Nonreciprocal Phase Separation

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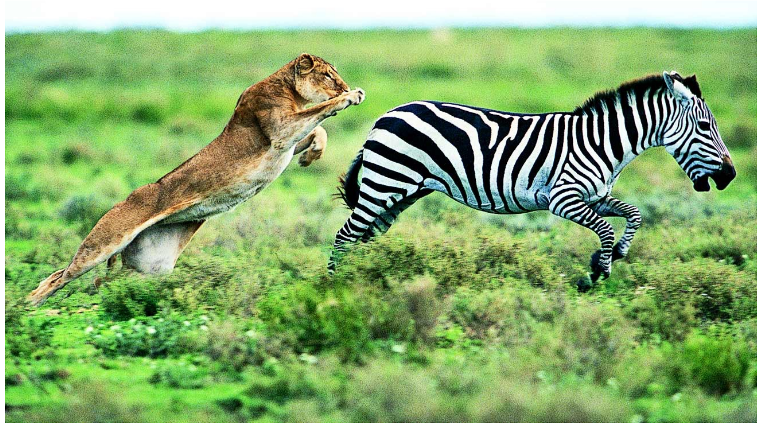
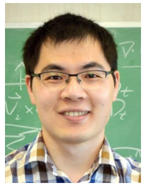


Fridtjof Brauns
KITP

Non-reciprocity as a generic mechanism for driving transitions from static to traveling patterns



Zhihong You
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SIMONS FOUNDATION

Outline

- Nonreciprocity ubiquitous out of equilibrium → Examples
- Activator-inhibitor models as NR dynamical systems
- From *global* to *local* dynamics: a generic model of spatiotemporal patterns
- Mapping of previously studied systems (in 1D) onto this generic form

→ formulate a general criterion for identifying a new class of NR pattern formation

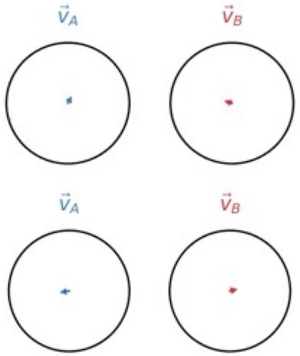
Nonreciprocal Phase Transitions

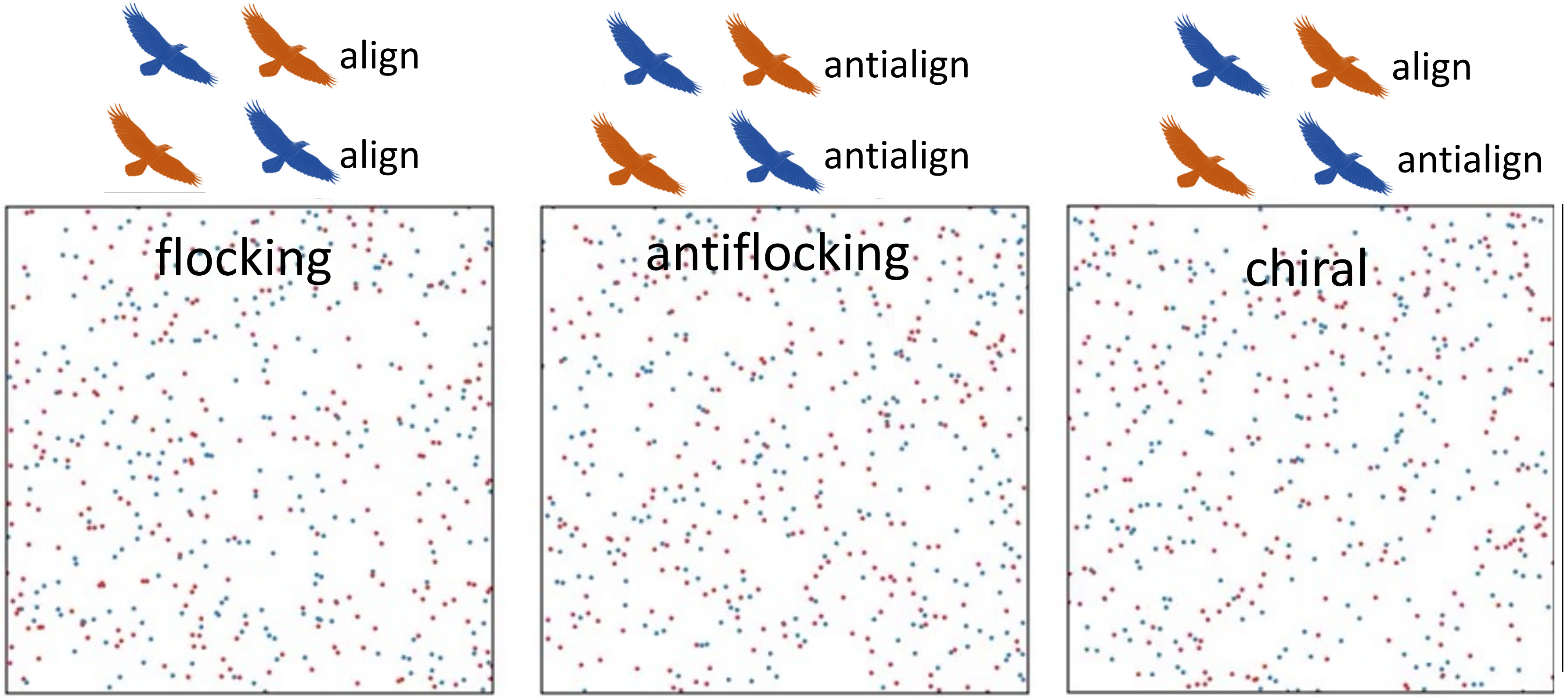
NR forces among species yield time-dependent self-organized phases

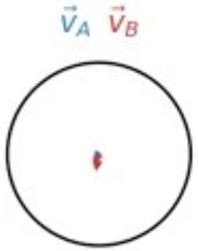
Reciprocal

Nonreciprocal

Two species flocking model







Static polar states , broken rotational symmetry

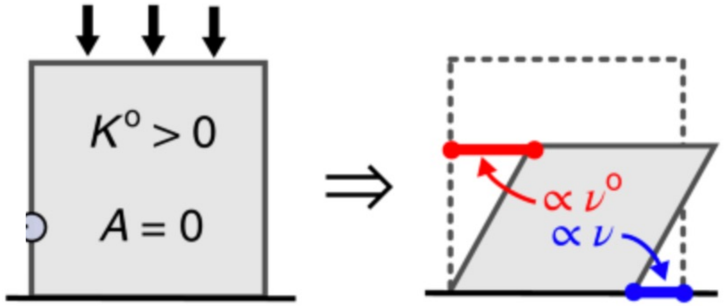
Time-dependent chiral state

M Fruchart, R Hanai, PB Littlewood, V Vitelli, Nature 2021

Nonreciprocal (odd) elasticity

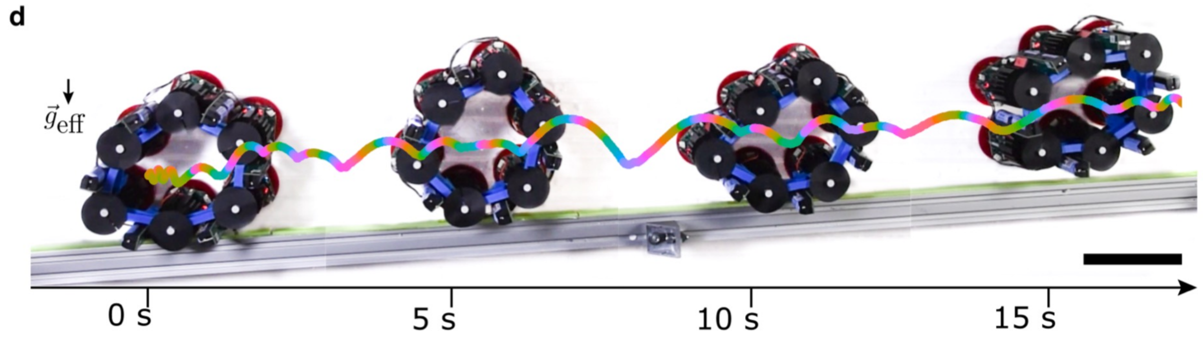
Nonconservative interactions yield antisymmetric elastic moduli and unusual response to deformations

Odd elasticity couples compression and shear
→ spontaneous shear under uniaxial compression



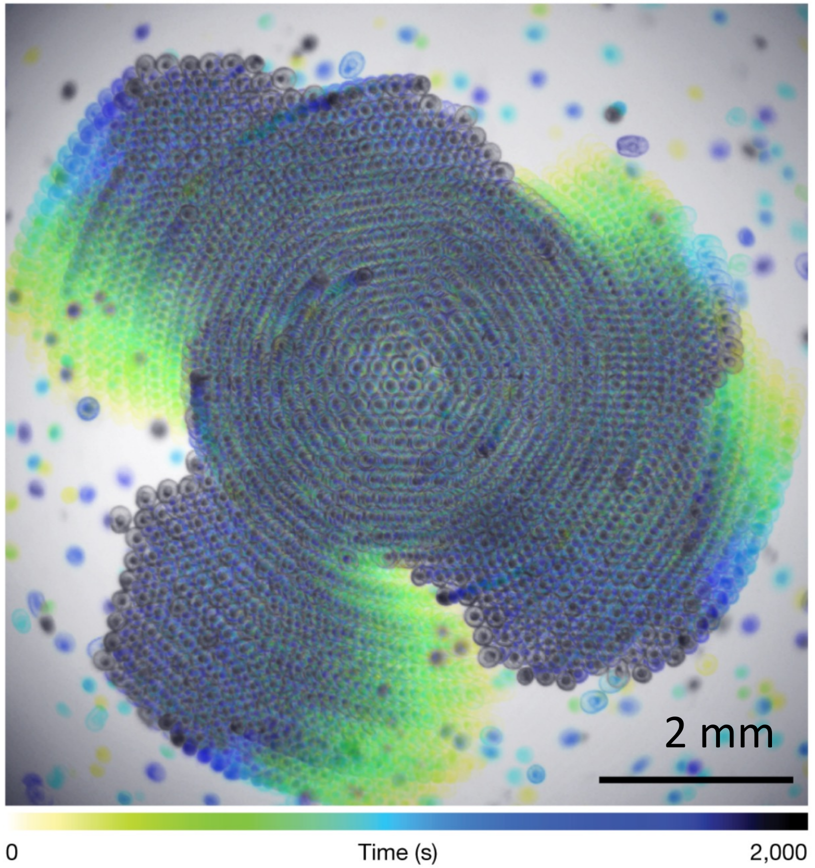
C Schneiber *et al.* Nat Phys 2020

Realization of odd-elastic engine cycle



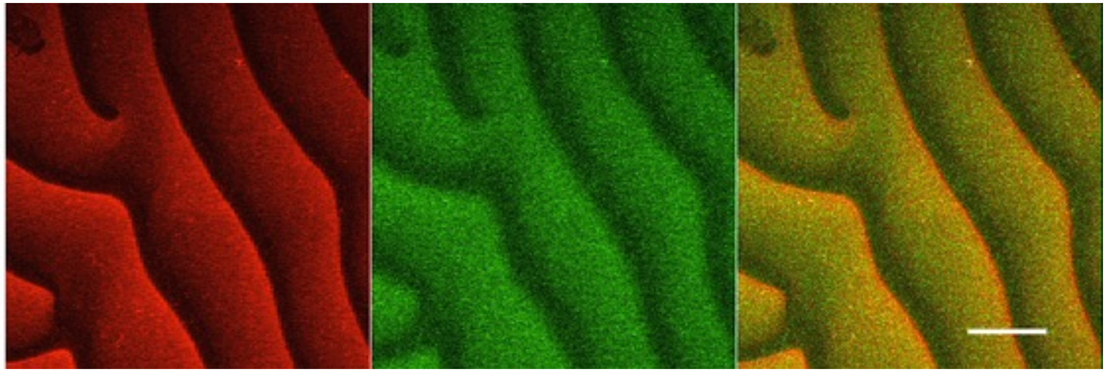
M Brandenbourger *et al.* arXiv:2108.08837

Self-sustained chiral strain cycles in crystals of starfish embryos TH Tan et al. Nature 2022

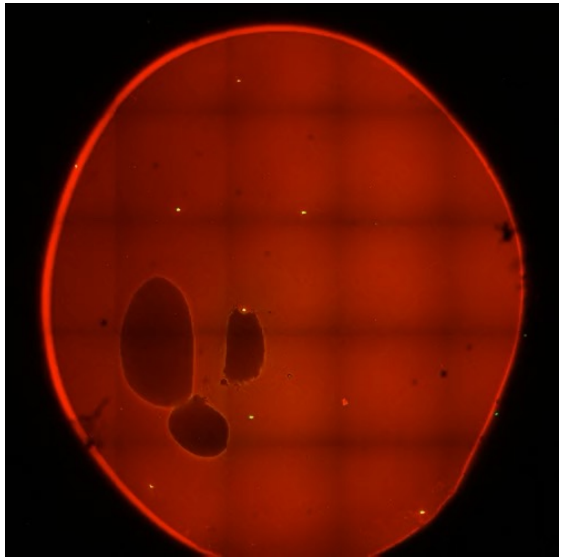


Traveling Waves of Conserved (Diffusive) Densities

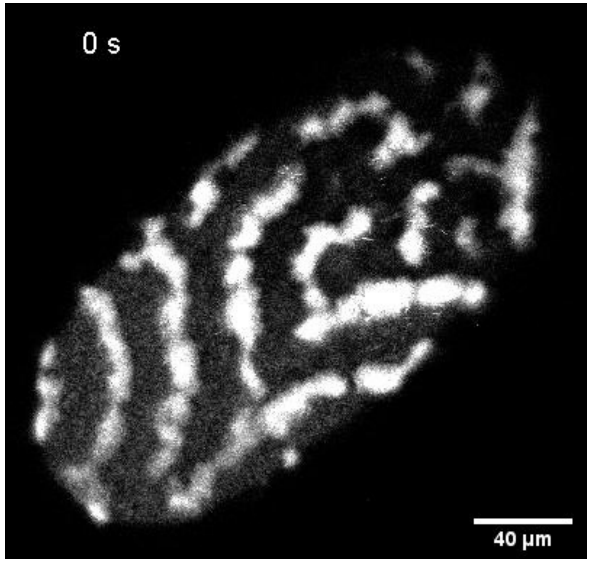
Mass-conserving reaction-diffusion: MinDE of *E.Coli*



M Loose *et al.*
Science 2008



P Schwille Lab
Munich

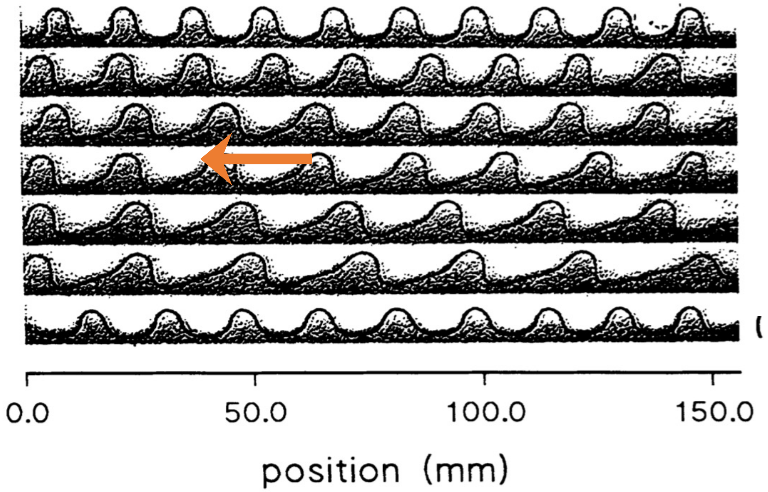


Protein (Rho-GTP) waves on the membrane of starfish egg cells

TH Tan *et al.*
Nat Phys 2020

Travelling patterns at driven fluid-air interface

L Pan JR de Bruyn
PRE 1994



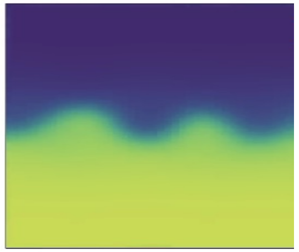
drive

Traveling and oscillatory states emerge from NR-coupled conserved Cahn-Hillard

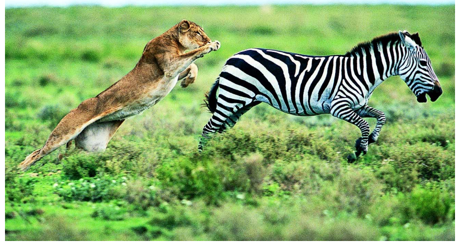
Z You, A Baskaran, MCM, PNAS 2020 & S Saha, J Agudo-Canalejo, R Golestanian PRX 2020

A generic model of nonreciprocal pattern formation of conserved fields

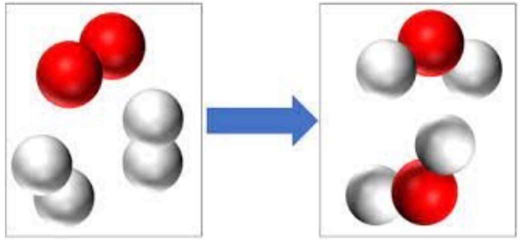
Static patterns

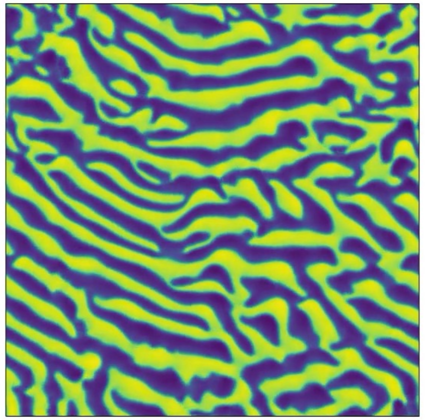


NR interactions



Mass conservation





- Unifies a broad class of pattern forming systems with conservation laws
- Provide a criterion for identifying them through linear stability analysis

F Brauns, MCM arXiv:2306.08868

Related work:
T Frohoff-Hülsmann, J Wrembel, U Thiele PRE 2021
S Saha, J Agudo-Canalejo, R Golestanian PRX 2020
S Saha, R Golestanian arXiv:2208.14985
T Frohoff-Hülsmann, U Thiele arXiv 2301.05568

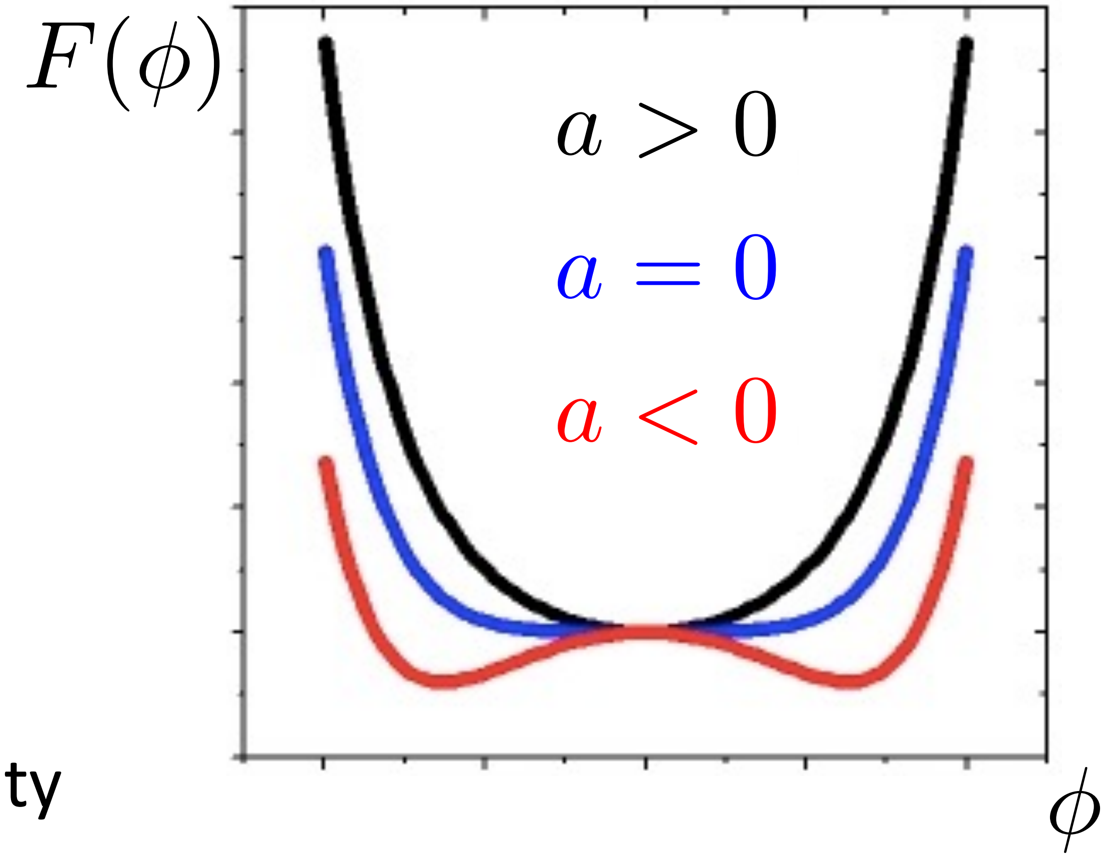
Equilibrium Phase Transitions captured by Free Energy Minimization

Landau free energy:

$$F(\phi) = a\phi^2 + b\phi^4$$

Stationary states are determined by free energy minimization

$$\frac{\partial F(\phi)}{\partial \phi} = 0$$ → bistability



Pattern formation with mass conservation: Cahn-Hilliard Equation

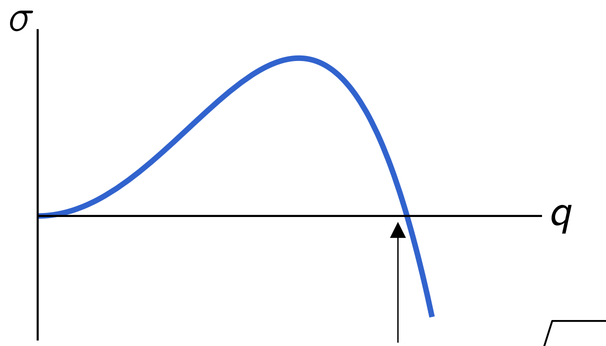
Conserved concentration: binary mixture of A and B molecules $\phi = \dfrac{\overline{n}_A - \overline{n}_B}{\overline{n}_A + \overline{n}_B}$

$$\partial_t \phi(x,t) = \nabla^2 \frac{\delta F}{\delta \phi} \qquad F = \int_{\mathbf{r}} \left[f(\phi) + \kappa (\nabla\phi)^2/2 \right]$$

$$\partial_t \phi(x,t) = \nabla^2 (D\phi + \phi^3 - \kappa \nabla^2 \phi)$$

$\overline{\phi} = \langle \phi \rangle_r$ conserved
tuning parameter

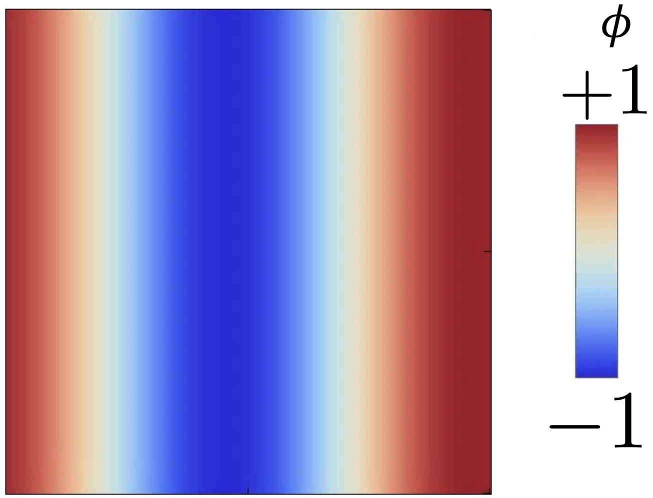
Spinodal instability:



$q_+ = \sqrt{-(D + 3\overline{\phi}^2)/\kappa}$

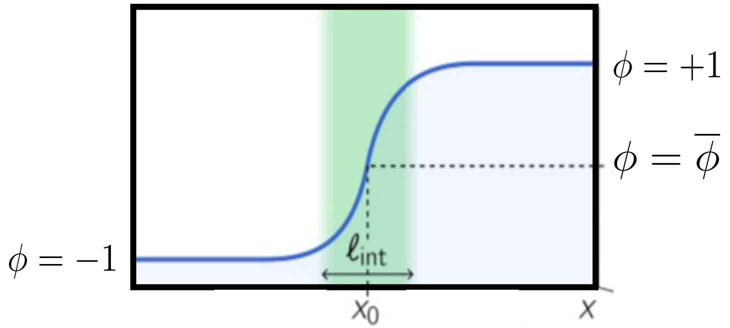
Band of unstable modes $[0, q_+]$

$D < 0$: phase separation



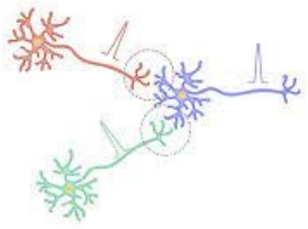
single scale:

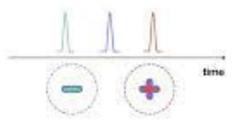
$$\ell_{int} \sim \sqrt{\frac{\kappa}{|D|}}$$



$$\ell_{int} = \frac{\pi}{q_+(\overline{\phi})}$$

Revisiting a classic model of excitable media
→ FitzHugh-Nagumo (FHN) model



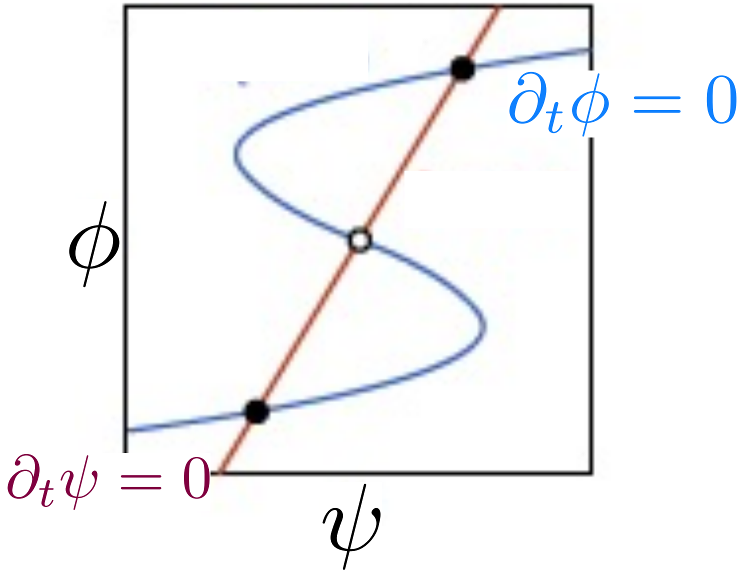


activation and deactivation dynamics of a spiking neuron

$\phi(t)$ fast voltage-like variable
$\psi(t)$ slower feedback

$$\partial_t \phi(t) = \phi - \phi^3 + c\psi$$
$$\partial_t \psi(t) = -b\psi + c\phi$$

$c > 0$

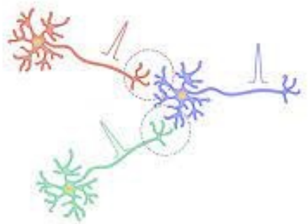


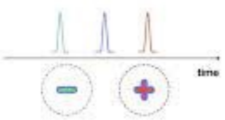
Stationary states are obtained from free energy minimization

$$F(\phi, \psi) = -\frac{1}{2}\phi^2 + \frac{1}{4}\phi^4 + \frac{1}{2}b\psi^2 + c\phi\psi$$

→ Bistability but no oscillatory/travelling states

Revisiting a classic model of excitable media
→ FitzHugh-Nagumo (FHN) model



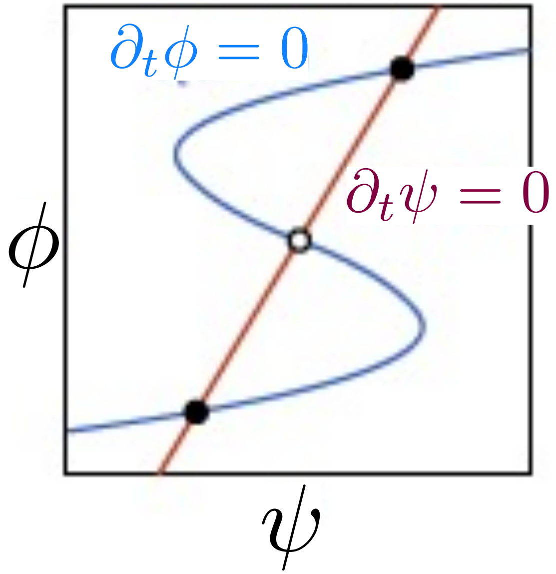


activation and deactivation dynamics of a spiking neuron

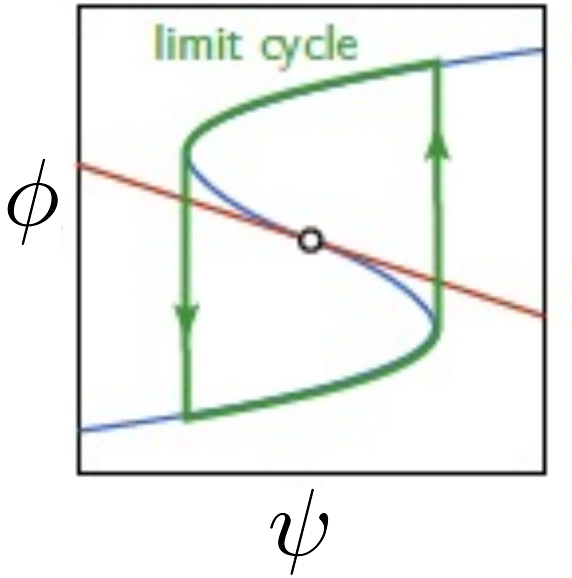
$\phi(t)$ fast voltage-like variable
$\psi(t)$ slower negative feedback

$$\partial_t \phi(t) = \phi - \phi^3 + c_{12}\psi$$
$$\partial_t \psi(t) = -b\psi + c_{21}\phi$$

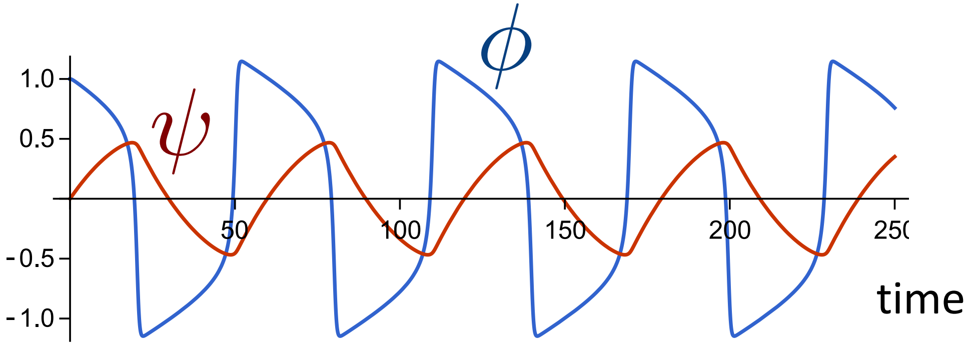
Reciprocal $c_{12}=c_{21}=c>0$



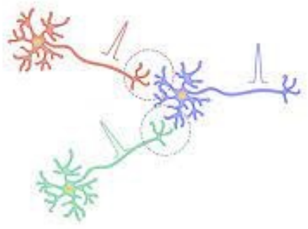
Anti-reciprocal $c_{12}=-c_{21}$

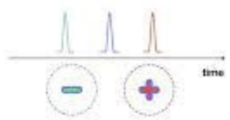


Dynamics cannot be obtained from free energy



Revisiting a classic model of excitable media
→ FitzHugh-Nagumo (FHN) model





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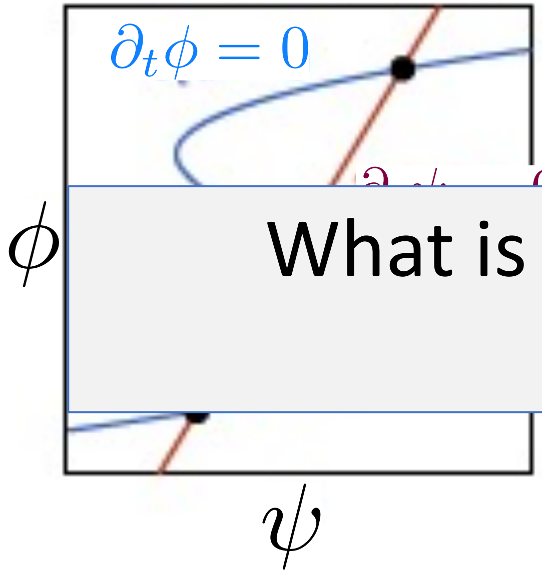

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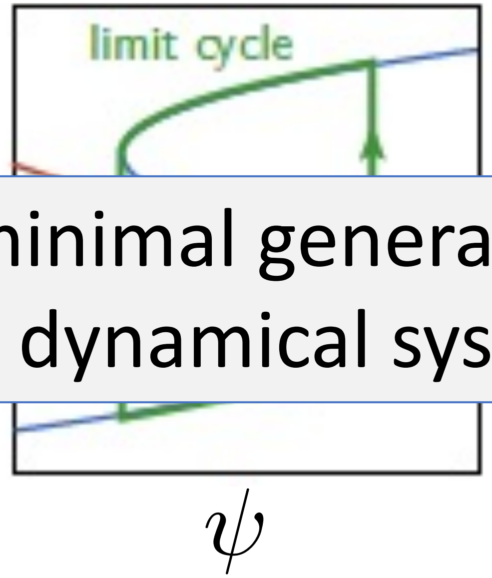
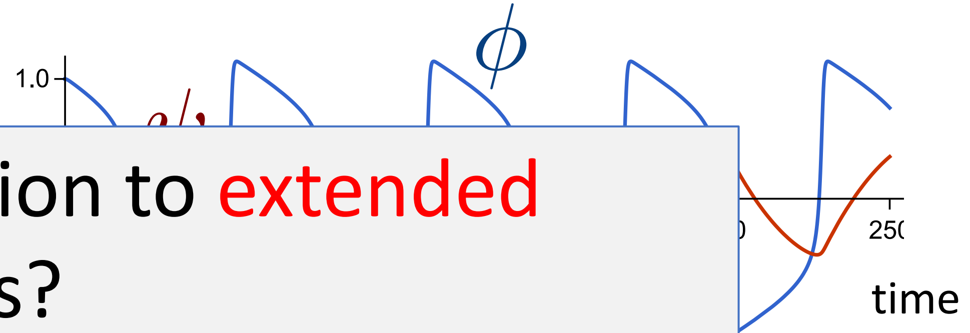


Dynamics cannot be obtained from free energy



What is the minimal generalization to extended dynamical systems?

From FHN to Extended System: coupled Cahn Hilliard & Diffusive Fields

Two conserved fields: $\overline{\phi} = \langle \phi \rangle_{\mathbf{r}}, \quad \overline{\psi} = \langle \psi \rangle_{\mathbf{r}}$

$$\partial_t \phi(x,t) = \nabla^2 \frac{\delta F}{\delta \phi}$$

$$\partial_t \psi(x,t) = \nabla^2 \frac{\delta F}{\delta \psi}$$

$$F = \int_{\mathbf{r}} \left[f_\phi(\phi) + \frac{1}{2}\kappa(\nabla\phi)^2 + f_\psi(\psi) + D\phi\psi \right]$$

$$\partial_t \phi(x,t) = \nabla^2 (D_{11}\phi + \phi^3 - \kappa\nabla^2\phi + D\psi)$$

$$\partial_t \psi(x,t) = \nabla^2 (D_{22}\psi + D\phi)$$

Allow for NR cross couplings:

$$\partial_t \phi(x,t) = \nabla^2 (D_{11}\phi + \phi^3 - \kappa\nabla^2\phi + D_{12}\psi)$$

$$\partial_t \psi(x,t) = \nabla^2 (D_{22}\psi + D_{21}\phi)$$

$$D_{11} < 0$$

Generic minimal model of excitable extended dynamical system

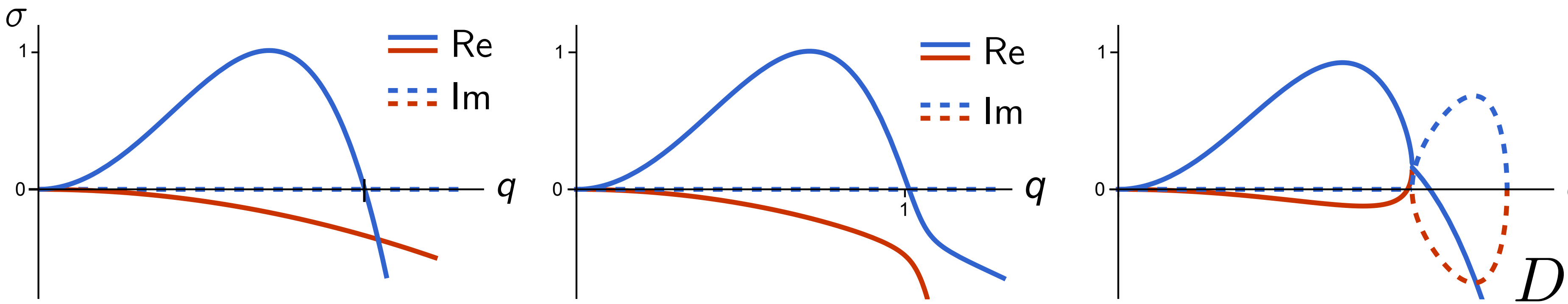
Z You A Baskaran MCM PNAS 2020; S Saha *et al.* PRX 2020; T Frohoff-Hülsmann *et al.* PRE 2021

Linear Stability of Homogeneous States

$$\partial_t \phi(x,t) = \nabla^2 (D_{11}\phi + \phi^3 - \kappa \nabla^2 \phi + D_{12}\psi)$$
$$\partial_t \psi(x,t) = \nabla^2 (D_{22}\psi + D_{21}\phi)$$

$$D_{11} < 0$$

Nonreciprocity controlled by sign of $D_{12}D_{21}$



$D_{12} = D_{21} = 0$

decoupled modes

spinodal instability

diffusion

$D_{12}D_{21} > 0$

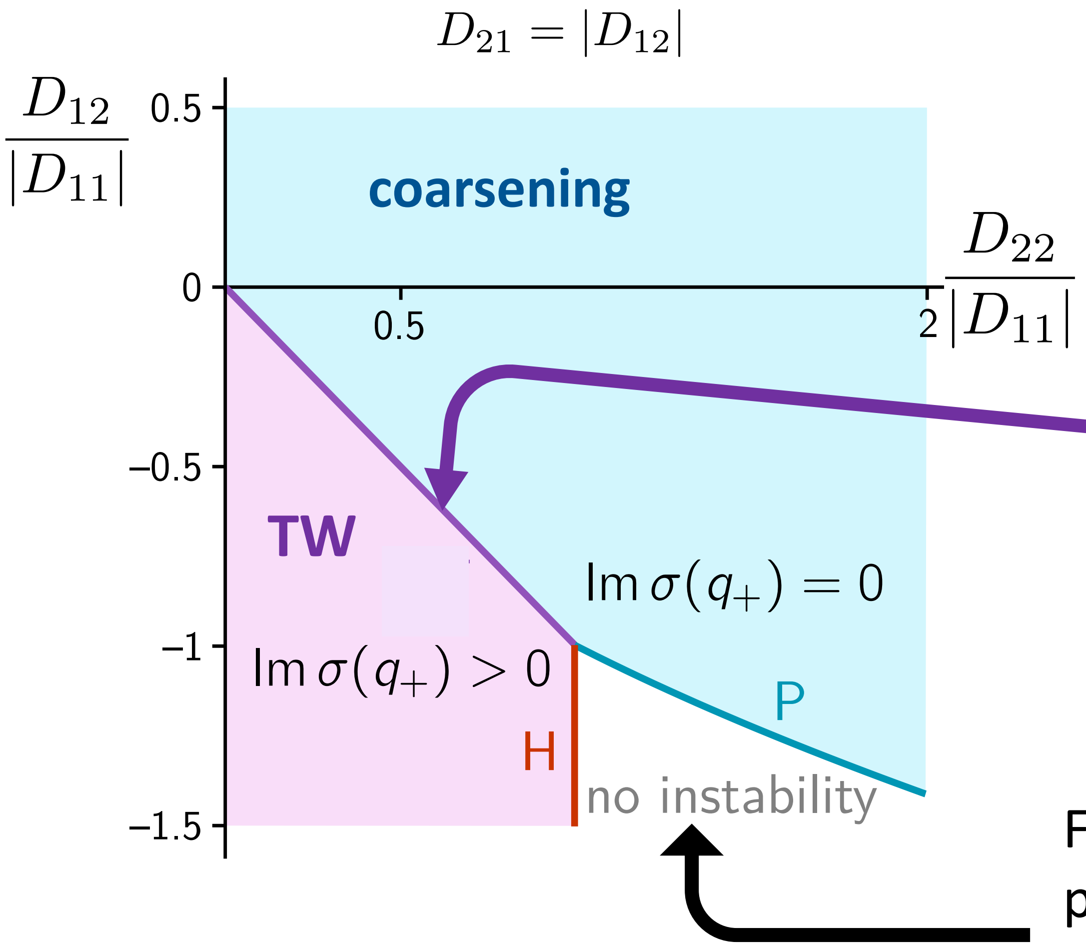
avoided crossing

$D_{12}D_{21} < 0$

Coalescence of hydrodynamic modes associated with mass conservation near q_+

→ band of propagating modes

Linear Stability Phase Diagram



Line of ``exceptional'' points a.k.a. Bogdanov-Takens bifurcation.

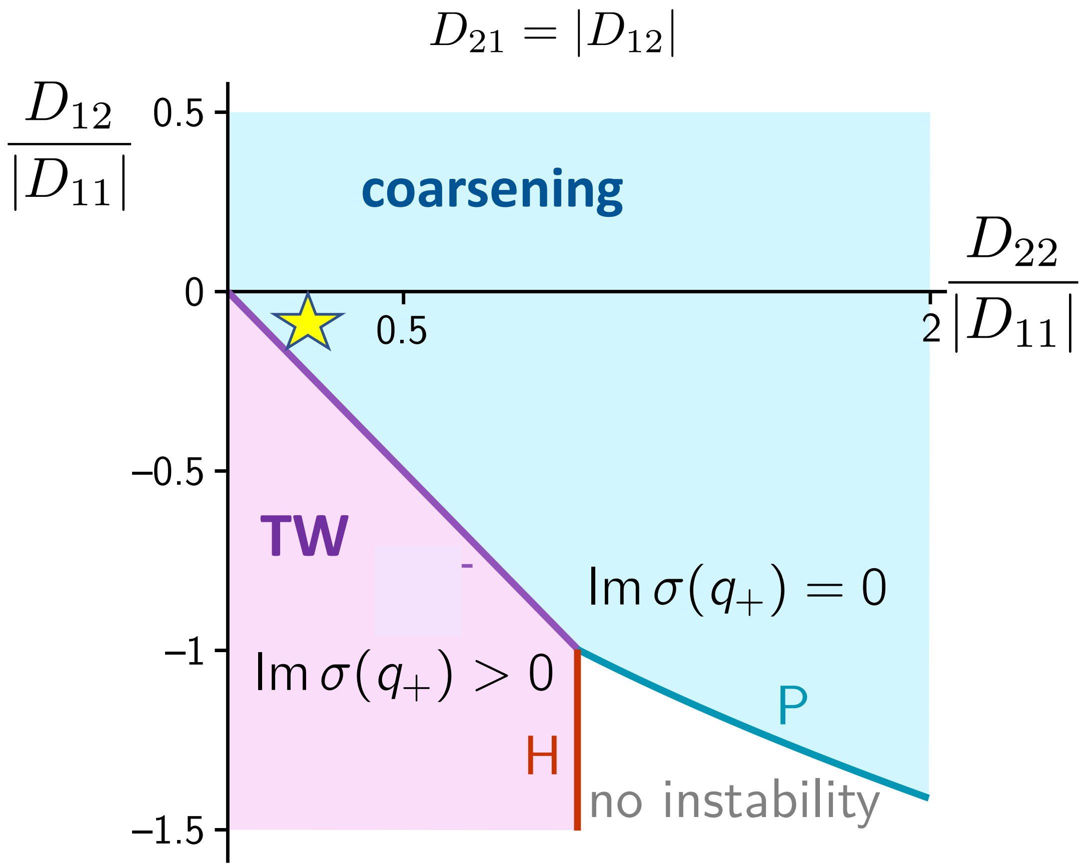
Mode coalescence:

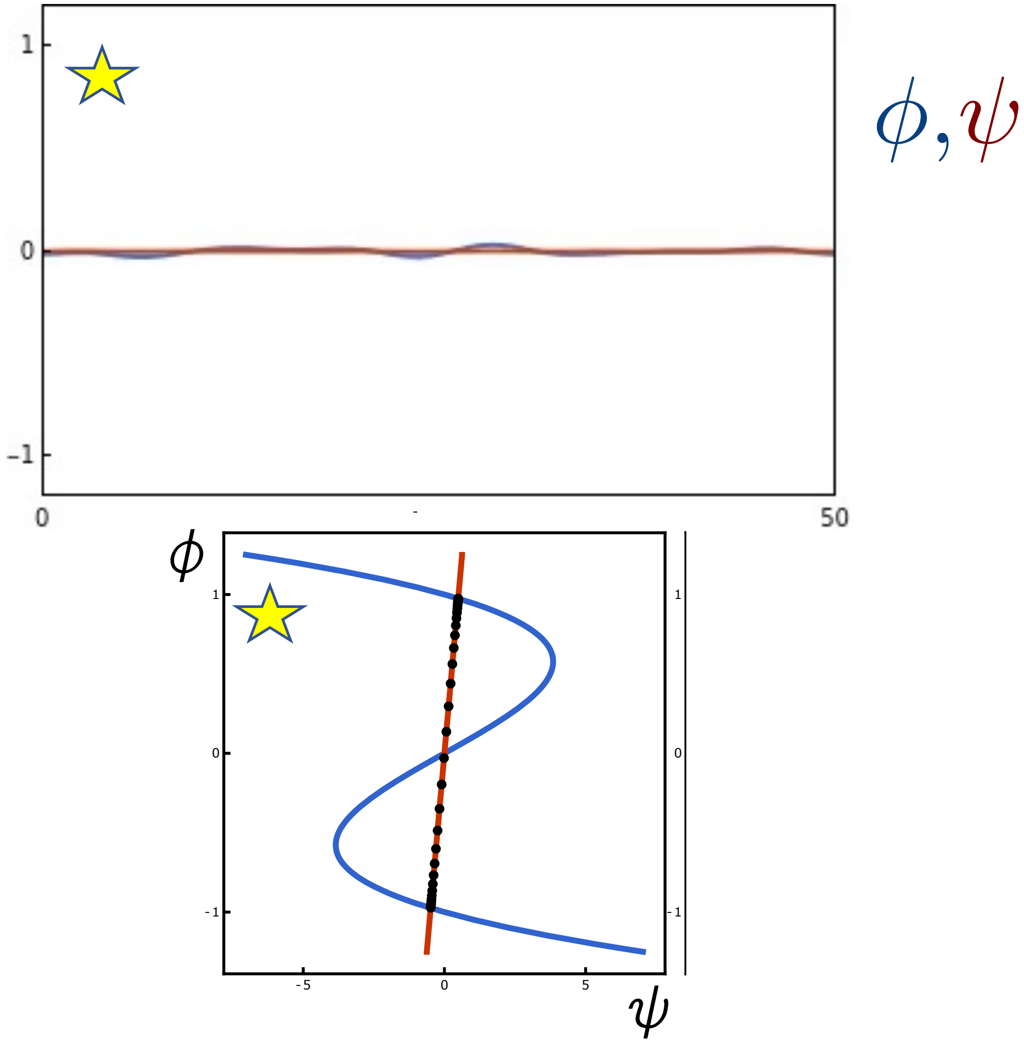
$$Im[\sigma(q_+)] = 0,\ \ Re[\sigma(q_+)] = 0$$

$$\rightarrow D_{12}D_{21} = -D_{22}^2$$

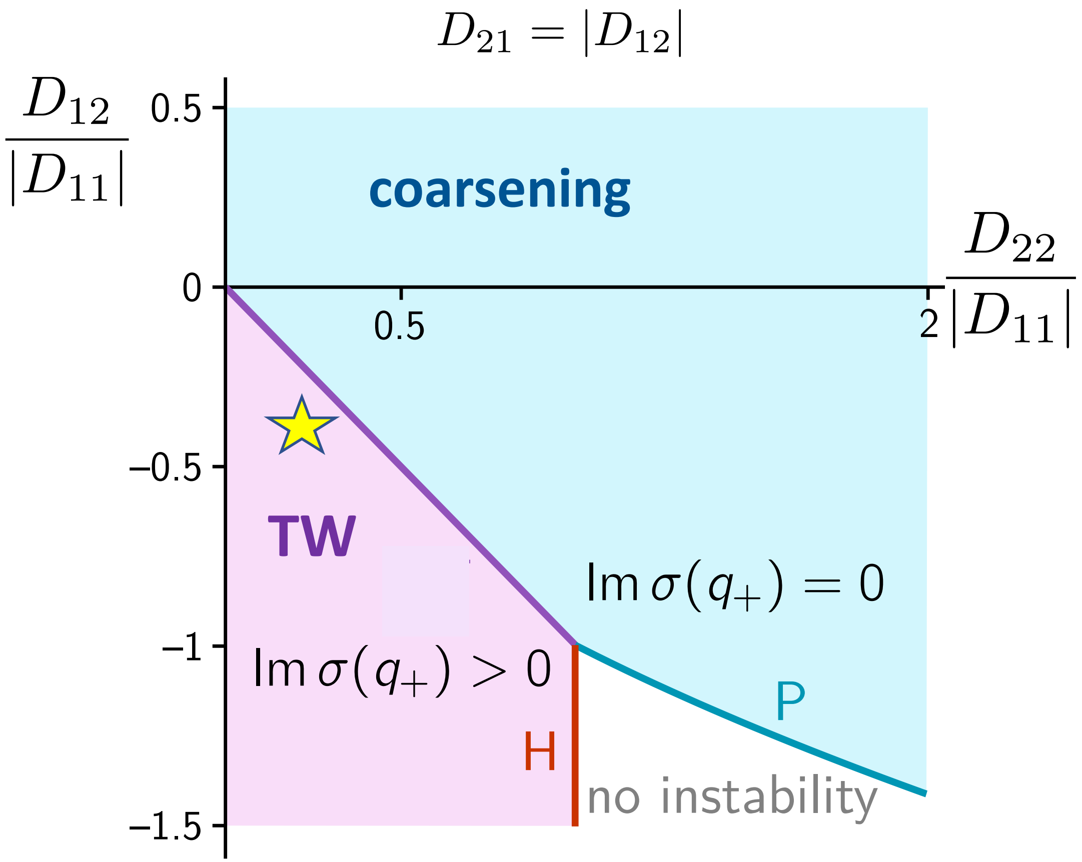
Fast decay of diffusive field ψ ($D_{22} >> |D_{11}|$) pushes down ϕ fluctuations and suppresses pattern forming instability

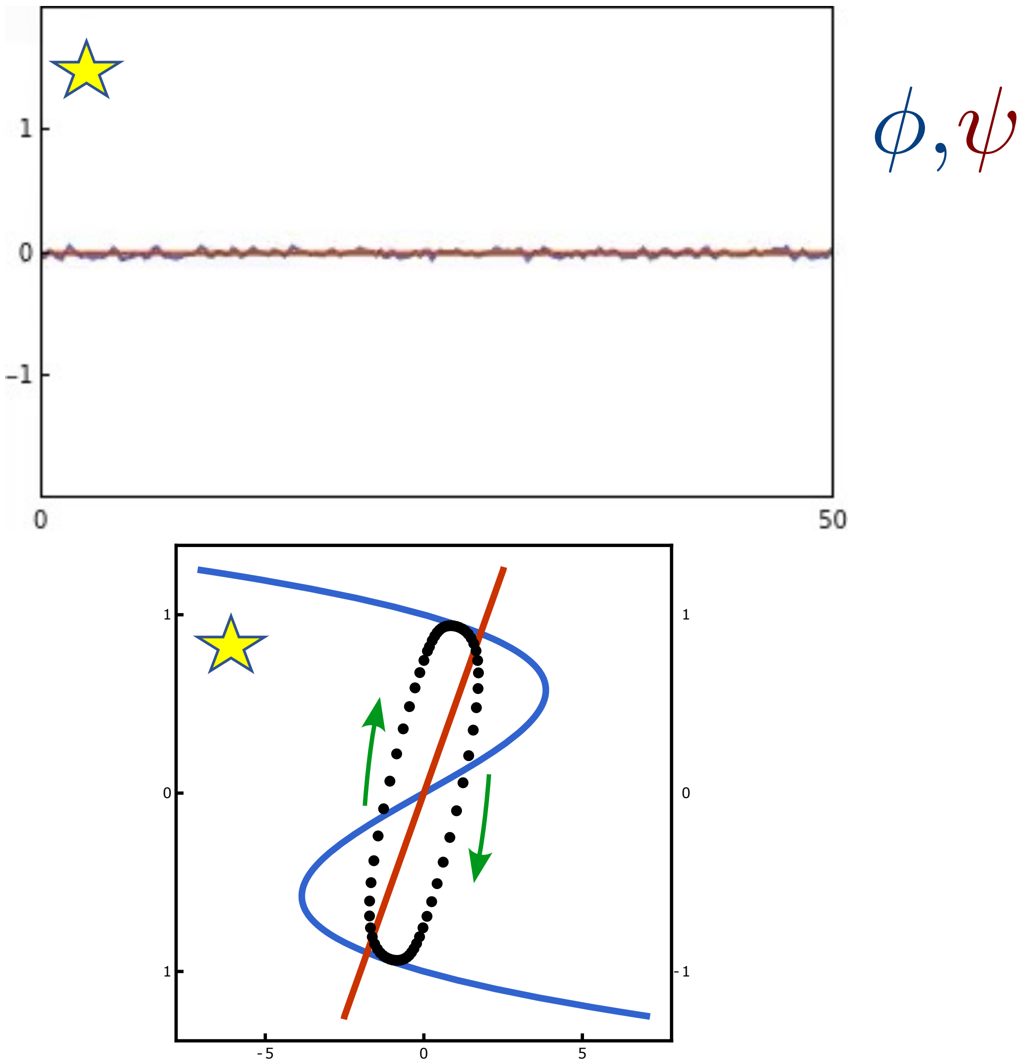
Weak Nonreciprocity → Uninterrupted Coarsening



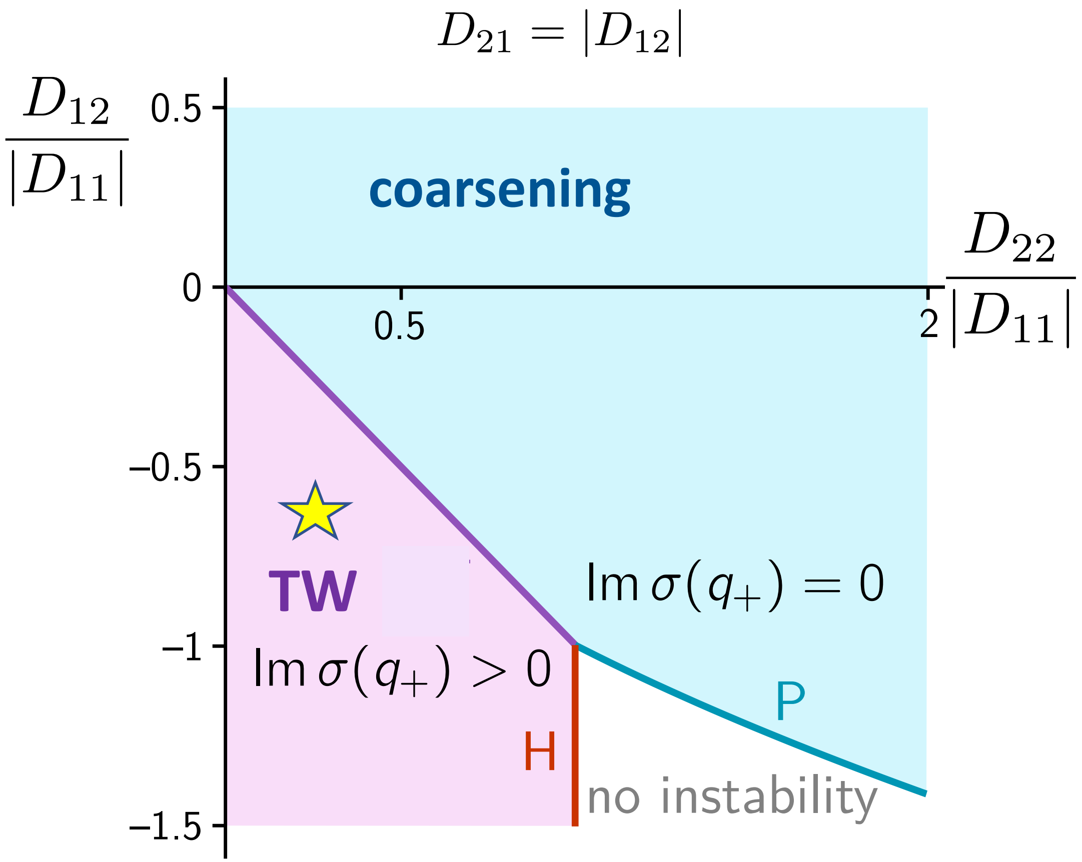


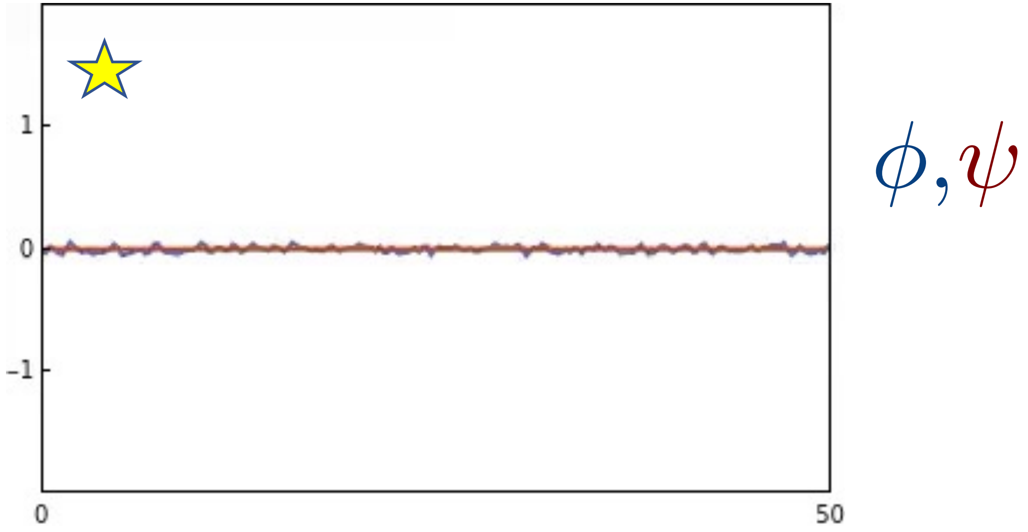
Stronger NR → Traveling Waves & Arrested Coarsening

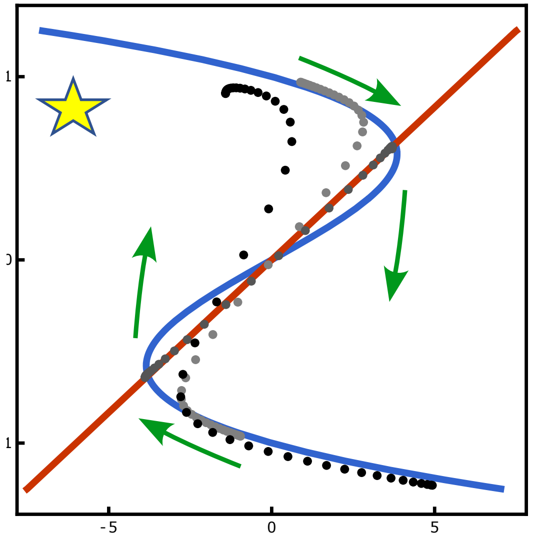




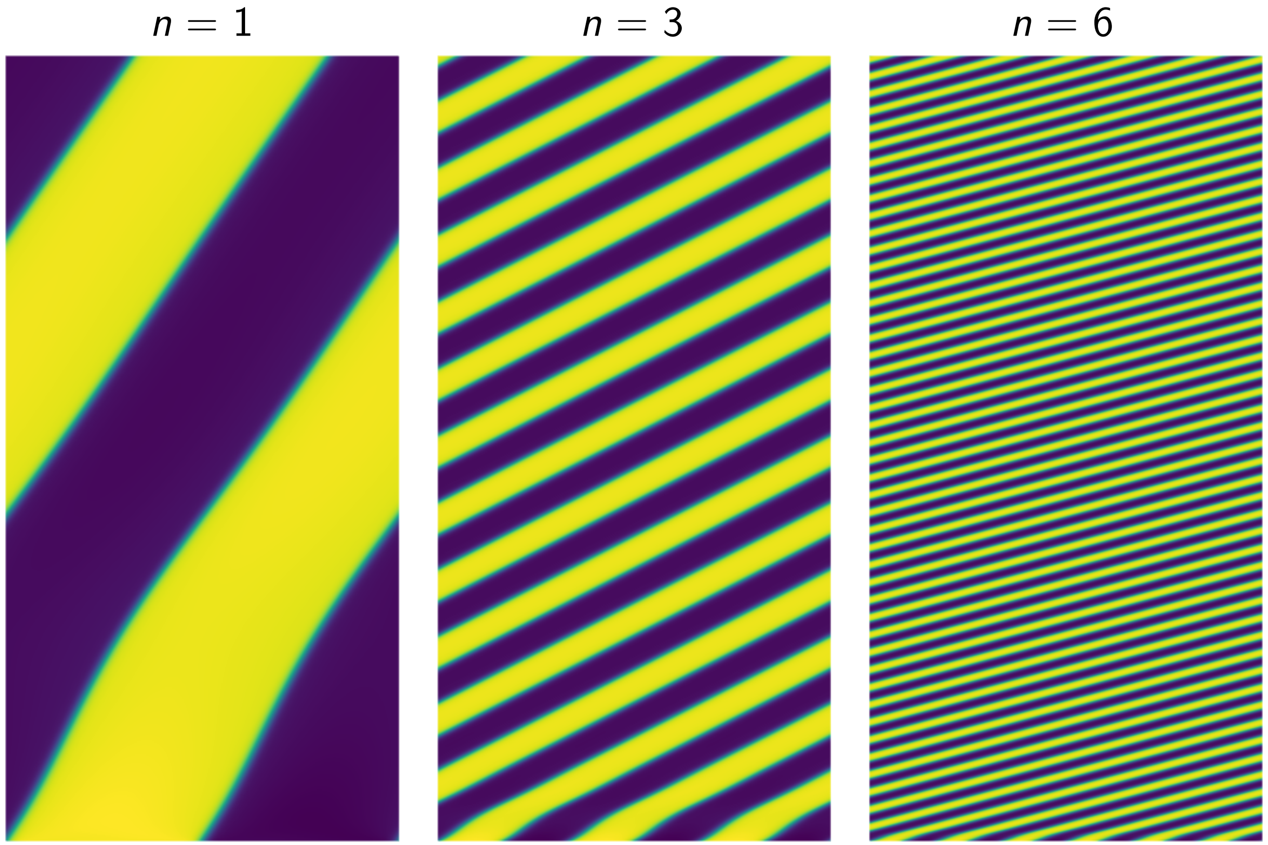
Strong NR + No Flux Boundary Condition → Standing Waves





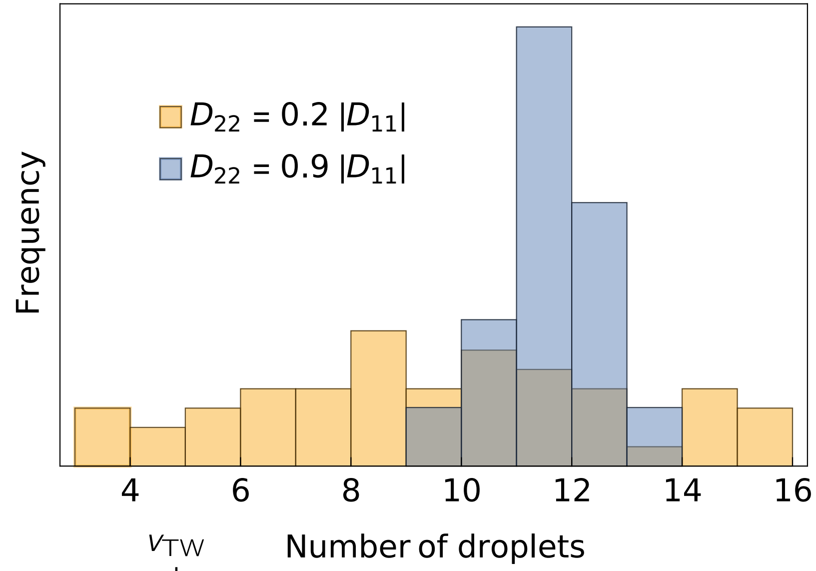


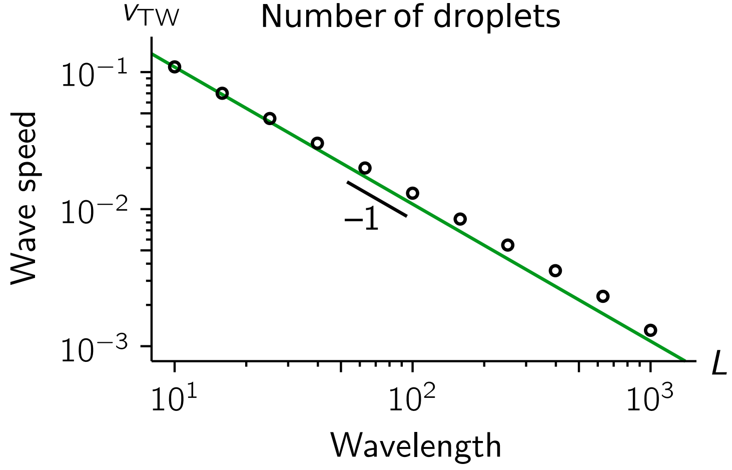
Multistability of Traveling Waves



Traveling states initiated with n ``droplets'' $D_{22}=0.1|D_{11}|$

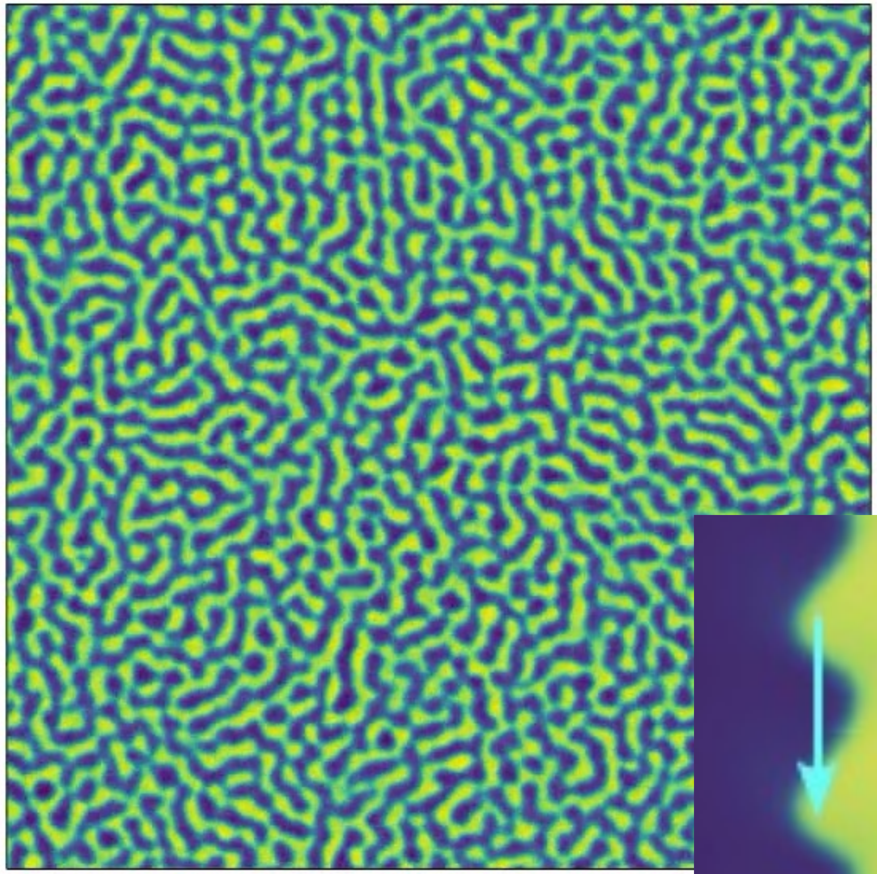
Wavelength selection controlled by $D_{22}/|D_{11}|$

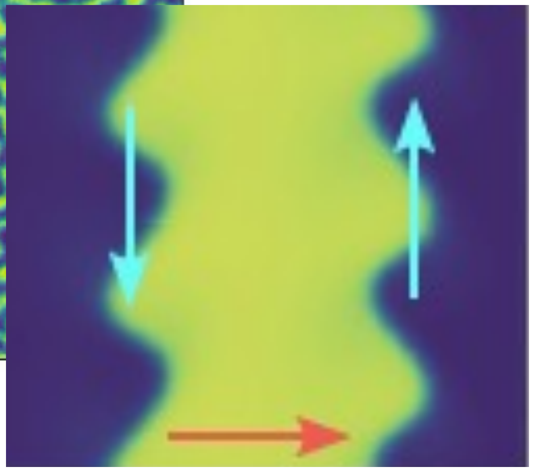




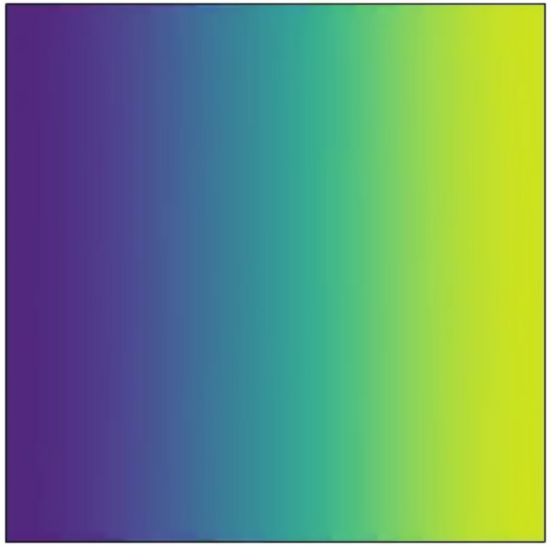
Two dimensions: undulation instability of traveling fronts

Periodic boundary conditions
Initial homogeneous state

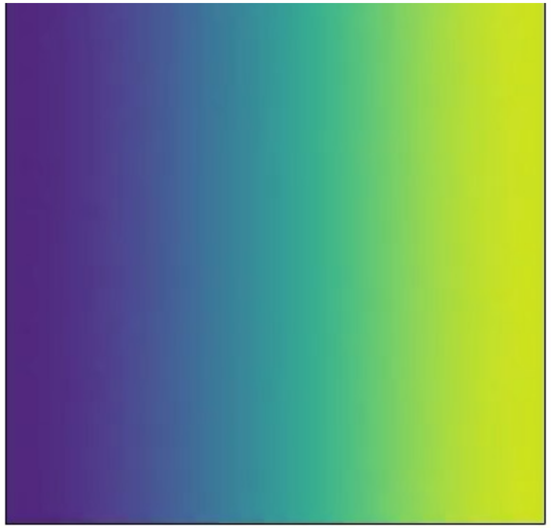




No-flux boundary conditions
Initial flat interface

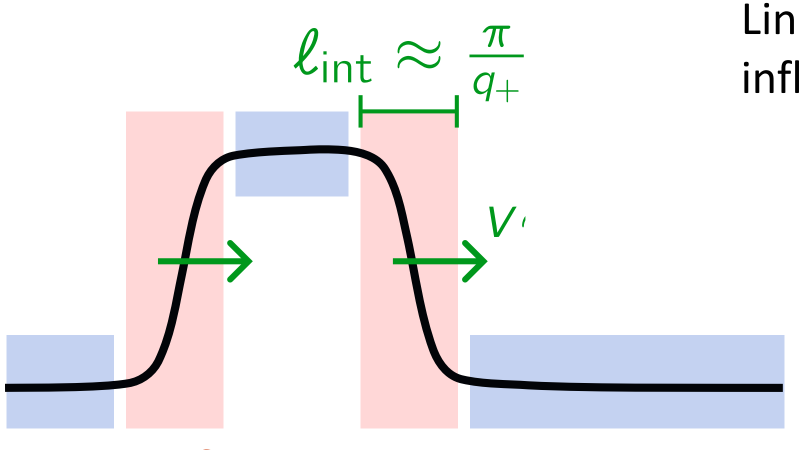


Weak anti-reciprocity
→ rotating wave



Strong anti-reciprocity
→ undulational instability

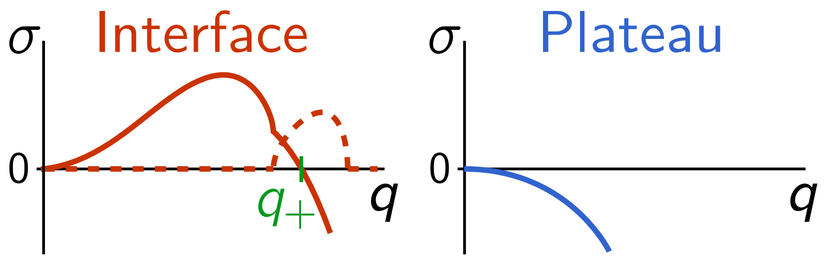
Interface mode predicts pattern propagation speed



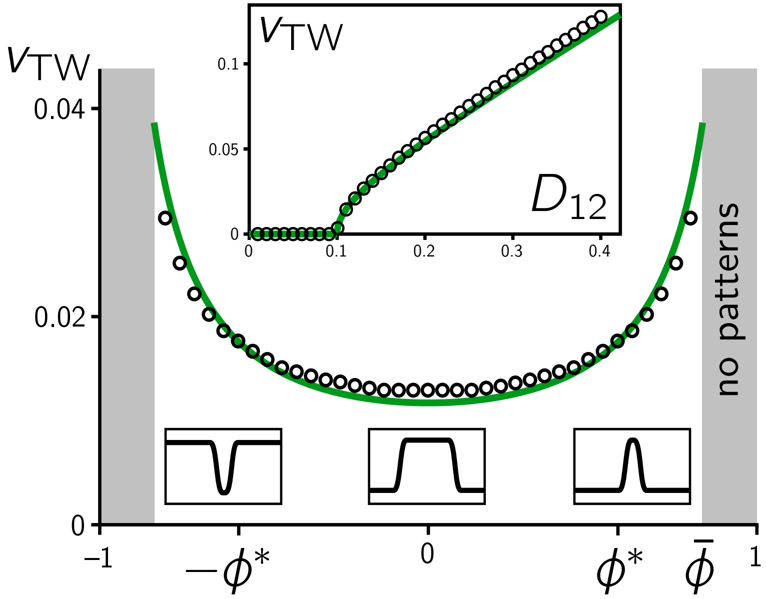
Linearization of the steady state profiles near the inflection point where $\overline{\phi} = \overline{\psi}$ → $\ell_{int} = \dfrac{\pi}{q_+(\overline{\phi})}$

The marginal mode at $q_{int} = q_+(\overline{\phi})$ controls the interface width and speed
→ Transition to traveling waves when $Im[\sigma(q_+^{int})] \neq 0$

``Regional'' dispersion relation [F Brauns et al. PRX 2020]



$$v_{\text{TW}} \propto \frac{Im[\sigma(q_+^{\text{int}})]}{q_+^{\text{int}}}$$

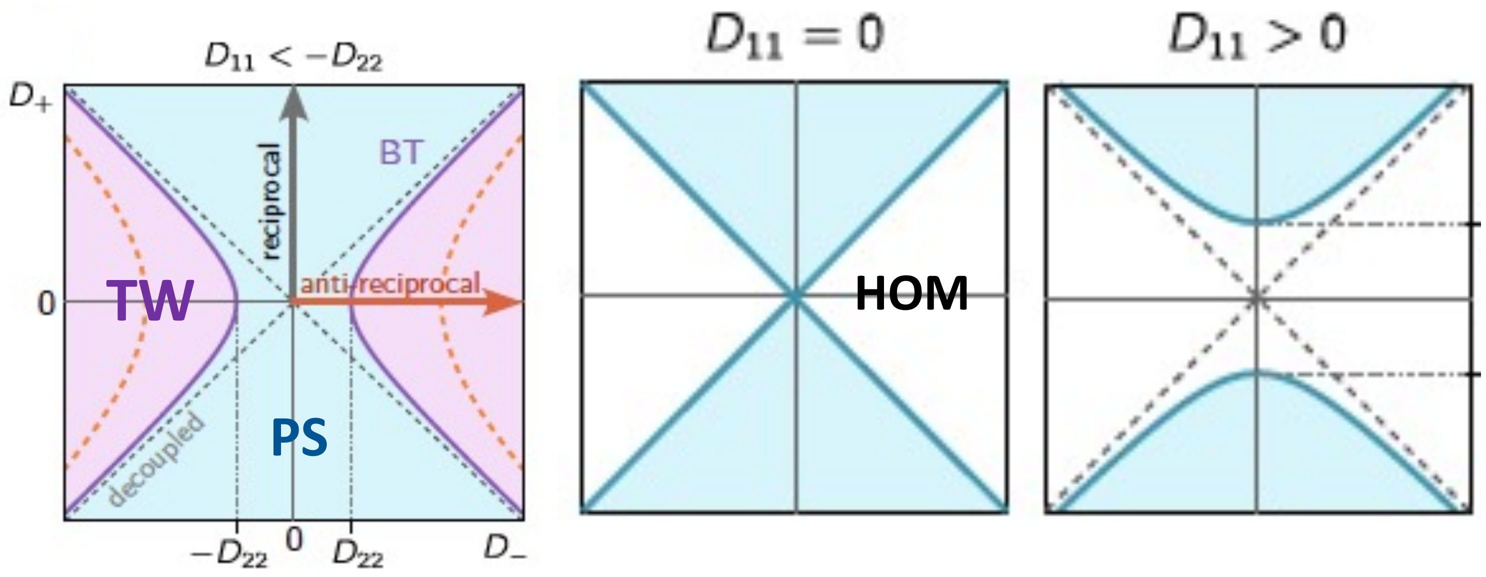


Generalization of single-mode approximation of You *et al.*
where bifurcation occurs at $q_+ \sim \frac{2\pi}{L}$ and $v_{TW} = \text{Im}[\sigma(q_+)]/q_+$

NR mass-conserving fields vs broken symmetry fields

$$D_{\pm} = \frac{D_{12} \pm D_{21}}{2}$$

- NR breaks polar symmetry → TW
- D_{11} tunes static phase separation

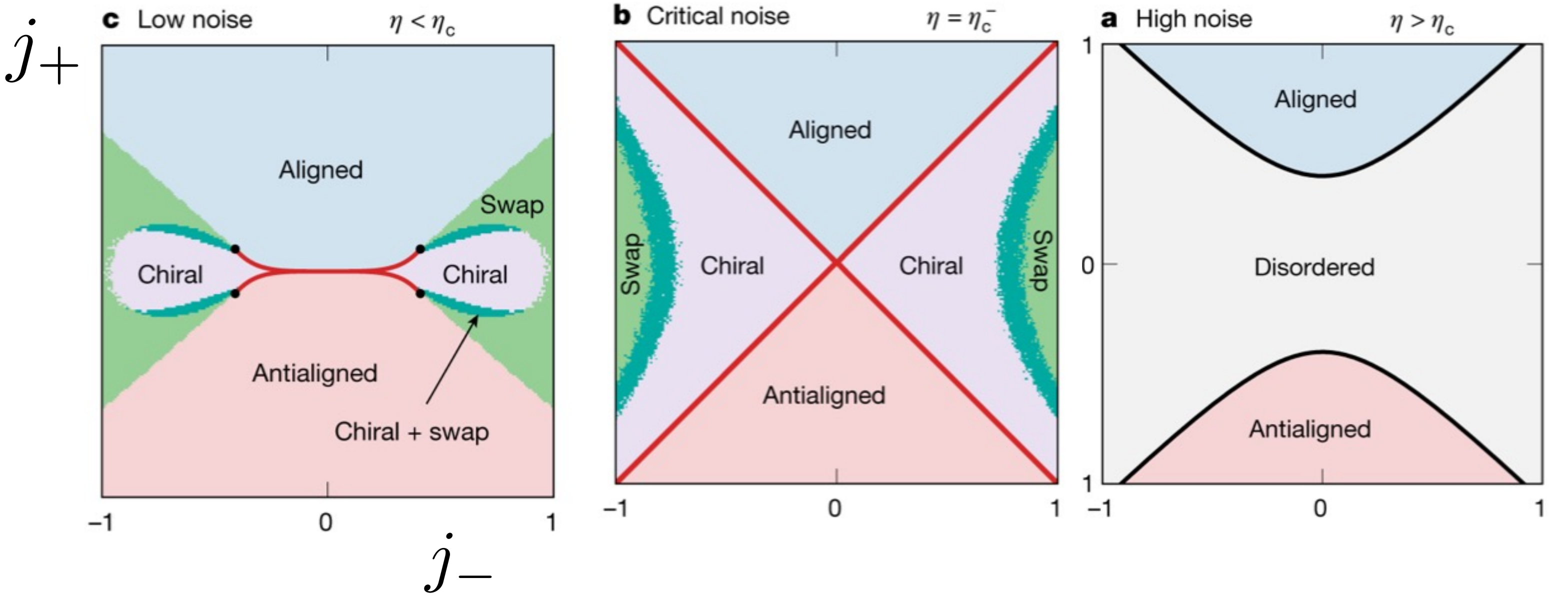


NR-coupled flocking agents:

- NR breaks chiral symmetry
- disorder tunes alignment transition

M Fruchart *et al.* Nature 2021

$$j_{\pm} = \frac{j_{AB} \pm j_{BA}}{2}$$



NR-coupled mass-conserving fields

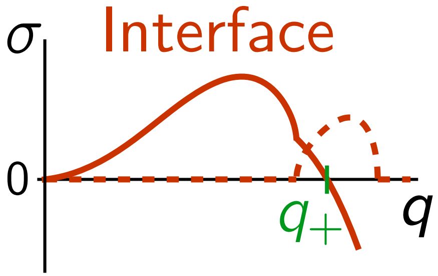
Traveling waves emerge from coalescence of two hydrodynamic modes (mass conservation/translational invariance)

Patterns (phase separation) a prerequisite

Dynamical states tuned by nonreciprocity and $D_{22}/|D_{11}|$

Behavior controlled by mode at the right edge of unstable band → **characteristic form of dispersion relation that identifies this class of systems**

$$v_{\mathrm{TW}} \propto \frac{\pi Im[\sigma(q_+^{\mathrm{int}})]}{q_+^{\mathrm{int}}}$$



NR-coupled broken symmetry fields

Chiral states emerge from coalescence of Goldstone mode (broken global rotational symmetry of OP/oscillator phase) and damped mode

Symmetry-breaking phase transition a prerequisite

Dynamical states tuned by nonreciprocity and noise

nonlinear pattern controlled by "self-organized" interfacial mode

Many other system can be mapped onto the same generic model

- Nonreciprocally coupled fluid mixtures, e.g., phoretic colloids Z You 2020, S. Saha 2020, 2022
- Mass-conserving reaction-diffusion systems, e.g., MinDE system of E. coli B Jacobs 2019, K John2005, F Brauns 2021
- Active-passive mixtures A Wysocki 2016, R Wittkowski 2017, Z You 2020
- Active (visco)elastic gels JS Bois 2011, S Banerjee 2015
- Active poroelastic media M Radszuweit 2013, CA Weber 2018

} actomyosin cortex, epithelia, cells in ECM, muscles

- Chemosensitive motile bacterial mixtures AI Curatolo 2020
- Chemotactic droplets H Zhao 2023, L Demarchi 2023

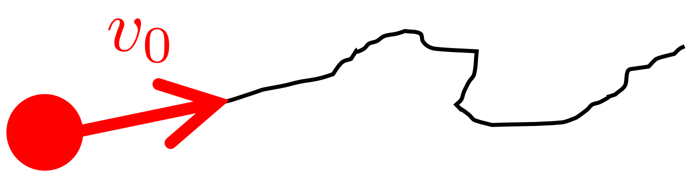
All share same characteristic dispersion relation → can be identified by linear stability

System	ϕ	ψ
Non-reciprocal binary mixtures	Pattern-forming field	Diffusive field
Active/passive particle mixtures	Density of active particles	Density of passive particles
Mass-conserving reaction–diffusion systems	MinD concentration	MinE concentration
Active gels	Density of contractile elements	Strain

→ Two Examples

Example 1: Mixture of Active & Passive Brownian Particles

ABPs: thermal noise + persistent self-propulsion

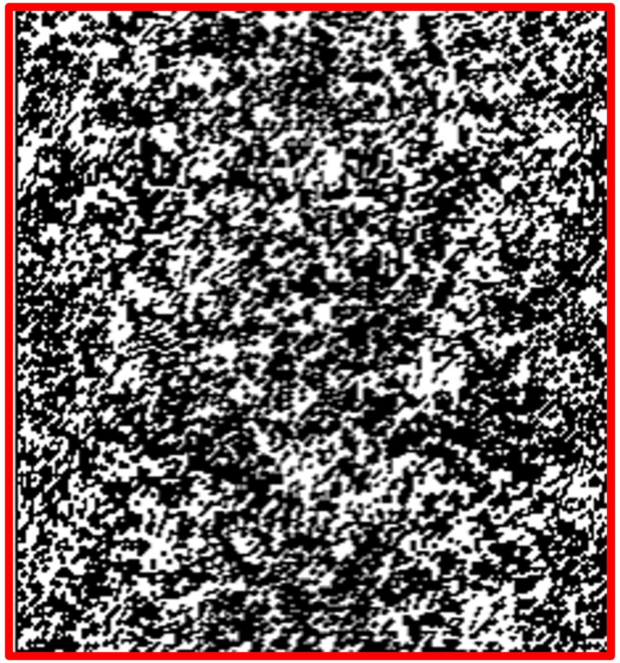


Passive particles: thermal noise

steric repulsion

Pattern-forming field ϕ → density ρ_A of ABPs undergoing Motility Induced Phase Separation (MIPS)

Diffusive field ψ → density ρ_P of passive particles



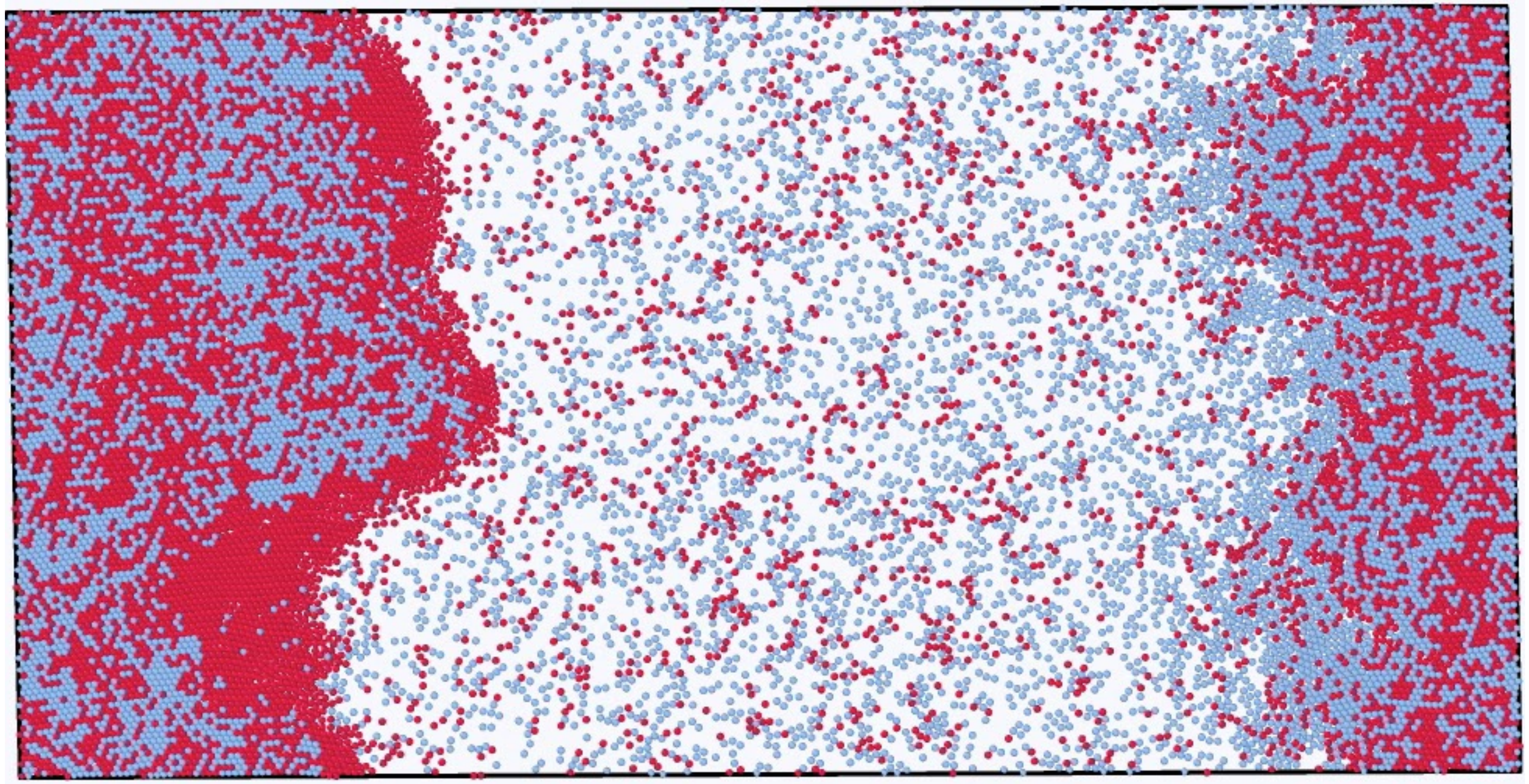
- Both active and passive particles slow down the persistent dynamics of ABPs → $D_{AA} < 0$, $D_{AP} < 0$
- Cross diffusion of passive particles is not affected by activity → $D_{PP} > 0$, $D_{PA} > 0$

Explicit mapping: Z You, A Baskaran, MCM PNAS 2020

Passive

Active

Emergent nonreciprocity



Also:

Wysocki *et al*, NJP (2016)

Wittkowski *et al*., NJP (2017)

Simulations by
Somaiyeh Shokri

Example 2: motile cells in viscoelastic ECM

JS Bois 2011, S Banerjee 2015
M Radszuweit 2013, CA Weber 2018

Conserved contractile elements/cell density *c*

Translationally invariant gel/ECM displacement *u*

$$\partial_t c + \partial_x(\dot{u}c) = D\partial_x^2 c$$

$$\gamma\dot{u} = \partial_x\left[\underbrace{\eta\partial_x\dot{u}}_{\text{viscosity}} + \underbrace{E\partial_x u}_{\text{elasticity}} + \underbrace{\sigma_a(c)}_{\text{active stress}}\right]$$

Instability & pattern formation: $\dot{u} \simeq \frac{1}{\gamma}\sigma_a'\partial_x c \quad \rightarrow \quad \partial_t c = \partial_x\left[D - c\sigma_a'/\gamma\right]\partial_x c \qquad \sigma_a' = \frac{\partial\sigma_a}{\partial c}$

$D_{eff}(c) < 0$

stabilized by viscosity at short scales

requires contractile activity $\sigma_a'(c_0) > 0$

Incorporating viscosity and elasticity:

$$\gamma\partial_t c = \partial_x\left[\gamma D_{eff}\partial_x c - cE\partial_x\varepsilon\right] - \kappa_{\text{eff}}\partial_x^4 c$$

$$\gamma\partial_t\varepsilon = \left[E\partial_x^2\varepsilon + \partial_x(\sigma_a'\,\partial_x c)\right]$$

$$\varepsilon = \partial_x u \qquad \kappa_{eff} \sim \eta$$

Negative feedback between gel elasticity and density c of active elements provides NR cross-diffusion

ARTICLES
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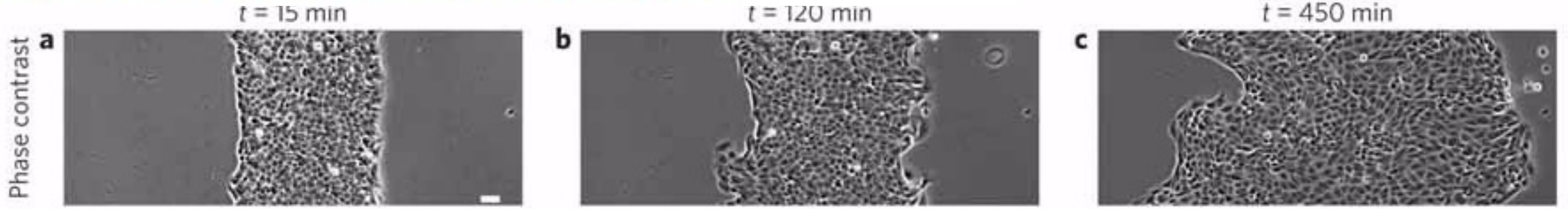
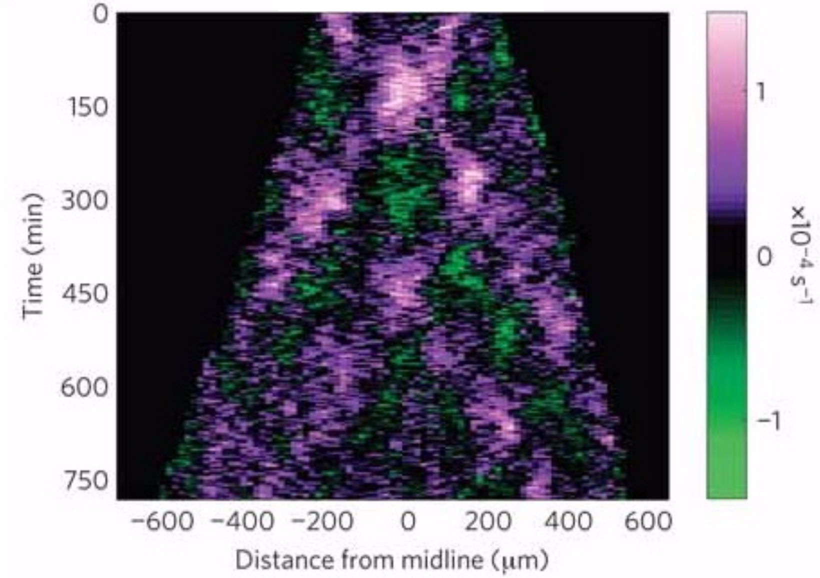
nature physics

Mechanical waves during tissue expansion

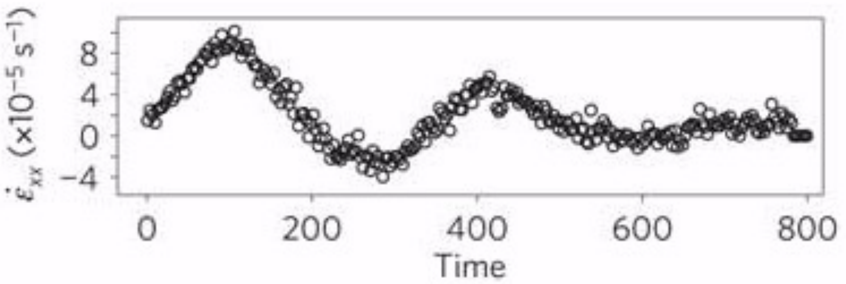
Xavier Serra-Picamal[1,2†], Vito Conte[1†], Romaric Vincent[1], Ester Anon[1,3], Dhananjay T. Tambe[4], Elsa Bazellieres[1], James P. Butler[4,5], Jeffrey J. Fredberg[4] and Xavier Trepat[1,2,6*]



strain rate



strain rate vs time



Conclusions and Outlook

- Cahn Hillard equation with NR coupling to diffusive field provides a generic minimal model for traveling and oscillating states in extended systems
  T Frohoff-Hülsman, U Thiele arXiv:2301.05568
- In 1D a variety of physical systems can be mapped onto this ``normal form''
- Interfacial mode as useful framework for investigating more complex patterns:
  - density dependent transport coefficients
    S Saha, R Golestanian arXiv:2208.14985
  - nonlinear wavelength selection due to broken mass conservation
  - spontaneous phase separation of ψ field

Fridtjof Brauns

Postdoctoral positions available

Soft & Living Matter @UCSB
http://biogroup.physics.ucsb.edu