Tracking nonequilibrium in living matter and self-propelled systems

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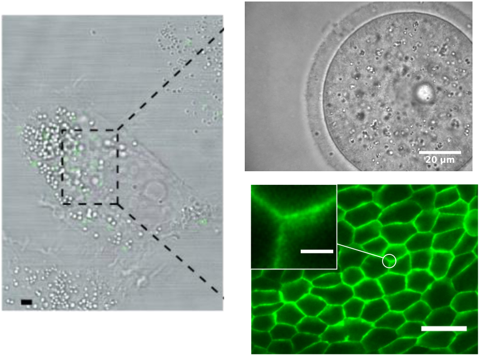
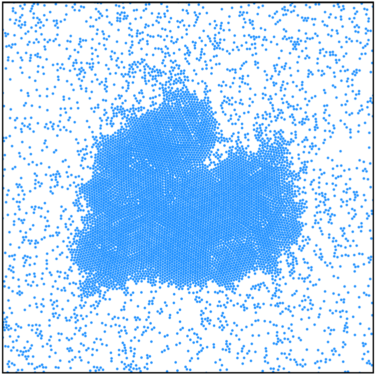
Introduction

From one tracer ... | ... to many active particles

Living matter | Collective effects





Introduction

From one tracer ...

Living matter

- Living melanoma cells

  D. A. Weitz, M. Guo (Harvard University)

  N. S. Gov (Weizmann Institute of Science)

- Living mouse oocytes

  W. W. Ahmed, M. Bussonnier, T. Betz (Curie Institute)

  M. Almonacid and M.-H. Verlhac (Collège de France)

- Epithelial tissues

  V. Mehandia, J. Comelles, R. Thiagarajan, D. Riveline

  (University of Strasbourg)

... to many active particles

Collective effects

Interacting active particles

J. Tailleur (University Paris Diderot)

C. Nardini, M. E. Cates (University of Cambridge)

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Outline

1. Vesicle dynamics in living oocytes
   - What can we measure?
   - What is equilibrium/nonequilibrium?
   - How can we quantify activity?

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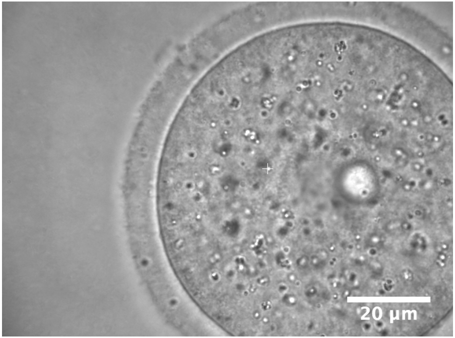
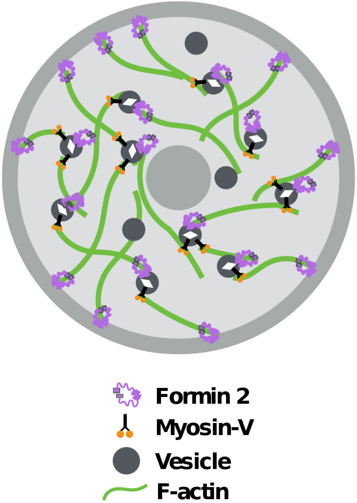
Vesicle dynamics in living oocytes

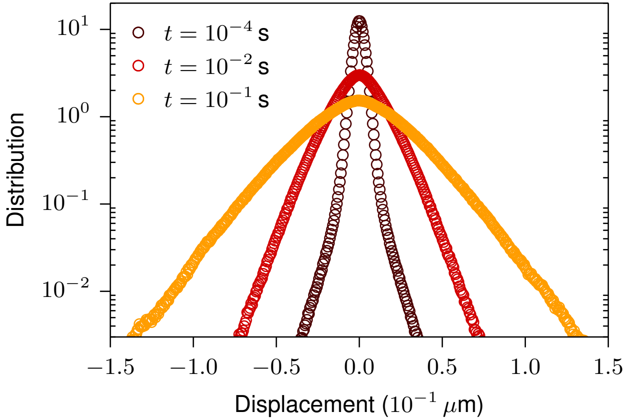




Oocyte = Immature egg

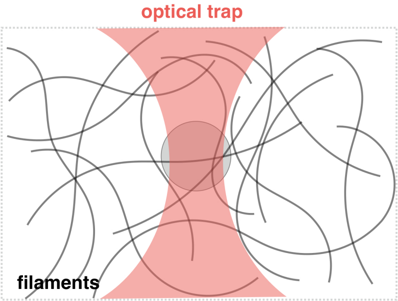
Tracers = Vesicles

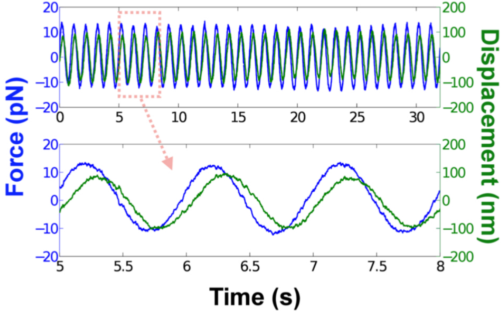
Statistics of tracer displacement



Vesicle dynamics in living oocytes

Measuring the mechanics



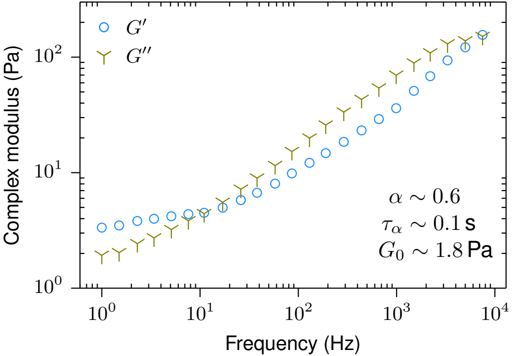


$$\langle \delta r(t) \rangle = \int_0^t \underbrace{R(t-s)}_{\text{Response}} F(s) \mathrm{d}s$$

Vesicle dynamics in living oocytes

Complex modulus

$$G^*(\omega) = \frac{1}{6\pi a R(\omega)}$$



$$G^* = \underbrace{G'}_{\text{Elastic mod.}} + \underbrace{\mathrm{i}G''}_{\text{Viscous mod.}}$$

$$G^*(\omega) = G_0\left[1 + (\mathrm{i}\omega\tau_\alpha)^\alpha\right]$$

Visco-elastic material

Vesicle dynamics in living oocytes

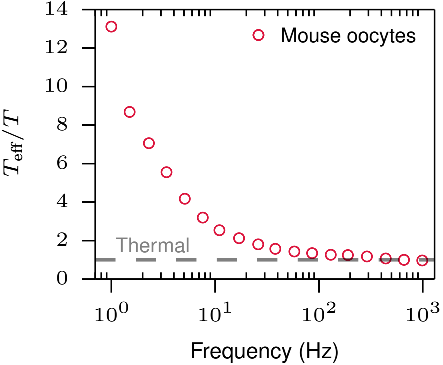
Trademark of equilibrium

$$R(t) = -\frac{1}{T}\frac{\mathrm{d}}{\mathrm{d}t}\underbrace{\langle x(t)x(0)\rangle}_{C(t)} \quad \rightarrow \quad T = \frac{\omega C(\omega)}{2R''(\omega)}$$

Fluctuation-dissipation theorem

Vesicle dynamics in living oocytes

Effective temperature



Violation of FDT

$$T_{\text{eff}}(\omega) = \frac{\omega C(\omega)}{2R''(\omega)}$$

D. Mizuno *et al.*, Science **315**, 370 (2007)

C. Wilhelm, Phys. Rev. Lett. **101**, 028101 (2008)

F. Gallet *et al.*, Soft Matter **5**, 2947 (2009)

H. Turlier *et al.*, Nat. Phys. **12**, 512 (2016)

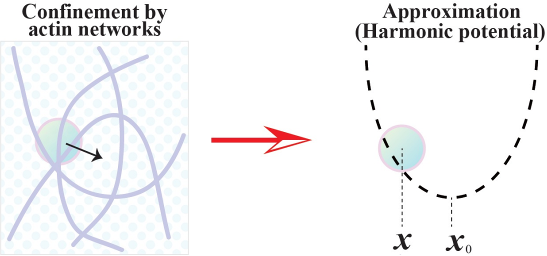
Bridging departure from equilibrium to the microscopics

Vesicle dynamics in living oocytes

Tracer dynamics: transitions between local cages

C. P. Brangwynne *et al.*, Trends Cell Biol. **19**, 423 (2009)

Vesicle dynamics in living oocytes

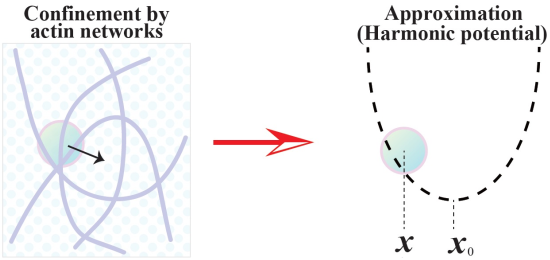


Tracer dynamics

$$m\frac{\mathrm{d}^2x}{\mathrm{d}t^2} = -k(x - x_0) - \gamma\frac{\mathrm{d}x}{\mathrm{d}t} + \xi$$

$$\langle\xi(t)\xi(0)\rangle = 2\gamma T\delta(t)$$

Vesicle dynamics in living oocytes



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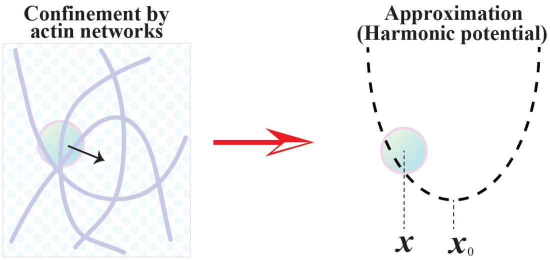
Vesicle dynamics in living oocytes



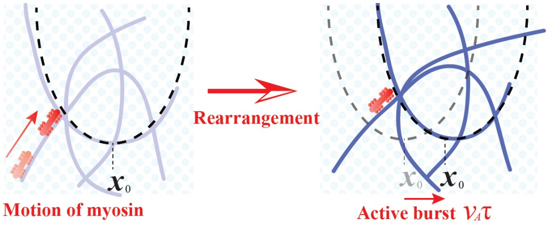
Tracer dynamics

$$\cancel{m\frac{\mathrm{d}^2x}{\mathrm{d}t^2}} = -k(x-x_0) - \gamma * \frac{\mathrm{d}x}{\mathrm{d}t} + \xi$$

$$\langle \xi(t)\xi(0) \rangle = T\gamma\left(|t|\right)$$

Vesicle dynamics in living oocytes

Active motion of local minimum

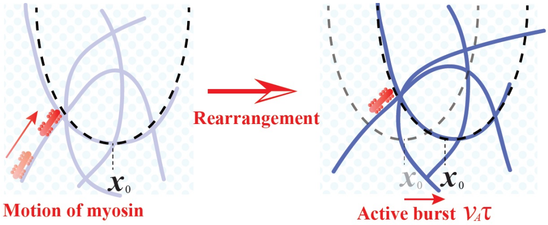


Tracer dynamics

$$\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} = -k(x - x_0) + \xi, \quad \gamma * \frac{\mathrm{d}x_0}{\mathrm{d}t} = F_{\mathrm{M}}$$

Vesicle dynamics in living oocytes

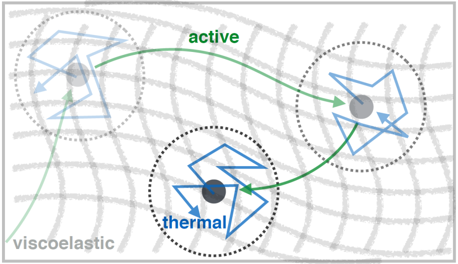
Active motion of local minimum

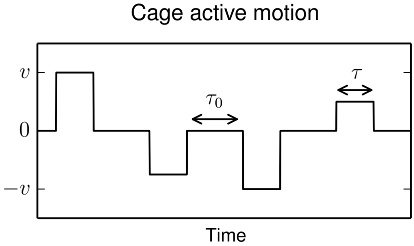


Tracer dynamics

$$\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} = -kx + \underbrace{F_A}_{kx_0} + \xi, \quad \gamma * \frac{\mathrm{d}x_0}{\mathrm{d}t} = F_M$$

Vesicle dynamics in living oocytes





$$\langle F_{\mathrm{M}}(t)F_{\mathrm{M}}(0)\rangle \propto D_{\mathrm{A}}\frac{\mathrm{e}^{-|t|/\tau}}{\tau}$$

Active diffusion $D_{\mathrm{A}} = \dfrac{(v\tau)^2}{3(\tau+\tau_0)}$

Vesicle dynamics in living oocytes

Spectrum of stochastic forces

$$S_{\text{cell}}(\omega) = \mathcal{F}\left\langle\left(\xi + F_{\text{A}}\right)(t)\left(\xi + F_{\text{A}}\right)(0)\right\rangle$$

Combining response and fluctuations

F. Gallet *et al.*, Soft Matter **5**, 2947 (2009)

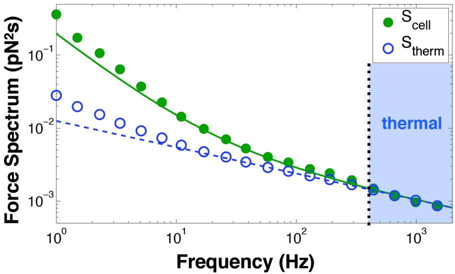
D. Robert *et al.*, PLoS One **5**, e10046 (2010)

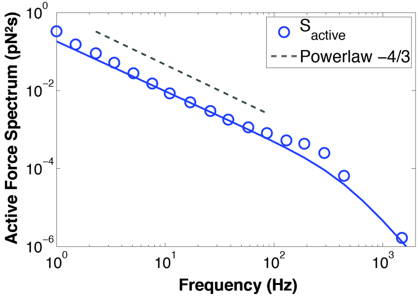
M. Guo *et al.*, Cell **158**, 822 (2014)

Active and thermal contributions

$$S_{\text{cell}}(\omega) \quad = \quad \underbrace{S_{\text{th}}(\omega)}_{\text{mechanics (FDT)}} \quad + \quad S_{\text{A}}(\omega)$$

Vesicle dynamics in living oocytes





Active diffusion $D_{\mathrm{A}} \sim 5 D_{\mathrm{th}}$

Persistence time $\tau \sim 0.3\,\mathrm{ms}$

Power stroke time of myosin-V $\sim 0.5\,\mathrm{ms}$

G. Cappello *et al.*, Proc. Natl. Acad. Sci. U.S.A. **104**, 15328 (2007)

Vesicle dynamics in living oocytes

Characterizing energy transfers

Active force power

$$J_{\text{tracer}} = F_{\text{A}} \frac{\mathrm{d}x}{\mathrm{d}t}$$

Vesicle dynamics in living oocytes

Characterizing energy transfers

Active force power

$$J_{\text{tracer}} = \left\langle F_{\text{A}} \frac{\mathrm{d}x}{\mathrm{d}t} \right\rangle$$

Stochastic energetics

Vesicle dynamics in living oocytes

Tracer dynamics

$$\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} = -kx + F_{\mathrm{A}} + \xi$$

Active force power

$$J_{\mathrm{tracer}} = \left\langle \left(\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} - \xi \right) \frac{\mathrm{d}x}{\mathrm{d}t} \right\rangle + \left\langle kx \frac{\mathrm{d}x}{\mathrm{d}t} \right\rangle$$

Vesicle dynamics in living oocytes

Tracer dynamics

$$\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} = -kx + F_{\mathrm{A}} + \xi$$

Active force power

$$J_{\mathrm{tracer}} = \underbrace{\left\langle \left(\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} - \xi \right) \frac{\mathrm{d}x}{\mathrm{d}t} \right\rangle}_{\text{Dissipated power}} + \cancel{\left\langle kx \frac{\mathrm{d}x}{\mathrm{d}t} \right\rangle}$$

Vesicle dynamics in living oocytes

Spectral decomposition

$$J_{\mathrm{tracer}} = \int I(\omega)\frac{\mathrm{d}\omega}{2\pi}$$

Vesicle dynamics in living oocytes

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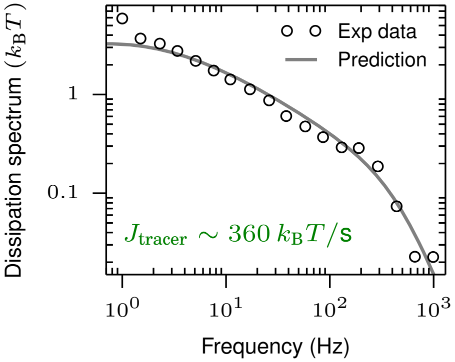


Spectrum of dissipated power

$$I(\omega) = \frac{2\left[T_{\text{eff}}(\omega) - T\right]}{1 + \left[G'(\omega)/G''(\omega)\right]^2}$$

Vesicle dynamics in living oocytes

Tracer dynamics

$$\gamma * \frac{\mathrm{d}x}{\mathrm{d}t} = -kx + F_{\mathrm{A}} + \xi, \quad \gamma * \frac{\mathrm{d}x_0}{\mathrm{d}t} = F_{\mathrm{M}}$$

Power injected by motors into cage

$$J_{\mathrm{cage}} = \left\langle F_{\mathrm{M}} \frac{\mathrm{d}x_0}{\mathrm{d}t} \right\rangle \sim 2 \cdot 10^5 \, k_{\mathrm{B}} T / s$$

Power injected by one myosin-V $\sim 10^4 \, k_{\mathrm{B}} T/\mathrm{s}$

K. Fujita *et al.*, Nat. Com. **3**, 956 (2012)

Vesicle dynamics in living oocytes

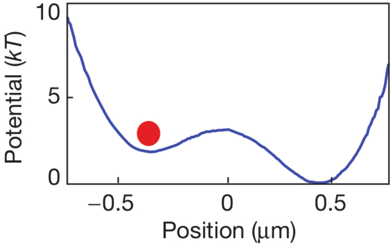
Efficiency of power transduction

$$\frac{\text{cage} \to \text{tracer}}{\text{motors} \to \text{cage}} = \frac{J_{\text{tracer}}}{J_{\text{cage}}} \sim 10^{-3}$$

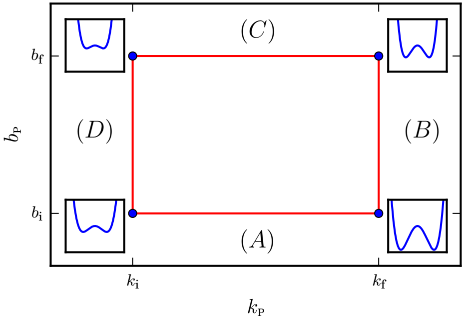
Main energy injection goes to network remodeling

Vesicle dynamics in living oocytes

Perspectives: Extract work from cyclic protocol



A. Bérut *et al.*, Nature **483**, 187 (2012)



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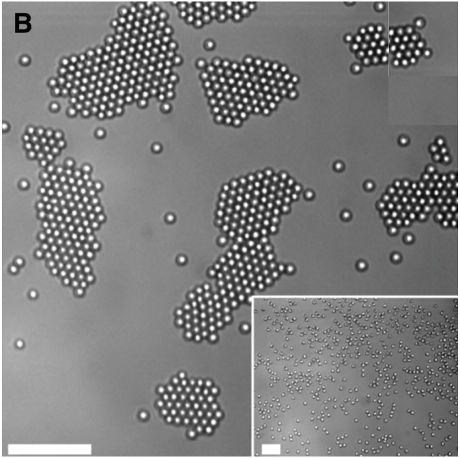
Interacting active particles

Light-induced clusters of colloids



J. Palacci *et al.*, Science **339**, 936 (2013)

Interacting active particles

Many-body dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\mu\nabla_i U + \xi_i$$

Equilibrium fluctuations ξ_i

No memory and Gaussian

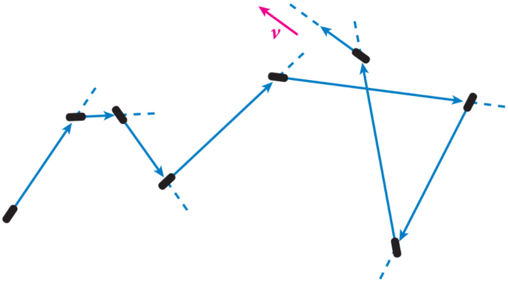
Boltzmann distribution

$$P_{\mathrm{S}} \propto \mathrm{e}^{-U/T}$$

Interacting active particles

Many-body dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\mu \nabla_i U + v_i$$



Nonequilibrium self-propulsion v_i

Memory and non-Gaussian

Non-Boltzmann distribution

M. E . Cates and J. Tailleur, Ann. Rev. CMP **6**, 219 (2015)

Interacting active particles

Many-body dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\mu \nabla_i U + v_i$$

Nonequilibrium self-propulsion v_i

Memory and Gaussian

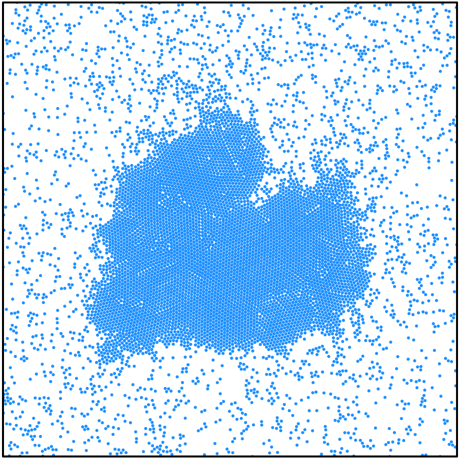
G. Szamel et al., Phys. Rev. E **91**, 062304 (2015)

C. Maggi *et al.*, Sci. Rep. **5**, 10724 (2015)

T. F. F. Farage *et al.*, Phys. Rev. E **91**, 042310 (2015)

Persistence time $\tau \quad \rightarrow \quad$ Equilibrium $\quad \tau = 0$

Interacting repulsive particles



Interacting active particles

Comparing forward and backward dynamics

Quantifying irreversibility

$$\sigma = \lim_{t\to\infty} \frac{1}{t} \ln \frac{\mathcal{P}}{\mathcal{P}^{\mathsf{R}}}$$

Entropy production rate

Equilibrium $\quad \sigma = 0$

Interacting active particles

Brownian particles + non-conservative force F_i

$$\sigma = \frac{\left\langle F_i \frac{\mathrm{d}x_i}{\mathrm{d}t} \right\rangle}{T} = \frac{\text{power of } F_i}{\text{temperature}}$$

Self-propelled particles

$$\sigma = \frac{\mu\tau^2}{2T} \left\langle \nabla_i^3 U \left(\frac{\mathrm{d}x_i}{\mathrm{d}t} \right)^3 \right\rangle$$

Interacting active particles

Many-body dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\mu\nabla_i U + v_i, \quad \tau\frac{\mathrm{d}v_i}{\mathrm{d}t} = -v_i + \xi_i$$

$$\langle\xi_i(t)\xi_j(0)\rangle = 2\mu T\delta_{ij}\delta(t)$$

Nonequilibrium underdamped dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = p_i, \quad \tau\frac{\mathrm{d}p_i}{\mathrm{d}t} = -p_i - \tau\mu p_j\nabla_i\nabla_j U - \mu\nabla_i U + \xi_i$$

Interacting active particles

Many-body dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\mu\nabla_i U + v_i, \quad \tau\frac{\mathrm{d}v_i}{\mathrm{d}t} = -v_i + \xi_i$$

$$\langle \xi_i(t)\xi_j(0)\rangle = 2\mu T\delta_{ij}\delta(t)$$

Nonequilibrium underdamped dynamics

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = p_i, \quad \cancel{\tau\frac{\mathrm{d}p_i}{\mathrm{d}t}} = -p_i - \tau\mu p_j \nabla_i\nabla_j U - \mu\nabla_i U + \xi_i$$

C. Maggi *et al.*, Sci. Rep. **5**, 10724 (2015)

Interacting active particles

Perturbative treatment in $\sqrt{\tau}$

$$p_i \to \sqrt{\tau} p_i$$

Scaled velocities

Stationary distribution: position and velocity

$$P_{\mathrm{S}} \propto \exp\left[-\frac{p_i^2}{2T} - \frac{U}{T} + \sum_{n=2}^{\infty} \tau^{n/2} \psi_n\left(\{x_i, p_i\}\right)\right]$$

Solving recursively the Fokker-Planck equation

Interacting active particles

Stationary distribution: position only

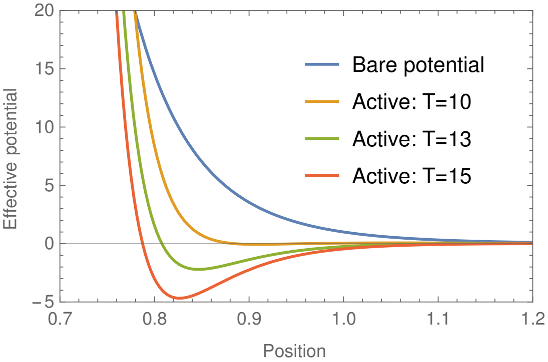
$$P_{\mathrm{S}} \propto \mathrm{e}^{-U_{\mathrm{eff}}/T}\left[1+\mathcal{O}\left(\tau^2\right)\right]$$

Effective potential

$$U_{\mathrm{eff}} = U + \tau\left[\frac{\left(\nabla_i U\right)^2}{2} - T\nabla_i^2 U\right]$$

Original pair-wise potential

$$U = \frac{1}{2}\sum_{i,j=1}^{N}\phi(x_i - x_j), \quad \phi \propto \frac{1}{x^{12}}$$



Consistent with

- C. Maggi *et al.*, Sci. Rep. **5**, 10724 (2015)
- T. F. F. Farage *et al.*, Phys. Rev. E **91**, 042310 (2015)

Entropy production rate

$$\sigma \propto \left\langle \nabla_i^3 U \left(\frac{\mathrm{d}x_i}{\mathrm{d}t}\right)^3 \right\rangle$$

$$\left\langle \nabla_i^3 U \left(\frac{\mathrm{d}x_i}{\mathrm{d}t}\right)^3 \right\rangle = \mathcal{O}\left(\tau^{3/2}\right)$$

$$\text{Effective equilibrium regime} \quad \begin{cases} \text{Non-thermal statistics} \\ \text{Time reversal} \end{cases}$$

Interacting active particles

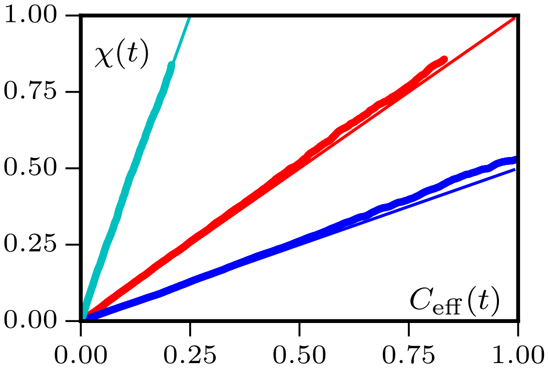
Fluctuation-dissipation relation

$$R(t) = -\frac{1}{T}\frac{\mathrm{d}}{\mathrm{d}t}\left\langle x_i(t)x_i(0) + \tau^2 \frac{\mathrm{d}x_i(t)}{\mathrm{d}t}\frac{\mathrm{d}x_i(0)}{\mathrm{d}t}\right\rangle$$

Probing effective equilibrium

Interacting active particles

Numerical simulations: 3 values of T



Susceptibility

$$\chi(t) = \frac{1}{N}\int_0^t R(t-s)\mathrm{d}s$$

Correlation

$$C_{\mathrm{eff}}(t) = \frac{1}{N}\left\langle x_i^2(t) + \tau^2\left[\frac{\mathrm{d}x_i(t)}{\mathrm{d}t}\right]^2\right\rangle - \frac{1}{N}\left\langle x_i(t)x_i(0) + \tau^2\frac{\mathrm{d}x_i(t)}{\mathrm{d}t}\frac{\mathrm{d}x_i(0)}{\mathrm{d}t}\right\rangle$$

Future directions

- Other models of self-propulsion

  Non-Gaussian without memory

- Hydrodynamics

  Dynamics passive tracer

Conclusion

Nonequilibrium properties of active systems

- Living matter

  Quantifying active fluctuations

  Energetics

- Interacting active particles

  Emergence of attractive effects

  Effective equilibrium regime

References

- Modeling fluctuations in living/glassy systems

  Phys. Rev. E **90**, 042724 (2014), `arXiv:1406.1732`

  Phys. Rev. E **92**, 012716 (2015), `arXiv:1507.00917`

  BBA – Molecular Cell Research **1853**, 3083 (2015)

  Phys Rev. E (2016), `arXiv:1601.06613`

- Living melanoma cells | EPL **110**, 48005 (2015), `arXiv:1505.06489`
- Living mouse oocytes | `arXiv:1510.08299`, `arXiv:1511.00921`
- Epithelial tissues | `arXiv:1512.01476`
- Self-propelled particles | Phys. Rev. Lett. (2016), `arXiv:1604.00953`

Interacting active particle

Density waves around an obstacle