Frontiers in Nonequilibrium Physics 2026
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Spontaneous oscillations and geometric cutoff in confined bacterial swarms

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arXiv:2603.26025

Dissipative structures and biological rhythms

Albert Goldbeter, *Chaos* 27, 104612 (2017)

Oscillations and waves of cyclic AMP in *Dictyostelium* amoebae	5-10 min
Segmentation clock in somitogenesis	
Zebrafish	30 min
Chicken	90 min
Mouse	2 h
NF-KB transcription factor oscillations	100 min
P53 tumor suppressor oscillations	3–4 h
Pulsatile hormone secretion	
Insulin	10 min
GnRH, LH, FSH	1 h
Growth hormone	3–5 h
Yeast respiratory oscillations	5 h
Synthetic oscillators	
Repressilator (first example)	3–4 h
Others	Tunable period (h)

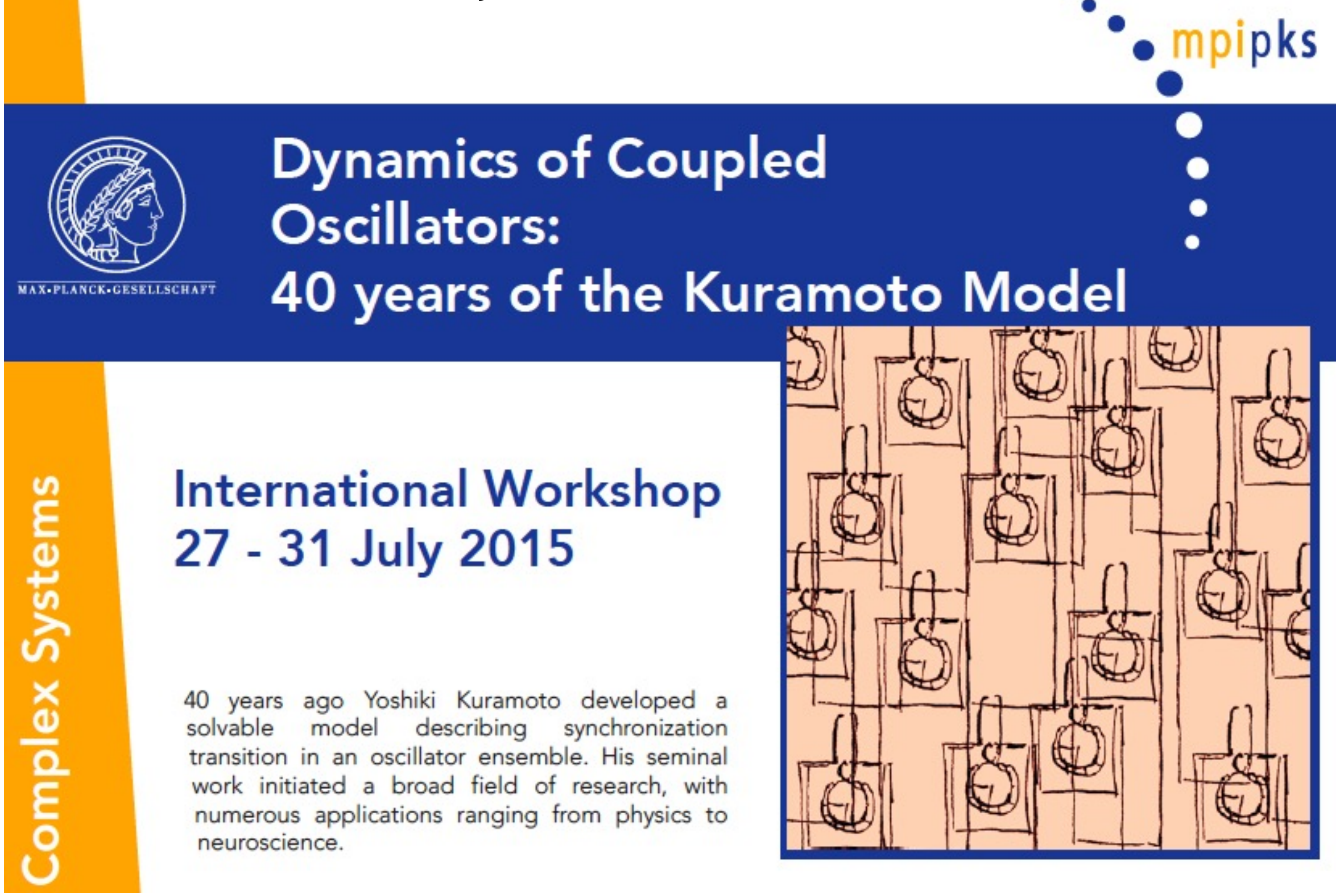
electrical, chemical, mechanical,...

Biological rhythm	Period
Cellular rhythms	
Neural rhythms	0.01 s–10 s
Individual neurons	
Bursting neurons (e.g., R15 in *Aplysia*)	
Neural networks	
Central pattern generators	
Muscle cells	0.01 s to s
Cardiac cells	1 s
Oscillatory peroxidase reaction	30 s
Min protein oscillations in *E. coli* bacteria	100 s
Glycolytic oscillations	
Individual yeast cells	10–30 s
Yeast cell extracts	5–8 min
Cardiac cells	1.5 min
Skeletal muscle extracts	20 min
Pancreatic β-cells	5–10 min
Ca^{++} oscillations and waves	s to min
Periodic reversal of direction in swarming *Myxococcus* bacteria (the *Frizzilator*)	2–50 min

organisms need a clock, or do they?

$$\frac{d\varphi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=1}^{N}\sin\left(\varphi_j - \varphi_i\right)$$

[Emergence](): each cell acquires a phase…



The Ising model of oscillatory dynamics

Yoshiki Kuramoto

Half a century of the theory of synchronization

JSTAT 2026 (4), 044001

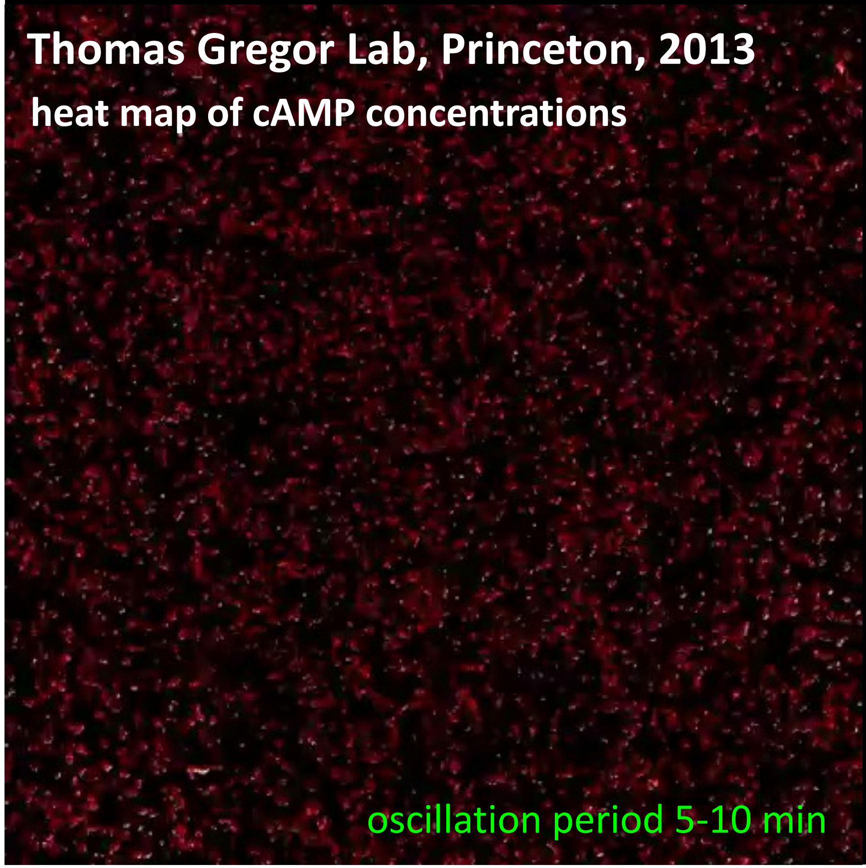
Outline: How Oscillations *Emerge*

- Biological rhythms without a **built-in clock** — the question of **collective origin**
- **A generic circuit**: active cells + passive communication channel (the response-function framework)
- The **chemical blueprint** — starved *Dictyostelium* and adaptation as phase-lead
- The mechanical blueprint — confined bacterial swimmers, shear-induced phase-lead, and the geometric cutoff
- **Quantitative comparison** with experiment and **predictions**

Active and communicating cells

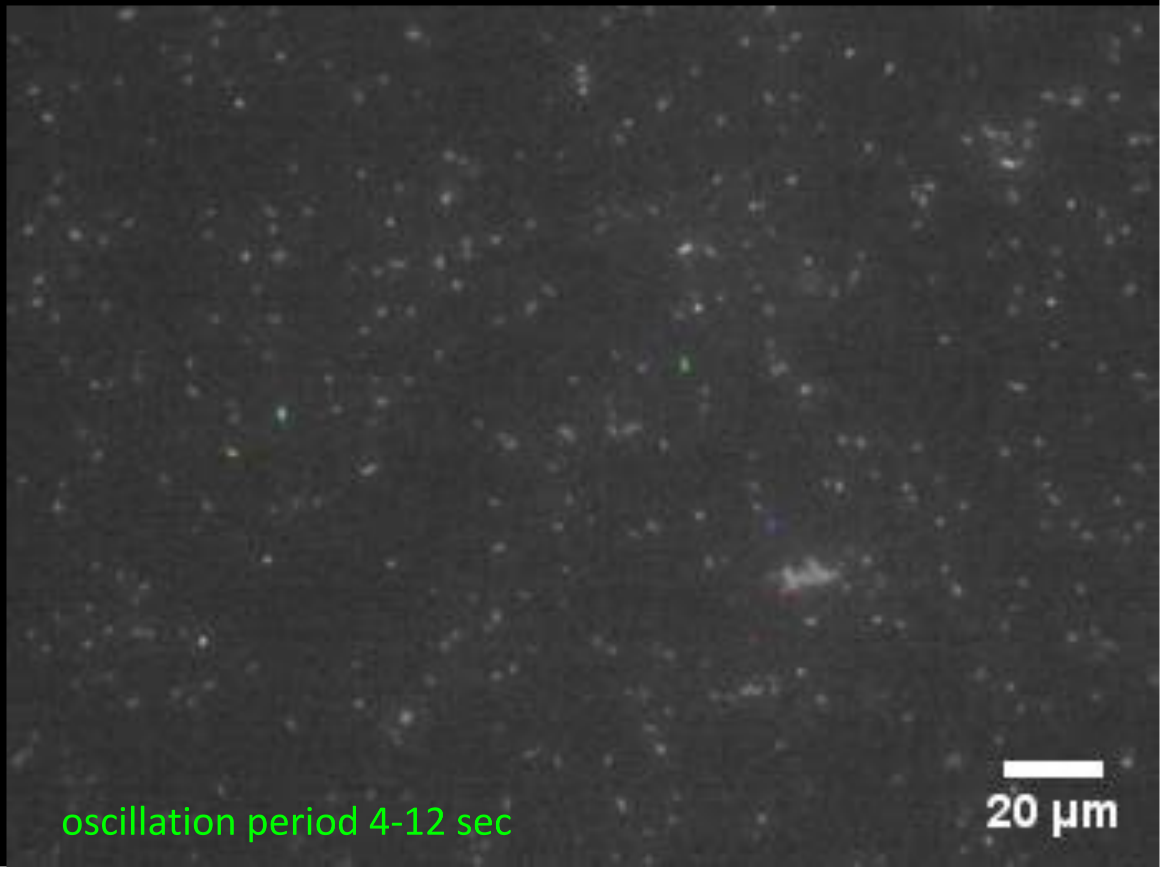
Case 1: social amoeba

Chemical Signal



Case 2: *B. subtilis*

Mechanical Signal



A Mean-Field Response Function Approach to Spontaneous Oscillations

focusing on
individual cells adapting to their environment

SW Wang and L-H Tang,
Nature Communications **10**, 5613 (2019)

A generic circuit for collective oscillations

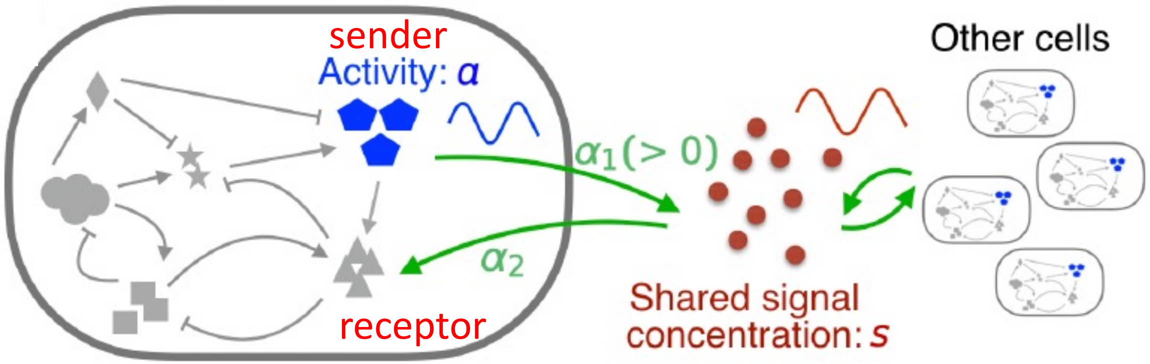
Sender node (active individual): $\langle a_j(t)\rangle = \langle a_j(t)\rangle_u + \int_{-\infty}^{t} R_{a_j}(t-\tau)\, s(\tau)\, d\tau$

Medium (passive): $\gamma \dot{s} = -Ks + \sum_{j=1}^{N} \alpha_1 a_j$

degradation

sender node activity

System A: active cells **System B: communication channel**



Dynamic equations in frequency domain:

$$\tilde{a}_j(\omega) = \tilde{R}_{a_j}(\omega)\tilde{s}(\omega)$$

$$\tilde{s}(\omega) = \frac{\alpha_1}{K - i\gamma\omega}\sum_{j=1}^{N}\tilde{a}_j(\omega)$$

Onset condition for *N* identical oscillators

$$\boxed{N\tilde{R}_a(\omega)\tilde{R}_s(\omega) = 1}$$

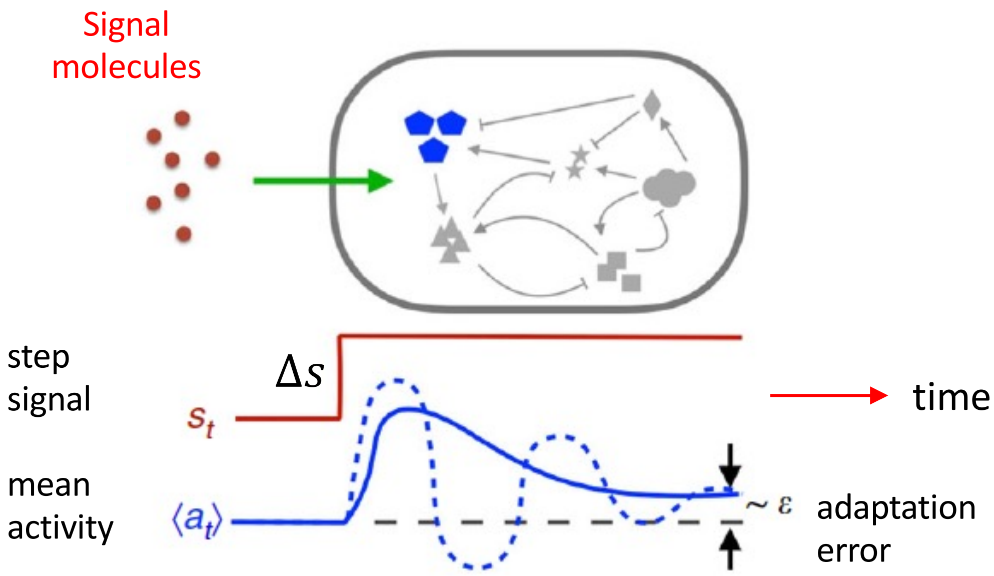
$\tilde{R}_{s,a}(\omega) = |\tilde{R}_{s,a}(\omega)| e^{-i\phi_{s,a}(\omega)}$

passive: phase lag
active: phase lead

i) $\phi_a(\omega) = -\phi_s(\omega)$ phase matching at ω

ii) $N = \frac{1}{|\tilde{R}_a(\omega)\tilde{R}_s(\omega)|}$ threshold cell density

Adaption is phase-leading



Linear response (noise-averaged):

$$\langle a_t \rangle = a_0 + \int_{-\infty}^{t} R(t-\tau) s_\tau d\tau$$

$$R(t) = \frac{1}{\Delta s} \frac{d\langle a_t \rangle}{dt} \quad \text{under a step stimulus}$$

Spectral property of the response function

Kramers-Krönig relation (causality):

$$\tilde{R}(\omega) = \tilde{R}'(\omega) + i\tilde{R}''(\omega)$$

$$\boxed{\tilde{R}'(\omega) = \frac{2}{\pi} \int_0^\infty \tilde{R}''(\omega_1) \frac{\omega_1}{\omega_1^2 - \omega^2} d\omega_1}$$

Adaptation:

$$\lim_{t\to\infty} \frac{\langle a_t \rangle - a_0}{\Delta s} = \int_0^\infty R(\tau) d\tau = \tilde{R}(0) = \epsilon$$

$$\lim_{\omega\to 0} \tilde{R}'(\omega) = \frac{2}{\pi} \int_0^\infty \tilde{R}''(\omega_1) \frac{d\omega_1}{\omega_1} = \varepsilon \to 0$$

sign change along
the frequency axis

Adaptive node can be employed as an active, phase-leading agent at a range of frequencies.

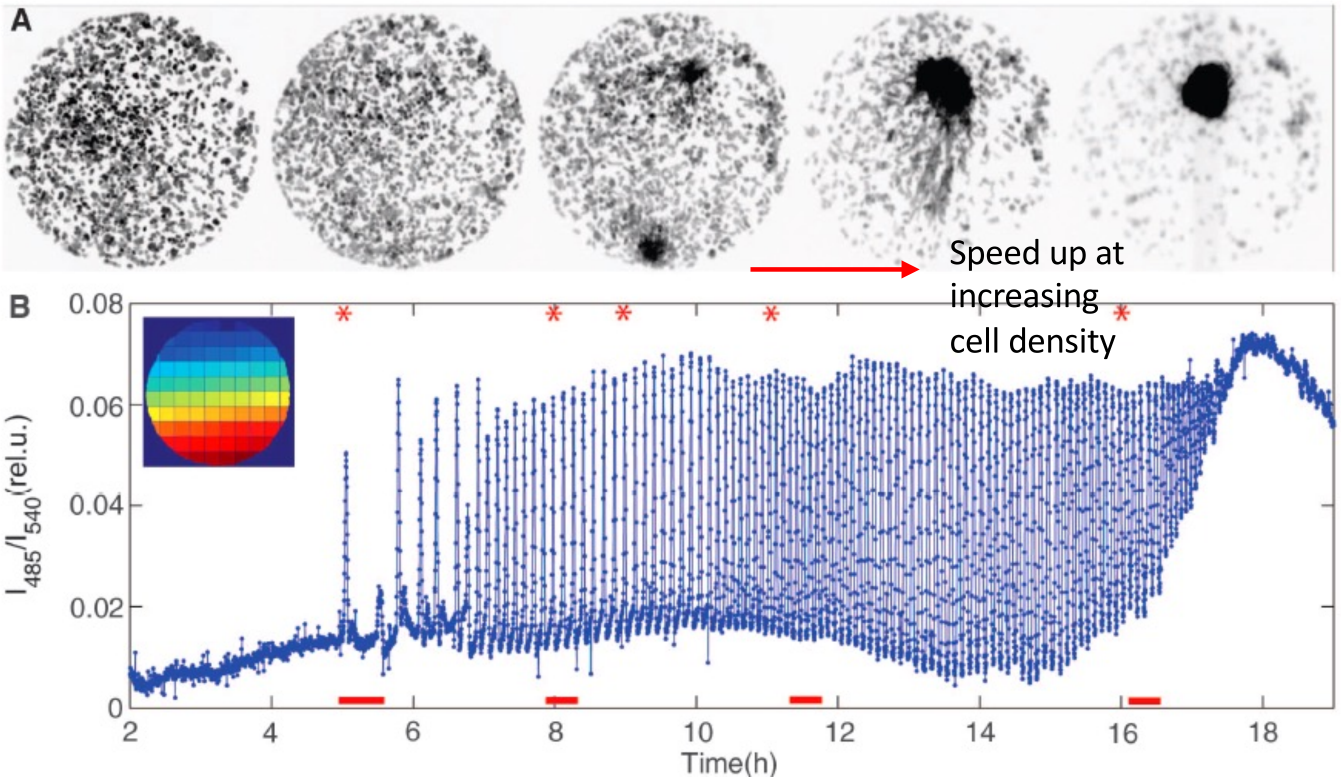
The Onset of Collective Behavior in Social Amoebae

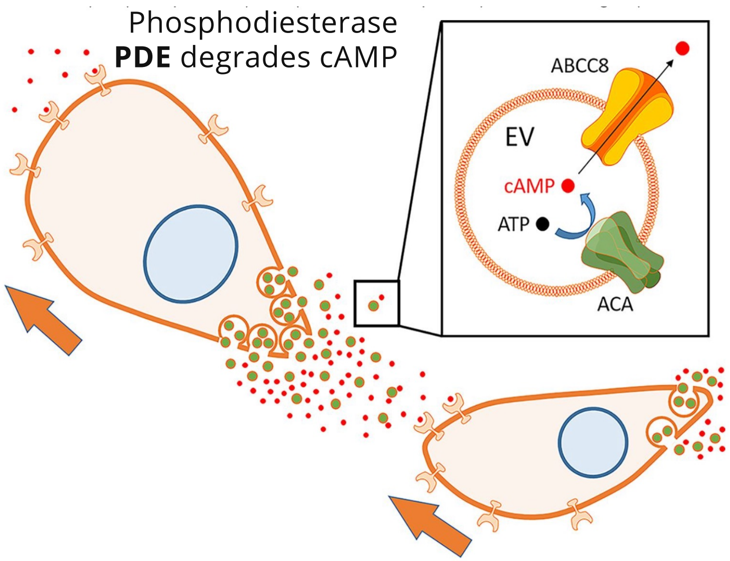
Science **328**:1021 (2010)

Thomas Gregor,[1*] Koichi Fujimoto,[2†] Noritaka Masaki,[2] Satoshi Sawai[1,2‡]

Period 15-30 min **Period 6-8 min**

https://exrna.org/blog-dicty-ev-chemotaxis/

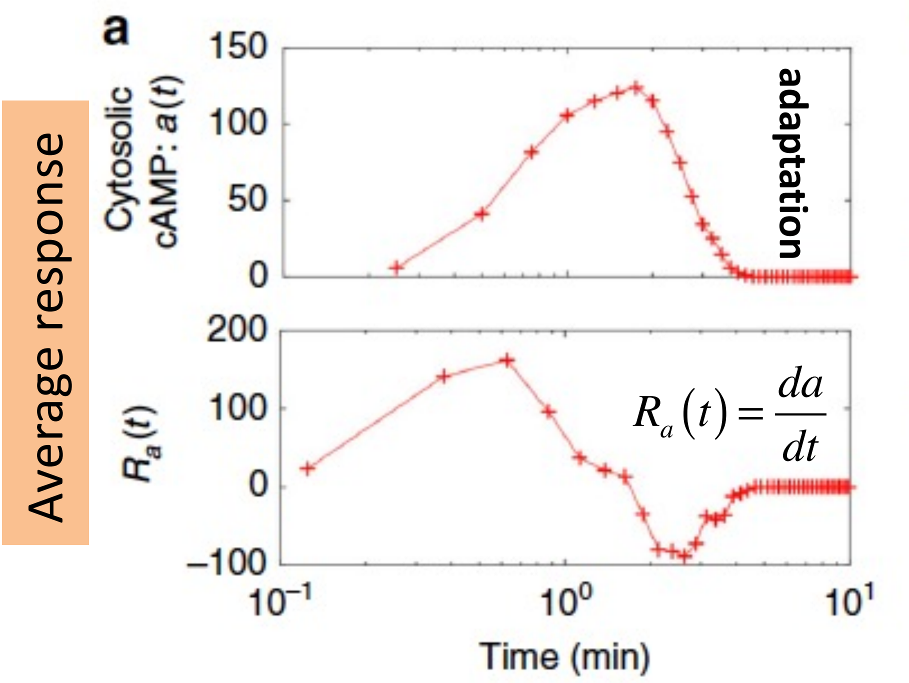




cAMP degradation in surrounding medium proportional to cell density

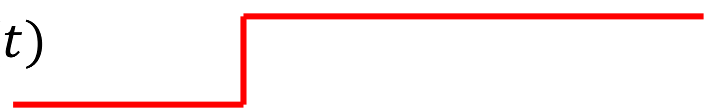
Adaptation in cAMP response

Single-cell measurement of cytosolic cAMP
upon a step increase (1nM) of extracellular cAMP



$$\langle a_j(t) \rangle = \langle a_j(t) \rangle_u + \int_{-\infty}^{t} R_{a_j}(t-\tau) s(\tau) d\tau$$

$s(t)$



$$\tilde{R}_a(\omega) = \int R_a(t) e^{-i\omega t} dt = |\tilde{R}_a(\omega)| e^{-i\varphi_a(\omega)}$$

AE Sgro et al., Mol. Syst. Biol. **11**, 779 (2015)

Adaptation in cAMP response

Extracellular cAMP

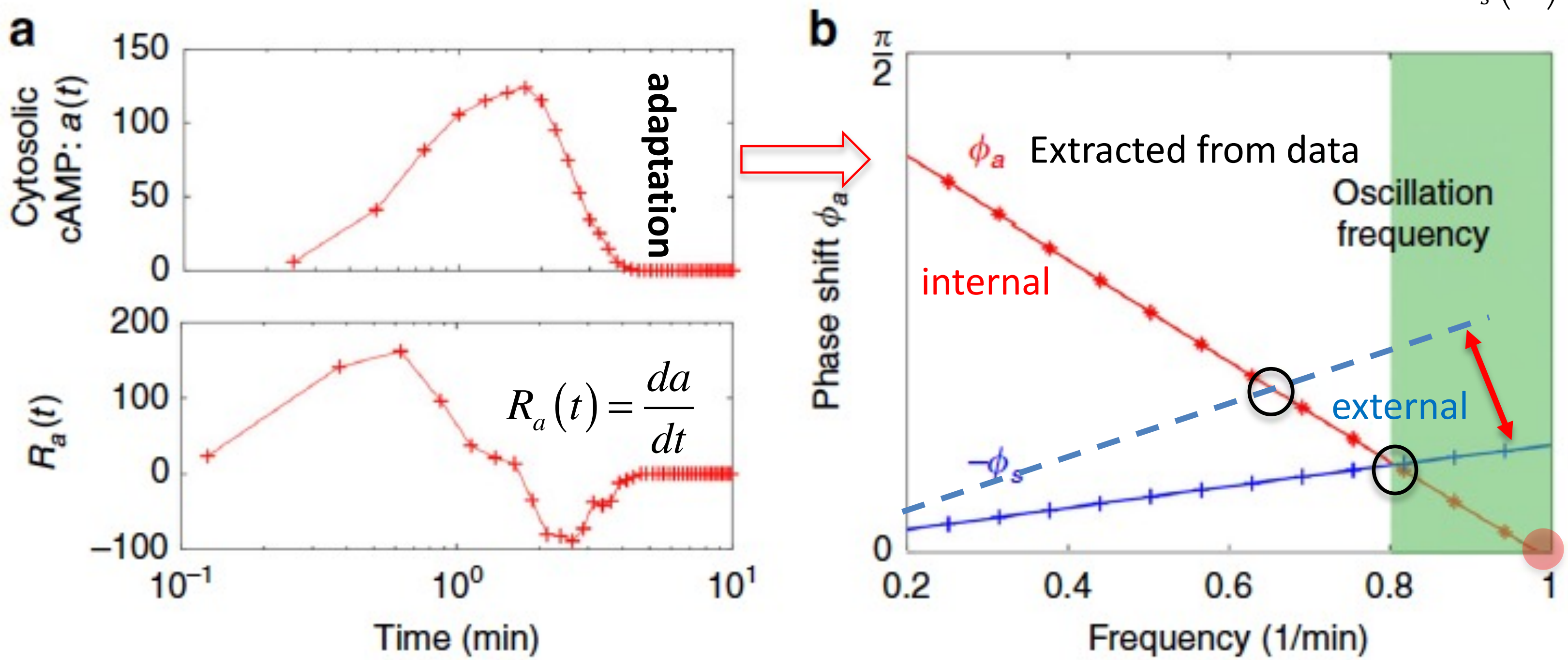
Theory:

$$\tilde{R}_s(\omega) = \frac{\alpha_1}{K - i\gamma\omega}$$

$$-\phi_s(\omega) = \tan^{-1}\frac{\gamma\omega}{K}$$

Single-cell measurement of cytosolic cAMP upon a step increase (1nM) of extracellular cAMP

Average response



Degradation rate K increases with cell density

$$T_{\min} = \frac{2\pi}{\omega_{\max}} = 6.5 \text{ min}$$

AE Sgro et al., Mol. Syst. Biol. **11**, 779 (2015)

SW Wang & LHT, Nature Comm **10**, 5613 (2019)

Can mechanical channel do the same?

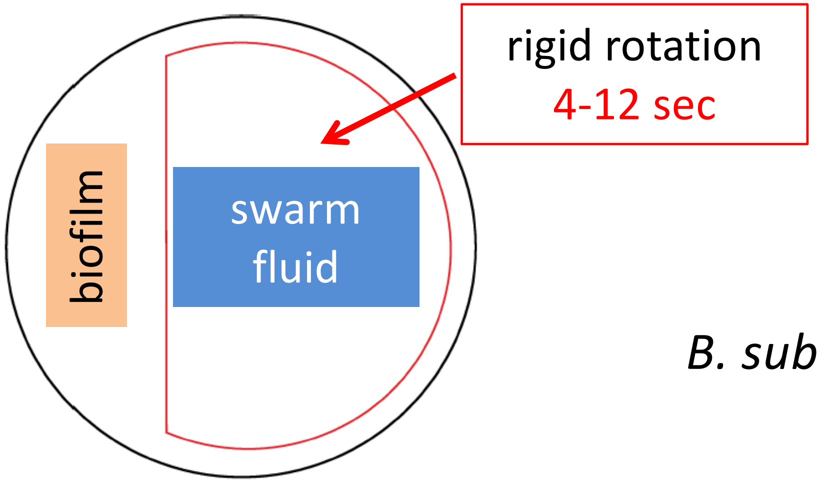
Circularly polarized motion of micro-swimmers

C Chen, S Liu, X-Q Shi, H Chate, YL Wu, *Nature* **542**: 210 (2017)

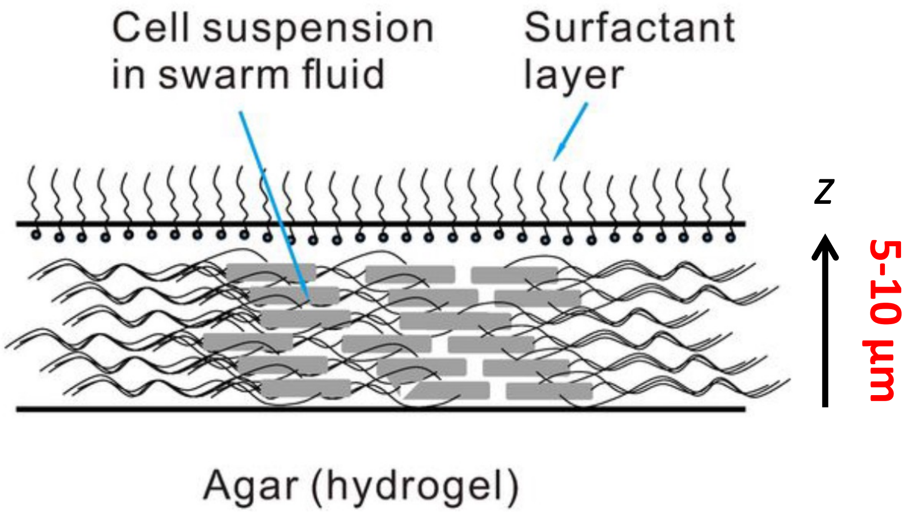
B Miao and L.-H. Tang, arXiv: 2603.26025

Experimental setup in Wu Lab

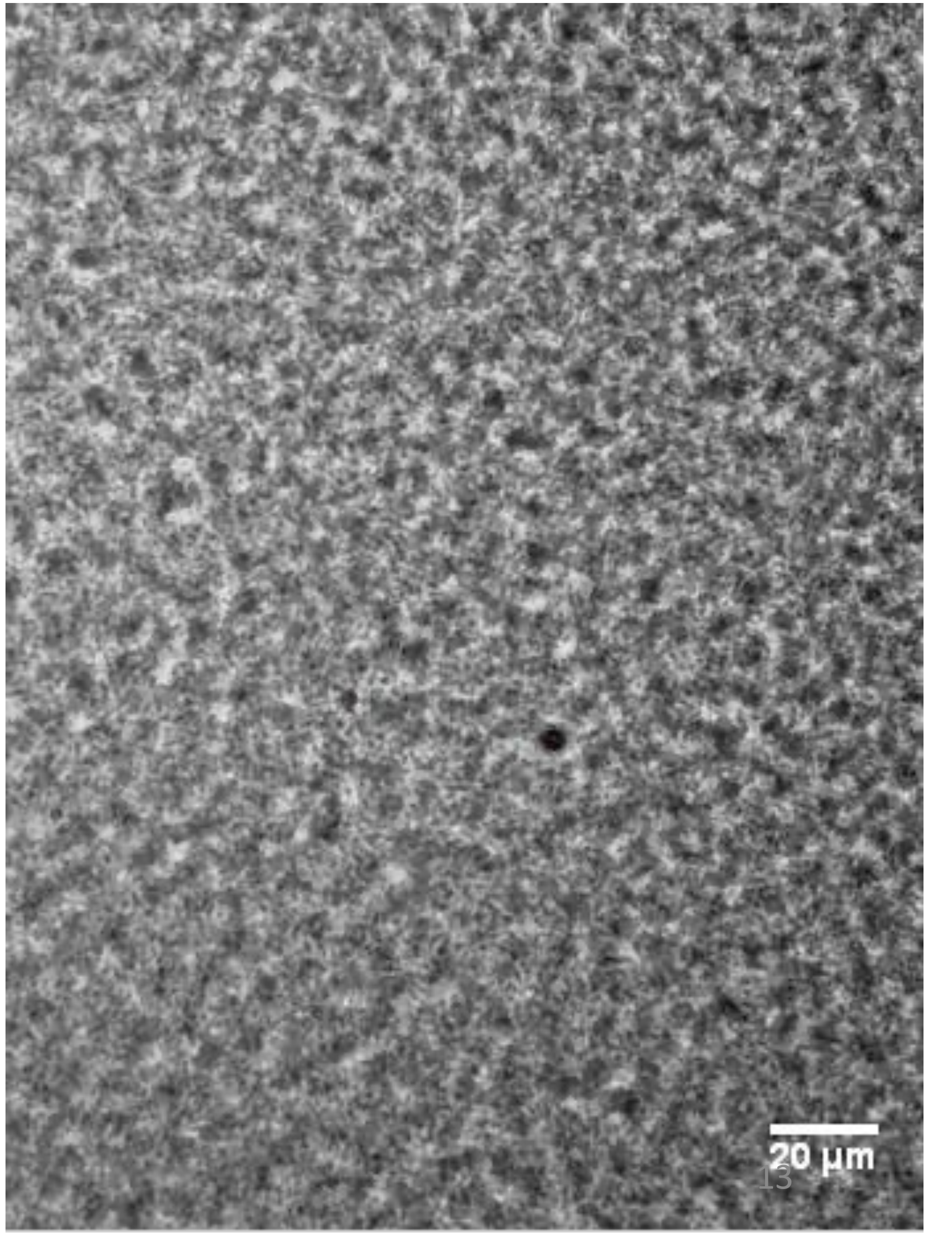
top view



side view



B. subtilis

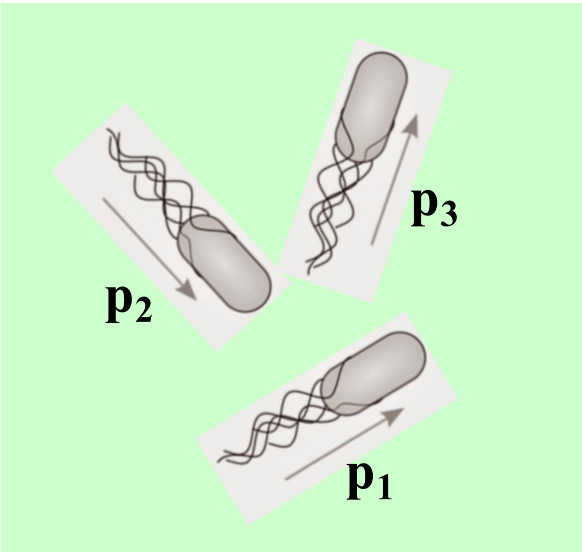


How bacteria communicate

swimming bacteria

+

fluid **u** (communication)

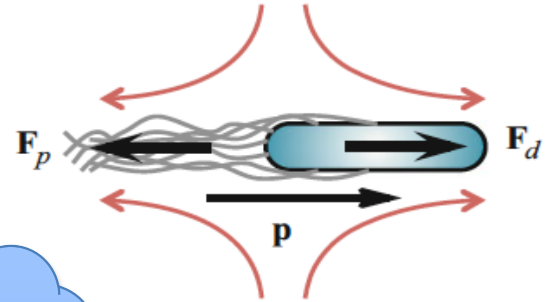


p = polarity vector

Disturbance on the fluid due to bacterial flagella + body movement

force dipole

Pusher (e.g. *E. coli*)



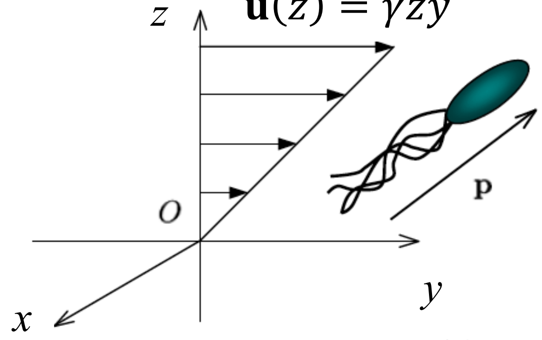
sender

fluid flow

receiver

Is it going to do the trick?

suspension



Jeffery equation (thin rod)

$$\dot{\mathbf{p}} = (\mathbf{I} - \mathbf{pp}) \cdot (\nabla \mathbf{u}) \cdot \mathbf{p}$$

turning in shear flow

A minimal model for microswimmers

David Saintillan and **Michael J. Shelley**, 2008

$$P(\mathbf{r},\mathbf{p},t) = \text{PDF of a bacterium at } \mathbf{r} \text{ with orientation } \mathbf{p}$$

Smoluchowski equation: $\dfrac{\partial P(\mathbf{r},\mathbf{p},t)}{\partial t} = -\nabla\cdot(\dot{\mathbf{r}}P) - \nabla_{\mathbf{p}}\cdot(\dot{\mathbf{p}}P) + D_T\nabla^2 P + D_R\nabla^2_{\mathbf{p}} P$

Stochastic components of bacterial motion

translational diffusion

rotational diffusion

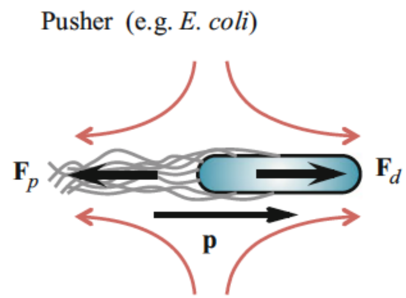
Swimmer in a flow field $\mathbf{u}$: $\dot{\mathbf{r}} = V_s\mathbf{p} + \mathbf{u}$

Jeffery's equation: $\dot{\mathbf{p}} = (\mathbf{I} - \mathbf{pp})\cdot(\nabla\mathbf{u})\cdot\mathbf{p}$

Moving to the population: mean polarity profile $P(\mathbf{r},\mathbf{p},t) \rightarrow cP(\mathbf{r},\mathbf{p},t)$, c = cell number density

Navier Stokes Equation (low R): $-\nabla q + \nabla\cdot\Sigma + \mu\nabla^2\mathbf{u} = 0$

Stress generated by swimmers: $\Sigma(\mathbf{r},t) = \sigma_0 \int \left(\mathbf{pp} - \dfrac{1}{3}\mathbf{I}\right) P(\mathbf{r},\mathbf{p},t)\, d\mathbf{p}$



$\sigma_0 < 0$ for pushers

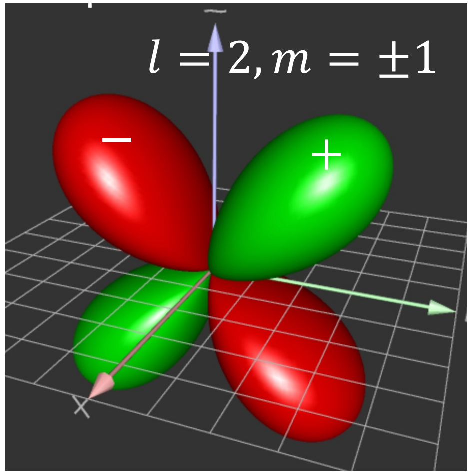
Linear response: nematic tilt as sender/receiver

Small deviations from a non-polarized state:

$$P = \frac{c}{4\pi} + \Psi(z, \mathbf{p}, t)$$ Mean polarity profile

$$\mathbf{u} = \mathbf{u}_{\parallel}(z, t)$$ Flow profile

Physical takeaway:
the off-diagonal nematic order parameter acts as both a ”sender” and a ”receiver” of the signal through the fluid



Linearized Smoluchowski Equation

$$\frac{\partial \Psi}{\partial t} + V_s p_z \frac{\partial \Psi}{\partial z} - D_T \frac{\partial^2 \Psi}{\partial z^2} - D_R \nabla_{\mathbf{p}}^2 \Psi = \boxed{\frac{3c}{4\pi} p_z \partial_z (\mathbf{u}_{\parallel} \cdot \mathbf{p})}$$

nonequilibrium

signal

Fluid motion

$$\boxed{-\mu \frac{\partial^2 \mathbf{u}_{\parallel}}{\partial z^2}} = \sigma_0 \frac{\partial}{\partial z} \int d\mathbf{p} \, p_z \mathbf{p}_{\parallel} \Psi(z, \mathbf{p}, t)$$

sender

Multipole expansion and eigenmode equations

Separation of variables (geometry and symmetries):

$$\mathbf{u}_{\parallel} = u_x \hat{\mathbf{x}} + u_y \hat{\mathbf{y}} \rightarrow u_{\pm} \hat{\mathbf{e}}_{\pm} \sin(kz)\, e^{-i\omega t/\tau}$$

$$\Psi(z, \mathbf{p}, t) = [A(\theta, \varphi) \sin(kz) + B(\theta, \varphi) \cos(kz)]\, e^{-i\omega t/\tau}$$

$$k = \frac{\pi}{2W} \qquad \tau = \frac{1}{D_R}$$

$$\tilde{a}_2 = \chi(\omega, \Lambda_{\mathrm{T}}, \mathrm{Pe_s}) B$$

Orientational dynamics of bacteria:

Multipole expansion:

$$A(\theta, \varphi) = \sum_{l \text{ odd}} \tilde{a}_l Y_l^{\pm 1}(\theta, \varphi)$$

$$B(\theta, \varphi) = \sum_{l \text{ even}} \tilde{a}_l Y_l^{\pm 1}(\theta, \varphi)$$

$$\boxed{(-i\omega + \Lambda_l)\tilde{a}_l + g_l \tilde{a}_{l-1} - g_{l+1}\tilde{a}_{l+1} = B\delta_{l,2}, \; l = 1, 2, \ldots}$$

$$\Lambda_l = \Lambda_{\mathrm{T}} + l(l+1), \qquad g_l = (-1)^l \mathrm{Pe_s} \sqrt{\frac{l^2 - 1}{4l^2 - 1}}$$

Fluid flow driven by swimmers (communication channel):

$$\boxed{B = -\left(\frac{c\sigma_0}{5\mu D_{\mathrm{R}}}\right) \tilde{a}_2}$$

onset of oscillations

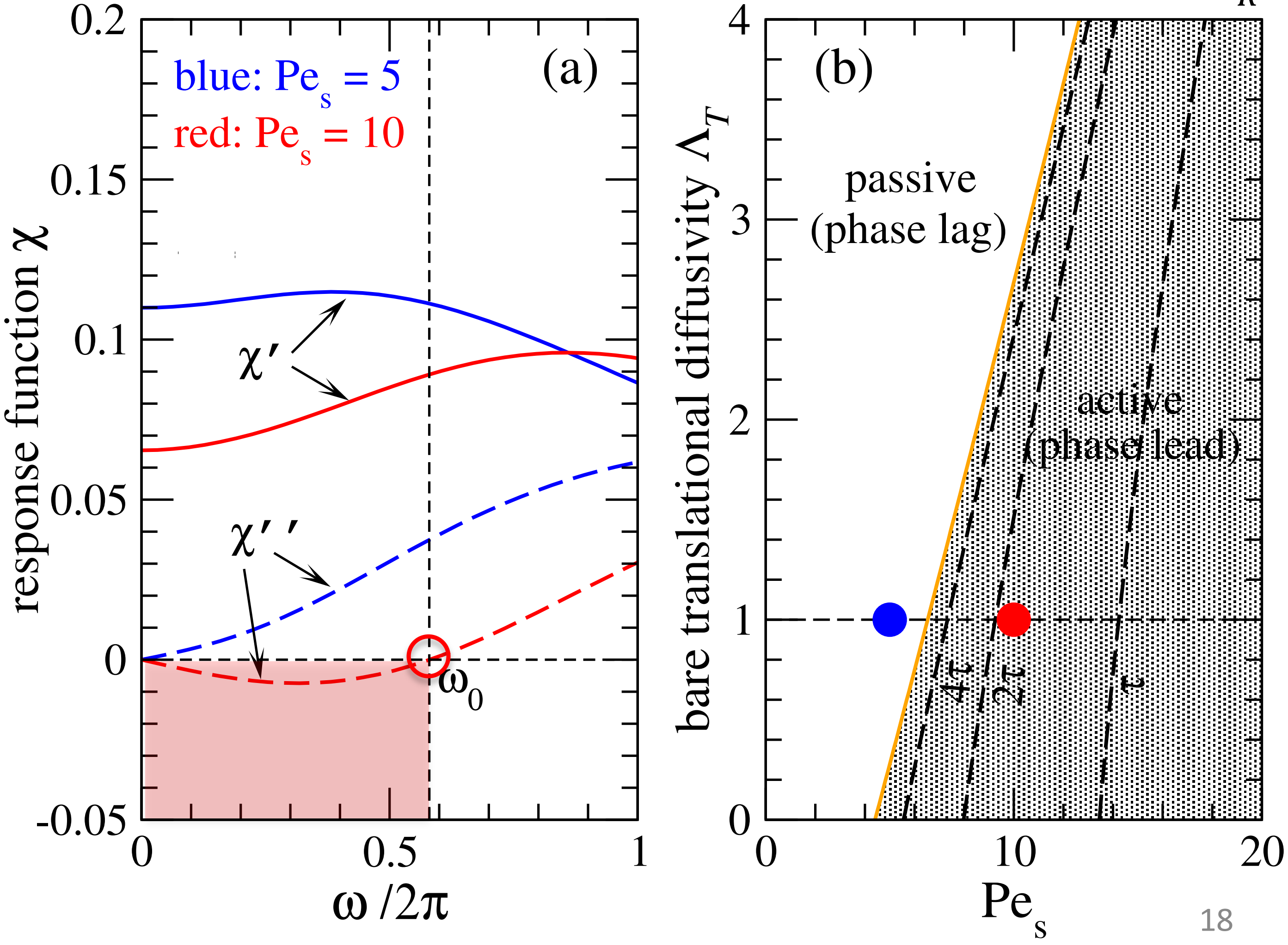
Result: phase-leading response at large Péclet number

$$\boxed{\chi(\omega) = \chi'(\omega) + \chi''(\omega)}$$

$$\mathrm{Pe}_s = \frac{\pi}{2}\frac{V_s}{D_R W} \approx \frac{\lambda_R}{W}$$

$$\Lambda_T = \frac{\pi^2 D_T}{4 D_R W^2} \leq 1$$

$\Lambda_T = 1$ onset frequency, $\tau = \frac{1}{D_R}$



Quantitative agreement with Wu lab's experiment

Onset cell density (theory):

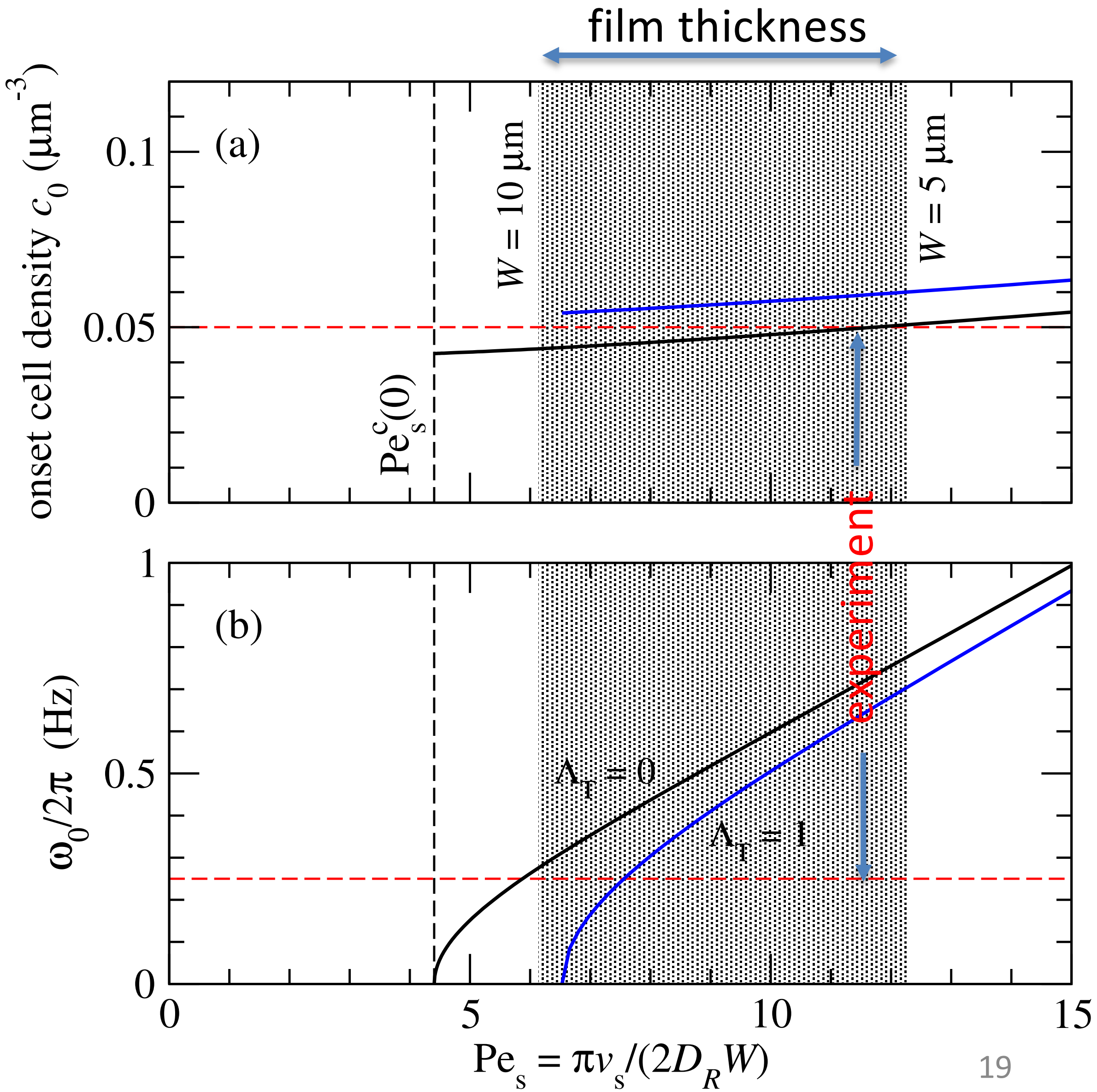
$$\boxed{c_0 = -\left(\frac{5\mu D_R}{\sigma_0}\right)[\chi'(\omega_0, \Lambda_\mathrm{T}, \mathrm{Pe_s})]^{-1}}$$

$$\frac{\mu V_s}{\sigma_0} = 0.025 - 0.05\ \mu\mathrm{m}^{-2}$$

$$V_s = 34\ \mu\mathrm{m/s}$$

$$D_R \approx 0.87\ \mathrm{s}^{-1}$$

Oscillation period: 4 - 12 sec



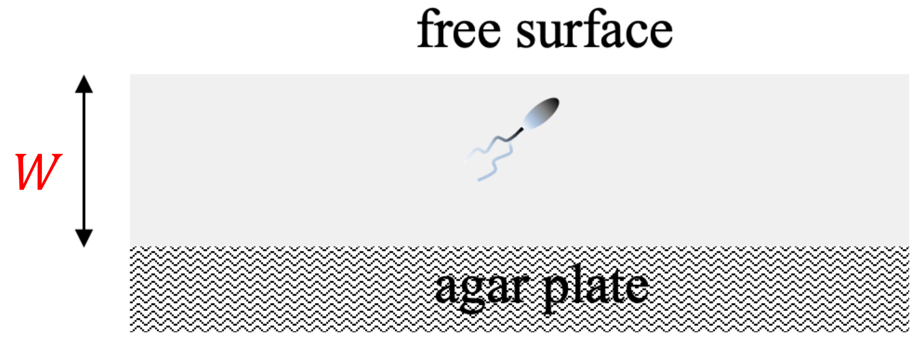
The geometric cutoff: physical mechanism and a new prediction

run length

$$\mathrm{Pe}_s = \frac{\pi}{2}\frac{V_s}{D_R W} \approx \frac{\lambda_R}{W}, \qquad \lambda_R = V_s/D_R = \boxed{V_s\tau}/(\Delta\theta)^2$$

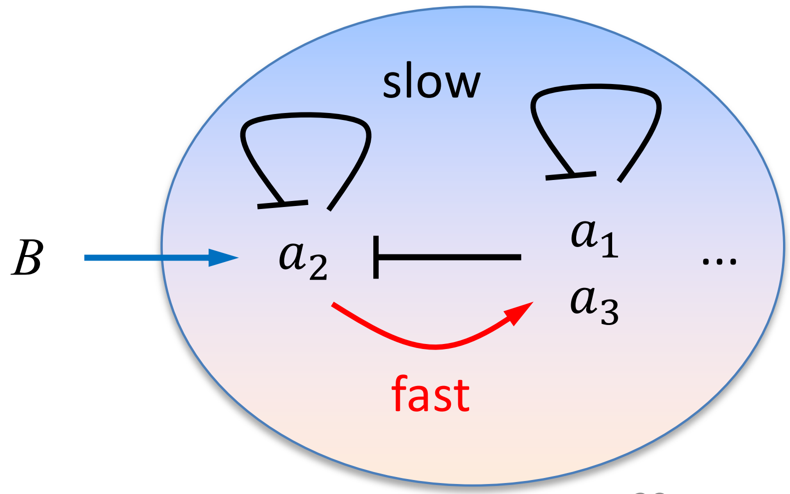
$$\boxed{(-i\omega+\Lambda_l)\tilde{a}_l+g_l\tilde{a}_{l-1}-g_{l+1}\tilde{a}_{l+1} = B\delta_{l,2},\ l=1,2,\ldots}$$

$$\Lambda_l = \Lambda_\mathrm{T} + l(l+1), \qquad g_l = (-1)^l \mathrm{Pe_s}\sqrt{\frac{l^2-1}{4l^2-1}}$$



phase-leading response: persistence of individual bacterial orientation across film thickness

excitable circuit at large Pe_s

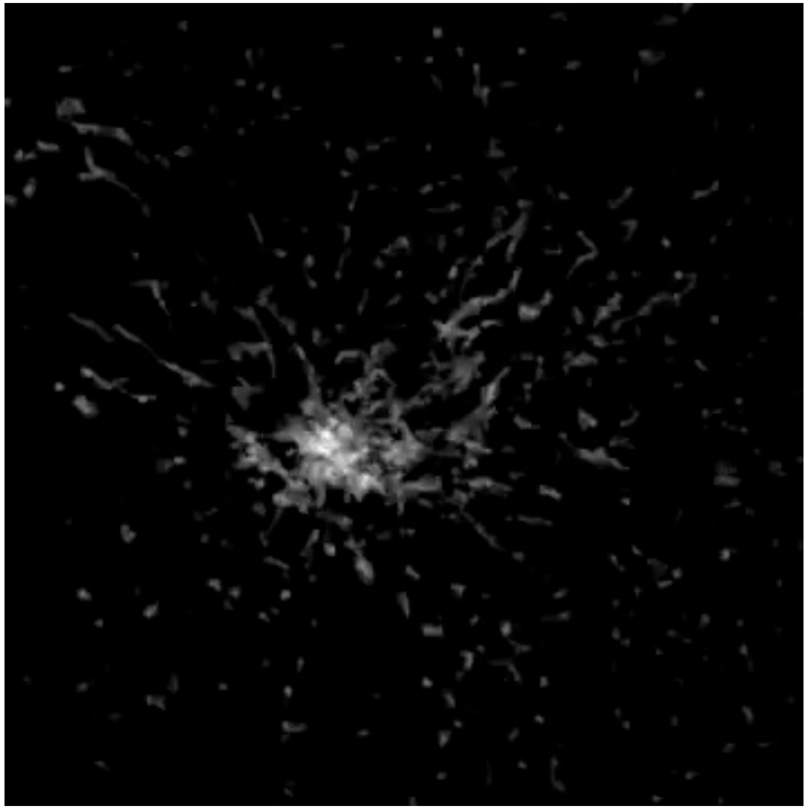


Summary

collective oscillations – cells find ways to communicate and excite each other

Dicty aggregation (chemical blueprint)

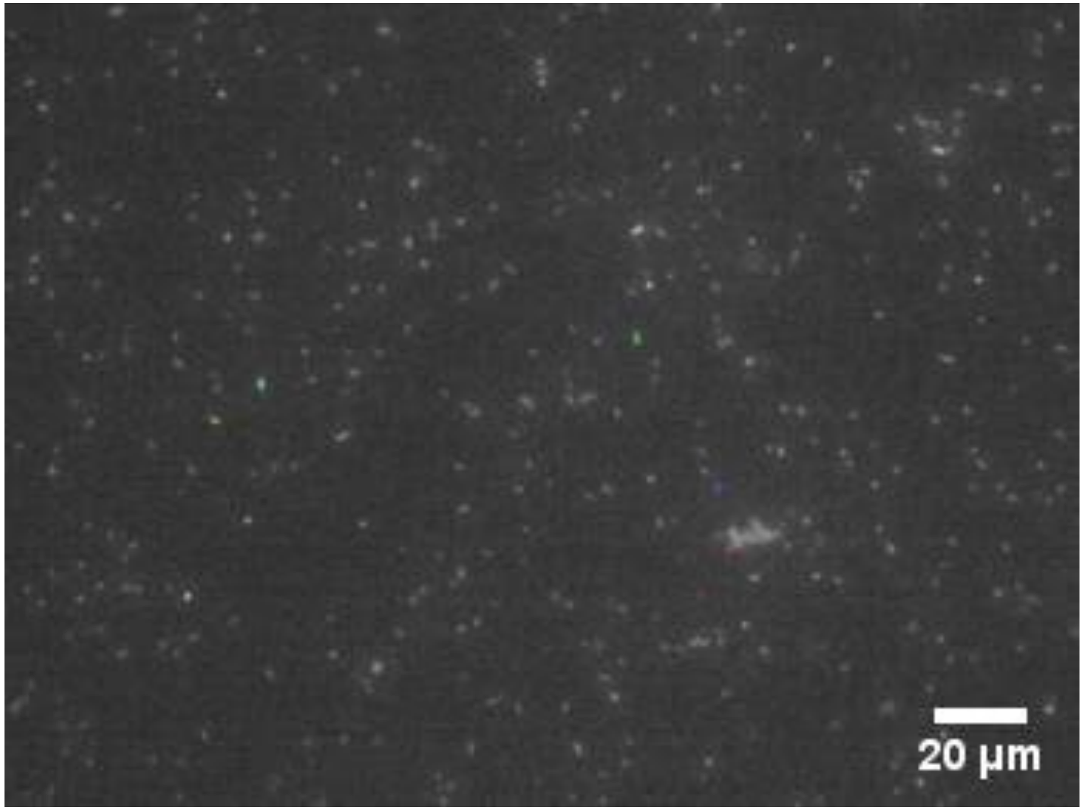
Adaptation → phase-lead → order



Nonequilibrium physics at work

Bacterial swimmers (mechanical blueprint)

Shear flow → phase-lead → order

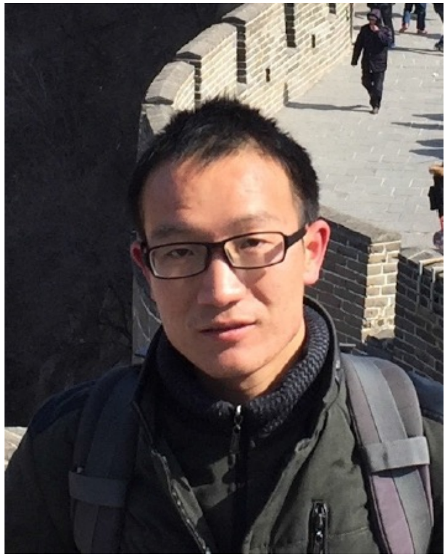


Conclusions

- Collective oscillations can emerge without an intrinsic oscillator at the single-cell level — the key ingredients are ***active agents*** coupled through a ***shared communication channel***.
- A unified criterion: oscillation onset requires **phase matching** (active lead cancels passive lag) and a **threshold density** (loop gain ≥ 1).
- Quantitative predictions (onset density ~0.03–0.05 μm^{-3}, period 4–12 s) agree with Wu lab experiments with no fitting parameters beyond known single-cell quantities.
- Film thickness W sets a **geometric cutoff** — oscillations require $\frac{\lambda_R}{W} \geq 1$.
- **Open direction**: What happens beyond onset? Nonlinear selection of amplitude, frequency, and spatial patterns in finite-size geometries (**cGL** and **KPZ phase dynamics**?).

Acknowledgements

General theory



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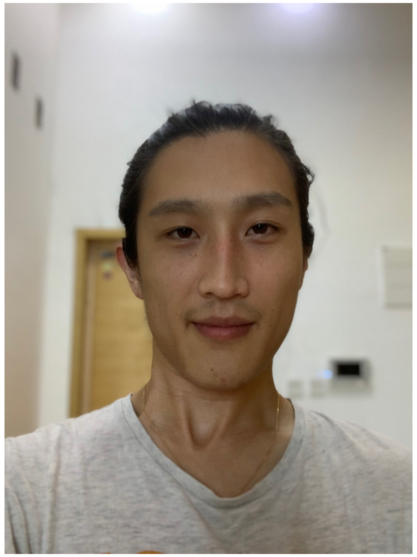
Active fluid



Francois Gu
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Bing Miao
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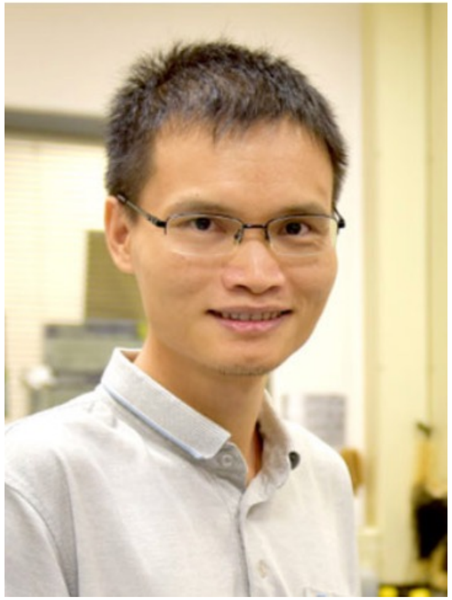

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Thank you very much
for your attention!
Center for Complex Systems
Westlake University

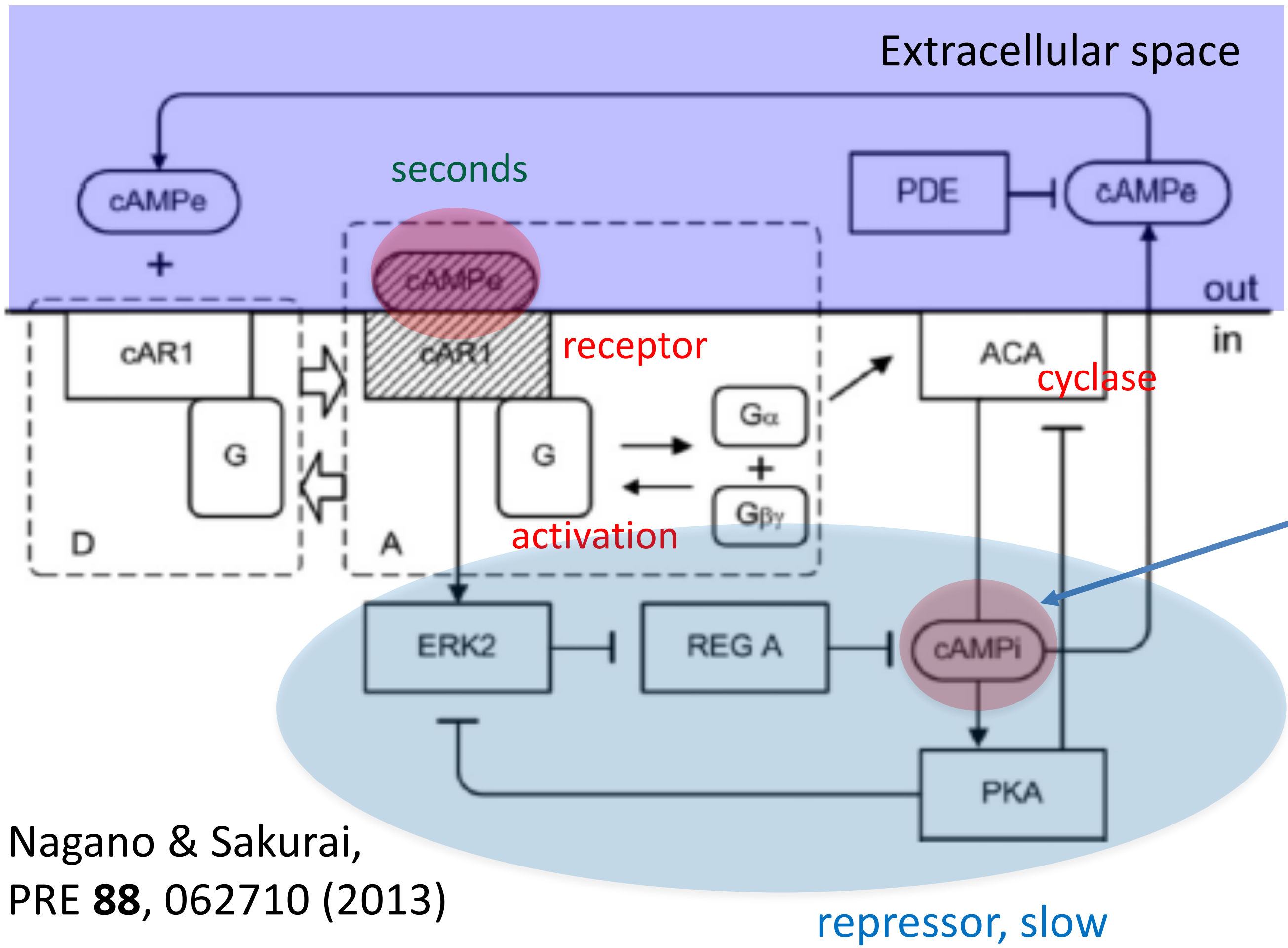
The Adaptation Route to Collective Oscillations

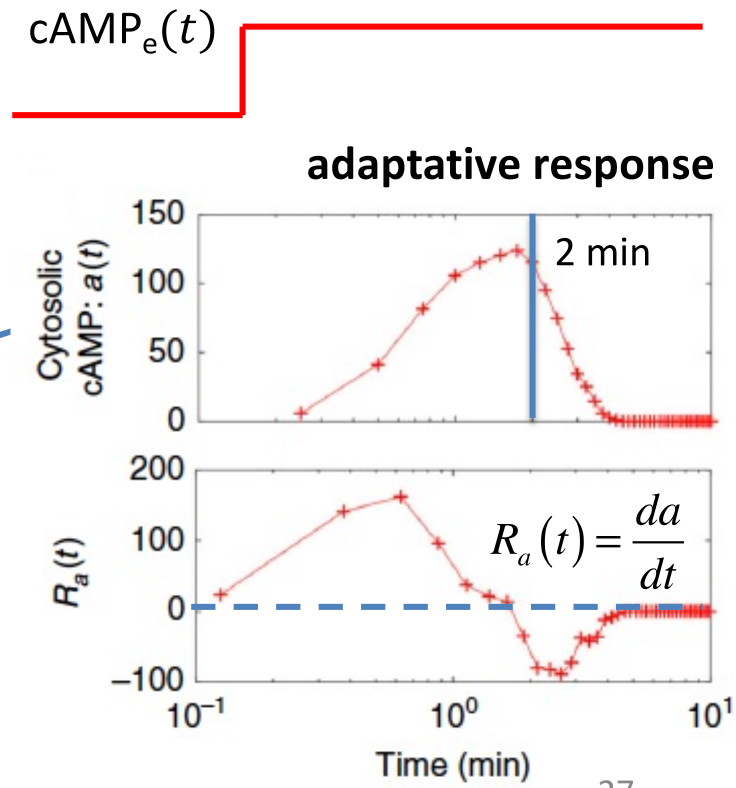
	System	sender a	Signal s	Interaction	Phenomena	Traditional interpretation	Adaptation
耳鸣	Inner ear	Hair bundle displacement	Pressure wave	Mechanical interaction	Spontaneous otoacoustic emission	Adaptation & energy flow	Yes
聚集	Social amoebae	Cytosolic cAMP	Extracellular cAMP	Ligand binding + active secretion	Oscillatory aggregation	Excitability & noise-induced oscillation	Yes
合成系统	Synthetic system	Cytosolic AHL	Extracellular AHL	Passive diffusion across membrane	Collective oscillation	Concrete modeling	Yes
糖酵解	Yeast	$\mathrm{NAD}^+/\mathrm{NADH}$ ratio	Acetaldehyde	Reversible conversion	Glycolytic oscillation	Controversial	Yes (hypothesis)

Careful study of individual response circuit

Dicty's cAMP signalling circuit

AE Sgro et al., Mol. Syst. Biol. **11**, 779 (2015)





Nagano & Sakurai,
PRE **88**, 062710 (2013)