Correlated cell movements drive epithelial finger formation

Yann-Edwin Keta

Sorbonne Université, Physique et Mécanique des Milieux Hétérogènes (PMMH)

5èmes journées du GDR IDE

4/5/2026

SORBONNE UNIVERSITÉ

Physique et Mécanique des Milieux Hétérogènes UMR 7636

S. C. Kammeraat

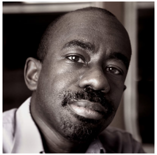
S. Henkes

Universiteit Leiden

I. Näthke

R. Sknepnek

University of Dundee



T. B. Liverpool

University of Bristol

What is active matter?

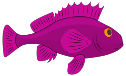
Definition (Active matter)

System composed of self-driven units, **active particles**, each capable of converting stored or ambient free energy into **systematic movement** [Marchetti, Joanny, *et al.*, Rev. Mod. Phys. (2013)].

What is active matter?

Definition (Active matter)

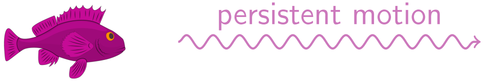
System composed of self-driven units, **active particles**, each capable of converting stored or ambient free energy into **systematic movement** [Marchetti, Joanny, *et al.*, Rev. Mod. Phys. (2013)].



What is active matter?

Definition (Active matter)

System composed of self-driven units, **active particles**, each capable of converting stored or ambient free energy into **systematic movement** [Marchetti, Joanny, *et al.*, Rev. Mod. Phys. (2013)].



What is active matter?

Definition (Active matter)

System composed of self-driven units, **active particles**, each capable of converting stored or ambient free energy into **systematic movement** [Marchetti, Joanny, *et al.*, Rev. Mod. Phys. (2013)].

What is active matter?

Definition (Active matter)

System composed of self-driven units, **active particles**, each capable of converting stored or ambient free energy into **systematic movement** [Marchetti, Joanny, *et al.*, Rev. Mod. Phys. (2013)].

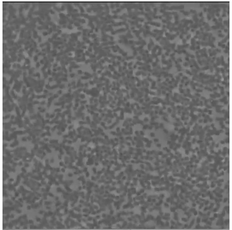
[BBC Earth (2017)]

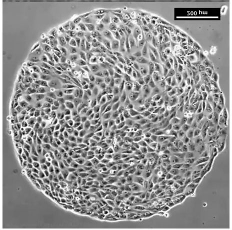
[Patel (2021)]

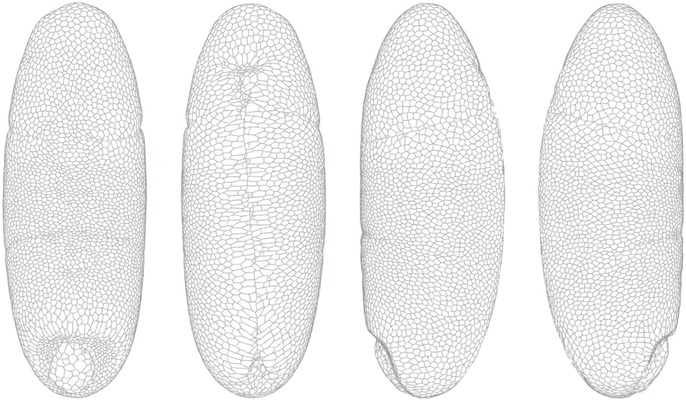
[Winter (2010)]

Dense active matter: cell tissues and dense suspensions

[Guillamat (2020)]





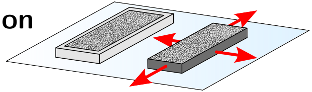


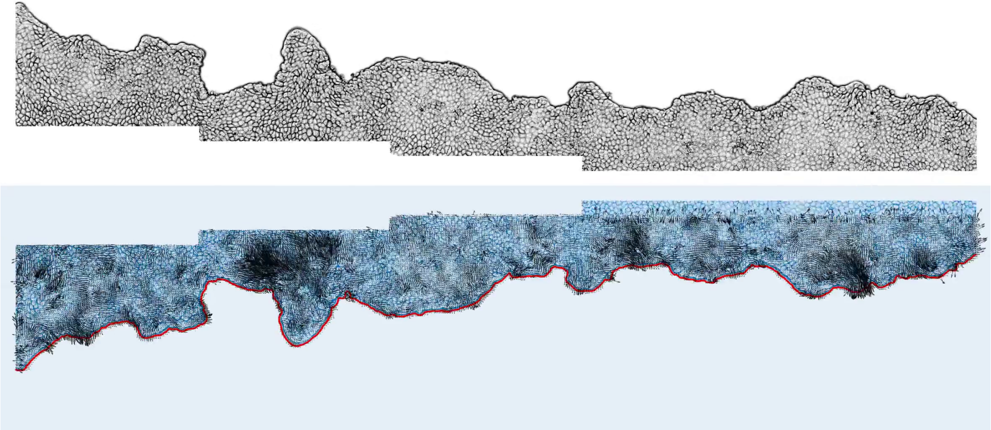
[Rabani, Ariel, Be'er, PLoS ONE (2013)]

[Stern, Shvartsman, Wieschaus, Curr. Biol. (2022)]

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

Epithelial finger formation





Finger-like protrusions form at the advancing edge of an MDCK cell tissue in a wound healing assay.

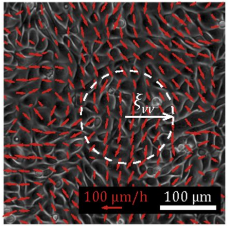
Origin of finger formation

- Chemical signaling? [Ouaknin, Bar-Yoseph, Biophys. J. (2009)]
- Curvature-enhanced motility? [Mark, Shlomovitz, *et al.*, Biophys. J. (2010)]
- Leader cells with special properties? [Sepúlveda, Petitjean, *et al.*, PLoS Comput. Biol. (2013)]
- Velocity gradient leading to accelerated front? [Alert, Blanch-Mercader, Casademunt, PRL (2019)]
- Pressure-dependent growth rate? [Ye, Lin, PRL (2024)]

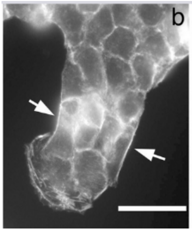
Origin of finger formation

- Chemical signaling? [Ouaknin, Bar-Yoseph, Biophys. J. (2009)]
- Curvature-enhanced motility? [Mark, Shlomovitz, *et al.*, Biophys. J. (2010)]
- Leader cells with special properties? [Sepúlveda, Petitjean, *et al.*, PLoS Comput. Biol. (2013)]
- Velocity gradient leading to accelerated front? [Alert, Blanch-Mercader, Casademunt, PRL (2019)]
- Pressure-dependent growth rate? [Ye, Lin, PRL (2024)]

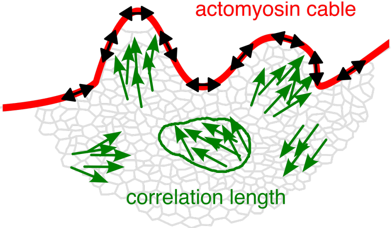
[Poujade, Grasland-Mongrain, *et al.*, PNAS (2007)]



+



→

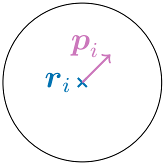


[Garcia, Hannezo, *et al.*, PNAS (2015)]

[Kammeraat, YEK, *et al.*, arXiv (2025)]

Self-propelled particles

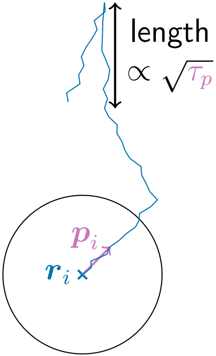
- Overdamped self-propelled particles.



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

Self-propelled particles

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

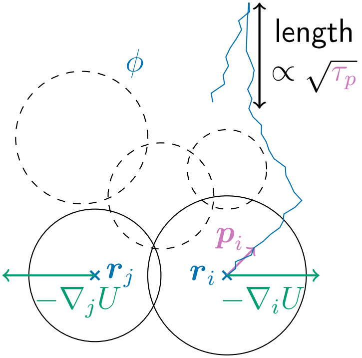


$$\zeta \dot{\boldsymbol{r}}_i = \boldsymbol{p}_i$$

$$\left\langle \boldsymbol{p}_i(t) \cdot \boldsymbol{p}_j(t') \right\rangle = \delta_{ij}\, \zeta k_B T_{\mathrm{eff}} \, \frac{e^{-|t-t'|/\tau_p}}{\tau_p}$$

Self-propelled particles

- Overdamped self-propelled particles.
- Propulsion forces $\boldsymbol{p}_i$ are stochastic with an autocorrelation time τ_p ($\equiv$ persistence time).
- Interaction potential U for N particles with packing fraction ϕ in 2D periodic box. No propulsion alignment.

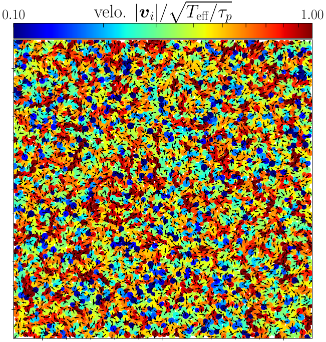


$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i U + \boldsymbol{p}_i$$

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

Emergence of velocity correlations

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

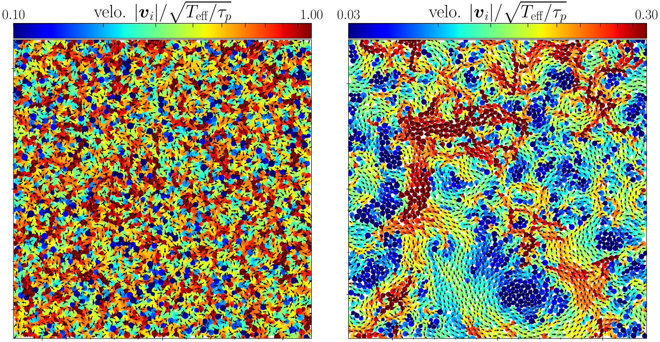


$\tau_p = 10^{-2}, \phi = 1.1$

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

Emergence of velocity correlations

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



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

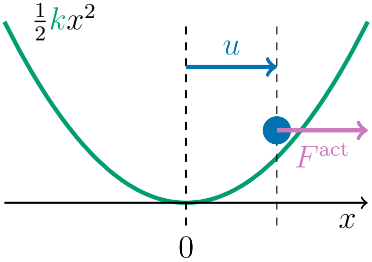
Equilibrium limit ($\tau_p \ll 1$): velocities and positions are independent (Maxwell-Boltzmann distribution), no velocity correlations.

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

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

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

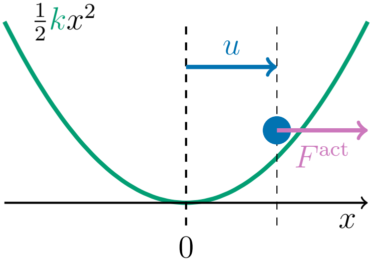


Heuristic argument for the emergence of velocity correlations

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

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

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

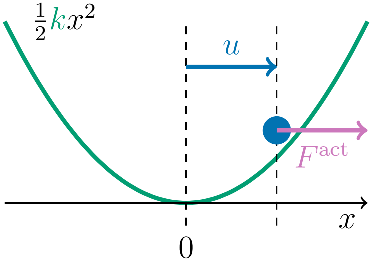


Heuristic argument for the emergence of velocity correlations

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

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

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



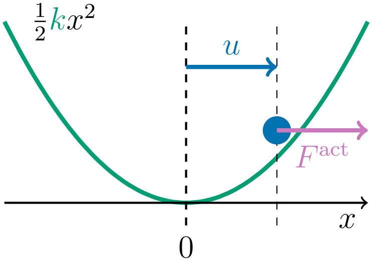
$$\zeta \dot{\boldsymbol{u}}_i = -\sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{u}_j + \boldsymbol{F}_i^{\mathrm{act}}$$ and eigenmodes $$\sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{e}_{j,n} = k_n \boldsymbol{e}_{i,n}$$

Heuristic argument for the emergence of velocity correlations

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

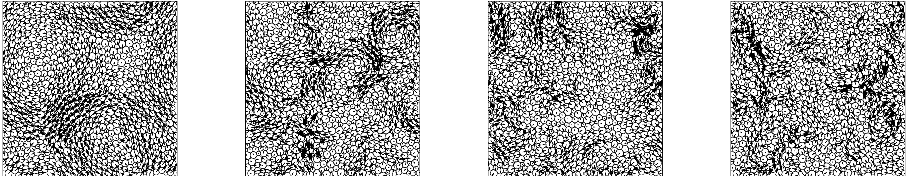
$$\left\langle F^{\mathrm{act}}(t) F^{\mathrm{act}}(t') \right\rangle = \zeta k_B T_{\mathrm{eff}} \frac{\exp(-|t-t'|/\tau_p)}{\tau_p}$$

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



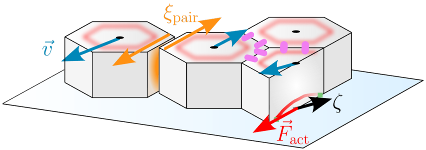
$$\zeta \dot{\boldsymbol{u}}_i = -\sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{u}_j + \boldsymbol{F}_i^{\mathrm{act}} \text{ and eigenmodes } \sum_j \frac{\partial^2 U}{\partial \boldsymbol{r}_i \partial \boldsymbol{r}_j} \boldsymbol{e}_{j,n} = k_n \boldsymbol{e}_{i,n}$$

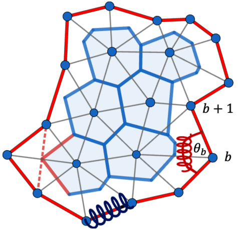
eigenmode k_1 | $k_2 > k_1$ | $k_3 > k_2$ | $k_4 > k_3$



Active Voronoi model (AVM)

Representing the dense confluent tissue as a 2D self-propelled (active) Voronoi model [Bi, Yang, *et al.*, PRX (2016)] and the actomyosin cable as a stretch- and bend-resisting chain.

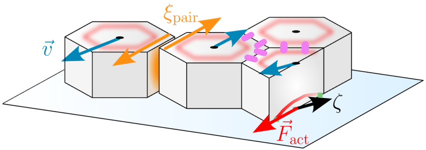


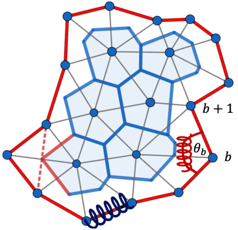


$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i (U_{\rm VM} + U_{\rm AMC}) + \boldsymbol{F}_i^{\rm act}$$

Active Voronoi model (AVM)

Representing the dense confluent tissue as a 2D self-propelled (active) Voronoi model [Bi, Yang, *et al.*, PRX (2016)] and the actomyosin cable as a stretch- and bend-resisting chain.



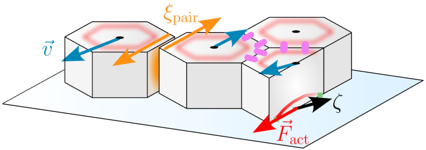


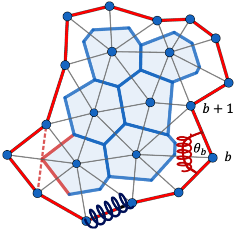
$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i (U_{\rm VM} + U_{\rm AMC}) + \boldsymbol{F}_i^{\rm act}$$

$$U_{\rm VM} = \sum_{\text{cells } i} \left[\frac{K}{2} (\text{Area}_i - A_0)^2 + \frac{\Gamma}{2} (\text{Perimeter}_i - P_0)^2 \right]$$

Active Voronoi model (AVM)

Representing the dense confluent tissue as a 2D self-propelled (active) Voronoi model [Bi, Yang, *et al.*, PRX (2016)] and the actomyosin cable as a stretch- and bend-resisting chain.





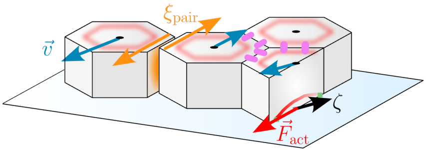
$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i (U_{\text{VM}} + U_{\text{AMC}}) + \boldsymbol{F}_i^{\text{act}}$$

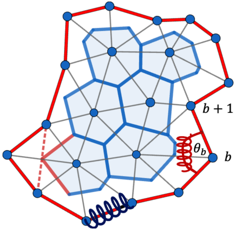
$$U_{\text{VM}} = \sum_{\text{cells } i} \left[\frac{K}{2} (\text{Area}_i - A_0)^2 + \frac{\Gamma}{2} (\text{Perimeter}_i - P_0)^2 \right]$$

$$U_{\text{AMC}} = \sum_{\text{bonds } b} \left[\frac{k_s}{2} \ell_{b,b+1}^2 + \frac{k_b}{2} (\theta_b - \pi)^2 \right]$$

Active Voronoi model (AVM)

Representing the dense confluent tissue as a 2D self-propelled (active) Voronoi model [Bi, Yang, *et al.*, PRX (2016)] and the actomyosin cable as a stretch- and bend-resisting chain.





$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i (U_{\text{VM}} + U_{\text{AMC}}) + \boldsymbol{F}_i^{\text{act}}$$

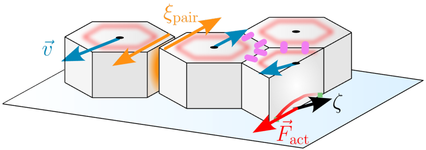
$$U_{\text{VM}} = \sum_{\text{cells } i} \left[\frac{K}{2} (\text{Area}_i - A_0)^2 + \frac{\Gamma}{2} (\text{Perimeter}_i - P_0)^2 \right]$$

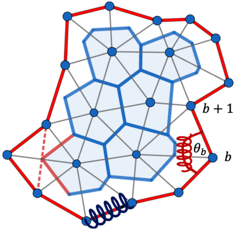
$$U_{\text{AMC}} = \sum_{\text{bonds } b} \left[\frac{k_s}{2} \ell_{b,b+1}^2 + \frac{k_b}{2} (\theta_b - \pi)^2 \right]$$

$$\boldsymbol{F}_i^{\text{act}} = \zeta v_0 (\cos\theta_i, \sin\theta_i);\ \dot{\theta}_i = \sqrt{2/\tau_p}\, \eta_i;\ \langle \eta_i(0) \eta_j(t) \rangle = \delta_{ij}\, \delta(t)$$

Active Voronoi model (AVM)

Representing the dense confluent tissue as a 2D self-propelled (active) Voronoi model [Bi, Yang, *et al.*, PRX (2016)] and the actomyosin cable as a stretch- and bend-resisting chain.





$$\zeta \dot{\boldsymbol{r}}_i = -\nabla_i (U_{\rm VM} + U_{\rm AMC}) + \boldsymbol{F}_i^{\rm act} + \xi \sum_{\langle i,j \rangle} (\dot{\boldsymbol{r}}_j - \dot{\boldsymbol{r}}_i)$$

$$U_{\rm VM} = \sum_{\text{cells } i} \left[\frac{K}{2} (\text{Area}_i - A_0)^2 + \frac{\Gamma}{2} (\text{Perimeter}_i - P_0)^2 \right]$$

$$U_{\rm AMC} = \sum_{\text{bonds } b} \left[\frac{k_s}{2} \ell_{b,b+1}^2 + \frac{k_b}{2} (\theta_b - \pi)^2 \right]$$

$$\boldsymbol{F}_i^{\rm act} = \zeta v_0 (\cos\theta_i, \sin\theta_i);\ \dot{\theta}_i = \sqrt{2/\tau_p}\, \eta_i;\ \langle \eta_i(0) \eta_j(t) \rangle = \delta_{ij}\, \delta(t)$$

Derivation of bulk velocity correlations

Continuous model of viscoelastic self-propelled solid.

$$\zeta \dot{\boldsymbol{u}} = B \nabla (\nabla \cdot \boldsymbol{u}) + \mu \nabla^2 \boldsymbol{u} + K \nabla (\nabla \cdot \dot{\boldsymbol{u}}) + \eta \nabla^2 \dot{\boldsymbol{u}} + \zeta v_0 \hat{\boldsymbol{n}}$$

$$\langle \hat{\boldsymbol{n}}(\boldsymbol{r}, t) \cdot \hat{\boldsymbol{n}}(\boldsymbol{r}', t') \rangle = a^2 \, \delta(\boldsymbol{r} - \boldsymbol{r}') \, e^{-|t-t'|/\tau_p}$$

Derivation of bulk velocity correlations

Continuous model of viscoelastic self-propelled solid.

$$\zeta \dot{\boldsymbol{u}} = B \nabla (\nabla \cdot \boldsymbol{u}) + \mu \nabla^2 \boldsymbol{u} + K \nabla (\nabla \cdot \dot{\boldsymbol{u}}) + \eta \nabla^2 \dot{\boldsymbol{u}} + \zeta v_0 \hat{\boldsymbol{n}}$$

$$\langle \hat{\boldsymbol{n}}(\boldsymbol{r}, t) \cdot \hat{\boldsymbol{n}}(\boldsymbol{r}', t') \rangle = a^2 \, \delta(\boldsymbol{r} - \boldsymbol{r}') \, e^{-|t-t'|/\tau_p}$$

(1) Velocity $\boldsymbol{v} \equiv \dot{\boldsymbol{u}}$ spectrum *i.e.* Fourier transform of velocity-velocity correlations.

$$\langle \tilde{\boldsymbol{v}}(\boldsymbol{q}, t) \cdot \tilde{\boldsymbol{v}}(\boldsymbol{q}', t) \rangle \propto \frac{v_0^2 \, a^2 \, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\parallel,\mathrm{d}}^2 q^2)(1 + \xi_{\parallel,\mathrm{p}}^2 q^2)} + \frac{v_0^2 \, a^2 \, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\perp,\mathrm{d}}^2 q^2)(1 + \xi_{\perp,\mathrm{p}}^2 q^2)}$$

Derivation of bulk velocity correlations

Continuous model of viscoelastic self-propelled solid.

$$\zeta \dot{\boldsymbol{u}} = B\nabla(\nabla \cdot \boldsymbol{u}) + \mu \nabla^2 \boldsymbol{u} + K\nabla(\nabla \cdot \dot{\boldsymbol{u}}) + \eta \nabla^2 \dot{\boldsymbol{u}} + \zeta v_0 \hat{\boldsymbol{n}}$$

$$\langle \hat{\boldsymbol{n}}(\boldsymbol{r}, t) \cdot \hat{\boldsymbol{n}}(\boldsymbol{r}', t') \rangle = a^2\, \delta(\boldsymbol{r} - \boldsymbol{r}')\, e^{-|t-t'|/\tau_p}$$

(1) Velocity $\boldsymbol{v} \equiv \dot{\boldsymbol{u}}$ spectrum *i.e.* Fourier transform of velocity-velocity correlations.

$$\langle \tilde{\boldsymbol{v}}(\boldsymbol{q}, t) \cdot \tilde{\boldsymbol{v}}(\boldsymbol{q}', t) \rangle \propto \frac{v_0^2\, a^2\, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\parallel,\mathrm{d}}^2 q^2)(1 + \xi_{\parallel,\mathrm{p}}^2 q^2)} + \frac{v_0^2\, a^2\, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\perp,\mathrm{d}}^2 q^2)(1 + \xi_{\perp,\mathrm{p}}^2 q^2)}$$

$$\xi_{\parallel,\mathrm{d}} = \sqrt{(K + \eta)/\zeta};\ \xi_{\parallel,\mathrm{p}} = \sqrt{(B + \mu)\tau_p/\zeta + \xi_{\parallel,\mathrm{d}}^2};\ \xi_{\perp,\mathrm{d}} = \sqrt{\eta/\zeta};\ \xi_{\perp,\mathrm{p}} = \sqrt{\mu\tau_p/\zeta + \xi_{\perp,\mathrm{d}}^2}$$

Derivation of bulk velocity correlations

Continuous model of viscoelastic self-propelled solid.

$$\zeta \dot{\boldsymbol{u}} = B \nabla(\nabla \cdot \boldsymbol{u}) + \mu \nabla^2 \boldsymbol{u} + K \nabla(\nabla \cdot \dot{\boldsymbol{u}}) + \eta \nabla^2 \dot{\boldsymbol{u}} + \zeta v_0 \hat{\boldsymbol{n}}$$

$$\langle \hat{\boldsymbol{n}}(\boldsymbol{r}, t) \cdot \hat{\boldsymbol{n}}(\boldsymbol{r}', t') \rangle = a^2 \, \delta(\boldsymbol{r} - \boldsymbol{r}') \, e^{-|t-t'|/\tau_p}$$

(1) Velocity $\boldsymbol{v} \equiv \dot{\boldsymbol{u}}$ spectrum *i.e.* Fourier transform of velocity-velocity correlations.

$$\langle \tilde{\boldsymbol{v}}(\boldsymbol{q}, t) \cdot \tilde{\boldsymbol{v}}(\boldsymbol{q}', t) \rangle \propto \frac{v_0^2 \, a^2 \, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\parallel,\mathrm{d}}^2 q^2)(1 + \xi_{\parallel,\mathrm{p}}^2 q^2)} + \frac{v_0^2 \, a^2 \, \delta(\boldsymbol{q} - \boldsymbol{q}')}{(1 + \xi_{\perp,\mathrm{d}}^2 q^2)(1 + \xi_{\perp,\mathrm{p}}^2 q^2)}$$

$$\xi_{\parallel,\mathrm{d}} = \sqrt{(K + \eta)/\zeta}; \; \xi_{\parallel,\mathrm{p}} = \sqrt{(B + \mu)\tau_p/\zeta + \xi_{\parallel,\mathrm{d}}^2}; \; \xi_{\perp,\mathrm{d}} = \sqrt{\eta/\zeta}; \; \xi_{\perp,\mathrm{p}} = \sqrt{\mu\tau_p/\zeta + \xi_{\perp,\mathrm{d}}^2}$$

(2) Short-time decay of velocity temporal autocorrelation is dominated by τ_p.

Derivation of bulk velocity correlations

Continuous model of viscoelastic self-propelled solid.

$$\zeta \dot{\boldsymbol{u}} = B\nabla(\nabla\cdot\boldsymbol{u}) + \mu\nabla^2\boldsymbol{u} + K\nabla(\nabla\cdot\dot{\boldsymbol{u}}) + \eta\nabla^2\dot{\boldsymbol{u}} + \zeta v_0\hat{\boldsymbol{n}}$$

$$\langle\hat{\boldsymbol{n}}(\boldsymbol{r},t)\cdot\hat{\boldsymbol{n}}(\boldsymbol{r}',t')\rangle = a^2\,\delta(\boldsymbol{r}-\boldsymbol{r}')\,e^{-|t-t'|/\tau_p}$$

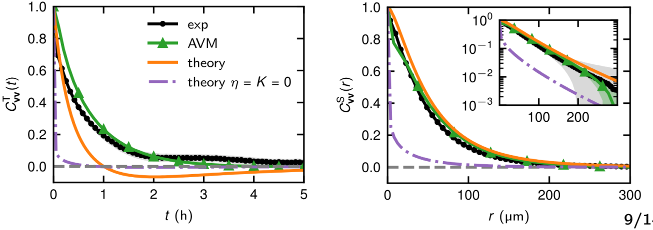
(1) Velocity $\boldsymbol{v}\equiv\dot{\boldsymbol{u}}$ spectrum *i.e.* Fourier transform of velocity-velocity correlations.

$$\langle\tilde{\boldsymbol{v}}(\boldsymbol{q},t)\cdot\tilde{\boldsymbol{v}}(\boldsymbol{q}',t)\rangle \propto \frac{v_0^2\,a^2\,\delta(\boldsymbol{q}-\boldsymbol{q}')}{(1+\xi_{\parallel,\mathrm{d}}^2q^2)(1+\xi_{\parallel,\mathrm{p}}^2q^2)} + \frac{v_0^2\,a^2\,\delta(\boldsymbol{q}-\boldsymbol{q}')}{(1+\xi_{\perp,\mathrm{d}}^2q^2)(1+\xi_{\perp,\mathrm{p}}^2q^2)}$$

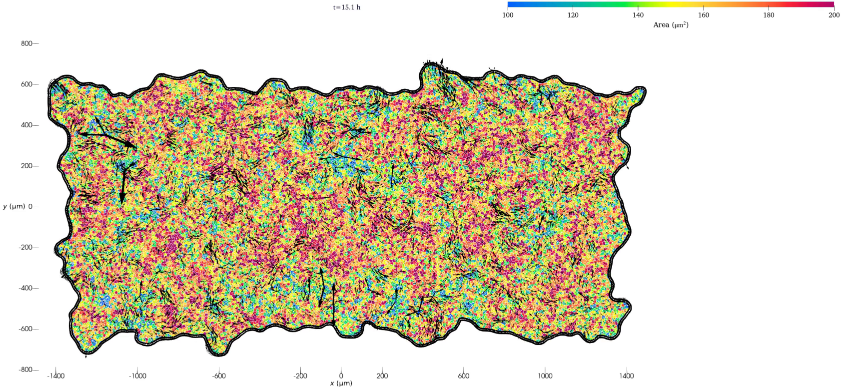
$$\xi_{\parallel,\mathrm{d}} = \sqrt{(K+\eta)/\zeta};\ \xi_{\parallel,\mathrm{p}} = \sqrt{(B+\mu)\tau_p/\zeta+\xi_{\parallel,\mathrm{d}}^2};\ \xi_{\perp,\mathrm{d}} = \sqrt{\eta/\zeta};\ \xi_{\perp,\mathrm{p}} = \sqrt{\mu\tau_p/\zeta+\xi_{\perp,\mathrm{d}}^2}$$

(2) Short-time decay of velocity temporal autocorrelation is dominated by τ_p.

Continuous model parameters are tuned against experimental velocity correlations. AVM parameters are derived via dimensional analysis.



Matching self-propelled Voronoi model with experiments



Height equation theory for finger formation

Actomyosin cable as a stretch- and band-resisting viscoelastic cable driven by a correlated noise v^{f} and described by $h(x,t)$ in the limit of small deformations.

$$\zeta_h \dot{h} = \lambda \frac{\partial^2 h}{\partial x^2} - \kappa \frac{\partial^4 h}{\partial x^4} + \eta \frac{\partial^2 \dot{h}}{\partial x^2} + \zeta_h v^f$$

Height equation theory for finger formation

Actomyosin cable as a stretch- and band-resisting viscoelastic cable driven by a correlated noise v^{f} and described by $h(x,t)$ in the limit of small deformations.

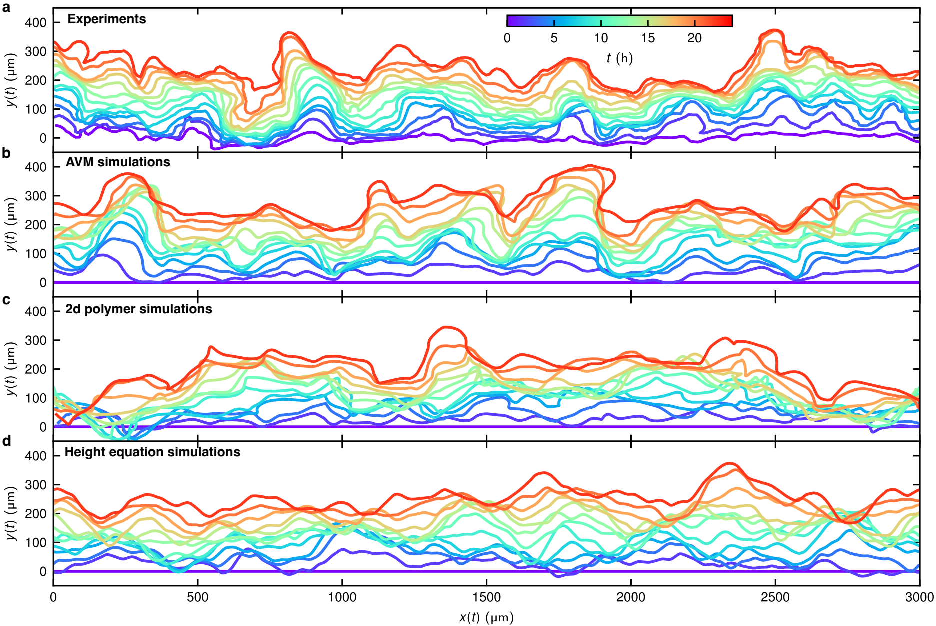
$$\zeta_h \dot{h} = \lambda \frac{\partial^2 h}{\partial x^2} - \kappa \frac{\partial^4 h}{\partial x^4} + \eta \frac{\partial^2 \dot{h}}{\partial x^2} + \zeta_h v^f$$

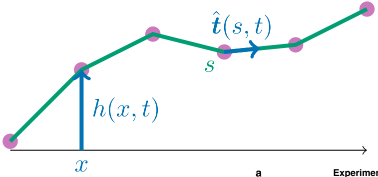
Effective time- and space-correlated noise generated by a chain model.

$$v^f \equiv \dot{y};\; \zeta_y \dot{y} = \mu \frac{\partial^2 y}{\partial x^2} + \eta \frac{\partial^2 \dot{y}}{\partial x^2} + \zeta_y v_0 \eta$$

$$\langle \eta(x,t)\eta(x',t')\rangle = \frac{1}{2} a\, \delta(x-x')\, e^{-|t-t'|/\tau_p}$$

Fingers (qualitative)



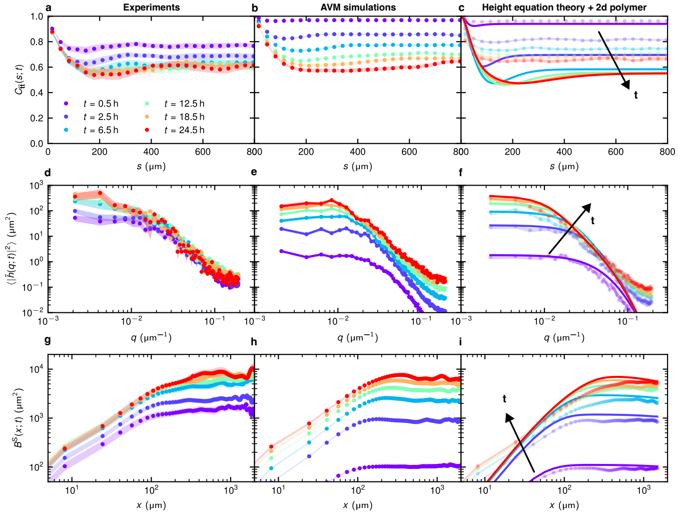


Fingers (quantitative)

(tangent correlation) $C_{\hat{t}\hat{t}}(s;t) = \langle \hat{t}(s,t) \cdot \hat{t}(0,t) \rangle$

(height spectrum) $\langle |\tilde{h}(q,t)|^2 \rangle$

(roughness) $B^S(x;t) = \langle [h(x,t) - h(0,t)]^2 \rangle$



Conclusion

Conclusion

- Epithelial fingers are long-lived fluctuations of the boundary driven by bulk collective motion.

Conclusion

- Epithelial fingers are long-lived fluctuations of the boundary driven by bulk collective motion.
- Fingers reach steady state and there is no evidence of finite-wavelength instability.

Conclusion

- Epithelial fingers are long-lived fluctuations of the boundary driven by bulk collective motion.
- Fingers reach steady state and there is no evidence of finite-wavelength instability.
- Leader cells, cell-cell signaling, and division modulate an intrinsic process instead of causing it.

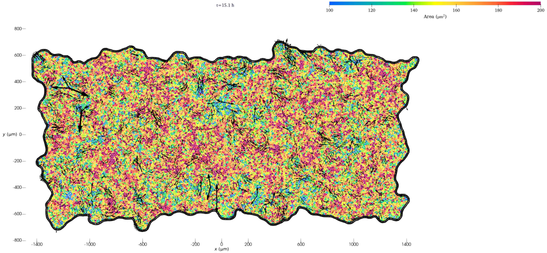
Conclusion

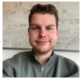
- Epithelial fingers are long-lived fluctuations of the boundary driven by bulk collective motion.
- Fingers reach steady state and there is no evidence of finite-wavelength instability.
- Leader cells, cell-cell signaling, and division modulate an intrinsic process instead of causing it.

Conclusion

- Epithelial fingers are long-lived fluctuations of the boundary driven by bulk collective motion.
- Fingers reach steady state and there is no evidence of finite-wavelength instability.
- Leader cells, cell-cell signaling, and division modulate an intrinsic process instead of causing it.

arXiv:2508.01046





S. C. Kammeraat

S. Henkes

U. Leiden

I. Näthke

R. Sknepnek

U. Dundee

T. B. Liverpool

U. Bristol

Thank you for your attention!

References

Alert, R., C. Blanch-Mercader, J. Casademunt (Mar. 2019). "Active Fingering Instability in Tissue Spreading". In: *Physical Review Letters* 122.8, p. 088104. ISSN: 0031-9007, 1079-7114.

BBC Earth (Feb. 2017). *Amazing Fish Form Giant Ball to Scare Predators | Blue Planet | BBC Earth*. YouTube. URL: https://www.youtube.com/watch?v=15B8qN9dre4.

Bi, D., X. Yang, M. C. Marchetti, M. L. Manning (Apr. 2016). "Motility-Driven Glass and Jamming Transitions in Biological Tissues". In: *Physical Review X* 6.2, p. 021011. ISSN: 2160-3308.

Garcia, S., E. Hannezo, J. Elgeti, J.-F. Joanny, P. Silberzan, N. S. Gov (Dec. 2015). "Physics of Active Jamming during Collective Cellular Motion in a Monolayer". In: *Proceedings of the National Academy of Sciences* 112.50, pp. 15314–15319. ISSN: 0027-8424, 1091-6490.

Guillamat, P. (Mar. 2020). *Cellular turbulent swirl - MDCK flows*. YouTube. URL: https://www.youtube.com/watch?v=0DY0UV50TRY.

Henkes, S., K. Kostanjevec, J. M. Collinson, R. Sknepnek, E. Bertin (Dec. 2020). "Dense Active Matter Model of Motion Patterns in Confluent Cell Monolayers". In: *Nature Communications* 11.1, p. 1405. ISSN: 2041-1723.

Kammeraat, S. C., YEK, P. Appleton, I. P. Newton, T. B. Liverpool, R. Sknepnek, I. Näthke, S. Henkes (Aug. 2025). "Correlated Cell Movements Drive Epithelial Finger Formation". In: *arXiv* arXiv:2508.01046. arXiv: 2508.01046 [cond-mat].

Marchetti, M. C., J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, R. A. Simha (July 2013). "Hydrodynamics of Soft Active Matter". In: *Reviews of Modern Physics* 85.3, pp. 1143–1189. ISSN: 0034-6861, 1539-0756.

Mark, S., R. Shlomovitz, N. S. Gov, M. Poujade, E. Grasland-Mongrain, P. Silberzan (Feb. 2010). "Physical Model of the Dynamic Instability in an Expanding Cell Culture". In: *Biophysical Journal* 98.3, pp. 361–370. ISSN: 00063495.

Ouaknin, G. Y., P. Z. Bar-Yoseph (Oct. 2009). "Stochastic Collective Movement of Cells and Fingering Morphology: No Maverick Cells". In: *Biophysical Journal* 97.7, pp. 1811–1821. ISSN: 00063495.

Patel, L. (2021). *Sheel Timelapse*. URL: https://www.bravozuluaerials.com/copy-of-construction?pgid=liepp2m9-ad6d559e-e387-4bf3-b310-42d8e9c7f00a.

Poujade, M., E. Grasland-Mongrain, A. Hertzog, J. Jouanneau, P. Chavrier, B. Ladoux, A. Buguin, P. Silberzan (Oct. 2007). "Collective Migration of an Epithelial Monolayer in Response to a Model Wound". In: *Proceedings of the National Academy of Sciences* 104.41, pp. 15988–15993. ISSN: 0027-8424, 1091-6490.

Rabani, A., G. Ariel, A. Be'er (Dec. 2013). "Collective Motion of Spherical Bacteria". In: *PLoS ONE* 8.12. Ed. by M. S. Kellermayer, e83760. ISSN: 1932-6203.

Sepúlveda, N., L. Petitjean, O. Cochet, E. Grasland-Mongrain, P. Silberzan, V. Hakim (Mar. 2013). "Collective Cell Motion in an Epithelial Sheet Can Be Quantitatively Described by a Stochastic Interacting Particle Model". In: *PLoS Computational Biology* 9.3. Ed. by M. P. Brenner, e1002944. ISSN: 1553-7358.

Stern, T., S. Y. Shvartsman, E. F. Wieschaus (Apr. 2022). "Deconstructing Gastrulation at Single-Cell Resolution". In: *Current Biology* 32.8, 1861–1868.e7. ISSN: 09609822.

Winter, D. (2010). URL: https://www.youtube.com/watch?v=eakKfY5aHmY.

Ye, Y., J. Lin (Jan. 2024). "Fingering Instability Accelerates Population Growth of a Proliferating Cell Collective". In: *Physical Review Letters* 132.1, p. 018402. ISSN: 0031-9007, 1079-7114.

YEK, R. L. Jack, L. Berthier (July 2022). "Disordered Collective Motion in Dense Assemblies of Persistent Particles". In: *Physical Review Letters* 129.4, p. 048002.