Correlations and order from active fluctuations in two-dimensional model cell sheets

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STATPHYS29: Driven and active amorphous matter, Göttingen

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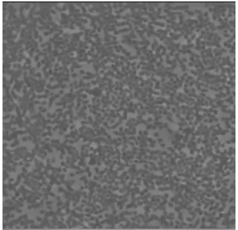
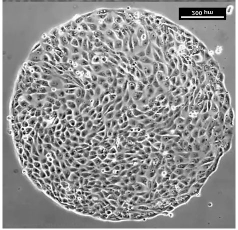
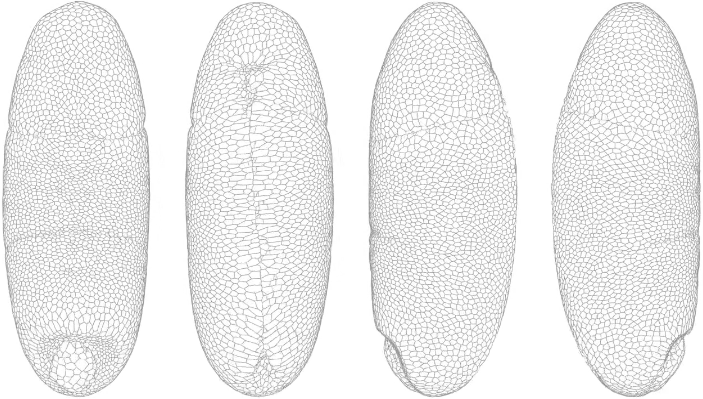
Dense active matter: cell tissues and dense suspensions

[Guillamat (2020)]







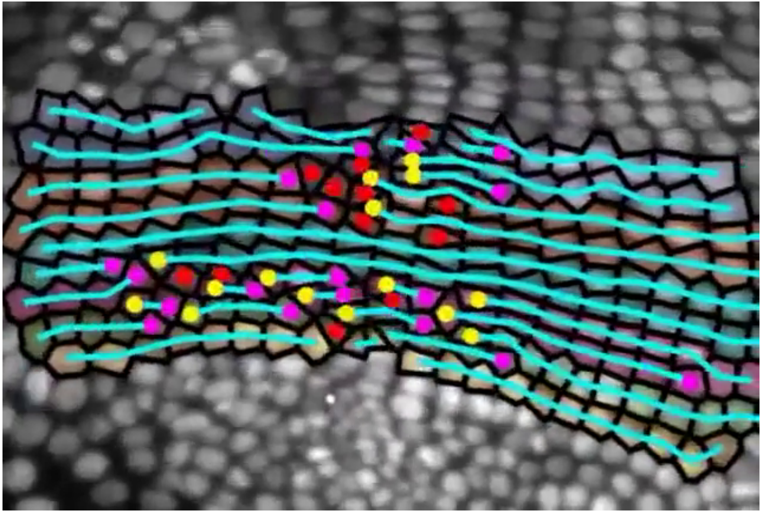
[Rabani, Ariel, Be'er, PLoS ONE (2013)]

[Stern, Shvartsman, Wieschaus, Current Biology (2022)]

How may the competition between crowding effects and particle-level active forcing on microscopic scales result in collective motion on larger scales?

Generation and stabilisation of order

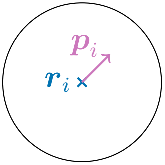
[Cislo, Yang, *et al.*, Nat. Phys. (2023)]



How may active forces generate and stabilise structural order?

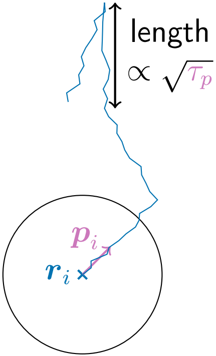
Self-propelled particles

- Overdamped self-propelled particles.



$$\cancel{m\ddot{\boldsymbol{r}}_i} = -\zeta\dot{\boldsymbol{r}}_i + \boldsymbol{p}_i$$

- Overdamped self-propelled particles.
- Propulsion forces $\boldsymbol{p}_i$ are stochastic with an autocorrelation time τ_p ($\equiv$ persistence time).



$$\zeta \dot{\boldsymbol{r}}_i = \boldsymbol{p}_i$$

$$\left\langle \boldsymbol{p}_i(t) \cdot \boldsymbol{p}_j(t') \right\rangle = f^2 \; e^{-|t-t'|/\tau_p} = \frac{k_B T_{\text{eff}}}{\zeta} \frac{e^{-|t-t'|/\tau_p}}{\tau_p}$$

Self-propelled particles

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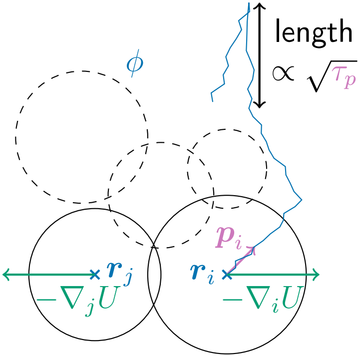
- Pairwise interaction potential U for N particles with packing fraction ϕ in 2D periodic box. No propulsion alignment.



$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i U + \boldsymbol{p}_i$$

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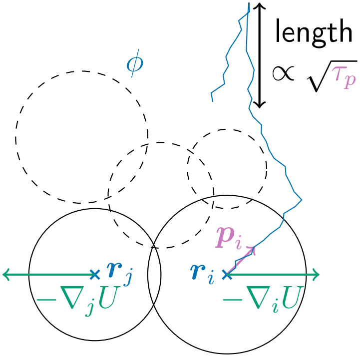
- Propulsion forces $\boldsymbol{p}_i$ are stochastic with an autocorrelation time τ_p ($\equiv$ persistence time).
- Pairwise interaction potential U for N particles with packing fraction ϕ in 2D periodic box. No propulsion alignment.
- With units $\zeta = 1$ and $k_B = 1$, there are only 3 control parameters: f or T_{eff}, τ_p, and ϕ.

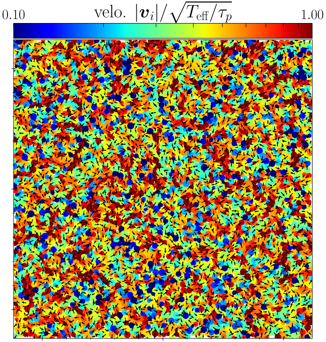


$$\boldsymbol{v}_i = -\nabla_i U + \boldsymbol{p}_i$$

$$\langle \boldsymbol{p}_i(t) \cdot \boldsymbol{p}_j(t') \rangle = f^2 \, e^{-|t-t'|/\tau_p} = T_{\text{eff}} \, \frac{e^{-|t-t'|/\tau_p}}{\tau_p}$$

Emergence of velocity correlations

[YEK, Jack, Berthier, PRL (2022)]



$\tau_p = 10^{-2}, \phi = 1.1$

Equilibrium limit ($\tau_p \ll 1$): velocities and positions are independent (Maxwell-Boltzmann distribution), no velocity correlations.

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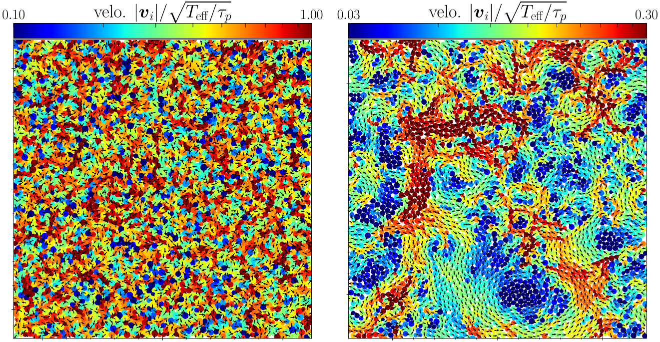


$\tau_p = 10^{-2}, \phi = 1.1$ $\tau_p = 10^{3}, \phi = 0.84$

Equilibrium limit ($\tau_p \ll 1$): velocities and positions are independent (Maxwell-Boltzmann distribution), no velocity correlations.

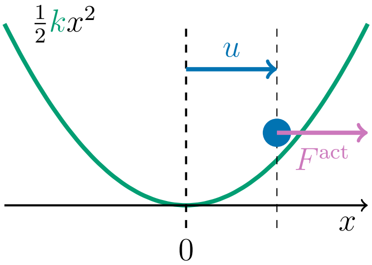
Far from equilibrium ($\tau_p \gg 1$): nonequilibrium velocity correlations, correlation length grows with τ_p [Henkes, Kostanjevec, *et al.*, Nat. Commun. (2020)].

Heuristic argument for the emergence of velocity correlations

$$\zeta \dot{u} = -ku + F^{\mathrm{act}}$$

$$\left\langle F^{\mathrm{act}}(t) F^{\mathrm{act}}(t') \right\rangle = \zeta k_B T_{\mathrm{eff}} \frac{\exp(-|t-t'|/\tau_p)}{\tau_p}$$

$$\left\langle \frac{1}{2} k u^2 \right\rangle = \frac{k_B T_{\mathrm{eff}}}{2} \frac{1}{1 + \frac{k\tau_p}{\zeta}}$$



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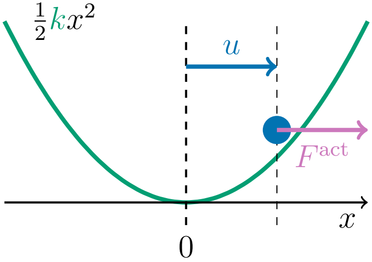

$$\zeta \dot{\boldsymbol{u}}_i = -\sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{u}_j + \boldsymbol{F}_i^{\mathrm{act}}$$ and eigenmodes $$\sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{e}_{j,n} = k_n \boldsymbol{e}_{i,n}$$

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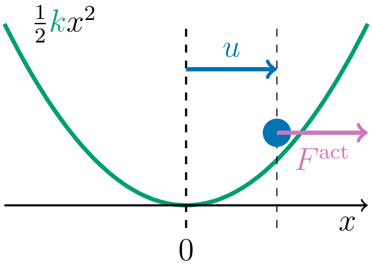

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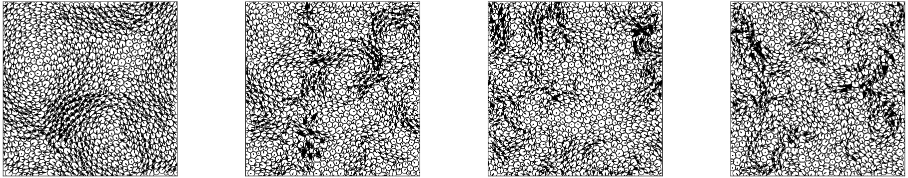
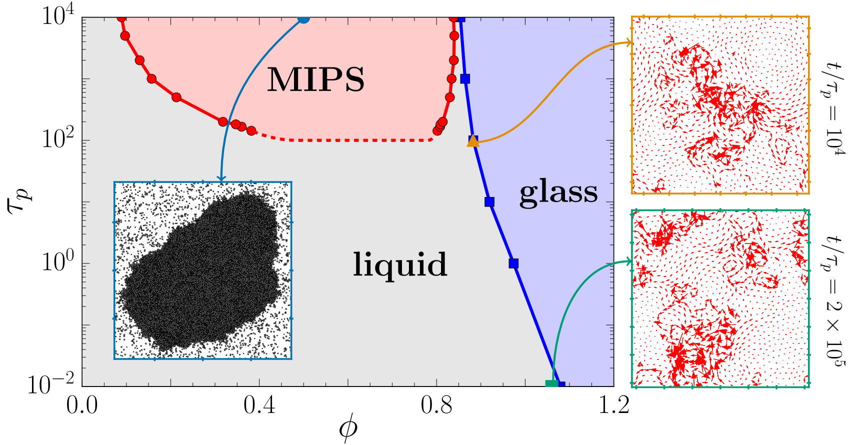
eigenmode k_1 | $k_2 > k_1$ | $k_3 > k_2$ | $k_4 > k_3$



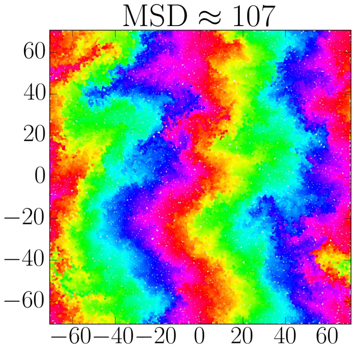
Phase diagram

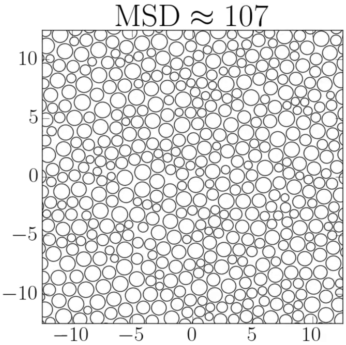


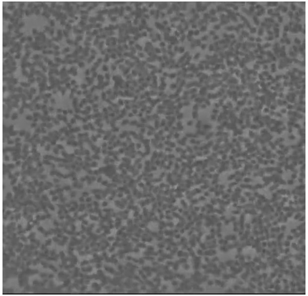
[YEK, Jack, Berthier, PRL (2022)]

Emergence of chaotic advective flows

[YEK, Klamser, *et al.*, PRL (2024)]





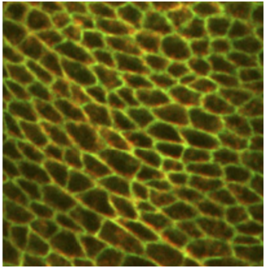


[Rabani, Ariel, Be'er, PLoS ONE (2013)]

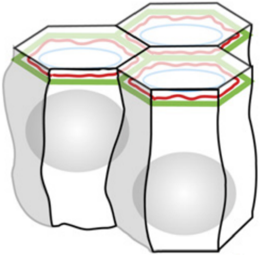
$$\tau_p = 10^4, \phi = 0.8425, T_{\text{eff}} = 1$$

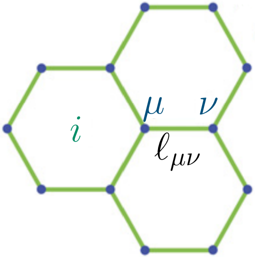
Qualitative behaviour reminiscent of active turbulence [Alert, Casademunt, Joanny, Annu. Rev. Condens. Matter Phys. (2022)] in the absence of aligning interactions, correlations emerge solely from the competition between persistence and crowding.

Cell tissues as vertex models



[Farhadifar, Röper, *et al.*, Curr. Biol. (2007)]





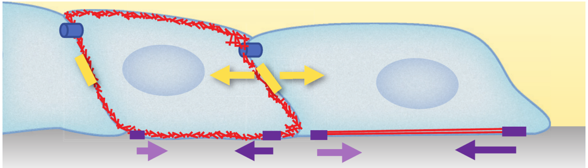
H1 Cell tissue is confluent (= without holes).

H2 Cell tissue is represented by the two-dimensional polygonal tiling of cell junctions.

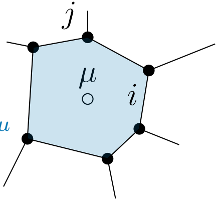
We describe the system as a planar mesh where the vertices are the degrees of freedom, and enclose the physical cells.

Forces in cell tissues

[Alert, Trepat, Ann. Rev. Cond. Matt. Phys. (2020)]



area A_μ
perimeter P_μ



$$\text{energy potential } U = \underbrace{\frac{1}{2}K(A_\mu - A_0)^2}_{\text{compression}} + \underbrace{\frac{1}{2}\Gamma(P_\mu - P_0)^2}_{\text{tension}}$$

Multiple origins for forces: cell shape constraints,

Forces in cell tissues

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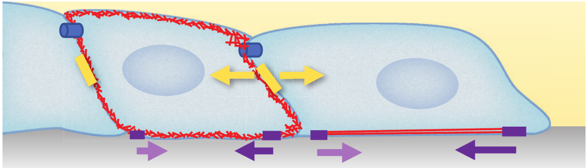

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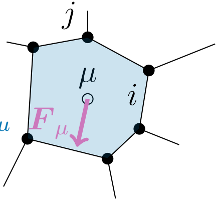

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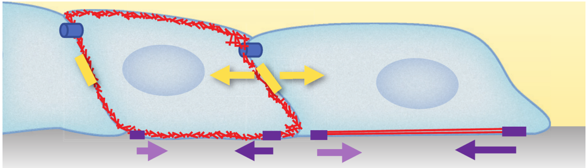

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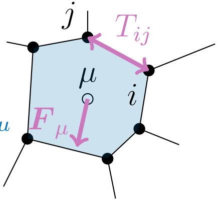

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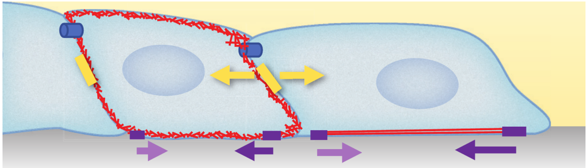

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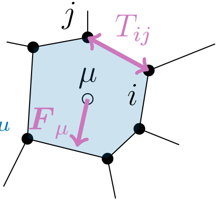

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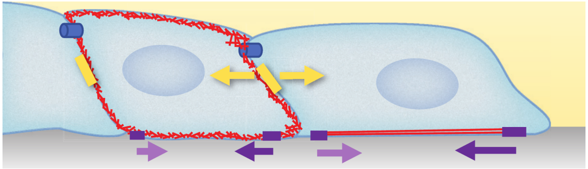

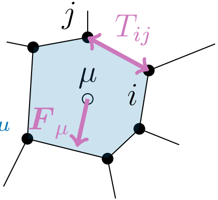

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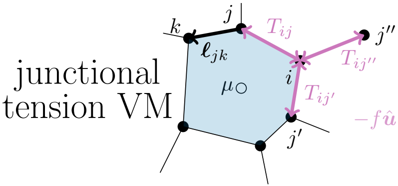
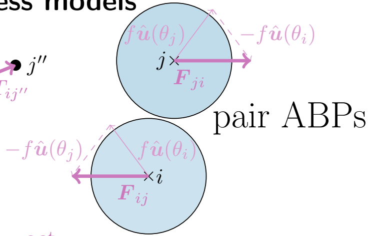
Some two-dimensional tissues, such as developing germ layers, develop on substrates from which they cannot extract momentum. Active stresses arise from the contractile activity of the cytoskeleton, with dissipation provided by the three-dimensional surroundings.

Active stress models





overdamped EOM $\quad \zeta \dot{\boldsymbol{r}}_i = -\nabla_i U + \boldsymbol{F}_i^{\mathrm{act}}$

active stress (pair-wise fluctuations)

$$\boldsymbol{F}_i^{\mathrm{act}} = \begin{cases} \sum_{\langle j,i \rangle} T_{ij} \hat{\boldsymbol{\ell}}_{ij} & \text{(junctional tension VM)} \\ \sum_{\langle j,i \rangle} f(\hat{\boldsymbol{u}}(\theta_i) - f\hat{\boldsymbol{u}}(\theta_j)) & \text{(pair ABPs)} \end{cases}$$

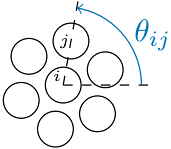
OU process: $\tau_p \dot{T}_{ij} = -T_{ij} + \sqrt{2 f^2 \tau_p}\, \eta_{ij}^{\mathrm{GWN}}$

Brownian process: $\dot{\theta} = \sqrt{2/\tau_p}\, \eta_i^{\mathrm{GWN}}, \quad \hat{\boldsymbol{u}}(\theta) = \begin{pmatrix} \cos\theta \\ \sin\theta \end{pmatrix}$

active force (particle-wise fluctuations) $\quad \boldsymbol{F}_i^{\mathrm{act}} = f\hat{\boldsymbol{u}}(\theta_i)$

Order-to-disorder transition in systems with active stress

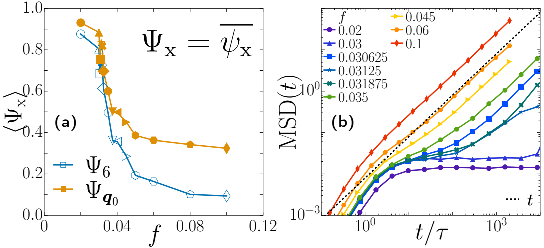
orientational order parameter $$\psi_{6,i} = \frac{1}{\#\mathcal{N}_i} \sum_{i \in \mathcal{N}_i} e^{\mathrm{i}6\theta_{ij}}$$



translational order parameter $$\psi_{\boldsymbol{q}_0,i} = e^{\mathrm{i}\boldsymbol{q}_0 \cdot \boldsymbol{r}_i}$$

mean squared displacement $$\mathrm{MSD}(t) = \left\langle \left| (\boldsymbol{r}_i(t) - \overline{\boldsymbol{r}}(t)) - (\boldsymbol{r}_i(0) - \overline{\boldsymbol{r}}(0)) \right|^2 \right\rangle$$

junctional tension VM



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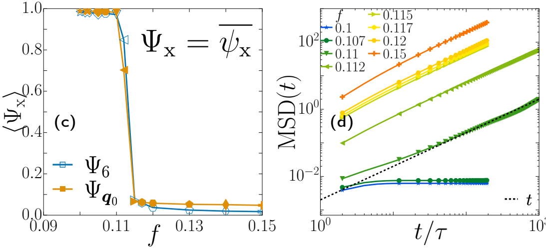
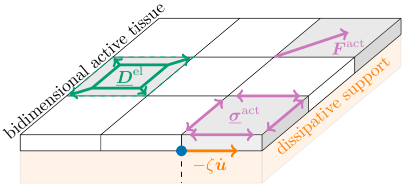


Displacement correlations in active solids



active elastic solid

$$\zeta\dot{\boldsymbol{u}} = -\underline{\boldsymbol{D}}^{\rm el} * \boldsymbol{u} + \boldsymbol{F}^{\rm act}$$

$$\underline{\tilde{\boldsymbol{D}}}^{\rm el}(\boldsymbol{q}) \sim K q^2$$

self-propulsion

$$\left\langle \boldsymbol{F}^{\rm act}(\boldsymbol{r},t) \cdot \boldsymbol{F}^{\rm act}(\boldsymbol{r}',t') \right\rangle = f^2 \, e^{-|t-t'|/\tau_p} \left[a^2\delta(\boldsymbol{r}-\boldsymbol{r}')\right]$$

$$\left\langle \tilde{\boldsymbol{u}}(\boldsymbol{q},t) \cdot \tilde{\boldsymbol{u}}(\boldsymbol{q}',t) \right\rangle = \boxed{\frac{f^2\tau_p}{2\zeta K q^2}} \frac{1}{1+q^2\xi^2} \left[(2\pi a)^2\delta(\boldsymbol{q}-\boldsymbol{q}')\right] \xrightarrow[q\to 0]{} \infty$$

characteristic length $\xi = \sqrt{K\tau_p/\zeta}$

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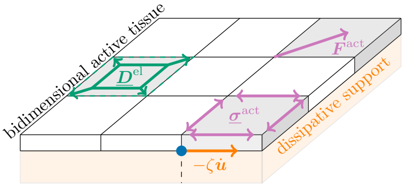

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characteristic length $\xi = \sqrt{K \tau_p / \zeta}$

active stress

$$\boldsymbol{F}^{\mathrm{act}} = \nabla \cdot \underline{\boldsymbol{\sigma}}^{\mathrm{act}}$$

$$\left\langle \boldsymbol{F}^{\mathrm{act}}(\boldsymbol{r}, t) \cdot \boldsymbol{F}^{\mathrm{act}}(\boldsymbol{r}', t') \right\rangle = -f^2 a^2 \, e^{-|t-t'|/\tau_p} \, [a^2 \nabla^2 \delta(\boldsymbol{r} - \boldsymbol{r}')]$$

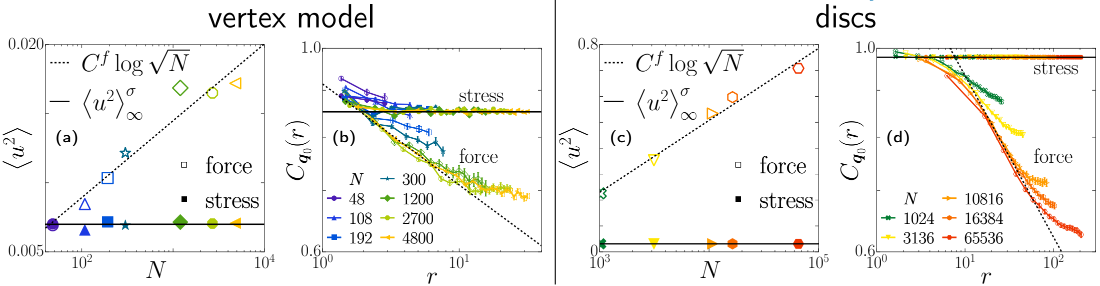
$$\left\langle \tilde{\boldsymbol{u}}(\boldsymbol{q}, t) \cdot \tilde{\boldsymbol{u}}(\boldsymbol{q}', t) \right\rangle = \boxed{\frac{f^2 a^2 \tau_p}{2\zeta K}} \frac{1}{1 + q^2 \xi^2} \, [(2\pi a)^2 \delta(\boldsymbol{q} - \boldsymbol{q}')] \underset{q \to 0}{=} \mathcal{O}(1)$$

Long-range displacement correlations in systems with active stress

displacement variance $\left\langle u^2 \right\rangle = \left\langle |\boldsymbol{u}_i|^2 \right\rangle$

translational order correlations $C_{\boldsymbol{q}_0}(r) = \left\langle \psi_{\boldsymbol{q}_0,i} \psi_{\boldsymbol{q}_0,j} \right\rangle_{|\boldsymbol{r}_j - \boldsymbol{r}_i| = r}$

$= \left\langle e^{\mathrm{i}\boldsymbol{q}_0 \cdot (\boldsymbol{r}_j - \boldsymbol{r}_i)} \right\rangle_{|\boldsymbol{r}_j - \boldsymbol{r}_i| = r}$

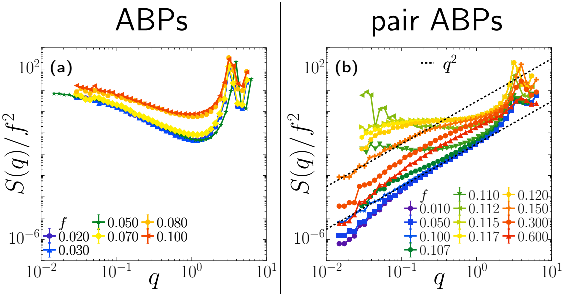


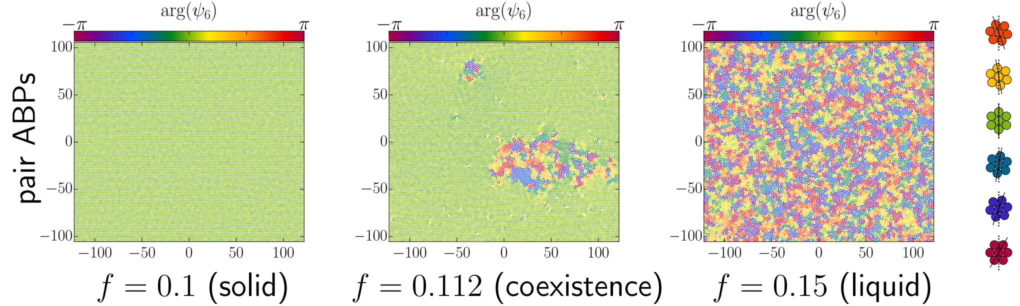
$$C_{\boldsymbol{q}_0}(r) \underset{\substack{L\to\infty \\ r\to\infty}}{\sim} \begin{cases} r^{-\frac{1}{2}|\boldsymbol{q}_0|^2 C^f} & \text{(self-propulsion – QLRO)} \\ e^{-\frac{1}{2}|\boldsymbol{q}_0|^2 \left\langle u^2 \right\rangle_\infty^\sigma} & \text{(active stress – LRO)} \end{cases}$$

Hyperuniformity in systems with active stress

structure factor $S(\boldsymbol{q}) = \frac{1}{N} \sum_{i,j=1}^{N} \left\langle e^{\mathrm{i}\boldsymbol{q}\cdot(\boldsymbol{r}_j - \boldsymbol{r}_i)} \right\rangle$

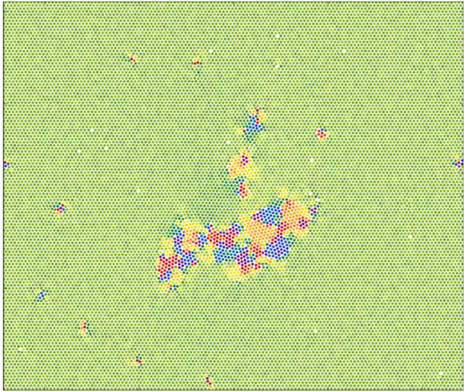
$$\underset{\substack{L\to\infty \\ q\to 0}}{\sim} \begin{cases} f^2 & \text{(self-propulsion)} \\ f^2 q^2 & \text{(active stress)} \end{cases}$$





Summary

1. Self-propelled particles and vertex models can be used to model biological cell tissues.
2. Velocity correlations emerge in dense persistently self-propelled systems.
3. Systems under active stresses are a class of systems encompassing nonmotile active matter. These are realised by pair-wise fluctuating forces.
4. Active stresses lead to finite large-wavelength displacement fluctuations, and thus long-range translational order and hyperuniformity.



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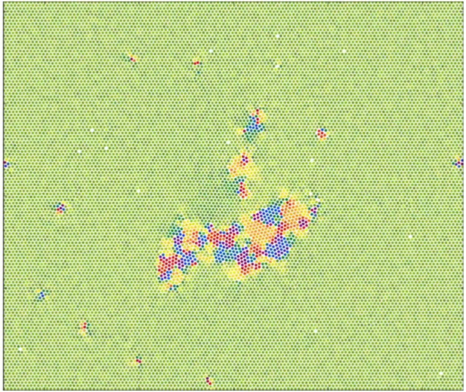

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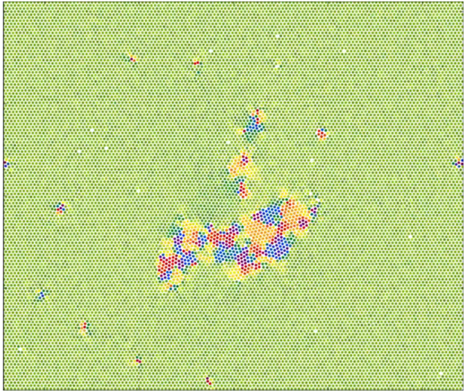

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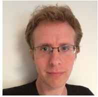

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Thank you for your attention!

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