Membrane Rotors

and Membrane Proteins

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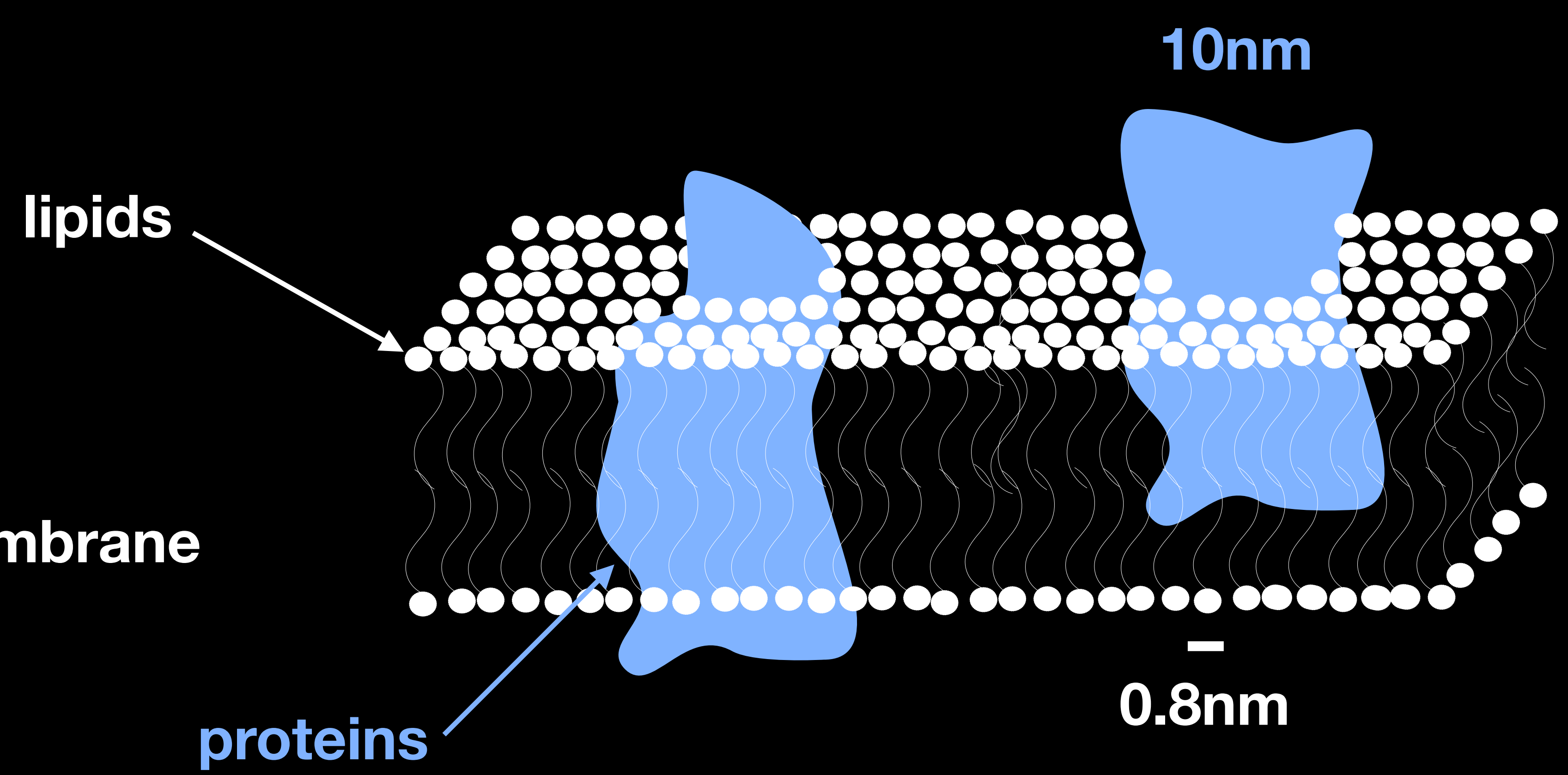
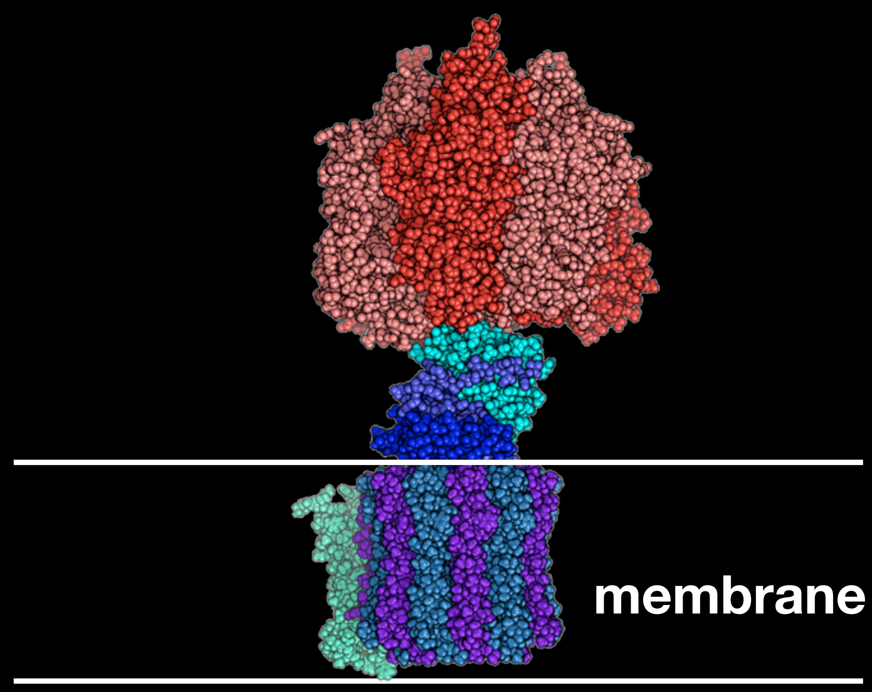
Biological Membranes



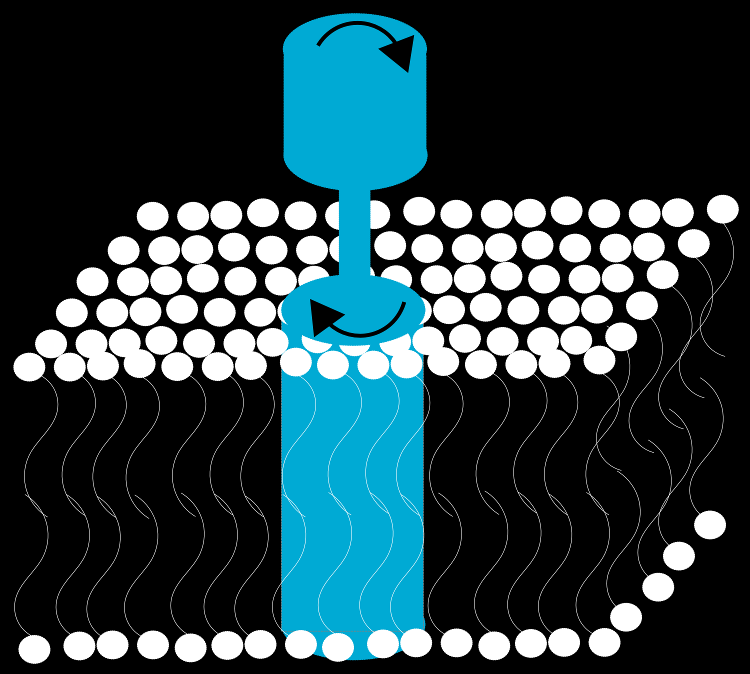
Lipids and proteins
move freely in the membrane

biomembrane = 2D fluid (like a soap bubble)

ATP synthase
a Rotating Protein



Molecular model

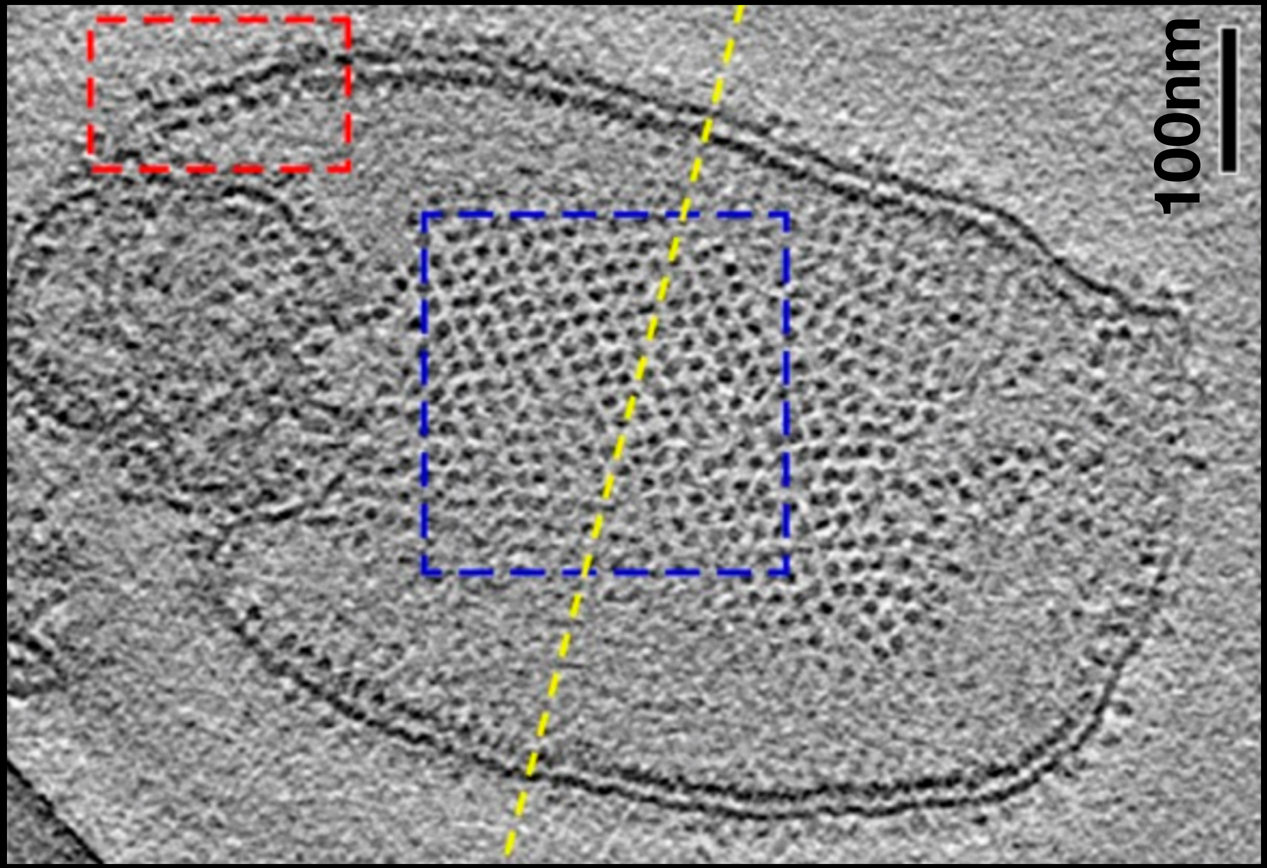


Our model

Creates ATP (fuel of life)

Rotates in the membrane

Forming a Lattice - Why?

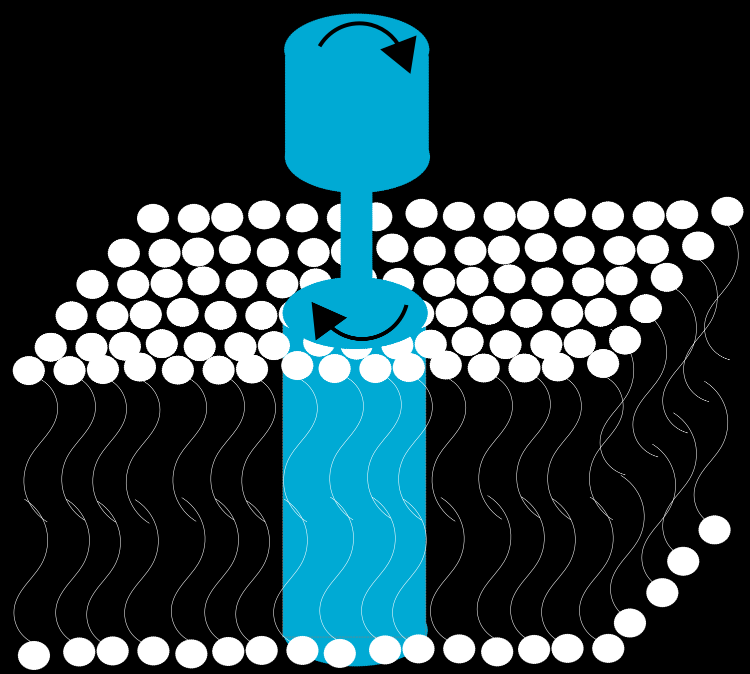


ATP synthase in a membrane
Jiko, Gerle et. al, eLife. 2015

Lattice formation could be explained with just hydrodynamics!

Suggested by: Lenz, Joanny, Julicher, Prost, PRL 2003

Protein vs. Hurricane



	ATP synthase protein	Hurricane Rita
Scale	10 nm	10 km
Dominated by	Viscosity	Inertia

Vorticity in a 2D Ideal Fluid

Incompressibility $\nabla \cdot \mathbf{u} = 0$

Stream Function $u_x = -\frac{\partial \Psi}{\partial y}$ $\quad u_y = \frac{\partial \Psi}{\partial x}$

Define $\mathbf{u} = \nabla^{\perp} \Psi$

Vorticity $\omega = \nabla \times \mathbf{u} \quad = \nabla^2 \Psi$

For a point vortex $\omega = \Gamma \delta(r)$

$$\Gamma \delta(r) = \nabla^2 \Psi$$

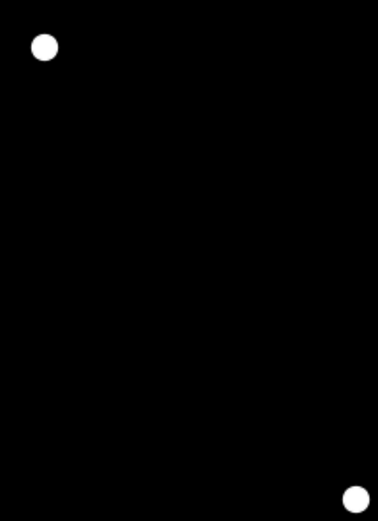
$$\boxed{\Psi = \frac{\Gamma}{2\pi} \log r}$$

The Hamiltonian

For N point vortices $$H = \frac{1}{2\pi} \sum_{i \neq j} \Gamma_i \Gamma_j \log |r_i - r_j|$$

Equations of motion $$\Gamma_i \dot{x}_i = -\frac{\partial H}{\partial y_i} \qquad \Gamma_i \dot{y}_i = \frac{\partial H}{\partial x_i}$$

Conservation of: H, Linear momentum, Angular momentum



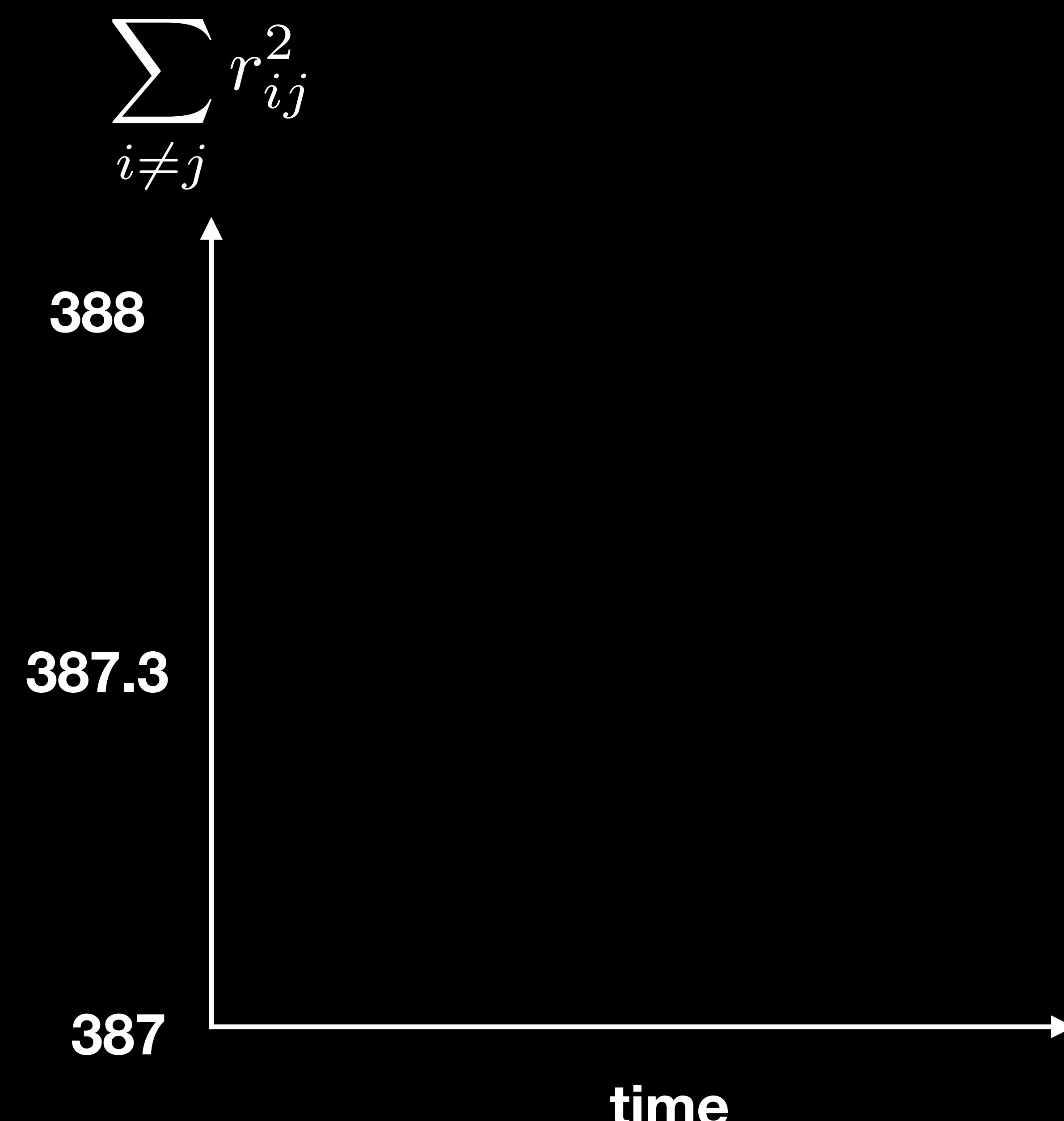
Same sign

100 Vortices

Sum of distances is conserved

Can’t collapse to a point

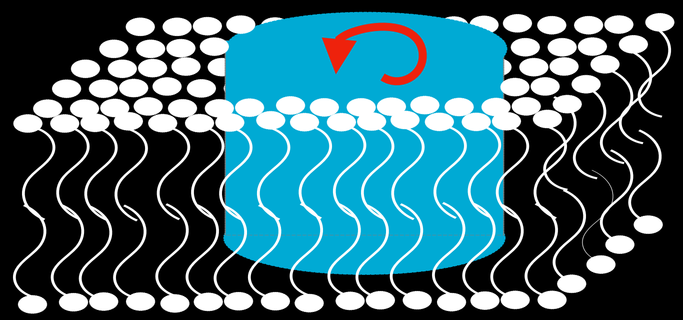
can’t diverge to infinity



Rotors in a membrane

$\mathbf{u}$, $\eta_{3\mathrm{D}}$

$\mathbf{v}$, $\eta_{2\mathrm{D}}$



Momentum conservation

$$0 = \eta_{2\mathrm{D}} \nabla^2 \mathbf{v} - \cancel{\nabla P} + \mathbf{f} \quad + \eta_{3\mathrm{D}} \left. \frac{\partial \mathrm{u}}{\partial z} \right|_{z=0}$$

In Fourier Space

$$-\eta_{2\mathrm{D}} q^2 \tilde{\mathbf{v}} - \eta_{3\mathrm{D}} \tilde{\mathbf{v}} q + \tilde{\mathbf{f}} = 0 \qquad (\, \tilde{\mathbf{u}} = \tilde{\mathbf{v}} e^{-|\mathbf{q}|z})$$

The velocity is

$$\tilde{\mathbf{v}} = \frac{\tilde{\mathbf{f}}(\mathbf{q})}{\eta_{2\mathrm{D}} q (q + \kappa)} \qquad \kappa = \frac{\eta_{3\mathrm{D}}}{\eta_{2\mathrm{D}}}$$

Deriving the Stream Function Ψ

$$\tilde{\mathbf{v}} = \frac{\tilde{\mathbf{f}}(\mathbf{q})}{\eta_{2\mathrm{D}} q(q+\kappa)}$$

Rotlet $$\mathbf{f} = \tau_0 \nabla^{\perp} \delta(r)$$

We can define $$\tilde{\mathbf{v}} = \tau_0 \nabla^{\perp} \tilde{\Psi} \qquad \tilde{\Psi} = \frac{1}{\eta_{2\mathrm{D}} q(q+\kappa)}$$

In real space $$\Psi = \frac{\pi}{2}\left(H_0(\kappa r) - Y_0(\kappa r)\right)$$

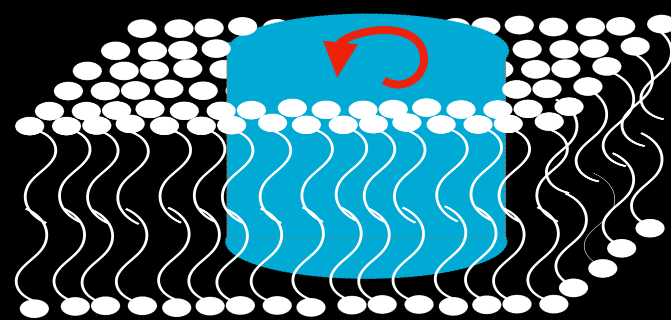
$r \ll \kappa^{-1}$ → $\log(\kappa r)$

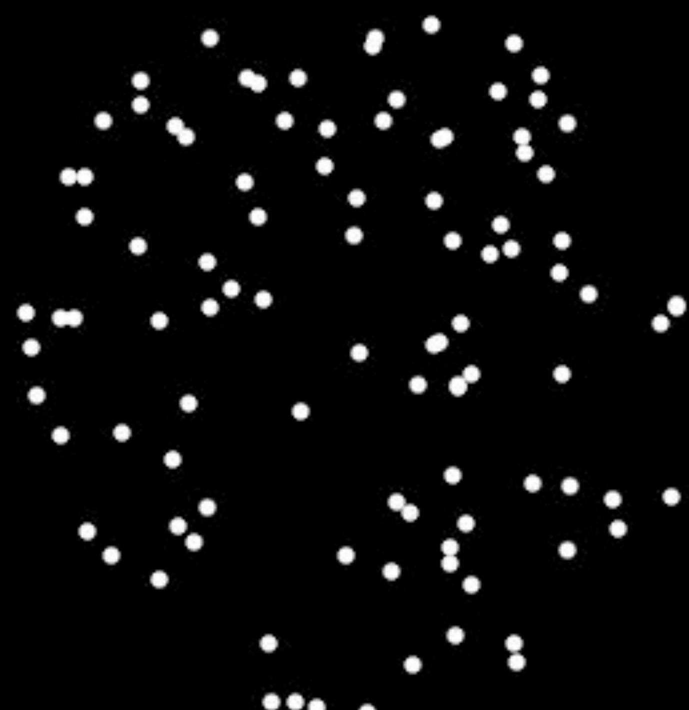
Ideal fluid (Euler)

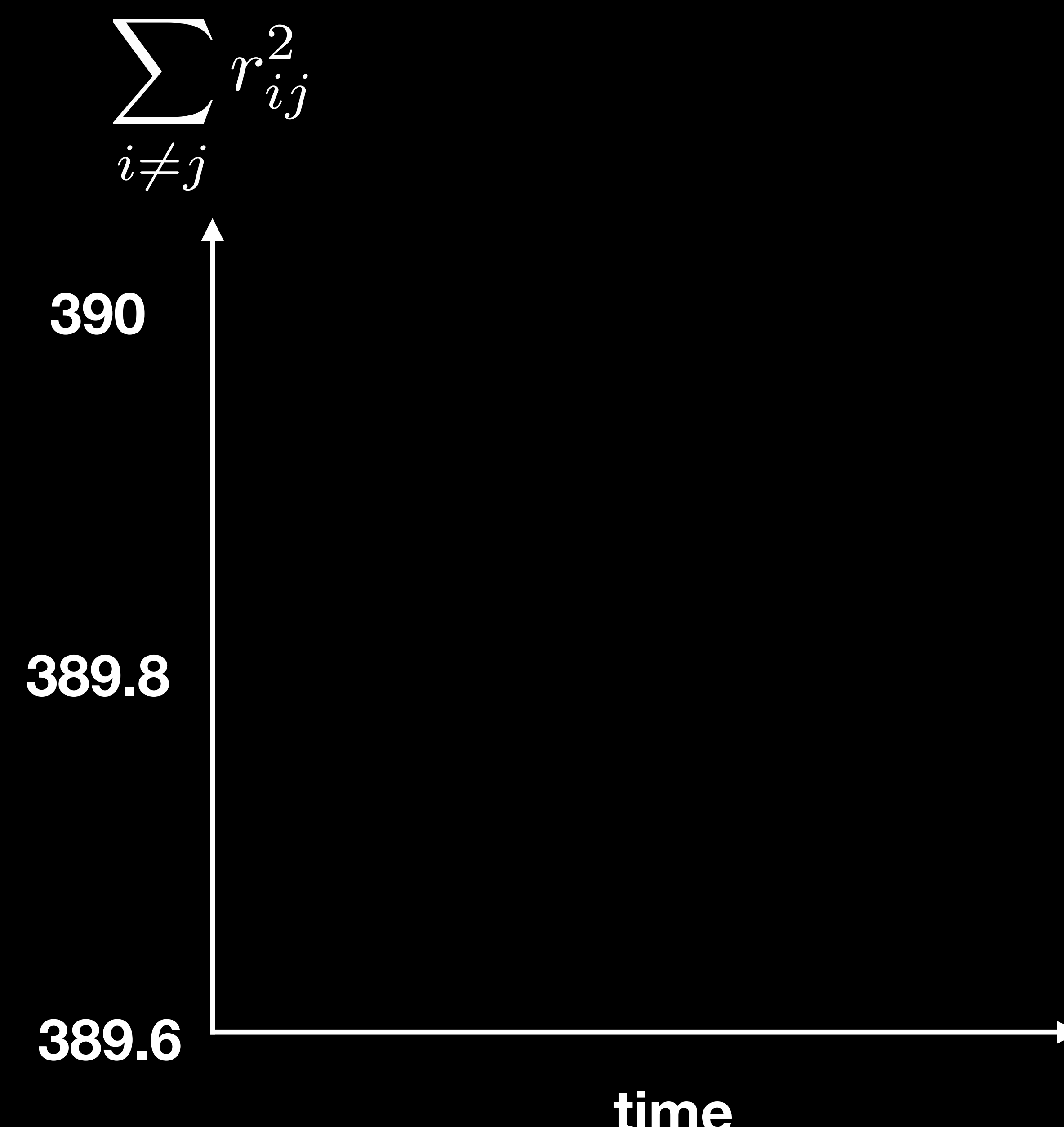
$r \gg \kappa^{-1}$ → $\frac{1}{r}$

Quasi geostrophic

100 Rotors in a Membrane

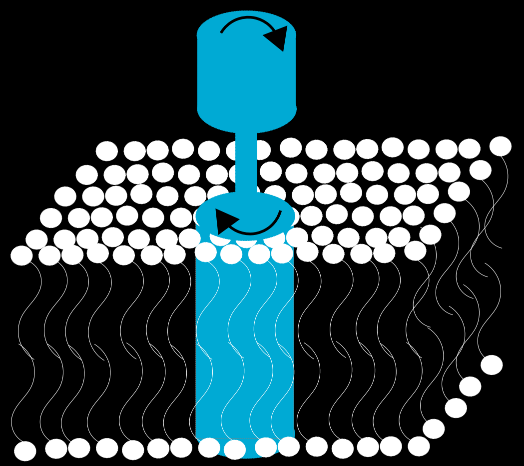






Proteins + Short Ranged Repulsion

Proteins are torque free



yet they act like vortices

$$\Psi = -\frac{1}{\kappa r} + \frac{\pi}{2}\left(H_0(\kappa r) - Y_0(\kappa r)\right)$$

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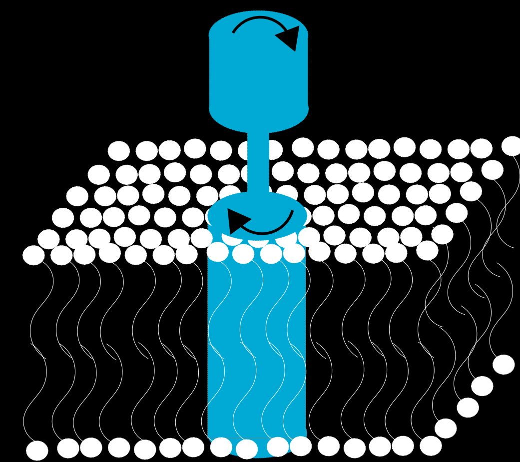

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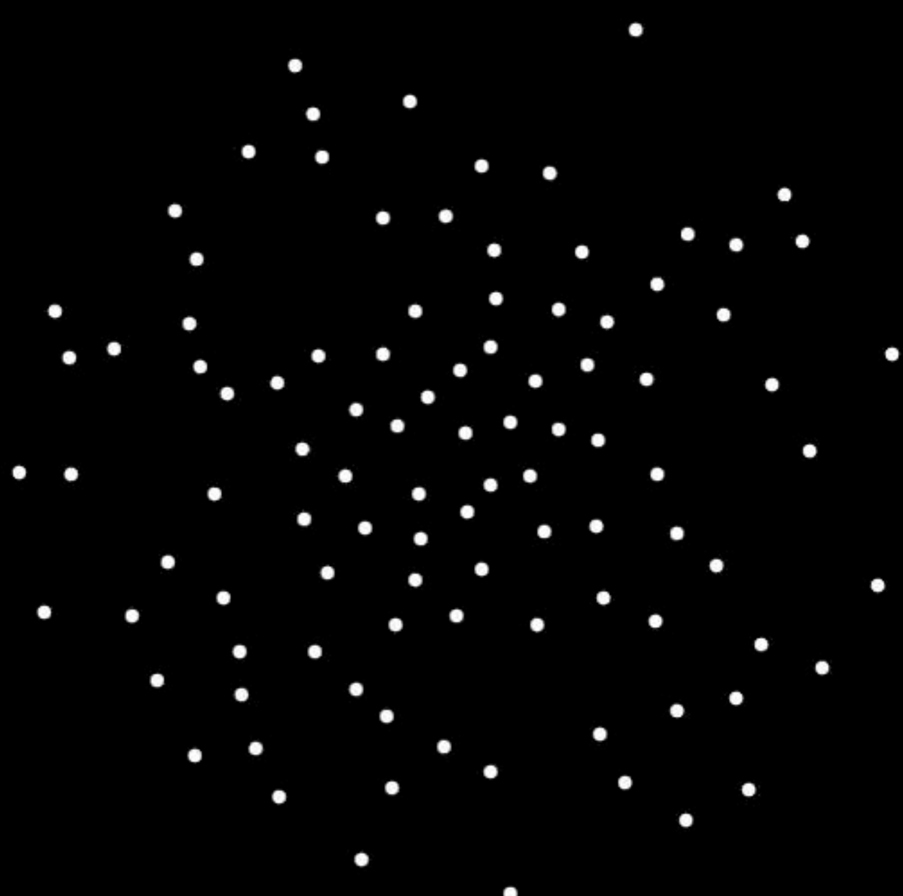
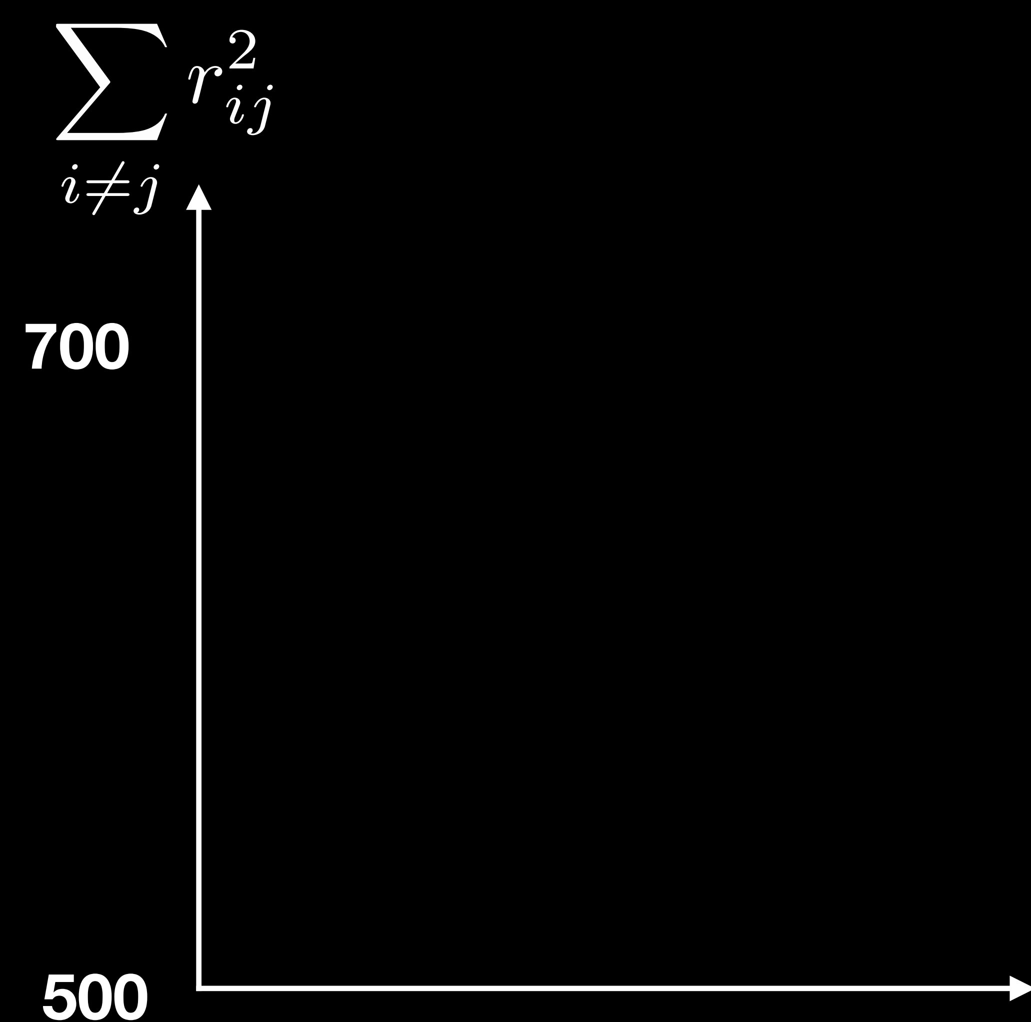
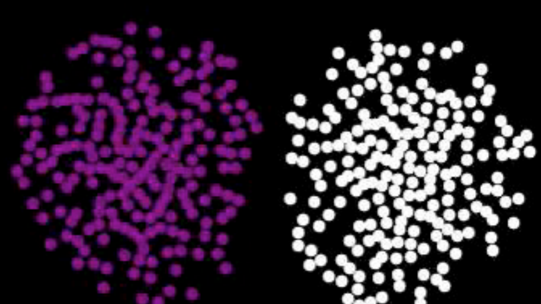


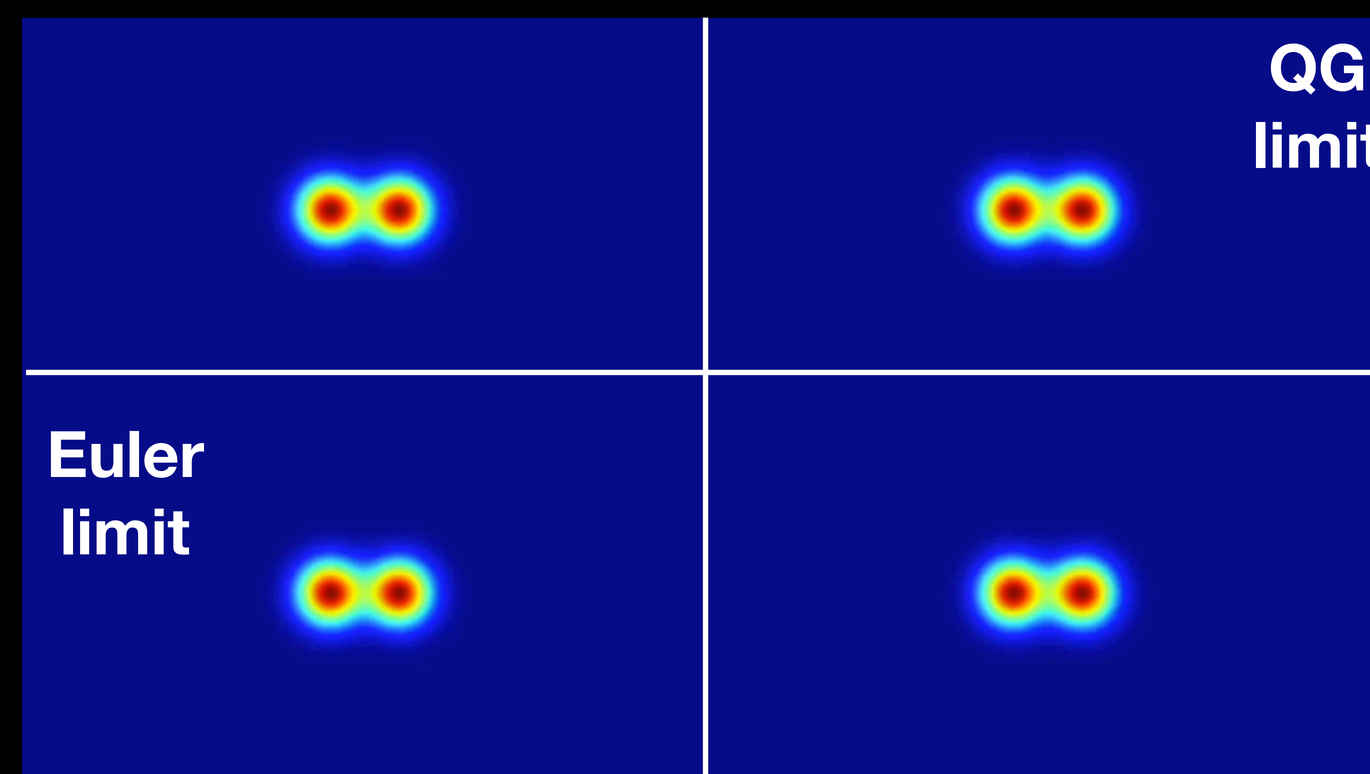


Discrete to Continuous

Discrete → **Continuous**



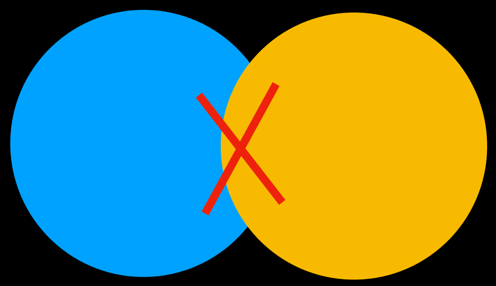
$\kappa r = 10$ $\kappa r = 1$



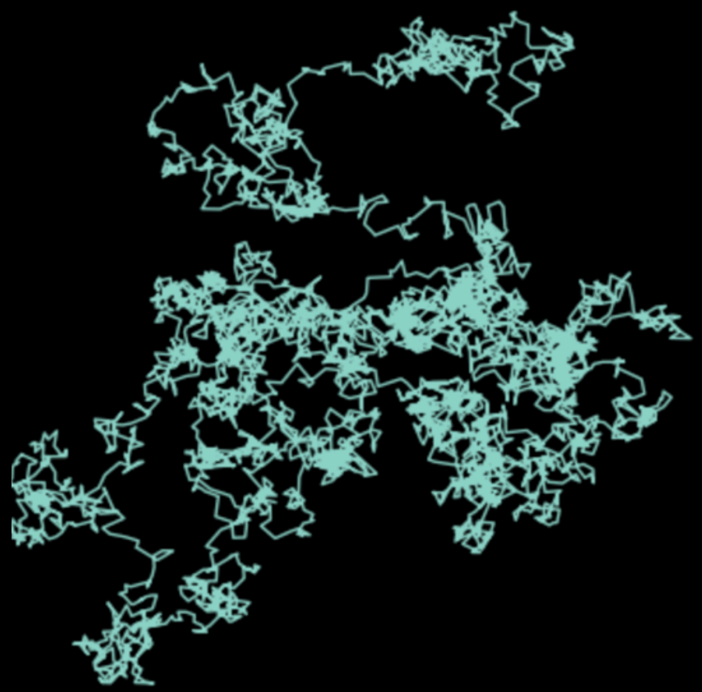
$\kappa r = 0.01$ $\kappa r = 0.1$

Difference from Ideal Vorticity

- Short-ranged repulsion

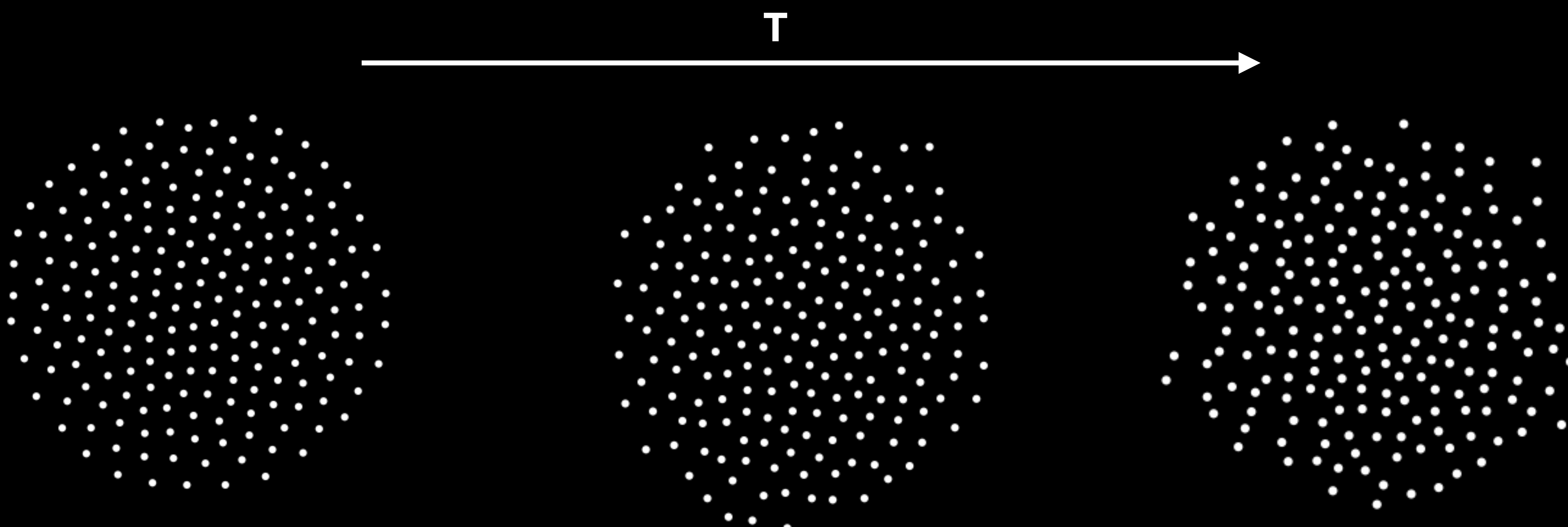


- Brownian motion



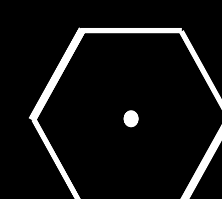
Brownian Motion

Destroying order



The hexatic order parameter

$$\Psi_6 = \frac{1}{N}\sum_{i=1}^{N} e^{6i\theta}$$

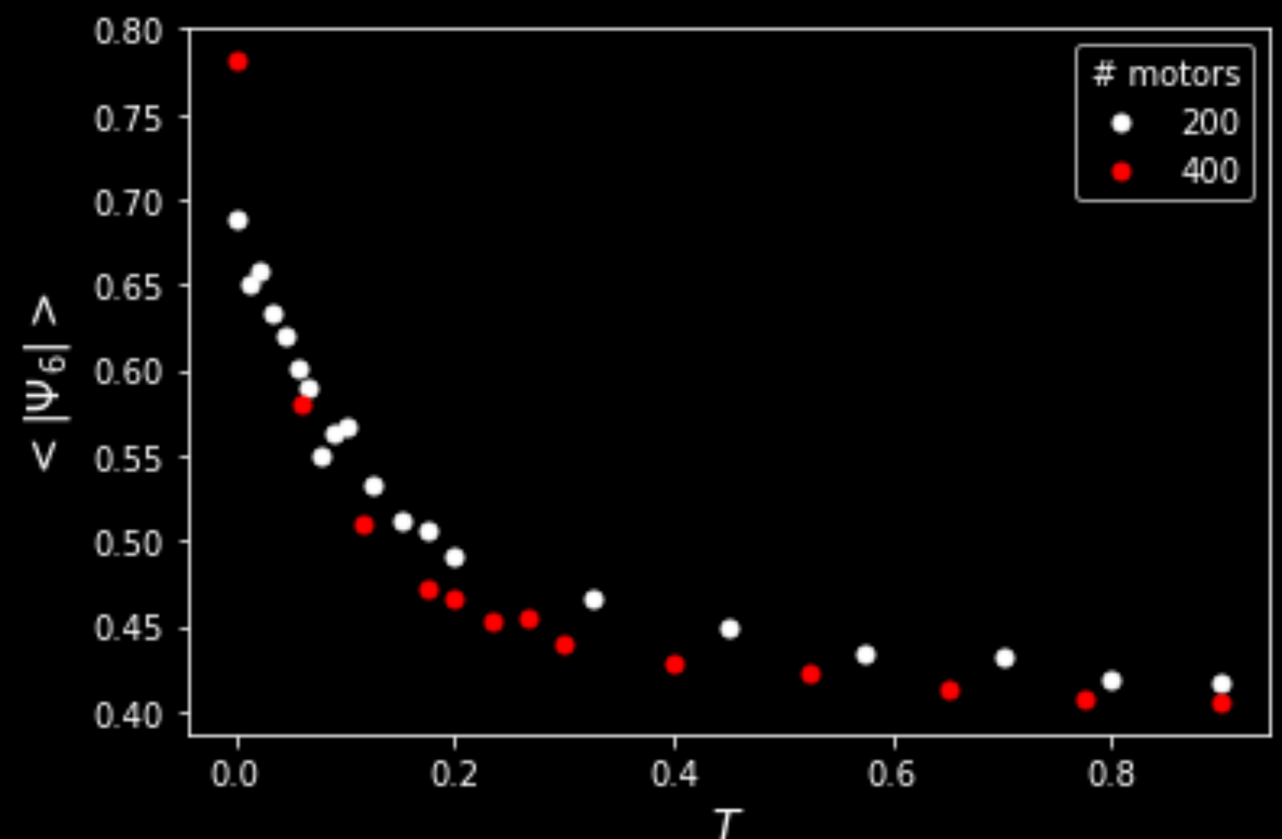


Sokolov-Diamant Mobility Tensor

$$B^{12}_{\alpha\beta} = \frac{1}{4\pi\eta_m}\left[\left(\log\frac{2}{\kappa r} - \gamma - \frac{1}{2} + \frac{a^2}{r^2}\right)\delta_{\alpha\beta} + \left(1 - \frac{2a^2}{r^2}\right)\frac{r_\alpha r_\beta}{r^2}\right]$$

Y. Sokolov and H. Diamant JCP 2018

The Rotne-Prager analog for a membrane = positive definite mobility tensor



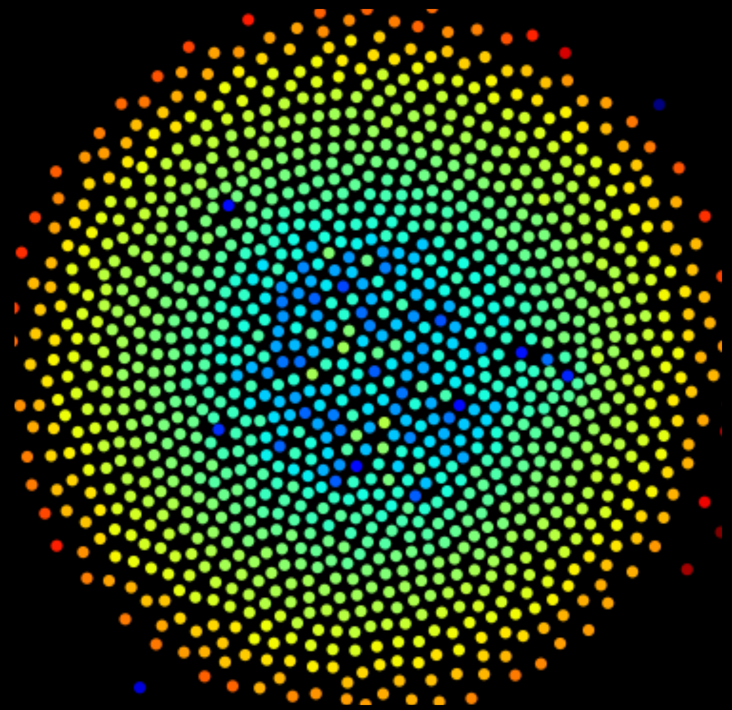
average over local hexagonal order

Conclusions

- At short distances membrane rotors act just like vortices in an ideal fluid
- Motor proteins self assemble into a lattice when short ranged repulsion is included
- Continuous dynamics: Hurricane in a membrane?

Next

Distribution of Velocities



Understanding the density variation