Self-organization of bacterial mixtures using motility regulation

J. Tailleur

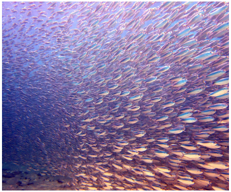
Laboratoire MSC
CNRS - Université Paris Diderot

active20@KITP

[A. I. Curatolo, N. Zhou, Y. Zhao, C. Liu, A. Daerr, J. Tailleur, J.-D. Huang, BioRxiV:798827, Nat. Phys. in Press.]

Active matter

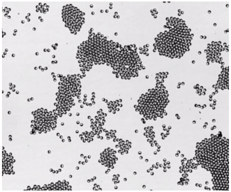
Drive at the microscopic level → *Strongly out of equilibrium* → *Fundamentally new physics*



- Biological relevance
- Explore new dynamical phenomenology

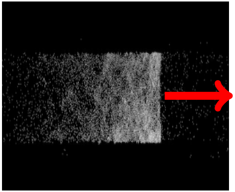
Active matter

Drive at the microscopic level → *Strongly out of equilibrium* → *Fundamentally new physics*



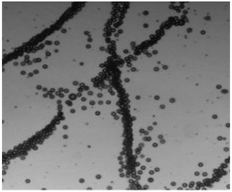
Clusters without attractive interactions

[van der Linden, PRL 2019]



Solitonic waves

[Bricard , Nature 2013]



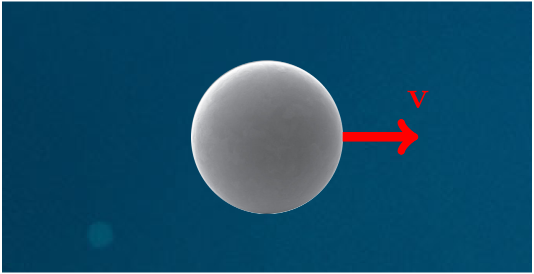
Filaments

[Thutupalli, PNAS 2018]

- Biological relevance
- Active Soft Materials

- Explore new dynamical phenomenology
- Build generic framework for Active Matter

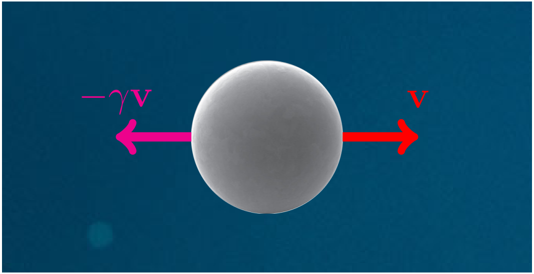
Active vs Passive particles



$$m\dot{v} = -V'_{\rm ext}(x) - \gamma v + \sqrt{2\gamma kT}\eta$$

- Colloid in a fluid at equilibrium:

Active vs Passive particles

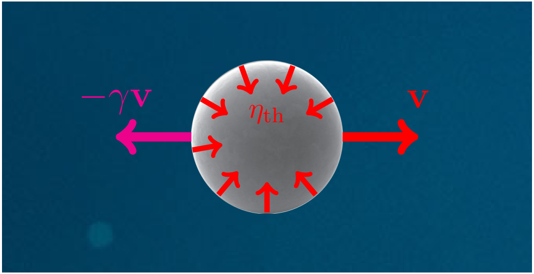


$$m\dot{v} = -V'_{\mathrm{ext}}(x) - \gamma v + \sqrt{2\gamma k T}\eta$$

- Colloid in a fluid at equilibrium:

  → Dissipation: mean (drag) force from the fluid $\propto \gamma$

Active vs Passive particles



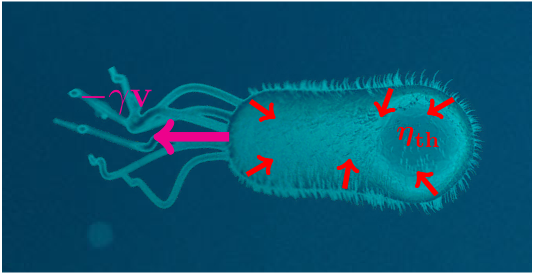
$$m\dot{v} = -V'_{\rm ext}(x) - \gamma v + \sqrt{2\gamma kT}\eta$$

- Colloid in a fluid at equilibrium: Fluctuation-Dissipation theorem $D = kT/\gamma$

⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma kT$

Active vs Passive particles



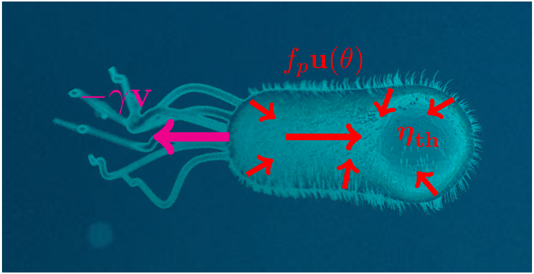
$$m\dot{v} = -V'_{\mathrm{ext}}(x) - \gamma v + \sqrt{2\gamma k T}\,\eta$$

- Active matter:

⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma k T$

Active vs Passive particles



$$m\dot{v} = -V'_{\mathrm{ext}}(x) - \gamma v + \sqrt{2\gamma kT}\eta + f_p\mathbf{u}(\theta)$$

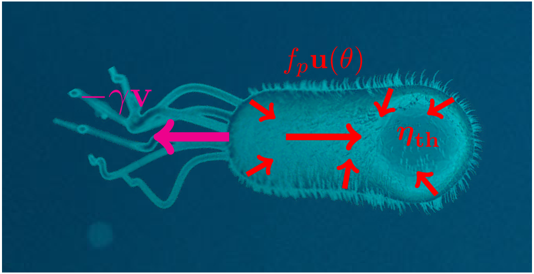
- Active matter:

⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma kT$

⟶ Injection of energy: self-propulsion force $f_p\mathbf{u}(\theta)$

Active vs Passive particles



$$m\dot{v} = -V'_{\text{ext}}(x) - \gamma v + \sqrt{2\gamma k T}\eta + f_p \mathbf{u}(\theta)$$

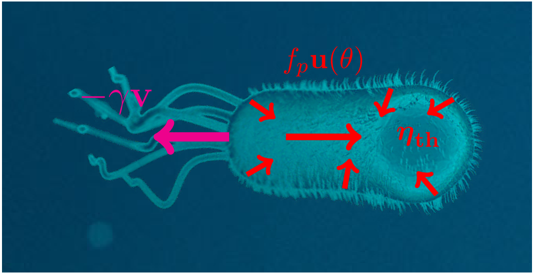
- Active matter: ⟶ No FDT: system driven out of equilibrium

⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma k T$

⟶ Injection of energy: self-propulsion force $f_p \mathbf{u}(\theta)$

Active vs Passive particles



$$0 = m\dot{v} = -V'_{\rm ext}(x) - \gamma v + \tilde{\eta}$$

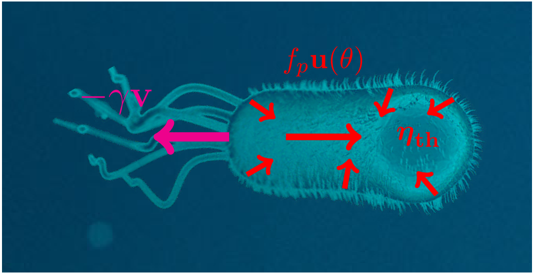
- Active matter: ⟶ No FDT: system driven out of equilibrium

⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma kT$

⟶ Injection of energy: self-propulsion force $f_p\mathbf{u}(\theta)$

Active vs Passive particles



$$0 = m\dot{v} = -V'_{\rm ext}(x) - \gamma v + \tilde{\eta}$$

- Active matter: ⟶ No FDT: system driven out of equilibrium

  ⟶ Dissipation: mean (drag) force from the fluid $\propto \gamma$

  ⟶ Injection of energy: fluctuating force from the fluid $\propto \gamma kT$

  ⟶ Injection of energy: self-propulsion force $f_p\mathbf{u}(\theta)$

- Breakdown of detailed-balance ⟶ Steady-state not easily infered from dynamics

Passive vs active dynamics

$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \sqrt{2D}\boldsymbol{\eta}$

Gaussian white noise $\boldsymbol{\eta}$

Equilibrium Stat. Mech.

$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \boldsymbol{v_p}$

Non-Gaussian persistent noise $\boldsymbol{v_p}$

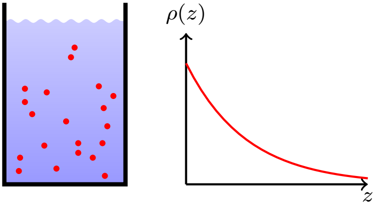
No working theory

Passive vs active dynamics

$$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \sqrt{2D}\boldsymbol{\eta}$$

Gaussian white noise $\boldsymbol{\eta}$

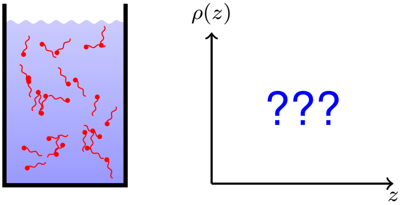
Equilibrium Stat. Mech.



$$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \boldsymbol{v_p}$$

Non-Gaussian persistent noise $\boldsymbol{v_p}$

No working theory

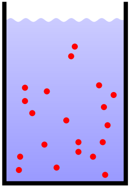


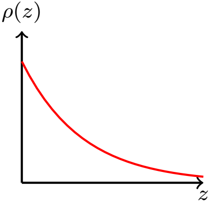
Passive vs active dynamics

$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \sqrt{2D}\boldsymbol{\eta}$

Gaussian white noise $\boldsymbol{\eta}$

Equilibrium Stat. Mech.

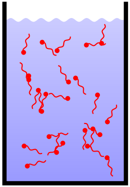


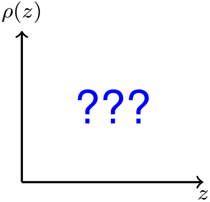


$\dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \boldsymbol{v_p}$

Non-Gaussian persistent noise $\boldsymbol{v_p}$

No working theory





→ Rather frustrating situation: what can be saved from (near-) equilibrium methods?

Outside the limit in which $\boldsymbol{v_p}$ amounts to a Gaussian white noise

Self-organization in & out of equilibrium

- Thermal Equilibrium
  - ⟶ Time-reversal symmetry in steady-state
  - ⟶ Boltzman weight: guides our intuition

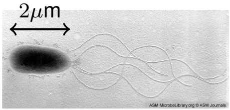
Self-organization in & out of equilibrium

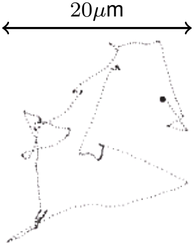
- Thermal Equilibrium
  - ⟶ Time-reversal symmetry in steady-state
  - ⟶ Boltzman weight: guides our intuition
- Example: Liquid-gas phase transition
  - ⟶ Passive Brownian particles with attractive interactions
  - ⟶ Entropy vs Energy : disorder vs cohesion
  - ⟶ Lowering T: transition from gas to liquid (with coexistence)

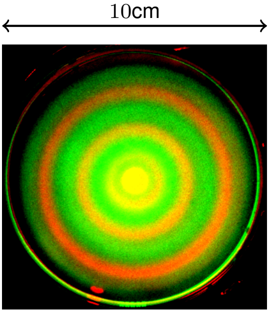
Self-organization in & out of equilibrium

- Thermal Equilibrium
  - ⟶ Time-reversal symmetry in steady-state
  - ⟶ Boltzman weight: guides our intuition
- Example: Liquid-gas phase transition
  - ⟶ Passive Brownian particles with attractive interactions
  - ⟶ Entropy vs Energy : disorder vs cohesion
  - ⟶ Lowering T: transition from gas to liquid (with coexistence)
- Outside equilibrium
  - ⟶ No generic formula for steady-state distribution
  - ⟶ Little basis upon which to build intuition
  - ⟶ Few guiding principles for self-assembly

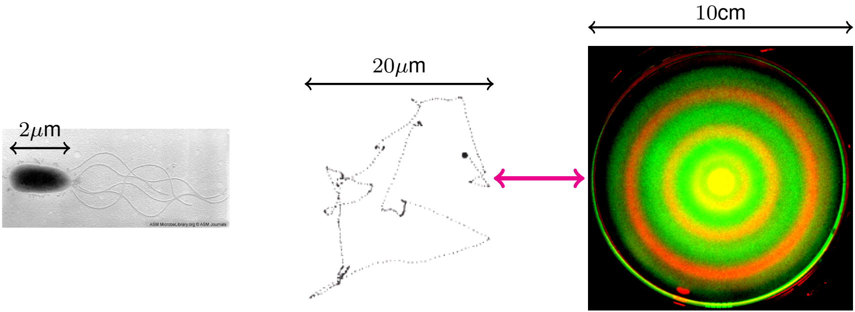
A statistical-mechanics framework for Active Matter







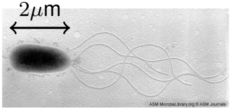
A statistical-mechanics framework for Active Matter



- How to go from micro to macro ?

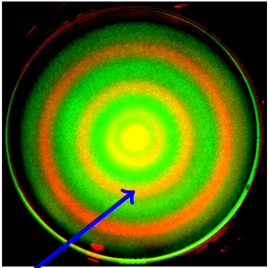
A statistical-mechanics framework for Active Matter

2μm



20μm

10cm

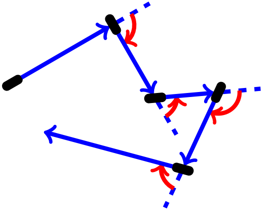


- How to go from micro to macro ?
- To understand and control (self-)organization ?

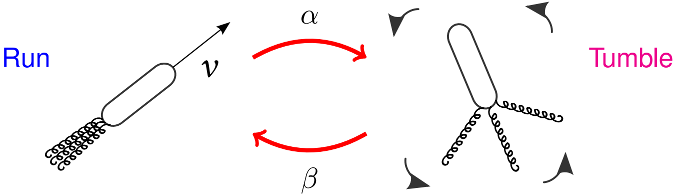
Run-and-tumble bacteria [Berg & Brown, Nature, 1972]

- Run: straight line (velocity $v \simeq 20\,\mu\mathrm{m.s}^{-1}$)
- Tumble: new direction (rate $\alpha \simeq 1\,\mathrm{s}^{-1}$, duration $\tau \simeq 0.1s$)

Run-and-tumble bacteria [Berg & Brown, Nature, 1972]

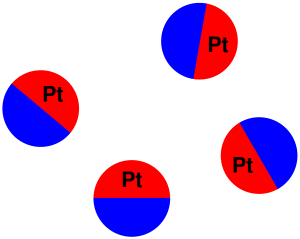


- Run: straight line (velocity $v \simeq 20\,\mu\mathrm{m.s}^{-1}$)
- Tumble: new direction (rate $\alpha \simeq 1\,\mathrm{s}^{-1}$, duration $\tau \simeq 0.1s$)



Self-propelled colloids

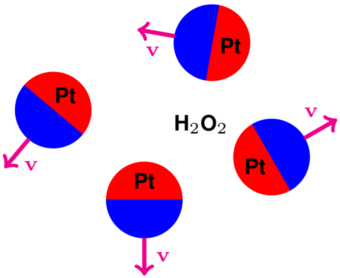
- E.g. Janus colloids with asymmetric coating



Self-propelled colloids

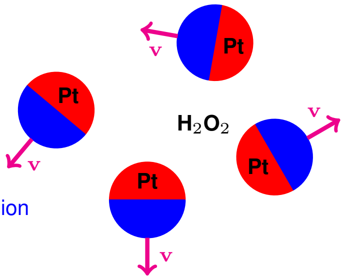
- E.g. Janus colloids with asymmetric coating

- Self [diffusio-] phoresis



Self-propelled colloids

- E.g. Janus colloids with asymmetric coating



- Self [diffusio-] phoresis

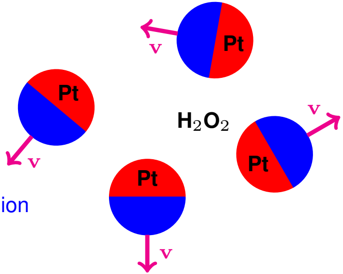
- Active Brownian Particles: continuous rotational diffusion

$$\dot{\mathbf{r}}(t) = v\mathbf{u}(\theta) + \sqrt{2D_t}\boldsymbol{\eta}; \qquad \dot{\theta}(t) = \sqrt{2D_r}\xi$$

$$v \simeq 1\mu.s^{-1}; \qquad D_t \simeq .3\mu^2.s^{-1}; \qquad D_{\text{eff}} \simeq 1-4\mu^2.s^{-1}$$

Self-propelled colloids

- E.g. Janus colloids with asymmetric coating



- Self [diffusio-] phoresis

- Active Brownian Particles: continuous rotational diffusion

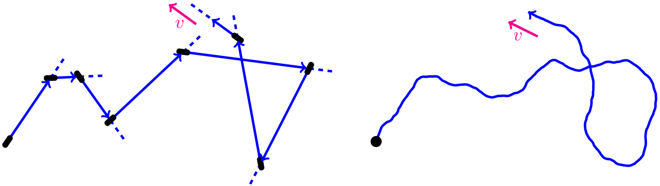
$$\dot{\mathbf{r}}(t) = v\mathbf{u}(\theta) + \sqrt{2D_t}\boldsymbol{\eta}; \qquad \dot{\theta}(t) = \sqrt{2D_r}\xi$$

$$v \simeq 1\mu.s^{-1}; \qquad D_t \simeq .3\mu^2.s^{-1}; \qquad D_{\rm eff} \simeq 1 - 4\mu^2.s^{-1}$$

- Many other types of self-propelled colloids...

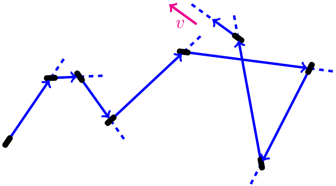
- Light-controlled [Palacci *et al.* Science **339**, 936 (2013)] •

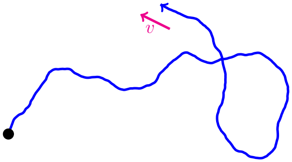
Motility-control as a self-organization principle



- Self-propelled particles with propelling speed v
- Diverse reorientation mechanisms (ABPs, RTPs, AOUPs, etc.)
- Generic: properties of v $\longrightarrow$ Control steady states

Motility-control as a self-organization principle





- Self-propelled particles with propelling speed v
- Diverse reorientation mechanisms (ABPs, RTPs, AOUPs, etc.)
- Generic: properties of v $\longrightarrow$ Control steady states

I. Non-interacting particles with spatially varying speed $v(\mathbf{r})$

II. Quorum-sensing: density-dependent speed $v(\rho)$

III. Application to bacterial pattern formation

IV. Multi-component systems

Position-dependent self-propulsion speed $v(\mathbf{r})$

- Master-equation for the probability density $P(\mathbf{r},\theta)$

$$\partial_t P(\mathbf{r},\theta;t) = -\nabla\cdot[v(\mathbf{r})\mathbf{u}(\theta)P(\mathbf{r},\theta)] + \Theta P$$

- ΘP: Randomization of orientation

$$\Theta_{ABP}P = D_r\Delta_\theta P(\mathbf{r},\theta); \qquad \Theta_{RTP}P = -\alpha P(r,\theta) + \int d\theta' \frac{\alpha}{2\pi}P(\mathbf{r},\theta')$$

Position-dependent self-propulsion speed $v(\mathbf{r})$

- Master-equation for the probability density $P(\mathbf{r},\theta)$

$$\partial_t P(\mathbf{r},\theta;t) = -\nabla\cdot[v(\mathbf{r})\mathbf{u}(\theta)P(\mathbf{r},\theta)] + \Theta P$$

- ΘP: Randomization of orientation

$$\Theta_{ABP}P = D_r \Delta_\theta P(\mathbf{r},\theta); \qquad \Theta_{RTP}P = -\alpha P(r,\theta) + \int d\theta' \frac{\alpha}{2\pi} P(\mathbf{r},\theta')$$

- Any isotropic function: $\Theta f(\mathbf{r}) = 0 \longrightarrow P_{\rm stat}(\mathbf{r}) \propto \frac{1}{v(\mathbf{r})}$ (up to normalization issues)

- SPPs spend more time where they go slower [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]

Position-dependent self-propulsion speed $v(\mathbf{r})$

- Master-equation for the probability density $P(\mathbf{r},\theta)$

$$\partial_t P(\mathbf{r},\theta;t) = -\nabla\cdot[v(\mathbf{r})\mathbf{u}(\theta)P(\mathbf{r},\theta)] + \Theta P$$

- ΘP: Randomization of orientation

$$\Theta_{ABP}P = D_r\Delta_\theta P(\mathbf{r},\theta); \qquad \Theta_{RTP}P = -\alpha P(r,\theta) + \int d\theta' \frac{\alpha}{2\pi} P(\mathbf{r},\theta')$$

- Any isotropic function: $\Theta f(\mathbf{r}) = 0 \longrightarrow P_{\rm stat}(\mathbf{r}) \propto \frac{1}{v(\mathbf{r})}$ (up to normalization issues)

- SPPs spend more time where they go slower [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]

- (A bit of) translational diffusion only changes this *quantitatively*

$$P_{\rm stat} \propto \frac{1}{\sqrt{D+v^2\tau}}; \qquad \tau^{-1} = d(d-1)D_r + d\alpha$$

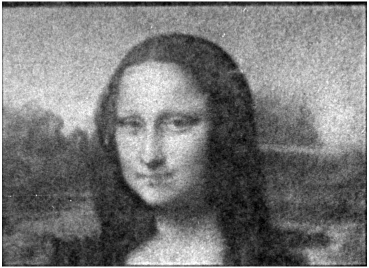
Experiments with bacteria

- Flagellar rotor can be controlled using light (proteorhodopsin)

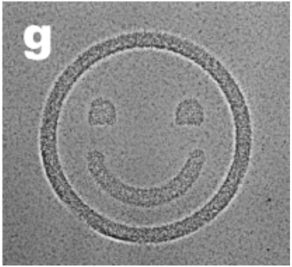
- Quantitative check that $\rho(\mathbf{r}) \propto \frac{1}{v(\mathbf{r})}$ [Arlt et al., arxiv:1902.10083]

Experiments with bacteria

- Flagellar rotor can be controlled using light (proteorhodopsin)
- Quantitative check that $\rho(\mathbf{r}) \propto \frac{1}{v(\mathbf{r})}$ [Arlt et al., arxiv:1902.10083]
- Painting with bacteria (and light modulation)



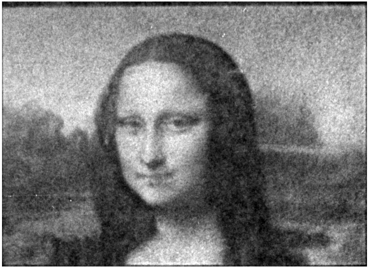
[Vizsnyiczai *et al.*, Nat. Com. (2017)]



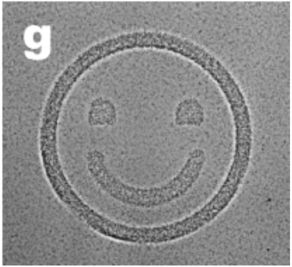
[Arlt *et al.*, Nat. Com. (2018)]

Experiments with bacteria

- Flagellar rotor can be controlled using light (proteorhodopsin)
- Quantitative check that $\rho(\mathbf{r}) \propto \frac{1}{v(\mathbf{r})}$ [Arlt et al., arxiv:1902.10083]
- Painting with bacteria (and light modulation)



[Vizsnyiczai *et al.*, Nat. Com. (2017)]



[Arlt *et al.*, Nat. Com. (2018)]

- Accumulation can be triggered by $v(\mathbf{r}), \alpha(\mathbf{r}), \beta(\mathbf{r})$ $\longrightarrow$ Many ways of slowing down

Interactions: Quorum-Sensing

- Motility requires energy source → Interactions with the environment (food, fuel source, etc.)

Interactions: Quorum-Sensing

- Motility requires energy source ⟶ Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles

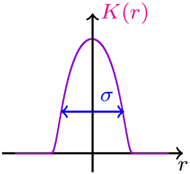
Interactions: Quorum-Sensing

- Motility requires energy source ⟶ Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles
- Simplest of model: Local in time, quasi-local in space [JT, Cates, PRL 2008]

$$\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)]\mathbf{u}(\theta_i); \qquad \dot{\theta}_i = [...]$$

- Particles measure an effective density $\tilde{\rho}(r)$

$$\tilde{\rho}(\mathbf{r}) = \int d\mathbf{r}' K(\mathbf{r}-\mathbf{r}')\rho(\mathbf{r}')$$



$$\rho(\mathbf{r}') = \sum_i \delta(\mathbf{r}' - \mathbf{r}_i)$$

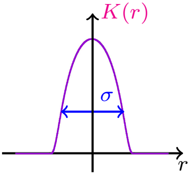
Interactions: Quorum-Sensing

- Motility requires energy source ⟶ Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles
- Simplest of model: Local in time, quasi-local in space [JT, Cates, PRL 2008]

$$\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)]\mathbf{u}(\theta_i); \qquad \dot{\theta}_i = [...]$$

- Particles measure an effective density $\tilde{\rho}(r)$

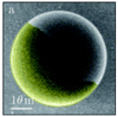
$$\tilde{\rho}(\mathbf{r}) = \int d\mathbf{r}' K(\mathbf{r} - \mathbf{r}')\rho(\mathbf{r}')$$



$$\rho(\mathbf{r}') = \sum_i \delta(\mathbf{r}' - \mathbf{r}_i)$$

- In reality, much more complex (*taxis*, time-delay, etc.)

Engineering quorum-Sensing [Bauerle *et al* Nat Com 2019]

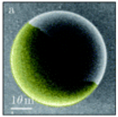


- Janus colloids in water-lutidine mixture with $T \leq T_c$
  [Volpe *et* al, Soft Mat. 2011]

- Light ⟶ Demixing on one side ⟶ Phoretic (self)-propulsive force

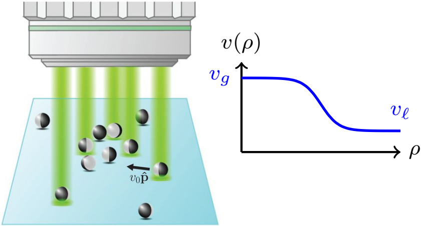
Engineering quorum-Sensing [Bauerle *et al* Nat Com 2019]

- Janus colloids in water-lutidine mixture with $T \leq T_c$
  [Volpe et al, Soft Mat. 2011]



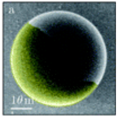
- Light ⟶ Demixing on one side ⟶ Phoretic (self)-propulsive force

- $v(\tilde{\rho})$ through feedback mechanism



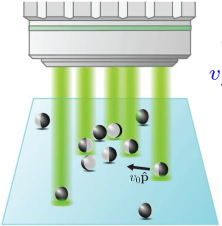
Engineering quorum-Sensing [Bauerle *et al* Nat Com 2019]

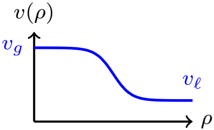
- Janus colloids in water-lutidine mixture with $T \leq T_c$
  [Volpe *et* al, Soft Mat. 2011]

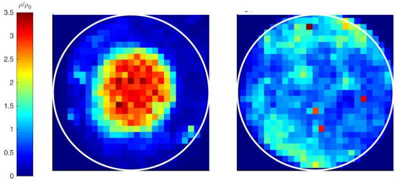


- Light ⟶ Demixing on one side ⟶ Phoretic (self)-propulsive force

- $v(\tilde{\rho})$ through feedback mechanism





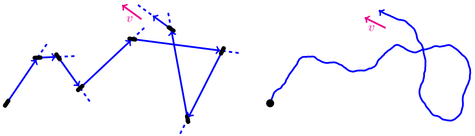


$v = v(\rho)$ $\qquad$ $v = v_0 \in \mathbb{R}$

- Can we understand this using our simple model?

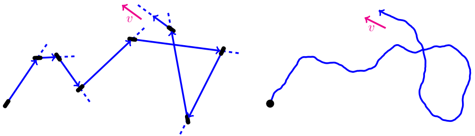
Quorum-sensing *in sillico*

- Consider RTPs and ABPs with QS interactions: $\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)]\mathbf{u}(\theta_i); \qquad \dot{\theta}_i = [...]$
  [JT & M. Cates; PRL 2008, EPL 2013; Solon *et al.* EPJST 2015, PRE 2016, NJP 2018]



Quorum-sensing *in sillico*

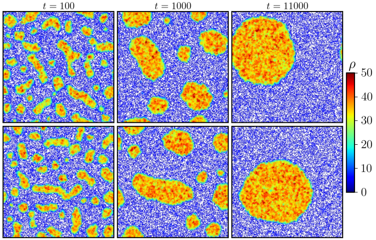
- Consider RTPs and ABPs with QS interactions: $\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)]\mathbf{u}(\theta_i); \qquad \dot{\theta}_i = [...]$
  [JT & M. Cates; PRL 2008, EPL 2013; Solon *et al.* EPJST 2015, PRE 2016, NJP 2018]



- $v(\rho)$ decreases as ρ increases ⟶ Generic phase separation

Tumble

Rotational diffusion



Hand-waving explanation

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\rm r}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$

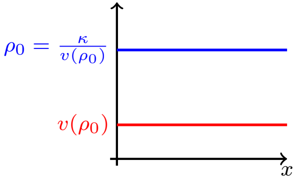
Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\rm r}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop



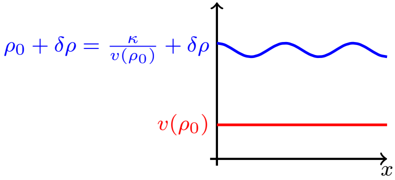
Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop



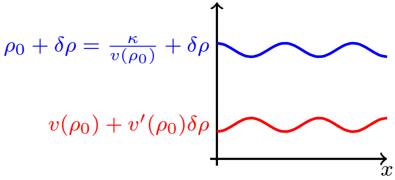
Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ → Feedback loop



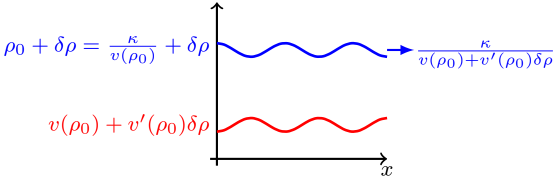
Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop



Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

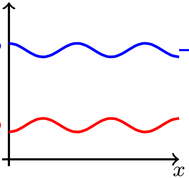
$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop

$\rho_0 + \delta\rho = \frac{\kappa}{v(\rho_0)} + \delta\rho$

$v(\rho_0) + v'(\rho_0)\delta\rho$



$\rightarrow \frac{\kappa}{v(\rho_0)+v'(\rho_0)\delta\rho} \simeq \frac{\kappa}{v(\rho_0)}\left(1 - \frac{v'(\rho_0)\delta\rho}{v(\rho_0)}\right)$

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

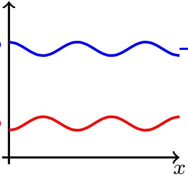
$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop

$\rho_0 + \delta\rho = \frac{\kappa}{v(\rho_0)} + \delta\rho$

$v(\rho_0) + v'(\rho_0)\delta\rho$



$$\longrightarrow \frac{\kappa}{v(\rho_0)+v'(\rho_0)\delta\rho} \simeq \frac{\kappa}{v(\rho_0)}\left(1 - \frac{v'(\rho_0)\delta\rho}{v(\rho_0)}\right) = \rho_0 - \frac{\rho_0 v'}{v}\delta\rho$$

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

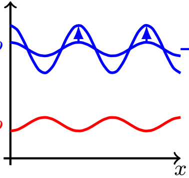
$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop

$\rho_0 + \delta\rho = \frac{\kappa}{v(\rho_0)} + \delta\rho$

$v(\rho_0) + v'(\rho_0)\delta\rho$



$\to \frac{\kappa}{v(\rho_0)+v'(\rho_0)\delta\rho} \simeq \frac{\kappa}{v(\rho_0)}\left(1 - \frac{v'(\rho_0)\delta\rho}{v(\rho_0)}\right) = \rho_0 - \frac{\rho_0 v'}{v}\delta\rho$

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

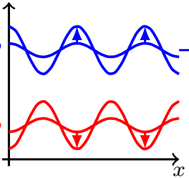
$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\rm r}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop

$\rho_0 + \delta\rho = \frac{\kappa}{v(\rho_0)} + \delta\rho$

$v(\rho_0) + v'(\rho_0)\delta\rho$



→ $\frac{\kappa}{v(\rho_0)+v'(\rho_0)\delta\rho} \simeq \frac{\kappa}{v(\rho_0)}\left(1 - \frac{v'(\rho_0)\delta\rho}{v(\rho_0)}\right) = \rho_0 - \frac{\rho_0 v'}{v}\delta\rho$

- Linear instab. if $1 \leq -\rho_0 \frac{v'(\rho_0)}{v(\rho_0)}$

Hand-waving explanation

- Non-uniform speed $v(\mathbf{r})$

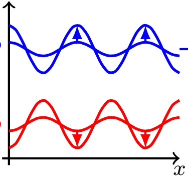
$$\dot{P}(\mathbf{r},\theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r})P(r,\theta)\mathbf{u}(\theta)] + D_{\mathrm{r}}\partial_\theta^2 P(\mathbf{r},\theta)$$

- Stationnary distribution $P(\mathbf{r},\theta) = \frac{\kappa}{v(\mathbf{r})}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ ⟶ Feedback loop

$\rho_0 + \delta\rho = \frac{\kappa}{v(\rho_0)} + \delta\rho$

$v(\rho_0) + v'(\rho_0)\delta\rho$



$\to \frac{\kappa}{v(\rho_0)+v'(\rho_0)\delta\rho} \simeq \frac{\kappa}{v(\rho_0)}\left(1 - \frac{v'(\rho_0)\delta\rho}{v(\rho_0)}\right) = \rho_0 - \frac{\rho_0 v'}{v}\delta\rho$

- Linear instab. if $1 \le -\rho_0 \frac{v'(\rho_0)}{v(\rho_0)}$ ⟶ Motility-induced phase-separation [Cates, JT Ann. Rev. Cond. Mat. Phys. 2015]

- How can we characterize this phase separation?

Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality

$$\dot{\rho} = -\nabla \cdot J[\rho] \qquad \text{where} \qquad J[\rho] = -M[\rho]\nabla \frac{\delta \mathcal{F}}{\delta \rho}$$

- Free energy: $\mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2}(\nabla\rho)^2] + \dots$

Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality

$$\dot{\rho} = -\nabla \cdot J[\rho] \qquad \text{where} \qquad J[\rho] = -M[\rho]\nabla \frac{\delta \mathcal{F}}{\delta \rho}$$

- Free energy: $\mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2}(\nabla\rho)^2] + \dots$

- Most probable profiles $\longleftrightarrow$ Minimize $\mathcal{F}[\rho]$ with $\int d\mathbf{r}\rho(\mathbf{r}) = V\rho_0$

Hydrodynamics of Equilibrium Phase-Separation

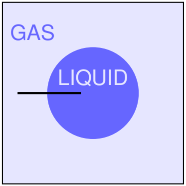
- Large-scale dynamics of phase-separating scalar systems away from criticality

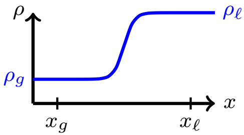
$$\dot{\rho} = -\nabla \cdot J[\rho] \qquad \text{where} \qquad J[\rho] = -M[\rho]\nabla \frac{\delta \mathcal{F}}{\delta \rho}$$

- Free energy: $\mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2}(\nabla \rho)^2] + \dots$

- Most probable profiles $\longleftrightarrow$ Minimize $\mathcal{F}[\rho]$ with $\int d\mathbf{r} \rho(\mathbf{r}) = V \rho_0$

- Phase-separated profiles:





Hydrodynamics of Equilibrium Phase-Separation

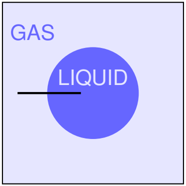
- Large-scale dynamics of phase-separating scalar systems away from criticality

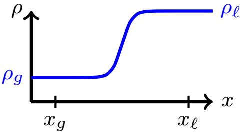
$$\dot{\rho} = -\nabla \cdot J[\rho] \qquad \text{where} \qquad J[\rho] = -M[\rho]\nabla \frac{\delta \mathcal{F}}{\delta \rho}$$

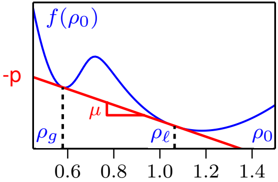
- Free energy: $\mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2}(\nabla\rho)^2] + \dots$

- Most probable profiles $\longleftrightarrow$ Minimize $\mathcal{F}[\rho]$ with $\int d\mathbf{r} \rho(\mathbf{r}) = V\rho_0$

- Phase-separated profiles: Common tangent construction on $f(\rho_0)$







Hydrodynamics of Equilibrium Phase-Separation

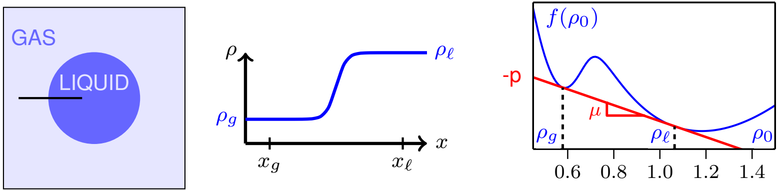
- Large-scale dynamics of phase-separating scalar systems away from criticality

$$\dot{\rho} = -\nabla \cdot J[\rho] \qquad \text{where} \qquad J[\rho] = -M[\rho]\nabla \frac{\delta \mathcal{F}}{\delta \rho}$$

- Free energy: $\mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2}(\nabla\rho)^2] + \dots$

- Most probable profiles $\longleftrightarrow$ Minimize $\mathcal{F}[\rho]$ with $\int d\mathbf{r}\rho(\mathbf{r}) = V\rho_0$

- Phase-separated profiles: Common tangent construction on $f(\rho_0)$



- $F \simeq V\rho_0$ and $\rho_0 = \frac{N}{V}$ $\longrightarrow$ Chemical potential $\mu = \frac{\partial F}{\partial N} = f'(\rho_0)$ and Pressure $p = -\frac{\partial F}{\partial V} = \rho f'(\rho) - f(\rho)$

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}}_\mathbf{i} = v[\tilde{\rho}(\mathbf{r}_\mathbf{i})]\mathbf{u}(\theta_i)$; $\quad \tilde{\rho}(\mathbf{r}_\mathbf{i}) = \sum_j K(|\mathbf{r}_\mathbf{i} - \mathbf{r}_\mathbf{j}|)$; $\quad \sigma^2 = \int drK(r)r^2$

- Rotational diffusivity D_r, tumbling rate α

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}_\mathbf{i}} = v[\tilde{\rho}(\mathbf{r_i})]\mathbf{u}(\theta_i); \quad \tilde{\rho}(\mathbf{r_i}) = \sum_j K(|\mathbf{r_i} - \mathbf{r_j}|); \quad \sigma^2 = \int drK(r)r^2$

- Rotational diffusivity D_r, tumbling rate α

- Assume $\tilde{\rho}(\mathbf{r})$ frozen $\longrightarrow$ Non-interacting $v(r_i)$ $\longrightarrow$ Determine $\partial_t \rho(\mathbf{r}, t)$

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}}_\mathbf{i} = v[\tilde{\rho}(\mathbf{r_i})]\mathbf{u}(\theta_i)$; $\tilde{\rho}(\mathbf{r_i}) = \sum_j K(|\mathbf{r_i} - \mathbf{r_j}|)$; $\sigma^2 = \int dr K(r) r^2$

- Rotational diffusivity D_r, tumbling rate α

- Assume $\tilde{\rho}(\mathbf{r})$ frozen ⟶ Non-interacting $v(r_i)$ ⟶ Determine $\partial_t \rho(\mathbf{r}, t)$

- Fluctuating hydro + Mean-field approximation ⟶ hydro eq.

$$\dot{\rho} = \nabla \cdot \left\{ \qquad \qquad \qquad \right\};$$

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}_\mathbf{i}} = v[\tilde{\rho}(\mathbf{r_i})]\mathbf{u}(\theta_i)$; $\quad \tilde{\rho}(\mathbf{r_i}) = \sum_j K(|\mathbf{r_i} - \mathbf{r_j}|)$; $\quad \sigma^2 = \int dr K(r) r^2$

- Rotational diffusivity D_r, tumbling rate α

- Assume $\tilde{\rho}(\mathbf{r})$ frozen ⟶ Non-interacting $v(r_i)$ ⟶ Determine $\partial_t \rho(\mathbf{r}, t)$

- Fluctuating hydro + Mean-field approximation ⟶ hydro eq.

$$\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[\frac{\delta \mathcal{F}}{\delta \rho} \qquad \qquad \right] \right\}; \qquad M = \rho \frac{v^2}{D_r d(d-1) + \alpha d}$$

- $\mathcal{F}[\rho(x)] = \int \mathrm{d}^d r \left[\rho(\log \rho - 1) + \int^\rho \mathrm{d}s \log[v(s)] \right] \equiv \int \mathrm{d}^d r f(\rho(r))$

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}}_{\mathbf{i}} = v[\tilde{\rho}(\mathbf{r}_{\mathbf{i}})]\mathbf{u}(\theta_i); \quad \tilde{\rho}(\mathbf{r}_{\mathbf{i}}) = \sum_j K(|\mathbf{r}_{\mathbf{i}} - \mathbf{r}_{\mathbf{j}}|); \quad \sigma^2 = \int dr K(r) r^2$

- Rotational diffusivity D_r, tumbling rate α

- Assume $\tilde{\rho}(\mathbf{r})$ frozen ⟶ Non-interacting $v(r_i)$ ⟶ Determine $\partial_t \rho(\mathbf{r}, t)$

- Fluctuating hydro + Mean-field approximation ⟶ hydro eq.

$$\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[\frac{\delta \mathcal{F}}{\delta \rho} + \sigma^2 \frac{v'}{v} \Delta \rho \right] \right\}; \qquad M = \rho \frac{v^2}{D_r d(d-1) + \alpha d}$$

- $\mathcal{F}[\rho(x)] = \int \mathrm{d}^d r \left[\rho(\log \rho - 1) + \int^{\rho} \mathrm{d}s \log[v(s)] \right] \equiv \int \mathrm{d}^d r f(\rho(r))$

- $\sigma^2 \frac{v'}{v} \Delta \rho$ does not derive from a free energy

Quorum sensing self-propelled particles

- $\dot{\mathbf{r}}_\mathbf{i} = v[\tilde{\rho}(\mathbf{r}_\mathbf{i})]\mathbf{u}(\theta_i)$; $\quad \tilde{\rho}(\mathbf{r}_\mathbf{i}) = \sum_j K(|\mathbf{r}_\mathbf{i} - \mathbf{r}_\mathbf{j}|)$; $\quad \sigma^2 = \int dr K(r) r^2$

- Rotational diffusivity D_r, tumbling rate α

- Assume $\tilde{\rho}(\mathbf{r})$ frozen ⟶ Non-interacting $v(r_i)$ ⟶ Determine $\partial_t \rho(\mathbf{r}, t)$

- Fluctuating hydro + Mean-field approximation ⟶ hydro eq.

$$\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[\frac{\delta \mathcal{F}}{\delta \rho} + \sigma^2 \frac{v'}{v} \Delta \rho \right] \right\}; \qquad M = \rho \frac{v^2}{D_r d(d-1) + \alpha d}$$

- $\mathcal{F}[\rho(x)] = \int \mathrm{d}^d r \left[\rho(\log \rho - 1) + \int^\rho \mathrm{d}s \log[v(s)] \right] \equiv \int \mathrm{d}^d r f(\rho(r))$

- $\sigma^2 \frac{v'}{v} \Delta \rho$ does not derive from a free energy

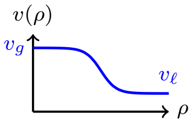
⟶ Common-tangent on $f(\rho)$ leads to a wrong phase diagram

[Wittkowski *et al.* Nat. Com. 5, 4351 (2014)]

Hydrodynamics of Quorum-sensing active particles

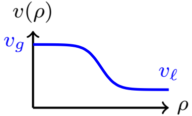
$$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$$

$$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$$



Hydrodynamics of Quorum-sensing active particles

$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$

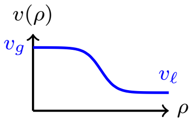


$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$

Unfortunately $g(\rho) \neq \frac{\delta \mathcal{F}[\rho]}{\delta \rho}$ ☹

Hydrodynamics of Quorum-sensing active particles

$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$



$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$

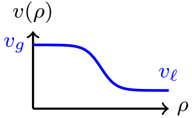
Unfortunately $g(\rho) \neq \frac{\delta \mathcal{F}[\rho]}{\delta \rho}$ ☹

A bit of magic: define $R'(\rho) \equiv \frac{1}{\kappa(\rho)}$ and $\phi'(R) = g_0(\rho)$

Hydrodynamics of Quorum-sensing active particles

$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$

$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$



Unfortunately $g(\rho) \neq \frac{\delta \mathcal{F}[\rho]}{\delta \rho}$ ☹

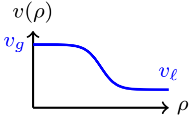
A bit of magic: define $R'(\rho) \equiv \frac{1}{\kappa(\rho)}$ and $\phi'(R) = g_0(\rho)$

Then $\dot{\rho} = \nabla\left[M \nabla \frac{\delta \mathcal{H}}{\delta R(\rho)}\right]$ with $\mathcal{H} = \int d\mathbf{r}[\phi(R) + \frac{\kappa}{2R'}(\nabla R)^2]$

Hydrodynamics of Quorum-sensing active particles

$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$

$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$

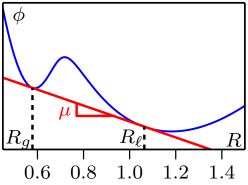


Unfortunately $g(\rho) \neq \frac{\delta \mathcal{F}[\rho]}{\delta \rho}$ ☹

A bit of magic: define $R'(\rho) \equiv \frac{1}{\kappa(\rho)}$ and $\phi'(R) = g_0(\rho)$

Then $\dot{\rho} = \nabla \left[M \nabla \frac{\delta \mathcal{H}}{\delta R(\rho)} \right]$ with $\mathcal{H} = \int d\mathbf{r} [\phi(R) + \frac{\kappa}{2R'} (\nabla R)^2]$

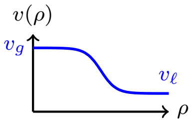
Common-tangent construction on the effective free energy density $\phi(R)$



Hydrodynamics of Quorum-sensing active particles

$\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \qquad g = g_0(\rho) - \kappa(\rho)\Delta\rho$

$g_0 = \log[\rho v(\rho)], \qquad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}$

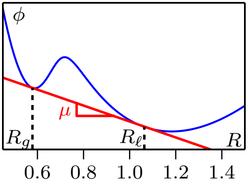


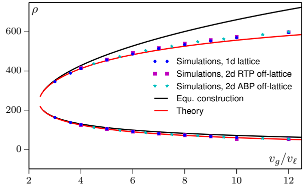
Unfortunately $g(\rho) \neq \frac{\delta \mathcal{F}[\rho]}{\delta \rho}$ ☹

A bit of magic: define $R'(\rho) \equiv \frac{1}{\kappa(\rho)}$ and $\phi'(R) = g_0(\rho)$

Then $\dot{\rho} = \nabla \left[M \nabla \frac{\delta \mathcal{H}}{\delta R(\rho)} \right]$ with $\mathcal{H} = \int d\mathbf{r} [\phi(R) + \frac{\kappa}{2R'} (\nabla R)^2]$

Common-tangent construction on the effective free energy density $\phi(R)$

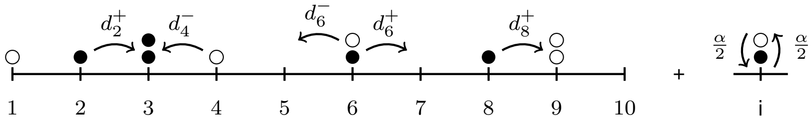




→ (Almost) quantitative agreement ☺

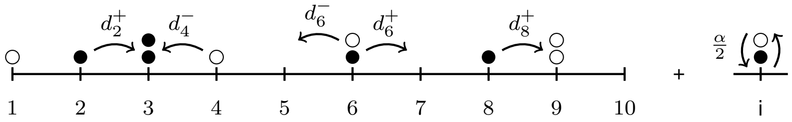
Be wise, discretize !

- Lattice-gas model of run & tumble particles (RTP)
  [Thompson et al. JSTAT 2011; Soto & Golestanian PRE 2014; Whitelam JCP 2018]

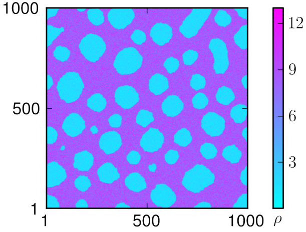


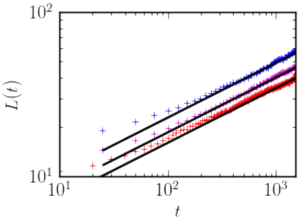
Be wise, discretize !

- Lattice-gas model of run & tumble particles (RTP)
  [Thompson et al. JSTAT 2011; Soto & Golestanian PRE 2014; Whitelam JCP 2018]



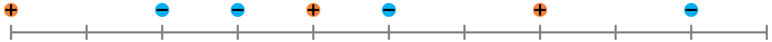
- Exclusion: $d_i^\pm = v_0(1 - \frac{n_{i\pm1}}{n_M})$





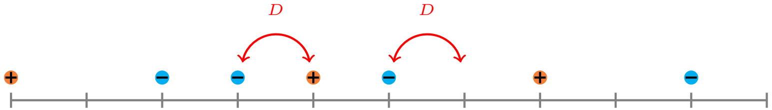
An exactly solvable case

- Lattice of αL sites with at most one particle per site



An exactly solvable case

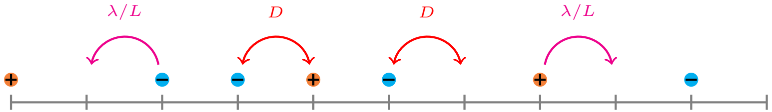
- Lattice of αL sites with at most one particle per site



- Symmetric diffusion/exchange at rate D

An exactly solvable case

- Lattice of αL sites with at most one particle per site

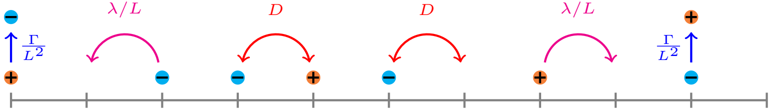


- Symmetric diffusion/exchange at rate D

- Asymmetric hopping on empty sites at rate λ/L

An exactly solvable case

- Lattice of αL sites with at most one particle per site



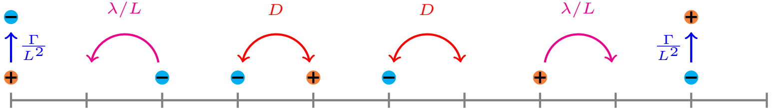
- Symmetric diffusion/exchange at rate D

- Asymmetric hopping on empty sites at rate λ/L

- Particles switch hopping direction at rate Γ/L^2

An exactly solvable case

- Lattice of αL sites with at most one particle per site



- Symmetric diffusion/exchange at rate D

- Asymmetric hopping on empty sites at rate λ/L

- Particles switch hopping direction at rate Γ/L^2

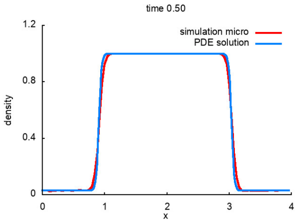
- Undergoes MIPS if $\rho_0 = N/L^d$ and λ are large enough

Phase equilibrium

- Exact hydrodynamic equations for density and magnetisation

$x = \frac{i}{L}, t = \frac{t_{\text{micro}}}{L^2}$ [M. Kourbane-Houssene *et al*, PRL (2018); C. Érignoux, arXiv:1608.04937]

$$\begin{aligned}\partial_t \rho(x,t) &= D\Delta\rho + \lambda\nabla[m(1-\rho)] \\ \partial_t m(x,t) &= D\Delta m + \lambda\nabla[\rho(1-\rho)] - 2\Gamma m\end{aligned}$$



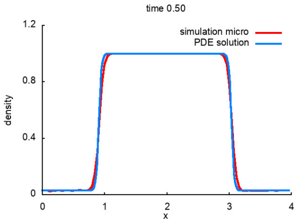
Phase equilibrium

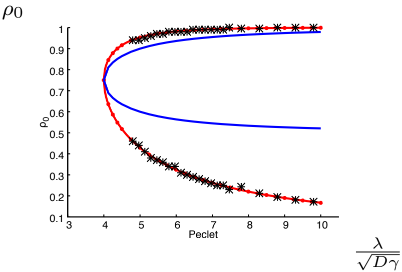
- Exact hydrodynamic equations for density and magnetisation

$x = \frac{i}{L}, t = \frac{t_{\rm micro}}{L^2}$ [M. Kourbane-Houssene *et al*, PRL (2018); C. Érignoux, arXiv:1608.04937]

$$\begin{aligned} \partial_t \rho(x,t) &= D\Delta\rho + \lambda\nabla[m(1-\rho)] \\ \partial_t m(x,t) &= D\Delta m + \lambda\nabla[\rho(1-\rho)] - 2\Gamma m \end{aligned}$$

- More complicated but can still be solved using the same transform





- Exact, parameter-free result

MIPS from repulsive forces

- Self-propelled particles with pairwise forces (PFAPs)
  [Fily & Marchetti PRL 2012, Redner et al. PRL 2013, Stenhammar et al. PRL 2013, Bialké et al. PRL 2013, . . .]

$$\dot{\mathbf{r_i}} = v\mathbf{u}(\theta_i) - \mu \sum_j F_{ij}(\mathbf{r_i} - \mathbf{r_j}) + \sqrt{2D_t}\eta_i; \qquad \dot{\theta}_i = \sqrt{2D_r}\xi_i$$

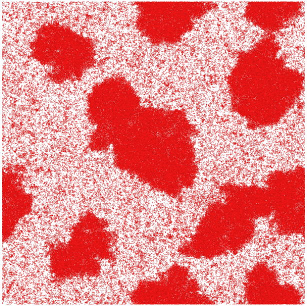
- Interactions yields decreasing $v(\rho) \equiv \sum_i \dot{\mathbf{r}}_i \cdot \mathbf{u}(\theta_i)$ [Fily et al PRL (2012)]

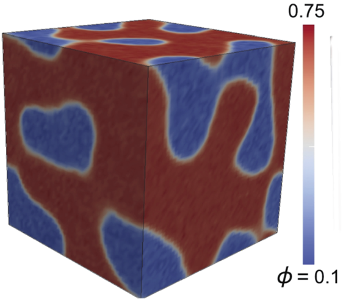
MIPS from repulsive forces

- Self-propelled particles with pairwise forces (PFAPs)
  [Fily & Marchetti PRL 2012, Redner et al. PRL 2013, Stenhammar et al. PRL 2013, Bialké et al. PRL 2013, . . .]

$$\dot{\mathbf{r}}_\mathbf{i} = v\mathbf{u}(\theta_i) - \mu \sum_j F_{ij}(\mathbf{r_i} - \mathbf{r_j}) + \sqrt{2D_t}\eta_i; \qquad \dot{\theta}_i = \sqrt{2D_r}\xi_i$$

- Interactions yields decreasing $v(\rho) \equiv \sum_i \dot{\mathbf{r}}_i \cdot \mathbf{u}(\theta_i)$ [Fily et al PRL (2012)]





⟶ Same phenomenology as QSAPs

- Interesting qualitative & quantitative differences [Tjhung *et al*, PRX 2018; Caporusso *et al*, arxiv:2005.06893]

Pressure-driven instability

- Hydrodynamic description [Solon *et al.*, PRE 2016, NJP 2018]

$$\dot{\rho}(\mathbf{r}) = -\nabla \cdot \mathbf{J} \qquad \text{where} \qquad \mathbf{J} = \mu \nabla \cdot \boldsymbol{\sigma}; \qquad \boldsymbol{\sigma} = \big[\text{Bunch of bulk correlators}\big]$$

Pressure-driven instability

- Hydrodynamic description [Solon *et al.*, PRE 2016, NJP 2018]

$$\dot{\rho}(\mathbf{r}) = -\nabla \cdot \mathbf{J} \qquad \text{where} \qquad \mathbf{J} = \mu \nabla \cdot \boldsymbol{\sigma}; \qquad \boldsymbol{\sigma} = \left[\text{Bunch of bulk correlators}\right]$$

- $P_{\rm tot} = -\sigma_{xx}$ is the equation of state of the mechanical pressure
  [Takatori *et al.* PRL 2014; Yang *et al.* Soft. Mat. 2014; Solon *et al.* PRL 2015]

Pressure-driven instability

- Hydrodynamic description [Solon *et al.*, PRE 2016, NJP 2018]

$$\dot{\rho}(\mathbf{r}) = -\nabla\cdot\mathbf{J} \qquad \text{where} \qquad \mathbf{J} = \mu\nabla\cdot\boldsymbol{\sigma}; \qquad \boldsymbol{\sigma} = \left[\text{Bunch of bulk correlators}\right]$$

- $P_{\rm tot} = -\sigma_{xx}$ is the equation of state of the mechanical pressure
  [Takatori *et al.* PRL 2014; Yang *et al.* Soft. Mat. 2014; Solon *et al.* PRL 2015]

$$P(\rho) = P_D + P_A \quad \text{where} \quad P_A = \rho\frac{v_0 v(\rho)}{2\mu D_r}; \quad v(\rho) = \langle\sum_i \dot{\mathbf{r}}_i\cdot\mathbf{u}(\theta_i)\rangle$$

- P_D passive pressure: mean force exerted through a plane

- P_a flux of active impulse & momentum through a plane [Fily et al. JPA (2018)]

Pressure-driven instability

- Hydrodynamic description [Solon *et al.*, PRE 2016, NJP 2018]

$$\dot{\rho}(\mathbf{r}) = -\nabla\cdot\mathbf{J} \quad \text{where} \quad \mathbf{J} = \mu\nabla\cdot\boldsymbol{\sigma}; \qquad \boldsymbol{\sigma} = [\text{Bunch of bulk correlators}]$$

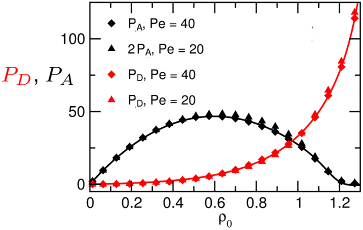
- $P_{\rm tot} = -\sigma_{xx}$ is the equation of state of the mechanical pressure
  [Takatori *et al.* PRL 2014; Yang *et al.* Soft. Mat. 2014; Solon *et al.* PRL 2015]

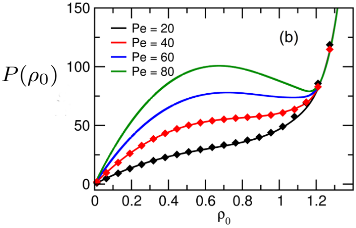
$$P(\rho) = P_D + P_A \quad \text{where} \quad P_A = \rho\frac{v_0 v(\rho)}{2\mu D_r}; \quad v(\rho) = \langle\sum_i \dot{\mathbf{r}}_i\cdot\mathbf{u}(\theta_i)\rangle$$

- P_D passive pressure: mean force exerted through a plane

- P_a flux of active impulse & momentum through a plane [Fily et al. JPA (2018)]

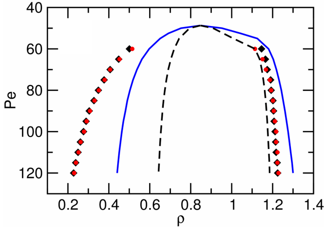
- $P'(\rho) < 0$ predicts linear instability

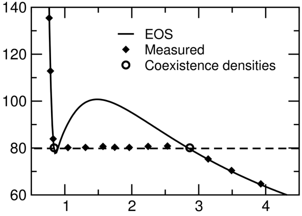




Pairwise forces—Summary

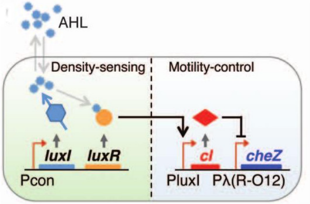
- Phase diagram in quantitative agreement with generalized thermodynamical construction

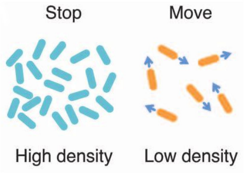


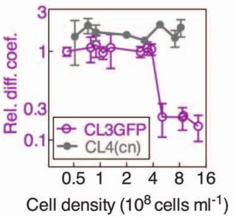


- Equal mechanical pressure in coexisting phases
- Can do isobaric ensemble
- Failure of Maxwell construction
- Quite rich physics still to be explored (surface tension, bubbles, etc.)

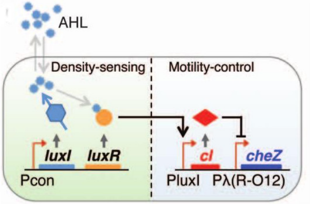
Back to bacteria: Motility-Induced Pattern Formation (MIPF)

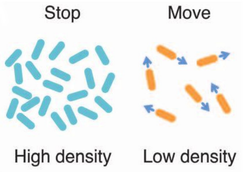


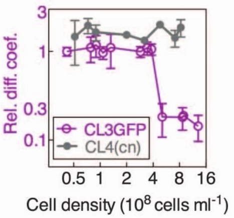


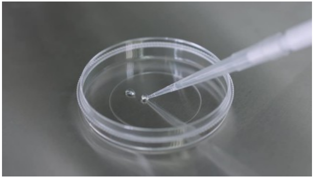


Back to bacteria: Motility-Induced Pattern Formation (MIPF)

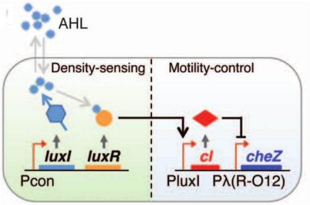


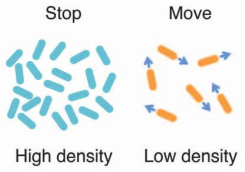


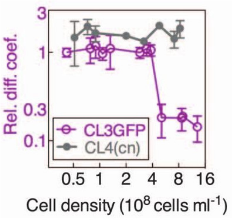


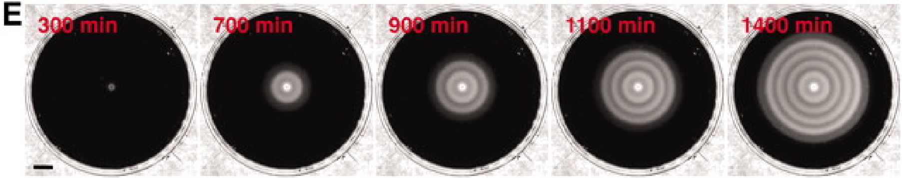


Back to bacteria: Motility-Induced Pattern Formation (MIPF)









Patterns instead of MIPS [Liu et al., Science (2011)]. Nice, but why ?

Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

  ⟶ Bacteria accumulate where they are less motile

  ⟶ Bacteria lose motility at high density

Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

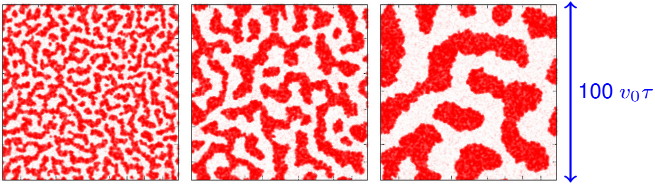
  → Bacteria accumulate where they are less motile

  → Bacteria lose motility at high density

  → Microscopic simulations starting from homogeneous systems

$t = 10^3\tau$ $t = 10^4\tau$ $t = 10^5\tau$

$v'(\rho) < 0$



Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

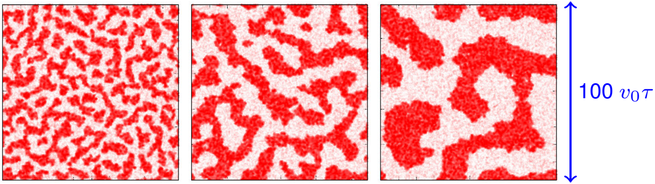
  → Bacteria accumulate where they are less motile

  → Bacteria lose motility at high density

  → Microscopic simulations starting from homogeneous systems

$t = 10^3\tau$ $t = 10^4\tau$ $t = 10^5\tau$

$\beta'(\rho) < 0$



Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

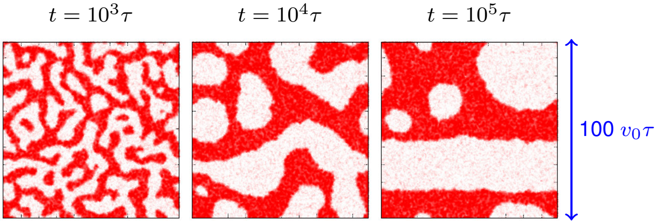
- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

  → Bacteria accumulate where they are less motile

  → Bacteria lose motility at high density

  → Microscopic simulations starting from homogeneous systems

$\alpha'(\rho) > 0$



Interplay between density and mobility: Quorum-sensing interactions

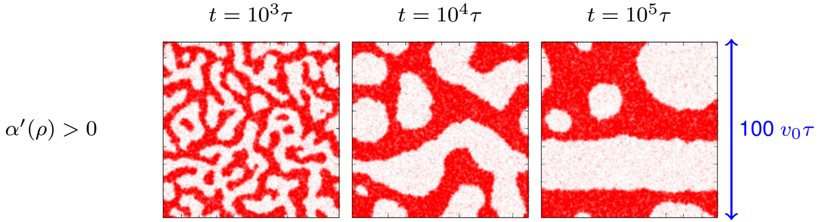
- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

  ⟶ Bacteria accumulate where they are less motile

  ⟶ Bacteria lose motility at high density

  ⟶ Microscopic simulations starting from homogeneous systems



- Slow coarsening leads to complete motility-induced phase separation

- No finite-size patterns: What is the missing ingredient?

Pattern formation in bacterial colonies: a simple mechanism

- Coarsening is slow ⟶ Long-time dynamics (24 hours)
- Large-scale description of run & tumble dynamics: $\dot{\rho} = \nabla \left[\frac{v^2 \beta}{d\alpha(\beta+\alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha+\beta} \right]$

Pattern formation in bacterial colonies: a simple mechanism

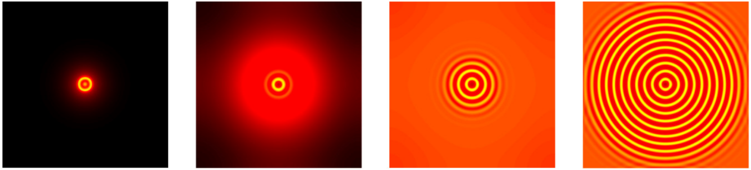
- Coarsening is slow $\longrightarrow$ Long-time dynamics (24 hours)
- Large-scale description of run & tumble dynamics: $\dot\rho = \nabla\left[\frac{v^2\beta}{d\alpha(\beta+\alpha)}\nabla\rho + \frac{v\rho}{d\alpha}\nabla\frac{v\beta}{\alpha+\beta}\right]$
- Missing ingredient: population dynamics

$$\dot\rho = -\nabla\cdot J[\rho] + \mu\rho\left(1-\frac{\rho}{\rho_0}\right)$$

Pattern formation in bacterial colonies: a simple mechanism

- Coarsening is slow ⟶ Long-time dynamics (24 hours)
- Large-scale description of run & tumble dynamics: $\dot{\rho} = \nabla\left[\frac{v^2\beta}{d\alpha(\beta+\alpha)}\nabla\rho + \frac{v\rho}{d\alpha}\nabla\frac{v\beta}{\alpha+\beta}\right]$
- Missing ingredient: population dynamics

$$\dot{\rho} = -\nabla\cdot J[\rho] + \mu\rho\left(1-\frac{\rho}{\rho_0}\right)$$



⟶ Qualitatively accounts for the experiments

- What happened to the phase-separation ?

Birth & death vs phase separation

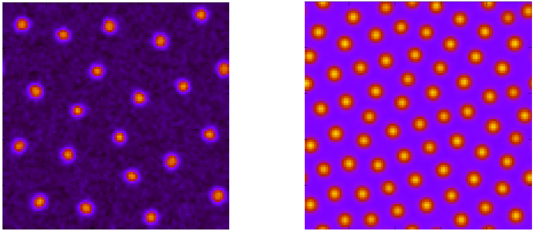
- Quorum-sensing ⟶ Motility-Induced Phase separation ⟶ $(\rho_{\rm low}, \rho_{\rm high})$

Birth & death vs phase separation

- Quorum-sensing ⟶ Motility-Induced Phase separation ⟶ $(\rho_{\rm low}, \rho_{\rm high})$
- Logistic growth: $\rho_{\rm low} \le \rho_0$ ⟶ division; $\rho_{\rm high} \ge \rho_0$ ⟶ death

Birth & death vs phase separation

- Quorum-sensing ⟶ Motility-Induced Phase separation ⟶ $(\rho_{\rm low}, \rho_{\rm high})$
- Logistic growth: $\rho_{\rm low} \leq \rho_0$ ⟶ division; $\rho_{\rm high} \geq \rho_0$ ⟶ death
- Competition ⟶ Micro-phase separation •



- Motility-induced phase separation + population dynamics ⟶ Finite-size patterns
  [Cates *et al.* PNAS 2010; Liu *el al.* Science 2011]

Mathematically: linear stability analysis

- Simplified model: $\partial_t \rho = \nabla \cdot [D_c(\rho) \nabla \rho + \rho \nabla D_c(\rho)] - \kappa \Delta^2 \rho + \alpha \rho \left(1 - \frac{\rho}{\rho_0}\right)$

Mathematically: linear stability analysis

- Simplified model: $\partial_t \rho = \nabla \cdot [D_c(\rho)\nabla\rho + \rho\nabla D_c(\rho)] - \kappa\Delta^2\rho + \alpha\rho\left(1 - \frac{\rho}{\rho_0}\right)$

- Linear stability analysis: $\rho(\mathbf{r}, t) = \rho_0 + \sum_{\mathbf{q}} \delta\rho_{\mathbf{q}}(t) e^{i\mathbf{q}\cdot\mathbf{r}} \longrightarrow \delta\rho_{\mathbf{q}}(t) = \delta\rho_{\mathbf{q}}(0) e^{\lambda_{\mathbf{q}} t}$

$$\lambda_{\mathbf{q}} = -[D_c(\rho_0) + \rho_0 D_c'(\rho_0)]q^2 - \kappa q^4 - \alpha$$

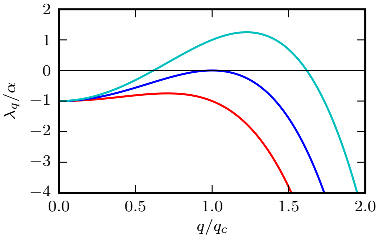
Mathematically: linear stability analysis

- Simplified model: $\partial_t \rho = \nabla \cdot [D_c(\rho)\nabla\rho + \rho\nabla D_c(\rho)] - \kappa\Delta^2\rho + \alpha\rho\left(1 - \frac{\rho}{\rho_0}\right)$

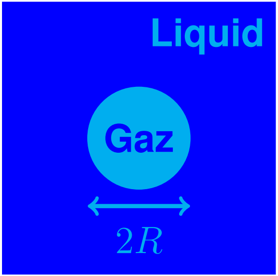
- Linear stability analysis: $\rho(\mathbf{r},t) = \rho_0 + \sum_{\mathbf{q}} \delta\rho_{\mathbf{q}}(t) e^{i\mathbf{q}\cdot\mathbf{r}} \longrightarrow \delta\rho_{\mathbf{q}}(t) = \delta\rho_{\mathbf{q}}(0)e^{\lambda_{\mathbf{q}} t}$

$$\lambda_{\mathbf{q}} = -[D_c(\rho_0) + \rho_0 D_c'(\rho_0)]q^2 - \kappa q^4 - \alpha$$

- Transition at finite q_c when $D_c(\rho_0) + \rho_0 D_c'(\rho_0)$ strongly negative $\longrightarrow$ Patterns

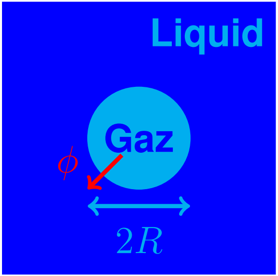


Selection of a lengthscale



- Droplet of radius R

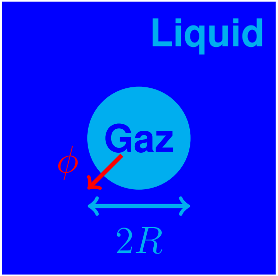
Selection of a lengthscale



- Droplet of radius R
- MIPS $\longrightarrow$ Flux through boundary $\phi > 0$

$$\frac{d}{dt}(\text{Mass in the droplet}) = -2\pi R\phi$$

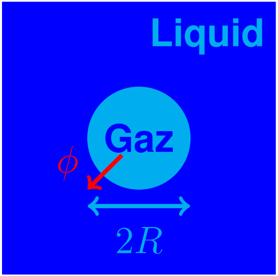
Selection of a lengthscale



- Droplet of radius R
- MIPS $\longrightarrow$ Flux through boundary $\phi > 0$
- Local birth/death rate $\alpha > 0$

$$\frac{d}{dt}(\text{Mass in the droplet}) = -2\pi R\phi + \alpha\pi R^2$$

Selection of a lengthscale



- Droplet of radius R
- MIPS ⟶ Flux through boundary $\phi > 0$
- Local birth/death rate $\alpha > 0$

$$\frac{d}{dt}\text{(Mass in the droplet)} = -2\pi R\phi + \alpha\pi R^2$$

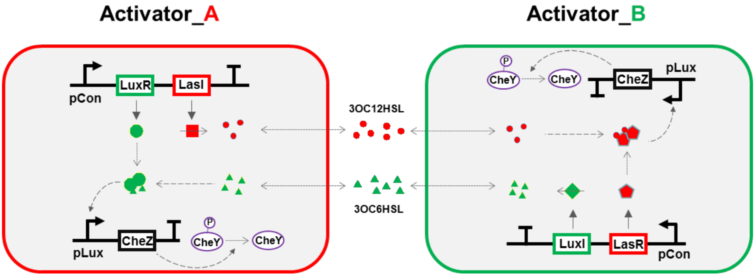
⟶ Steady-state radius $R \sim 2\phi/\alpha$

Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains A and B
- Reciprocal motility control

Multi-component bacterial colonies (with J. Huang, HKU)

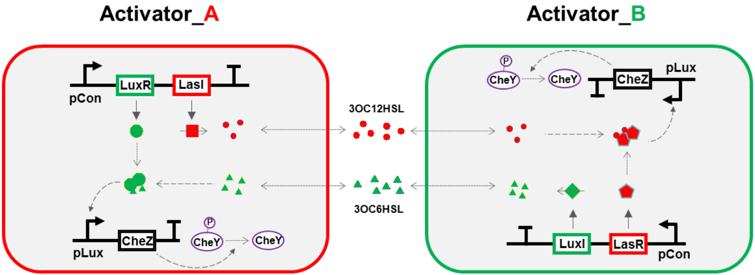
- Idea: two strains A and B
- Reciprocal motility control



Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains A and B

- Reciprocal motility control

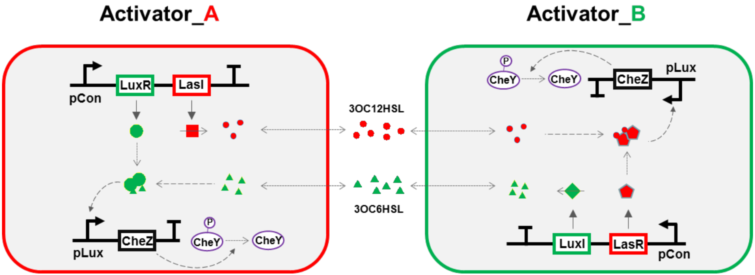


- Constant production of 3OC12HSL ⟶ Enhance expression of CheZ in B

- Enhance expression of CheZ in A ⟵ Constant production of 3OC6HSL

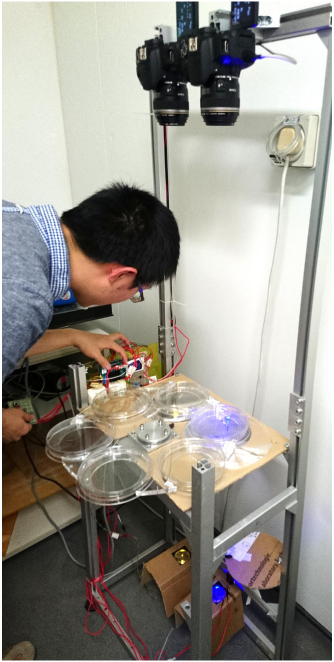
Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains A and B
- Reciprocal motility control

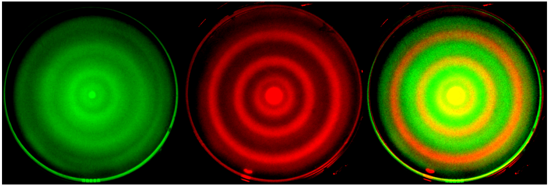


- Constant production of 3OC12HSL ⟶ Enhance expression of CheZ in B
- Enhance expression of CheZ in A ⟵ Constant production of 3OC6HSL
- Reciprocal enhancement or inhibition of motility can be implemented

Experimental results [N. Zhou, Y. Zhao, A. Daerr]

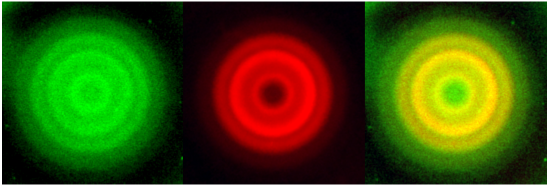


Mutual activation of motility



B A A+B

Mutual inhibition of motility



A B A+B

Macroscopic dynamics (Agnese Curatolo)

Time evolution of the density fields

- $\rho_A(\mathbf{r},t)=\sum_{\ell=1}^{N_A}\delta(\mathbf{r}-\mathbf{r}_\ell^A(t))$
- $\rho_B(\mathbf{r},t)=\sum_{\ell=1}^{N_B}\delta(\mathbf{r}-\mathbf{r}_\ell^B(t))$

Run-and-tumble dynamics + density-dependent swimming rate $\beta_A(\rho_B)$, $\beta_B(\rho_A)$

$$\dot{\rho}_A(\mathbf{r},t)=\nabla\cdot\Big(D_A(\rho_B)\nabla\rho_A-\mathbf{F}_A(\rho_B)\rho_A+\sqrt{2D_A(\rho_B)\rho_A}\,\Lambda_A\Big)$$

$$\dot{\rho}_B(\mathbf{r},t)=\nabla\cdot\Big(D_B(\rho_A)\nabla\rho_B-\mathbf{F}_B(\rho_A)\rho_B+\sqrt{2D_B(\rho_A)\rho_B}\,\Lambda_B\Big)$$

$$D_x(\rho_y)=\frac{v^2}{2\alpha\left(1+\frac{\alpha}{\beta_x(\rho_y)}\right)}\;;\quad \mathbf{F}_x(\rho_y)=-\frac{v^2}{2\alpha}\nabla\frac{1}{1+\frac{\alpha}{\beta_x(\rho_y)}}$$

The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta_A'(\rho_B^0)\beta_B'(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B}$$

The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta_A'(\rho_B^0)\beta_B'(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$$\beta'_A > 0 \qquad \beta'_B > 0$$

Mutual inhibition of the motility

$$\beta'_A < 0 \qquad \beta'_B < 0$$

The origin of the patterns

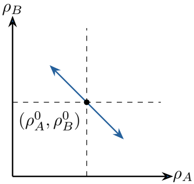
Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$$\beta'_A > 0 \qquad \beta'_B > 0$$



$$\delta\rho_A\delta\rho_B < 0$$

Mutual inhibition of the motility

$$\beta'_A < 0 \qquad \beta'_B < 0$$

The origin of the patterns

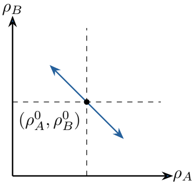
Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta_A'(\rho_B^0)\beta_B'(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$$\beta_A' > 0 \qquad \beta_B' > 0$$



$$\delta\rho_A\delta\rho_B < 0$$

Segregation

Mutual inhibition of the motility

$$\beta_A' < 0 \qquad \beta_B' < 0$$

The origin of the patterns

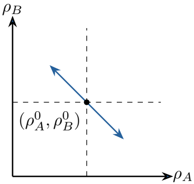
Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta_A'(\rho_B^0)\beta_B'(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$$\beta_A' > 0 \qquad \beta_B' > 0$$

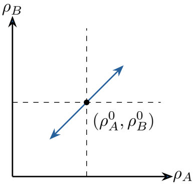


$$\delta\rho_A\delta\rho_B < 0$$

Segregation

Mutual inhibition of the motility

$$\beta_A' < 0 \qquad \beta_B' < 0$$



$$\delta\rho_A\delta\rho_B > 0$$

The origin of the patterns

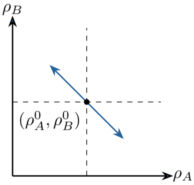
Linear analysis of the hydrodynamic equations around homogeneous profiles ρ_A^0 and ρ_B^0:

$$\rho_A = \rho_A^0 + \delta\rho_A \qquad \rho_B = \rho_B^0 + \delta\rho_B$$

$$\frac{\alpha^2}{(\alpha+\beta_A)(\alpha+\beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$$\beta'_A > 0 \qquad \beta'_B > 0$$

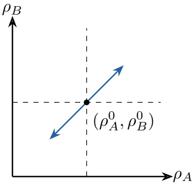


$$\delta\rho_A\delta\rho_B < 0$$

Segregation

Mutual inhibition of the motility

$$\beta'_A < 0 \qquad \beta'_B < 0$$



$$\delta\rho_A\delta\rho_B > 0$$

Colocalization

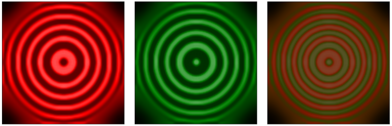
Overall dynamics

At longer time-scales: population growth

$$\dot{\rho}_A(\mathbf{r},t) = \nabla \cdot [D_A(\rho_B)\nabla\rho_A - \mathbf{F}_A(\rho_B)\rho_A] - \kappa\Delta^2\rho_A + \mu\rho_A\left(1 - \frac{\rho_A+\rho_B}{\rho_0}\right)$$

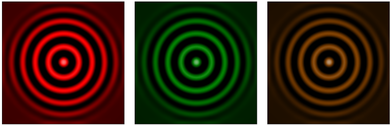
$$\dot{\rho}_B(\mathbf{r},t) = \underbrace{\nabla \cdot [D_B(\rho_A)\nabla\rho_B - \mathbf{F}_B(\rho_A)\rho_B]}_{\text{Quorum-sensing interactions}} - \kappa\Delta^2\rho_B + \underbrace{\mu\rho_B\left(1 - \frac{\rho_A+\rho_B}{\rho_0}\right)}_{\text{Population dynamics}}$$

Mutual activation of motility



A B A+B

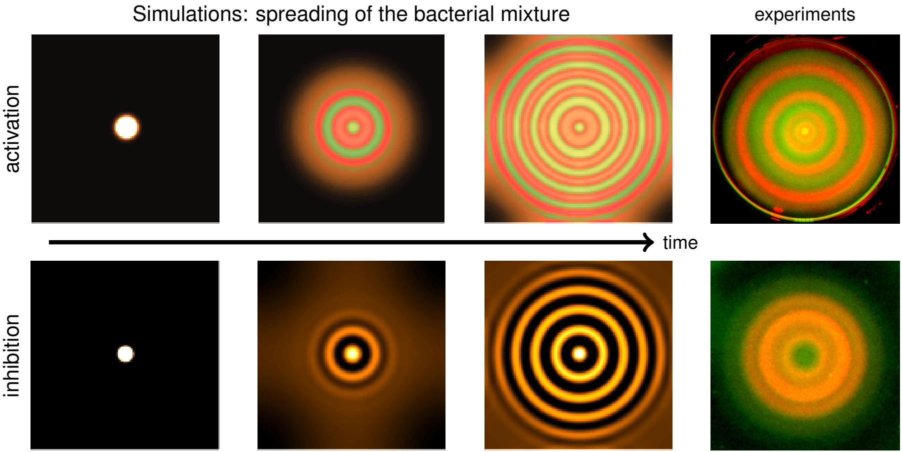
Mutual inhibition of motility



A B A+B

N-species MIPF

- N populations of interacting active particles
- Mutual inhibition ⟶ Phase separation with colocalization
- Mutual activation ⟶ Phase separation with demixing
- Population dynamics arrest growth: MIPS ⟶ MIPF



Summary

- A LOT can be achieved using motility-control to self-organize SPPs
- *In silico* & In experiments
- Theory starts to be well established

Summary

- A LOT can be achieved using motility-control to self-organize SPPs
- *In silico* & In experiments
- Theory starts to be well established

Thanks to: R. Blythe, T. Bodineau, M. Cates, A. Curatolo, A. Daerr, C. Erignoux, Y. Fily, J. Huang, Y. Kafri, M. Kardar, M. Kourbane-Houssenne, C. Liu, D. Marenduzzo, N. Zhou, J. O'Byrne, I. Pagonabarraga, A. Solon, J. Stenhammar, A. Thompson, R. Wittkowsky, Y. Zhao

A biased, unfair, restricted and incomplete view on MIPS & bacteria

- MIPS
  - → Quorum sensing: [Tailleur Cates PRL 100, 218103 (2008); Cates Tailleur EPL 101, 20010 (2013); Solon Cates Tailleur, EPSJT 224, 1231 (2015); . . .]
  - → Pairwise forces: [Fily Marchetti PRL 108, 235702 (2012); Redner, Baskaran, Hagan PRL 110, 055701 (2013); Solon et al, PRL 114, 198301 (2015); . . .]
  - → On lattice: [Thompson et al, JSM P02029 (2011); Soto & Golestanian, PRE 89, 012706 (2014); Manacorda & Puglisi, PRL 119, 208003 (2017); Whitelam at al, JCP 148, 154902 (2018); . . .]
  - → Generalized thermodynamics: [Solon et al., NJP 2018]
- Pattern formation in single-strain bacterial colonies
  - → Theory: [Cates et al, PNAS 2010]
  - → Experiments: [Liu et al, Science 2011]
- Pattern formation in two-strain bacterial colonies: [Curatolo et al, bioarxiv:2019]