

自走する粒子系としての  
細胞や生物集団のふるまい

**Collective behaviors of cells and lives  
modelled as self-propelled particles**

Ryoichi Yamamoto

# 70 unsolved problems in Physics (JPS 2017)

日本物理学会創立70周年記念企画

## 物理学70の不思議

- 16. 原子核の形
- 13. 陽子=クォーク3つ?
- 14. テトラクォーク
- 17. 超重原子核
- 4. クォーク・グルーオン・プラズマ
- 15. ストレンジ原子核
- 12. 反物質
- 21. 中性子星
- 33. 冷却原子
- 9. 宇宙の物質生成
- 22. 超大質量ブラックホール
- 23. ブラックホールと情報
- 70. 物理学はどこへ?
- 62. 経済物理
- 19. 格子QCD
- 11. ヒッグス粒子
- 6. ニュートリノ
- 10. クォークの閉じこめ
- 39. マヨラナ粒子
- 8. 暗黒エネルギー
- 7. 暗黒物質
- 2. 4次元時空
- 29. 核融合
- 20. 恒星
- 27. 太陽コロナ
- 24. 相対論的ジェット
- 25. 宇宙線
- 35. 量子通信
- 65. タンパク質
- 67. 分子機械
- 70. 物理学はどこへ?
- 64. シマウマの縞
- 69. 私たちと物理
- 5. 素粒子の世代
- 37. 素粒子と物性
- 38. モンテカルロ計算
- 45. 光誘起相転移
- 49. 物質設計
- 34. 量子力学の検証
- 48. 極限環境
- 50. 金属と絶縁体
- 60. ガラス
- 54. スピン・軌道相互作用
- 61. 粉体
- 66. 電子と生命
- 68. 物理と生命
- 36. 量子コンピュータ
- 53. フェルミ液体論
- 41. トポロジカル秩序
- 30. 乱流
- 44. メタマテリアル
- 55. 隠れた秩序
- 51. 超伝導
- 52. 銅酸化物高温超伝導
- 31. 量子電磁力学
- 57. 統計力学の基礎
- 47. スピントロニクス
- 59. 可積分系
- 43. 超短パルスレーザー
- 42. 観るの極み
- 40. 還元と創発

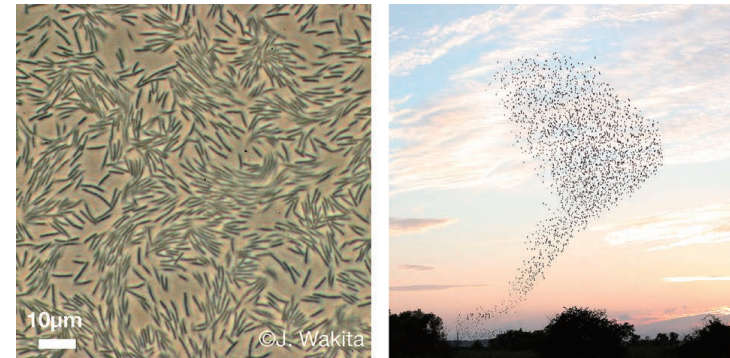
# #63: Collective behaviors of cells and lives modelled as self-propelled particles

63

## 自走する粒子系としての細胞や生物集団のふるまい

混雑した駅の通路や交差点を歩いているうちに、行き交う人の流れに自然と「レーン」が形成されていることに気づくことがある。こうしたヒトの群集に限らず、動物の群れや微生物の集団を観察してみると、何かに命令されることなく、運動の様子や配置・配列に、ある種のパターンや構造が自発的に現れる例がいくつも見つかる（図左：バクテリア（枯草菌）が集団運動している様子）。

互いに影響し合いながら運動する同種の粒子や要素が呈する巨視的なふるまいを知り、その背後にある数理的な共通性や差異を明らかにするのは、統計物理の重要なテーマの1つである。細胞や動物、人工的な移動物体である自動車など、自ら運動する粒子や物体を「同種の粒子」とみなし、自己駆動粒子系やアクティブマターとよんで、その多体的・統計的なふるまいを明らかにしようという試みが広がっている。自己駆動粒子系は複雑でその例は多岐にわたるため、それらをすっきりと分類することは難しい。一般に、粒子自体が異方的で、エネルギー散逸と注入をともない、粒子間の実効的な相互作用に作用・反作用の法則が成り立たない。また、局所的なゆらぎが緩和せず系全体におよび、疎密や対流、渦などが自己組織される（図右：竜巻



状の鳥（ムクドリ）の渦巻き）などの点において、アクティブではない粒子の系とはふるまいが大きく異なる。

ゆらぎをとめないながら自走する粒子を単純化した数理モデルとして、ビチェックモデル (Vicsek model) がよく調べられている。周囲と進行方向をそろえようとする効果とゆらぎとの競合によって、運動方向の秩序が不連続的に相転移することが知られている。はじめはランダムに歩行していた昆虫の集団が、ある密度を超えると1方向に行進をはじめめる現象などが、このモデルでよく説明できるという報告もある。こうした研究によって、生物や人工物の「群れ」の数理的な理解が進みつつある。

# Major categories of self-propelled particles

## Dry particles

in which hydrodynamics is not important  
ex. flock of birds

## Wet particles

in which hydrodynamics plays crucial role  
ex. school of fish





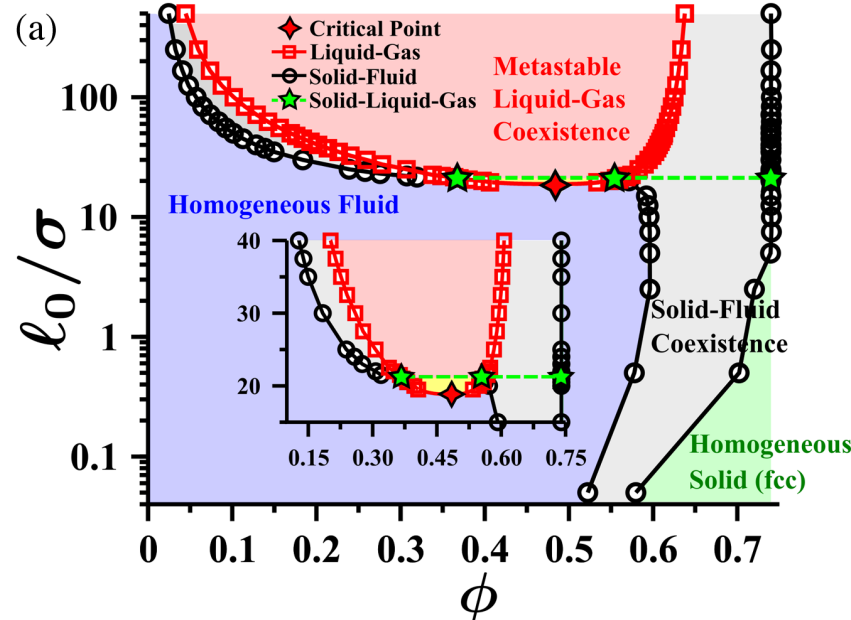
# A popular dry particles: Active Brownian particles

- **MIPS**: Cates, Tailleur, Ann. Rev. Cond. Matt. 6, 219 (2015)
- Omar, Klymko, GrandPre, Geissler, PRL 126, 188002 (2021)

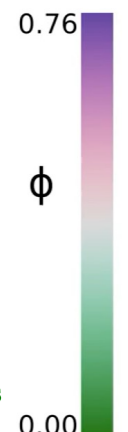
$$\dot{\mathbf{r}} = v_0 \hat{\mathbf{n}} - (m\xi)^{-1} \nabla V(\mathbf{r}) + \sqrt{2D} \boldsymbol{\eta}_{\text{trans}}(t)$$

$$\hat{\mathbf{n}} = (\cos \theta, \sin \theta)$$

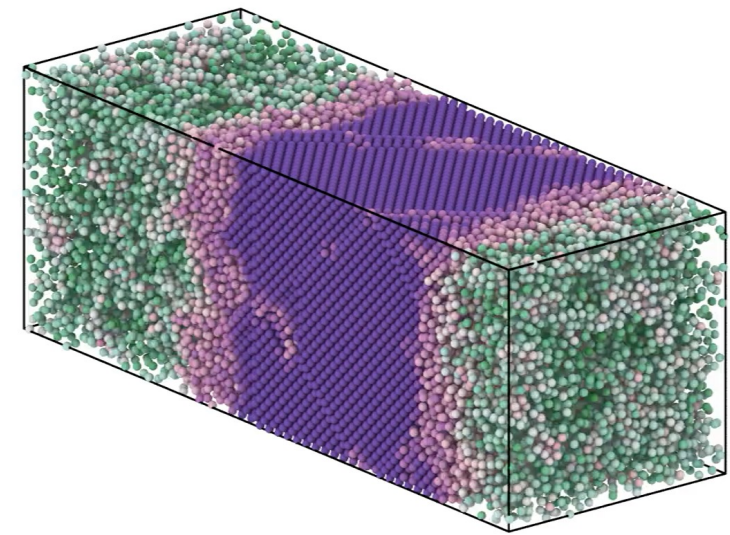
$$\dot{\theta} = \sqrt{2D_r} \eta_{\text{rot}}(t).$$



time = 0.0  $\tau$   
 $\phi = 0.5$

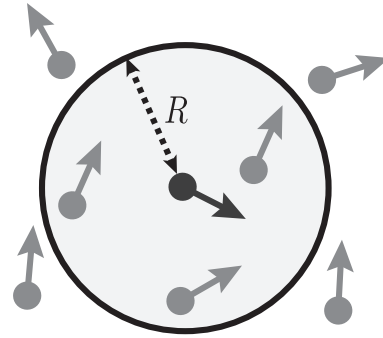


$l_0 / \sigma = 24$



# Another popular dry particles: **Vicsek model**

- Tamás Vicsek et al., PRL 75, 1226 (1986)



$$\theta_j^{t+1} = \arg \sum_{k \sim j} e^{i\theta_k^t} + \eta_j^t$$

$$\mathbf{r}_j^{t+1} = \mathbf{r}_j^t + v_0 \mathbf{e}_{\theta_j^{t+1}}$$

$$\begin{aligned} \partial_t \mathbf{v} + \lambda_1 (\mathbf{v} \cdot \nabla) \mathbf{v} + \lambda_2 (\nabla \cdot \mathbf{v}) \mathbf{v} + \lambda_3 \nabla (|\mathbf{v}|^2) \\ = \alpha \mathbf{v} - \beta |\mathbf{v}|^2 \mathbf{v} - \nabla P + D_B \nabla (\nabla \cdot \mathbf{v}) \\ + D_T \nabla^2 \mathbf{v} + D_2 (\mathbf{v} \cdot \nabla)^2 \mathbf{v} + \mathbf{f}, \end{aligned}$$

$$P = P(\rho) = \sum_{n=1}^{\infty} \sigma_n (\rho - \rho_0)^n,$$

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (\mathbf{v} \rho) = 0.$$

Vicsek model (discrete)  $\rightarrow$  **Toner-Tu model** (continuum)



## Other dry particles

There existed a few good models  
before Vicsek.

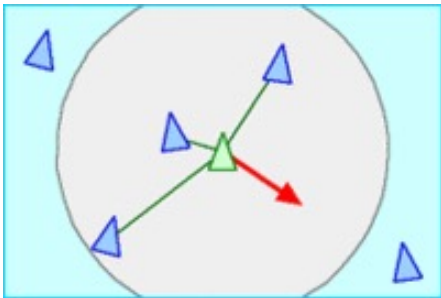


# Dry particles for CG: **Boids**

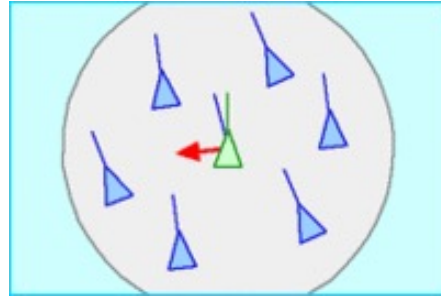
- artificial life program proposed by Craig Reynolds (1986)



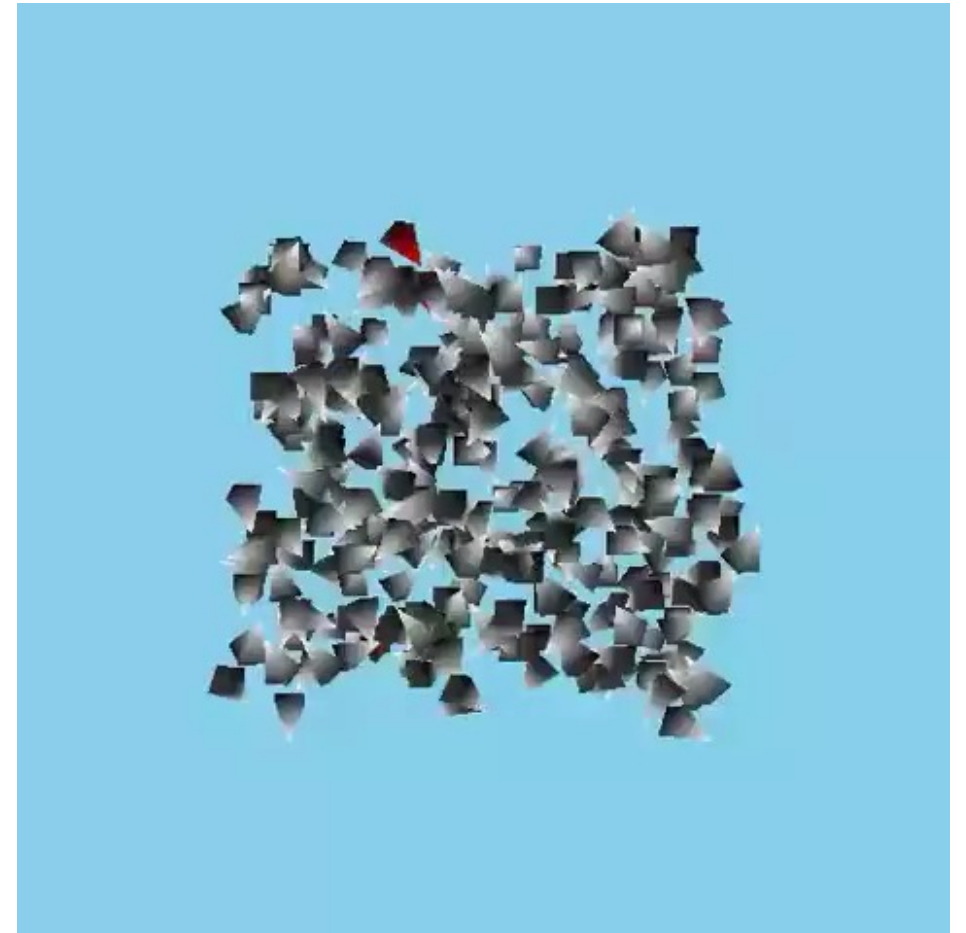
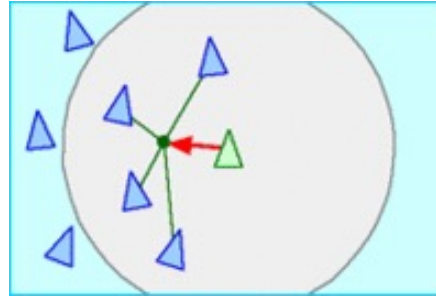
1) Separation



2) Alignment



3) Cohesion



# Dry particles in Japanese article: Sakai model

- Sumiko Sakai, 生物物理 13, 83 (1973)

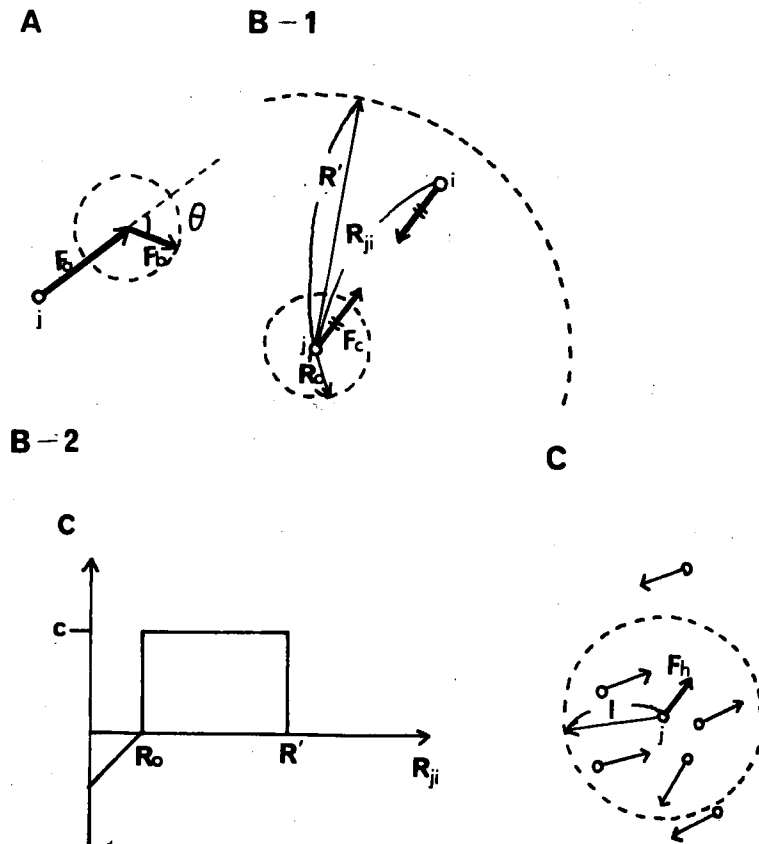


図1 モデルの説明  
 (A) 個体jの自己運動. (B) 接近運動 B-2は、引力Cと  
 個体間の距離  $R_{ji}$  との関係を示す. (C) 整列運動.

$$m \frac{d^2 \mathbf{X}}{dt^2} + \nu \frac{d\mathbf{X}}{dt} = \mathbf{F}, \quad (1)$$

$$\mathbf{F}_{a_j} = a \left( \frac{d\mathbf{X}_j}{dt} \right) \setminus \left| \frac{d\mathbf{X}_j}{dt} \right|, \quad (2) \text{ propulsion}$$

$$\mathbf{F}_{c_j} = \frac{1}{N-1} \sum_{i=1}^N \frac{C(R_{ji})(\mathbf{X}_i - \mathbf{X}_j)}{R_{ji}}, \quad (3) \text{ attraction} \\ \text{+ collision}$$

$$\mathbf{F}_{h_j} = \frac{1}{M} \sum_{\mathbf{X}_i \in A_j} h \left( \frac{d\mathbf{X}_i}{dt} - \frac{d\mathbf{X}_j}{dt} \right), \quad (4) \text{ aligning}$$

$$\mathbf{F}_b = \mathbf{b}(t) \quad (5) \text{ random}$$

# Dry particles in Japanese article: Sakai model

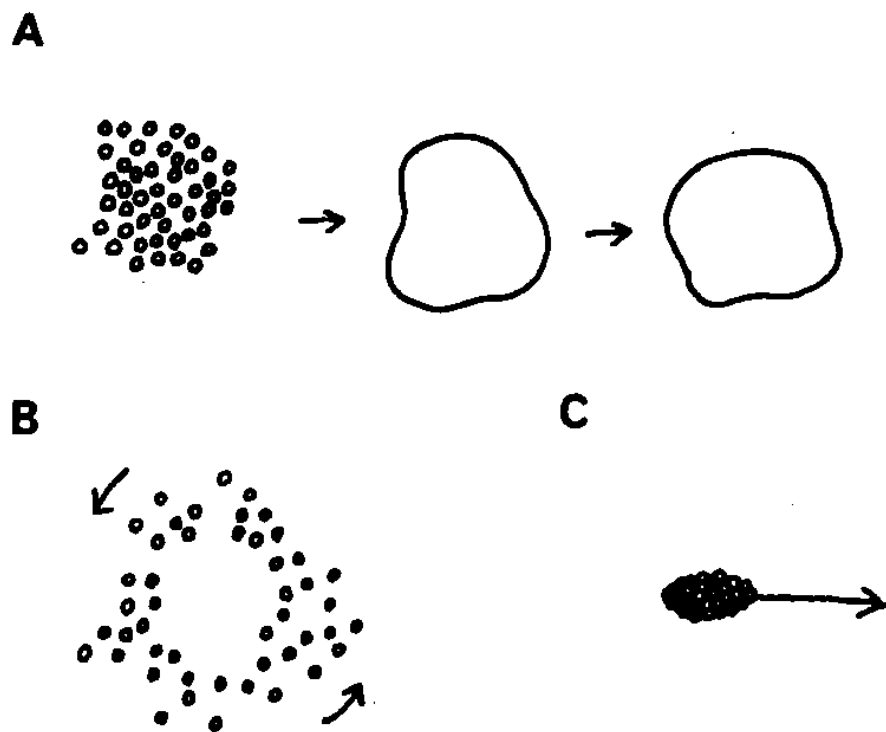


図 3 群れのパターンの種類

## (i) アメーバ状運動

推進力が小さく擾乱が大きいと、群れは小さくかたまりほとんど止っている。形はほぼ円形であるが、周辺の形状は刻々様々に変化する(図3-A)。

## (ii) ドーナツ形運動

推進力が大きくなると互いに輪状になって回転し、中心部に空洞のある群れになる。群れの重心はほとんど移動せず一ヶ所に止って回転している(図3-B)。

## (iii) 直進形運動

更に、整列作用が加わると小さくひとかたまりになって直進運動をする(図3-C)。

# Dry particles in Japanese article: Sakai model

$b > a$	$h = 0$	$h > 0$
$c \gg a$		
$c \sim a$		
$c \ll a$		
$0.5a < b < a$		
$c \gg a$		
$c \sim a$		
$c \ll a$		
$b < 0.5a$		
$c \gg a$		
$c \sim a$	$b=0$ 	 $l \sim a$
	$b \neq 0$ 	 $l \gg a$
$c \ll a$		

図 4 パラメータの変化による群れのパターンの変化

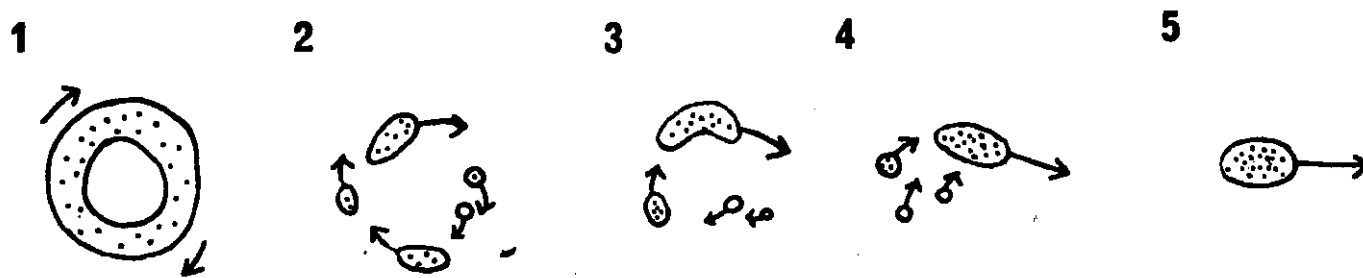


図 7 ドーナツ形から直進形の群れへの時間変化



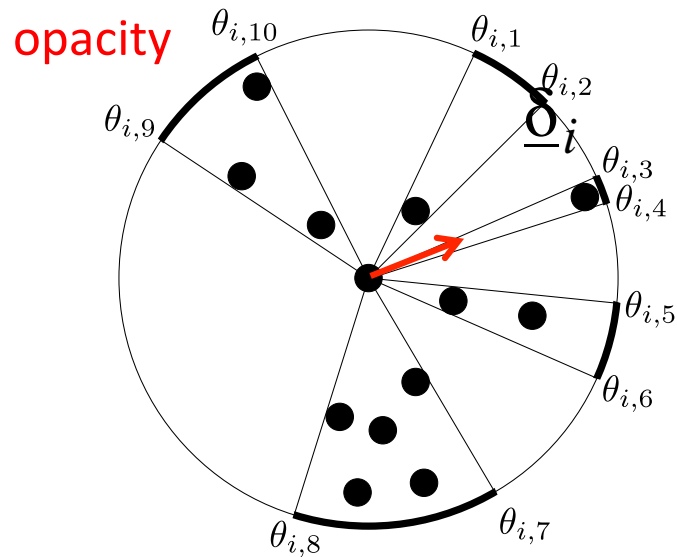
## Other dry particles

There proposed many models after Vicsek  
including ...

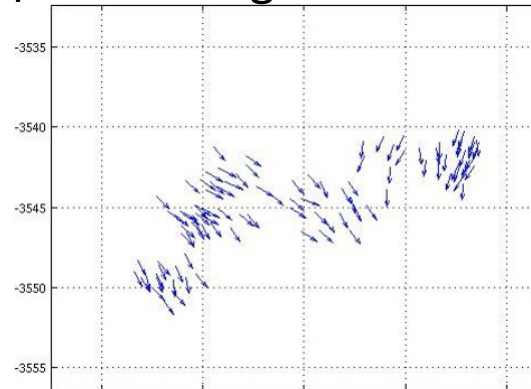
# Dry particles with vision: Hybrid Projection model

- Pearcea, Millera, Rowlandsa, Turner, PNAS 111, 10422 (2014)

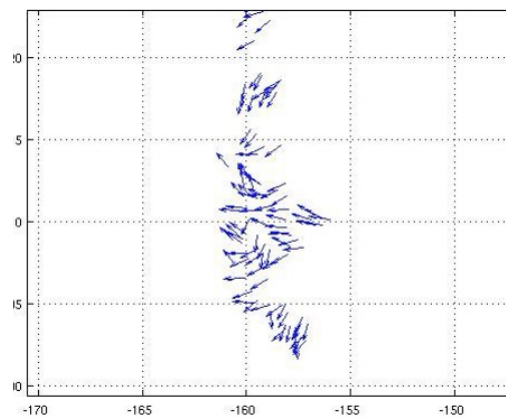
$$\underline{v}_i^{t+1} = \phi_p \underline{\delta}_i + \phi_a \langle \underline{v}_k \rangle_{n.n.} + \phi_n \underline{\eta}_i^t,$$



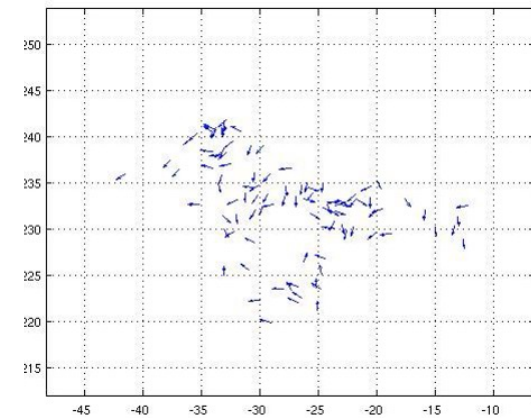
$\phi_p = 0.1, \phi_a = 0.75$   
w/o blind angle



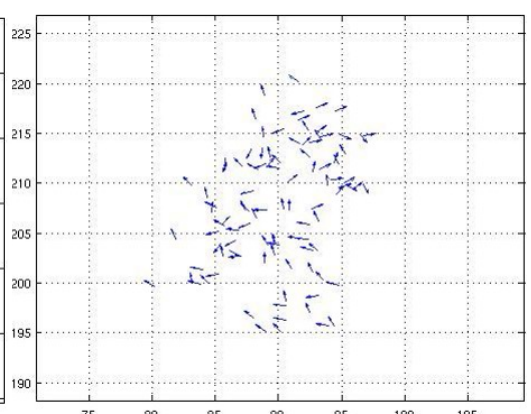
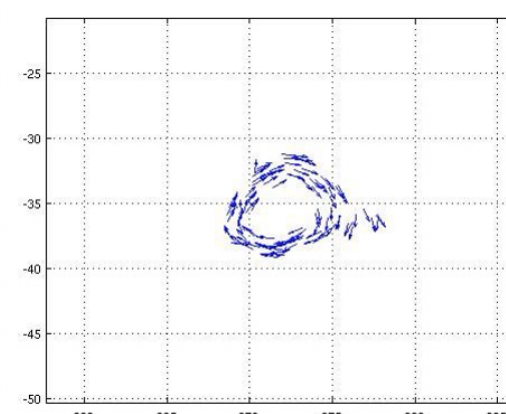
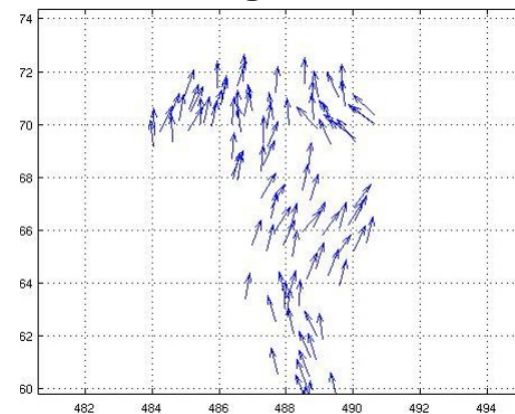
$\phi_p = 0.45, \phi_a = 0.45$



$\phi_p = 0.175, \phi_a = 0.45$



with blind angle



**Fig. 1.** Sketch showing the construction of the projection through a 2D swarm seen by the  $i^{\text{th}}$  individual, which here happens to be one near the center of the swarm. The thick dark arcs around the exterior circle (shown for clarity; there is no such boundary around the swarm) correspond to the angular regions where one or more others block the line of sight of the  $i^{\text{th}}$  individual to infinity. The sum of unit vectors pointing to each of these domain boundaries, at the angles shown, gives the resolved vector  $\underline{\delta}_i$ , shown in red, that enters our equation of motion. See [SI Appendix](#) for the extension to 3D.

# Major categories of self-propelled particles

## Dry particles

in which hydrodynamics is not important  
ex. flock of birds

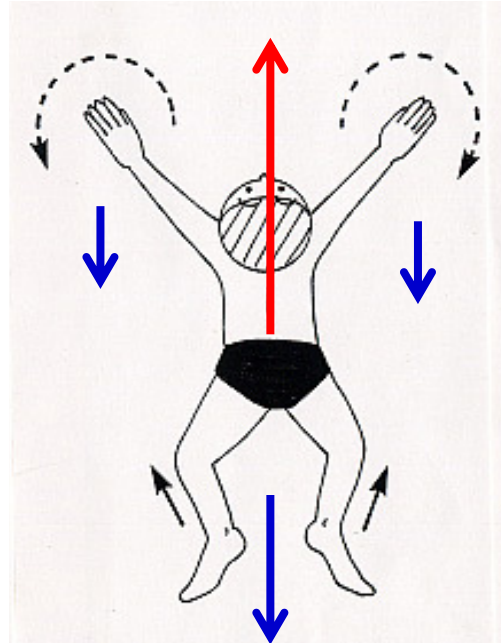
## Wet particles = Swimmers

in which hydrodynamics plays crucial role  
ex. school of fish



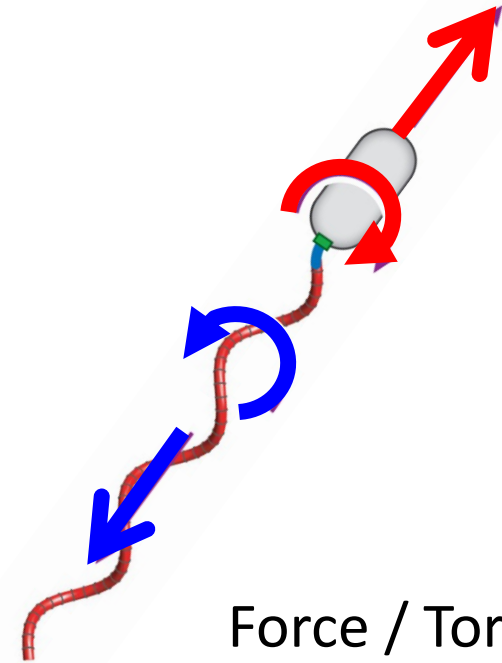
# How can swimmers swim?

Breaststroke



Force free

E-coli bacteria



Force / Torque free

Swimming = Propulsion without external Force or Torque

$$\mathbf{u}(\mathbf{r}) \sim |\mathbf{r}|^{-2}$$

cf. driven colloid

$$\mathbf{u}(\mathbf{r}) \sim |\mathbf{r}|^{-1}$$



# A detailed swimmer model

- **boundary element method:**

Ishikawa, Sekiya, Imai, Yamaguchi, Biophys. J. 93, 2217 (2007)

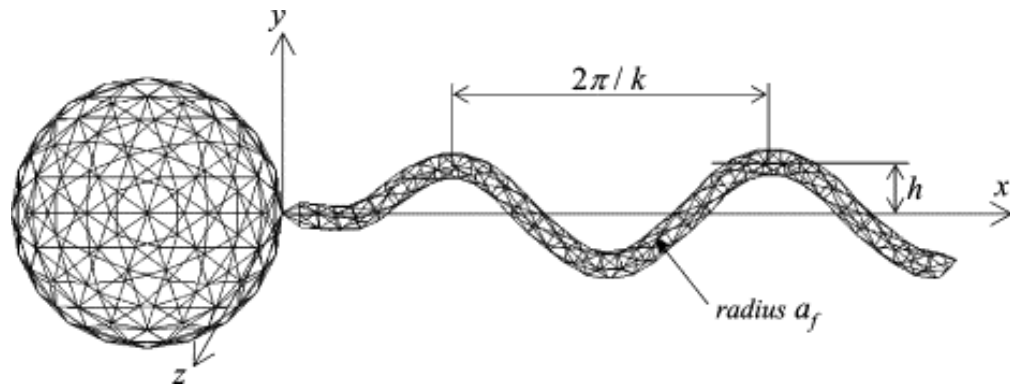
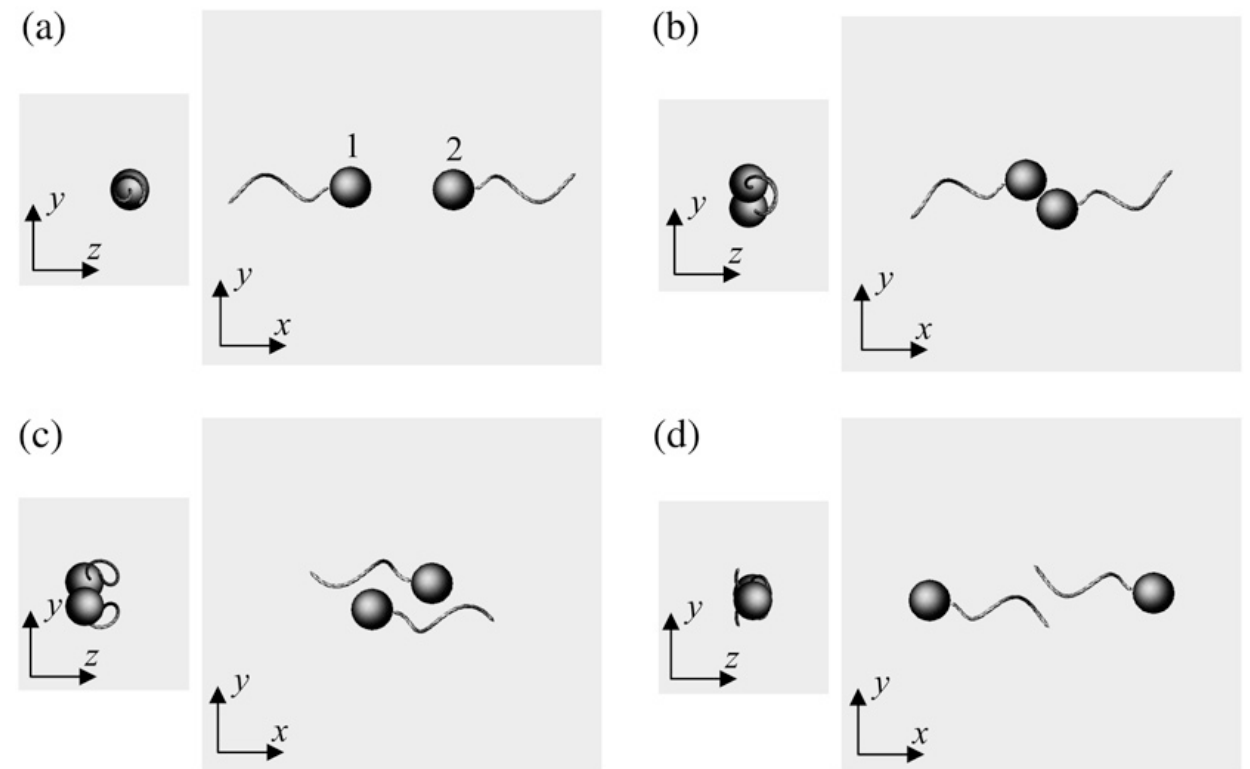


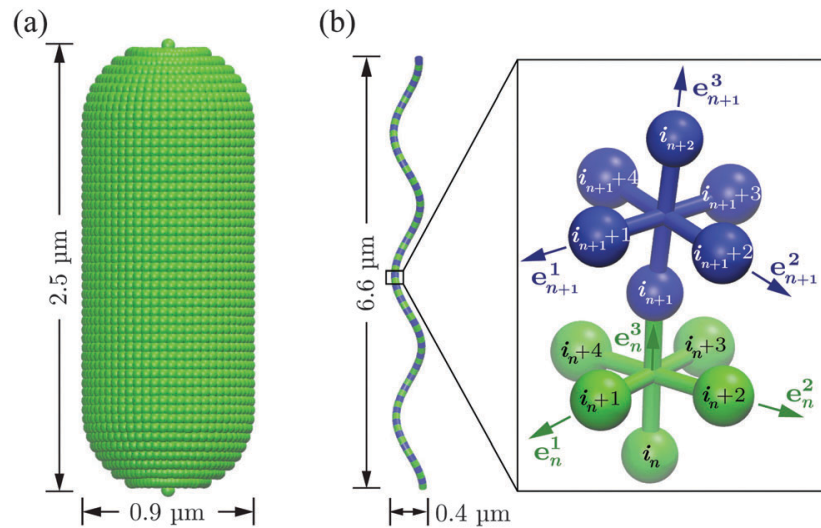
FIGURE 1 Shape parameters for a bacterial model with 360 and 320 triangle elements for the flagellum and spherical body, respectively. The total number of elements per bacterium is 680. (a) Shape A ( $h = 0.77$ ,  $k = k_E = 1.3$ , and  $a_f = 0.1$ ), (b) shape B ( $h = 0.77/2$ ), and (c) shape C ( $h = 0.77/2$ ,  $k = 2.6$ ).



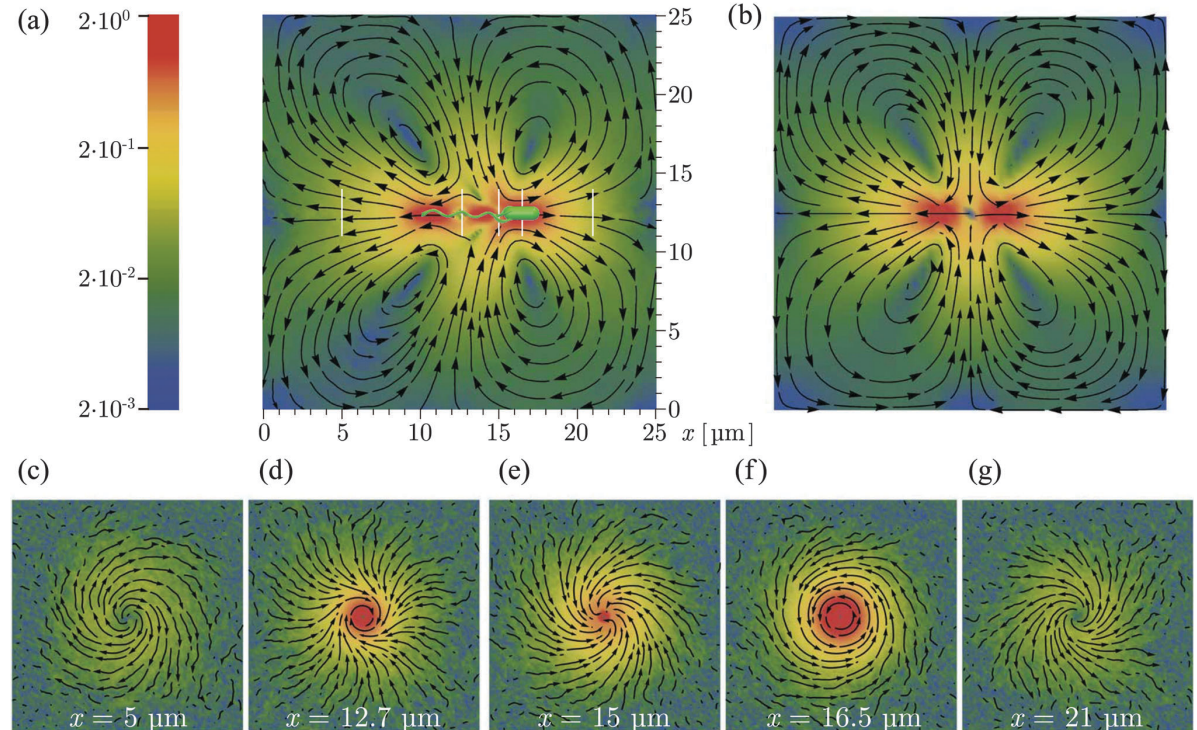
# More detailed swimmer model

- **PMC dynamics:**

Hu, Yang, Gompper, Winkler, *Soft Matter* 11, 7867 (2015)



**Fig. 2** (a) Model of the spherocylindrical cell body of diameter  $d = 0.9 \mu\text{m}$  and length  $l_b = 2.5 \mu\text{m}$ . It is composed of 51 circular sections of particles, which are connected by the bond potential of eqn (1). (b) The flagellum, a three-turn left-handed helix of radius  $R = 0.2 \mu\text{m}$ , pitch  $\lambda = 2.2 \mu\text{m}$  and contour length  $L_c = 7.6 \mu\text{m}$  (corresponding to the parallel length  $L_{||} = 6.6 \mu\text{m}$ ), consists of 76 consecutive segments.



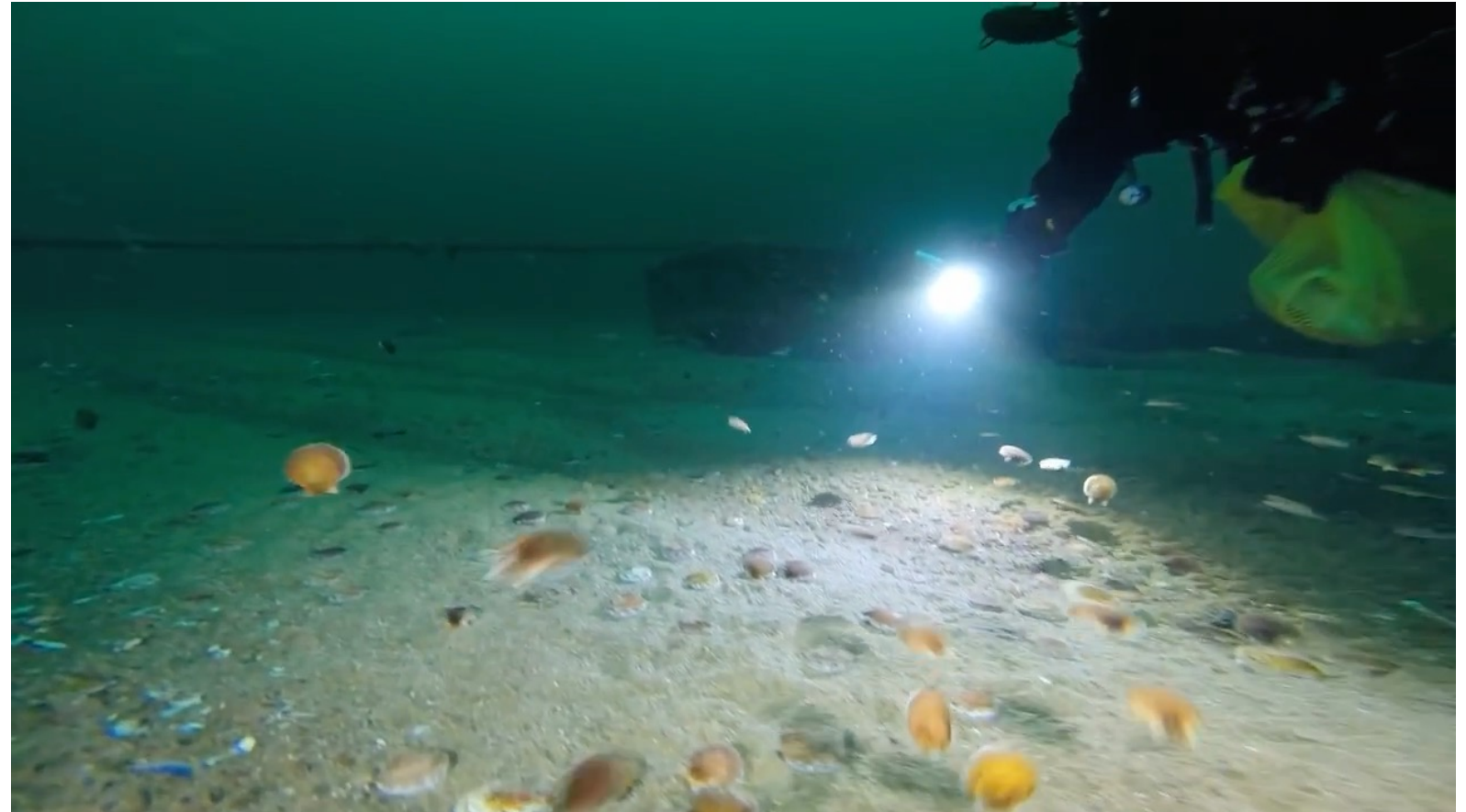
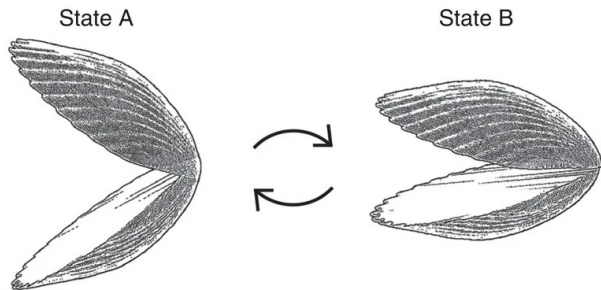
**Fig. 5** Time-averaged flow field generated by a single swimming bacterium as obtained from simulations: (a) flow field in the swimming plane (b) the theoretical flow pattern for a finite-distance force dipole as illustrated in Fig. 6(a) as superposition of two Stokeslets within the same periodic box as for our simulations. (c–g) Flow fields in planes perpendicular to the swimming plane at positions indicated by the white vertical lines in (a). The streamlines indicate the flow direction, and the logarithmic color scheme indicates the magnitude of the flow speed scaled by the bacterial swimming velocity.

# Simpler swimmers in a real-world

Q. Can scallops swim using simple reciprocal motion?

A. Yes, in a real-world (= at moderate  $Re$ ).

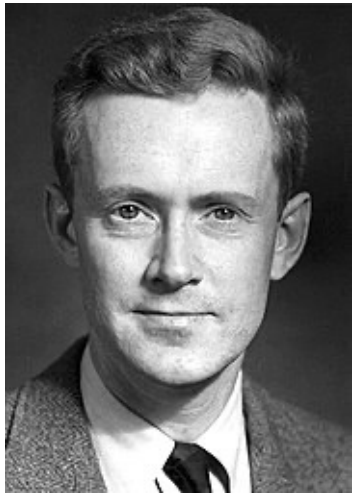
simple reciprocal motion



# Simpler swimmers in a small-scale

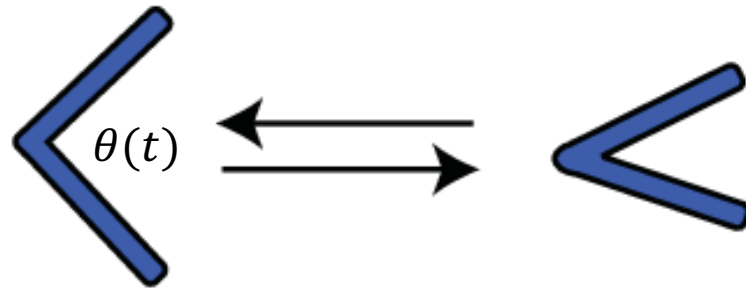
A. No, in a small-world (= at low Re).

- **Purcell theorem:** Purcell, AJP 45, 3 (1977)



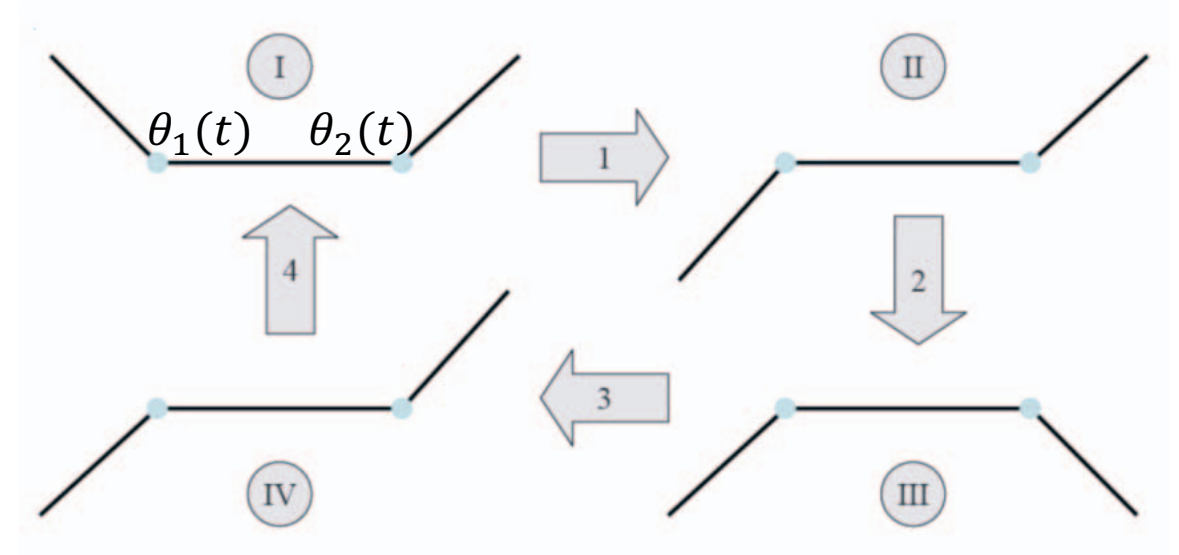
Edward Mills Purcell  
(1912 –1997)  
1952 Nobel Prize for  
Physics: Discovery  
of NMR

Reciprocal  
 $\langle V \rangle = 0$



Scallop

Non-reciprocal (Circulative)  
 $\langle V \rangle \neq 0$



Purcell's swimmer



# A model microswimmer (3-linked spheres)

- **3-sphere NG model:** Najafi, Golestanian, PRE 69, 062901 (2004)

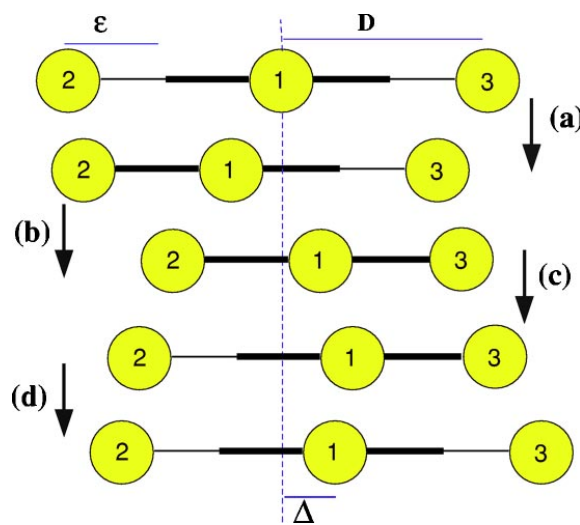


FIG. 2. Complete cycle of the proposed nonreciprocal motion of the swimmer, which is composed of four consecutive time-reversal breaking stages: (a) the left arm decreases its length with the constant relative velocity  $W$ , (b) the right arm decreases its length with the same velocity, (c) the left arm opens up to its original length, and finally, (d) the right arm elongates to its original size. By completing the cycle the whole system is displaced to the right side by an amount  $\Delta$ .

$$v_1 = \frac{f_1}{6\pi\eta a_1} + \frac{f_2}{4\pi\eta L_1} + \frac{f_3}{4\pi\eta(L_1 + L_2)}$$

$$v_2 = \frac{f_1}{4\pi\eta L_1} + \frac{f_2}{6\pi\eta a_2} + \frac{f_3}{4\pi\eta L_2}$$

$$v_3 = \frac{f_1}{4\pi\eta(L_1 + L_2)} + \frac{f_2}{4\pi\eta L_2} + \frac{f_3}{6\pi\eta a_3}$$

$$L_1 = l_1 + u_1, \quad u_1(t) = d_1 \cos(\omega t + \varphi_1)$$

$$L_2 = l_2 + u_2, \quad u_2(t) = d_2 \cos(\omega t + \varphi_2)$$

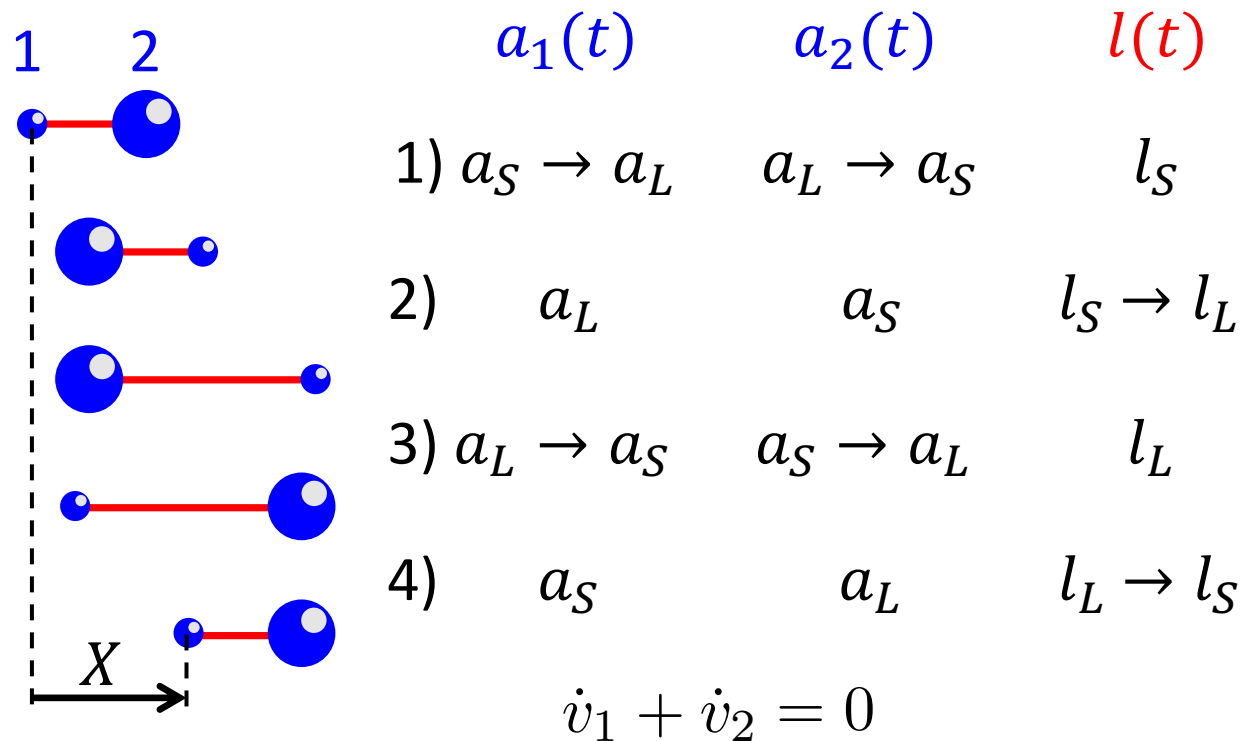
$$\overline{V}_0 = \frac{K}{2} d_1 d_2 \omega \sin(\varphi_1 - \varphi_2)$$

# A model microswimmer (2-linked spheres)

- **push-me-pull-you (PMPY) model:**

Avron, Kenneth, Oaknin, NJP 7, 234 (2005)

Silverberg et al., Bioinspiration and Biomimetics 15, 64001 (2020)



w/o HI (2005)

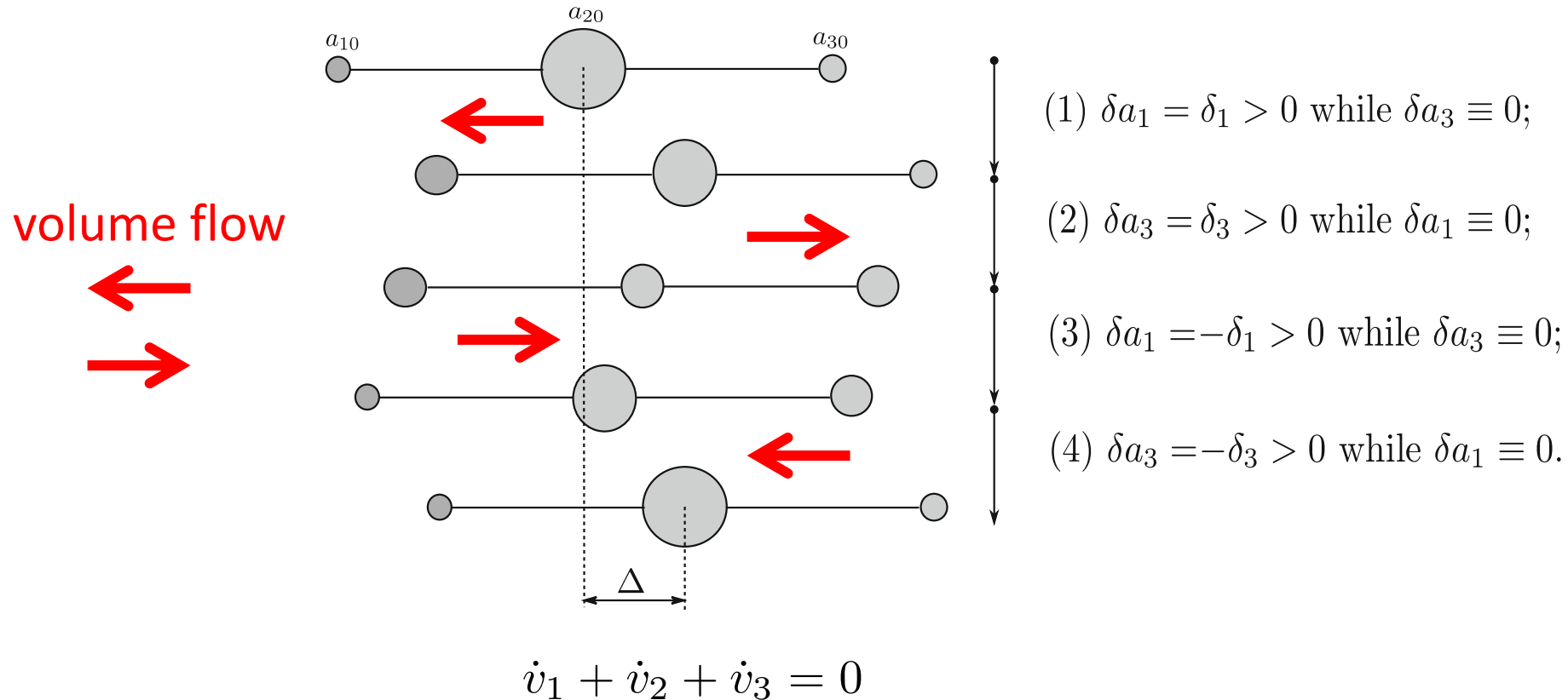
$$X = \frac{a_L - a_S}{a_L + a_S} (l_L - l_S)$$

with HI by Oseen tensor (2020)

$$X = \frac{a_L - a_S}{a_L + a_S} (l_L - l_S) + \frac{3a_S a_L}{(a_S - a_L)} \ln \frac{l_L}{l_S}$$

# A model microswimmer (3-linked spheres)

- 3-sphere volume exchange (VE) model:  
Wang, Hu, Othmer, IMA 155, 185 (2012)

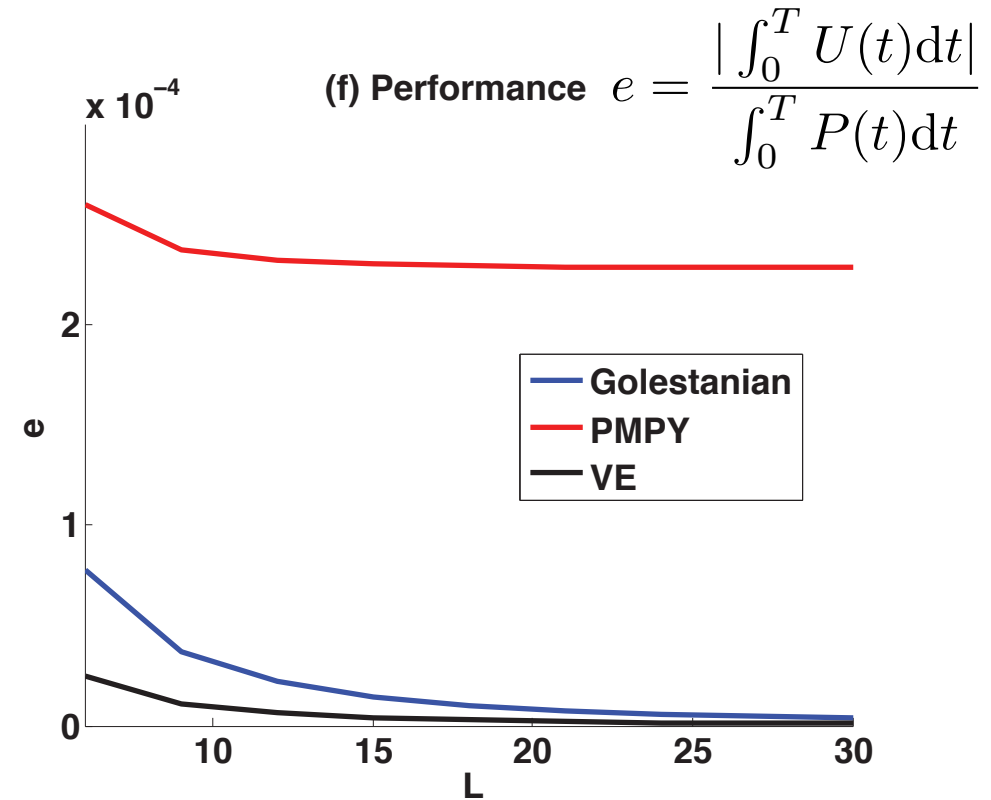
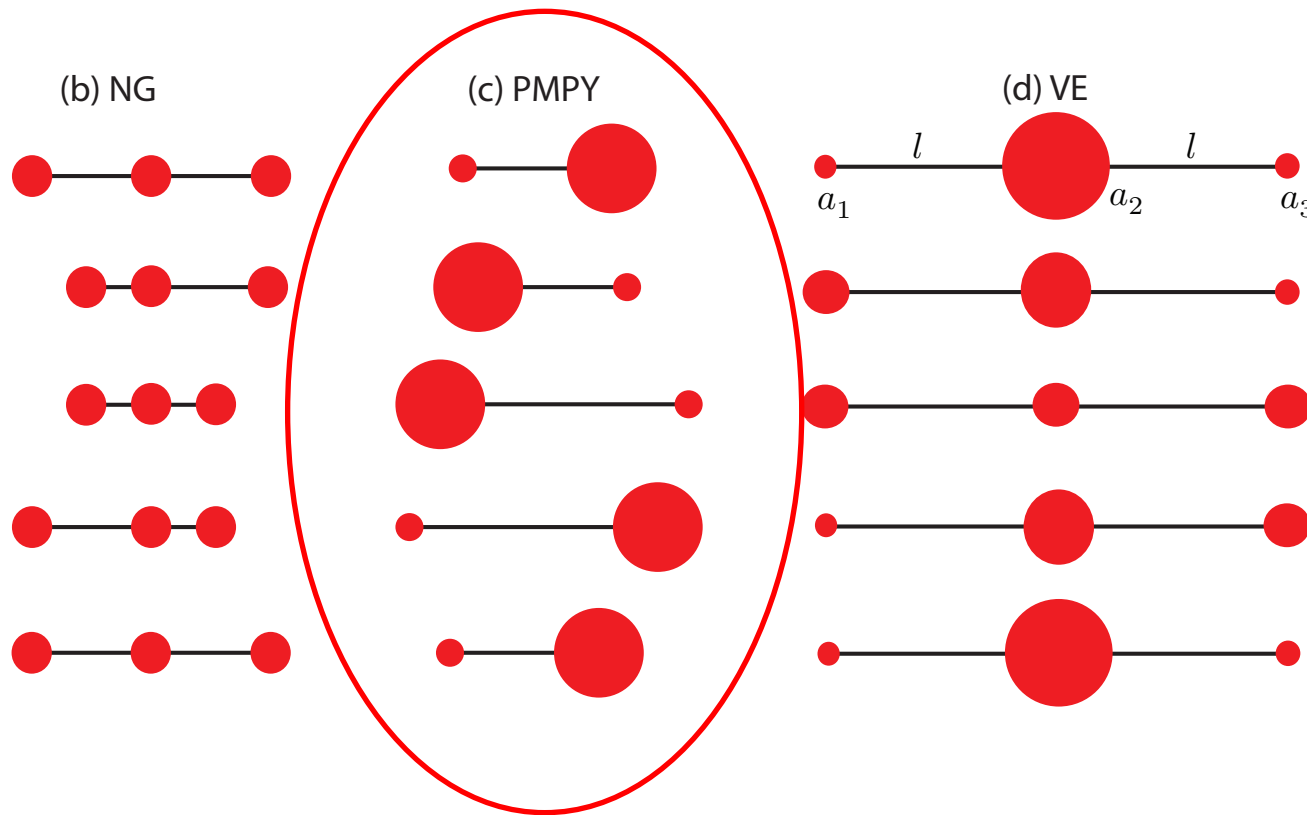


# Comparisons of model microswimmers

total volume in all spheres are the same, and the stroke amplitudes are the same for each mode.

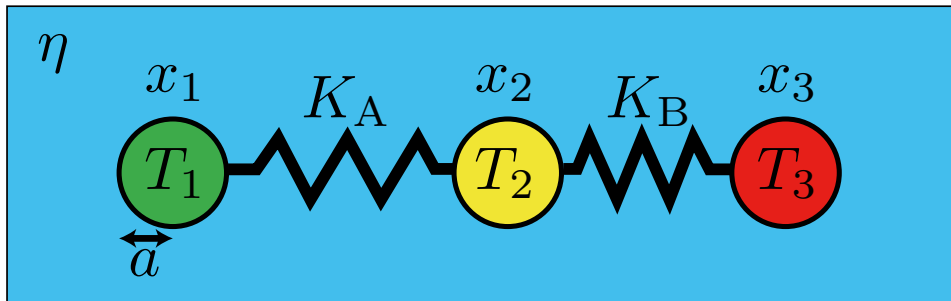
- **NG** vs **PMPY** vs **VE**

Wang, Othmer, MBE 12, 1303 (2015)



# A model microswimmer (3-linked spheres)

- **Thermally driven elastic microswimmer**: Hosaka, Yasuda, Sou, Okamoto, Komura, JPSJ 86, 113801 (2017)



$$F_A = -K_A(x_2 - x_1 - l)$$

$$F_B = -\lambda K_A(x_3 - x_2 - l)$$

$$f_1 = -F_A$$

$$f_2 = F_A - F_B,$$

$$f_3 = F_B$$

Oseen tensor

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \end{pmatrix} = \begin{pmatrix} M_{12} & M_{12} & M_{13} \\ M_{21} & M_{22} & M_{23} \\ M_{31} & M_{32} & M_{33} \end{pmatrix} \cdot \begin{pmatrix} f_1 \\ f_2 \\ f_3 \end{pmatrix} + \begin{pmatrix} \xi_1 \\ \xi_2 \\ \xi_3 \end{pmatrix}$$

$$\langle \xi_i(t) \xi_j(t') \rangle = k_B \bar{T}_{ij} M_{ij} \delta(t - t')$$

$$\bar{T}_{ii} = T_i, \quad \bar{T}_{ij} = \text{ave}[T_i, T_j]$$

$$\langle V \rangle \equiv \frac{(\dot{x}_1 + \dot{x}_2 + \dot{x}_3)}{3}$$

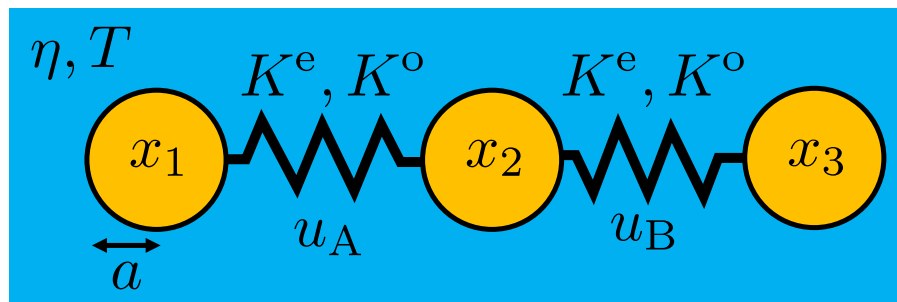
$$= \frac{k_B}{144\pi\eta l^2(1 + \lambda)} [(2 - 5\lambda)T_1 - (7 - 7\lambda)T_2 + (5 - 2\lambda)T_3]$$

Temperature gradient drives the elastic microswimmer

# A model microswimmer (3-linked spheres)

- Thermally driven odd-elastic microswimmer:

Yasuda, Hosaka, Sou, Komura, JPSJ 90, 075001 (2021)



$$\begin{pmatrix} F_A \\ F_B \end{pmatrix} = - \begin{pmatrix} K^e & K^o \\ -K^o & K^e \end{pmatrix} \cdot \begin{pmatrix} x_2 - x_1 - l \\ x_3 - x_2 - l \end{pmatrix}$$

$$\begin{aligned} f_1 &= -F_A \\ f_2 &= F_A - F_B, \\ f_3 &= F_B \end{aligned}$$

Oseen tensor

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \end{pmatrix} = \begin{pmatrix} M_{12} & M_{12} & M_{13} \\ M_{21} & M_{22} & M_{23} \\ M_{31} & M_{32} & M_{33} \end{pmatrix} \cdot \begin{pmatrix} f_1 \\ f_2 \\ f_3 \end{pmatrix} + \begin{pmatrix} \xi_1 \\ \xi_2 \\ \xi_3 \end{pmatrix}$$

$$\langle \xi_i(t) \xi_j(t') \rangle = k_B T M_{ij} \delta(t - t')$$

$$\langle V \rangle \equiv \frac{(\dot{x}_1 + \dot{x}_2 + \dot{x}_3)}{3} = \frac{7ak_B T \lambda}{8l^2 K^e \tau} + \mathcal{O}$$

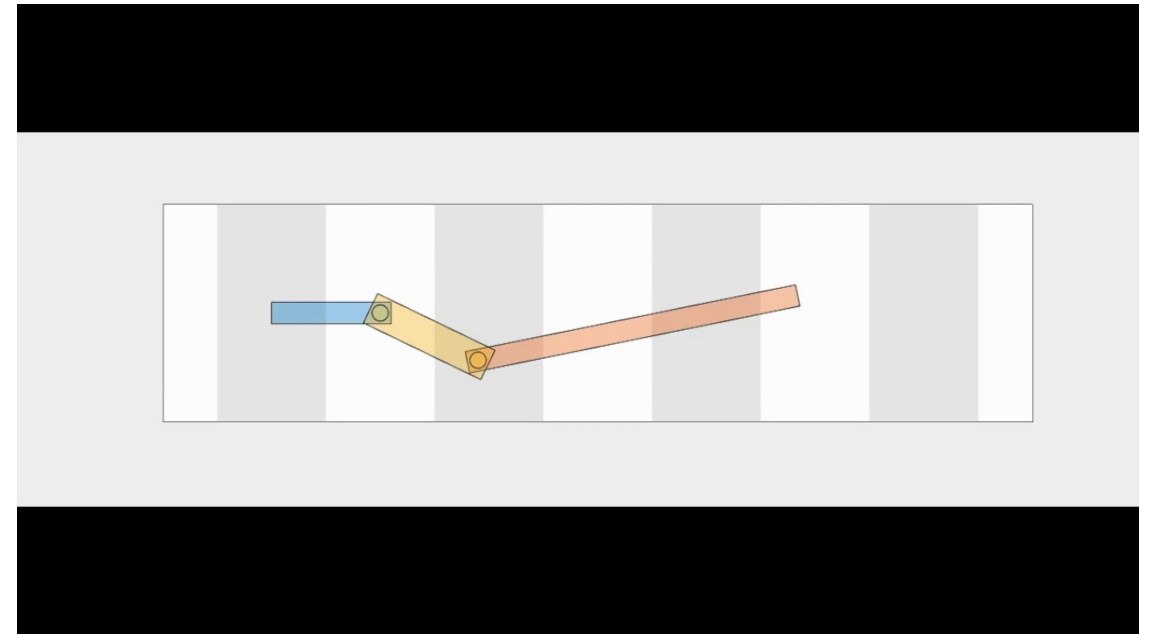
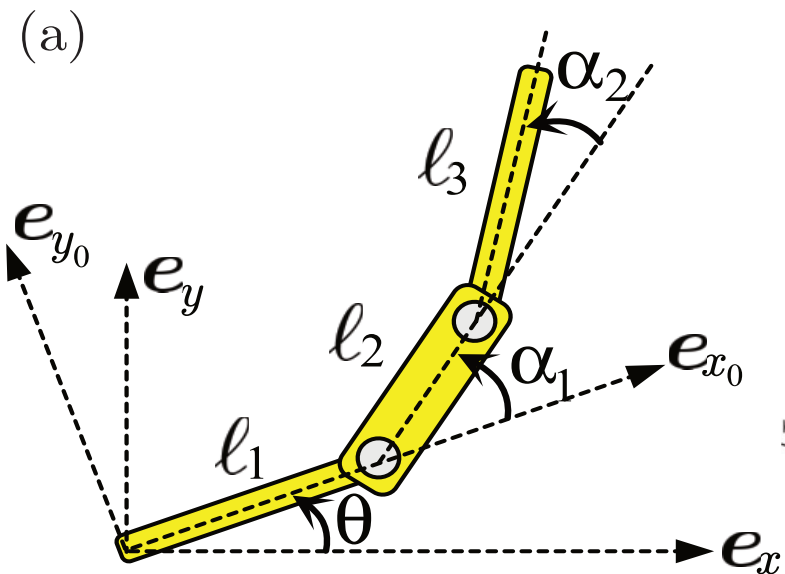
$$\begin{aligned} \lambda &\equiv K^o / K^e \\ \tau &\equiv 6\pi\eta a / K^e \end{aligned}$$

The odd-elastic microswimmer can spontaneously propel in a heat bath!!



# A model microswimmer (3-linked rods)

- Purcell's swimmer with odd-elasticity:  
Ishimoto, Moreau, Yasuda, PRE 105, 064603 (2022)



Spontaneous and autonomous motion can be sustained in viscous media by the odd-elasticity!!!

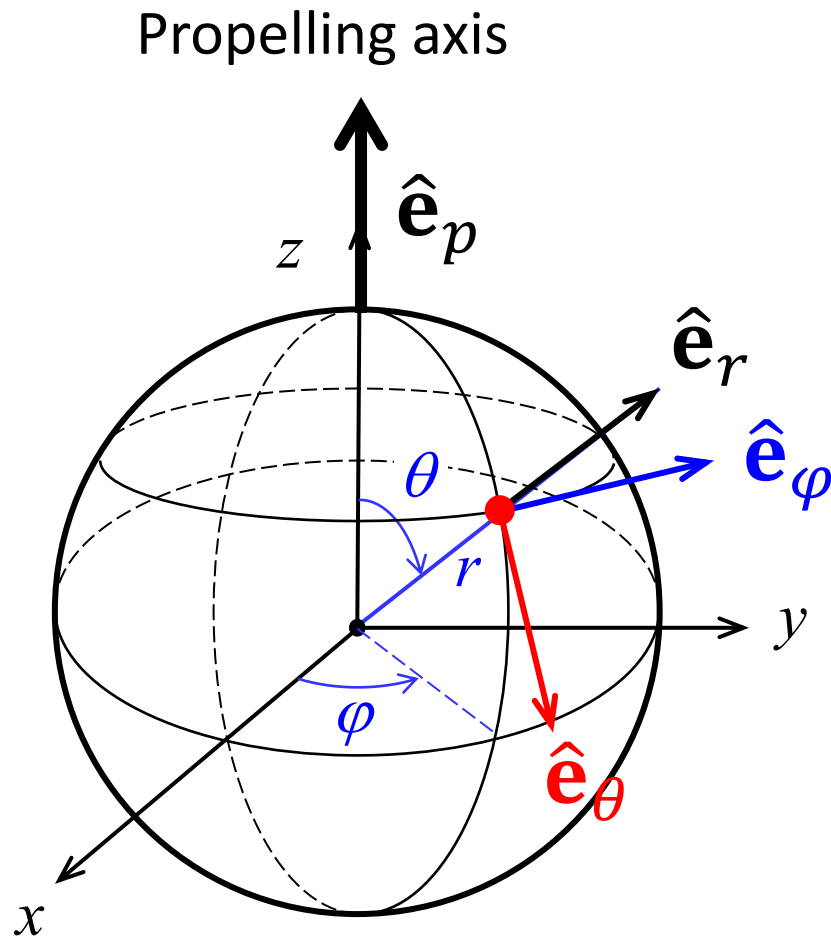
$$\begin{pmatrix} T_1 \\ T_2 \end{pmatrix} = - \begin{pmatrix} \kappa_e & \kappa_0 \\ -\kappa_0 & \kappa_e \end{pmatrix} \cdot \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} \quad \gamma \equiv \kappa_0 / \kappa_e$$

# Unsolved problems of microswimmers

(of my personal choice)

# A spherical microswimmer

- **Squirmer model:** Lighthill (1952), Blake (1971)



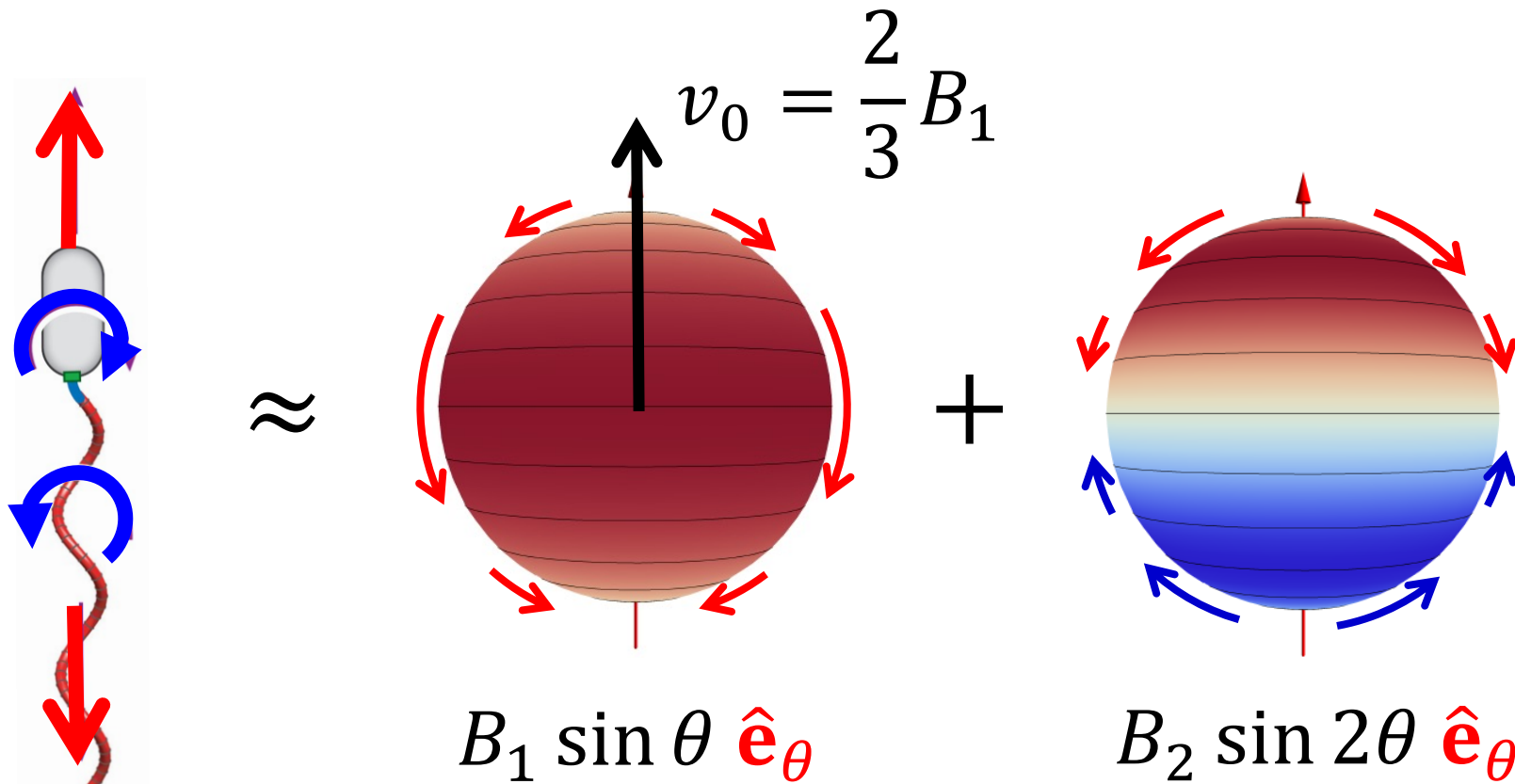
Sliding velocity  $\mathbf{u}^{(s)}$  using polynomial expansion

$$\begin{aligned} \mathbf{u}^{(s)} &= \sum_{n=1}^{n=\infty} \frac{2}{n(n+1)} B_n (\hat{\mathbf{e}} \cdot \hat{\mathbf{r}} \hat{\mathbf{r}} - \hat{\mathbf{e}}) P'_n(\hat{\mathbf{e}} \cdot \hat{\mathbf{r}}) \\ &= \sum_{n=1}^{\infty} \frac{2}{n(n+1)} B_n P'_n(\cos \theta) \sin \theta \hat{\boldsymbol{\theta}} \end{aligned}$$

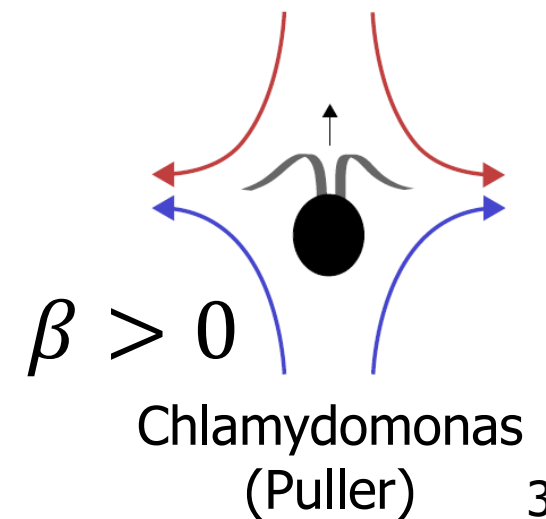
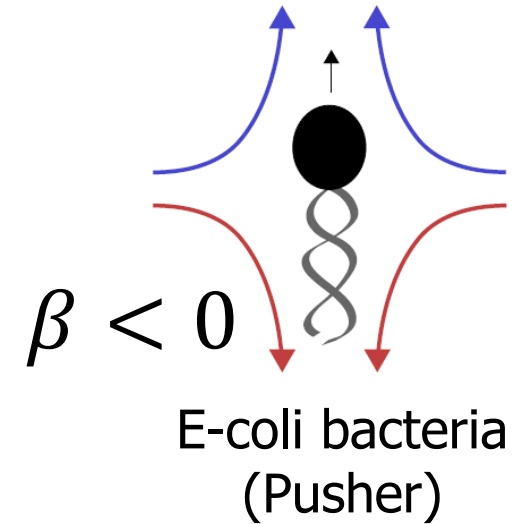
neglecting  $n > 2$

$$\mathbf{u}^{(s)} = (B_1 \sin \theta + B_2 \sin 2\theta) \hat{\boldsymbol{\theta}}$$

# A spherical microswimmer



$$\beta \equiv \frac{B_2}{B_1}$$



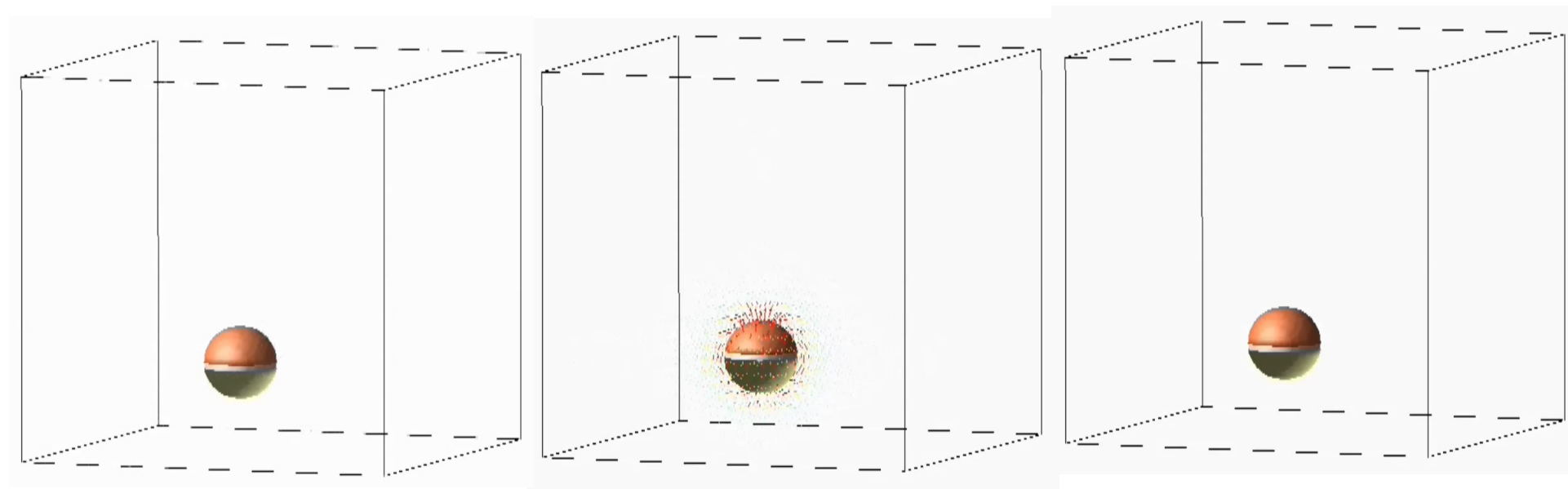
# Single squirmer motions

Pusher  
 $\alpha = -2$

Neutral  
 $\alpha = 0$

Puller  
 $\alpha = 2$

$$\alpha \equiv \frac{B_2}{B_1}$$



$$U = \frac{2}{3} B_1 \hat{e}$$

$$\mathbf{u}(\mathbf{r}) \sim |\mathbf{r}|^{-2}$$

$$\mathbf{u}(\mathbf{r}) \sim |\mathbf{r}|^{-3}$$

$$\mathbf{u}(\mathbf{r}) \sim |\mathbf{r}|^{-2}$$

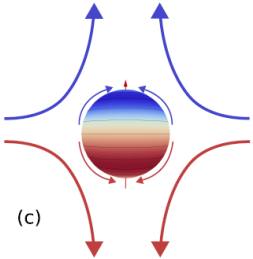
Box: 64 x 64 x 64 with PBC, Particle radius: a=6,  $\phi=0.002$   
Re=0.01, Pe= $\infty$ , Ma=0

# Collective behaviors of many pushers /pullers

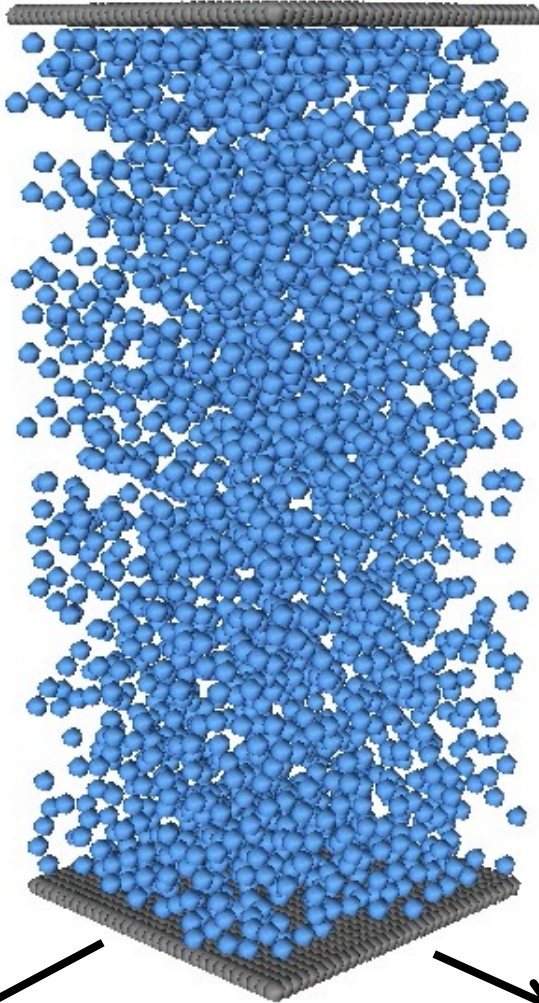
Confined in parallel walls (V.F. of Squirmer = 0.13)

$\alpha = -0.5$

Pusher

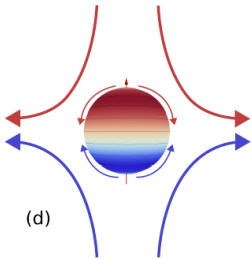


(c)

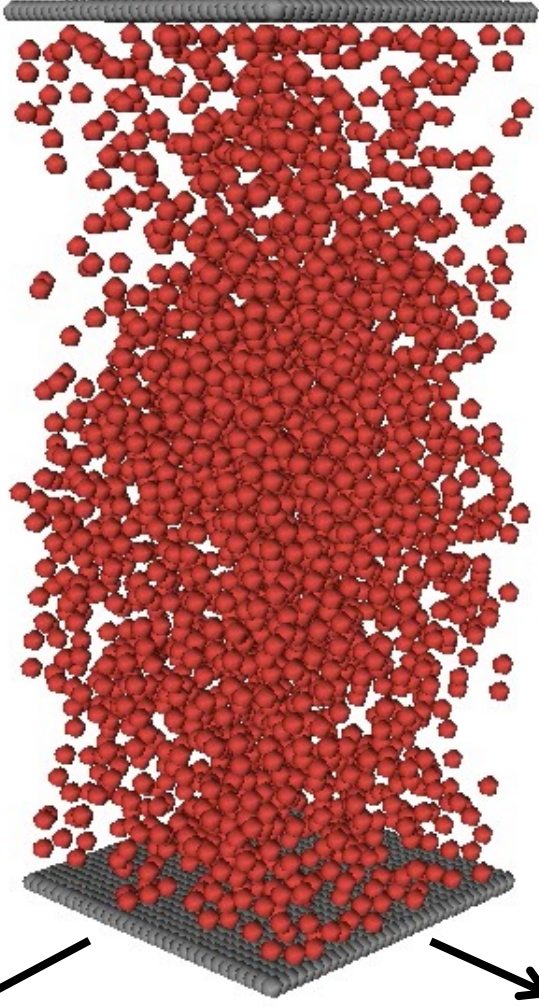


$\alpha = 0.5$

Puller



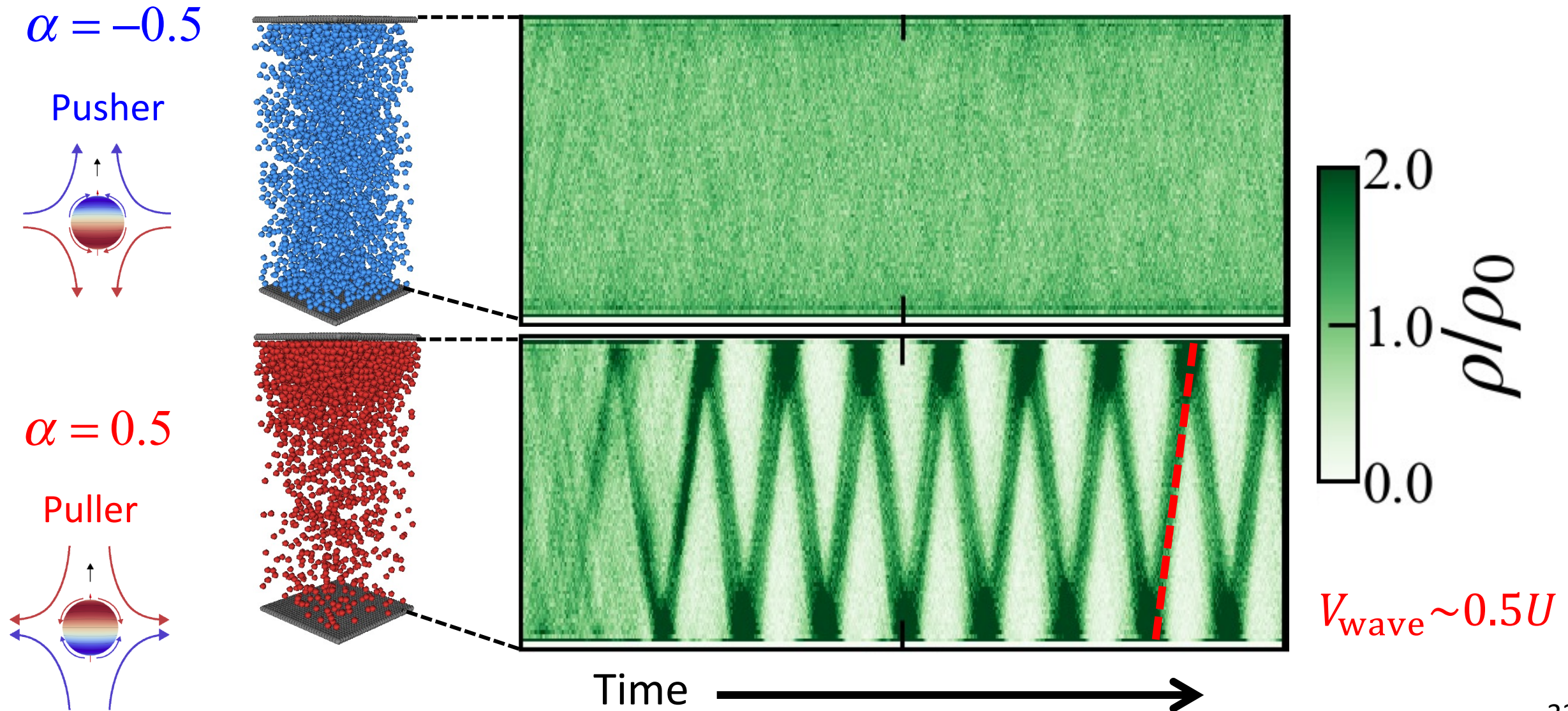
(d)



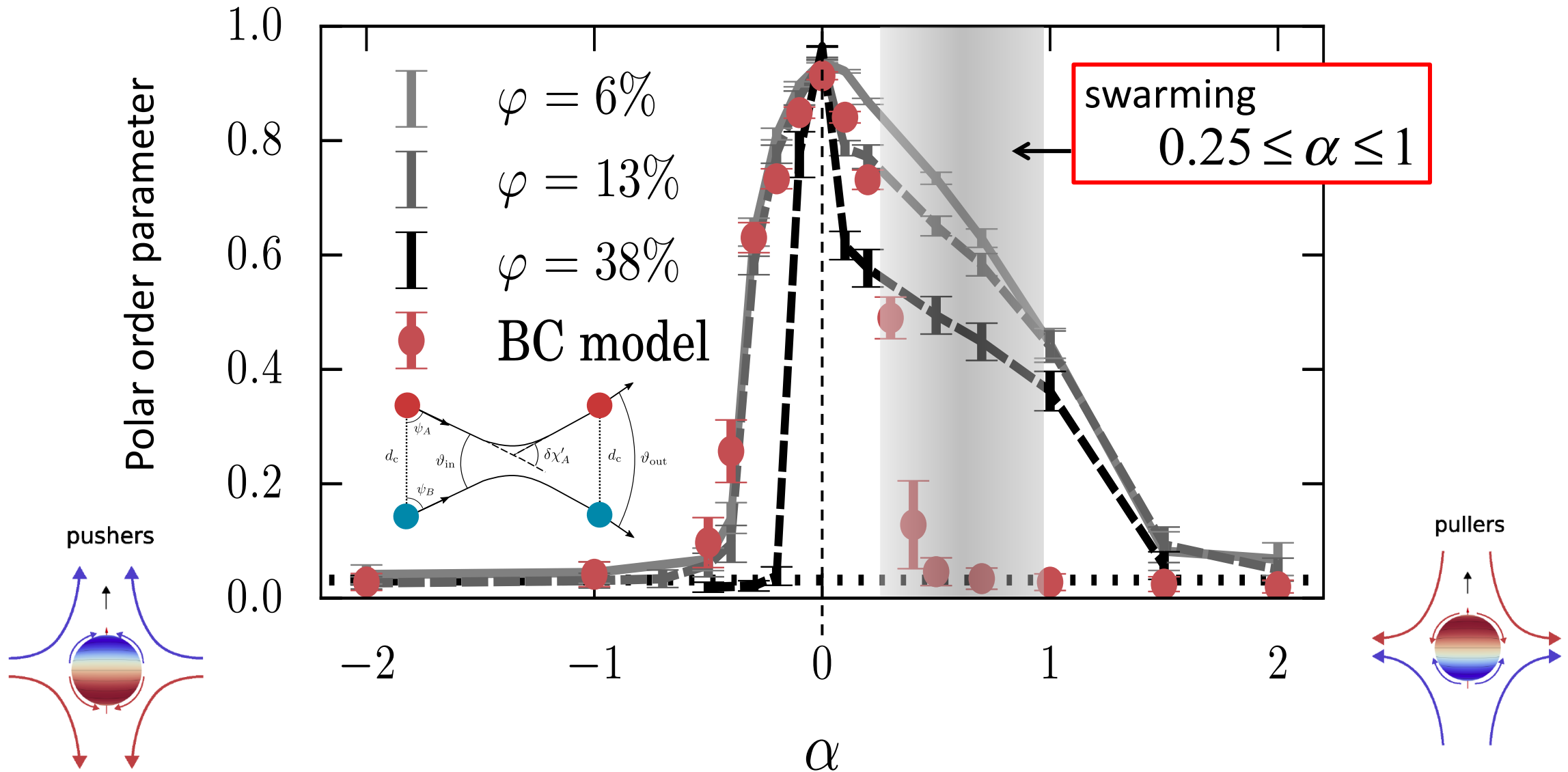
PBC



# Collective behaviors of many pushers /pullers



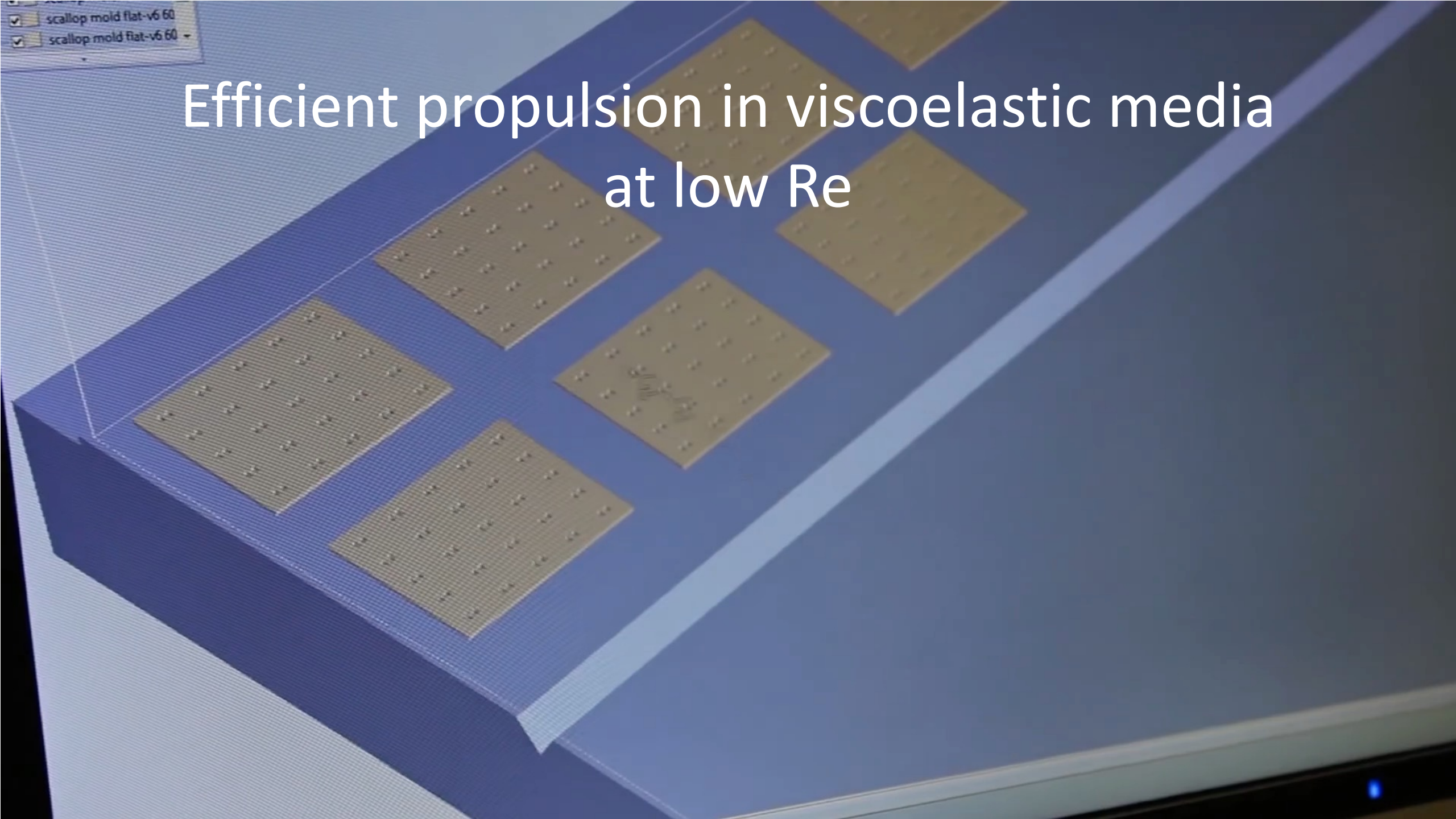
# Collective behaviors of many pushers /pullers





✓ scallop mold flat-v6 60  
✓ scallop mold flat-v6 60

# Efficient propulsion in viscoelastic media at low Re



# Squirmers in viscoelastic fluid

Oldroyd-B model

total stress:  $\mathbf{T} = 2\eta_s \mathbf{D} + \tau$   
 solvent polymer

where  $\tau + \lambda_1 \overset{\nabla}{\tau} = 2\eta_p \mathbf{D}$   
 upper convective Maxwell model

with

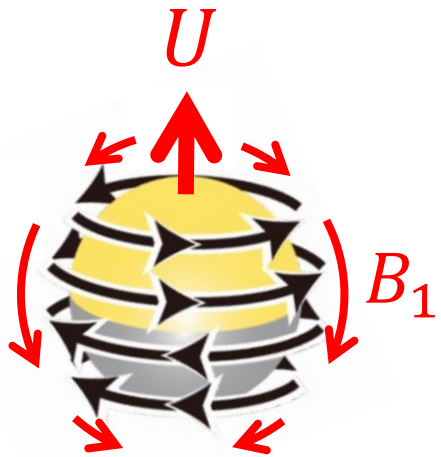
$$\overset{\nabla}{\mathbf{T}} = \frac{\partial}{\partial t} \mathbf{T} + \mathbf{v} \cdot \nabla \mathbf{T} - ((\nabla \mathbf{v})^T \cdot \mathbf{T} + \mathbf{T} \cdot (\nabla \mathbf{v}))$$

$$\mathbf{D} = \frac{1}{2} [\nabla \mathbf{v} + (\nabla \mathbf{v})^T]$$

$$\beta \equiv \frac{\eta_s}{\eta_s + \eta_p}$$

$$Wi \equiv \frac{\lambda_1 B_1}{a}$$

# Squirmers in viscoelastic fluid



Neutral swimmer

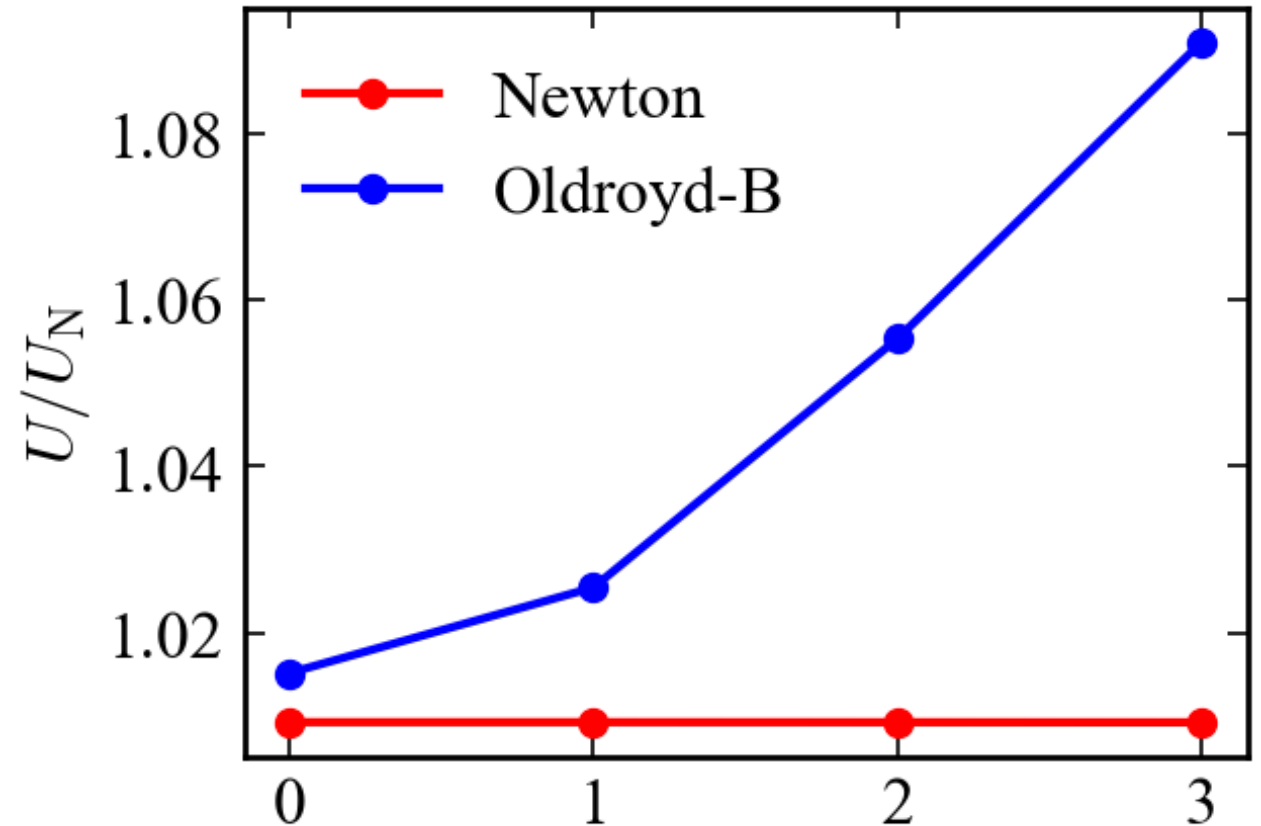
$$B_2 = 0$$

$$\alpha = 0$$

$$\zeta > 0$$

$$\beta \equiv \frac{\eta_s}{\eta_s + \eta_p} = 0.5$$

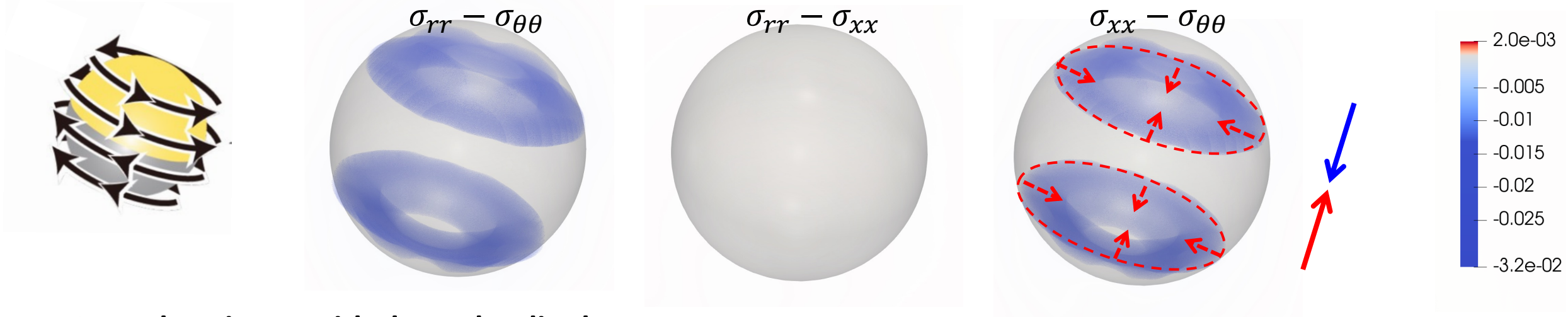
$$Wi \equiv \frac{\lambda_1 B_1}{a} = 0.2$$



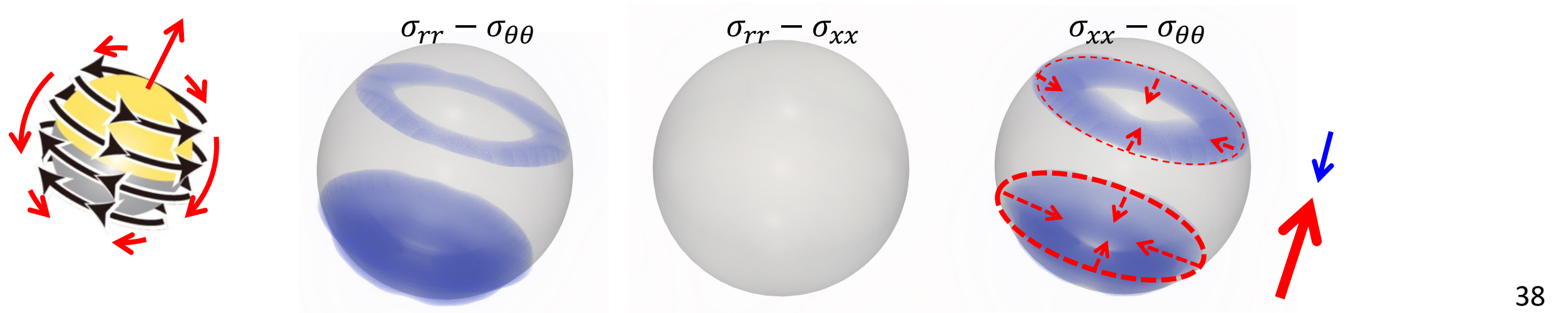
$$\zeta \equiv \frac{C_2}{B_1}$$

# Squirmers in viscoelastic fluid

Squirmer with only rotlet dipole



Neutral squirmer with the rotlet dipole

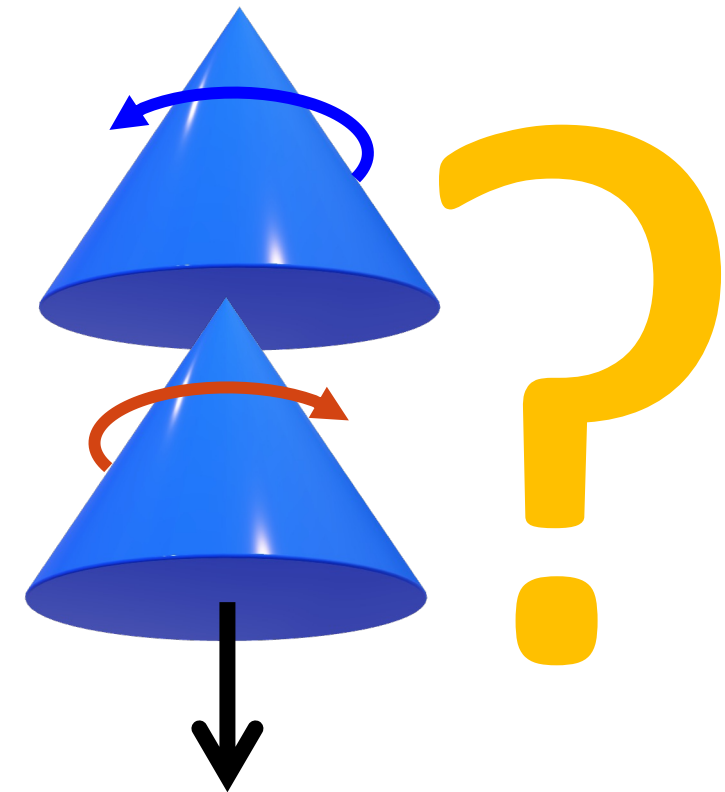




# Efficient propulsion in viscoelastic media



Weissenberg effect



Visco-elastic propeller

Thank you for your kind attention.

# Model microswimmer (1 sphere)

- **DDFT model:**

Menzel, Saha, Hoell, Löwen, JCP 144, 024115 (2016)

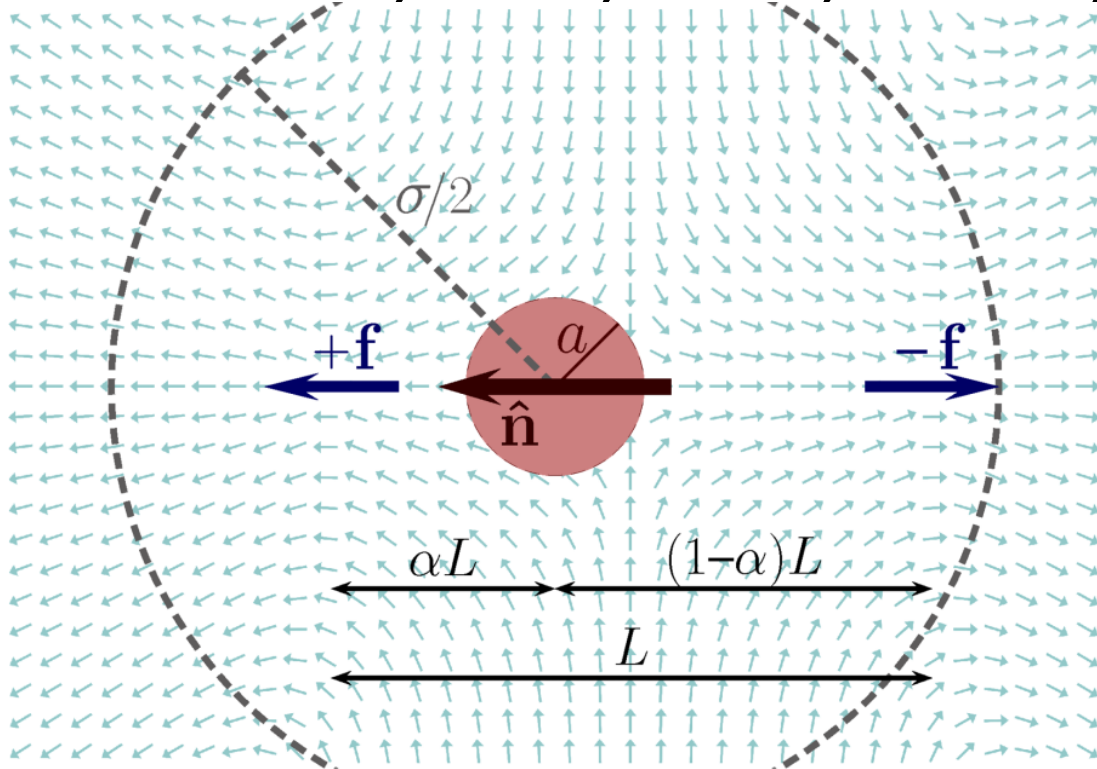
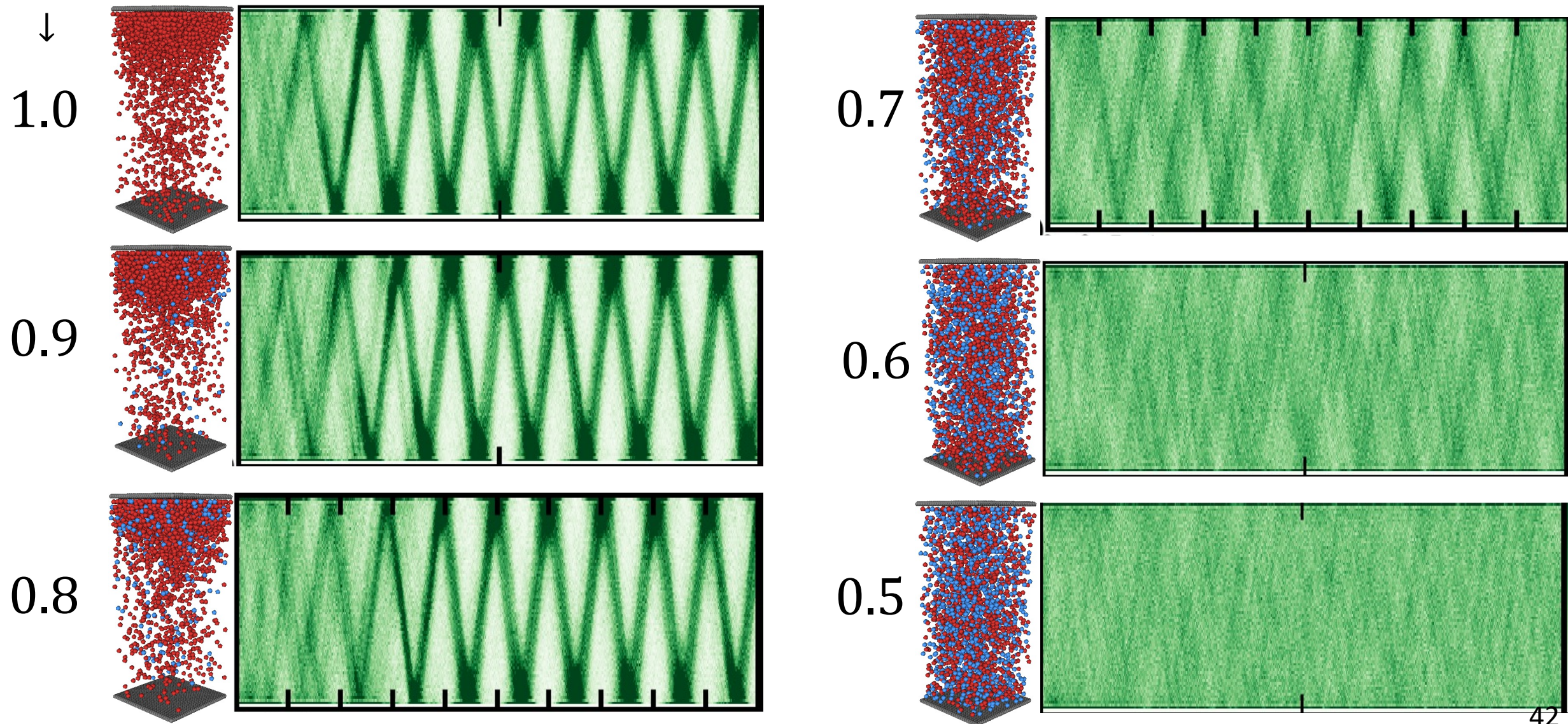


FIG. 1. Individual model microswimmer. The spherical swimmer body of hydrodynamic radius  $a$  is subjected to hydrodynamic drag. Two active point-like force centers exert active forces  $+\mathbf{f}$  and  $-\mathbf{f}$  onto the surrounding fluid. This results in a self-induced fluid flow indicated by small light arrows.  $L$  is the distance between the two force centers. The whole setup is axially symmetric with respect to the axis  $\hat{n}$ . If the swimmer body is shifted along  $\hat{n}$  out of the geometric center, leading to distances  $\alpha L$  and  $(1-\alpha)L$  to the two force centers, it feels a net self-induced hydrodynamic drag. The microswimmer then self-propels. In the depicted state (pusher), fluid is pushed outward. Upon inversion of the two forces, fluid is pulled inward (puller). We consider soft isotropic steric interactions between the swimmer bodies of typical interaction range  $\sigma$ , implying an effective steric swimmer radius of  $\sigma/2$ .



$x_{\text{Puller}}$

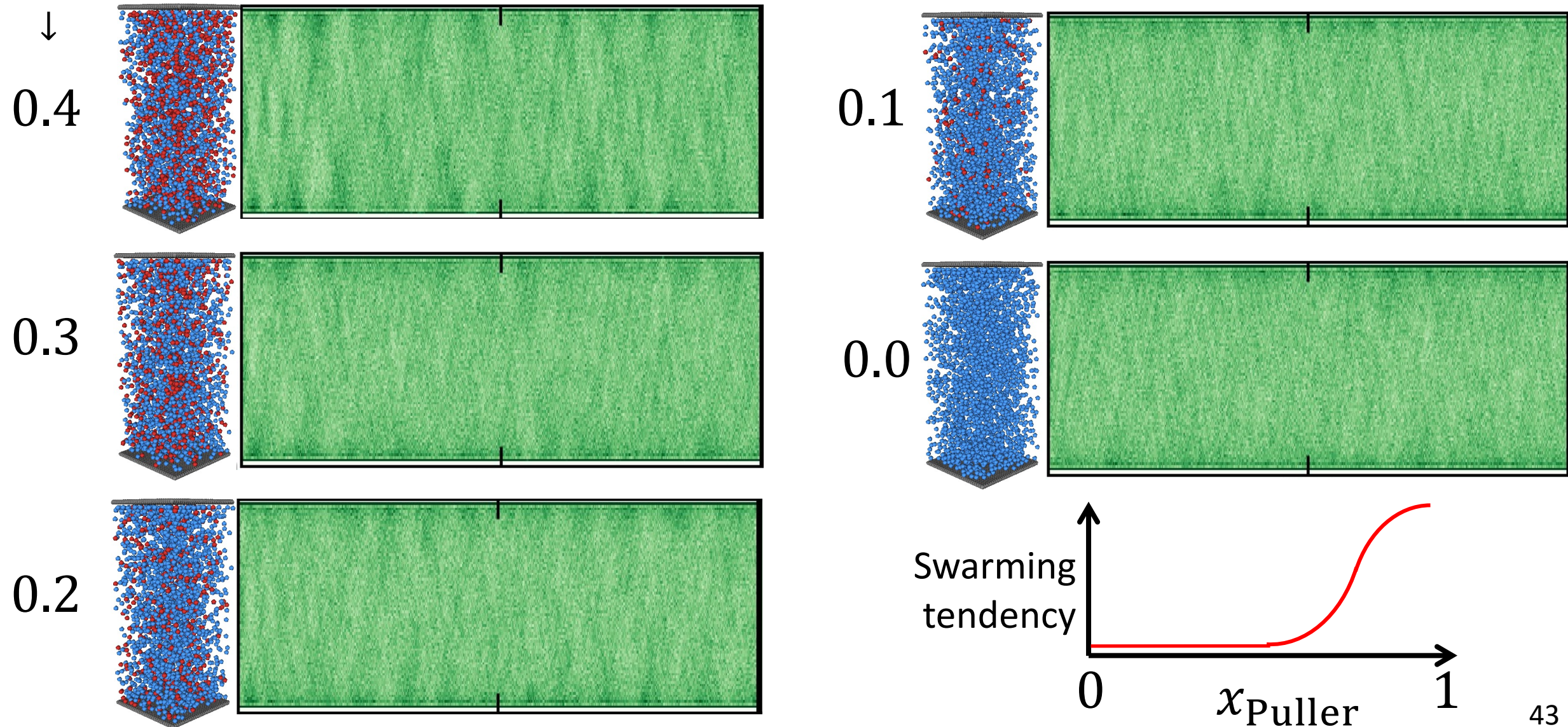
# Swarm propagation: Mixtures





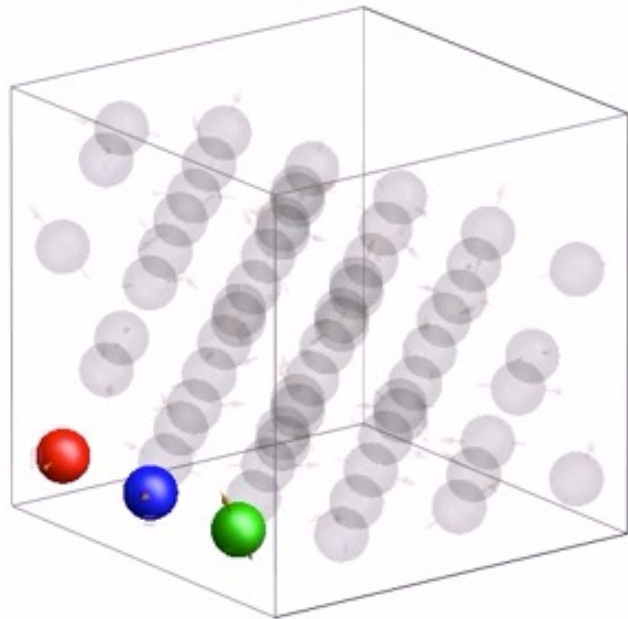
# Swarm propagation: Mixtures

$x_{\text{Puller}}$

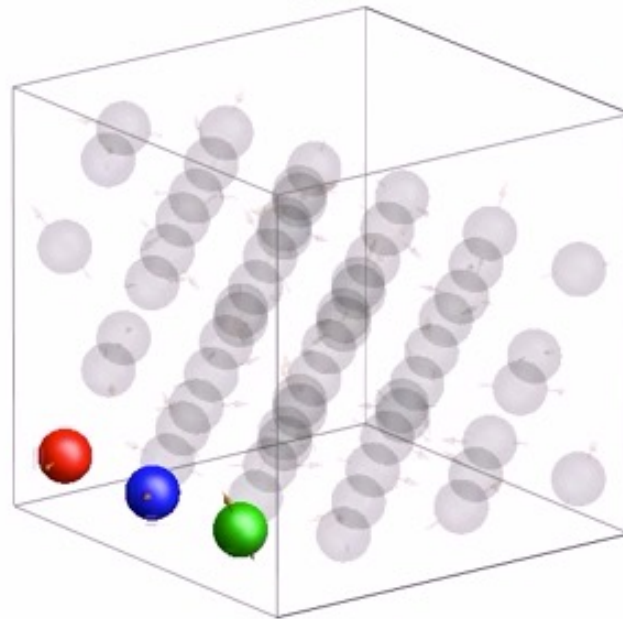


# Collective motions in bulk

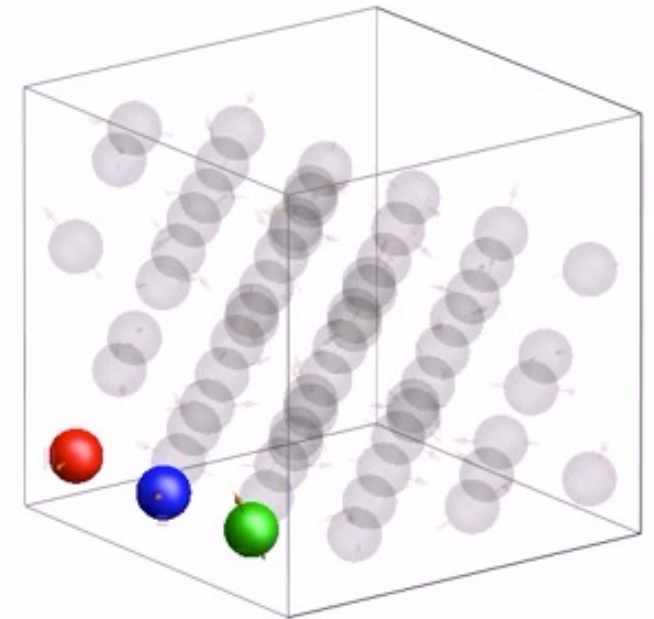
Pusher  
 $\alpha = -2$



Neutral  
 $\alpha = 0$



Puller  
 $\alpha = 2$





# Spherical micro-swimmer with rotlet

