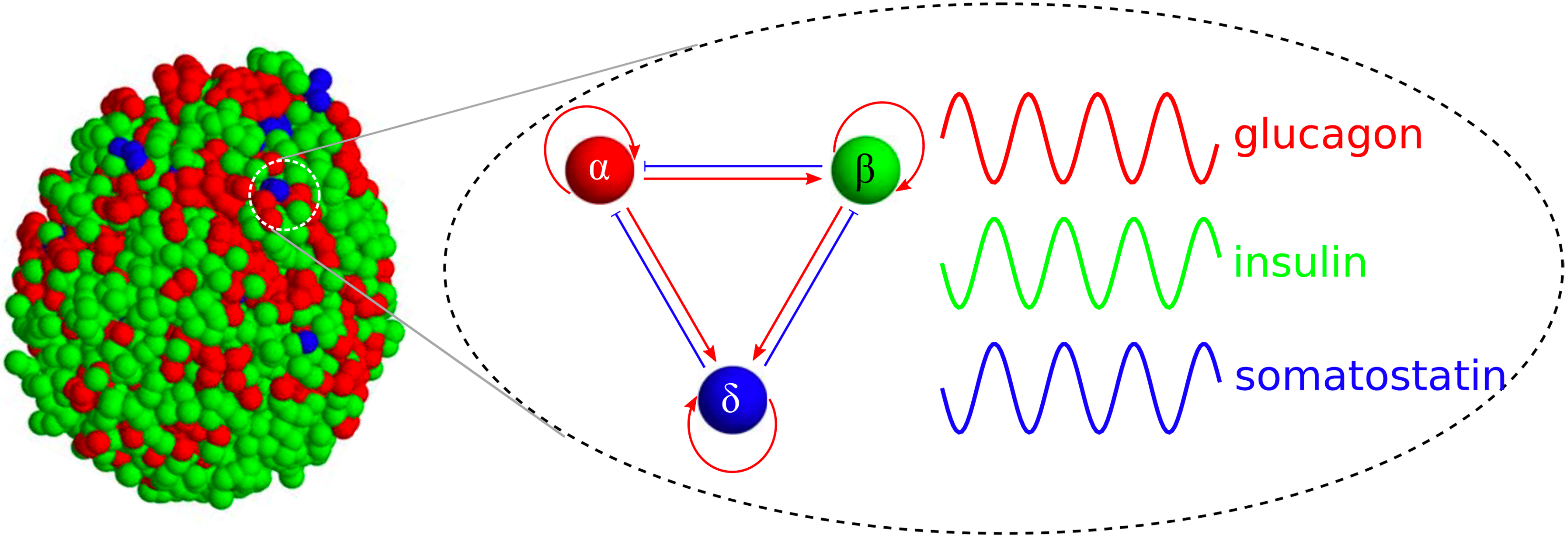
Conformist, contrarian oscillators



$$\frac{d\theta_i}{dt} = \omega_i + K_i \sum_{\langle i,j \rangle} \sin(\theta_j - \theta_i)$$

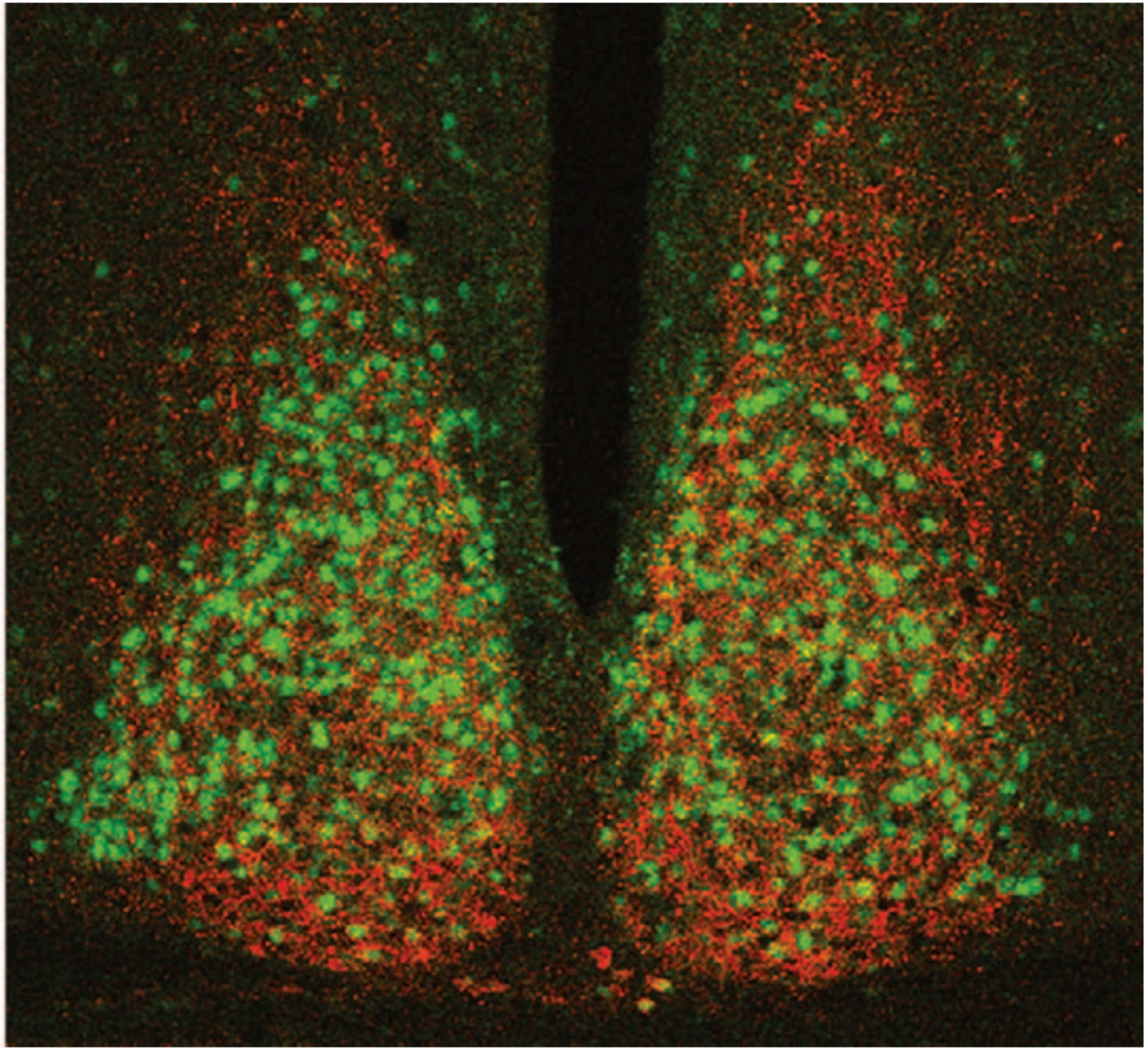
(Hoang, Jo, and Hong, PRE 2015)

Cellular oscillators



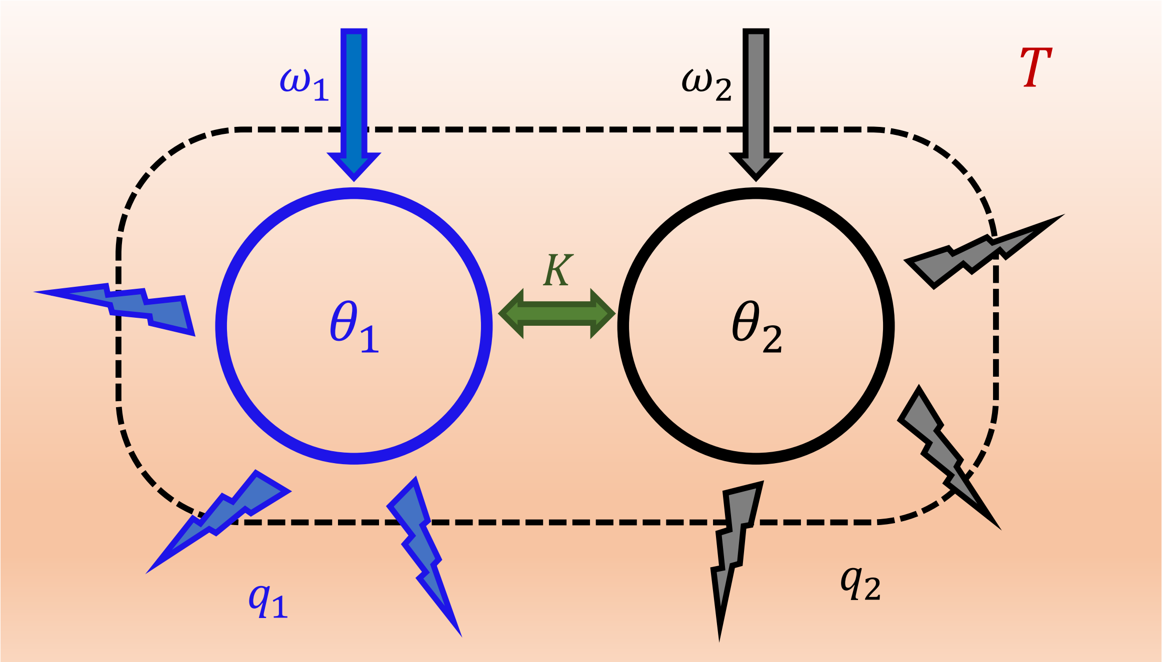
(Hoang, Hara, and Jo, PLoS ONE 2015)

Clock-cell oscillators



(Mohawk and Takahashi, Trends in Neurosciences, 2011)

Energy-accuracy trade-off of interacting subsystems



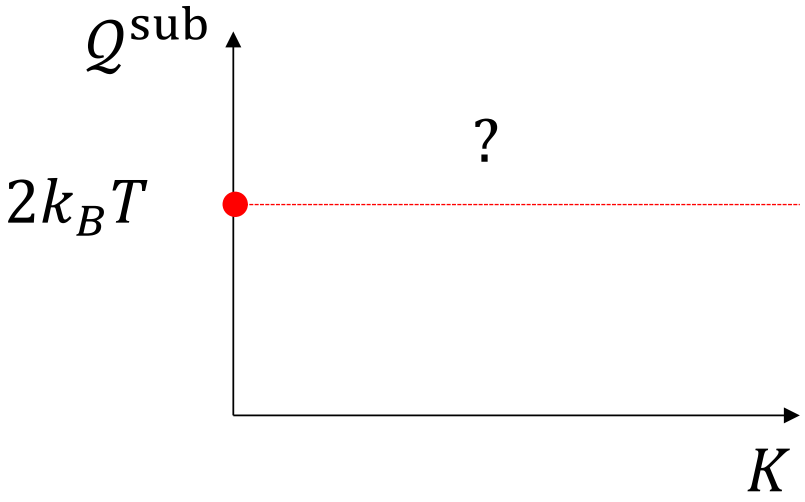
$$\mathcal{Q} = \langle q\ (t)\rangle \frac{\langle \delta\theta(t)^2\rangle}{\langle \theta(t)\rangle^2}$$

$$\mathcal{Q}^{\text{tot}} = \mathcal{Q}(\Sigma_i q_i, \theta_i)$$

$$\mathcal{Q}^{\text{sub}} = \mathcal{Q}(q_i, \theta_i)$$

Conservative interaction

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



Strong coupling limit ($K \to \infty$)

$$\frac{d\theta_1}{dt} = \omega_1 + \frac{K}{2}\sin(\theta_2 - \theta_1) + \eta_1(t)$$

$$\frac{d\theta_2}{dt} = \omega_2 + \frac{K}{2}\sin(\theta_1 - \theta_2) + \eta_2(t)$$

$$\frac{d\phi_1}{dt} = 2\bar{\omega} + \xi_1(t)$$

$$\frac{d\phi_2}{dt} = \Delta\omega - K\sin\phi_2 + \xi_2(t)$$

$$\phi_1 = \theta_1 + \theta_2$$

$$\phi_2 = \theta_1 - \theta_2$$

$$\bar{\omega} = (\omega_1 + \omega_2)/2 \qquad \Delta\omega = \omega_1 - \omega_2$$

$$\langle \xi_i(t)\xi_i(t')\rangle = 4D\delta(t - t')$$

$$v = \bar{\omega} \qquad \sigma = \bar{\omega}^2$$

$$D = \frac{\langle \delta\theta_1^2\rangle}{2t} = \frac{1}{2t}\frac{\langle \delta\phi_1^2 + \delta\phi_2^2\rangle}{4}$$

$$\langle \delta\phi_1^2\rangle = 4Dt$$

$$\frac{d\phi_2}{dt} = \Delta\omega - K\phi_2 + \xi_2(t)$$

$$\phi_2(t) = \int_0^t d\tau e^{-K(t-\tau)}(\Delta\omega + \xi_2)$$

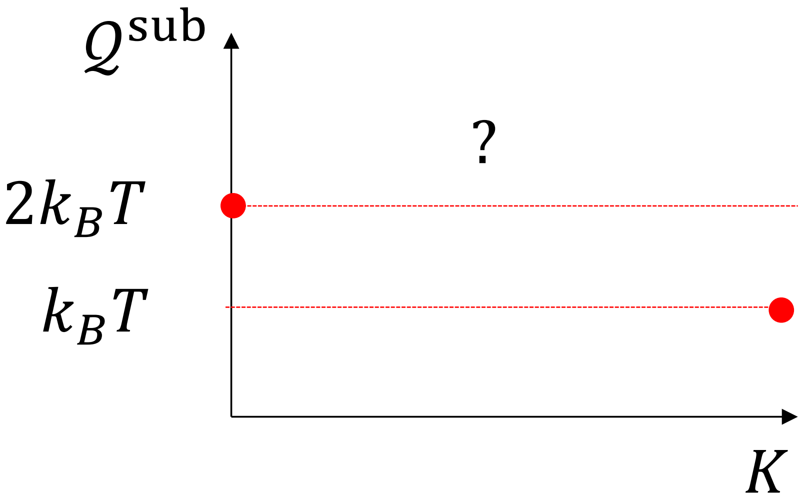
$$\langle \delta\phi_2^2\rangle = \frac{2D}{K}(1 - e^{-2Kt})$$

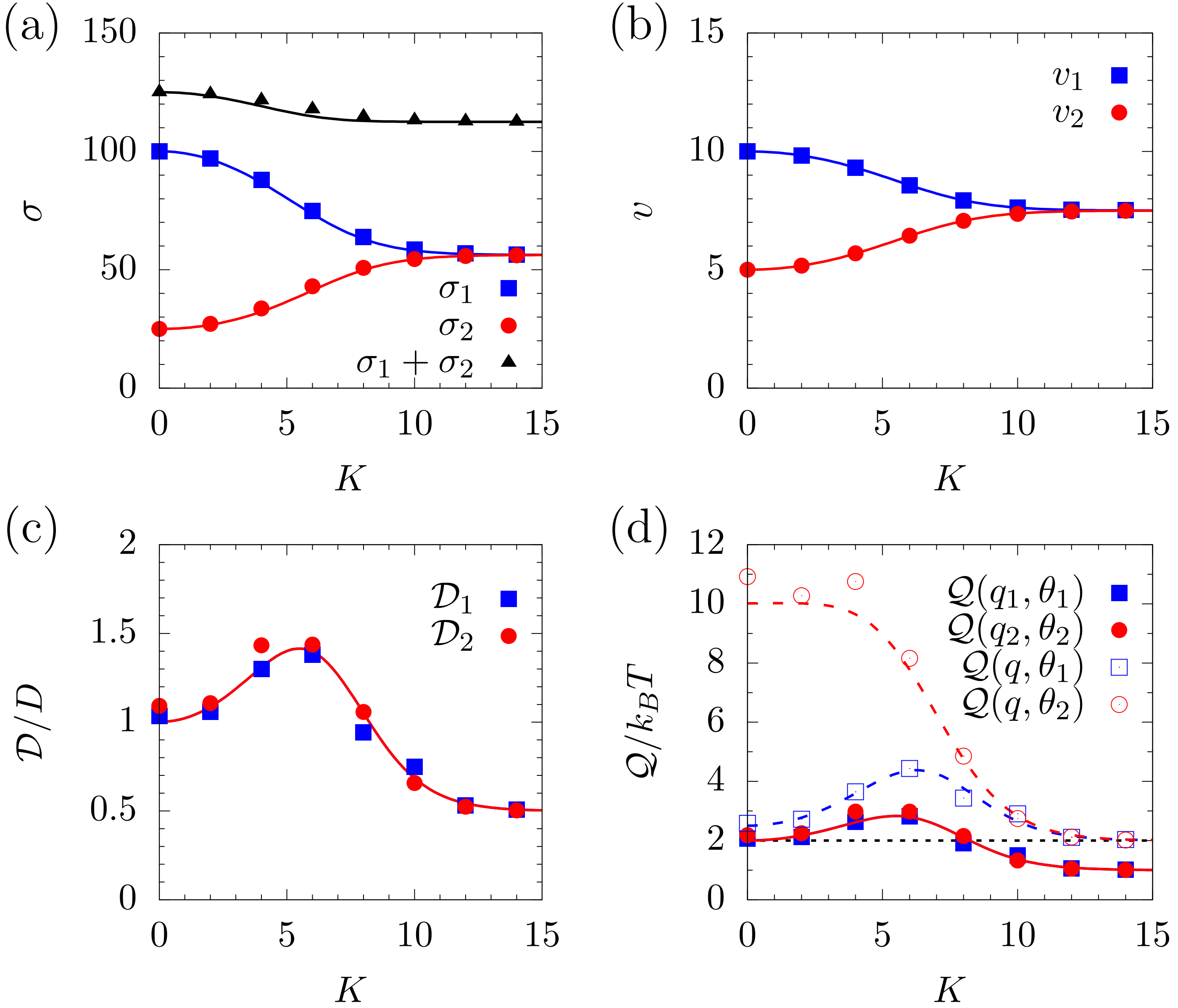
$$Q^{\mathrm{sub}} = \sigma\frac{2D}{v^2} = k_B T$$

Energy-accuracy trade-off of interacting subsystems

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

$$Q^{\mathrm{sub}} = \langle q_i \rangle \frac{\langle \delta\theta_i^2 \rangle}{\langle \theta_i \rangle^2}$$





Analytical approach

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

$$\frac{d\phi_1}{dt} = 2\bar{\omega} + \xi_1(t)$$
$$\frac{d\phi_2}{dt} = \Delta\omega - K\sin\phi_2 + \xi_2(t)$$

$$V(\phi_2) = -\phi_2\Delta\omega - K\cos\phi_2$$

$$P(\theta_1, \theta_2, t)$$

$$\frac{\partial P}{\partial t} = -\frac{\partial J_1}{\partial \theta_1} - \frac{\partial J_2}{\partial \theta_2}$$

Fokker-Planck equation

$$J_i = F_i P - D\frac{\partial P}{\partial \theta_i}$$

$$v_i = \int_0^{2\pi} d\theta_1 \int_0^{2\pi} d\theta_2 J_i^{ss}$$
$$\sigma_i = \int_0^{2\pi} d\theta_1 \int_0^{2\pi} d\theta_2 F_i J_i^{ss}$$

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

$$I_+(\phi_2) = \exp\left[\frac{V(\phi_2)}{2D}\right]\int_{\phi_2-2\pi}^{\phi_2} d\varphi \exp\left[-\frac{V(\varphi)}{2D}\right] \qquad I_-(\phi_2) = \exp\left[-\frac{V(\phi_2)}{2D}\right]\int_{\phi_2}^{\phi_2+2\pi} d\varphi \exp\left[\frac{V(\varphi)}{2D}\right]$$

Many oscillators

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

$$\frac{d\theta_i}{dt} = \omega_i + \sum_{j=1}^{N} M_{ij}\theta_j + \eta_i$$

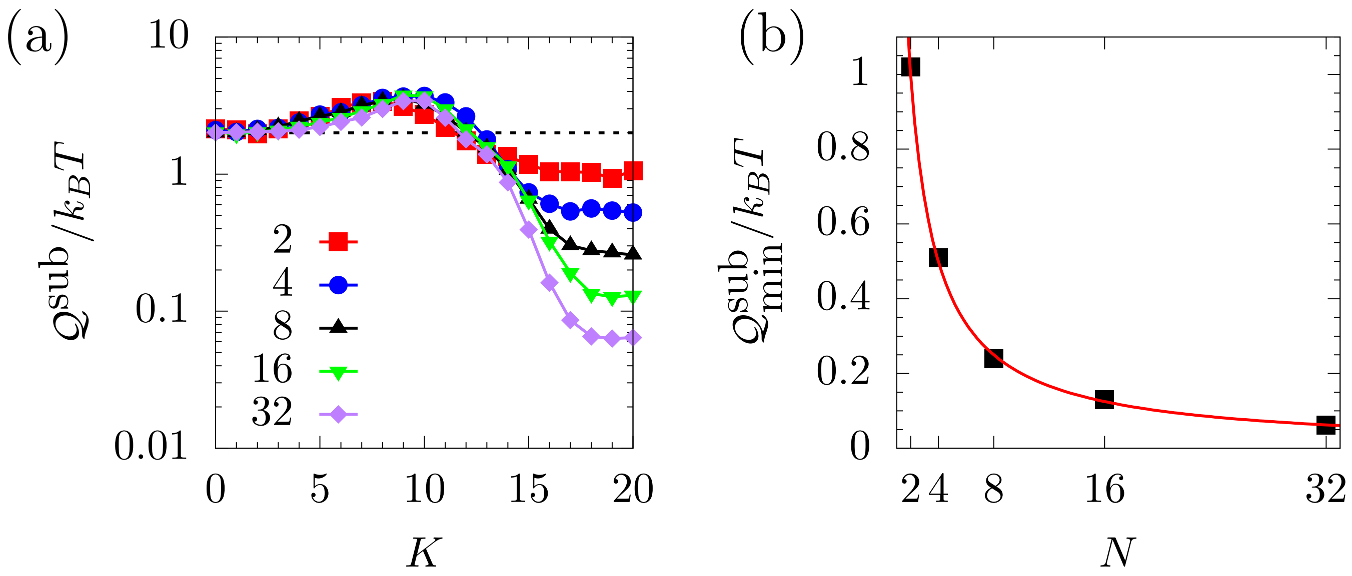
$$\mathbf{M} = \begin{bmatrix} -K & \frac{K}{N} & \frac{K}{N} & \cdots & \frac{K}{N} \\ \frac{K}{N} & -K & \frac{K}{N} & \cdots & \frac{K}{N} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{K}{N} & \frac{K}{N} & \frac{K}{N} & \cdots & -K \end{bmatrix}$$

$$\phi_1 = \theta_1 + \theta_2 + \cdots + \theta_N \qquad \lambda_1 = 0$$

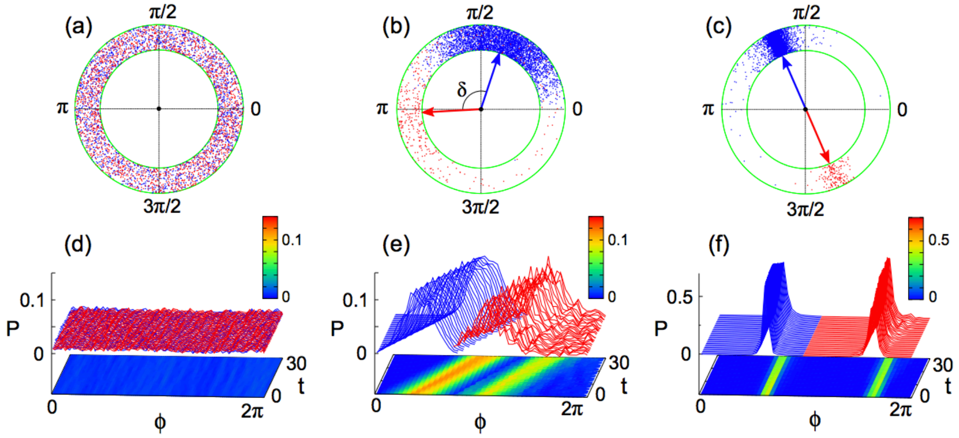
$$\phi_i = \theta_1 - \theta_i \qquad \lambda_i < 0 \quad (i \neq 1)$$

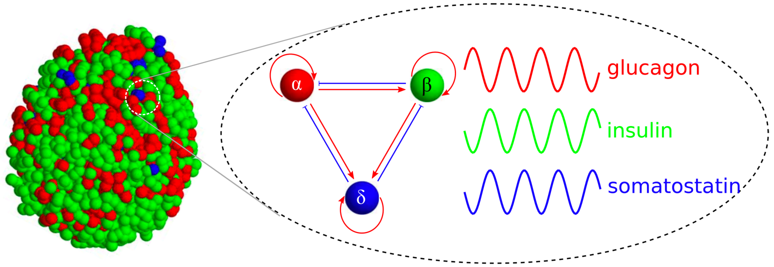
$$\langle \delta\theta_1^2 \rangle = \frac{\sum_{i=1}^{N}\langle \delta\phi_i^2 \rangle}{N^2} \approx \frac{\langle \delta\phi_1^2 \rangle}{N^2} = \frac{2Dt}{N}$$

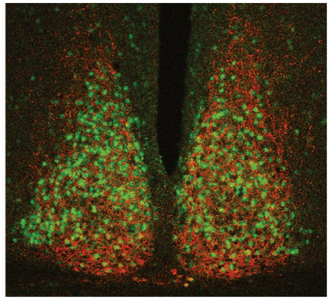
$$\mathcal{Q}^{\text{sub}} = \sigma\frac{2D}{v^2} = \frac{2k_BT}{N}$$

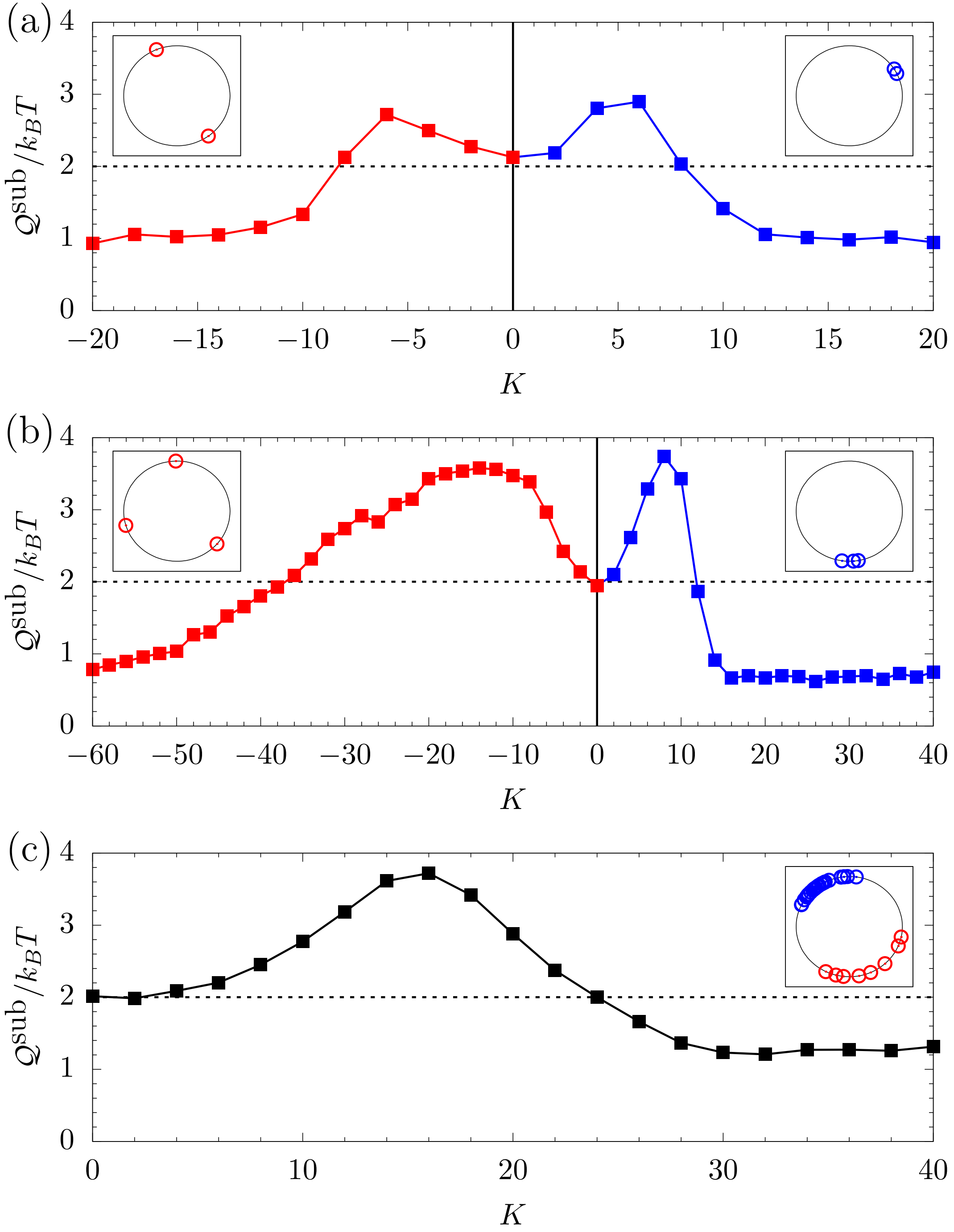


Collective dynamics









Summary

- Non-equilibrium thermodynamics, stochastic thermodynamics, and information thermodynamics provide new languages for understanding thermodynamic (energetic and informational) aspects of rich and collective dynamics of living systems (e.g., learning, computation, memory, …).
- Thermodynamic constraints are important for designing efficient molecular machines/robots operating under thermal fluctuations.
- The energetic cost for operational accuracy can be reduced by the cooperation between subsystems.

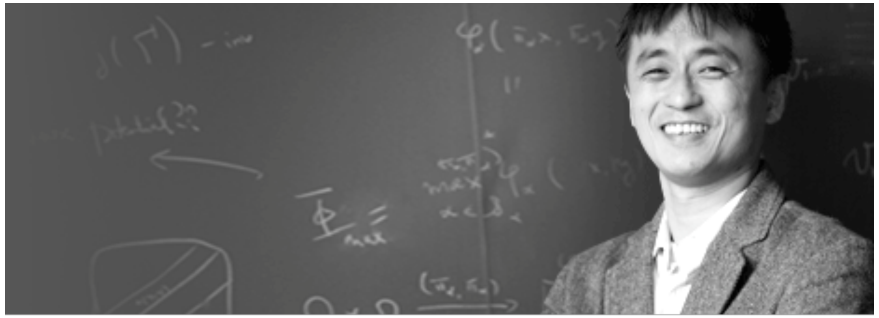
arXiv.org > cond-mat > arXiv:1804.10362

Condensed Matter > Statistical Mechanics

Thermodynamic uncertainty relation of interacting oscillators in synchrony

Sangwon Lee, Changbong Hyeon, Junghyo Jo

(Submitted on 27 Apr 2018)



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