Bacterial Glass

[Lama et al., arXiv:2205.10436]

Kazumasa A. Takeuchi
(Univ. Tokyo)

E. coli glasswork © Trilobite
(which I bought...)

Joint work in Takeuchi Lab

Hisay Lama

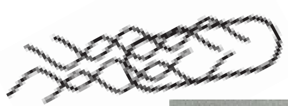
M. J. Yamamoto

Y. Furuta

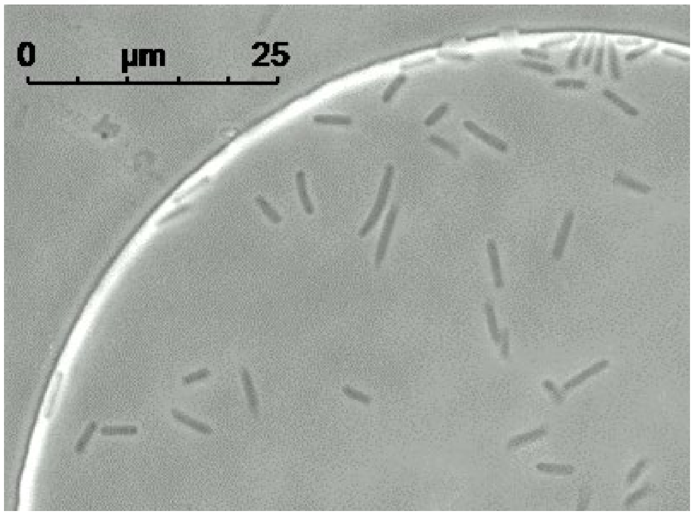
T. Shimaya

Active Matter & its Phases

= systems made of self-propelled particles

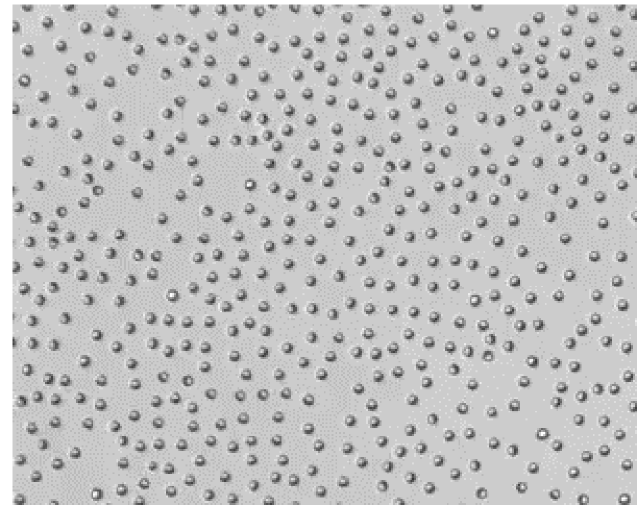


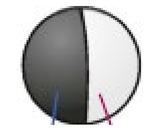
bacteria



[Shimaya, …, KaT, Comm. Phys. 2021]

active colloid





[Iwasawa, Nishiguchi, Sano PRR 2021]

Q. How do the phases of matter change in active systems?

Active gas, active liquid, active nematics, …

What about "active glass" ?

Are usual glass properties kept unchanged? Any novel feature?

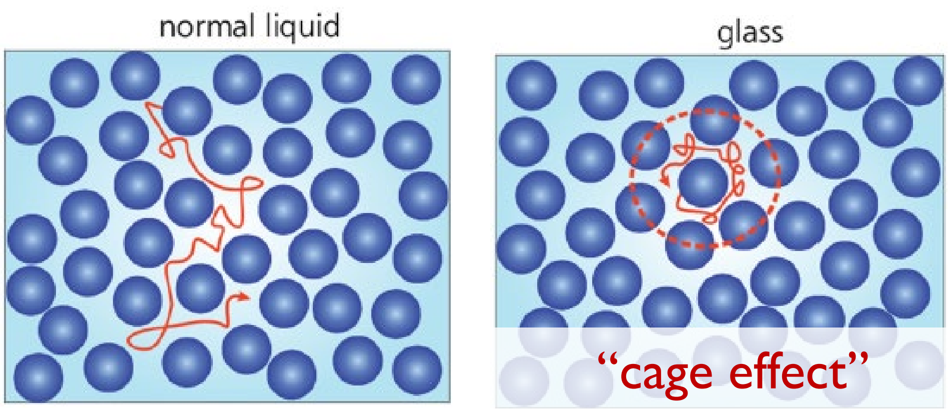
Glass

Solid-like material,
without long-range structural order

characteristic
structural relaxation

intermediate scattering function

$$F(k,t) = \langle \rho_k(t)\rho_{-k}(0)\rangle / N$$



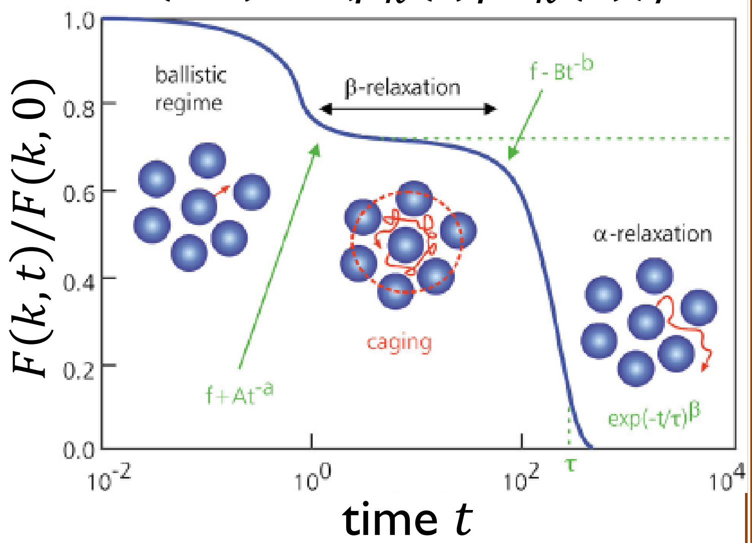
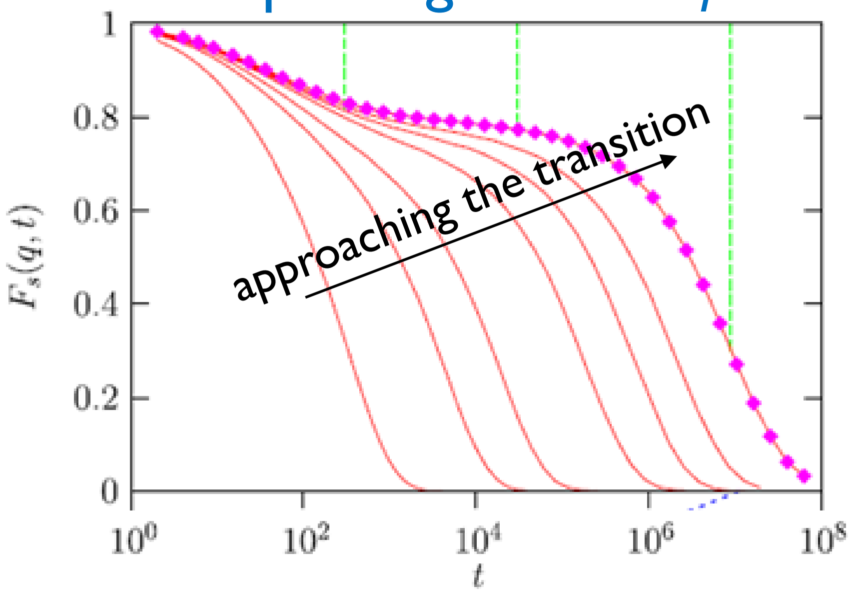
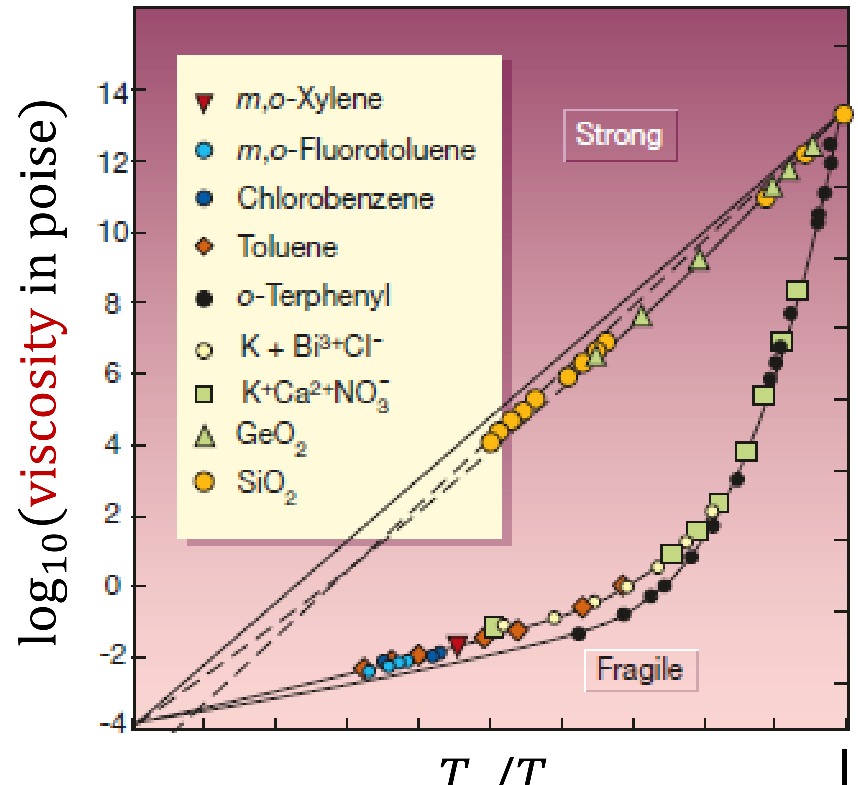


Figure source: Janssen, Front. Phys. 6, 97 (2018)

Glass' Hallmark 1: Rapid Dynamic Slowdown

Relaxation time ⮥
as temperature T ↘
or packing fraction ϕ ↗



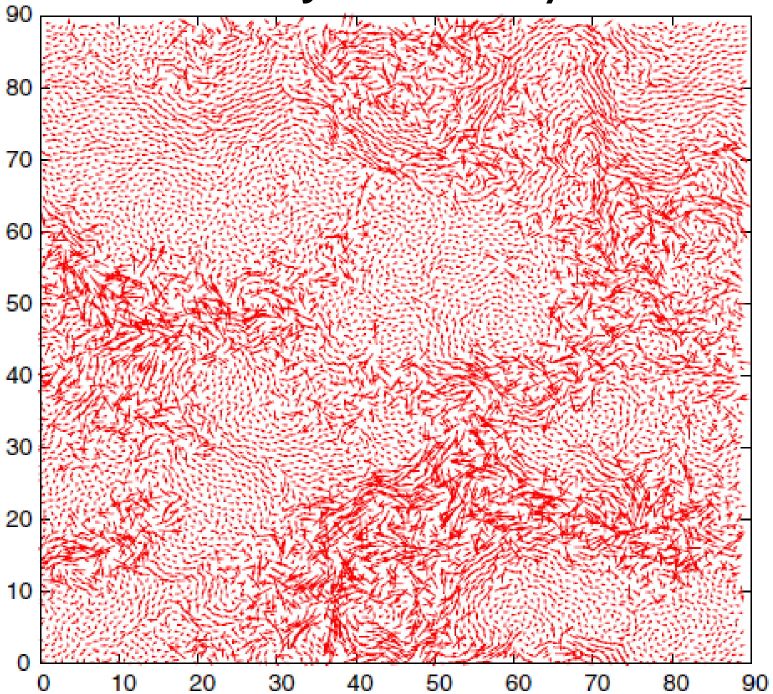


(T_g: glass transition temperature)

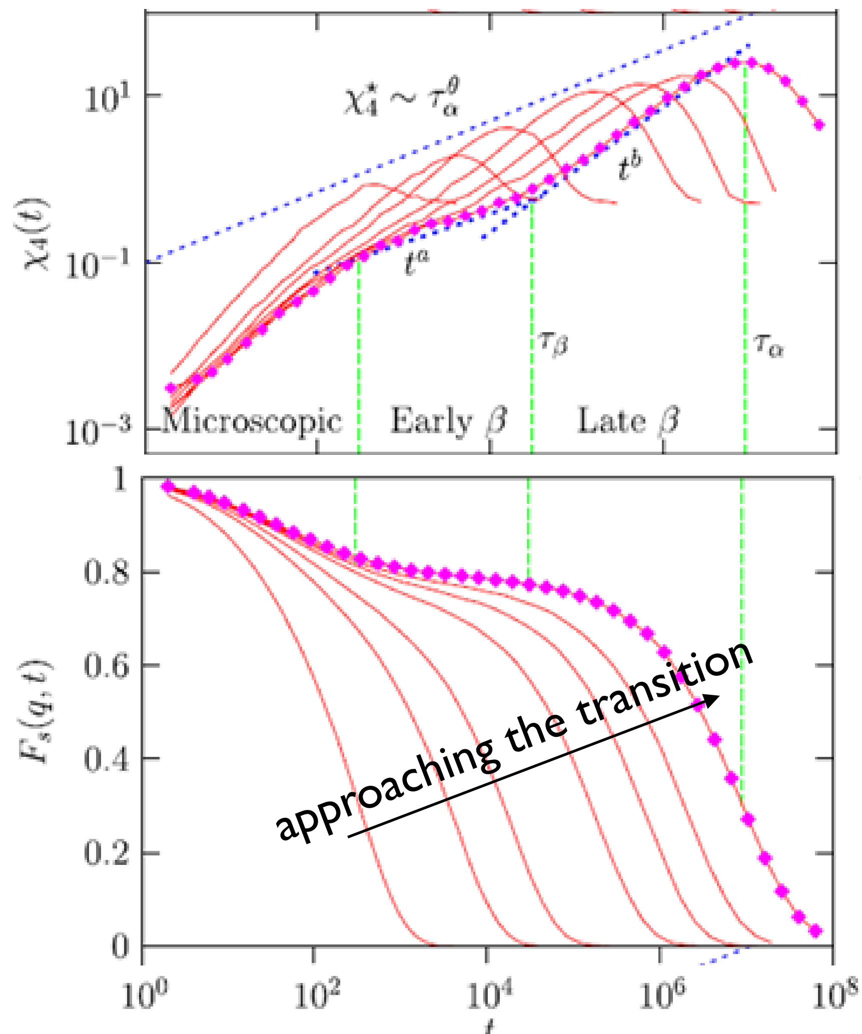
Figure source
Left: Berthier & Biroli, Rev. Mod. Phys. 83, 587 (2011)
Right: Debenedetti & Stillinger, Nature 410, 259 (2001)

Glass' Hallmark 2: Dynamic Heterogeneity

displacement vectors
in Lennard-Jones binary mixture



χ_4: dynamic susceptibility
(variance of space-time correlator)



All figures from
Berthier & Biroli, Rev. Mod. Phys. 83, 587 (2011)

Active Glass

[review: Janssen,
J. Phys. Cond. Mat. 31, 503002 (2019)]

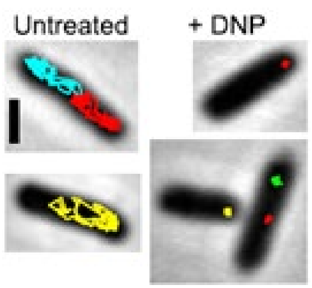
Numerics & theory

- Glassy dynamics observed in various self-propelled particle models.
- Glass hallmarks basically remain, with nontrivial effects of activity.
- Some glass theories (mode coupling, RFOT) extended to active systems.

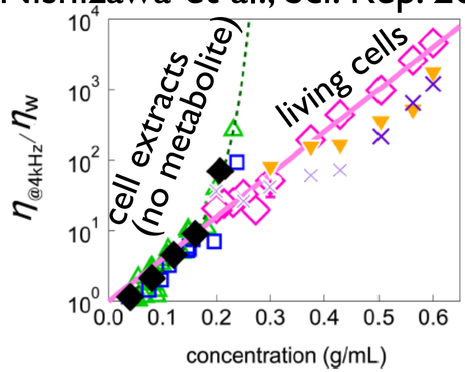
Experiments

Glassy dynamics in cytoplasm, cell extracts & cell sheets

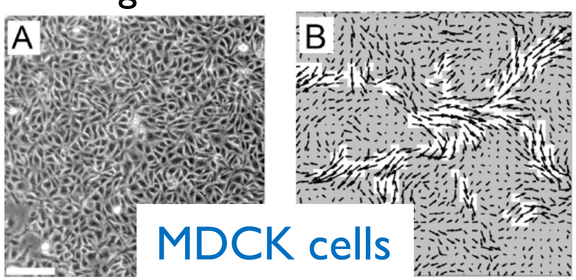
Parry et al. Cell 2014



Nishizawa et al., Sci. Rep. 2017



Angelini et al. PNAS 2011



MDCK cells

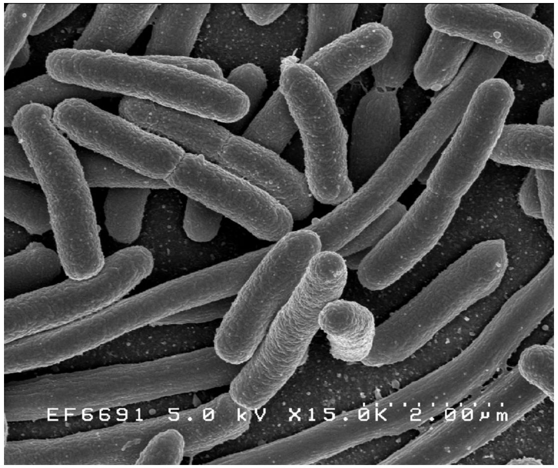
cell shape is important
[Park et al., Nat. Mater. 2015]

but, want a model experiment of particle-like cells! ⇨ bacteria !

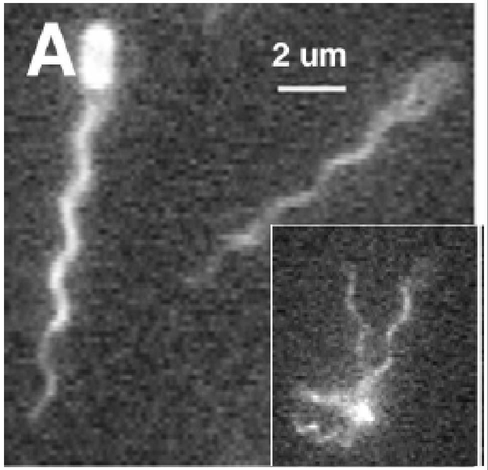
well-controlled condition — deformation negligible

Bacteria (*E. coli*) as our Constituent Particles

- Rod-like
  diameter $\approx 1\ \mu\mathrm{m}$
  length $\approx 2\sim 4\ \mu\mathrm{m}$
  rigidity ≈ 3 MPa
  [Perry et al. 2009]
  flagella $\approx 5\sim 10\ \mu\mathrm{m}$
  [Turner et al. 2000]



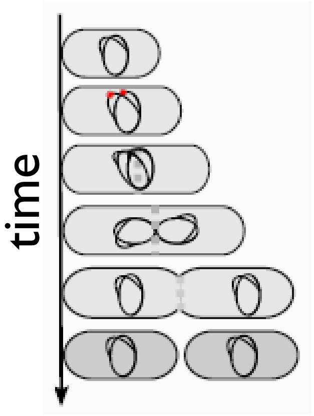
[SEM image by NIH, NIAID]



[Turner et al. 2000]

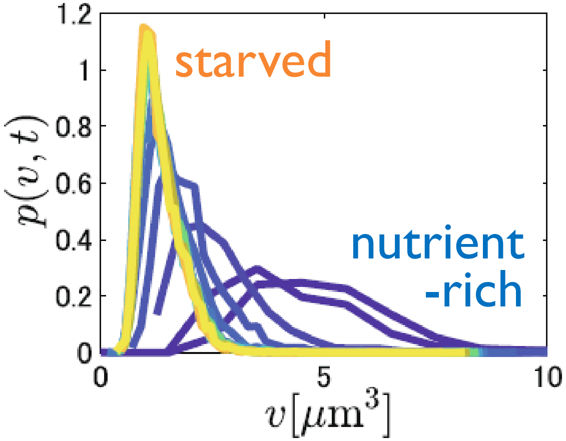
- Polydisperse
  (growth ➔ division)
  $\approx$ log normal dist.

E. coli cell cycle



[Micali et al., Sci. Adv. 2018]

cell volume distribution



[Shimaya, …, KaT, Comm. Phys. 2021]

- Swim speed $\approx 30\ \mu\mathrm{m/s}$
  ➔ propulsion ≈ 0.3 pN
  ➔ strain on collision
  $\approx 10^{-7} \ll 1$

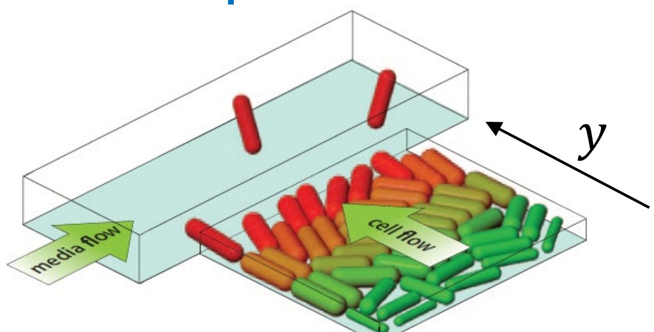
Controlled Experiment of Bacterial Populations

Want to culture bacteria under uniform & controlled environment

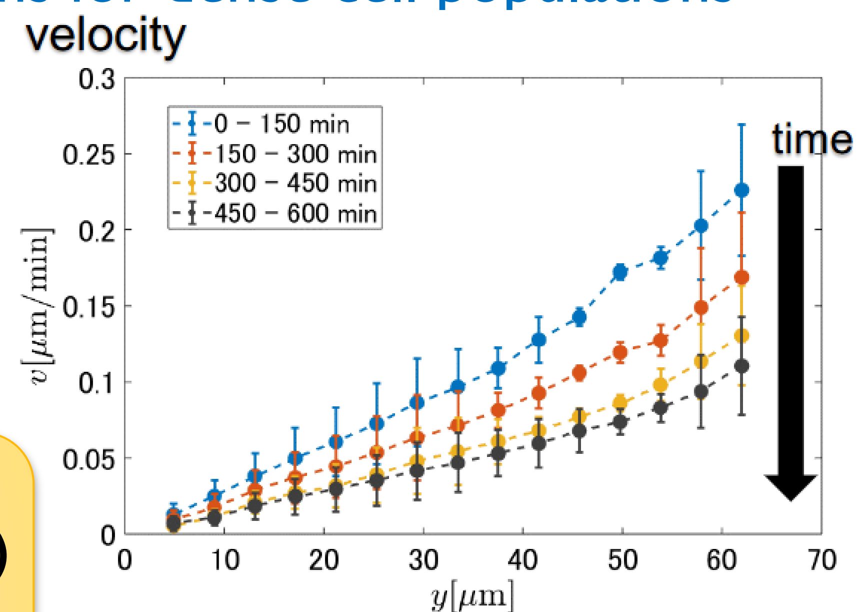
- choices: agar plates, cell suspensions, microfluidic devices, ...

long-time controllability 👍

However, conventional PDMS devices are unable to keep uniform conditions for dense cell populations



Mather et al., PRL 104, 208101 (2010)



our observation (*E. coli*)
(consistent with Mather et al.)

Nutrients used up near the inlet and don't reach far (only ~25μm)
Keeping uniform condition for dense cell populations is difficult!

Our Solution: Membrane-Type Device

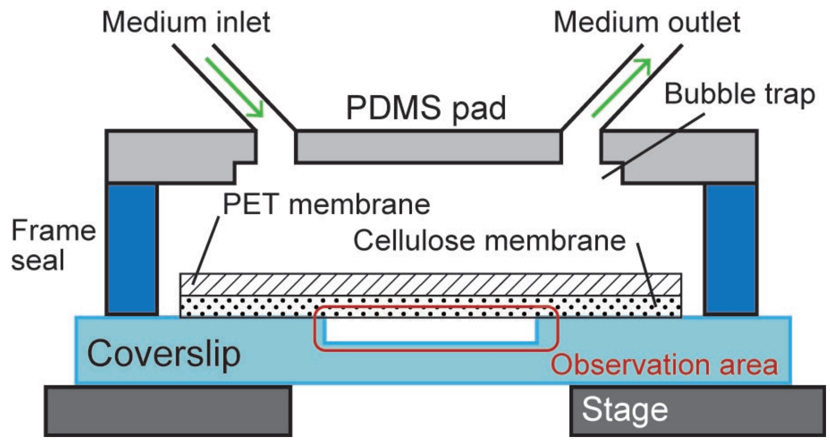
Takuro Shimaya

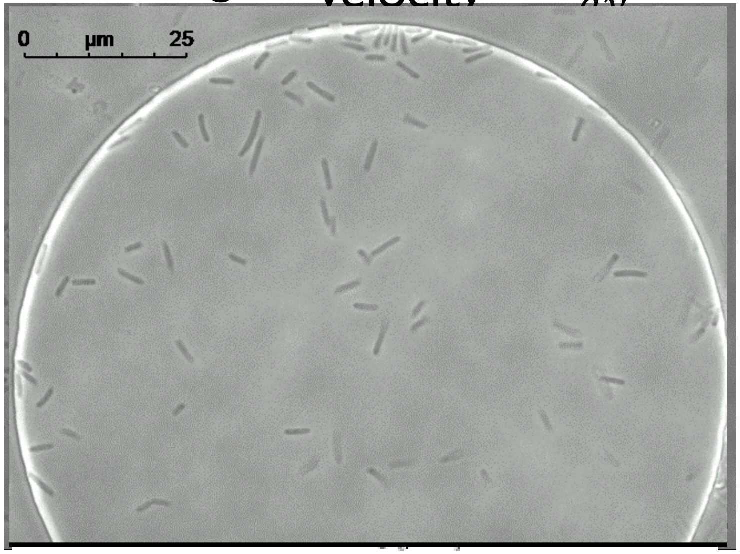
"Extensive Micro-Perfusion System" (EMPS)

[Shimaya *et al.*, Commun. Phys. 4, 238 (2021)]

growth rate $\lambda = \frac{du}{dx}$

velocity

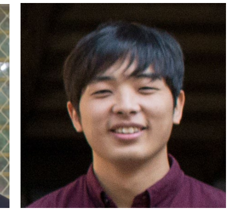


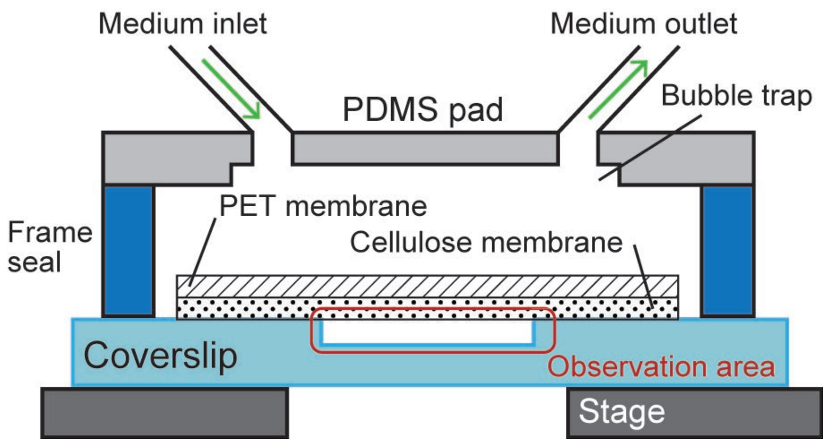


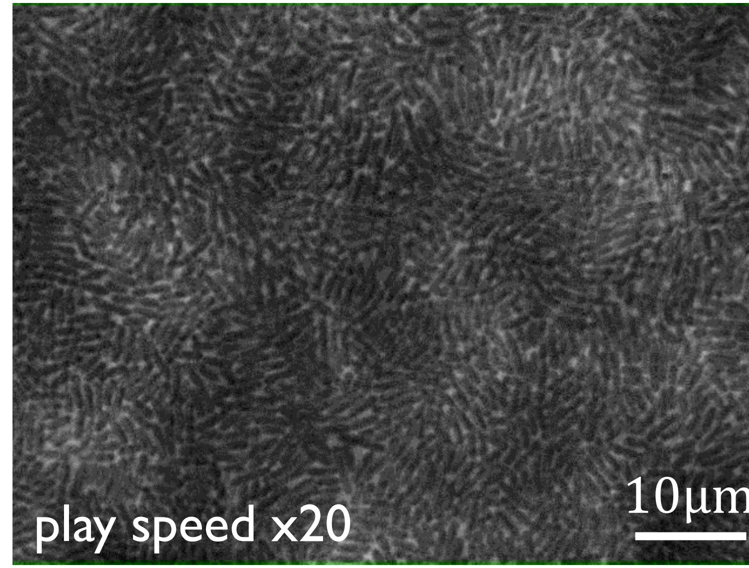
- Medium supplied uniformly through porous membrane (& wastes removed)
  ➜ bacteria grow uniformly, even in dense populations

- Rigid membrane (PET-cellulose double membrane)
  ➜ realized wide area (up to ~200 µm)

Bacterial Glass Experiment







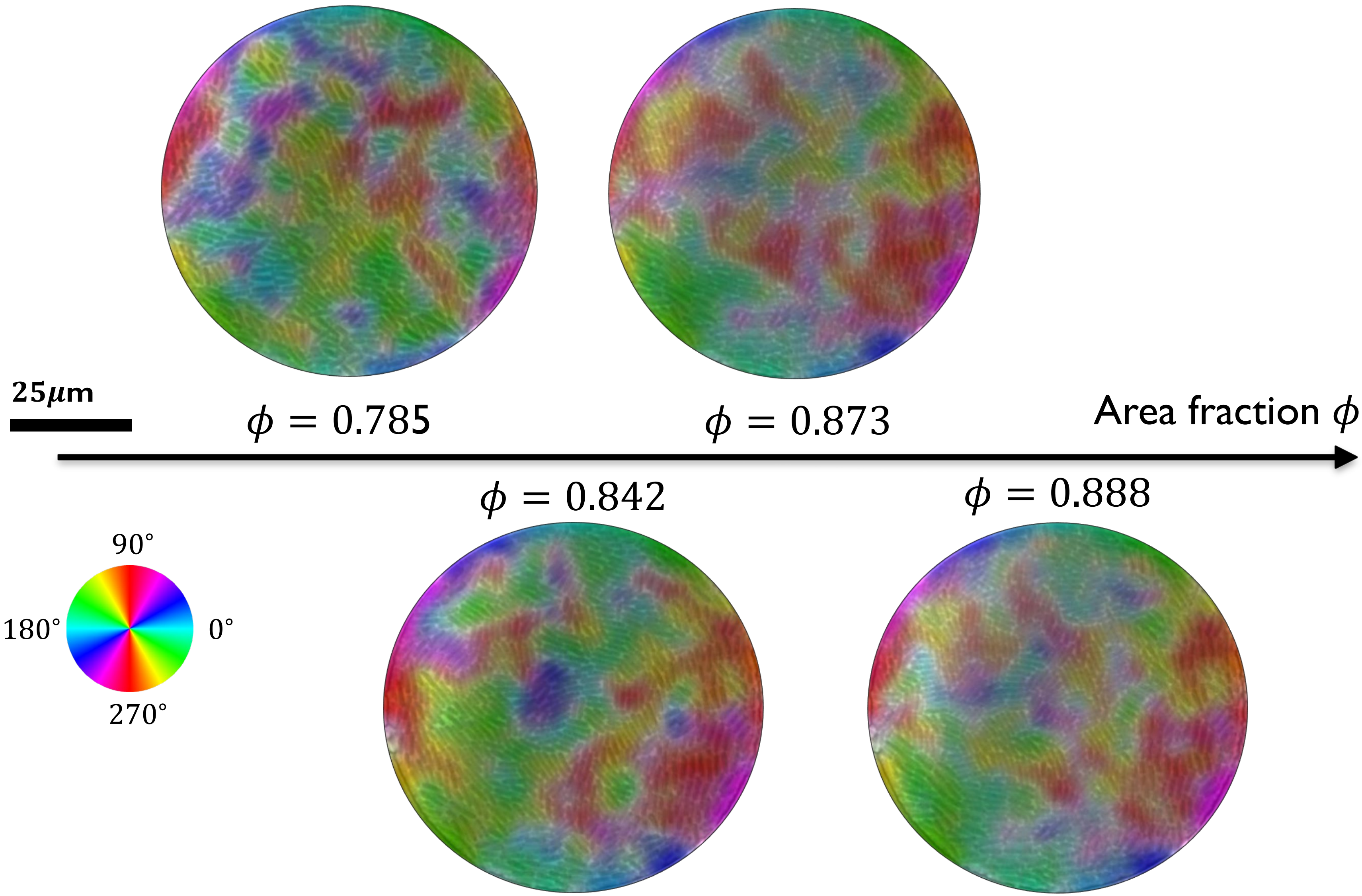
[only for this movie, RP437 Venus, M9 + Tween20, diam $200\mu\mathrm{m}$, depth $1.8\mu\mathrm{m}$]

Main experimental conditions

- Bacteria confined & cultured in a closed circular well with diam $\approx 70\mu\mathrm{m}$ & depth $\approx 1.4\mu\mathrm{m}$ ($< 2 \times$ cell diameter) $\therefore$2D
- Bacteria: *E. coli*, motile strain RP437 (wild type)
- Medium: Tryptone broth + 0.01% Tween20

Cell growth ➔ area fraction ϕ increases. Glass transition!

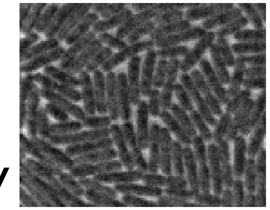
Movies at Various Area Fractions



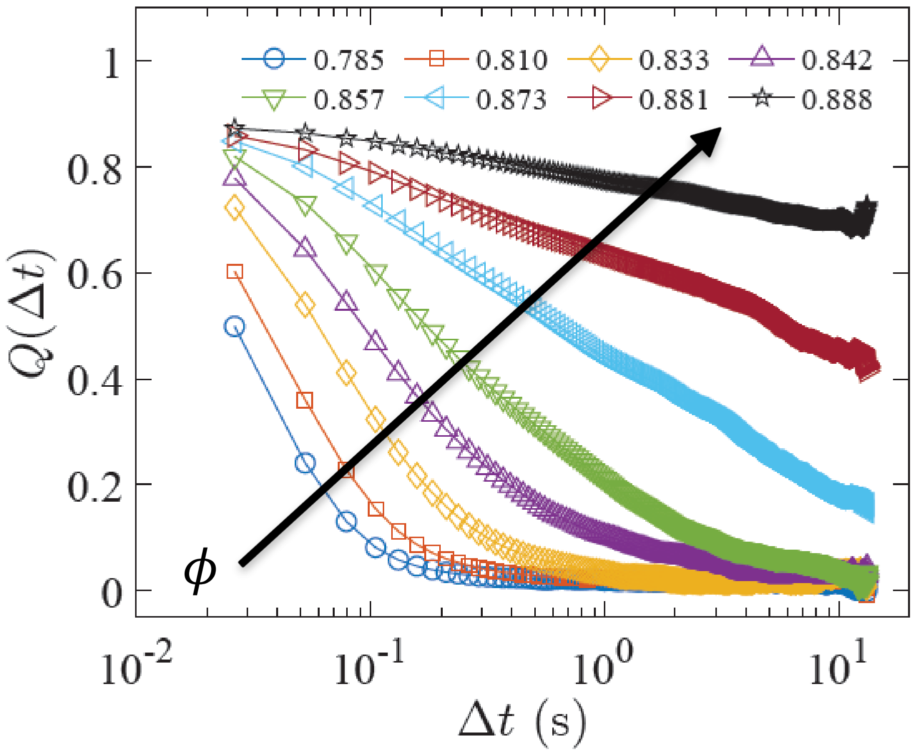
Let's characterize the transition!

Structural Relaxation

image intensity

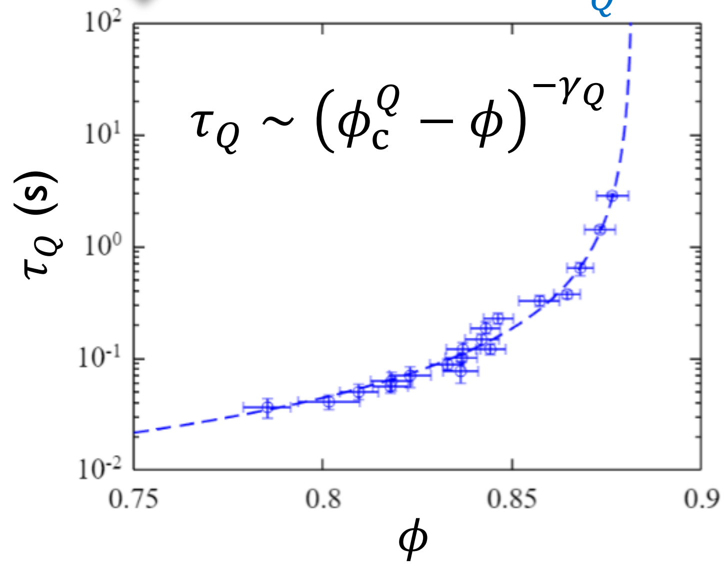


Overlap $Q(\Delta t) \approx \langle I(\vec{r}, t+\Delta t) I(\vec{r}, t) \rangle$ [method: Pastore *et al.* Sci. Rep. 2017]



$$Q(\Delta t) \sim \exp\left[-\left(\frac{\Delta t}{\tau_Q}\right)^{\beta}\right]$$

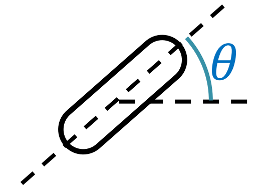
relaxation time τ_Q



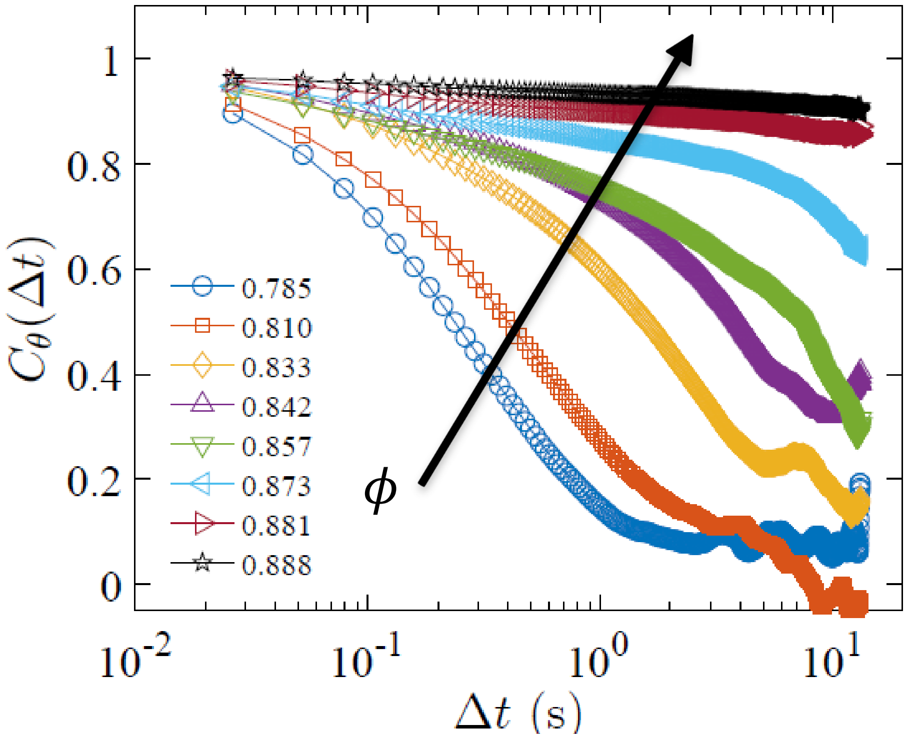
- Rapid dynamic slowdown is observed! Fragile glass.
- Behavior consistent with mode-coupling theory:

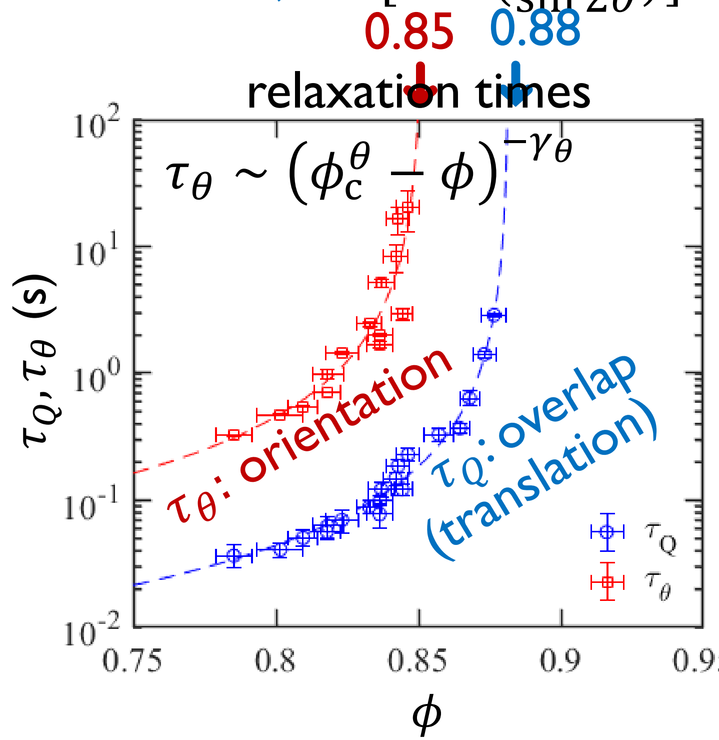
$\boxed{\tau_Q \sim \left(\phi_c^Q - \phi\right)^{-\gamma_Q}}$ $\phi_c^Q = 0.882(4)$ & $\gamma_Q = 1.5(3)$.

Orientational Relaxation



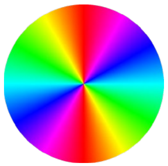
Measured $C_\theta(\Delta t) \equiv \langle \vec{n}(\vec{r}, t + \Delta t) \cdot \vec{n}(\vec{r}, t) \rangle_{\vec{r},t}$ $\left[\vec{n} \equiv \begin{pmatrix} \cos 2\theta \\ \sin 2\theta \end{pmatrix}\right]$



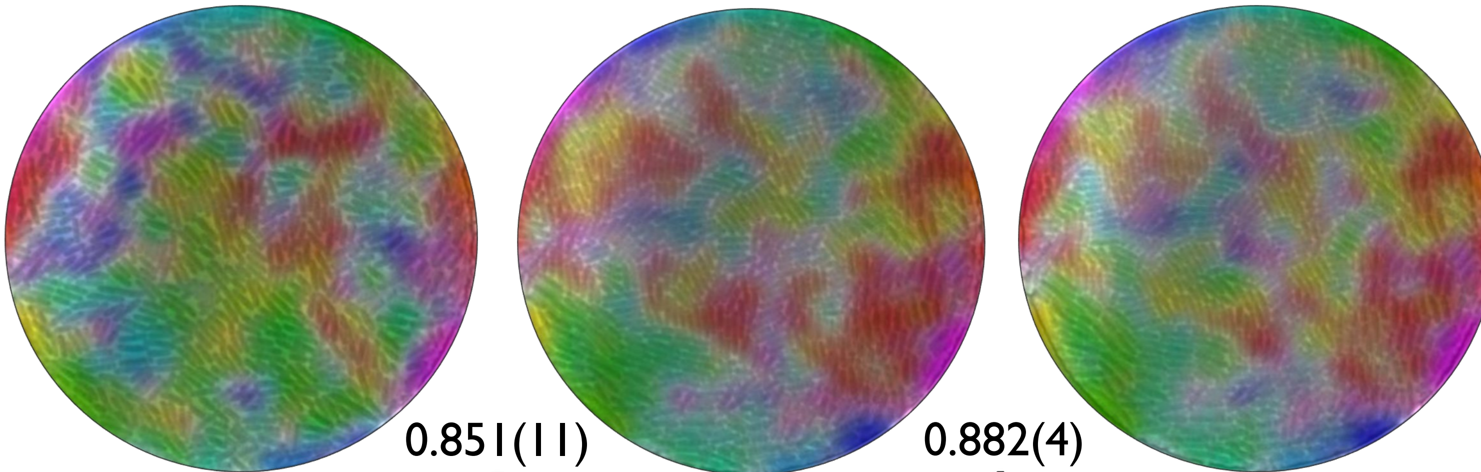


- Rapid dynamic slowdown in orientation, too!
- $\boxed{\tau_\theta \sim (\phi_c^\theta - \phi)^{-\gamma_\theta}}$ $\phi_c^\theta = 0.851(11)$ & $\gamma_\theta = 1.5(12)$.
- Importantly, $\phi_c^\theta < \phi_c^Q = 0.882(4)$. Orientation freezes first!

Phase Diagram



$\phi = 0.785$ $\phi = 0.873$ $\phi = 0.888$



25μm

0.851(11) 0.882(4) ϕ

active fluid ϕ_c^θ orientation glass ϕ_c^Q complete glass

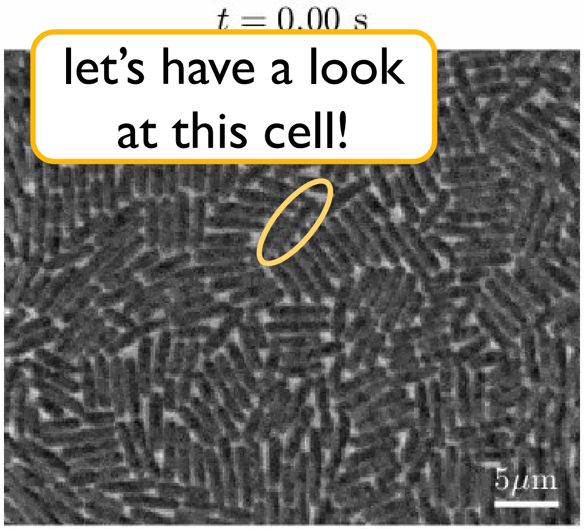
DOF's			
translation	evolving	evolving	frozen
orientation	evolving	frozen	frozen

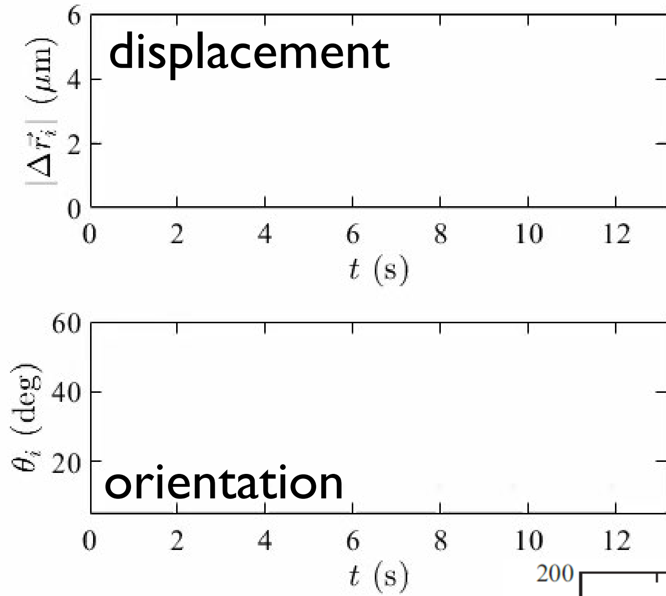
※ Similar 2-step transition observed in ellipsoidal colloids

[Yilong Han group 2011 & 2014; Ganapathy group 2013]

Orientation Glass

How do bacteria move? $(\phi = 0.873)$

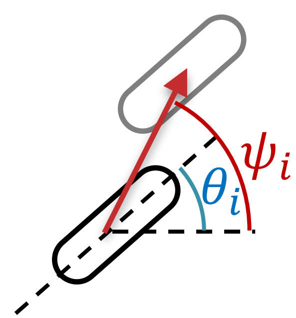


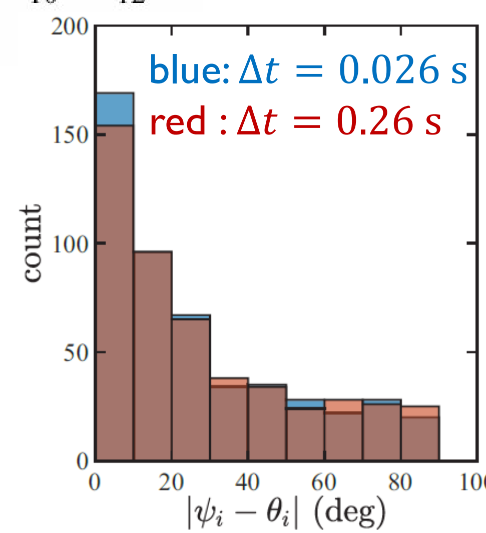


cage escape event!

Cells tend to move along orientation.

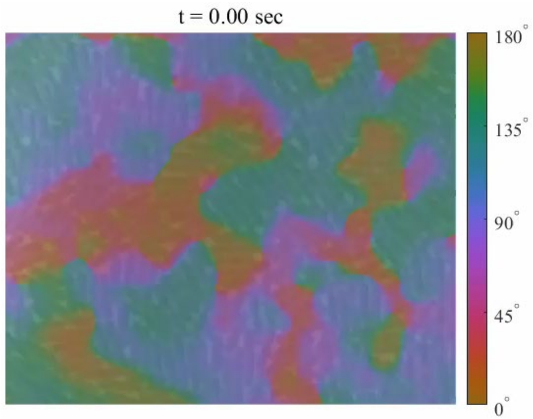
➔ Motion is guided by frozen orientation field!





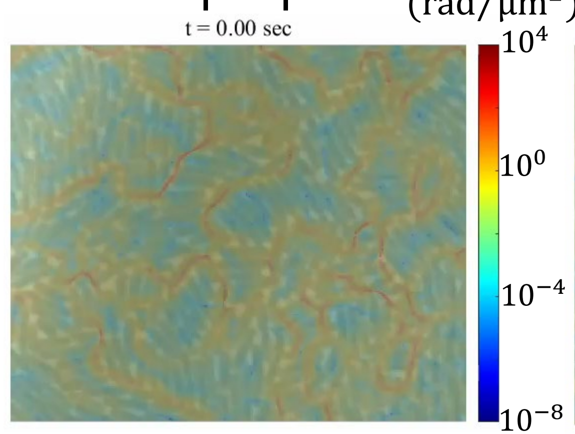
Domain Structure

$\theta(\vec{r},t)$



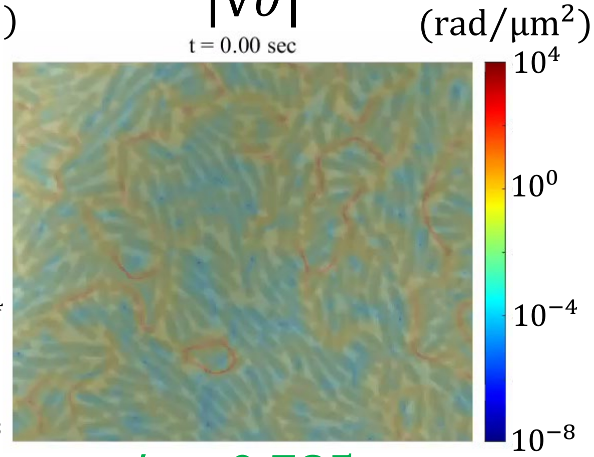
$\phi = 0.873$
(orientation glass)

$|\nabla\theta|^2$



$\phi = 0.873$
(orientation glass)

$|\nabla\theta|^2$

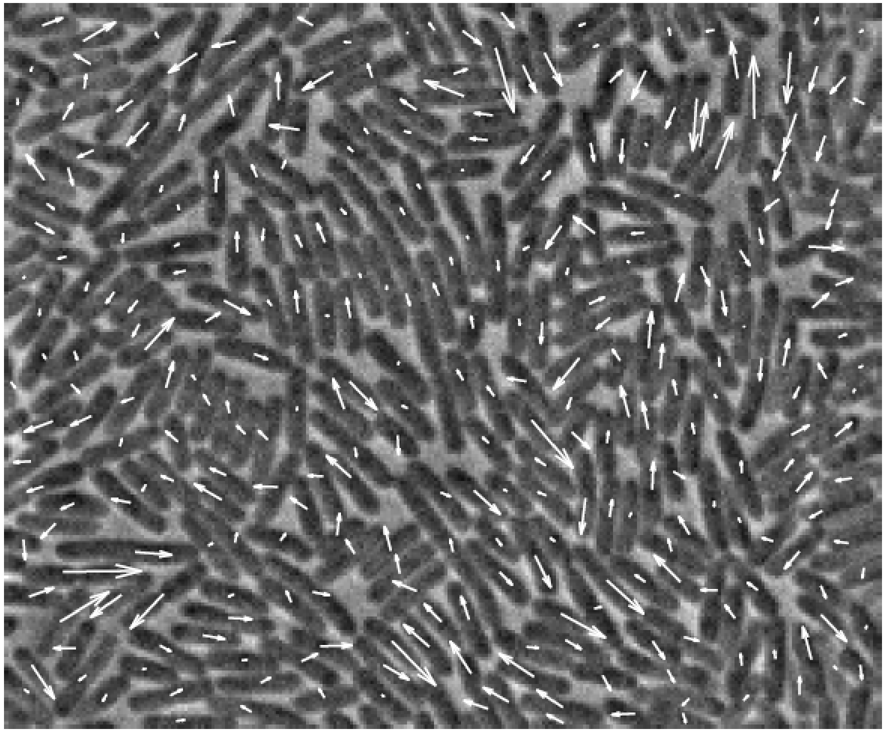


$\phi = 0.785$
(active fluid)

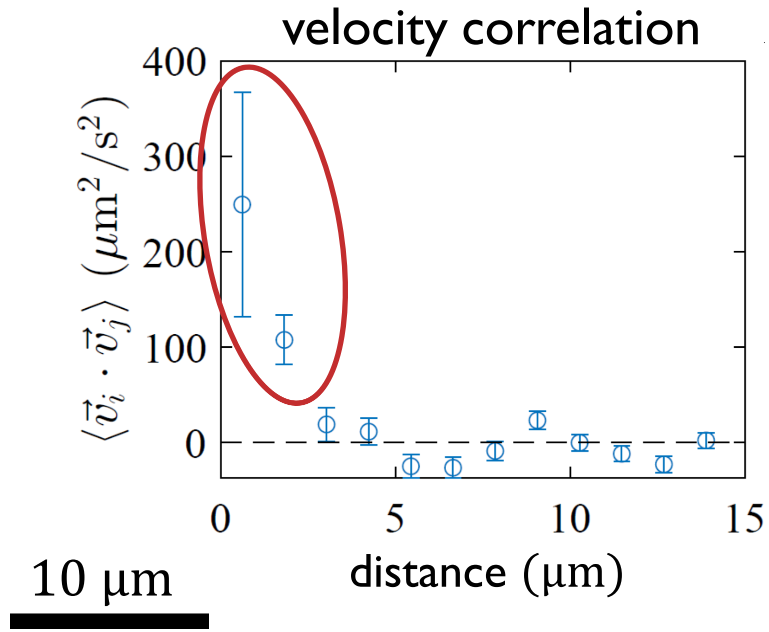
- Domains of locally aligned cells (typical area $\approx 8.3(21)\ \mu\mathrm{m}^2$)
- Domains are frozen in glassy phases.
- Domains are continuously rearranged in active fluid phase.
- Domain structure + motion along alignment
  ➜ collective motion! (especially in active fluid phase)

Collective Motion

Displacement $\Delta\vec{r}_i = \vec{r}_i(t + \Delta t) - \vec{r}_i(t)$ (in active fluid phase)



$\Delta t = 0.053\ s$



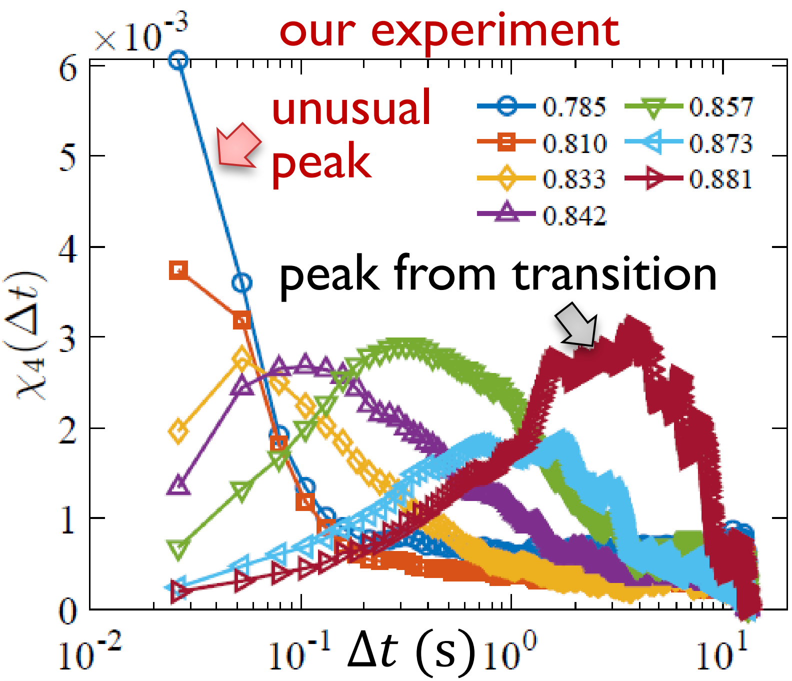
- Polar velocity correlation (despite nematic volume exclusion) with correlation length consistent with domain size.
- Dynamic heterogeneity?

Dynamic Heterogeneity

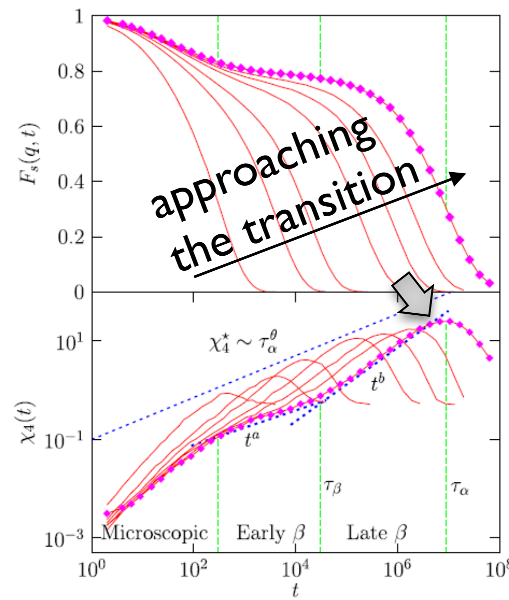
dynamic susceptibility

$$\boxed{\chi_4 = \phi[\langle Q(t,\Delta t)^2\rangle_t - \langle Q(t,\Delta t)\rangle_t^2]}$$

[Pastore et al., Sci. Rep. 2017]



typical behavior in thermal glass

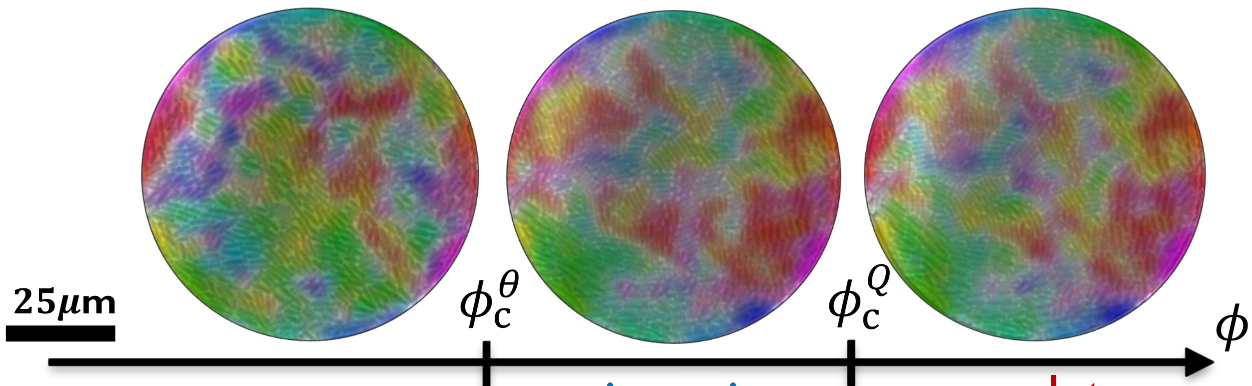


[Berthier & Biroli, Rev. Mod. Phys. 2011]

- Dynamic heterogeneity is observed!
- Unusual peak at low ϕ $\leftarrow$ due to collective motion?
  expected to arise generally in active rod glass.

Summary of Results

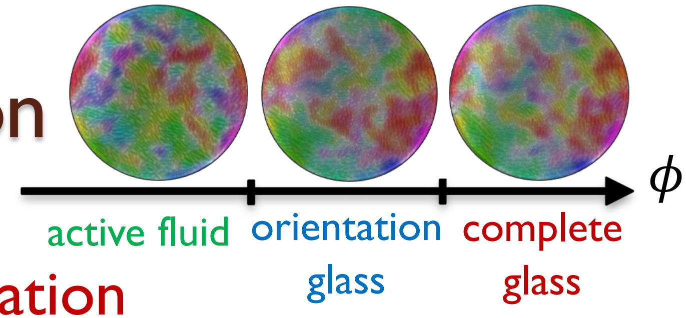
Spontaneous glass transition of motile *E. coli* populations
bottom lines: 2-step transition & collective motion



DOF's	active fluid	orientation glass	complete glass
translation	evolving	evolving	frozen
orientation	evolving	frozen	frozen

- Characteristic glassy dynamics
  (dramatic slowdown, fragility, cage escape, dynamic heterogeneity)
- Cell shape ➜ characteristic domain structure
  \+ Motility ➜ collective motion & unusual signal in χ_4 at low ϕ

Discussions on 2-Step Transition



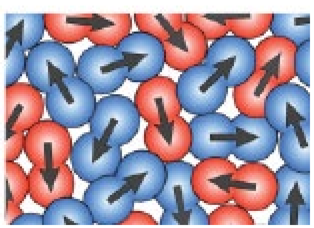
- Our transition: orientation ➜ translation

- Literature: both "ori ➜ trans" & "trans ➜ ori" exist.

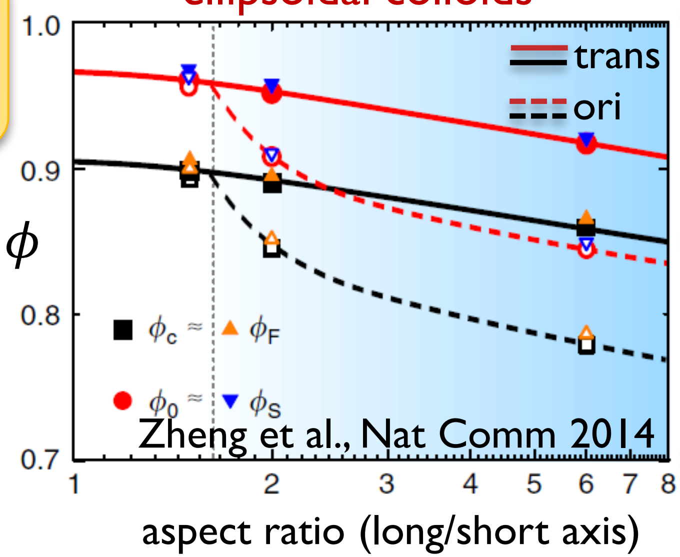
	ellipsoidal colloids Zheng et al. 2011 & 2014, etc.	rigid rods MCT Letz et al., PRE 2000
Small aspect ratio	Simultaneous	trans ➜ ori
Large aspect ratio	ori ➜ trans	Simultaneous

What determines the order?

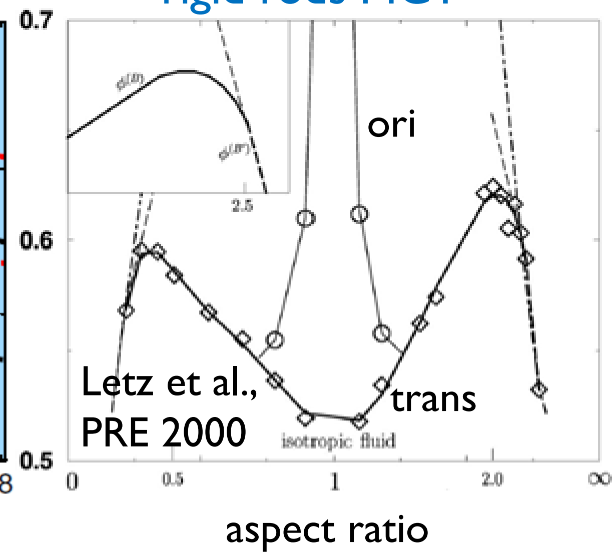
cf) active dumbbells:
trans ➜ ori
[Mandal et al. PRE 2017]



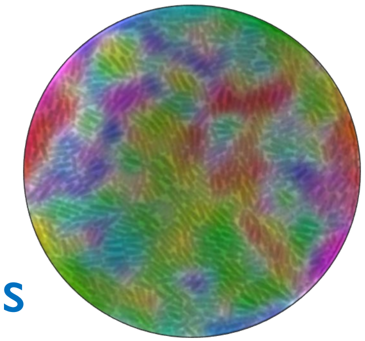
ellipsoidal colloids



rigid rods MCT



Non-Equilibrium Nature of Bacterial Glass

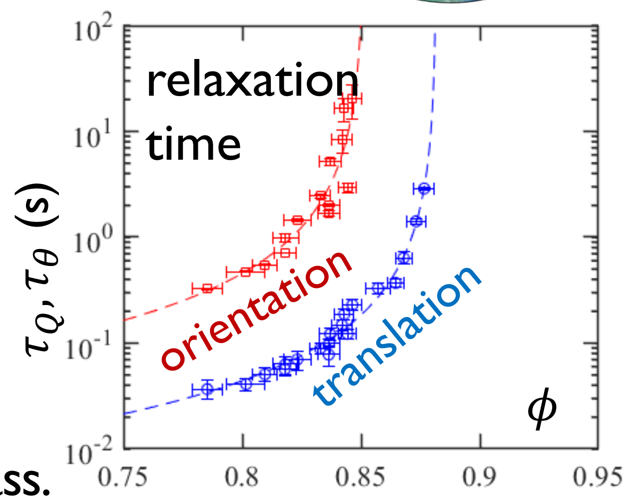


- Collective motion & unusual peak of χ_4 at low ϕ (maybe characteristic of active rod glass)

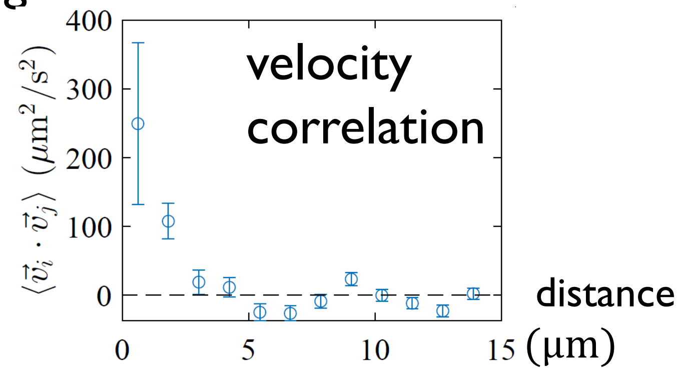
- Relaxation slowdown different from thermal glass

$\boxed{\tau_{Q,\theta} \sim \left(\phi_{\mathrm{c}}^{Q,\theta} - \phi\right)^{-\gamma_{Q,\theta}}}$ MCT power law

  - Here: $\gamma_\theta = 1.5(12)$
    $\gamma_Q = 1.5(3) < \gamma_0 \equiv 1.76\cdots$
  - In equilibrium: generally $\gamma \geq \gamma_0$
    [Götze's book 2009; thanks to Ikeda-san]
  - $\gamma < \gamma_0$ is possible only out of equilibrium.
    a kind of β relaxation impossible for thermal glass.



- Velocity correlation
  - Absent in equilibrium systems.
  - Used as input for active glass MCT
    [Szamel et al., PRE 2015; Szamel PRE 2016]



Summary

Refs

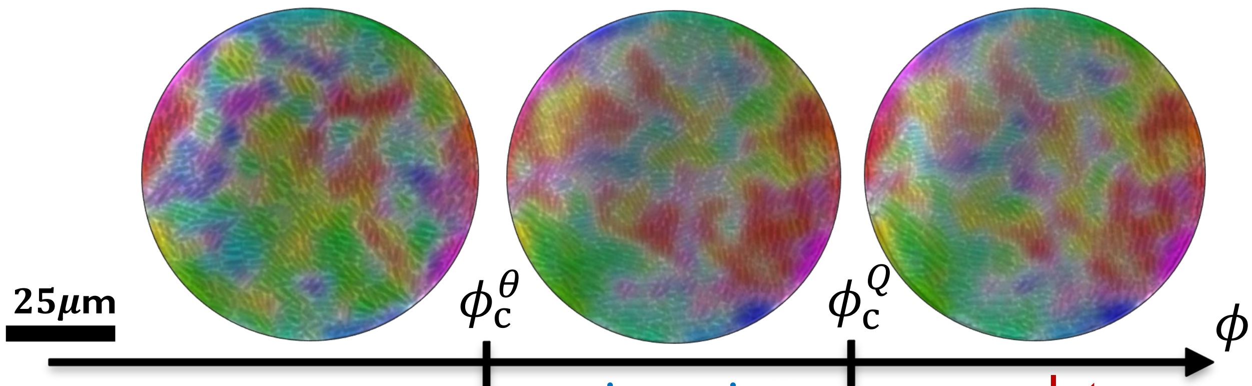
main: H. Lama et al., arXiv:2205.10436.

device: T. Shimaya et al., Commun. Phys. **4**, 238 (2021)

Spontaneous glass transition of motile *E. coli* populations

bottom lines: 2-step transition & collective motion

preprint



DOF's	active fluid	orientation glass	complete glass
translation	evolving	evolving	frozen
orientation	evolving	frozen	frozen

- Characteristic glassy dynamics

  (dramatic slowdown, fragility, cage escape, dynamic heterogeneity)

- Cell shape ➜ characteristic domain structure

  \+ Motility ➜ collective motion & unusual signal in χ_4 at low ϕ