MIPS: from phase separation to pattern formation

Julien Tailleur



M2-ICFP

Run-and-tumble bacteria

[Berg & Brown, Nature, 1972]



- Run •: straight line, velocity $v \simeq 20 \, \mu m.s^{-1}$, duration $\tau_r \simeq 1s$
- Tumble •: new direction, duration $\tau_{\rm t}\simeq 0.1s$

Run-and-tumble bacteria

[Berg & Brown, Nature, 1972]



- Run •: straight line, velocity $v \simeq 20 \,\mu {\rm m.s}^{-1}$, duration $\tau_{\rm r} \simeq 1 s = \alpha^{-1}$
- Tumble •: new direction, duration $\tau_{\rm t}\simeq 0.1s=\beta^{-1}$



• Non-uniform speed $v(\mathbf{r})$, tumbling rate $\alpha(\mathbf{r}) = \tau_{\mathrm{r}}^{-1}(\mathbf{r})$, swimming rate $\beta(\mathbf{r}) = \tau_{\mathrm{t}}^{-1}(\mathbf{r})$

- Non-uniform speed $v(\mathbf{r})$, tumbling rate $\alpha(\mathbf{r}) = \tau_{\mathbf{r}}^{-1}(\mathbf{r})$, swimming rate $\beta(\mathbf{r}) = \tau_{\mathbf{t}}^{-1}(\mathbf{r})$
- Steady-state distribution

 $P_{
m s}({f r}) \propto rac{ au_{
m r}({f r}) + au_{
m t}({f r})}{ au_{
m r}({f r}) \, v({f r})}$

- Non-uniform speed $v(\mathbf{r})$, tumbling rate $\alpha(\mathbf{r}) = \tau_{\mathbf{r}}^{-1}(\mathbf{r})$, swimming rate $\beta(\mathbf{r}) = \tau_{\mathbf{t}}^{-1}(\mathbf{r})$
- Steady-state distribution

$$P_{\rm s}({\bf r}) \propto \frac{\tau_{\rm r}({\bf r}) + \tau_{\rm t}({\bf r})}{\tau_{\rm r}({\bf r}) v({\bf r})} = \frac{1}{\text{fraction of time swimming at } {\bf r}} \times \frac{1}{\text{speed at } {\bf r}} \simeq \frac{1}{\text{Effective speed at } {\bf r}}$$

Self-propelled particles accumulate where they are less motile

[Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]

- Non-uniform speed $v(\mathbf{r})$, tumbling rate $\alpha(\mathbf{r}) = \tau_{\mathbf{r}}^{-1}(\mathbf{r})$, swimming rate $\beta(\mathbf{r}) = \tau_{\mathbf{t}}^{-1}(\mathbf{r})$
- Steady-state distribution

 $P_{\rm s}({\bf r}) \propto \frac{\tau_{\rm r}({\bf r}) + \tau_{\rm t}({\bf r})}{\tau_{\rm r}({\bf r}) \, v({\bf r})} = \frac{1}{\text{fraction of time swimming at } {\bf r}} \times \frac{1}{\text{speed at } {\bf r}} \simeq \frac{1}{\text{Effective speed at } {\bf r}}$

- Self-propelled particles accumulate where they are less motile [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]
- Experiments: Light-controlled flagella rotor (proteorhodopsin)

- Non-uniform speed $v(\mathbf{r})$, tumbling rate $\alpha(\mathbf{r}) = \tau_{\mathbf{r}}^{-1}(\mathbf{r})$, swimming rate $\beta(\mathbf{r}) = \tau_{\mathbf{t}}^{-1}(\mathbf{r})$
- Steady-state distribution

 $P_{\rm s}({\bf r}) \propto \frac{\tau_{\rm r}({\bf r}) + \tau_{\rm t}({\bf r})}{\tau_{\rm r}({\bf r}) \, v({\bf r})} = \frac{1}{\text{fraction of time swimming at } {\bf r}} \times \frac{1}{\text{speed at } {\bf r}} \simeq \frac{1}{\text{Effective speed at } {\bf r}}$

- Self-propelled particles accumulate where they are less motile [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]
- Experiments: Light-controlled flagella rotor (proteorhodopsin)
- 'Painting with bacteria'



[Frangipane et al., e-life (2018)]



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

- Bacteria produce diffusing molecules that regulates protein expressions
- cheZ favors swimming over tumbling



- Bacteria produce diffusing molecules that regulates protein expressions
- cheZ favors swimming over tumbling



- Concentration of AHL molecules: proxy for density $\rho(\mathbf{r})$
- Density-dependent swimming-rate -> Self-inhibition of motility

- Bacteria produce diffusing molecules that regulates protein expressions
- cheZ favors swimming over tumbling



- Concentration of AHL molecules: proxy for density $\rho(\mathbf{r})$
- Density-dependent swimming-rate -> Self-inhibition of motility



- Bacteria produce diffusing molecules that regulates protein expressions
- cheZ favors swimming over tumbling



- Concentration of AHL molecules: proxy for density $\rho(\mathbf{r})$
- Density-dependent swimming-rate -----> Self-inhibition of motility



- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$



- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$
 - ->Particle accumulate at high density: instability

 $v'(\rho) < 0$

• Microscopic simulations [A. Curatolo]: slower at high density





- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$
 - ->Particle accumulate at high density: instability

 $\tau_{\rm t}'(\rho) > 0$

• Microscopic simulations [A. Curatolo]: longer tumbles at high density





- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$
 - --->Particle accumulate at high density: instability

 $\tau_{\rm r}'(\rho) < 0$

• Microscopic simulations [A. Curatolo]: more tumbles at high density



• All ways leading to motility reduction are qualitatively equivalent and lead to MIPS [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]



- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$
 - --->Particle accumulate at high density: instability

 $\tau_{\rm r}'(\rho) < 0$

• Microscopic simulations [A. Curatolo]: more tumbles at high density



- All ways leading to motility reduction are qualitatively equivalent and lead to MIPS [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]
- No finite-size patterns: What is the missing ingredient?



- Particle are less motile at high density (QS interactions)
- Bacteria accumulate where they are less motile $\rho \propto \frac{\tau_r(\mathbf{r}) + \tau_t(\mathbf{r})}{\tau_r(\mathbf{r})v(\mathbf{r})}$
 - ->Particle accumulate at high density: instability
 - Microscopic simulations [A. Curatolo]: more tumbles at high density



 $\tau_{\rm r}'(\rho) < 0$

- All ways leading to motility reduction are qualitatively equivalent and lead to MIPS [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]
- No finite-size patterns: What is the missing ingredient?
- Slow coarsening: population dynamics !



• Large-scale description of run & tumble dynamics: [Tailleur, Cates PRL (2008), Curatolo *et al.*, Nat. Phys. (2020)]

$$\dot{\rho} = \nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right]$$

• Large-scale description of run & tumble dynamics:

[Tailleur, Cates PRL (2008), Curatolo et al., Nat. Phys. (2020)]

Stabilizing
$$\downarrow$$

 $\dot{\rho} = \nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right]$
Destabilizing $_$

- Large-scale description of run & tumble dynamics: [Tailleur, Cates PRL (2008), Curatolo *et al.*, Nat. Phys. (2020)]
- Long times: population dynamics

$$\begin{split} & \text{Stabilizing} \underbrace{\qquad } \\ & \dot{\rho} = \nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v \rho}{d\alpha} \nabla \frac{v \beta}{\alpha + \beta} \right] \\ & \text{Destabilizing} \underbrace{\qquad } \end{split}$$

- Large-scale description of run & tumble dynamics: [Tailleur, Cates PRL (2008), Curatolo *et al.*, Nat. Phys. (2020)]
- Long times: population dynamics

& tumble dynamics:
al., Nat. Phys. (2020)]
ics

$$\dot{\rho} = -\nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right]$$
Destabilizing

$$\dot{\rho} = -\nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right] + \mu \rho \left(1 - \frac{\rho}{\rho_0} \right)$$

- Large-scale description of run & tumble dynamics: [Tailleur, Cates PRL (2008), Curatolo *et al.*, Nat. Phys. (2020)]
- Long times: population dynamics

Stabilizing
ble dynamics:
Phys. (2020)]

$$\dot{\rho} = \nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right]$$
Destabilizing

$$-\nabla \cdot \left[\frac{v^2 \beta}{d\alpha(\beta + \alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha + \beta} \right] + \mu \rho \left(1 - \frac{\rho}{\rho_0} \right)$$

• Population dynamics promote $\rho(\mathbf{r}) = \rho_0 \longrightarrow$ Stabilizes long wave-length

 $\dot{\rho} =$

- Large-scale description of run & tumble dynamics: [Tailleur, Cates PRL (2008), Curatolo *et al.*, Nat. Phys. (2020)]
- Long times: population dynamics

$$\dot{\rho} = \nabla \cdot \left[\frac{v^{2}\beta}{d\alpha(\beta+\alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha+\beta} \right]$$

$$Destabilizing \longrightarrow$$

$$-\nabla \cdot \left[\frac{v^{2}\beta}{d\alpha(\beta+\alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha+\beta} \right] + \mu\rho \left(1 - \frac{\rho}{\rho_{0}}\right)$$

• Population dynamics promote $\rho(\mathbf{r}) = \rho_0 \longrightarrow$ Stabilizes long wave-length

 $\dot{\rho} =$



→ Qualitatively accounts for the experiments