

Near-wall Dynamics of Active and Passive
Particles at Low Reynolds Number

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Abstract

Moving particles at low Reynolds number are categorized into two types. The first are passive particles driven by an external force, such as red blood cells in a vessel and microfluidic droplets. The second are active particles, which exchange energy for kinetic motion and are self-driven, such as swimming cells and artificial microswimmers. By use of the Stokes equation, we can derive an exact flow field and a drag force on a single particle, but the “near-wall” motions, which contain arbitrary boundary conditions, become complex and unpredictable.

In this thesis, the dynamics of passive and active particles at low Reynolds number are revealed. Specifically, we focused on near-wall motions of a few micrometer-scale particles, including the oscillation and clustering of passive microfluidic droplets in a microchannel and the motions of a swimming microorganism interacting with a wall and with a shear flow. Statistical analysis cannot be used to assess the concrete activities of near-wall systems. Based on experimental observations and numerical calculations, we quantified the interactions of individual particles in detail and identified the mechanisms of the dynamic behaviors. In addition, micro-systems of moving particles near a wall exist *in vivo* or in nature, such as red blood cells flowing in a capillary vessel as passive particles and aquatic microorganisms living in the sea, ponds or lakes. From the viewpoint of the evolution of a cell or an organism, their motilities should be optimized, in other words, biogenic or effective for survival and growth. The physical approach to the near-wall dynamics of micrometer-scale particles has the potential to provide a new aspect for unsolved microbiological problems.

As an attractive form of motion of passive particles, a 1-dimensional crystal of homogeneous droplets flowing in a microchannel exhibits wave propagation generated from hydrodynamic interactions. In Chapter 2, the motion of flowing droplets with heterogeneous sizes was investigated. We developed a microchannel to alternately generate small and large water-in-oil droplets aligned in one line. We observed that small droplets oscillate between two large droplets flowing in the microchannel. The hydrodynamic numerical calculation demonstrated that the phenomenon of a small droplet can be explained by a 3-dimensional rotational flow generated in a space surrounded by two large droplets and top-bottom walls.

The oscillatory motion was obtained from a low Reynolds system, where complex structures, such as vortices, do not arise. In addition, such a rotationally attractive flow phenomenon, called bolus flow, has also been observed between two red blood cells in a microcapillary. Bolus flow is considered important for material transportation by blood flow. The present study represents an experimental advance because no microfluidic device has previously been able to observe bolus flow or periodically ordered large and small particles.

As an active particle, we focused on a swimming microorganism. In Chapter 3, the dynamics of a swimming microorganism near a wall was investigated. Ciliates, a class of protists, exhibit rapid swimming motion in bulk water propelled by beating cilia around the cell body. Ciliates are known to aggregate near a wall. The biological mechanisms determining these behaviors have not yet revealed, but physical or hydrodynamic issues underlying the motion of active particle(s) near a boundary is a fundamental and complex problem. By use of the squirmer model, the hydrodynamic properties of ciliates were approximately represented as a neutral swimmer. However, the neutral swimmer experiences hydrodynamic repulsion and moves away from the wall. In short, the motion of the model contradicts biological knowledge. We investigated the difference between the ciliate and the neutral swimmer experimentally to relate cilia dynamics to the hydrodynamic interactions. We determined that the well-studied ciliate, *Tetrahymena pyriformis*, frequently did not swim away from the wall but slid on the wall. During cell sliding, the part of the cilia attached to the wall exhibits little beating, indicating that the thrust forces were asymmetrical on the whole body. By comparing the experimental results for the “real swimmer” with the numerical calculation including the asymmetry of the thrust force, we found that the sliding motion could be explained not by a complex biological behavior only but by two simple physical factors. One is the asymmetry of the thrust force, and the other is the anisotropic shape of the cell body. In Chapter 4, we studied the dynamics of the ciliate swimming under a shear flow. Microswimmers, such as mammalian sperms and bacteria, are known to swim against shear flow, and this behavior is called positive rheotaxis. We observed that *T. pyriformis* also underwent positive rheotaxis in shear flow and determined the mechanisms through experimental and numerical studies. The above two results revealed that the simple physical properties decided the behavior of the cell. Both the sliding motion and the positive rheotaxis are ethologically efficient for the survival and growth of the cell in nature, and thus, the present studies on cell motility are meaningful for biology.

This thesis has identified novel rules governing passive and active particles under simple but realistic conditions at low Reynolds number through a combination of quantitative measurements and hydrodynamic numerical calculations. The simple

dynamics that we observed provide a basis for extension to many-body systems or complex boundary conditions observed in the real world.

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List of publications

Publications covered in this thesis

Ohmura, T., Ichikawa, M., Kamei, K. I. and Maeda, Y. T. Oscillation and collective conveyance of water-in-oil droplets by microfluidic bolus flow. *Applied Physics Letters*, 107(7), 074102 (2015).

Ohmura, T., Nishigami, Y., Taniguchi A., Nonaka, S., Manabe, J., Ishikawa, T., and Ichikawa, M. Simple mechano-sense and response of cilia motion determine the intrinsic habits of ciliates. submitted.

Chapter 1

General introduction

1.1 Particle motions in low Reynolds world

All moving objects and organisms not only are subject to drag forces from the surrounding fluid but also produce kinetic and thermal effects on the surrounding fluid. “Flow” is generally described by the Navier-Stokes equation, and its features change depending on the Reynolds number (Re), which is a ratio of inertial effect and viscous effect. At high Reynolds number, the inertial term dominates in the Navier-Stokes equation. When Re is smaller than 1, the flow field around a spherical particle in continuous flow is almost symmetrical, whereas when Re is higher than $10 - 10^2$, vortexes are generated back to the particle. These vortices cause unexpected motions of the particle, such as a no-rotational shut in soccer and a knuckle ball in baseball. Those wandering phenomena are derived from non-linear flow, which is called turbulence.

At low Reynolds number, the flow field is described by the Stokes equation $\nabla P = \mu \nabla^2 \cdot \mathbf{u}$, which is derived from the Navier-Stokes equation but ignores the inertial and time-dependent terms. The Stokes equation is linear, and therefore the dynamics of a simple system in a low Reynolds world can be solved analytically.

We classify systems of particle motion at low Reynolds number based on the number of particles and the driving force. Considering a spherical particle driven by continuous flow, the flow field around the particle and the drag force on the particle can be solved exactly (Fig. 1.1: top-left). This solution has been approximately used to describe non-linear dynamics of many-body systems, such as the segmentation of colloidal suspensions, aggregation or electrophoresis (Fig. 1.1: bottom-left). We focus on a simpler system than a many-body system that consists of particles aligned 1-dimensionally. Interestingly, when particles are placed in a narrow space, they show non-trivial phenomena similar to those observed in many-body systems, such as wave propagation in a 1-dimensional droplet crystal,

clustering of red blood cells flowing in a microcapillary and rhythmic motion of driven colloids on a ring (Fig. 1.1: middle-left). To reveal the dynamics and mechanism of these spatio-temporally ordered motions, theoretical or numerical models including strict wall interactions of each particle are necessary.

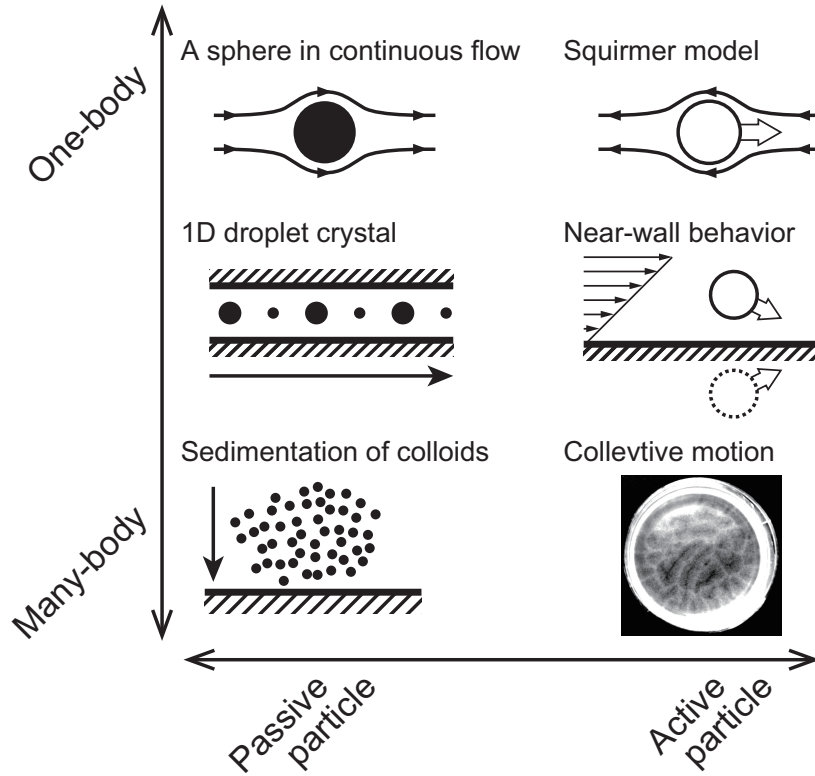


Fig. 1.1 Schematic diagram of particle motion at low Reynolds number.

Next, we discuss active particles. Active particles are self-driven, such as living cells, Janus colloidal particles and swimming droplets. Active particles continue to convert chemical energy to kinetic energy as long as they are in motion, and the systems of their motions are usually in a non-equilibrium state. Therefore, an exact formulation of a single active particle is very complex. To express the hydrodynamic effect of an active particle qualitatively, a simple hydrodynamic model called the ‘squirmer model’ has been developed (Fig. 1.1: top-right). The squirmer model has been used to represent a microswimmer, especially a swimming cell, with an approximate flow field around the body. The squirmer model enables the solution of the numerical dynamics of many-body active particles. The many-body systems of swimming cells occasionally form macroscopic interactive patterns called collective motion, such as bioconvection, bacterial turbulence or aggregation (Fig. 1.1: bottom-right). However, it is still difficult to describe all of the dynamics of these patterns using only the simplified model because ac-

tual active particles are influenced by various factors, such as hydrodynamic and chemotic interactions, collisions, and the response to an external field. Thus, we focus on the quantification of such factors, e.g., an interface or external flow (Fig. 1.1: middle-right).

In this thesis, the near-wall phenomena of passive and active particles at low Reynolds number in a one-body and many-body system were compared (Fig. 1.1: middle). To identify the mechanisms and quantify their motions, we performed both experimental and numerical calculations and compared the results. The important aim is not to reproduce motions using an advanced numerical model but to identify the interactions by reproducing the motion to explain the origin of the motion of interest.

1.2 Passive and active particles

In this thesis, moving particles at low Reynolds number are categorized into two types. The first is a passive particle driven by an external force. A single passive particle tends to behave linearly because of viscous resistance, whereas a many-body system of passive particles in a non-equilibrium state becomes non-linear without changing the external field. The second is an active particle, which exchanges energy for kinetic motion and is driven by itself. Active particles maintain a non-equilibrium state as long as they are in motion, and thus, an interactive system of active particles is unpredictable, even if it is a very simple system, such as a single particle interacting with a flat wall. In this section, passive particles and active particles in a non-equilibrium state are introduced.

1.2.1 Passive particle

The dynamics of a many-body system is mainly described by the interactions between particles. The interactions of micrometer-scaled particles in viscous fluid include collisions and electromagnetic or hydrodynamic interactions in, for example, electrophoresis of charged colloidal particles, aggregation and sedimentation. Intuitively, the collisions and electromagnetic interactions seem crucial for the dynamics. However, a simulation without hydrodynamic interactions cannot reproduce the clustering patterns of charged colloids in an experiment[1, 2], which indicates the importance of the hydrodynamic interactions in a many-body system as well as other interactions.

In addition, there are also some pattern formations due only to hydrodynamic interactions. Here, we introduce two types of these hydrodynamic phenomena at low Reynolds number.

Red blood cells in a capillary vessel

The many-body system at low Reynolds number exists *in vivo*, which is red blood cells (RBCs) flowing in a capillary vessel.

RBCs occupy 96% of blood cells and play a crucial role in body processes by transporting and circulating oxygen. Recent studies have included not only medical research on RBCs but also quantifications of their physical properties[3]. One of these physical approaches includes numerical calculations on RBCs flowing in microvessels in medical engineering research[4, 5]. Numerical calculations have shown that RBCs form a cluster of cells and align in one line in microcapillaries. The clustering and alignment occur by hydrodynamic interactions[6, 7]. The clustering of RBCs is a factor related to vascular occlusion. In addition, periodic flow can occur between two RBCs in a capillary vessel, which is called bolus flow[8, 9]. Bolus flow is a closed flow, and thus, small particles and chemicals are trapped and transported in the bolus flow.

As mentioned above, particles flowing only in a narrow capillary show interesting phenomena *in vitro*.

Microfluidic droplets

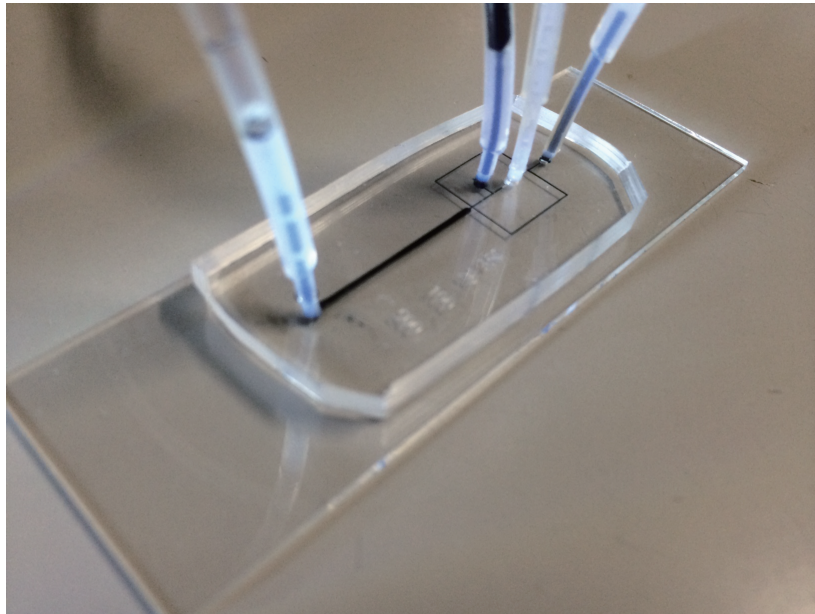


Fig. 1.2 Microfluidic device.

Microdroplets are generated in a microfluidic device and flow in a microchannel (Fig. 1.2). By controlling the pressure and designing the channel, it is possible to flow homogeneous droplets periodically (Fig. 1.3(a)). These droplets show wave

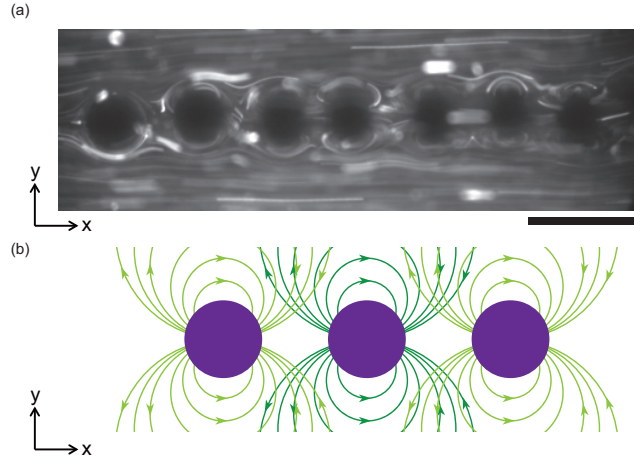


Fig. 1.3 Microfluidic droplets and the surrounding flow field. (a) Visualized flow around the droplets flowing in a microchannel. The scale bar is 200 μm . (b) Schematic figure of velocity potentials around a droplet.

propagation of distances between droplets or many-body structures [10, 11, 12, 13] ((Fig. 1.4)). This phenomenon can be explained by hydrodynamic interactions of the velocity potential of each droplet (Fig. 1.3(b)). In addition, this behavior is an attractive non-linear phenomenon in a simple experimental system with only hydrodynamic interactions. The mechanisms are written in detail in Chapter 2.

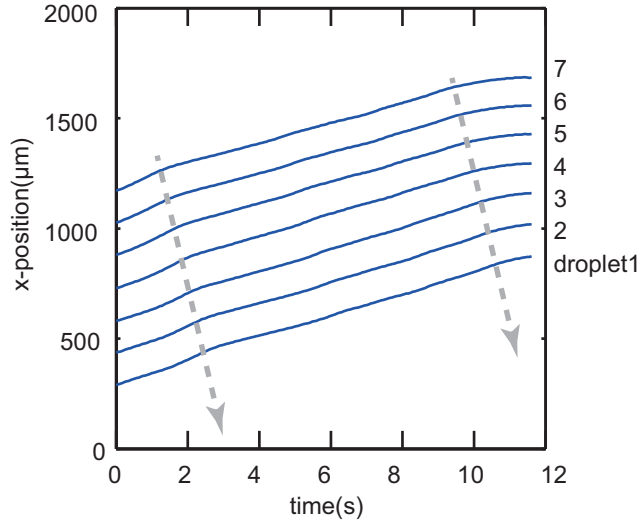


Fig. 1.4 Wave propagation of the distance between droplets. The horizontal axis represents time (s), and the vertical axis represents x -positions of droplets. The gray vectors represent the propagation of the distance deviation.

1.2.2 Active particle

In this section, we introduce active particles. In the last 10 years, research on “active matter” has developed within the field of non-equilibrium physics. Ramaswamy[14] defined active matter as “driven systems in which energy is supplied directly, isotropically and independently at the level of the individual constituents—active particles—which, in dissipating it, generally achieve some kind of systematic movement.” In active matter, the phenomena of self-propelled particles are targeted regardless of whether the particles are organisms or non-organisms. For example, this research area encompasses cellular motion, micrometer-scaled particles driven by the Marangoni effect[15, 16, 17] and the collective motion of animals [18, 19, 20, 21].

In the above examples, self-propelled micrometer-scaled particles in Newtonian fluids are observed.

Artificial swimmers

An artificial swimmer is a self-propelled particle that is artificially fabricated. In such swimmers, micrometer-scaled particles are propelled by the Marangoni effect. The Marangoni effect refers to the generation of flow by some type of gradient in space, such as a thermal gradient or gradient of chemical concentration, for example, Janus particles[22, 23, 24, 25, 26] or active droplets[15]. The behaviors of self-propelled swimmers include some non-linear motions, such as transitions, which are observed not only in many-body systems but also in individual swimmers.

Active droplets are artificial liquid droplets that move themselves without an external force when immersed in a second liquid. Some types of active droplets (water-in-oil droplet[27], oil-in-water droplet[16], alcohol droplet[28], liquid crystal droplet[29]) are self-propelled systems that are influenced by the Marangoni effect. Distributing surfactant into one layer, the concentration of surfactant becomes asymmetrical near the interface of droplet; subsequent Marangoni flow, which is generated by the difference in interfacial tension, drives the droplets. When a non-deformable spherical droplet is driven to one direction, the flow field around the droplet must satisfy the spherical boundary condition and break isotropic symmetry, which indicates that the flow contains a hydrodynamic source dipole. The hydrodynamic source dipole is also derived from the potential flow around a droplet in continuous flow, such as a microfluidic droplet. Therefore, the hydrodynamic properties of an active droplet without other droplets and boundary conditions appear similar to those of a passive droplet. However, a passive particle, for which

the flow field is dependent on the direction of the external field, is radically different from an active particle, for which the moving direction is dependent on the internal force.

In addition, active droplets also interact with a surfactant gradient that they generate. To describe the dynamics of active droplets, an advection-diffusion equation must be solved for the whole system, which is complicated.

Swimming microorganisms

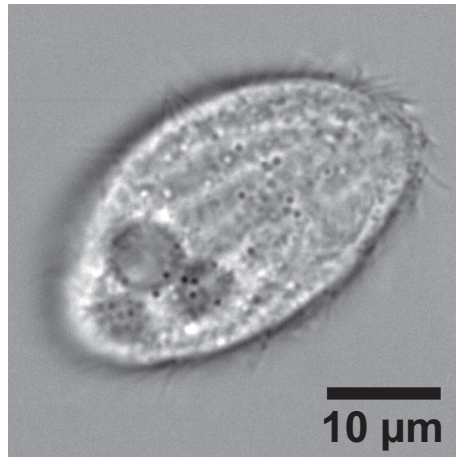


Fig. 1.5 Swimming microorganism; *Tetrahymena pyriformis*. It swims by ciliary beating around the body.

Living cells exchange chemical energy in the cell membrane into kinetic energy and show center-of-mass motion or deformation. The focus here is on cell swimming (Fig. 1.5). Swimming cells do not creep on a substrate by deforming their bodies but swim in bulk water by beating organelles called flagellar or cilia, which are constructed from filaments and motor proteins.

Recent experiments and analyses have focused on specific organisms, including mammalian sperm [30, 31, 31, 32], archaea [33], and *Chlamydomonas* [34]. Swimming microorganisms can exhibit collective motions, which are of interest as phenomena in non-equilibrium physics. Examples include bacterial vortices and turbulence [35, 36, 37] and bioconvection [38, 39, 40, 41, 42].

Microorganisms can secrete chemicals and show responses to concentration gradients via a process called chemotaxis. However, swimming microorganisms generally swim faster than the diffusion velocity in bulk water. Consequently, to describe the motility of swimming microorganisms, we need to know not how the chemicals diffuse but how the propulsion force is transmitted to their motion and influences the flow field around them.

At low Reynolds number in Newtonian fluids, a swimmer must break the time-reversal of deformation, which is theoretically described by the Scallop theorem [43, 44]. Approaches to the motions of swimming microorganisms using low Reynolds hydrodynamics have been developed [45, 46, 47].

1.3 Hydrodynamic theory

1.3.1 Stokes equation

In this section, we derive the Stokes equation that describes low Reynolds flow.

“Flow” indicates the macroscopic kinetics of material components as an ensemble, and the flow consists of the “fluid”. For a liquid or gas fluid, the component is a molecule, and thermal agitation in the flow vanishes because the dynamics is regarded as an averaged ensemble.

Using the mean free path of the component λ and a characteristic length of the system L , the Knudsen number is defined as $Kn = \lambda/L$. The Knudsen number determines whether the flow system can be treated as a continuum or not. If Kn is much lower than 1, the system is continuous. Because the mean free path is small and the characteristic length is large, the components frequently collide with each other, and the momentum and the energy are averaged.

As mentioned above, fluids are categorized by how body forces, such as gravity, or area forces, such as pressure, work. One such categorization focuses on the property of fluid called viscosity. A viscous fluid undergoes shear deformation under shear stress. Here, to form the equation of motion for a viscous fluid, we consider the fluid dynamics and area force.

The component of a fluid, in contrast to a rigid body, exhibits not only parallel motion but also deformation. The differences in velocity and coordinates between one component and the same component after a unit time are defined as $d\mathbf{u} = (du, dv, dw)$, $d\mathbf{x} = (dx, dy, dz)$. To deform the component, $d\mathbf{u} = (du, dv, dw)$ must be non-zero. Neglecting second-order terms in the Taylor expansion of $d\mathbf{u}$ by $d\mathbf{x}$, the equation can be expressed as a product of a tensor and a vector.

$$\begin{pmatrix} du \\ dv \\ dw \end{pmatrix} = \begin{pmatrix} \frac{\partial u}{\partial x} & \frac{\partial u}{\partial y} & \frac{\partial u}{\partial z} \\ \frac{\partial v}{\partial x} & \frac{\partial v}{\partial y} & \frac{\partial v}{\partial z} \\ \frac{\partial w}{\partial x} & \frac{\partial w}{\partial y} & \frac{\partial w}{\partial z} \end{pmatrix} \begin{pmatrix} dx \\ dy \\ dz \end{pmatrix} \quad (1.1)$$

This tensor also contains rotation. Thus, it is necessary to divide the term of

deformation by the term of rotation.

$$\frac{\partial u_i}{\partial x_j} = \frac{1}{2} \left(\frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i} \right) + \frac{1}{2} \left(\frac{\partial u_i}{\partial x_j} - \frac{\partial u_j}{\partial x_i} \right) \quad (1.2)$$

$$\equiv e_{ij} + \Omega_{ij} \quad (1.3)$$

e_{ij} is a symmetric tensor called the strain rate tensor. Ω_{ij} is an asymmetric tensor and expresses rotation. The strain rate tensor can be divided into two terms: the rate-of-expansion tensor and rate-of-shear tensor.

Next, we consider the stress force for deforming an object. Separating a space filled with fluid into cuboids (Δx , Δy , Δz), three pressures per unit area are defined: $\mathbf{p}_x$ parallel to the x -axis, $\mathbf{p}_y$ parallel to the y -axis, and $\mathbf{p}_z$ parallel to the z -axis. By using these three pressures, the forces on the six surfaces of the cuboid can be calculated. Each of $\mathbf{p}_x$, $\mathbf{p}_y$ and $\mathbf{p}_z$ has three components. Using the expression for the tensor,

$$P_{ij} = \begin{pmatrix} \mathbf{p}_x \\ \mathbf{p}_y \\ \mathbf{p}_z \end{pmatrix} = \begin{pmatrix} p_{xx} & p_{xy} & p_{xz} \\ p_{yx} & p_{yy} & p_{yz} \\ p_{zx} & p_{zy} & p_{zz} \end{pmatrix} \quad (1.4)$$

This tensor is called the stress tensor and can express all area forces in arbitrary directions at once.

Newton derived that the response of a fluid to a simple shear stress is proportional to the velocity gradient. A fluid that satisfies this relationship is called a Newtonian fluid. The constant of proportion μ is called the viscosity coefficient and depends on the type of fluid components. Assuming that the stress tensor p_{ij} is a first-order equation of the strain rate tensor e_{ij} , the relationship between the stress tensor and the strain tensor with shear velocity is as follows

$$p_{ij} = -p\delta_{ij} + \lambda e_{kk}\delta_{ij} + 2\mu e_{ij} \quad (1.5)$$

where $-p\delta_{ij}$ is the isotropic pressure and $\lambda e_{kk}\delta_{ij}$ is the expansive effect of pressure. λ is a constant called the second viscosity coefficient. This equation contains two viscosity coefficients, μ and λ . To simplify the equation, the following relationship is assumed (the Stokes assumption)

$$\lambda + \frac{2}{3}\mu = 0 \quad (1.6)$$

$\lambda + \frac{2}{3}\mu$ is called the volume viscosity. It is generally difficult to measure λ , and the volume viscosity is usually assumed to be zero. Using this assumption,

$$p_{ij} = -\left(p + \frac{2}{3}\mu e_{kk}\right)\delta_{ij} + 2\mu e_{ij} \quad (1.7)$$

Finally, we derive the two equations for viscous fluid. For the first equation, the mass conservation law is applied to the fluid component. For a unit cuboid of fluid, the mean density ρ and the mean velocity $\mathbf{u}$ are defined. The mass flowing out from the unit cuboid per unit time is expressed as $\nabla \cdot (\rho \mathbf{v})$. Therefore, the general equation is established as follows:

$$\frac{\partial \rho}{\partial t} = -\nabla \cdot (\rho \mathbf{v}) \quad (1.8)$$

This equation is called the continuity equation.

For the second equation, the equation of motion is derived using the stress tensor p_{ij} . Considering the motion of the fluid cuboid, the acceleration is given as follows: $D\mathbf{u}/Dt = \rho \left(\frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla) \mathbf{v} \right)$. The external forces include the body force $\mathbf{K}$ and the area force derived by the stress tensor p_{ij} . The above terms are combined into one equation as follows:

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} \right) = \rho \mathbf{K} - \nabla p + \frac{1}{3} \mu \nabla (\nabla \mathbf{u}) + \mu \nabla^2 \mathbf{u} \quad (1.9)$$

This equation is well-known as the Navier-Stokes equation, which generally describes the dynamics of viscous fluid.

The second term on the left side of Eq. (1.9) expresses the inertial force, and the third and fourth terms on the left side express the viscous force. The ratio of the inertial term to the viscous term is defined as the Reynolds number Re .

$$Re = \frac{\rho U L}{\mu} \quad (1.10)$$

where U is the characteristic velocity of the flow and L is the characteristic length of the flow. Re is generally used as the barometer of a flow system. If the velocities, lengths and viscosities of two flows are different but Re is the same, the two flows are regarded as having the same properties (Reynolds similarity).

For a high Reynolds number $Re \gg 1$, the viscous terms in the eq. (1.9) can be neglected to give the Euler equation.

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} \right) = \rho \mathbf{K} - \nabla p \quad (1.11)$$

The inertial term has non-linearity, and hence, the dynamics of fluid often becomes complex. The Euler equation is used in aerodynamic research, where large-scale flow is observed.

By contrast, for a low Reynolds number $Re \ll 1$, the inertial term in the eq. (1.9) can be neglected.

$$\rho \frac{\partial \mathbf{u}}{\partial t} = \rho \mathbf{K} - \nabla p + \frac{1}{3} \mu \nabla (\nabla \mathbf{u}) + \mu \nabla^2 \mathbf{u} \quad (1.12)$$

Here, assuming that the fluid is incompressible, $\rho = \text{const.}$, the continuity equation is as follows:

$$\nabla \cdot \mathbf{u} = 0 \quad (1.13)$$

This is called the incompressible condition. Then, the eq. (1.12) becomes

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} \right) = -\nabla p + \mu \nabla^2 \mathbf{u} \quad (1.14)$$

This equation is called the Stokes equation, which generally describes incompressible flow at low Reynolds number. As a divergence of eq. (1.14),

$$\Delta p = 0 \quad (1.15)$$

This is the Laplace equation, and the pressure is a harmonic function.

In addition, considering steady flow in which the terms are not dependent on time, $\partial \mathbf{u} / \partial t = 0$. Thus, eq. (1.14) is

$$\nabla \cdot p = \mu \nabla^2 \mathbf{u} \quad (1.16)$$

The solutions of this equation can be superimposed, and the fundamental solution is given as the Stokeslet.

1.3.2 Boundary condition

For incompressible flow at low Reynolds number, boundary conditions are important because the solution of eq. (1.16) is specified if deciding the boundary condition. There are two types of hydrodynamic boundary conditions: slip boundary and non-slip boundary.

The slip boundary is generally set at the fluid-fluid interface, for example, liquid-air and liquid-air. Under the slip boundary condition, the flow cannot pass through the interface to the perpendicular direction $\mathbf{n}$. Therefore, the following equation governs the interface.

$$\mathbf{u} \cdot \mathbf{n} = 0 \quad (1.17)$$

By contrast, the non-slip boundary is generally set at the solid-fluid interface. Under the non-slip boundary condition, the flow is given by the friction force and stops. Therefore, the condition is more restricted than the slip boundary.

$$\mathbf{u} = \mathbf{0} \quad (1.18)$$

Although the boundary conditions of a wall and a particle in viscous fluid are slip, the boundary conditions of an air-liquid interface and a liquid droplet are non-slip. Adequate boundary conditions must be chosen for each system.

1.3.3 Oseen tensor

In this section, the Oseen tensor is derived from the eq. (1.16). The Oseen tensor is a Green function that relates a point force to a velocity and a pressure field generated by the point force in an incompressible fluid at low Reynolds number.

First, introducing the point force $-\mathbf{F}\delta(\mathbf{r})$ into the eq. (1.16),

$$-\nabla p + \mu \nabla^2 \mathbf{u}(\mathbf{r}) = -\mathbf{F}\delta(\mathbf{r}) \quad (1.19)$$

Here, the flow field at infinity must vanish, i.e., $|\mathbf{u}(\mathbf{r})| = 0$ ($r = \infty$). Taking the divergence of eq. (1.19) and using eq. (1.13), a Poisson equation is obtained.

$$\nabla^2 p = \mathbf{F}\delta(\mathbf{r}) \quad (1.20)$$

The Fourier transform is applied to the above equation.

$$k^2 \hat{p}(\mathbf{k}) = -i\mathbf{k}\mathbf{F} \quad (1.21)$$

The Fourier transform is also applied to eq. (1.19).

$$ik\hat{p}(\mathbf{k}) + \mu k^2 \hat{\mathbf{u}}(\mathbf{k}) = \mathbf{F} \quad (1.22)$$

From above two equations,

$$\hat{p}(\mathbf{k}) = -i \frac{\mathbf{k} \cdot \mathbf{F}}{k^2} \quad (1.23)$$

$$\hat{\mathbf{u}}(\mathbf{k}) = \frac{1}{\mu k^2} \left[\mathbf{F} - \mathbf{k} \left(\frac{\mathbf{k} \cdot \mathbf{F}}{k^2} \right) \right] \quad (1.24)$$

Using the definition of the inverse Fourier transform,

$$p(\mathbf{r}) = \frac{i}{8\pi^3} \int_{\mathbb{R}} d\mathbf{k} \frac{e^{i\mathbf{k} \cdot \mathbf{r}}}{k^2} (\mathbf{k} \cdot \mathbf{F}) \quad (1.25)$$

$$\mathbf{u}(\mathbf{r}) = \frac{1}{8\mu\pi^3} \int_{\mathbb{R}} d\mathbf{k} \frac{e^{i\mathbf{k} \cdot \mathbf{r}}}{k^2} \left[\mathbf{F} - \mathbf{k} \left(\frac{\mathbf{k} \cdot \mathbf{F}}{k^2} \right) \right] \quad (1.26)$$

The expression in Fourier space is derived from fundamental solutions of the Laplace equation.

$$\frac{i}{(2\pi)^3} \int_{\mathbb{R}} d\mathbf{k} \frac{\mathbf{k}}{k^2} e^{i\mathbf{k} \cdot \mathbf{r}} = \nabla \left(\frac{1}{4\pi r} \right) \quad (1.27)$$

Taking eq. (1.27) into eq. (1.25), the expression of $p(\mathbf{r})$ is obtained.

$$p(\mathbf{r}) = -\mathbf{F} \cdot \nabla \left(\frac{1}{4\pi r} \right) = \frac{\mathbf{F} \cdot \mathbf{r}}{4\pi r^3} \quad (1.28)$$

In the same way, by using the two expressions in Fourier space

$$\frac{1}{(2\pi)^3} \int_{\mathbb{R}} d\mathbf{k} \frac{1}{k^2} e^{i\mathbf{k} \cdot \mathbf{r}} = \left(\frac{1}{4\pi r} \right) \quad (1.29)$$

$$\begin{aligned} \frac{1}{(2\pi)^3} \int_{\mathbb{R}} d\mathbf{k} \frac{\mathbf{k}\mathbf{k}}{k^4} e^{i\mathbf{k} \cdot \mathbf{r}} &= \nabla \nabla \left(\frac{r}{8\pi} \right) \\ &= -\frac{1}{8\pi} \frac{\mathbf{r}\mathbf{r}}{r^3} + \frac{\mathbb{I}}{8\pi r} \end{aligned} \quad (1.30)$$

The expression of $\mathbf{u}(\mathbf{r})$ is obtained as follows:

$$\begin{aligned} \mathbf{u}(\mathbf{r}) &= \frac{\mathbf{F}}{4\pi\mu r} - \frac{1}{8\mu\pi^3} \int_{\mathbb{R}} d\mathbf{k} \frac{e^{i\mathbf{k} \cdot \mathbf{r}}}{k^2} \mathbf{k} \left(\frac{\mathbf{k} \cdot \mathbf{F}}{k^2} \right) \\ &= \frac{\mathbf{F}}{4\pi\mu r} - \frac{\mathbf{F}}{\mu} \cdot \nabla \nabla \left(\frac{r}{8\pi} \right) \\ &= \frac{\mathbf{F}}{8\pi\mu r} \cdot \left(\mathbb{I} + \frac{\mathbf{r}\mathbf{r}}{r^2} \right) \end{aligned} \quad (1.31)$$

These expressions are often used to express hydrodynamic interactions between micrometer-scaled particles approximately.

1.3.4 Squirmer model

Lighthill proposed and Blake expanded the squirmer model as a swimming model for microorganisms [48, 49]. This model has been used in many studies [30, 50, 51, 52, 53, 54]. In this section, the squirmer model is derived.

First, considering a sphere of radius R set in incompressible axisymmetric flow at low Reynolds number, the flow around the sphere can be described by the continuity equation (eq. 1.13) and the Stokes equation (eq. 1.16). Next, the boundary condition of the sphere is decided as follows in spherical polar coordinates.

$$\begin{aligned} u_r|_{r=R} &= \sum_n A_n(t) P_n(\cos \theta) \\ u_\theta|_{r=R} &= \sum_n B_n(t) V_n(\cos \theta) \end{aligned} \quad (1.32)$$

where P_n is the n th Legendre polynomial and V_n is defined as

$$V_n(\cos \theta) = \frac{2}{n(n+1)} \sin \theta P'_n(\cos \theta) \quad (1.33)$$

The sphere that has the above properties is defined as a squirmer. When the swimming direction of the squirmer is $\theta = 0$, the solution can be obtained analytically

as follows [49].

$$u_r = -U \cos \theta + A_0 \frac{R^2}{r^2} + \frac{2}{3}(A_1 + B_1) \frac{R^3}{r^3} P_1 + \sum_{n=2}^{\infty} \left[\left(\frac{n}{2} \frac{R^n}{r^n} - \left(\frac{n}{2} - 1 \right) \frac{R^{n+2}}{r^{n+2}} \right) A_n P_n + \left(\frac{R^{n+2}}{r^{n+2}} - \frac{R^n}{r^n} \right) B_n P_n \right] \quad (1.34)$$

$$u_\theta = U \sin \theta + \frac{1}{3}(A_1 + B_1) \frac{R^3}{r^3} V_1 + \sum_{n=2}^{\infty} \left[\left(\frac{n}{2} \frac{R^{n+2}}{r^{n+2}} - \left(\frac{n}{2} - 1 \right) \frac{R^n}{r^n} \right) B_n P_n + \frac{n}{2} \left(\frac{n}{2} - 1 \right) \left(\frac{R^n}{r^n} - \frac{R^{n+2}}{r^{n+2}} \right) A_n V_n \right] \quad (1.35)$$

$$p = \mu \sum_{n=2}^{\infty} \frac{2n-1}{n+1} (nA_n - 2B_n) \frac{R^n}{r^{n+1}} P_n \quad (1.36)$$

The condition for the squirmer to experience no net force is

$$U = \frac{1}{3}(2B_1 - A_1) \quad (1.37)$$

In addition, assuming the squirmer as a spherical object, the radial velocity at the surface is zero.

$$A_n = 0 \quad (n = 0, 1, 2, \dots) \quad (1.38)$$

Therefore, eq. (1.34) and eq. (1.35) are

$$u_r = \frac{2}{3} \left(\frac{R^3}{r^3} - 1 \right) B_1 P_1 + \sum_{n=2}^{\infty} \left(\frac{R^{n+2}}{r^{n+2}} - \frac{R^n}{r^n} \right) B_n P_n \quad (1.39)$$

$$u_\theta = \frac{2}{3} \left(\frac{R^3}{2r^3} + 1 \right) B_1 V_1 + \sum_{n=2}^{\infty} \frac{1}{2} \left(n \frac{R^{n+2}}{r^{n+2}} + (2-n) \frac{R^n}{r^n} \right) B_n P_n \quad (1.40)$$

Here, we focus on only the first two modes of the eq. (1.39) and the eq. (1.40) because the higher modes are very small and decrease drastically depending on the increase in r . Using $P_1(\cos \theta) = \cos \theta$, $P_2(\cos \theta) = \frac{1}{2}(\cos^2 \theta - \frac{1}{2})$, $V_1(\cos \theta) = \sin \theta$ and $V_2(\cos \theta) = \frac{1}{2} \sin 2\theta$,

$$\begin{aligned} u_r &= \frac{2}{3} \left(\frac{R^3}{r^3} - 1 \right) B_1 P_1 + \left(\frac{R^4}{r^4} - \frac{R^2}{r^2} \right) B_2 P_2 \\ &= U \left(\frac{R^3}{r^3} - 1 \right) \cos \theta + \beta U \frac{3}{4} \left(\frac{R^4}{r^4} - \frac{R^2}{r^2} \right) (3 \cos^2 \theta - 1) \end{aligned} \quad (1.41)$$

$$\begin{aligned}
u_\theta &= \frac{2}{3} \left(\frac{R^3}{2r^3} + 1 \right) B_1 V_1 + \frac{R^4}{r^4} B_2 P_2 \\
&= U \left(\frac{R^3}{2r^3} + 1 \right) \sin \theta + \beta U \frac{3}{4} \frac{R^4}{r^4} \sin 2\theta
\end{aligned} \tag{1.42}$$

where $\beta = B_2/B_1$. From above two equations, the velocity at the surface ($r = R$) can be derived.

$$u_r = 0 \tag{1.43}$$

$$u_\theta = \frac{3}{2} U \sin \theta (1 + \beta \cos \theta) \tag{1.44}$$

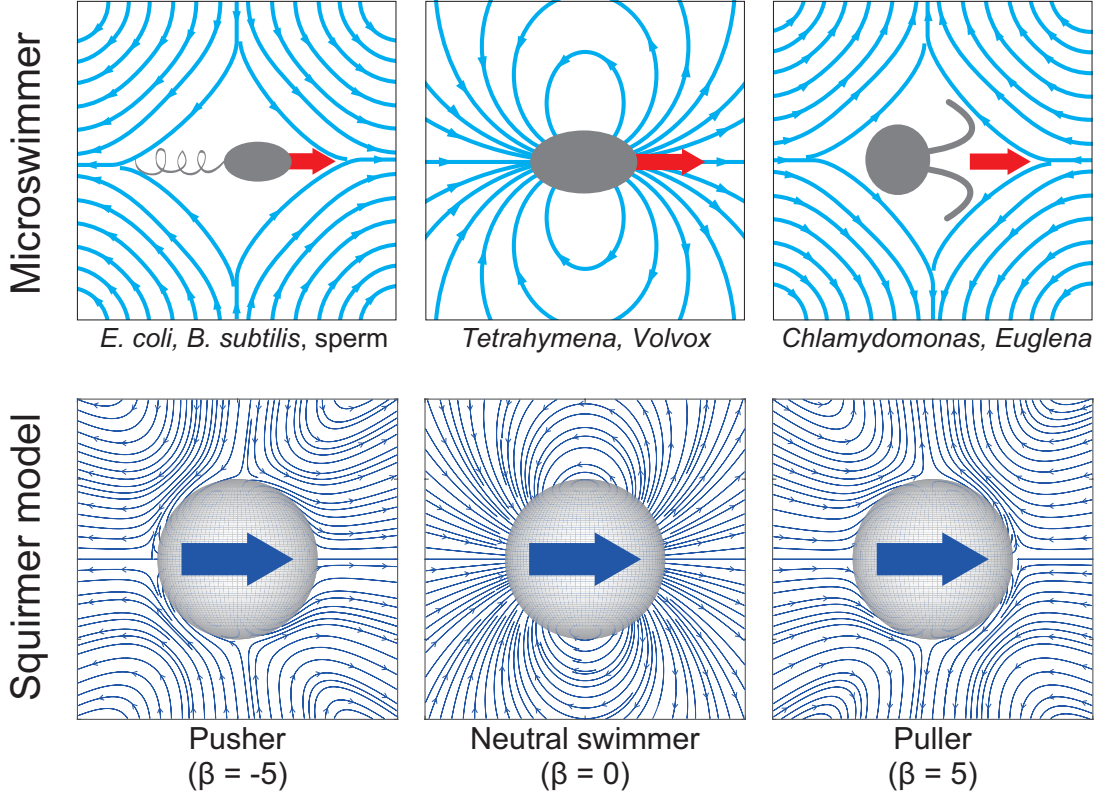


Fig. 1.6 Flow fields around a microswimmer (top) and flow fields around a squirmer (bottom) in lab frame.

This approximation has been used often in recent research, and eq. (1.41) and eq. (1.42) can represent the flow field around an actual microorganism. In this expression, the flow fields around swimming microorganisms are categorized into three patterns: a pusher ($\beta < 0$), a puller ($\beta > 0$) and a neutral swimmer ($\beta = 0$). Swimming microorganisms categorized as pushers are mainly propelled by flagella at the rear of the body, for example, mammalian sperms[30, 31, 31, 32], *Escherichia coli*[37], *Bacillus subtilis*[35], and *Halobacterium salinarum*[33].

Pullers are mainly propelled by flagella at the head of the body, for example, *Euglena*[42] and *Chlamydomonas*[34, 55]. Neutral swimmers are mainly propelled by multi-flagella or cilia on the whole body, for example, *Volvox*[55] and *Tetrahymena*[56].

The swimming motions of pushers and pullers have been extensively studied by experiment and simulation, but few studies have focused on neutral swimmers.

1.3.5 Numerical calculation

Numerical calculations for fluid dynamics are called Computational Fluid Dynamics (CFD) and are used to solve turbulent phenomena because the inertial term in the Navier-Stokes equation is non-linear. If considering low Reynolds phenomena neglecting inertia, the numerical method is also effective for complex systems, such as many-body systems and interactions between self-propelled swimmers. The system containing boundary conditions is too complex to solve analytically. The details of the numerical methods used in this thesis, the Lattice Boltzmann Method and Boundary Element Method, are provided in the Appendix.

1.4 Outline of this thesis

In this thesis, near-wall dynamics of passive and active particles at low Reynolds number are revealed. We performed quantitative experiments and obtained schematic mechanisms of the phenomena. We then identified the dynamics by using hydrodynamic numerical calculations.

In Chapter 2, we report the motion of passive particles, which are heterogeneous droplets in a microchannel in one line. In this study, we first developed a microfluidic device that can flow small droplets (diameter: $20\ \mu\text{m}$) and large droplets (diameter: $140\ \mu\text{m}$) alternately in one line. The flowing small droplets were trapped and oscillating between two large droplets. The wave propagation of the homogenous droplets can be explained by a quasi-2-dimensional model [10], but this model cannot represent our results. More precise experiments revealed that the oscillating orbit of the small droplet was 3-dimensional. Finally, we performed 3-dimensional numerical calculations by the Lattice Boltzmann Method. Comparing the experimental results with the numerical results, we identified the critical parameters representing the oscillation, which were the distance between the two large droplets and the ratio of the channel height to the large droplet size. In addition, some small droplets were trapped immediately in the periodic flow between two large droplets, and therefore this study could be applied to the transportation of micrometer-scaled particles.

In Chapters 3 and 4, studies of the motility of a swimming microorganism are presented. Among the many types of swimming microorganisms, we focus on ciliates, which have the hydrodynamic properties of a neutral swimmer in the squirmer model. Ciliates are eukaryotic organisms that swim in fluid by using cilia, which are organelles that beat periodically around the body surface. Among ciliates, *Tetrahymena* has been used as a model organism in cell biology[57], but there have been few physical studies of its swimming motility. Swimming microorganisms with the properties of a pusher or puller have been studied extensively, and some of their motilities have been revealed by hydrodynamic analysis. Therefore, we regarded *Tetrahymena* as a neutral swimmer and approached the dynamic mechanism of the motility of *Tetrahymena* by experimental and numerical calculation approaches.

In Chapter 3, we focus on swimming motion near a wall. A spherical neutral swimmer is theoretically repelled from a non-slip boundary by hydrodynamic interaction[52, 54, 58], but we found that *Tetrahymena pyriformis* was not repelled and slid adjacent to the wall. To identify the source of this discrepancy, we first observed the sliding motion quantitatively. *T. pyriformis* continued to

slide on the wall without cell adhesion and gravity. Precise observations of the ciliary beating revealed that the part of the cilia touching the wall nearly stopped compared to the other parts, indicating that the thrust force near the wall was different from the force far from the wall. We attribute the sliding motion to this asymmetry. To validate this assumption, we performed a 3-dimensional numerical calculation by using the Boundary Element Method. The numerical results showed that the ciliary stopping and the anisotropic cell-body shape are important for representing the cell motion. In addition, these experimental and numerical results are consistent with biological observations that ciliates in nature aggregate near a solid-liquid interface.

In Chapter 4, we focus on the response of the microorganism to shear flow. River fishes swim against the stream in rivers, a behavior that is called positive rheotaxis[59, 60]. Positive rheotaxis is also observed for micrometer-scaled swimmers, such as mammalian sperm cells[61, 62], bacteria[63, 64] and artificial swimmers[65]. In fish, rheotaxis is due to a complex biomechanical system, but the rheotaxis of a microswimmer can be explained by simple dynamics. In the case of mammalian sperm, the flagellar beating pattern causes the rheotaxis against shear flow near a wall[32, 66]. First, we examined the rheotaxis of *T. pyriformis* in a microchannel. The cells far from the wall flowed downstream, whereas the cells near the wall swam upstream until encountering a certain shear rate, even if the mean flow speed in the channel was greater than the swimming speed. To realize this rheotaxis near the wall, the swimming motion under shear flow must be considered. The numerical calculation revealed that the ciliary stopping and the anisotropic cell-body shape were also critical for rheotaxis. Based on these two properties, *T. pyriformis* prefers to swim near the wall and shows positive rheotaxis to the shear flow near the wall. These behaviors are very effective for survival under the severe conditions found in nature because abundant feed accumulates on the wall and organisms tend to stay in the same place in a changing environment.

Finally, in Chapter 5, we conclude the thesis and remark on future work on the phenomena of passive and active particles at low Reynolds number.

Chapter 2

Oscillatory motion of passive particles in a microchannel

2.1 Background phenomenon: Wave propagation of the microfluidic droplets

In this section, the hydrodynamic model for droplets flowing in a thin microchannel is exhibited.

First, we consider flow in a rectangular channel, which z -length is enough shorter than x - and y -length. In this channel, the flow velocity $\mathbf{v}(x, y, z)$ can be transformed to $\mathbf{u}(x, y) f(z)$, which channel flow is expressed as quasi-2-dimensional flow ($2\frac{1}{2}$ D flow)[67]. Then, a non-slip boundary condition influences in z -axis and the flow in z -axis is regarded approximately parabolic, which approximation is called Darcy approximation.

$$f(z) = 1 - (2z/h)^2 \quad (2.1)$$

At Darcy approximation, following equation is also established.

$$\frac{\partial^2}{\partial z^2} \gg \frac{\partial^2}{\partial x^2}, \frac{\partial^2}{\partial y^2} \quad (2.2)$$

Substituting eq.(2.1) into eq. (1.16),

$$\nabla p(x, y) = \mu \left((\nabla^2 \mathbf{u}(x, y)) f(z) - \frac{8}{h^2} \mathbf{u}(x, y) \right) \quad (2.3)$$

In addition, using eq. (2.2), $\frac{8}{h^2} \gg \frac{\partial^2}{\partial x^2}, \frac{\partial^2}{\partial y^2}$ Therefore, the velocity on xy plain $\mathbf{u}(x, y)$ is following expression.

$$\mathbf{u}(x, y) = -\frac{h^2}{8\mu} \nabla p(x, y) \quad (2.4)$$

Using Darcy approximation, flow in $2\frac{1}{2}$ dimension is described by potential flow. Defining velocity potential as $\phi = -h^2 p / 8\mu$,

$$\mathbf{u}(x, y) = \nabla \phi \quad (2.5)$$

Here, using incompressible condition $\nabla \cdot \mathbf{u} = 0$, the velocity satisfies Laplace equation $\Delta \phi = 0$. The solutions of this equation can be superimposed, therefore if the boundary condition is fixed, quasi-2-dimensional flow sometimes can be calculated analytically [68].

Next, using this velocity potential, we consider the dynamics of the droplets flowing in thin microchannel. Beatus, *et al.* observed homogeneous droplets (diameter $20\mu m$) flowing in a Hele-Shaw channel (height $10\mu m$) at even intervals and found that the 1-dimensional crystal of the droplets showed the propagation of longitudinal and transversal waves[68]. Defining the direction of the flow as x -axis and the height direction as z -axis, the droplet is extended in xy -plane. Therefore, the droplets can be regarded as putting in quasi-2-dimensional flow (neglecting z -axis). In addition, the Darcy approximation is adaptable so that Re of the system is 10^{-4} order. Considering a circular boundary in continuous flow, the velocity potential of the oil around the droplet ϕ_d is obtained by solving eq. (2.5). The velocity potential which is a harmonic function and satisfies a circular boundary condition must be a doublet.

$$\phi_d(\mathbf{r}) = R^2 (u_{oil}^\infty - u_d) \frac{\mathbf{r}\hat{x}}{r^2} \quad (2.6)$$

where R is the radius of the droplet, u_{oil}^∞ is the flow speed at infinity, u_d is the speed of the droplet flowing without interaction of the other droplets and $\hat{x}$ is the unit vector of x -axis. This solution is a dipole-like potential.

Then, by superimposing the potentials, the velocity potential of the whole system in the view of one droplet represents.

$$\phi(\mathbf{r}) = u_{oil}^\infty \mathbf{r}\hat{x} + \sum_j \phi_d(\mathbf{r} - \mathbf{r}_j) \quad (2.7)$$

The relative velocity of the oil in the droplet frame u_{oil} is derived by gradient of the above expression.

Here, considering that the drag force of the droplet from the flow is equal to the friction force of the droplet with the wall,

$$\nu_d u_d = \xi_d (u_{oil} - u_d) \quad (2.8)$$

u_{oil}^∞ is linearly proportional to u_d^∞ .

$$u_d = (1 + \nu/\xi_d)^{-1} u_{oil} = (u_d^\infty / u_{oil}^\infty) u_{oil} \quad (2.9)$$

where ν_d is the friction coefficient and ξ_d is the drag coefficient. Hereby, the relative velocity of the droplet represents by the expression of the relative velocity of the oil.

$$\dot{\mathbf{r}} = (u_d^\infty / u_{oil}^\infty) \sum_{j \neq n} \nabla \phi(\mathbf{r}_n - \mathbf{r}_j) \quad (2.10)$$

Next, we consider a deviation of the relative coordinates (x_n, y_n) by the interactions of the droplets. Assuming the deviation is much smaller than the mean distance between the two droplets, which indicates $(x_n, y_n) \ll a$, $(\dot{x}_n, \dot{y}_n)$ is as following

$$\dot{x}_n = (3C_s / \pi^2 a) \sum_{j=1}^{\infty} (x_{n+j} - x_{n-j}) / j^3 \quad (2.11)$$

$$\dot{y}_n = - (3C_s / \pi^2 a) \sum_{j=1}^{\infty} (y_{n+j} - y_{n-j}) / j^3 \quad (2.12)$$

where $C_s \cong (2\pi^2/3) (u_d^\infty / u_{oil}^\infty) (u_{oil}^\infty - u_d^\infty) (R^2/a^2)$. Considering that (x_n, y_n) is oscillating and the wave length is enough long, the eq. (2.11) and the eq. (2.12) are expressed as a first-order wave equation. $\partial x_n / \partial t \cong C_s \partial x_n / \partial x$, $\partial y_n / \partial t \cong -C_s \partial y_n / \partial x$, Defining x_n, y_n as

$$x_n = \alpha \exp i(kx_n - \omega_x t) \quad (2.13)$$

$$y_n = \beta \exp i(kx_n - \omega_y t) \quad (2.14)$$

These expressions are taken into eq. (2.11),

$$\dot{x}_n = \alpha (-i\omega_x) \exp i(kx_n - \omega_x t) \quad (2.15)$$

$$= \frac{3C_s}{\pi^2 a} \sum_{j=1}^{\infty} \alpha (\exp(i k x_{n+j} - \omega_x t) - \exp(i k x_{n-j} - \omega_x t)) / j^3 \quad (2.16)$$

$$i\omega_x = -\frac{3C_s}{\pi^2 a} \sum_{j=1}^{\infty} \alpha (\exp(i k x_{n+j} - x_n) - \exp(i k x_{n-j} - x_n)) / j^3 \quad (2.17)$$

Approximating $x_{n+j} - x_n = ja$, $x_{n-j} - x_n = -ja$, the part of the second term inside $\sum$ is

$$\exp(i k x_{n+j} - x_n) - \exp(i k x_{n-j} - x_n) \cong \exp(i k ja) - \exp(-i k ja) \quad (2.18)$$

$$= 2i \sin(jka) \quad (2.19)$$

Considering the wave in y -axis as well as,

$$\omega_x(k) = -\frac{6C_s}{\pi^2 a} \sum_{j=1}^{\infty} \frac{\sin(jka)}{j^3} \quad (2.20)$$

$$\omega_y(k) = \frac{6C_s}{\pi^2 a} \sum_{j=1}^{\infty} \frac{\sin(jka)}{j^3} \quad (2.21)$$

ω depends on the wavenumber and satisfies dispersion relation.

The relationship of the longitudinal and the transversal waves in the experiment is shown to be consistent to eq. (2.20) and eq. (2.21), which indicates that this velocity potential in quasi-2-dimension is valid for the propagation of the droplet crystal. This results also revealed that the hydrodynamic interaction works at the long distance as several hundred μm .

The velocity potential model in this study is also very smart and widely useful for many-body systems of quasi-2-dimensional droplets[12]. Here, the important point is that what makes the system quasi-2-dimensional is the ratio of the droplet size and the channel height. Namely, if the droplet is smaller than the channel height, the Darcy approximation is not adequate.

2.2 Introduction

Recent developments in the fabrication of miniaturized devices have permitted the creation of micro-total analysis systems (μTAS) in the fields of bioengineering, systems biology, and single cell genomics[69, 70]. These small devices can perform many types of biological and chemical analyses, from trapping and sorting of cells to droplet PCR[71, 72], using only tiny amounts of solution. In addition, their low production costs allow them to be used disposably for diagnostic purposes in clinical medicine[73]. Typical devices are composed of circuits, solenoid valves, microchambers, and other functional modules such as electrodes, a configuration which enables highly accurate and high-throughput microanalyses[74, 75]. Some of the most indispensable modules are those that realize the efficient separation and trapping of particles. Although optical tweezers can trap particles, its local weak force makes it difficult to handle in a fast flow. To overcome this difficulty, the S-shaped microchannel can separate differently sized particles owing to the interplay between shear-induced stress and inertial lift force and eventually align the sorted particles in a line[76, 77]. In addition, an interfacial tension gradient across two laminar flows has been used[78, 79]. The use of hydrodynamic effects for particle manipulations has received much attention, but there is a less explored effect which is also relevant—namely, collective dynamics.

A group of micro-objects individually interacting is the simplest realization of a many-body system. In colloidal particles[80, 81], charged plasma[82, 83], red blood cells in capillaries[7, 84], micro-droplets[13, 85, 86] or motile living cells[18, 21], ordered motion or patterns are emerged owing to their interactions through while single element behaves randomly. These organized dynamics emerge through long-range interactions in passive many-body systems[20]. One relevant system for trapping in microfluidics is the 1-dimensional (1D) array of water-in-oil (W/O) droplets, which consists of a lattice of W/O droplets in a line and is maintained under immiscible oil flow in a microchannel. In this droplet array, individual droplets interact hydrodynamically with each other, and it is known that, under a strong confinement by floor and ceiling plates, longitudinal wave propagation occurs[10, 87, 12, 88, 89]. On the other hand, the array of droplets is more remindful of a transport system, with the small objects being trapped in their grid and conveyed in a single direction. To realize a droplet conveyor using an array of other droplets, it is first necessary to understand hydrodynamics in a crystal composed of differently sized droplets dragged by immiscible oil flow. However, this subject has yet to be addressed.

In this Letter, we study the trapping and sequential transport of W/O droplets in a newly developed microfluidic device. We placed each droplet in one of the grids in a 1-dimensional array of other larger W/O droplets, and found that the droplet was conveyed at the same velocity as the large droplets in the lattice. Interestingly, the droplet embedded in the lattice was periodically moved in a back-and-forth manner relative to the large droplets, while the large droplets were dragged at a constant velocity by the oil fluid. This periodic motion was not symmetric to and from adjacent large droplets. That is, the small droplet moved faster (slower) from (toward) the large droplet behind it. To account for the trapping of droplets and oscillation, we performed a numerical simulation based on the lattice Boltzmann method. In the reference frame of large droplets, the parabolic profile of fluid velocity in the z axis and the reduced velocity of large droplets cause the streamlines to close. Furthermore, as more than one droplet was trapped in the grid of the large droplet array, these droplets assembled into a stable cluster with dynamic reposition and were conveyed at a velocity identical to that of the droplet array.

2.3 Method

The microfluidic setup developed in this study is depicted in Fig. 2.1(a). Polydimethylsiloxane (PDMS) was cast on a silicone wafer in which the microstructure of SU-8 positive photoresist was patterned through conventional photolithography

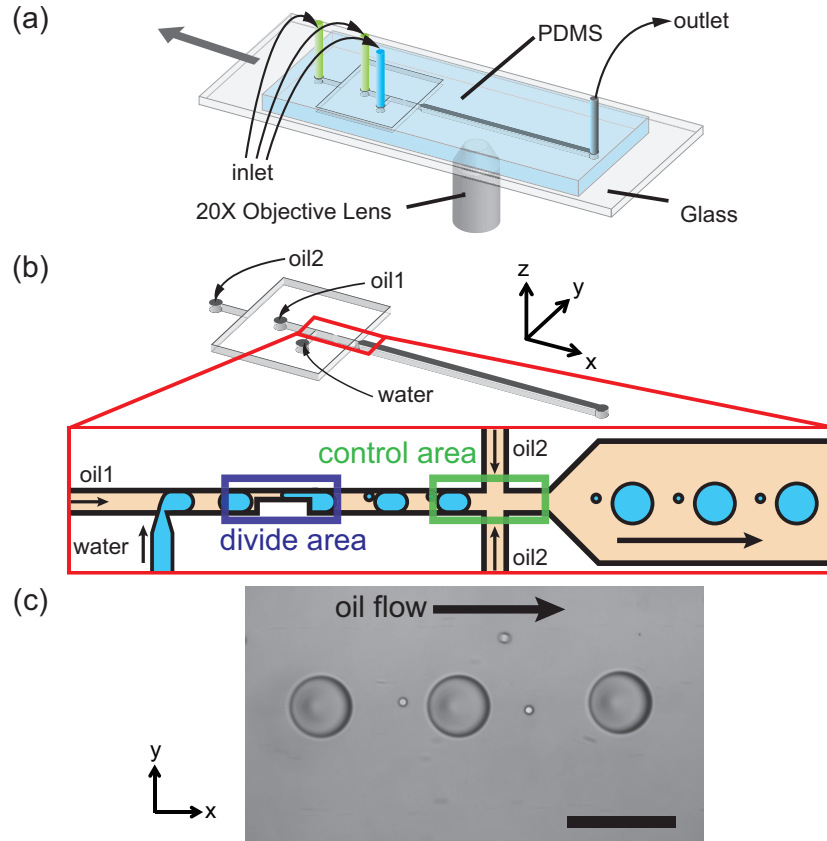


Fig. 2.1 Microfluidic setup. (a) A schematic of the microfluidic setup used in this study. A patterned PDMS was bonded onto slide glass. The PDMS microfluidic device was placed on a motorized stage in an inverted microscope. In order to observe the W/O droplets in a moving frame, we moved the motorized stage at a speed equal to the droplet motion but in the opposite direction. (b) Design of the microfluidic channel used in this study. While W/O droplet was generated at T-shaped junction, it was divided into two different sized droplets at divide area. In order to control the distance between two large droplets, we added another flow channel shown as control area. This module allowed us to control the distance of droplets without affecting the division of the W/O droplet. (c) A representative image of W/O droplets arranged in a line in an alternating sequence of large and small. The scale bar represents $200\ \mu\text{m}$.

and then cured at 80 °C for 1 hour. The PDMS layer was cut carefully and then bonded with pre-cleaned slide glass by treating with oxygen plasma for 30 s. To strengthen the bonding of PDMS to the glass surface, we kept the PDMS devices at 80°C for 1 hour. The inlet and outlet ports were punched-out with a biopsy punch and then the capillary tubes were connected. We used mineral oil supplemented with 2.0% Span80 surfactant and pure water so that the water-in-oil (W/O) droplets were generated by sheath flow. The experiment was carried using a velocity range of 1500-2700 $\mu\text{m/s}$ for mineral oil and 500-1100 $\mu\text{m/s}$ for W/O droplets. The flow rate of fluids was precisely controlled with a pressure-regulated pump system (MFCS System; Fluigent). Please note that the viscosity of fluids was 22 mPas for oil and 0.89 mPas for water, and the typical Reynolds number was $4.3\text{-}8.5 \times 10^{-3}$, indicating that inertia was negligible.

2.4 Result

We first investigated the dynamics of droplets arranged in a line in an alternating sequence of small and large. We generated successive W/O droplets at a T-shaped junction and then split one droplet into two differently sized droplets (Fig. 2.1(b)) [90, 91]. In the divide area, the channel becomes narrow from 100 μm to 20 μm and the length of the narrow part was 350 μm . The small droplet was 10 to 40 μm in diameter and the large one was 100 to 200 μm in diameter. The 1-dimensional array of different sized droplets was dragged by the surrounding oil flow in a microchannel whose width and entire length were 700 μm and 20 mm, respectively (Fig. 2.1(c)). The velocity of the large droplet was always slower than that of the oil flow owing to the friction with the ceiling and floor surfaces. One would expect that the small droplets would be moved by the oil at a comparable velocity because they are free from the frictional influence. However, we found that the small droplets exhibited a periodic back-and-forth motion relative to the large droplets (Fig. 2.2(a) and (b)), while the large droplets were conveyed at a constant velocity (Fig. 2.2(b), 1.2 mm/s for large droplets, oil flow of 2.7 mm/s). Neither longitudinal nor transverse waves were observed in this droplet array. In addition, after the small droplets turned away from the large droplets ahead of them, they continued to move astern until they came close the large droplets behind them. This result implies that the small droplets were repelled by the large droplets, and eventually their repeated approaches and rejections resulted in an oscillatory motion. In addition, the observed oscillation could not be easily explained based on hydrodynamic interactions via a potential flow in the xy plane alone: According to the superposition of the dipole-like potential, the motion of droplets can propagate as a density wave in a droplet crystal but cannot have a

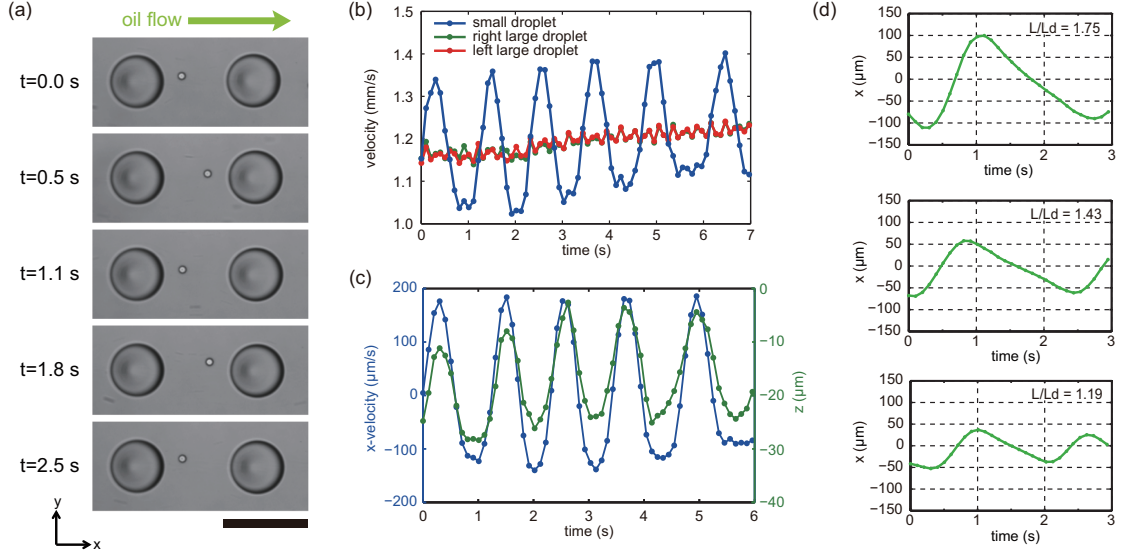


Fig. 2.2 Asymmetric, back-and-forth motion, and conveyance of droplets. (a) Snapshots of single small droplet between two large droplets (forward and backward). Small droplet moves in back-and-forth manner relative to the large droplets. (b) The dynamics of relative velocity. While large droplets move at a constant speed of 1.2 mm/s, the oscillation of relative velocity is clearly found for the small droplet. (c) The brightness of a small droplet, which reflects its z -position, shows anti-phase oscillation against its relative velocity. (d) The back-and-forth motion is asymmetric. The motion of a small droplet, relative to a forward-moving large droplet, in the forward direction is faster than that in the backward direction. L represents the distance between large droplets and L_d is the diameter of large droplets. The scale bar represents $200 \mu\text{m}$.

stable orbit reminiscent of oscillation[10, 12, 87, 88, 89]. The approximation of a 2-dimensional potential flow was no longer valid in this experiment, and therefore we needed to take the z -axis into account.

Next, we examined whether the small droplets were moved in the z -direction in the course of the back-and-forth motion. We can infer the z -position of small droplets by measuring their brightness, because drifting in the z -axis means defocusing, which alters the intensity of droplets. We found that the brightness of small droplets was periodically changed in the anti-phase of the oscillation of the droplet motion (Fig. 2.2(c)). The center of mass of small droplets was approximately $30 \mu\text{m}$ above the floor surfaces when the droplets moved backward relative to the large droplets. Moreover, we also analyzed the speed of small droplets in their forward and backward motions. As clearly seen in Fig. 2.2(d), the speed in the forward direction was greater than that in the backward motion. This asym-

metric velocity was mostly observed in our experiments and it did not depend on the distance between large droplets, which suggests that hydrodynamic interaction with large droplets had little influence on the origin of the asymmetry. One possible mechanism to explain the speed asymmetry is the deceleration of the fluid flow when the small droplets moved close to the PDMS wall in their backward motion: The fluid of the oil phase sticks to the solid floor surface under a no-slip condition. Thus, our results highlight the importance of considering the interaction among W/O droplets, oil fluid, and solid walls.

These experimental results motivated us to propose a schematic model for the oscillation of single small droplets (Fig. 2.3(a)). In the reference frame of large droplets, a small droplet moves in the forward direction if it lies midway between the top and bottom walls. To test whether this model recapitulates the asymmetric oscillation of small droplets, we performed a numerical simulation based on the lattice Boltzmann method[92, 93]. We performed the numerical simulation as follows: Two hard spheres were confined under two solid walls using a periodic boundary condition. The diameter of the large droplets was set at $120\text{ }\mu\text{m}$, whereas the height of the microchannel was $123\text{ }\mu\text{m}$. A pressure difference was applied in order to generate fluid flow at velocity $v = U_1$ in the laboratory frame. In order to determine the reference frame of large droplets, we had the top and bottom walls move in an opposite (backward) direction at $v = -U_2$, thereby the relative velocity of the oil fluid is $v = U_1 - U_2$. One small sphere of $20\text{ }\mu\text{m}$ was placed between two large droplets under a given set of initial conditions, and then its trajectory was analyzed. We note that no-slip boundaries existed among the oil phase, droplets and solid wall during the simulation because we added a sufficient amount of surfactant in the experiments.

Figure 2.3(b) shows the simulated streamlines of a fluid passing through large droplets. We found that the closed streamlines appeared between two large droplets. The results of a detailed comparison between the simulation and experiment are presented in Fig. 2.3(c). The simulated and experimental trajectories of a small droplet in a single period were strikingly similar, supporting the notion that such a droplet moves along a closed streamline. In addition, the small droplet moved faster in the forward direction in both the simulation and the experiment (Fig. 2.3(d)). The asymmetric nature of oscillation was always observed at $U_1 < U_2$, irrespective of the distance between large droplets. The ceiling and floor plates slowed down the surrounding fluid, as well as single small particle, at $U_1 - U_2$, and therefore asymmetric oscillation arose from the closed streamlines. We call this pattern of circulating streamlines a microfluidic bolus flow.

Next, in order to project the region where the small droplets are conveyed while

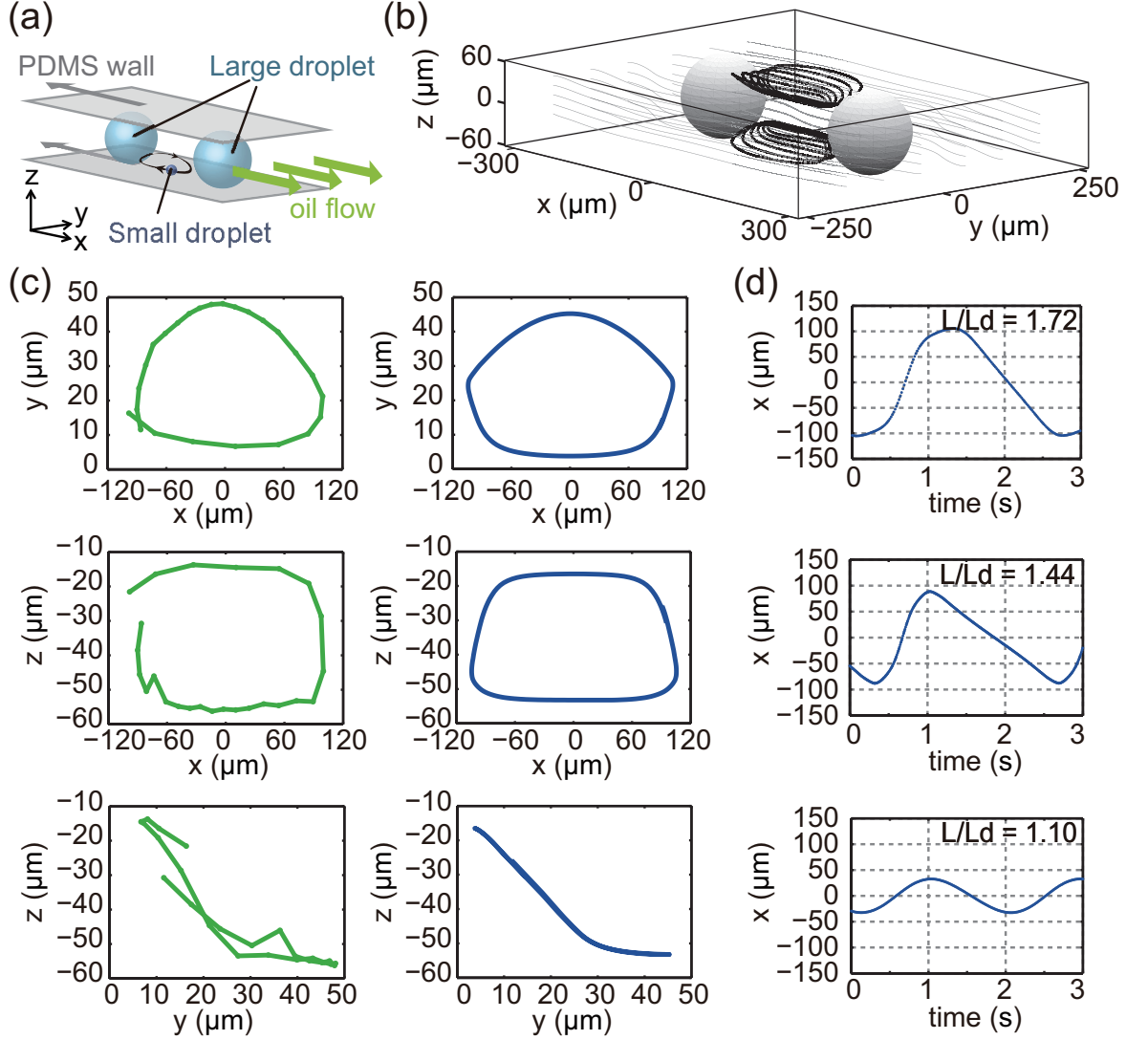


Fig. 2.3 Numerical simulation of microfluidic bolus flow. (a) A schematic of the simulated setup, showing the PDMS walls, large spheres and tracer particle. We assume that two large spheres whose diameter ($120 \mu\text{m}$) is comparable to the height of a channel ($123 \mu\text{m}$) are placed in the fluid flow. In addition, we also make the boundary of the channel, i.e., ceiling and bottom surfaces, move at a certain velocity in a direction opposite to the oil flow. (b) The streamline obtained in numerical simulation is shown in 3-dimensions. (c) Comparison of the trajectories of a small droplet observed experimentally (top) and those of a small sphere obtained by simulation (bottom). (d) Asymmetric back-and-forth motion of single small sphere.

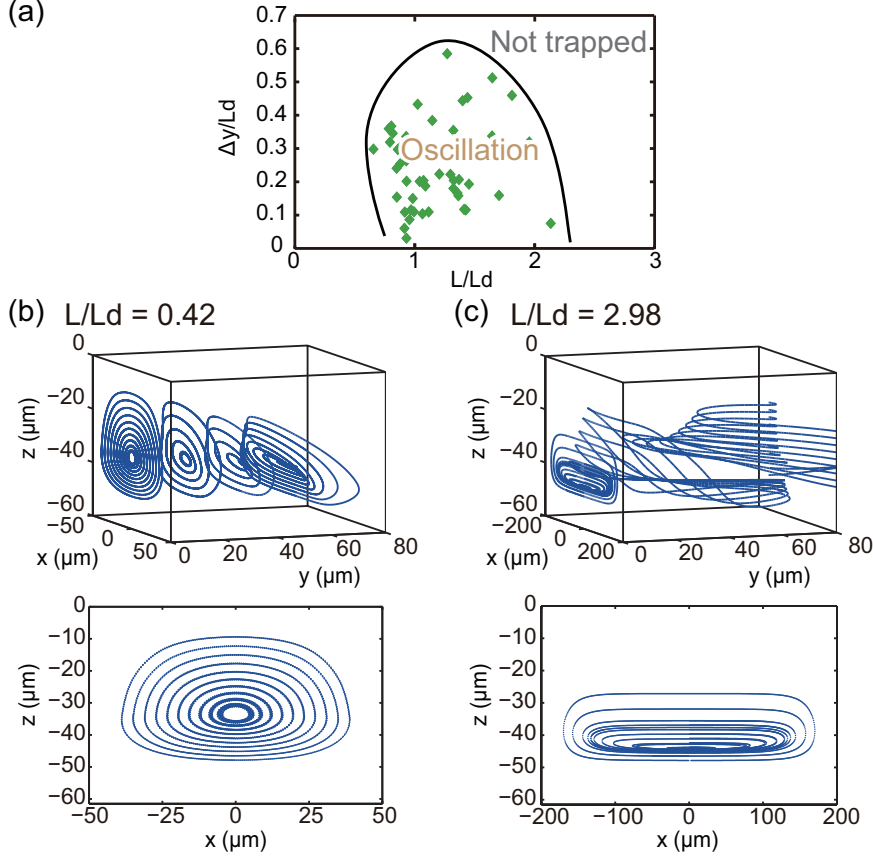


Fig. 2.4 Existence domain of microfluidic bolus flow. (a) A diagram of the trapping of small droplets with periodic motion. The horizontal axis is the distance between forward- and backward-moving large droplets, and the perpendicular axis is the deviation in the y -direction. (b),(c) The streamlines in short ((b), $L/L_d = 0.42$) and long ((c), $L/L_d = 2.98$) interspaces of the droplet array. Data are shown in 3D (top) and for the zx -plane (bottom).

showing the periodic motion, we draw a diagram with two axes, one representing the distance between two large droplets, L , and the other the distance in the y direction, y (Fig. 2.4(a)). In the experiment, we found that the optimal region was trapped with periodic motion at midst L ($L_d/2 < L < 2L_d$) and small y ($y < L_d/2$), whereas closed streamlines representing microfluidic bolus flow were always present irrespective of L (the numerical simulation data are not shown here). To resolve the difference between experiment and simulation, we numerically examined the area of microfluidic bolus flow by changing L . As L/L_d was increased in simulation, this bolus flow was distorted and the center of the vortex moved close to either the ceiling or floor plates (Fig. 2.4(b) and (c)). Given that small droplets were placed in the middle of the z -axis for large L/L_d , the probability of being trapped

in the microfluidic bolus flow could be decreased. In addition, y also limited the observable region of the oscillation according to the relation $y < Ld/2$, which agreed with the numerical simulation (data not shown). In summary, microfluidic bolus flow existed over a wide range of our droplet array, but the initial position in the z -axis appeared to affect the efficiency of trapping.

Finally, we investigated a group of small droplets placed between two large droplets. We found that a quadruplet cluster was generated after four droplets were trapped simultaneously (Fig. 2.5(a)). The cluster was stably moved at the same velocity with large droplets, while exhibiting dynamic repositioning: Small droplets switched their position periodically while the four droplets maintained the cluster. The period of rotating was 3.6 ± 0.2 s. In addition, the formation of a doublet cluster was observed for two small droplets as well as the formation of a quadruplet cluster for four small droplets, indicating that more than one small droplet was trapped to form a dynamic cluster spontaneously in the grid of large droplet array. In addition, we plotted the velocity of droplets in a cluster with respect to time (Fig. 2.5(b)). The change of velocity at repositioning described a sharp rather than a smooth oscillation (Fig. 2.5(b)). The asymmetric shape of droplet clusters may affect the dynamics of flipping while groups of small droplets still maintain rotation in time as well as the single small droplets. Additional effect involved in the rotation of clustered droplets may be the parabolic profile of laminar oil flow in z direction. Once the stable cluster that can be assumed as rigid body is formed, the fluid shear at the vicinity of the wall may cause rotational motion as seen in asymmetric Janus particles or yeast cells with a shmoo[94]. Detailed analysis of the effect of shape remains to be addressed in the future because hydrodynamic attraction to form asymmetric cluster is out of focus in this study.

2.5 Conclusion

In conclusion, we have shown the oscillatory motion of W/O droplets in a 1-dimensional array of large droplets dragged by oil flow in a microfluidic channel. Single small droplets placed in the interspace of the droplet array were transported at the same velocity of the array while showing asymmetric oscillation by microfluidic bolus flow. The device in this study had a thickness of $123 \mu\text{m}$ and thus additional freedom in the z -direction led to dynamically organized motion such as the oscillation of single small droplets and even the clustering of multiple droplets. The bolus flow is thought to be a general phenomenon for which one can find many relevant biological and biomedical examples such as closed streamlines between red blood cells in vessels [7, 8, 9]. This bolus flow may trap microvesicles

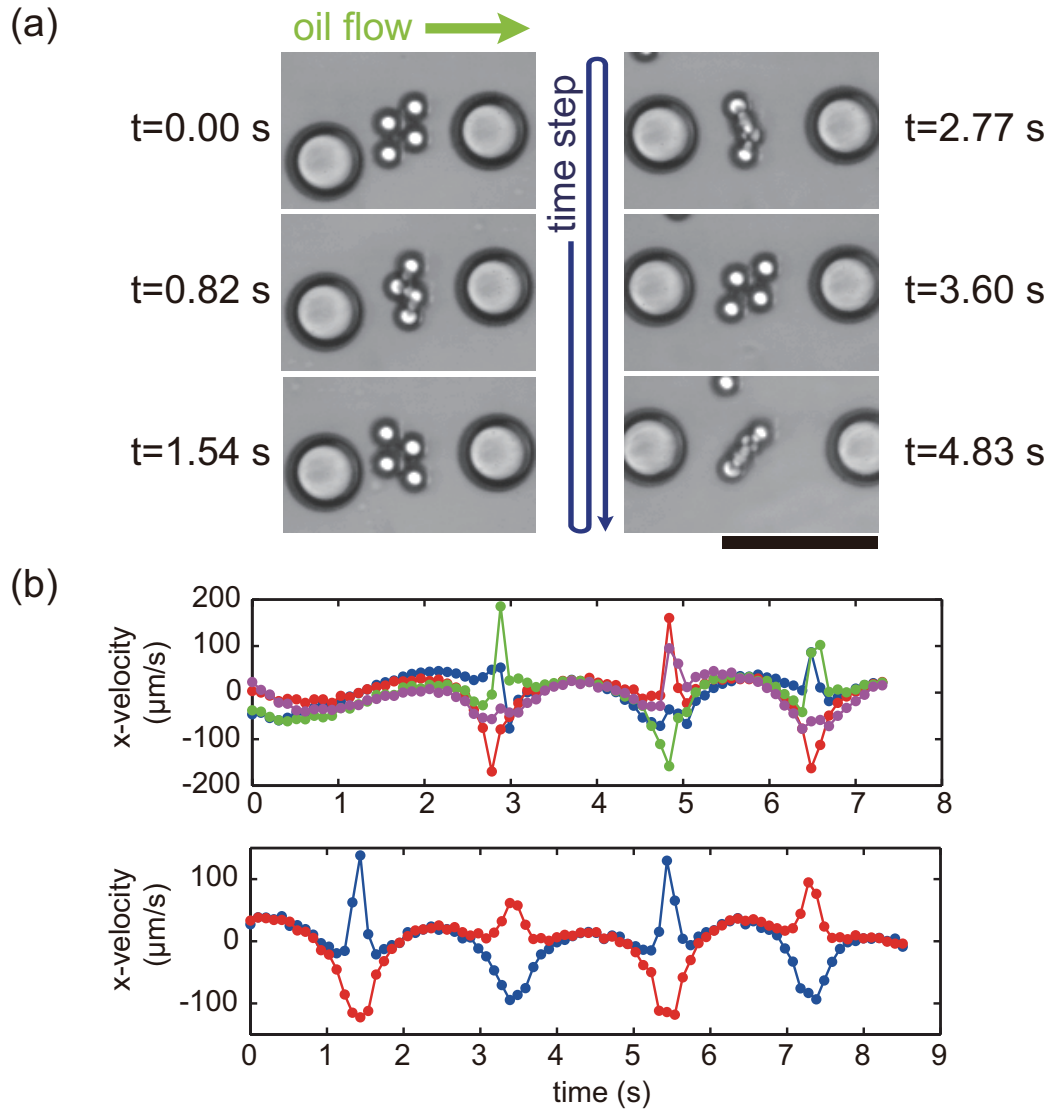


Fig. 2.5 Dynamic clustering of droplets. (a) The formation of a quadruplet cluster from four small droplets. Small droplets were readily trapped to form single cluster showing dynamic reposition. The scale bar represents $200 \mu\text{m}$. (b) Plot of the relative velocity of small droplets in the quadruplet cluster (top) and doublet cluster (bottom) as a function of time. The time course of each droplet is shown in different colors. Increase and decrease of velocity reflects dynamic repositions inside a cluster.

involved in intercellular communications and then make its clustered aggregation at the interspace of red blood cells for transport[95]. Further studies in other relevant systems, e.g. electrophoresis of the colloidal suspensions[96], will offer better understanding of the separation of particles in microfluidics.

Chapter 3

Wall-preferring motion of active living matter

3.1 Introduction

Microorganisms play crucial roles in ecosystems and are essential to life on Earth[97, 98, 99, 100, 101]. Eukaryotic unicellular microorganisms (i.e., protists) are dominant microorganisms in aquatic ecosystems[102, 103, 104, 105, 106]. One class of protists, ciliates, exhibits a rapid translational swimming motion. Ciliates have a large number of hair-like organelles, termed cilia, that beat around the whole body to induce thrust force. While the remarkable activity of ciliates is usually observed in bulk water[50, 107, 108, 109, 110], they frequently accumulate on air-fluid and solid-fluid interfaces in nature[56, 111, 112, 113, 114]. Although these two major characteristics (i.e., sliding on surfaces and traveling rapidly in bulk water) are commonly recognized as instinctive behaviors, the mechanism of the sliding motion remains unclear. Ciliates likely have sensing systems to detect walls or external boundary conditions and have a response mechanism connected to the transition between the modes of motion. To our knowledge, the mechanisms of sensing and response have not been revealed; however, this “wall taxis system” must be integrated into the life strategies of ciliates.

Are there clues about these mechanisms in biological studies or any hints related to their behavior in biophysical and hydrodynamic studies? Recent progress in numerical analysis and simulation has revealed the swimming mechanisms of various water microorganisms[32, 33]. Studies of the interactions between a swimmer and a wall have shown that pusher and puller swimmers accumulate on a non-slip wall boundary[47, 52, 54, 58, 115, 116, 117, 118, 119]. Pusher, puller and neutral swimmers are swimming styles categorized by hydrodynamic models for active swimmers. Pusher swimmers driven by rear propellers (e.g., *Escherichia*

coli) are known to show repulsive motions from the wall. Puller swimmers, which are driven by anterior flagella (e.g., *Chlamydomonas*), have been numerically analyzed to determine their attractive motions towards a wall. Finally, the neutral swimmer is used as a model for ciliates that represents the uniform driving force covering the swimmer surface, assuming that cilia are beating all over the cell surface, as in *Volvox*[55] and *Tetrahymena*[56]. Trajectories of neutral swimmers near a wall have been analytically and numerically reported. A wall repels neutral swimmers; specifically, the propelling direction of the swimmer orients its departure from the wall. This property inhibits the accumulation of neutral swimmers on the wall. Although a recent simulation study with numerous neutral swimmers reported the accumulation of swimmers near the wall due to their many-body effects[54], this finding was not applicable to accumulation or wall-preferring behavior at the individual cell level. Hydrodynamic studies have not yet explained the behaviors of ciliates on a wall. Our motivation for understanding the deviation between model swimmers and real ciliates near a wall drove us to observe *Tetrahymena pyriformis*, a model organism of ciliates[57].

3.2 Analytical calculation

The trajectory of a spherical neutral swimmer approaching non-slip boundary by hydrodynamic analytical calculation is exhibited. According to Chapter 1, a neutral swimmer has slip velocity on the surface $u_\theta = \frac{3}{2}U \sin \theta$, which is derived from eq. (1.44) in the case of $\beta = 0$. In 2-dimensional Stokes flow, the exact dynamics of a circular neutral swimmer near the non-slip wall can be calculated by complex variable formulation[120]. The detailed derivation is written as Möbius mapping in Appendix. Defining the swimmer angle θ , the surface velocity $U_s = 2V \sin(\phi - \theta)$ and the swimmer radius r , the center velocity and the angular velocity of the neutral swimmer is expressed as following

$$\frac{dx}{dt} = \frac{(c + \tilde{c})}{4}(2\rho^4 - 2\rho^2 + 1) \quad (3.1)$$

$$\frac{dy}{dt} = \frac{-i(c - \tilde{c})}{2(1 + \rho^2)}(2\rho^6 + \rho^2 - 1) \quad (3.2)$$

$$\frac{d\theta}{dt} = -\frac{2\rho^3(c + \tilde{c})}{r(1 + \rho^2)} \quad (3.3)$$

where

$$c = Ve^{i\theta}, \quad \rho = \frac{y}{r} - \sqrt{\left(\frac{y}{r}\right)^2 - 1} \quad (3.4)$$

From above equations, the trajectories were obtained (Fig. 3.1). Seeing Fig. 3.1, the swimmer was repelled from the wall if any incident angle. This repulsion

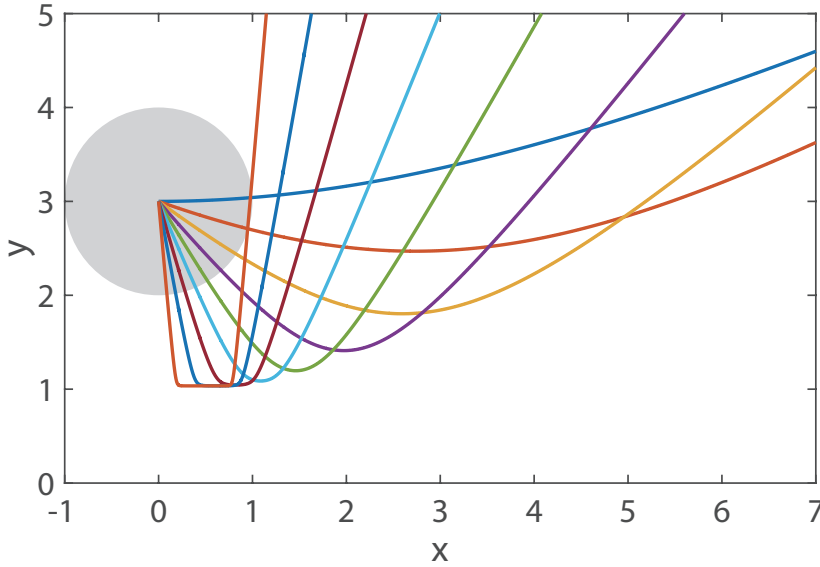


Fig. 3.1 The trajectories of a spherical neutral swimmer in 2-dimension. The color variation indicates the incident angle.

arose only from hydrodynamic interaction. Therefore, not only hydrodynamic interaction but also other factors are necessary to represent the property of actual ciliates.

3.3 Experimental Method

3.3.1 Preparation of *Tetrahymena pyriiformis*

T. pyriiformis were kindly gifted by Prof. Osamu Numata (University of Tsukuba, Japan). The cells were cultured in growth medium (1.2% (w/v) Bacto Proteose Peptone [Becton, Dickinson and Company], 0.6% (w/v) Paticase [Kyokuto] and 0.2% (w/v) Bact Yeast Extract [Becton, Dickinson and Company]) at room temperature (20 to 25°C) with aeration (e-AIR6000WB, GEX). Serial transfer of the cells was performed twice a week. Before observation, cells in middle-log phase growth were washed three times with an observation solution (10 mM Mops/Tris [pH 7.2], 1-mM KCl, 1-mM NaCl and 1-mM CaCl₂)[121] and equilibrated with the observation solution for more than 1 hour prior to observation.

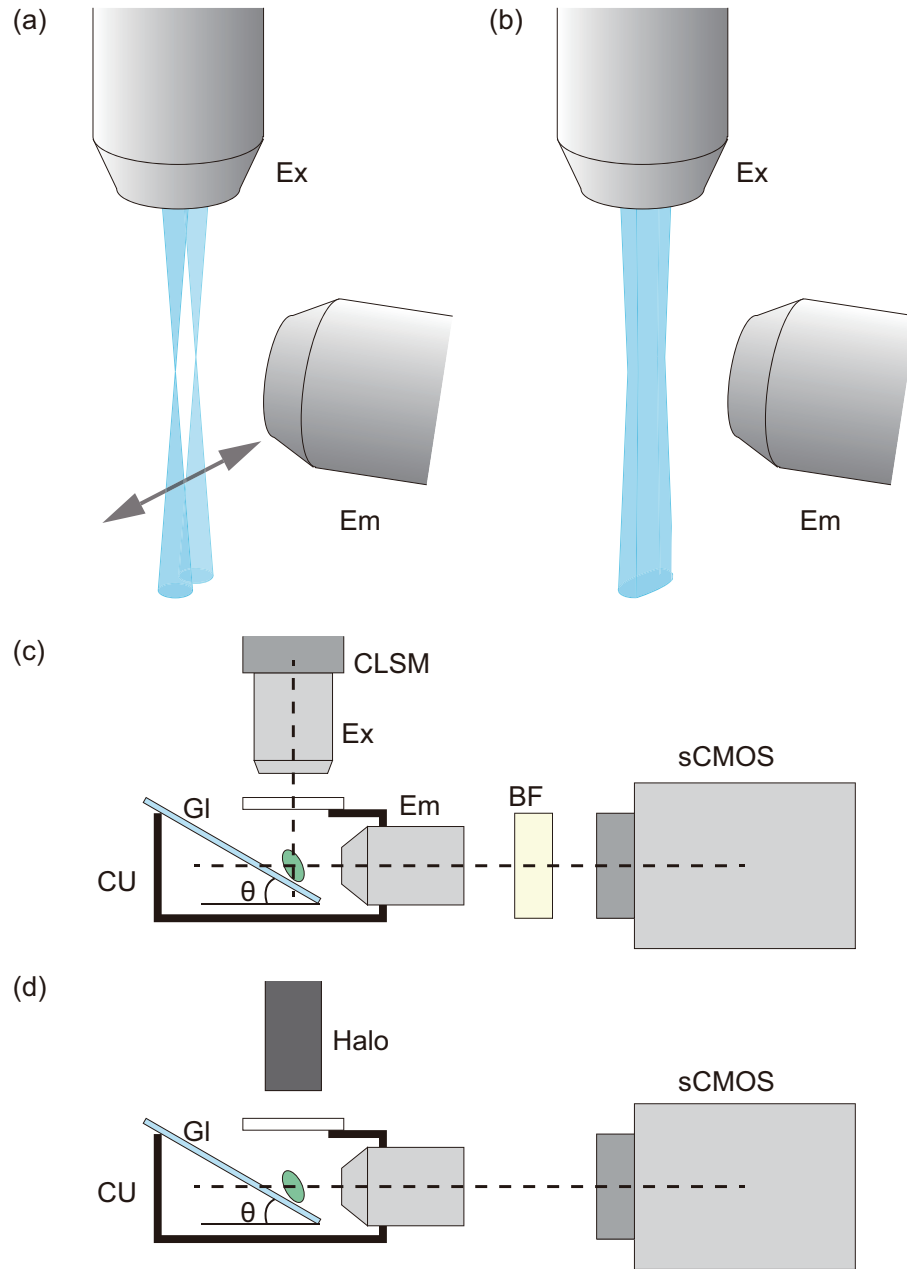


Fig. 3.2 A linearly scanned laser beam (a) was performed to generate a light-sheet (b). The light-sheet was used as the excitation light source for low-angle fluorescence observation. The optical axis of the objective used for excitation (Ex) was orthogonal to that for emission (Em). (c, d) Schematic side views of the observation systems. The optical axes of the objectives (Obj) for excitation (Ex) and emission (Em) are described as dashed lines. (c) The light-sheet was generated by a confocal laser-scanning microscope (CLSM) and used to irradiate cells on the glass (Gl) set at an angle of 28 degrees to the emission optical axis (θ). The chamber unit (CU) was filled with the observation solution, and cells were added to the CU. A time series of an optical section of the cell was acquired through the band-pass filter (BF) using an sCMOS camera. (d) For bright-field observation, a halogen lamp (Halo) was substituted for the light-sheet.

3.3.2 Bright- and dark-field observations of *T. pyriformis* at perpendicular and parallel angles

To prevent nonspecific binding between cells and the surface of the cover glasses, the cover glasses (thickness No. 1, 30x40 mm, Matsunami) were coated with 2-methacryloyloxyethyl phosphorylcholine (MPC) polymer (Lipidure-CM5206, NOF Corporation). Specifically, MPC polymer was dissolved in ethanol to a final concentration of 0.5% (w/v), and 20 μl of the MPC polymer solution was placed on the cover glass. To dry the coating solution, the glass was left at room temperature for more than 2 hours. The observation solution containing *T. pyriformis* was deposited between the MPC-coated cover glasses with a spacer (a silicone sheet (thickness: 400 μm) with a square hole (side length: 10 mm)). *T. pyriformis* was observed and recorded using bright-field and dark-field inverted microscopy (Eclipse Ti, Nikon) with an sCMOS camera (ORCA-Flash4.0, Hamamatsu). To observe side views of *T. pyriformis* in a bright field, the cover glasses (thickness No. 1, Matsunami) were substituted for silicone spacers, and *T. pyriformis* on the glass spacers were observed using the methods described above.

3.3.3 Fluorescence and bright-field observations of *T. pyriformis* at a low angle

To acquire low-angle fluorescence images of *T. pyriformis* attached to a glass surface, observations were performed as described previously[122]. In brief, a light-sheet, which was used as the excitation light, was generated by line scanning a laser beam (FV10-LD559, Olympus) (Fig. 3.2(a) and (b)) using a confocal laser-scanning microscope (FV1000, Olympus). An sCMOS camera (ORCA-Flash4.0, Hamamatsu) with an optical axis orthogonal to the plane of the excitation light was used for image acquisition. A cover glass was set at an angle of 28° to the optical axis (Fig. 3.2(c)). After the chamber unit was filled with the observation solution, *T. pyriformis* was stained for 10 min in the observation solution containing 10 $\mu\text{g/ml}$. CellMask Orange plasma membrane stain (Molecular Probes) and washed three times with the observation solution. It was then added to the chamber unit, and the cells on the glass were observed through a band-pass filter (BA570-625HQ, Olympus). In bright-field observation, a halogen lamp (LG-PS2, Olympus) was used as the light source (Fig. 3.2(d)).

3.3.4 Particle Imaging Velocimetry (PIV) analysis

The flow velocity field and the speed intensity around the cell body (Fig. 3.7(e) and (f)) were obtained using an open source MATLAB code (PIVlab)[123]. The raw movie was recorded at 2000 fps, and the snapshots at 1.5 ms interval were used for PIV analysis.

3.4 Numerical methods

3.4.1 Three surfaces in our numerical model

In this calculation, there are three defined boundaries: body surface, stress surface and cilia surface (Fig. 3.3(b)). The body surface is rigid and has a non-slip boundary condition; the shape is spherical or prolate ellipsoidal. An actual ciliate is anisotropic in shape, as in the prolate ellipsoid. The diameter of the spherical surface is 2.0. The major and minor lengths of the ellipsoidal surface are 2.0 and 1.0, respectively. The cilia surface is located outside the body surface. The length of the cilia in this model is fixed at 0.1, which is estimated from actual cells. The stress surface is defined to reproduce the stress force of ciliary beating per unit area. Usually, the squirmer model is given a velocity field on the surface, but we used a thrust stress force instead of a velocity field to reproduce the actual beating precisely (Fig. 3.3(a)). The stress surface is located between the body surface and the cilia surface (Fig. 3.3(d)). We use a boundary element method (BEM) for numerical calculation[32]. All surfaces are discretized by 162 material points far from the boundary and 2,562 material points near the boundary. The length unit is normalized by the radius of the spherical swimmer (i.e., 1.0).

3.4.2 Dominant equation

We derived a numerical method assuming $\mathbf{x} = (x, y, z)$ is an observation point, and $\mathbf{y}$ is a source point. Assuming surface traction acting on the cell surface $\mathbf{q}(\mathbf{y})$ and thrust force per unit area $\mathbf{F}(\mathbf{x})$, the flow field is given by a boundary integral equation[124],

$$\mathbf{u}(\mathbf{x}) = \mathbf{u}_\infty(\mathbf{x}) - \int \mathbf{J}_0(\mathbf{x}, \mathbf{y}) \cdot \mathbf{q}(\mathbf{y}) dS_b(\mathbf{y}) - \int \mathbf{J}_0(\mathbf{x}, \mathbf{y}) \cdot \mathbf{F}(\mathbf{y}) dS_c(\mathbf{y}) \quad (3.5)$$

where dS_b and dS_c are the body surface and stress surface, respectively. $\mathbf{J}_0(\mathbf{x}, \mathbf{y}) = \frac{1}{8\pi\mu} \left(\frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right)$ represents the single-layer potentials of Green function, which is the second-order tensor called the Oseen tensor. $\mathbf{u}_\infty(\mathbf{x})$

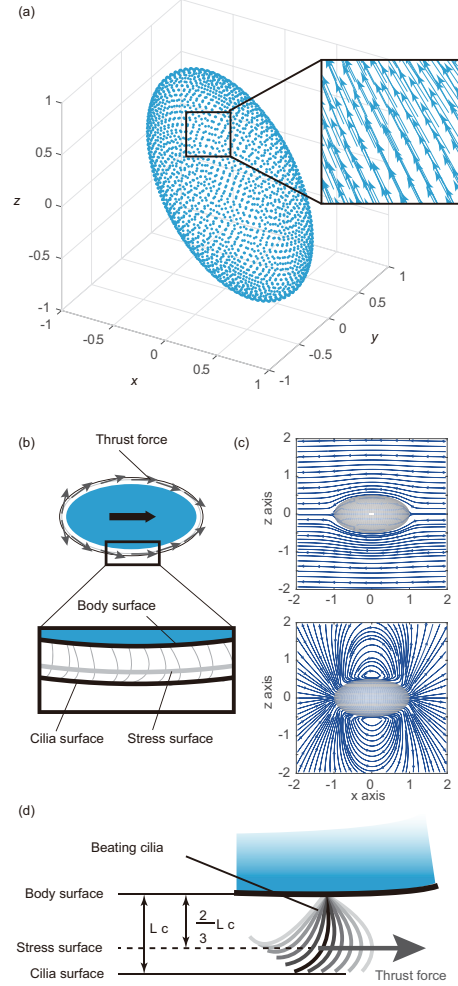


Fig. 3.3 Schematic diagram of the swimmer model used in the simulation. (a) Blue points indicate the nodes of the mesh surface in the numerical model. As shown in the inset, the beating thrust force along a curved line connecting the head point with the rear point is given at each node. (b) The model approximates the body shape of *T. pyriformis* as ellipsoidal, and the beating force acts around the body. The beating thrust force is uniformly set at the lattice points all over the body, as indicated by grey arrows. As in the inset, three surfaces (i.e., the body surface, cilia surface and stress surface) are included the model. The body surface is rigid and experiences hydrodynamic forces from other elements expressed by the Oseen tensor. The cilia surface is used to determine whether the swimmer touches the wall. (c) The streamlines are shown around the swimmer. Top: in lab frame; bottom: in swimmer frame. Both figures show streamlines generated from the source dipole, which is a feature of the neutral swimmer. (d) The configuration of the cilia length and stress surface. The stress surface is $2L_c/3$ away from the body surface.

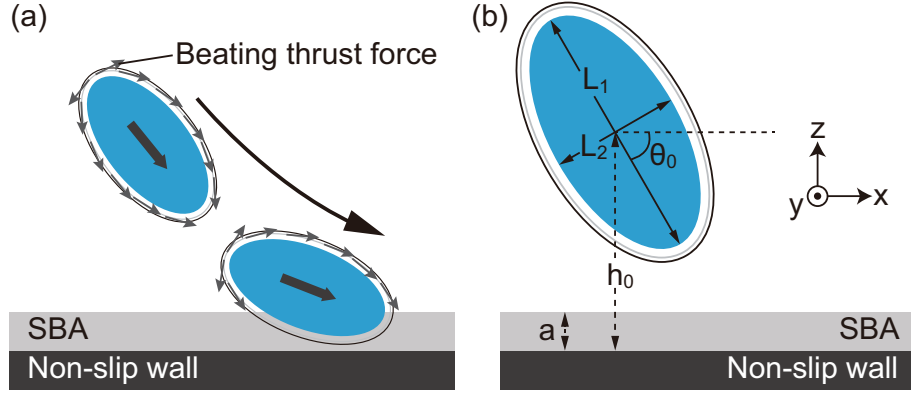


Fig. 3.4 Schematic illustrations of the simulation indicating the geometries of SBA and parameters. (a) Beating thrust forces (reaction force due to cilia strokes) along the surface driving the swimmer. We defined the “Stop Beating Area (SBA)” as the grey area on the bottom wall shown in the figure. If the surface is included within the SBA, the beating thrust force vanishes. (b) Parameter setup of the simulation. The shape of the force swimmer was determined by the ratio of the main axis length L_1 defined by the propelling direction to the waistline diameter L_2 . The parameters were set as $L_1 = 2$ and $L_2 = 1$ or 2 . $L_1/L_2 = 1$ corresponded to a spherical shape, and $L_1/L_2 = 2$ corresponded to an ellipsoidal shape. The SBA range was the defined length a . The initial angle was θ_0 , and the initial height was fixed at $h_0 = 2$.

expresses the external flow field. In this Chapter, $\mathbf{u}_\infty(\mathbf{x})$ is defined as zero. Next, the flow field on the body surface $\mathbf{u}_S(\mathbf{x})$ is determined using the velocity of the mass $\mathbf{U}$ and the turning angular velocity $\mathbf{\Omega}$ considering the non-slip boundary condition. Kinetic velocity on the body surface is as in

$$\mathbf{u}_S(\mathbf{x}) = \mathbf{U} + \mathbf{\Omega} \wedge (\mathbf{y} - \mathbf{X}_0) \quad (3.6)$$

Here, external force $\mathbf{F}$ and torque $\mathbf{T}$ are decided as boundary conditions.

$$\mathbf{F} = \int \mathbf{q}(\mathbf{y}) dS_b(\mathbf{y}) = \int \mathbf{F}(\mathbf{y}) dS_c(\mathbf{y}) \quad (3.7)$$

$$\mathbf{T} = \int \mathbf{q}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_b(\mathbf{y}) = \int \mathbf{F}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_c(\mathbf{y}) \quad (3.8)$$

By solving simultaneous equations eq. (3.5), (3.6), (3.7) and (3.8), $\mathbf{U}$, $\mathbf{\Omega}$ and $\mathbf{q}(\mathbf{x})$ can be derived. Once the translational and angular velocities are obtained, the material points are updated by a 4th-order Adams-Bashforth method. The time step was set to $\Delta t = 1.0 \times 10^{-4}$. The swimming speed at infinity was adjusted to $U = 1.0$. Figure S3(c) shows the streamlines of this model. The swimmer has dipole-like velocity potential, which is the property of a neutral swimmer.

3.4.3 Wall interactions

Assuming that a wall is a rigid, non-slip boundary, the swimmer experiences some forces and torques from the wall. First, we consider hydrodynamic interactions with the wall. The hydrodynamic interactions are derived using a modified Oseen tensor[125]. The Oseen tensor $\mathbf{J}_0$ in the second term of eq. (3.5) is changed to

$$\mathbf{J}(\mathbf{x}, \mathbf{y}) = \mathbf{J}_0(\mathbf{x}, \mathbf{y}) - \mathbf{J}_w(\mathbf{x}, \mathbf{y}') \quad (3.9)$$

$$\mathbf{J}_w(\mathbf{x}, \mathbf{y}') = -\mathbf{J}_0(\mathbf{x}, \mathbf{y}') + 2h^2 \mathbf{J}_D(\mathbf{x}, \mathbf{y}') - 2h \mathbf{J}_{SD}(\mathbf{x}, \mathbf{y}') \quad (3.10)$$

where h is the height of the center of the swimmer.

$$\mathbf{J}_D(\mathbf{x}, \mathbf{y}') = (1 - 2\delta_{i3}) \left(\frac{\delta_{ij}}{r'^3} + \frac{3r'_i r'_j}{r'^5} \right) \quad (3.11)$$

$$\mathbf{J}_{SD}(\mathbf{x}, \mathbf{y}') = (1 - 2\delta_{i3}) \left(\frac{\delta_{ij} r'_3 - \delta_{i3} r'_j + \delta_{j3} r'_i}{r'^3} - \frac{3r'_i r'_j r'_3}{r'^5} \right) \quad (3.12)$$

Next, we consider repulsion from the rigid wall. When the swimmer is approaching the wall, the swimmer sometimes overlaps the wall. Therefore, the repulsion force and torque from the collision are added to eq. (3.7), and eq. (3.8)

$$\mathbf{F}_{rep} = \int \mathbf{F}'_{rep}(\mathbf{y}) dS_a(\mathbf{y}) \quad (3.13)$$

$$\mathbf{T}_{rep} = \int \mathbf{F}'_{rep}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_a(\mathbf{y}) \quad (3.14)$$

$\mathbf{F}'_{rep}(\mathbf{y})$ is expressed as the repulsion force between the cilia and wall per unit area. To reproduce the interaction between cilia and the wall, we suppose that cilia are linear springs, and $\mathbf{F}'_{rep}(\mathbf{y}) = k l_c(\mathbf{y}) \mathbf{e}_z$, where $l_c(\mathbf{y})$ is the shrinking length of the cilia, k is the spring constant, and S_a is the area of cilia touching the wall. We do not consider friction with the wall in this calculation. Therefore, the repulsion force has only a z-axis component. Finally, we introduce a novel boundary condition. To reproduce the stopping of cilia near the wall, we define the ‘‘Stop Beating Area (SBA)’’ as the grey area on the bottom wall shown in Fig. 3.4(a). The ciliary beating inside the SBA stops, and thus, the thrust force $\mathbf{F}(\mathbf{y})$ near the wall vanishes. We define length a as the parameter of the SBA range in Fig. 3.4(b). When the ellipsoidal swimmer touches the bottom wall at a swimming angle of 11.9° , the ratio of the projected area of cilia stopping at $a = 0.3$ as 69.9%, which almost corresponds to the value estimated by the experiment.

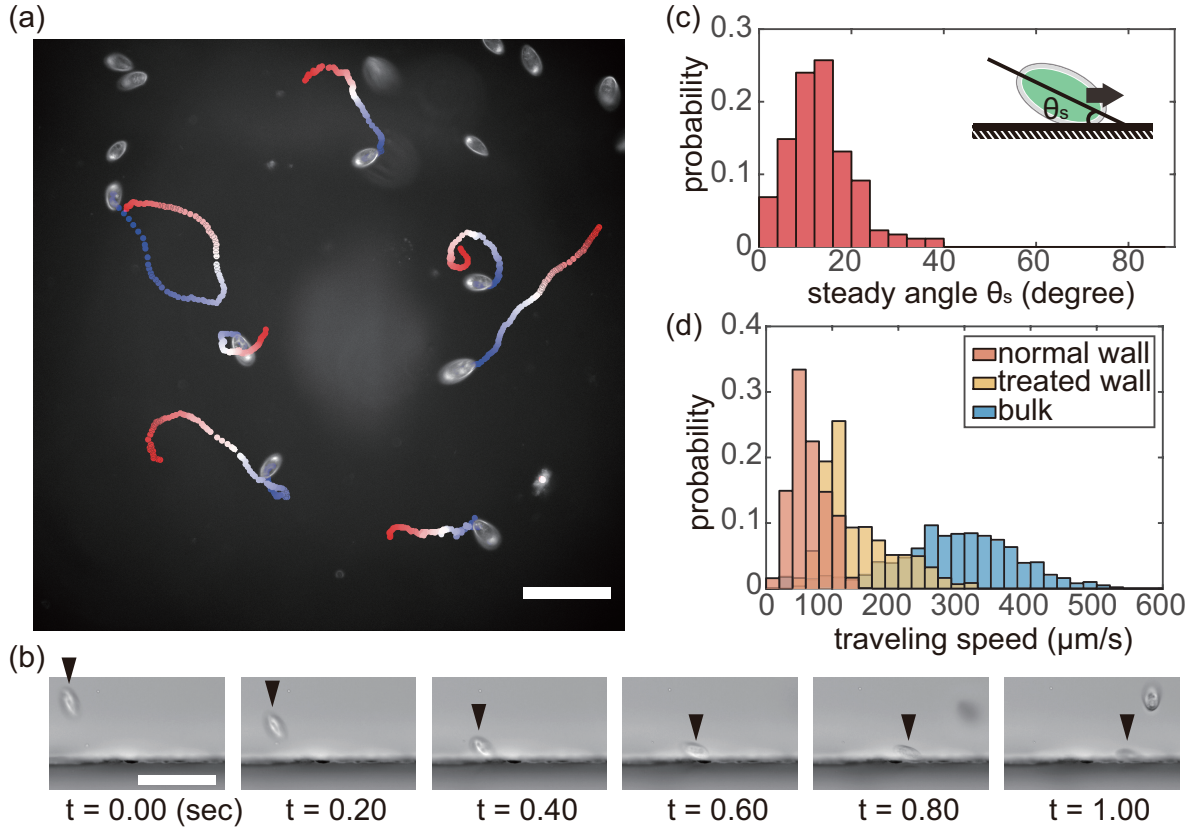


Fig. 3.5 Swimming behavior of individual *T. pyriformis* cells near walls. (a) Trajectories of *T. pyriformis* cells on a bottom wall. Most cells maintained their heights during contiguous swimming. Scale bar is 100 μm . (b) Snapshots of *T. pyriformis* swimming towards a side wall. After touching the wall, the cell slid along the wall. Scale bar is 100 μm . (c) Histogram of terminal or steady swimming angles θ_s between the wall and longitudinal axis of the cell body. The angle was defined as in the inset figure. The arithmetic average of the angle was 13.2°. (d) Histogram of the propelling speeds of cells in the bulk (yellow), near the treated glass wall (blue) and near the normal glass wall (red). While the mean speed in the bulk was 281.4 $\mu\text{m/s}$, the speed near the treated wall was 138.2 $\mu\text{m/s}$, and that near the normal wall was 64.9 $\mu\text{m/s}$.

3.5 Results

The swimming behavior of *T. pyriformis* in bulk water and near the bottom of a wall are shown in Fig. 3.5. *T. pyriformis* in bulk water passed across the observation window over several seconds (Fig. 3.6(a)), while others remained on the wall (Fig. 3.5(a) and 3.6(b)). Tracking their motion over 2.0 seconds revealed straight trajectories in bulk and straight or rotational motion on the wall, as shown

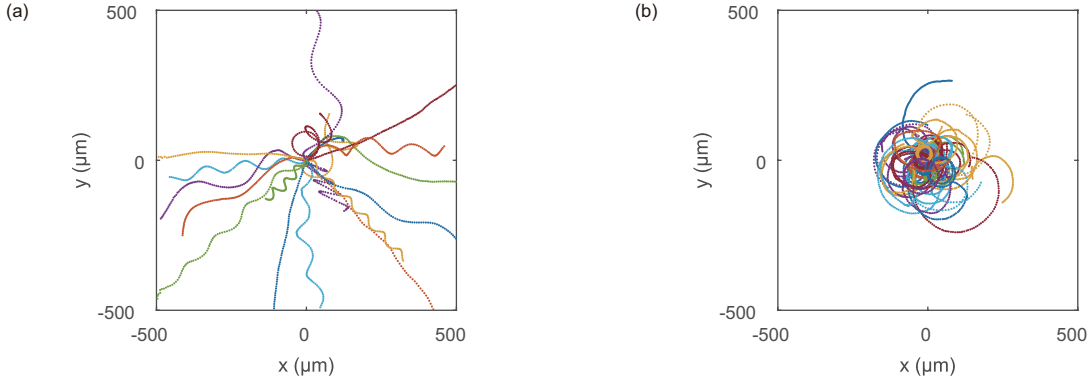


Fig. 3.6 Projected trajectories in bulk and near a wall. Both trajectories were acquired over 2.0 sec. (a) Projected trajectories on the XY -plane. The cells looked wavy while swimming in the 2-dimensional projection, indicating 3-dimensional helical motion. (b) Trajectories of cell near a wall coated with MPC polymer. Cells follow circular trajectories on the wall with orbital radii distributed between 10 and 150 μm .

in Figs. 3.6(a) and (b), respectively. Almost all rotation directions of the cilia on the wall were the same as the normal vector of the glass surface. *T. pyriformis* remained for 26.8 ± 4.7 s (mean $\pm$ SEM, $n = 20$) on the glass coated with 2-methacryloyloxyethyl phosphorylcholine (MPC; an anti-adhesion agent) and 5.2 ± 1.1 s (mean $\pm$ SEM, $n = 20$) on the uncoated glass. This process was commonly observed on the top wall (when it existed) and on the side wall (Fig. 3.5(b)). The steady swimming angle measured from the observation at this side wall was 13.2° on average (Fig. 3.5(c)) and was distributed below 40.0° .

The travel speed in bulk water (up to 100 μm from the bottom wall) was 281.4 $\mu\text{m/s}$ on average, while the travel speed on the MPC-coated glass was 138.2 $\mu\text{m/s}$ and the travel speed on the uncoated glass plate was 64.9 $\mu\text{m/s}$ (Fig. 3.5(d)). The travel speeds on the MPC-coated glass bottom walls were 49.1% as fast as those in bulk water, while those on the uncoated glass were 23.1% as fast as those in bulk water. These results confirm the interesting features of *T. pyriformis* on the wall; namely, *T. pyriformis* prefer a surface where they are not fixed but can slide. In this paper, “sliding” is defined as the observed motion adjacent to the wall. Considering the function of the MPC coat used to prevent the adhesion of proteins and biomacromolecules, the adhesive interaction strength between the substrate and the cilia was relatively inhibited on the coated surface. In addition, the sliding motions were observed on the anti-adhesive glass for longer than on the normal glass. Thus, the adhesive bond pinning the cilia during long-duration beating is not the immediate cause of the sliding phenomenon. In other words,

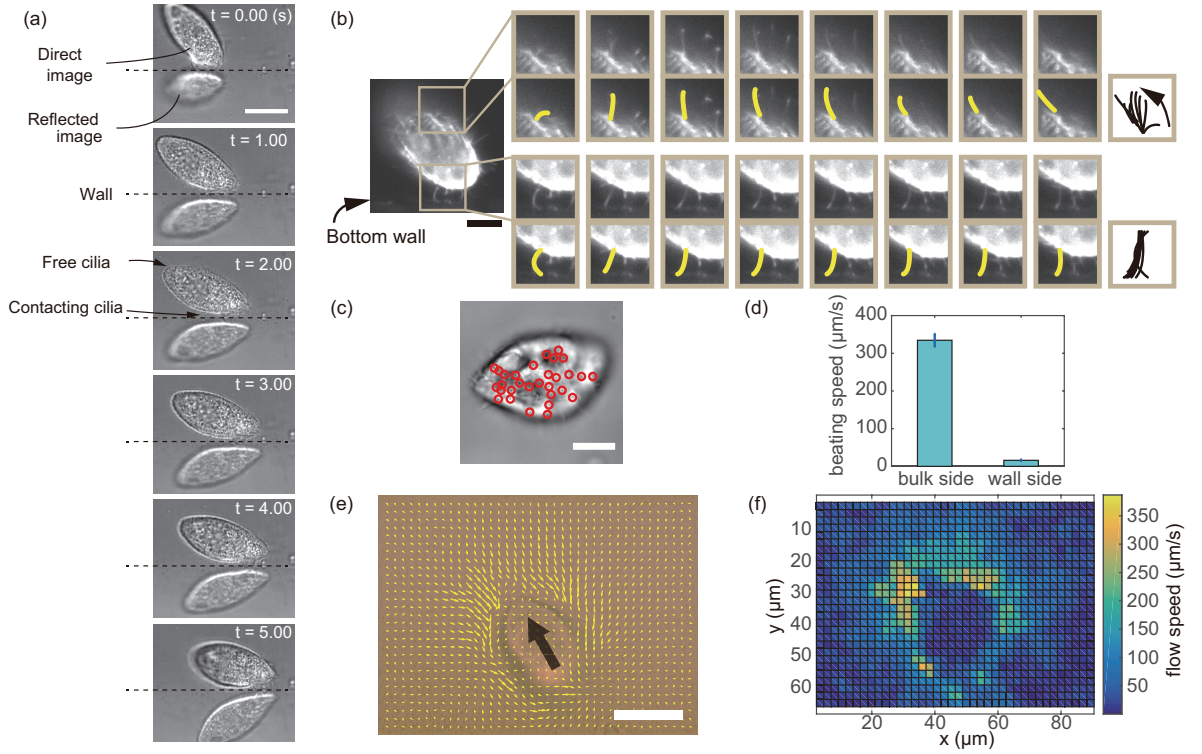


Fig. 3.7 Beating status of *T. pyriformis* cilia near the glass substrate. (a) Snapshots of *T. pyriformis* contacting the glass plate. The cell repeatedly touched and slid on the wall. Scale bar is $20\ \mu\text{m}$. (b) Snapshots of ciliary beating. Top: Normal beat, bottom: Sticking beat touching the wall. The snapshots were taken at 10 ms intervals. (c) Snapshot of a cell swimming adjacent to a wall. The retained cilia standing perpendicular to the wall are identified as black areas in phase-contrast microscopy. The black points indicated by red circles are cilia stopping their stroke in several frames around the picture. Scale bar is $10\ \mu\text{m}$. (d) Comparison of beating speeds in the bulk with those near the wall. The beating speeds of cilia in the bulk were estimated from the beating frequencies and a mean cilia length of $3.2\ \mu\text{m}$ (20 individual cilia). The beating speeds of cilia contacting the wall were measured at the black points, as shown in (c). (e) Flow field around the swimming cell estimated by particle image velocimetry (PIV) analysis. The analysis detected the motion of $0.5\ \mu\text{m}$ silica beads at a height less than $1\ \mu\text{m}$ from the bottom wall. Scale bar is $20\ \mu\text{m}$. (f) Intensity map of flow velocity in (e). The velocity between the cell body and wall was very small but non-zero.

the pressure generated by other factors towards the wall should be investigated.

To examine the contributions and interactions of cilia and the wall according to their hydrodynamics, we visualized microscopic motion and flow fields around the single cells. Fig. 3.7(a) show bright-field images of a single *T. pyriformis* from a 28° depression angle between the bottom glass plate and the cell. The surface

of the bottom plate was identified based on the horizon between the direct image and the reflected virtual image. The estimated distances between the cell body and the wall were approximately $3 \mu\text{m}$, which is almost equal to the natural cilium length of *T. pyriformis*. The distances and motions of the cell reveal that *T. pyriformis* swam by contacting the wall only with its cilia. This observation was confirmed by fluorescent live cell imaging using the same perspective as in Fig. 3.7(b), in which the cilia contacting the wall almost stopped beating (bottom series of pictures), whereas other intact cilia (e.g., those on the opposite side of the cell) continued beating (upper series). Stoppage of the cilia beating on the wall side of the cell was also noted in phase-contrast observations from the bottom view. Fig. 3.7(c) shows numerous stopped cilia at the face of the bottom wall, where vertically standing cilia are visualized as black dots (indicated by red circles) in phase-contrast imaging. The beating speeds of the stopped cilia were estimated as 1/10th of those on the bulk side (Fig. 3.7(d)). Since the stopping of individual cilia occurred transiently with an average duration of 0.16 s at the single-cilium level, it is appropriate to refer to this phenomenon as a beating stall. In fact, the motion of probe beads indicated that the cilia in the upper and lateral areas of the cell paddled normally, whereas cilia at the bottom hardly paddled, as shown in the intensity and direction maps (Figs. 3.7(e) and (f)). These experimental results indicate that the force generation was disturbed due to the presence of stalled cilia between the cell and the wall only. This phenomenon contributes to the sliding motion. Next, we incorporated the stalled phenomenon of cilium into a hydrodynamic cilium model to reveal the direct mechanism of the sliding motion of *T. pyriformis* on the wall.

Squirmer models have been used as mathematical models of swimming microswimmers[45, 48, 49, 52, 53, 54, 116, 126, 127, 125]. We prescribe the mean shear stress generated by the beating flagella as acting tangentially. This model can approximate ciliary swimming by selecting a parameter to be neutral (i.e., the neutral swimmer). The details of numerical setup are presented in Fig. 3.3. We simulate this model using the boundary element method to introduce the boundary condition mimicking the experimental results, where “Stop Beating Area (SBA)” is defined as beside a wall to reproduce cilia stuck near the wall (Fig. 3.4(a)). The SBA range can be optimized to represent the stuck ratio observed in the experiments. The parameter setup is shown in Fig. 3.4(b).

First, we checked the motion of the model swimmers near the non-slip boundary wall without SBA (Fig. 3.8(a) and (b)). Both spherical and ellipsoidal swimmers oriented their swimming direction against the wall, as observed in previous numerical and mathematical works[52, 54, 116]. The spherical swimmer is a neutral swimmer, and the ellipsoidal one mimics *T. pyriformis*’s shape. Without SBA,

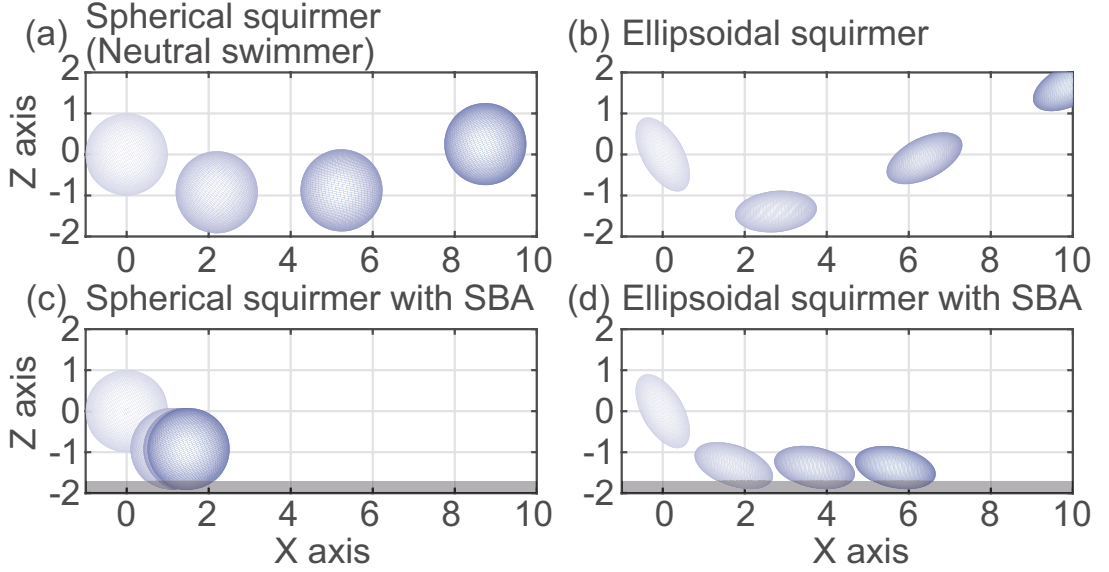


Fig. 3.8 Snapshots of simulation results reproducing swimmers approaching the wall. The initial angle is $\theta_0 = 60^\circ$. The non-slip wall is located at $z = -2$. The grey area indicates SBA. (a) $a = 0.0$; the spherical swimmer without SBA approached the wall and then swam away from the wall. (b) $a = 0.0$; the ellipsoidal swimmer without SBA swam away from the wall, similar to the spherical swimmer (a). (c) $a = 0.3$; the spherical swimmer with SBA did not swim away but stopped on the wall. (d) $a = 0.3$; the ellipsoidal swimmer with SBA swam adjacent to the wall.

neither swimmer exhibited a stable sliding mode on the wall, and both swam away from the wall under any initial conditions (Fig. 3.11). These behaviors are also shown in the graphs in Fig. 3.10(e) and (f) with $a = 0.0$, where the swimmer gradually oriented its direction near the wall. However, no stagnated or stable angle beside the wall was noted. Indeed, swimmers landing on the non-slip wall with SBA did not take off; the range of SBA was $a = 0.3$, and the wall was located at $z = -2$. Notably, the spherical swimmer with SBA stopped to fix on the wall (Fig. 3.8(c)), whereas the ellipsoidal swimmer swam and slid adjacent to the wall (Fig. 3.8(d)). The latter is a qualitative representation of the sliding motion on the wall observed in the experiments. The trajectories and swimming angles of the swimmers with SBA are shown in Fig. 3.9. The swimming angle of the spherical swimmer became perpendicular to the wall, and then the translational (X -direction) motion stopped (Fig. 3.9(a)). The swimming angle of the ellipsoidal swimmer converged to a certain angle and, after colliding, continued to slide on the wall (Fig. 3.9(b)). The terminal angle of the ellipsoidal swimmer was 11.9° , while that of the spherical swimmer was 90.0° . The terminal angle in the ellipsoidal

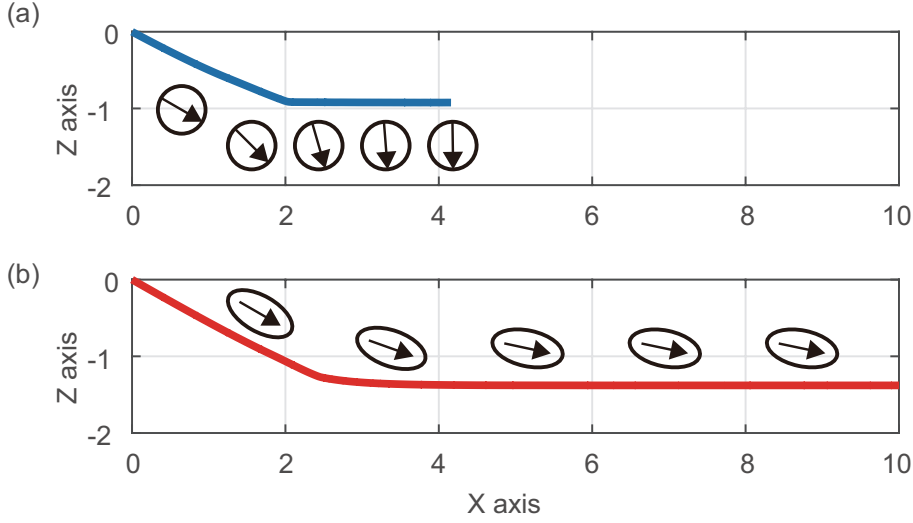


Fig. 3.9 Trajectories of spherical and ellipsoidal swimmers in the XZ -plane according to the head direction. (a) The blue line indicates the trajectory of the spherical swimmer. After colliding with the bottom wall, the swimming direction of the spherical swimmer became perpendicular to the wall. (b) The red line indicates the trajectory of the ellipsoidal swimmer. The ellipsoidal swimmer slid on the wall and maintained its swimming angle.

model was close to the experimental value of 13.2° at $a = 0.3$, confirming the experimental result shown in Fig. 3.5(c). The terminal angles are not dependent on the initial entry angles $\theta_0 = 10^\circ$ to 80° but are instead attributed to the SBA range $a = 0.00$ to 0.50 , as noted in the supplementary graphs (Fig. 3.12 and 3.13, respectively). Summarizing the simulation results, the ellipsoidal swimmer slid on the wall at $a > 0.20$, and the terminal swimming angle varied as a function of a ; in contrast, the spherical swimmer tended to have an angle of 90.0° . The adjacent motions of swimmers were bifurcated by certain thresholds: $0.05 < a < 0.10$ for the spherical swimmer and $0.20 < a < 0.25$ for the ellipsoidal swimmer.

3.6 Discussion

We discuss the applicability of the model in terms of a qualitative comparison between the experimental and simulated behaviors. The actual body of *T. pyriformis* has an oral apparatus and a pear shape, which correspond to an anterior-posterior asymmetry and rotational asymmetry in the locomotive direction axis. Although the present simulation did not generate angular momentum along the axis, in the experiments, *T. pyriformis* did not exhibit rotational motion during its sliding motion. Therefore, the effects of asymmetry due to the oral apparatus are negligible for qualitative comparison in the present work. The anterior-

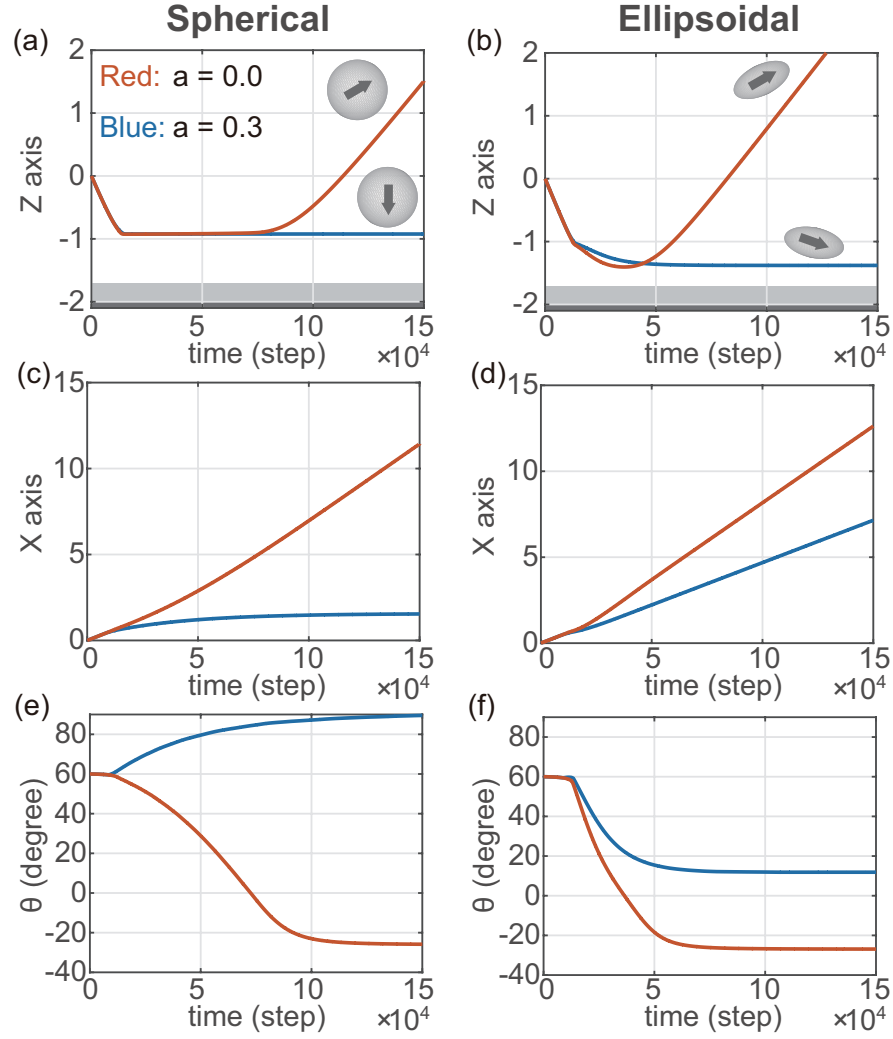


Fig. 3.10 Comparison of Z and X positions and swimming angle. Red lines represent trajectories without the SBA where length $a = 0.0$, and blue lines indicate $a = 0.3$. (a),(c),(e) Spherical swimmer; (b),(d),(f) ellipsoidal swimmer. The gray area in (a) and (b) represents the SBA. From (a) and (b), both the spherical and ellipsoidal swimmers showed similar changes in Z position. From (c) and (d), while the spherical swimmer stopped on the X axis when $a = 0.3$, the ellipsoidal swimmer stably slid on the wall. From (e) and (f), the swimming angles indicate asymptotic values. The angles below 0.0° indicate swimmers swimming away from the wall. The terminal angle of the spherical swimmer was 90.0° , which corresponds to a swimmer oriented vertically against the wall. The terminal angle of the ellipsoidal swimmer was 11.9° .

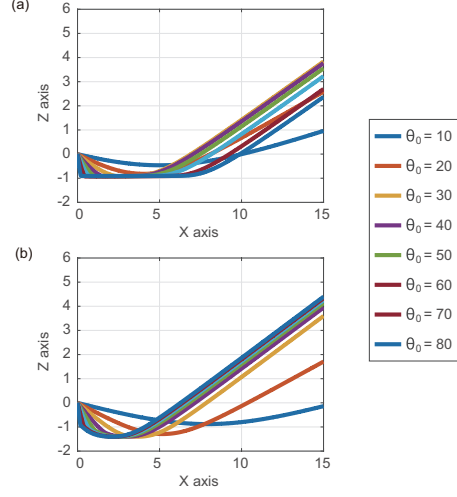


Fig. 3.11 Trajectories of numerical swimmers in the XZ -plane as the initial angle θ_0 changes with fixed SBA length $a = 0.3$. (a) Beginning from any initial angle, the spherical swimmer swam away from the wall. (b) The ellipsoidal swimmer also swam away from the wall from any initial angle.

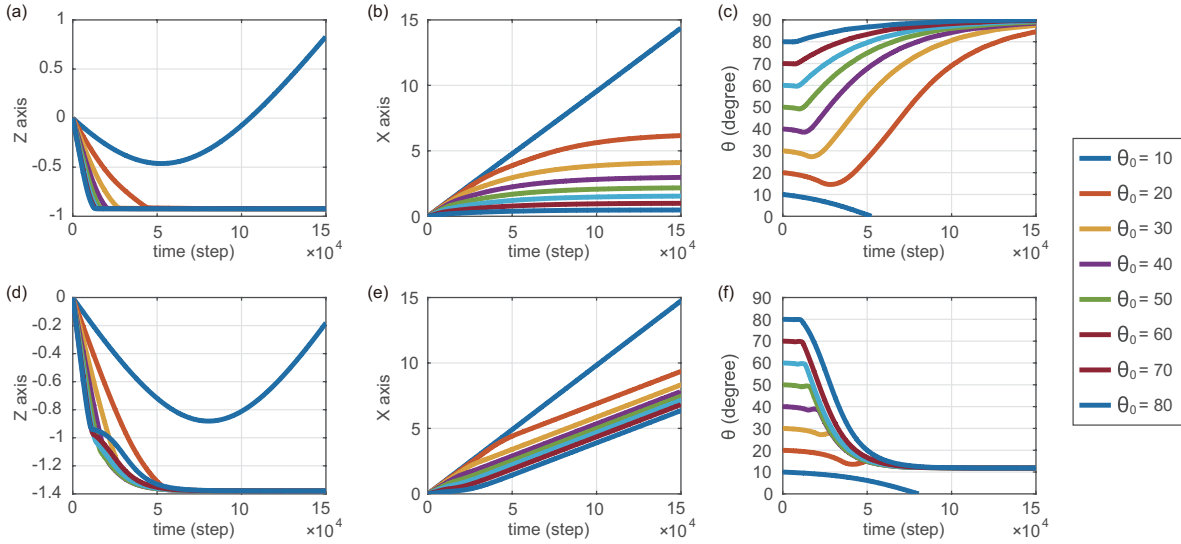


Fig. 3.12 Z and X positions and swimming angles of a swimmer with various initial angles θ_0 and fixed SBA length $a = 0.3$. (a)-(c) Spherical swimmer, (d)-(f) ellipsoidal swimmer. (a)-(c) The spherical swimmer stopped on the wall, and the angles approached 90.0° , except when $\theta_0 = 10.0$. (d)-(f) The ellipsoidal swimmer swam adjacent to the wall, and every terminal angle was 11.9° , except when $\theta_0 = 10.0$. In both cases of $\theta_0 = 10.0$, the swimmers were reflected by the wall without touching it.

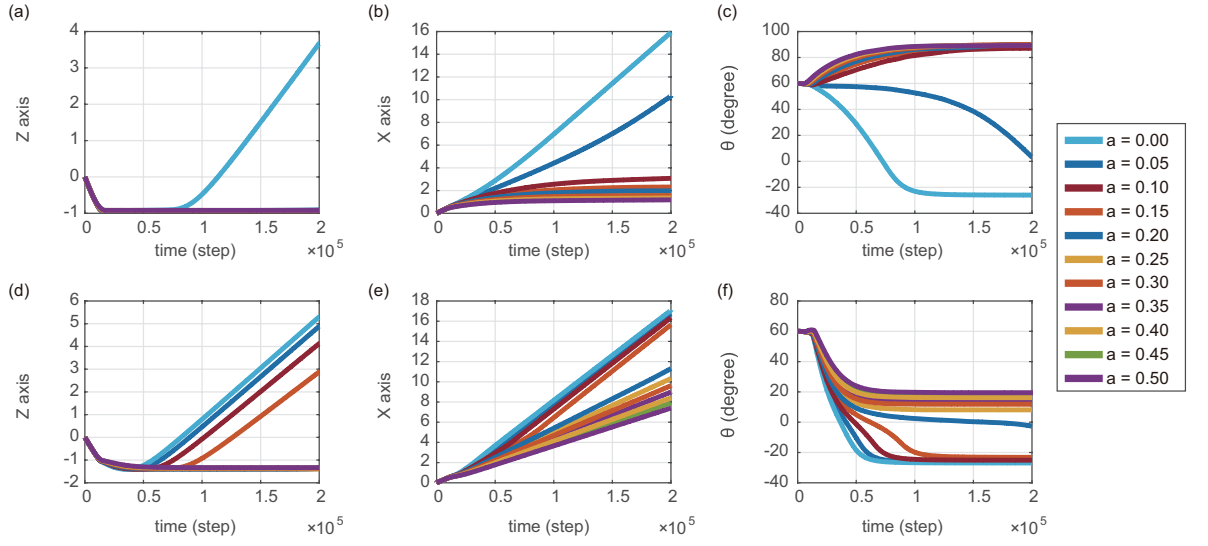


Fig. 3.13 Z and X positions and swimming angles of a swimmer with various SBA lengths a and fixed initial angles $\theta_0 = 60$. (a)-(c) Spherical swimmer, (d)-(f) ellipsoidal swimmer. (a)-(c) The spherical swimmer stopped on the wall, and every swimming angle approached 90.0° , except for $a = 0.00$ and 0.05 . (d)-(f) The ellipsoidal swimmer swam adjacent to the wall, and the angles approached a certain value except for $a < 0.20$. The spherical swimmer stuck to the wall at a lower a than the ellipsoidal swimmer, but the spherical swimmer did not slide in any of the cases.

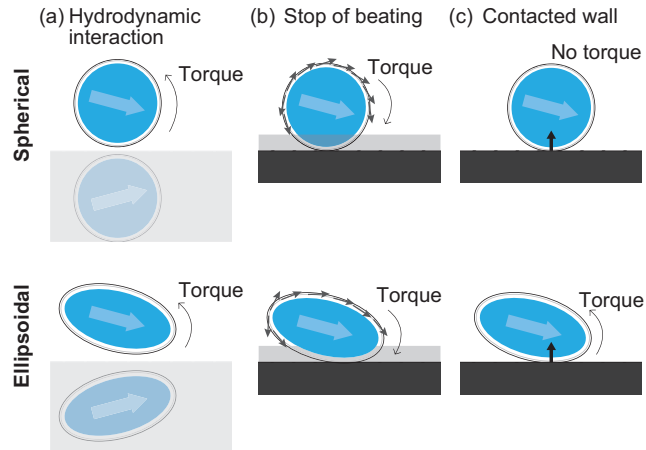


Fig. 3.14 Schematic illustrations of torques for a spherical swimmer (left) and ellipsoidal swimmer (right) approaching a wall from the left side. (a) Hydrodynamic interactions caused by the wall apply nose-up torques. (b) Stopping the cilia beating inside the SBA affects the total propelling force around bodies, leading to asymmetry and nose-down torques. (c) Mechanical repulsion from the wall. The spherical swimmer experiences no torque, whereas the ellipsoidal swimmer experienced nose-up torque.

posterior asymmetry of the shape requires more detailed study, but the present ellipsoidal shape can represent the experimental results semi-quantitatively. Therefore, the crucial factor impacting the sliding motion must be the disruption of the spherical-ellipsoidal symmetry. In practical comparisons, the ellipsoidal swimmer slid on the wall in a manner similar to the behavior observed experimentally; that is, the terminal swimming angles of the cell body were close to each other: 13.2° (nose-down, experiment) and 11.9° (nose-down, numerical calculation for the ellipsoidal swimmer at $a = 0.3$), where the ratio of the projected area of cilia stopping at $a = 0.3$ was almost the same as that estimated by the experiment. In addition, the match between the swimming speeds of the experiments and the simulations was achieved. The speed-reducing ratios of the sliding speed on the wall V_w over the speed in the bulk V_b were $\frac{V_w}{V_b} = 0.49$ (experiment; on the MPC coated glass) and $\frac{V_w}{V_b} = 0.55$ (simulation), which indicated that the boundary condition on the MPC-coated glass had possibly little lateral friction, inhibited the adhesion between cilia and the substrate and was quantitatively represented by simulation with no-lateral friction. In contrast, the ratio on the uncoated glass in the experiment was $\frac{V_w}{V_b} = 0.23$, and the difference must result from lateral friction. In addition, the force that the respective cilium experienced from the wall was at least 1.87 pN according to a comparison between the results of the experiment (approximately 30 cilia stalled) and the simulation (56.2 pN was applied). In any event, the surface sliding phenomena of *T. pyriformis* accompanied by the stopping of ciliary beating were observed. According to the abovementioned features, our simulation qualitatively reproduced actual ciliate swimming near the wall. Thus, the disruption of spherical-ellipsoidal symmetry and the cessation of ciliary beating near the wall are critical factors for ciliates swimming adjacent to a wall.

Since head-tail polar swimming direction(s) with angular velocity contribute primarily to determining whether a swimmer stops, slides, or departs from the wall, any torque balance that influences the swimmer and develops angular velocity should be considered. The causes of this torque are categorized into three patterns: hydrodynamic interaction, stopping of beating and wall repulsion (Fig. 3.14). If the swimmer approaches the wall from the top left, the hydrodynamic interaction from the wall has a nose-up torque, and asymmetric propelling force due to the stoppage of beating acts as a nose-down torque. Both torques act on both spherical and ellipsoidal swimmers. In contrast, wall repulsion does not give rotational torque to the spherical swimmer but to the ellipsoidal swimmer. Under this simplified scheme, the spherical swimmer touching the wall is given total torque from two factors without a balance point, and thus, the swimming direction is downward when $a > 0.2$ and the top right when $a < 0.15$ (Fig. 3.13). These

values correspond to stop and departure, respectively. However, the torque from the wall repulsion additionally acts on the ellipsoidal swimmer, affecting the total torque with a stationary fixed point of a certain angle θ_m , $-90.0^\circ < \theta_m < 0.0^\circ$. Thus, the ellipsoidal swimmer could slide on the wall, and the adjacent swimmer was stable at a certain angle (Figs. 3.10 and 3.12).

Finally, we discuss the biological relevance and applicability of the present results through comparison with other species. One well-studied ciliate, *Paramecium caudatum*, usually exhibits a back-and-forth motion against the uncoated wall, which is caused by a mechano-sensing system at the anterior region of the cell [109]. However, with the MPC-coated glass, *P. caudatum* also showed sliding motion for a long time, as did *T. pyriformis*, which would arise from the same dynamics. Ciliates are known to exist at air-fluid and solid-fluid interfaces in nature because these interfaces provide biofilm scaffolds composed of diatoms, alga, bacteria, polysaccharides and proteins[128, 129, 130, 131]. These components are favorite foods for ciliates[99, 105, 106]. In the case of the water/air interface (WAI), Ferracci et al. determined that *Tetrahymena* is also trapped at the WAI. However, the trapped cells did not stop their ciliary beating[56]. This finding indicates that the cell does not have SBA at the WAI, and the mechanisms of entrapment at the water/air interface will differ from those at the water/wall interface presented here. Adapting these facts to our results, the coupling of the mechanical and hydrodynamical responses allows ciliates to easily remain on solid interfaces, which is one of their preferred environments. This is a discovery of the ethology of ciliates accompanied by the mechanism coupling cilia motion and swimming behavior, and the finding also suggests why many ciliates have evolved ellipsoidal shapes. Spherical ciliates have a disadvantage in finding nutrients when sliding on surfaces. In the experiments, when *T. pyriformis* slid on a wall, its oral apparatus was located at the most appropriate position (i.e., close to the wall) (Fig. 3.7(a)). As for the spherical swimmer, which was propelled by means of multiple flagella on the surface (*Volvox carteri*), it continued swimming near the top and bottom walls, which was explained by geotaxis[132], which has different dynamics from the observed phenomenon because the sliding motion of *T. pyriformis* arose without gravity.

3.7 Conclusion

In conclusion, we reveal that *T. pyriformis* swims adjacent to the wall using the mechano-hydrodynamics of beating cilia, without cell adhesion, many-body effects[54] and chemotaxis. This phenomenon is essentially attributable to the ellipsoidal shape of the ciliate and the mechano-sensing and response of the beating

cilia against the attached surface. Although future biochemical investigations are required on the detailed mechano-sense/response in the ciliary motion, the present results should be considered in analyses of the collective motion of ciliates and bioconvection[39, 40].

Chapter 4

Positive rheotaxis of active living matter in microchannel

4.1 Introduction

Organisms show directed responses of motion in response to a stimulus or gradients against the input signal. These responses are known as taxis[133]. For example, organisms change directions upon sensing the presence of food. Taxis plays a crucial role in survival and is influenced by the surroundings. There are many types of taxis, such as chemotaxis[134, 135], phototaxis[136, 137], geotaxis[138, 139] and magnetotaxis[140].

Taxis moving against a flow is called positive rheotaxis. Rheotaxis is an important property of aquatic organisms[59]. If the living environment changes due to floating with a flow, organisms may die. Therefore, organisms attempt to stay in the same place against the flow, for example, fishes in a river. Not only macroscopic organisms but also microscopic organisms exhibit rheotaxis. The rheotaxis of fish is the product of complex biological sensing by a neural network in the brain, but the rheotaxis of microscopic organisms arises from physical mechanisms, such as in the case of mammalian sperm[115] or bacteria[63]. For mammalian sperm, the swimming motion due to flagellar beating and the shape of the cell can generate rheotaxis in a shear flow close to a wall without sensing the flow [32, 66]. Rheotaxis of *Bacillus subtilis* in a shear flow has also been observed. Shear flow must be a key factor for defeating or sensing the direction of flow in a microscopic world.

We investigated the shear response of a simple biological microswimmer. The ciliate *Tetrahymena pyriformis* can swim against a shear flow near a wall. However, in contrast to mammalian sperm, the dynamics of flagellar beating do not apply to the rheotaxis of ciliates propelled by ciliary beating. Thus, we attempted

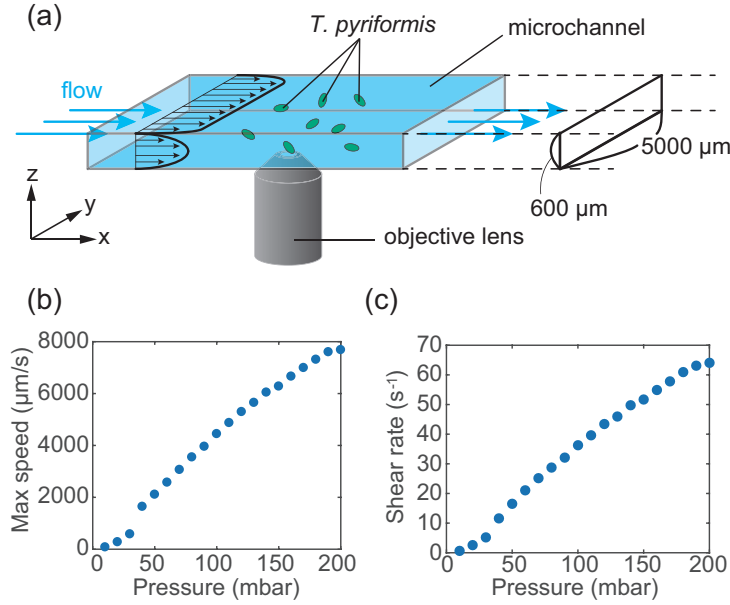


Fig. 4.1 Experimental setup for the observation of microorganisms in a microchannel. (a) A schematic illustration of the microfluidic device used in the experiment. The microchannel consisted of patterned PDMS bonded onto a glass slide. (b) The max flow speed in the x -axis around the center of the y -axis as a function of the pumping pressure rate. (c) The shear rate near the wall as a function of the pumping pressure rate.

to reveal the novel dynamics of *T. pyriformis* rheotaxis.

4.2 Experimental method

4.2.1 Preparation of *T. pyriformis*

The methodologies for cultivation and preparation were performed as described in Chapter 3. The shape of the cells used in the experiments was approximated as an ellipse, where the mean major length was $52.3 \mu\text{m}$ and the mean minor length was $24.8 \mu\text{m}$. The mean swimming speed far from a wall without external flow was $281.4 \mu\text{m/s}$.

4.2.2 Observation of *T. pyriformis* in a microfluidic channel

To observe the response of *T. pyriformis* to the flow and shear, we used microfluidics as depicted in Fig. 4.1(a). Upon applying a flow into a microchannel, the cells in the microchannel were observed by microscopy.

The length (x -axis) of the microchannel (produced from ibidi μ -Slide I Luer

with no coating) was 50 mm, the width (y -axis) was 5000 μm , and the height (z -axis) was 600 μm . The inside surface of the microchannel was coated with 2-methacryloyloxyethyl phosphorylcholine (MPC) polymer (Lipidure-CM5206, NOF Corporation) to prevent cell adhesion to the substrate.

The flow in the channel was controlled by a microfluidic pump (Elveflow OB1 MK3). The pressure applied by the pump generated a flow (Fig. 4.1(b)) and a shear near the bottom wall (Fig. 4.1(c)), proportionally. The flow profiles were obtained using a confocal microscope and fluorescent beads. The microchannel was a Hele-Shaw cell, and the flow profile in the z -axis became parabolic. Thus, assuming the z -flow profile was linear near a bottom wall, the shear rate near the wall was approximately calculated from the flow speed 24.8 μm (the cell minor length) away from the wall. The flow profile on the xy -plane was continuous at the field of view.

4.3 Experimental results

We observed that *T. pyriformis* in a shear flow exhibited positive rheotaxis on the bottom wall (Fig. 4.2(a)). If the cells swim far from the wall, they flow downstream. For this rheotaxis, we measured the velocity and lateral direction angle of the cell as a function of the shear rate (Fig. 4.2(a)inset). All data were obtained from the cell moving on the wall, and the cells flowing away were excluded.

The x -velocity in Fig. 4.2(b) indicates the intensity of rheotaxis. Positive rheotaxis began to be expressed at shear rates from 16.6 to 63.1 s^{-1} , which indicates that the cells swam against the flow that was faster than their mean swimming speed. The x -velocity increased to the peak value at a shear rate of 46.0 s^{-1} and then decreased.

As the shear rate increased, the standard deviation of the angle decreased, and θ_{xy} was distributed around 25 degrees (Fig. 4.2(c)). The smaller deviation indicates that the angle aligned with the one direction, and the converged angle slightly deviated from the flow direction. As the shear rate increased, the y -velocity became positive (Fig. 4.2(d)). At a shear rate of 36.3 s^{-1} , the y -velocity exhibited a positive peak value. The alignment and the response in the y -axis also indicate the properties of rheotaxis as a directing motion. We attributed these properties to the helical ciliary beating but do not discuss it in this study because the properties vertical to the flow direction do not directly concern the rheotaxis parallel to the flow direction. The speed had little correlation with the shear rate between 0.6 and 32.1 s^{-1} and decreased at shear rates greater than 36.3 s^{-1} (Fig. 4.2(e)).

Positive rheotaxis was observed without cell adhesion, and thus, there might be

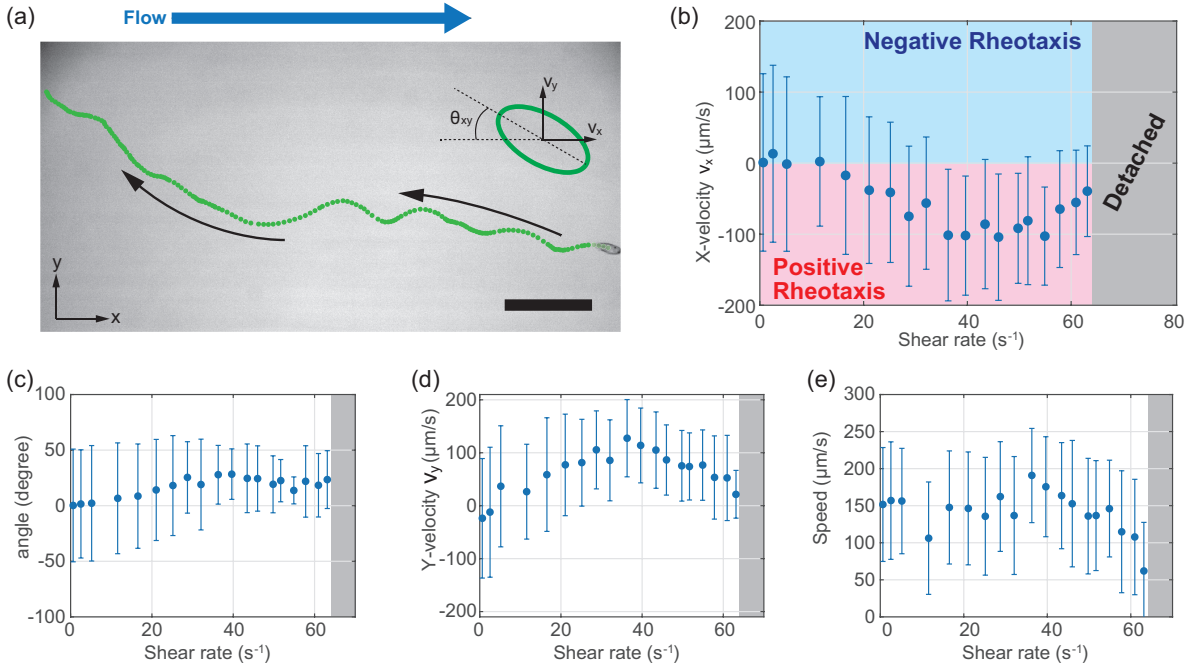


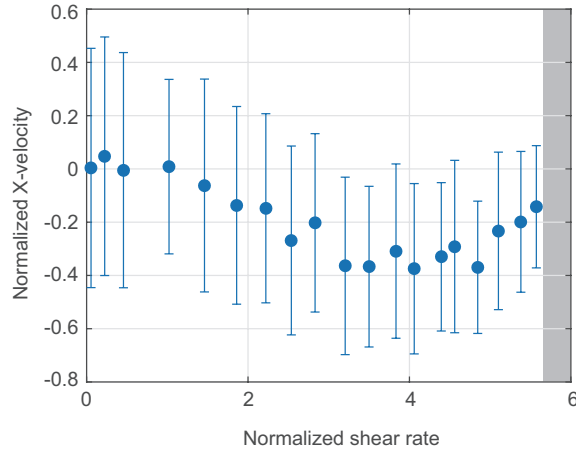
Fig. 4.2 The responses of *T. pyriformis* to a shear flow. (a) A typical trajectory of a cell in the snapshot. The cell swam against the flow on the bottom wall. The shear rate was 28.7 s^{-1} . The blue vector represents the flow direction. The black vectors represent the moving direction of the cell. The time interval of the position is 30 ms, and the scale bar is $200 \text{ } \mu\text{m}$. The inset figure represents a schematic picture of the parameters. (b) Plot of the x -velocity v_x as a function of the shear rate. Plots in the blue area represents negative rheotaxis, and plots in the red area represents positive rheotaxis. When the shear rate is higher than 64.0 s^{-1} (gray area), almost all cells are detached from the wall. (c) Plot of the xy -angle θ_{xy} as a function of the shear rate. (d) Plot of the y -velocity v_y as a function of the shear rate. (e) Plot of the speed as a function of the shear rate.

a dynamic mechanism of this phenomenon. We assumed that the dynamics of the wall-preferring motion (Chapter 3) was critical for the rheotaxis because rheotaxis was observed only near a wall in the experiment. Using the numerical method described in Chapter 3, we approached the dynamics of the rheotaxis.

To compare the experimental results with the numerical results, the parameters in the experiments were normalized by the swimming speed and the minor length of the cell (Table 4.1). In the numerical calculation, the swimming speed and the length were set to 1.0, and hence, the shear rate was given as $\dot{\gamma}_*$. Fig. 4.3 shows the normalized x -velocity as a function of the normalized shear rate.

Table 4.1 Experimental parameters and normalized parameters

	Experiments	Normalized
Swimming speed (without wall, shear)	v ; 281.4 $\mu\text{m/s}$	v_* ; 1
Length (minor length)	L ; 24.8 μm	L_* ; 1
Shear rate	$\dot{\gamma}$; 0.6-64.0 s^{-1}	$\dot{\gamma}_*$; 0.1-5.7

Fig. 4.3 Plot of the experimental normalized v_x as a function of the experimental normalized shear rate $\dot{\gamma}_*$.

4.4 Numerical method

The numerical method for ciliary swimming was the Boundary Element Method, as described in Chapter 3 and the Appendix.

In this study, a shear flow was added as the external flow $\mathbf{u}_\infty$. The shear flow was applied to the whole system and was dependent on the distance from the wall. The direction of the shear flow was along the x -axis, and therefore the flow velocity $\mathbf{u}_\infty$ at a point $\mathbf{x} = (x, y, z)$ was defined as

$$\mathbf{u}_\infty = (u_f, 0, 0), \quad \text{with} \quad u_f = \dot{\gamma}_*(z - z_{wall}) \quad (4.1)$$

where z_{wall} is the z -coordinate of the wall, and $z_{wall} = -2$ in this calculation. By adding this expression of $\mathbf{u}_\infty$ to eq. (3.5), the arbitrary flow field was obtained.

Fig. 4.4 shows the schematic figure of the numerical setup. The flow direction was along the x -axis. At $z = -2$, the velocity was zero. a indicates the Stop

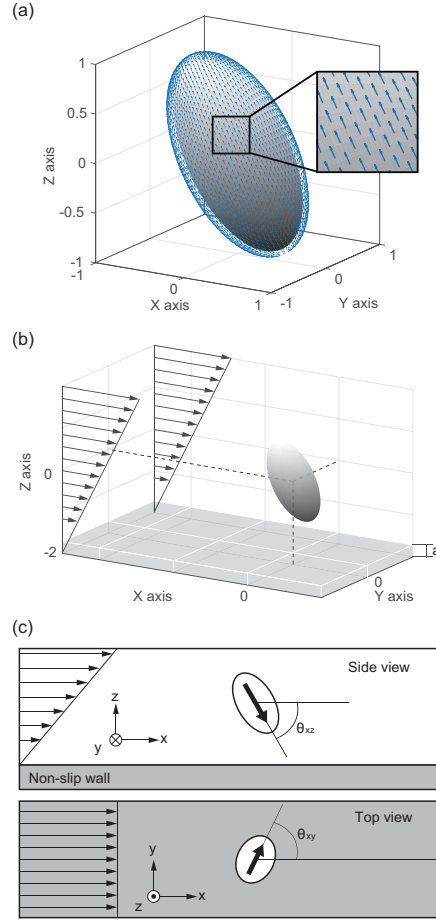


Fig. 4.4 Numerical setup. (a) A numerical swimmer. It has a thrust point force on discrete surface nodes. (b) A 3-dimensional schematic of the numerical system. (c) Parameter setup. Top: A schematic on the xz -plane. Bottom: A schematic on the xy -plane.

Beating Area (SBA) length (according to Chapter 3). The swimming angle on the xz -plane was defined as θ_{xz} , and the swimming angle on the xy -plane was defined as θ_{xy} . The shape of the swimmer was spherical or prolate ellipsoidal (aspect ratio 1:2). The diameter of the spherical swimmer was 2. The major length of the ellipsoidal swimmer was 2, and the minor length was 1. The time interval was $dt = 0.01$. The minor length of the swimmer was $L = 1.0$, and the speed of the swimmer without a wall was $U = 1.0$. The shear rate $\dot{\gamma}_*$ was normalized by U, L .

4.5 Numerical results

First, we investigated a spherical swimmer and an ellipsoidal swimmer in shear flow approaching the non-slip wall in the presence or absence of SBA. Fig. 4.5(a) shows the trajectories of the swimmers approaching the wall when $\dot{\gamma}_* = 0.5$. In

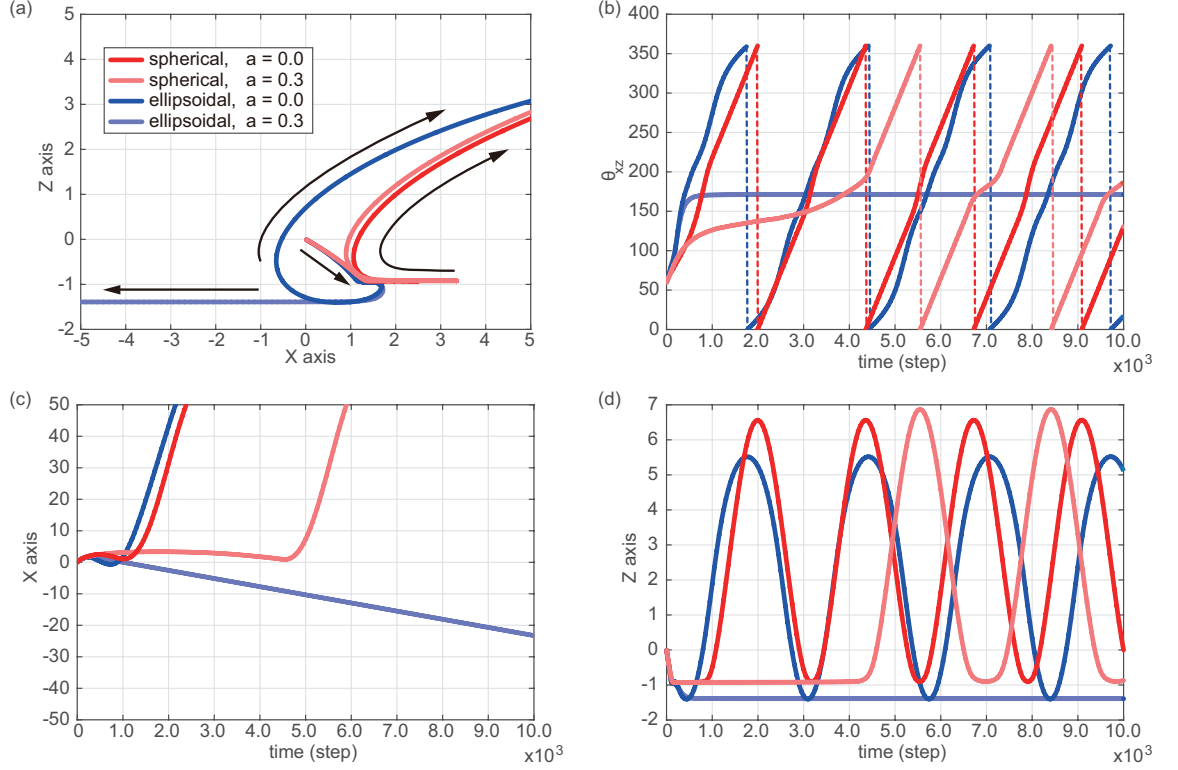


Fig. 4.5 Trajectories and time evolutions of spherical and ellipsoidal swimmers. The following parameters were fixed: $\dot{\gamma}_* = 0.5$, initial $\theta_{xz} = 60$ and initial $\theta_{xy} = 0$. In all plots, the dark red line indicates the spherical swimmer without SBA ($a = 0.0$), the light red line is the spherical swimmer with SBA ($a = 0.3$), the dark blue line indicates the ellipsoidal swimmer without SBA ($a = 0.0$), and the light blue line is the ellipsoidal swimmer with SBA ($a = 0.3$). (a) Trajectories on the xz -plane. The swimmers started from $x = 0, y = 0, z = 0$. (b) Time evolutions of θ_{xz} . (c) Time evolutions of the x -position. (d) Time evolutions of the z -position.

these cases, the initial swimming directions were parallel to the flow direction, and hence, the trajectories did not contain the y -component. The spherical swimmer flowed away from the wall regardless of SBA. The ellipsoidal swimmer without SBA also flowed similar to the spherical swimmer, but the ellipsoidal swimmer with SBA slid on the wall against the flow (Fig. 4.5(a)). All swimmers were rotated by the shear flow and immediately directed against the flow, but none of the swimmers, except the ellipsoidal one with SBA, could maintain a stable direction and thus flowed in the flow direction periodically (Fig. 4.5(b)(c)(d)).

Next, we checked the dependence on the shear rate with SBA. As $\dot{\gamma}_*$ increased, the ellipsoidal swimmer flowed away from the wall when $\dot{\gamma}_* = 1.75$ (Fig. 4.6(c)), and the spherical swimmer flowed away from the wall when $\dot{\gamma}_* = 0.5$ (Fig. 4.6(d)).

The ellipsoidal swimmer showed positive rheotaxis when $0.50 \leq \dot{\gamma}_* \leq 1.00$ and negative rheotaxis when $\dot{\gamma}_* = 0.25, 1.25, 1.50$ (Fig. 4.6(a)). As $\dot{\gamma}_* = 0.25$, the swimmer was directed to the flow because the shear was too weak and the swimmer attached to the wall could not turn on xz -plane (Fig. 4.6(e)). We discuss the weak shear flow in the following. The spherical swimmer did not exhibit positive rheotaxis at any shear rate (Fig. 4.6(b)). Even when the swimming direction was against the flow, the swimmer was pushed to the flow direction by the drag force.

Figure 4.7 indicates the motions of the ellipsoidal swimmer as the initial xy -angle θ_i changes. At any θ_i , the swimmer finally showed positive rheotaxis, directed parallel to the flow and attached on the wall (Fig. 4.7).

Figure 4.8 indicates the motions of the spherical swimmer with changing initial xy -angle θ_i . At any θ_i , the swimmer was also directed parallel to the flow and attached to the wall, but it did not show positive rheotaxis (Fig. 4.8).

Finally, the motions of the ellipsoidal swimmer as $\dot{\gamma}_*$ were observed. As shown in Figure 4.5, the ellipsoidal swimmer could not turn to the opposite flow direction and exhibited negative rheotaxis at $\dot{\gamma}_* = 0.25$ (Fig. 4.5 and Fig. 4.9 blue line). As shown in Figure 4.5, the motion was restricted to 2 dimensions because the system was always symmetrical in the y -axis. When the swimmer was permitted to move 3-dimensionally by $\theta_i = 1$, the swimmer turned on the xy -plane and moved against the flow (Fig. 4.9).

4.6 Discussion

We discuss the mechanism of the numerical swimmer showing positive rheotaxis on the wall. If there is no shear flow, the swimmer is assumed to move on the wall with SBA. First, when the swimmer moves to a downward flow near the wall, it is rotated by the shear flow and is directed to the upward flow. It is then unclear whether the swimmer can continue to move on the wall or not. The swimmer experiences two torques: one is a nose-down torque to keep moving on the wall T_b , and the other is a nose-up torque experienced by the shear flow T_s (Fig. 4.10). If T_s is higher than T_b , the head of the swimmer directs up to the wall, and the swimmer flows away. If T_s is lower than T_b , the head of the swimmer directs down to the wall, and the swimmer can move on the wall to the upward flow.

Next, the turn against a shear rate in the xy -plane is discussed. Even if the initial xy -angle is not zero, the swimmer finally begins to move parallel to the x -axis (Fig. 4.7, 4.8). In addition, in a weak shear flow, an ellipsoidal swimmer can rotate and turn to an upward flow on the wall in the xy -plane (Fig. 4.9). How the swimmer turns in the xy -plane is non-trivial because the flow has only the x -component and is a continuous flow in the xy -plane. This turn of the swimmer

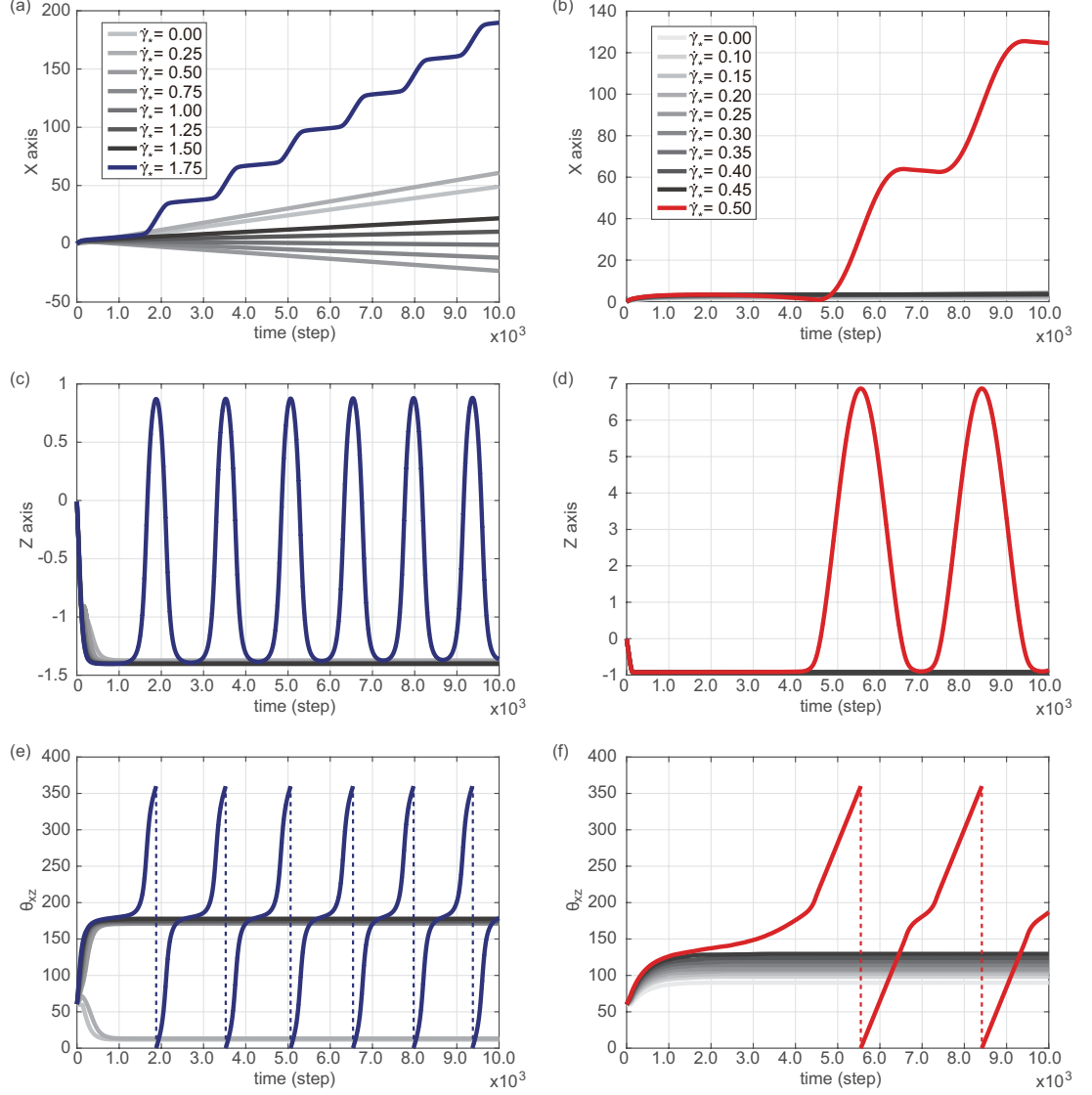


Fig. 4.6 Time evolutions of the swimmers with changing $\dot{\gamma}_*$. $a = 0.3$ and initial $\theta_{xy} = 0$. (a),(c),(e): The spherical swimmer. (b),(d),(f): The ellipsoidal swimmer. (a),(b) The time evolution of the x -position. In this plot, only the ellipsoidal swimmer showed positive rheotaxis when $0.50 \leq \dot{\gamma}_* \leq 1.0$. (c),(d) The time evolution of the z -position. The spherical swimmer moved away from the wall when $\dot{\gamma}_* = 0.5$, and the ellipsoidal swimmer moved away from the wall when $\dot{\gamma}_* = 1.75$. (e),(f) The time evolution of θ_{xz} . θ_{xz} of the spherical swimmer converged when $0.0 \leq \dot{\gamma}_* \leq 0.45$. θ_{xz} of the ellipsoidal swimmer converged when $0.0 \leq \dot{\gamma}_* \leq 1.5$, and In the cases of $\dot{\gamma}_* = 0.0, 0.25$, the swimming direction of the ellipsoidal swimmer was along the shear flow, whereas in the cases of $\dot{\gamma}_* \geq 0.5$, the swimming direction was against the shear flow.

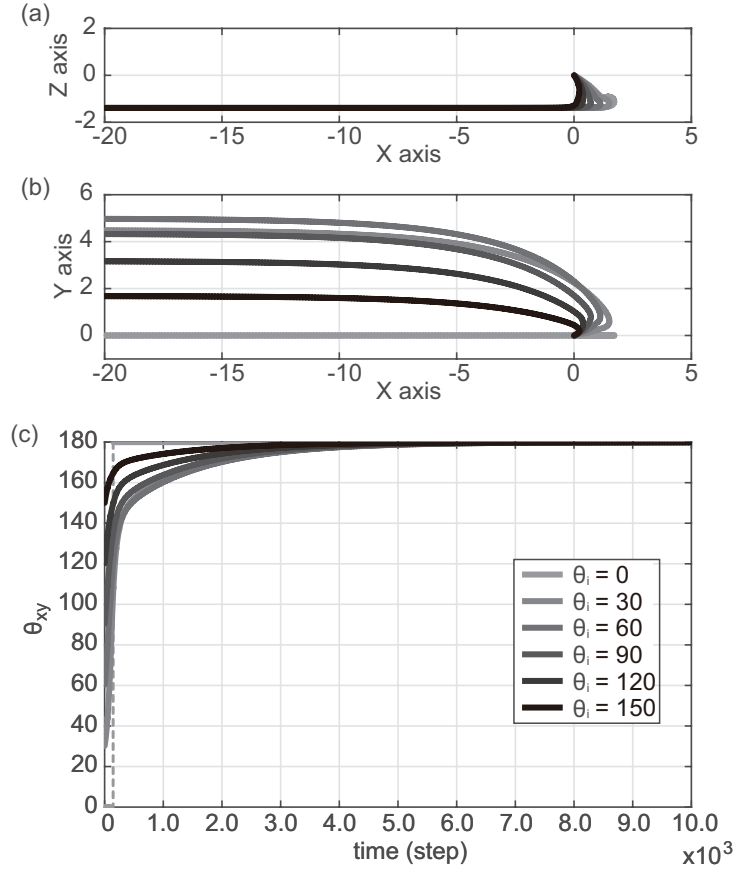


Fig. 4.7 Trajectories and time evolutions of an ellipsoidal swimmer with changing initial xy -angle θ_i when $\dot{\gamma}_* = 0.5$ and initial $\theta_{xz} = 60$. (a) Trajectories on the xz -plane. In all the cases, the swimmer remained attached to the wall. (b) Trajectories on the xy -plane. In all the cases, the swimmer exhibited positive rheotaxis parallel to the x -axis. (c) Time evolutions of the xy -angle. In all the cases, θ_{xz} converged to 180.

can be divided into two steps (Fig. 4.11). In the first step, the swimmer with a finite inclination angle to the flow direction rotates and falls down because of shear flow as shown in the left side of Figure 4.11. In the second step, the rear of the swimmer rises up because of T_b in the right side of Figure 4.11. These steps occur continuously, and the swimmer repeats these steps until its swimming direction aligns with the upward flow in the xy -plane. Thus, the swimmer on a wall with SBA can show rheotaxis until a certain shear rate regardless of the incident angle.

The degree of rheotaxis is valued quantitatively. Figure 4.12 shows the converged x -velocities of a spherical and an ellipsoidal swimmer moving on the wall. A negative value of x -velocity indicates positive rheotaxis. The converged x -velocity of the ellipsoidal swimmer was linearly proportional to the shear rate (Fig. 4.12(b)). The positive rheotaxis shifted to negative rheotaxis at shear rates between 1.0

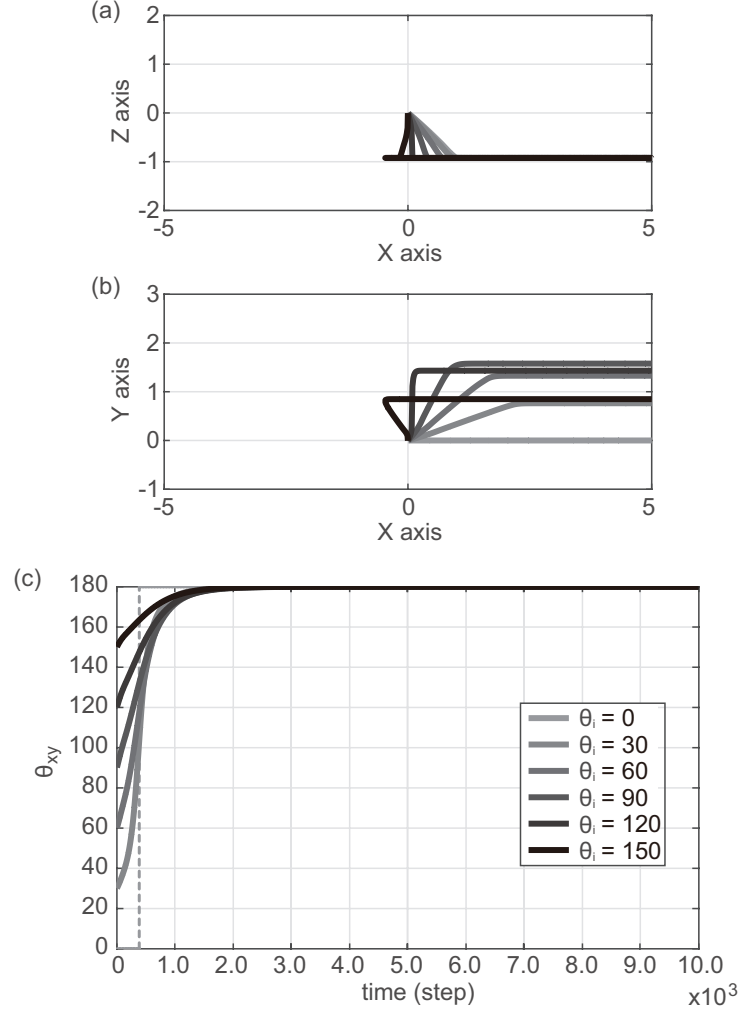


Fig. 4.8 Trajectories and time evolutions of a spherical swimmer with changing initial xy -angle θ_i when $\dot{\gamma}_* = 0.25$ and initial $\theta_{xz} = 60$. (a) Trajectories on the xz -plane. In all the cases, the swimmer remained attached to the wall. (b) Trajectories on the xy -plane. In all the cases, the swimmer exhibited negative rheotaxis parallel to the x -axis. (c) Time evolutions of the xy -angle. In all the cases, θ_{xz} converged to 180.

and 1.25. By contrast, the converged x -velocity of the spherical swimmer was not proportional to the shear rate and was higher than -0.01 under $\dot{\gamma}_* < 0.5$ (Fig. 4.12(a)), which indicates that a spherical shape shows less effective rheotaxis than an ellipsoidal shape. When the shear rate was between 0.2 and 0.3, the value of the x -velocity was maximum. As the shear rate increases, the drag force experienced by the flow increases, and the thrust force in x -direction also increases because the swimming direction becomes more parallel to the wall. The summation of these two factors is considered responsible for the non-linearity of the x -velocity. An order of x -velocity smaller than 10^{-2} may contain numerical errors. Hence, the

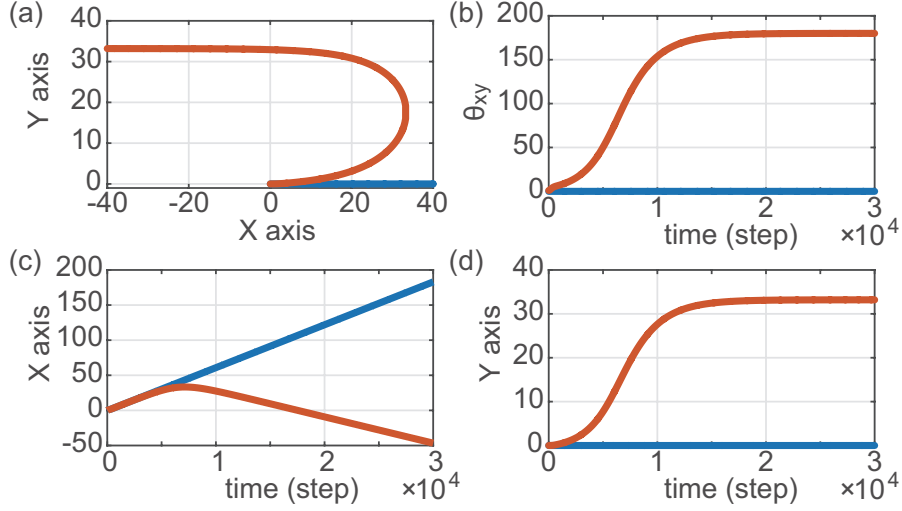


Fig. 4.9 Trajectories and time evolutions of the ellipsoidal swimmer. $\dot{\gamma}_* = 0.25$ and initial $\theta_{xz} = 60$. The red line represents the case of $\theta_i = 0$, and the blue line represents the case of $\theta_i = 1$. (a) Trajectories on the xy -plane. (b) Time evolutions of the xy -angle. (c) Time evolutions of the x -position. (d) Time evolutions of the y -position.

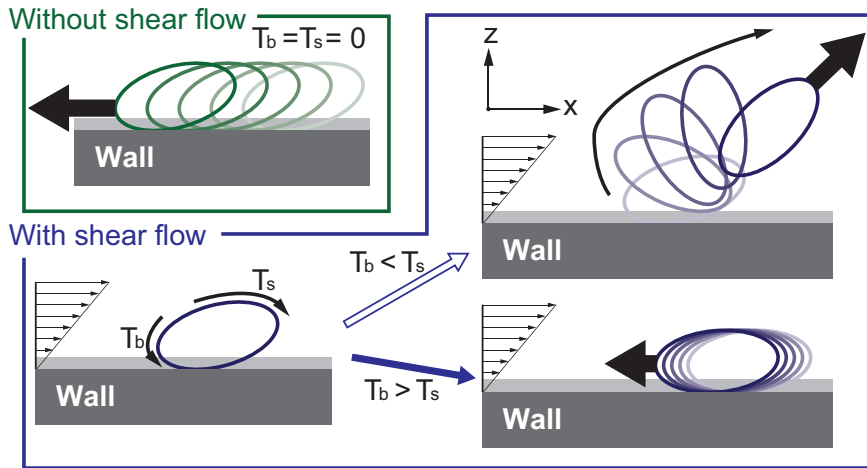


Fig. 4.10 Schematic figure of the swimmer sliding on the wall in shear flow. The green and blue ellipsoids represent the swimmer, and the gray area represents SBA. T_b is the torque at which the swimming angle converges on the wall. T_s is the torque that the swimmer experiences from shear flow.

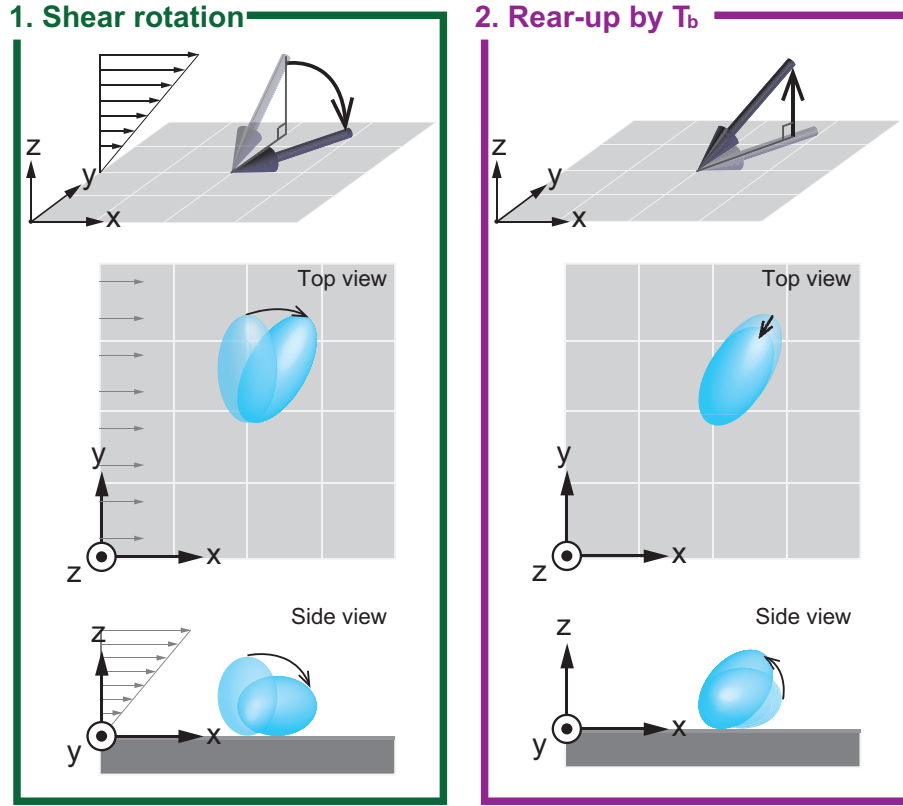


Fig. 4.11 Schematic figure of the alignment of the swimming angle with the flow direction.

x -velocity of the spherical swimmer cannot be valued precisely.

Finally, the numerical results are compared with the experimental results. The numerical ellipsoidal swimmer reproduced the positive rheotaxis and alignment with the flow direction, which indicates that the dynamic mechanism of the rheotaxis was qualitatively identified as discussed above. However, the ranges of the shear rate are different. In the experiment, rheotaxis was observed at shear rates between 1.5 and 5.7 (Fig. 4.3), whereas in the calculations, rheotaxis was observed at shear rates between 0.25 and 1.75 (Fig. 4.12(b)). This difference in range indicates that the cell has a larger T_b than the numerical swimmer or that there are some attractive forces at the wall other than cell adhesion. This numerical calculation did not resolve these questions.

4.7 Conclusion

We observed that *T. pyriformis* exhibited positive rheotaxis and aligned with the flow direction in the microchannel. This motion was observed only on a wall, which indicates that the cells tend to swim against a shear flow near the wall.

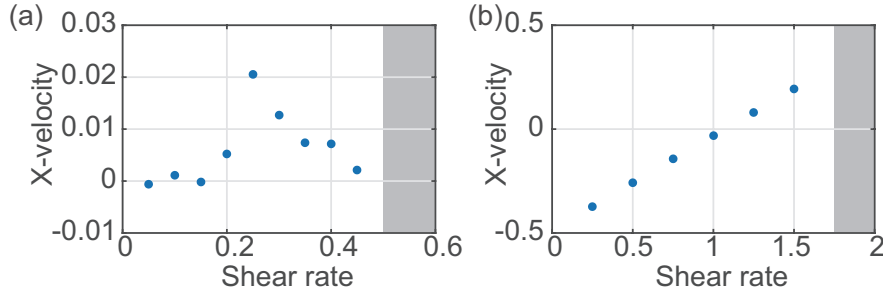


Fig. 4.12 Converged x -velocities of the swimmers. The gray area in both figures represents the swimmer flowing away from the wall. (a) In the plot, the x -axis is the shear rate, and the y -axis is the converged x -velocity of the spherical swimmer. (b) In the plot, the x -axis is the shear rate, and the y -axis is the converged x -velocity of the ellipsoidal swimmer.

Therefore, to investigate the rheotaxis near a non-slip boundary theoretically, we performed a hydrodynamic numerical calculation. The numerical swimmer with SBA in a shear flow exhibited positive rheotaxis on the boundary until a certain shear rate was reached. In addition to SBA, the ellipsoidal shape of the swimmer was critical for effective rheotaxis.

In the calculation, rheotaxis was observed at a low shear rate where alignment of *T. pyriformis* did not occur. A possible reason for this difference is that the actual cells experience the wall-adhesive effect more strongly than the shear effect. In future work, we will attempt to observe the ciliary beating motion of a single cell in a shear flow.

Chapter 5

Conclusion

5.1 General conclusions

In this thesis, the near-wall dynamics of passive and active particles at low Reynolds number were revealed. Specifically, we focused on the motions of micrometer-scaled particles, including the oscillation and clustering of passive microfluidic droplets in a microchannel and the motions of a swimming microorganism interacting with a wall and shear flow. Statistical analysis is meaningless for elucidating the concrete activities of these systems. By using experimental observations and numerical calculations, we quantified the interactions of the individual particles in detail and identified the dynamic mechanisms. In addition, microsystems of moving particles exist *in vivo* or in nature, such as red blood cells flowing in a microvessel as passive particles and aquatic microorganisms living in the sea, ponds or lakes. From the viewpoint of evolution, their motilities should be biogenic or effective for survival and growth. This physical approach to the dynamics of micrometer-scaled particles has the potential to provide a new perspective for unclear microbiological problems.

With respect to the phenomenon of passive particles, a 1-dimensional crystal of homogeneous droplets flowing in a microchannel was known to show wave propagation generated from hydrodynamic interactions. In Chapter 2, the motion of heterogeneous passive droplets was investigated. First, we developed a microchannel to generate small and large water-in-oil droplets aligned in one line. The small droplets were observed to oscillate between two large droplets flowing in the microchannel. The hydrodynamic numerical calculation demonstrated that these phenomena of the small droplet can be explained by the periodic flow generated in the space surrounded by two large droplets and top-bottom walls. The oscillatory motion was obtained from a low Reynolds system, where complex structures such as vortices do not arise. In addition, this periodic flow, called bolus flow, has

also been observed between two red blood cells in a microcapillary and is considered important for material transportation in blood flow. However, no microfluidic device that can observe bolus flow or periodic motions of large and small particles has been reported previously. Our developed microchannel can be used for medical engineering transportation of micrometer-scaled particles.

In Chapter 3, we studied the dynamics near a wall of a swimming microorganism as an active particle. Ciliates, a class of protists, show rapid swimming motion in bulk water propelled by beating cilia around the cell body. Ciliates are also known to aggregate near a wall. The motion of such a particle near a boundary is a fundamental and complex hydrodynamic problem. In the squirmer model, the hydrodynamic property of ciliates is represented as a neutral swimmer. When a spherical neutral swimmer approaches a wall at low Reynolds number, the swimmer experiences hydrodynamic repulsion and moves away from the wall. This motion of the model contradicts biological knowledge. Thus, we investigated the difference between the ciliate and the neutral swimmer, which is subject to dynamics other than hydrodynamics. The ciliate, *T. pyriformis*, was observed to slide on the wall rather than swim away from the wall. During cell sliding, the part of the cilia attached to the wall hardly beat, indicating that the thrust forces were asymmetrical. By comparing the experimental results for the “real swimmer” with the numerical calculation including the asymmetry of the thrust force, we determined that the sliding motion could be explained not by a complex biological behavior only but by two simple physical factors. One is the asymmetry of the thrust force, and the other is the anisotropic shape of the cell body. In Chapter 4, we studied the dynamics of the ciliate under a shear flow. Microswimmers, such as mammalian sperm and bacteria, swim against a shear flow in a process called positive rheotaxis. We observed that *T. pyriformis* also exhibited positive rheotaxis in a shear flow near a wall. The numerical calculation indicated that the same two factors, asymmetry of the thrust force and the anisotropic shape of the cell body, were responsible for the positive rheotaxis, as well as the sliding motion. The above two results revealed that simple physical properties decide the behavior of the cell. Both the sliding motion and the positive rheotaxis are ethologically efficient for survival and growth of the cell in nature, and thus, the present studies on cell motility are meaningful for biology.

In this thesis, we have identified near-wall rules of a few particles at low Reynolds number. The oscillation of the passive droplet occurred at $Re = 4.3 \sim 8.5 \times 10^{-3}$ and the swimming motion of the active microorganism was regarded as a hydrodynamic phenomenon at $Re = 7.9 \times 10^{-3}$. We intuitively cannot predict such motions of particles because the scales, the speeds and the viscosities are different from our living environments. However, by use of quantitative experiment and

physical analysis, the dynamics of the motions have been clear in recent years. The established approach coupling quantitative measurements and hydrodynamic numerical calculation will be useful for studying other phenomena at low Reynolds number. Moreover, the simple dynamics we identified can be extended to a many-body system or complex boundary conditions observed in the real world.

5.2 Future problems

With respect to the microfluidic droplets examined in Chapter 2, the dynamics of the two phenomena observed in our experiments remain unclear. The first phenomenon is the attraction of a small droplet outside the bolus flow into the flow. We attributed this attraction to the small deformation of the droplet. To verify this assumption, further numerical calculations including a deformable particle are necessary. The second phenomenon was the clustering of a few small droplets in the bolus flow. The cluster rotated periodically and maintained its structure. Although the periodic rotation can be explained by Jeffery's orbit, the formation process of clustering remains unknown. A cluster of charged colloidal particle has been reported, but it is not clear how uncharged droplets form a cluster. There are few data for droplet clusters; hence, further relevant experiments are necessary.

With respect to the swimming microorganism in Chapters 3 and 4, we already performed two experiments on many-body systems using the same microorganism. The first experiment focused on bioconvection, in which a 3-dimensional structure is formed by a dense suspension of swimming microorganisms. The bioconvection of *T. pyriformis* was reported previously, and a continuum model was established. However, that model did not reproduce the observed complex structure completely. We believe that the near-wall swimming property observed in Chapter 3 can be applied to the previous model. The second experiment involved a many-body system with ordered boundary condition. As shown in a previous study, a suspension of swimming bacteria confined in a microchamber with pillars forms a macroscopic structure called bacterial turbulence. The flow field and boundary response of *T. pyriformis* differ from those of bacteria, thus, the behavior of a suspension of *T. pyriformis* under such conditions cannot be predicted. We attempted to observe the suspension in a micro channel with pillars allowing the external flow to be controlled.

The phenomena mentioned above arise due to the interactions of particles in a confined boundary condition. We believe that quantification of these interactions is necessary, in addition to the existing statistic approach, to describe more concretely many-body dynamics, such as collective motions of animals. To demonstrate this idea, we will first work with micrometer-scaled many-body systems.

Appendix

Lattice Boltzmann Method

In this section, the Lattice Boltzmann Method, which is referenced in Chapter 2, is exhibited.

The Lattice Boltzmann Method (LBM) is a method for hydrodynamic numerical calculation [92, 141]. The LBM has the significant advantage of flexibility, e.g., defining the Reynolds number, arbitrary shape of the boundary, and multi-component fluids. Researchers can precisely calculate many types of systems as long as the computer power and calculation time allow it. The LBM has been employed for various systems, for example, Karman vortexes in high Reynolds flow [142] and red blood cells flowing in vessel in low Reynolds flow [143]. Many studies on microfluidic droplets also adopt the LBM [144, 145]. Therefore, we considered that the LBM is suitable for complex systems in which heterogeneous droplets are alternately placed in a microchannel.

The steps of the LBM are described as follows:

1. Define the densities of virtual particles, which are placed on each node of the lattice and have velocity.
2. Calculate the diffusion and collision of particles using a velocity distribution function that obeys a Boltzmann distribution.
3. Obtain the macroscopic flow of the density from the moment of the updated velocity distribution function.

Considering the 3-dimensional hydrodynamics inside the square boundary, we define the lattice points (nodes) in space, their virtual points and the 15 vectors directed from each node to neighbor nodes (Fig. 5.1)

At coordinate $\mathbf{x}$ and time t , the velocity distribution function of the virtual particles $f_i(\mathbf{x}, t)$ obeys the following discrete Boltzmann equation because the velocity of particle c_i is fixed.

$$\text{Sh} \frac{\partial f_i(\mathbf{x}, t)}{\partial t} + \mathbf{c}_i \cdot \nabla f_i(\mathbf{x}, t) = \frac{1}{\epsilon} \Omega_i, \quad i = 0, 1, \dots, 14 \quad (5.1)$$

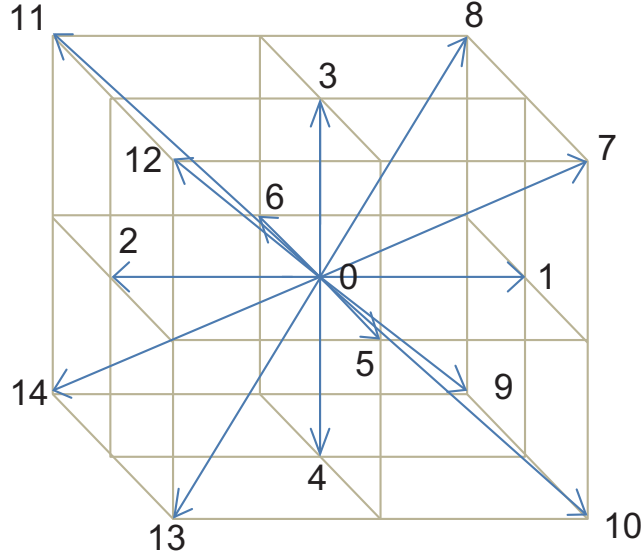


Fig. 5.1 Discrete velocity vectors on a node in the case of D3Q15.

where $Sh = U/c$ is the Strouhal number, ϵ corresponds to the Knudsen number, and Ω_i is the collision operator of the particle. The distance between two neighbor nodes is defined as δx , and the time interval in which the virtual particle moves from one node to a neighbor node is defined as $\delta t = Sh\delta x$. Approximating the left terms in eq. (5.1) by the primary difference, the following equation is obtained:

$$f_i(\mathbf{x} + \mathbf{c}_i\delta x, t + \delta t) - f_i(\mathbf{x}, t) = \Omega_i, \quad i = 0, 1, \dots, 14 \quad (5.2)$$

The density and the momentum of the virtual particle on each node can be derived by the velocity distribution function, and the velocity of the fluid is calculated by dividing the density by the momentum.

$$\rho(\mathbf{x}, t) = \sum_i f_i(\mathbf{x}, t) \quad (5.3)$$

$$\rho(\mathbf{x}, t) \mathbf{u}(\mathbf{x}, t) = \sum_i \mathbf{c}_i f_i(\mathbf{x}, t) \quad (5.4)$$

To derive a collision operator, approximation by the Bhatnagar-Gross-Krook (BGK) model is applied. In the BGK model, the velocity distribution arrives at an equilibrium state after the relaxation time τ , and the mass and the momentum are locally conserved when the particles collide. Using this approximation, the collision operator is

$$\Omega_i = -\frac{1}{\tau} (f_i(\mathbf{x}, t) - f_i^{eq}(\mathbf{x}, t)), \quad i = 0, 1, \dots, 14 \quad (5.5)$$

where $f_i^{eq}(\mathbf{x}, t)$ is referred to as a local equilibrium distribution function. τ is dependent on the fluid viscosity; thus, the viscosity is expressed using τ ,

$$\nu = c_s^2 \left(\tau - \frac{1}{2} \right) \delta t \quad (5.6)$$

where c_s is the speed of sound and is defined as $c_s = 1/\sqrt{3}$ in this thesis.

The local equilibrium distribution function of the right-hand terms in eq. (5.5) is derived by Maxwell's distribution function in the case where the Mach number $Ma = |\mathbf{u}|/\sqrt{RT}$ is sufficiently smaller than one.

$$f_i^{eq}(\mathbf{x}, t) = \frac{\rho}{(2\pi RT)^{D/2}} \exp\left(-\frac{\mathbf{c}_i^2}{2RT}\right) \left(1 + \frac{\mathbf{c}_i \cdot \mathbf{u}}{RT} + \frac{(\mathbf{c}_i \cdot \mathbf{u})^2}{2RT} - \frac{\mathbf{u}^2}{2RT}\right), \quad i = 0, 1, \dots, 14 \quad (5.7)$$

Translating this expression in the LBM system,

$$f_i^{eq}(\mathbf{x}, t) = \omega_i \rho \left(1 + \frac{\mathbf{c}_i \cdot \mathbf{u}}{c_s^2} + \frac{(\mathbf{c}_i \cdot \mathbf{u})^2}{2c_s^4} - \frac{\mathbf{u}^2}{2c_s^2}\right), \quad i = 0, 1, \dots, 14 \quad (5.8)$$

In this thesis, D3Q15 (3-dimensional fifteen discrete velocities) is utilized. The values of the coefficients are as follows: $\omega_0 = 2/9$, $\omega_i = 1/9$ ($i = 1, 2, \dots, 6$) and $\omega_i = 1/72$ ($i = 7, 8, \dots, 14$)

Boundary condition parallel to lattice

The calculation method for a simple straight boundary condition is explained. In this explanation, the D2Q9 model is employed (Fig. 5.2).

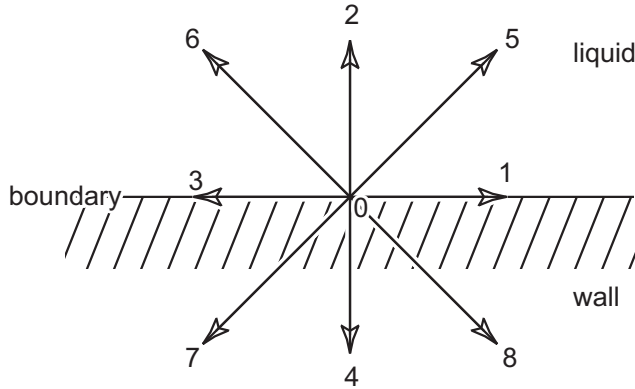


Fig. 5.2 Discrete velocity on the surface lattice point in the D2Q9 model

Slip boundary

At a slip boundary, the vertical velocity is zero. In the setup in Fig. 5.2, the condition is expressed as follows:

$$f_2 = f_4 \quad (5.9)$$

$$f_5 = f_8 \quad (5.10)$$

$$f_6 = f_7 \quad (5.11)$$

Non-slip boundary

At a non-slip boundary, the velocity is zero. One of the methods frequently employed is referred to as the bounce-back condition.

$$f_2 = f_4 \quad (5.12)$$

$$f_5 = f_7 \quad (5.13)$$

$$f_6 = f_8 \quad (5.14)$$

In the bounce-back condition, the vertical velocity becomes zero, but the parallel velocity does not become zero, and a slip velocity occurs. Then, the method by Zou *et al.* is applied for a more precise non-slip boundary condition[146]. This method is also adopted in the case where the non-slip boundary moves at the velocity (u_x, u_y) . The conditional equation is expressed as follows:

$$f_2 = f_4 + \frac{2}{3}\rho u_y \quad (5.15)$$

$$f_5 = f_7 - \frac{1}{2}(f_1 - f_3) + \frac{1}{2}\rho u_x + \frac{1}{6}\rho u_y \quad (5.16)$$

$$f_6 = f_8 + \frac{1}{2}(f_1 - f_3) - \frac{1}{2}\rho u_x + \frac{1}{6}\rho u_y \quad (5.17)$$

Periodic boundary and pressure gradient

We consider that the boundaries at $x = 0$ and $x = L$ are periodic in D2Q9 and the pressure gradient from $x = 0$ to $x = L$ is given. Defining the difference between the pressure at $x = 0$ and the pressure at $x = L$ as βL , the periodic boundary condition is imposed by

$$Inlet : \quad f_i(x_0, y, t + \delta t) = f'_i(x_L, y - c_{iy}\delta, t) \frac{\rho_0 + \beta/c_s^2}{\rho_{out}}, \quad i = 1, 5, 8 \quad (5.18)$$

$$Outlet : \quad f_i(x_L, y, t + \delta t) = f'_i(x_0, y - c_{iy}\delta, t) \frac{\rho_0 - \beta/c_s^2}{\rho_{in}}, \quad i = 3, 6, 7 \quad (5.19)$$

where ρ_0 is the initial density of the virtual particle, ρ_{in} is the density of the virtual particle at $x = 0$ and ρ_{out} is the density of the virtual particle at $x = L$.

Curved non-slip boundary

To represent a boundary condition of a static sphere, the method for a 2-dimensional curved boundary by Filippova *et al.* was developed into the method for a 3-dimensional curved boundary[147, 148]. For a simple explanation, the D2Q9 model is employed.

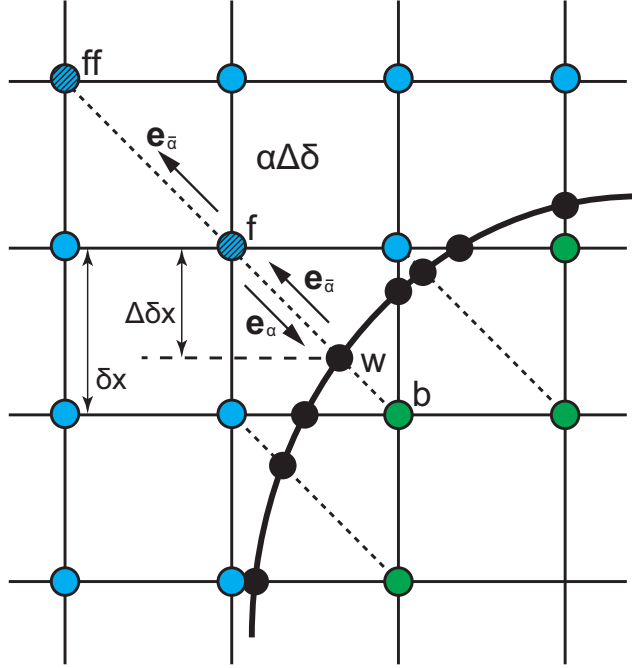


Fig. 5.3 Schematic of lattice points and curved boundary.

The point b in Fig. 5.3 is a lattice point inside a spherical boundary, and the point f is the nearest lattice point to the surface outside the spherical boundary. The coordinates of b and f are defined as $\mathbf{x}_b$ and $\mathbf{x}_f$. The black point w (coordinate: $\mathbf{x}_w$) is on the surface, and the velocity on w is defined as $\mathbf{u}_w$. The distance between f and the surface is expressed as follows:

$$\Delta = \frac{|\mathbf{x}_f - \mathbf{x}_w|}{|\mathbf{x}_f - \mathbf{x}_b|} \quad (5.20)$$

The velocity of the virtual particle from $\mathbf{x}_f$ to $\mathbf{x}_b$ is $\mathbf{c}_i$, and the velocity of the virtual particle from $\mathbf{x}_b$ to $\mathbf{x}_f$ is $\mathbf{c}_{\tilde{i}}$.

To calculate the advection on the lattice points, with the exception of inside the static sphere, $f_{\tilde{i}}(\mathbf{x}_b, t)$ is needed. Using a Taylor expansion and linear interpola-

tion, f_i^* is derived from the known information about the boundary.

$$f_i^*(\mathbf{x}_b, t) = (1 - \chi) f_i(\mathbf{x}_f, t) + \chi f_i^*(\mathbf{x}_b, t) + 2\omega\rho \frac{3}{|\mathbf{c}|^2} \mathbf{c}_i \cdot \mathbf{u}_w \quad (5.21)$$

where $f_i^*(\mathbf{x}_b, t)$ is the virtual equilibrium distribution function, which is given as

$$f_i^*(\mathbf{x}_b, t) = \omega_i \rho(\mathbf{x}_f, t) \left(1 + \frac{\mathbf{c}_i \cdot \mathbf{u}_{bf}}{c_s^2} + \frac{(\mathbf{c}_i \cdot \mathbf{u}_f)^2}{2c_s^4} - \frac{|\mathbf{u}_f|^2}{2c_s^2} \right), \quad i = 0, 1, \dots, 14 \quad (5.22)$$

The definition of χ , $\mathbf{u}_{bf}$ varies. In this case, the method of separation by the value of Δ was employed.

$$\mathbf{u}_{bf} = \frac{(\Delta - 1)}{\Delta} \mathbf{u}_f + \frac{1}{\Delta} \mathbf{u}_w \text{ and } \chi = \frac{(2\Delta - 1)}{\tau} \quad \text{for } \Delta \geq 1/2 \quad (5.23)$$

$$\mathbf{u}_{bf} = \mathbf{u}_{ff} = \mathbf{u}_f(\mathbf{x}_f + \mathbf{c}_i \delta t, t) \text{ and } \chi = \frac{(2\Delta - 1)}{(\tau - 2)} \quad \text{for } \Delta < 1/2 \quad (5.24)$$

This method can be expanded into a 3-dimensional method because the equations are almost equivalent, and only the coefficients need to be changed.

Immersed boundary method in the LBM

In this section, the method for representing a moving particle in the LBM, the Immersed Boundary Method (IBM), is introduced.

When an object, such as a sphere or a circle, moves in a fluid, we calculate the force that the object experiences from the fluid and redefine the boundary of the moved object. Then, the surface of the object needs to be expressed not by using the Euler lattice points of the LBM but by using new Lagrangian points (Fig. 5.4). As the method to calculate the force on the Lagrangian points from the fluid and to move the surface, we employed the IBM in the LBM (ILBM) [149, 150, 151].

Lagrangian points (coordinate: $\mathbf{X}_l$) are placed on the surface of the object, as shown in Fig. 5.4. The velocity distribution function of the virtual particle on each of the points is derived from the velocity distribution functions on the LBM lattice points (coordinate: $\mathbf{r}_{ijh} = (x_{ijh}, y_{ijh}, z_{ijh})$).

$$f_i(\mathbf{X}_l, t) = \sum_{ijh} \left(\prod_{k=1, k \neq i}^{i_{\max}} \frac{X_l - x_{kjh}}{x_{ijh} - x_{kjh}} \right) \left(\prod_{m=1, m \neq j}^{j_{\max}} \frac{Y_l - y_{imh}}{y_{ijh} - y_{imh}} \right) \quad (5.25)$$

$$\times \left(\prod_{n=1, n \neq h}^{h_{\max}} \frac{Z_l - z_{ijn}}{z_{ijh} - z_{ijn}} \right) f_i(\mathbf{r}_{ijh}, t) \quad (5.26)$$

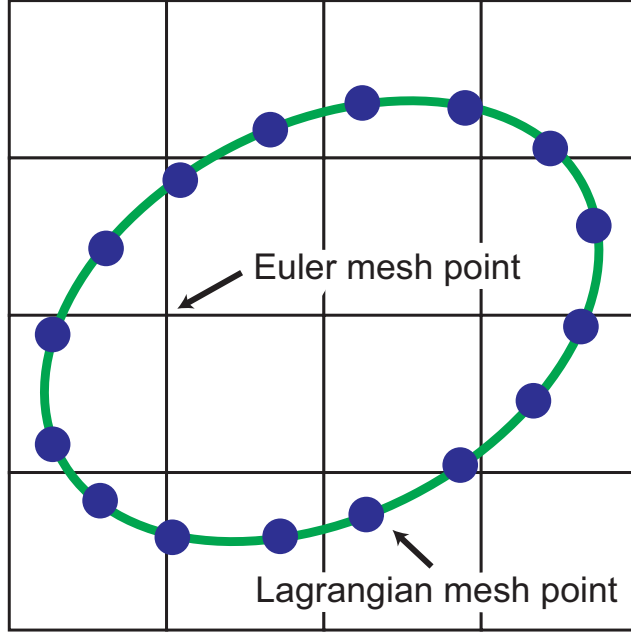


Fig. 5.4 Schematic figure of Lagrangian points (IBM) and Euler lattice points (LBM)

At the points on the surface, the velocities are zero; thus, the time evolution equation of the virtual particle is derived.

$$f_{\tilde{i}}(\mathbf{X}_l, t + \delta t) = f_i(\mathbf{X}_l, t) - 2\omega_i \rho \frac{\mathbf{c}_i \cdot \mathbf{U}_{BC}}{c_s^2} \quad (5.27)$$

Using the velocity of the particle $\mathbf{U}_p$ and the angular velocity of the particle Ω_p , the surface velocity $\mathbf{U}_{BC}$ is expressed as

$$\mathbf{U}_{BC} = \mathbf{U}_p + \Omega_p \times (\mathbf{X}_l - \mathbf{X}_p) \quad (5.28)$$

From $f_i(\mathbf{X}_l, t)$, the force from the surface to the fluid $\mathbf{g}(\mathbf{X}_l, t)$ is calculated as

$$\mathbf{g}(\mathbf{X}_l, t) = \sum_{\tilde{i}} \mathbf{c}_{\tilde{i}} (f_{\tilde{i}}(\mathbf{X}_l, t) - f_i(\mathbf{X}_l, t)) \quad (5.29)$$

Previously, the effect from the surface to the fluid was considered. The force from the surface to the lattice points in the LBM $\mathbf{F}(\mathbf{r}, t)$ is derived from $\mathbf{g}(\mathbf{X}_l, t)$.

$$\mathbf{F}(\mathbf{r}, t) = \sum_l \mathbf{g}(\mathbf{X}_l, t) D_{ijh}(\mathbf{r}_{ijh} - \mathbf{X}_l) \Delta s_l \quad (5.30)$$

where Δs_l is the area occupied by each of the nodes on the surface. The relationship between the lattice point and the node on the surface is defined as the function $D_{ijh}(\mathbf{r}_{ijh} - \mathbf{X}_l)$.

$$D_{ijh}(\mathbf{r}_{ijh} - \mathbf{X}_l) = \frac{1}{\Delta^3} \delta\left(\frac{x_{ijh} - X_l}{\Delta}\right) \delta\left(\frac{y_{ijh} - Y_l}{\Delta}\right) \delta\left(\frac{z_{ijh} - Z_l}{\Delta}\right) \quad (5.31)$$

where $\delta(a)$ is as follows:

$$\delta(a) = \begin{cases} \frac{1}{4} (1 + \cos(\frac{\pi a}{2})) & (|a| \leq 2) \\ 0 & (|a| > 2) \end{cases} \quad (5.32)$$

To integrate the force $\mathbf{F}(\mathbf{r}, t)$ into the time evolution equation of the virtual particle velocity distribution function, the force is transformed as

$$F_b = \left(1 - \frac{1}{2\tau}\right) \omega_i \left(\frac{\mathbf{c}_i - \mathbf{u}}{c_s^2} + \frac{\mathbf{c}_i \cdot \mathbf{u}}{c_s^4} \mathbf{c}_i \right) \cdot \mathbf{F}(\mathbf{r}, t) \quad (5.33)$$

By adding $F_b \delta t$ to the right side in eq. (5.5), the contribution from the surface to the fluid is calculated.

Next, we consider the motion of the surface. The force from the fluid to the surface is expressed using $\mathbf{g}(\mathbf{X}_l, t)$.

$$\mathbf{F}(\mathbf{X}_l, t) = -\mathbf{g}(\mathbf{X}_l, t) \quad (5.34)$$

Integrating the area forces, the entire force $\mathbf{F}_T$ and the entire torque $\mathbf{T}_T$ to the surface are derived.

$$\mathbf{F}_T = \sum_l \mathbf{F}(\mathbf{X}_l, t) \Delta s_l \quad (5.35)$$

$$\mathbf{T}_T = \sum_l (\mathbf{X}_l - \mathbf{X}_p) \times \mathbf{F}(\mathbf{X}_l, t) \Delta s_l \quad (5.36)$$

Using this force and torque, the equation of the surface motion is established.

$$m(\mathbf{U}_T(t + \delta t) - \mathbf{U}_T(t)) = \mathbf{F}_T \quad (5.37)$$

$$I(\Omega_T(t + \delta t) - \Omega_T(t)) = \Omega_T \quad (5.38)$$

In this case, the moving particle is a rigid sphere; thus, the moment of inertia is $I = 2mR^2/5$.

Möbius mapping for a 2-dimensional squirmer

In this section, the analytic method for calculating the squirmer near a flat non-slip boundary in a 2-dimensional xy -plane in Chapter 3 is exhibited according to the expressions proposed by Crowdy (2011) [120].

Complex variable formulation

In a 2-dimensional xy -plane, the stream function $\Psi(x, y)$ that describes an incompressible Stokes flow satisfies the following equation:

$$\left(\frac{\partial \Psi}{\partial y}, -\frac{\partial \Psi}{\partial x} \right) = (u, v) \quad (5.39)$$

$$\nabla^4 \Psi = 0 \quad (5.40)$$

$$\omega = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial y} = -\nabla^2 \Psi \quad (5.41)$$

where u, v are the x - and y -velocities, and ω is vorticity.

The stream function Ψ has a general complex variable presentation.

$$\Psi(x, y) = \text{Im}[\bar{z}f(z) + g(z)] \quad (5.42)$$

where $f(z)$ and $g(z)$ are two analytic functions of the complex variable $z = x + iy$. Using the terms $f(z)$ and $g(z)$, all physical quantities can be expressed.

$$\frac{P}{\mu} - i\omega = 4f'(z) \quad (5.43)$$

$$u + iv = -f(z) + z\overline{f'(z)} + \overline{g'(z)} \quad (5.44)$$

The non-slip boundary along x -axis ($z = \bar{z}$) is expressed as

$$-f(z) + z\overline{f'(z)} + \overline{g'(z)} = 0 \quad (5.45)$$

Considering the infinite cylinder that moves in a viscous fluid, the boundary condition is given using the center z_a , complex speed U and angular velocity Ω ,

$$-f(z) + z\overline{f'(z)} + \overline{g'(z)} = U + i\Omega(z - z_a) \quad (5.46)$$

on the cylinder boundary. These boundary conditions are unaffected if $f(z) \mapsto f(z) + bz + k$ and $g'(z) \mapsto g'(z) + k$ are constants.

Defining the stress tensor σ_{ij} as

$$\sigma_{ij} = -p\delta_{ij} + 2\mu e_{ij} \quad (5.47)$$

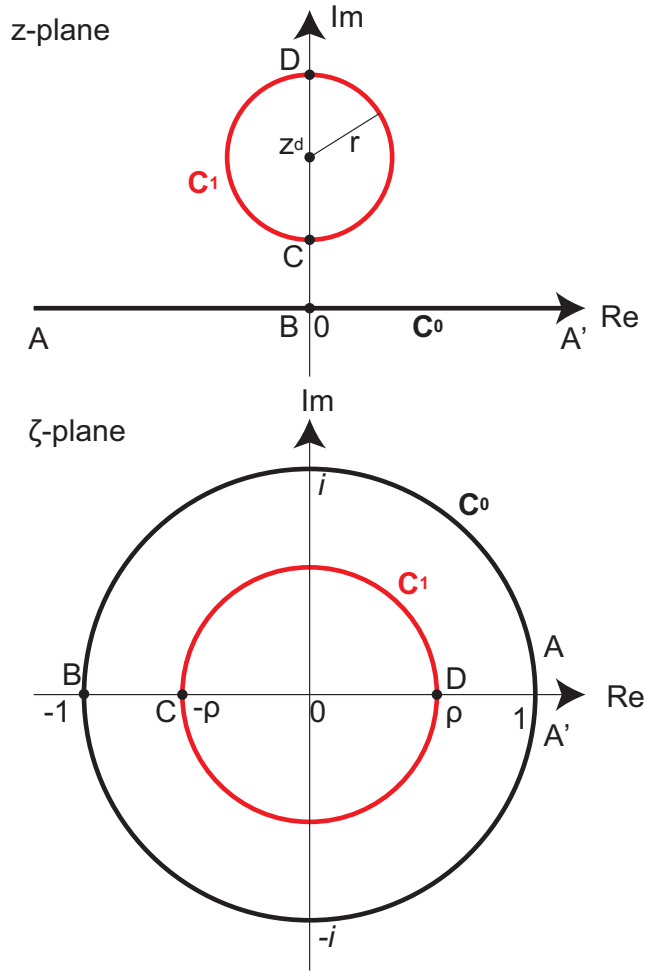


Fig. 5.5 Möbius transformation.

the unit normal vector as $\mathbf{n}$ and the arc length along some curve with a unit normal vector as ds , the complex form of the quantity $\sigma_{ij}n_j ds$ is described as

$$\sigma_{ij}n_j ds = 2\mu i \frac{dH}{ds} ds, \quad H(z) \equiv f(z) + z\overline{f'(z)} + \overline{g'(z)} \quad (5.48)$$

Möbius mapping: Circular and linear boundary conditions

First, we define the following translation for a complex z -plane

$$z(\zeta) = iR \left(\frac{\zeta + 1}{\zeta - 1} \right) \quad (5.49)$$

where R is a real constant. $|\zeta| = 1$ maps to the real axis, $|\zeta| = \rho$ maps to the cylinder and $\zeta = 1$ maps to the point at positive or negative infinity (Fig.5.5). On the z -plane, the radius of the cylinder is r , and the coordinate of the center of the

cylinder is $(0, id)$. Therefore,

$$2ri = z(\rho) - z(-\rho) = \frac{4iR\rho}{\rho^2 - 1} \quad (5.50)$$

which implies

$$r = \frac{2R\rho}{\rho^2 - 1} \quad (5.51)$$

At the point on the cylinder closest to the wall, the following equation is formed:

$$i(d - r) = z(-\rho) = iR \left(\frac{\rho + 1}{\rho - 1} \right) \quad (5.52)$$

Using equation (5.51) (5.52),

$$d = R \left(\frac{\rho^2 + 1}{\rho^2 - 1} \right) \quad (5.53)$$

In the same manner,

$$\rho = \frac{d}{r} - \sqrt{\left(\frac{d}{r}\right)^2 - 1}, \quad \frac{1}{\rho} = \frac{d}{r} + \sqrt{\left(\frac{d}{r}\right)^2 - 1} \quad (5.54)$$

$$z_a = id = iR \left(\frac{\rho^2 + 1}{\rho^2 - 1} \right) \quad (5.55)$$

Cylinder motion near a non-slip boundary

The hydrodynamic force and torque on the cylinder were calculated by Jeffrey and Onishi [152]. Defining the composed analytic functions

$$F(\zeta) \equiv f(z(\zeta)), \quad G(\zeta) \equiv g'(z(\zeta)) \quad (5.56)$$

the boundary condition in eq. (5.45) can be written as

$$-F(\zeta) + z(\zeta) \frac{\overline{F'}(\zeta^{-1})}{\overline{z'}(\zeta^{-1})} + \overline{G}(\zeta^{-1}) = 0 \quad (5.57)$$

where

$$\overline{\zeta} = \zeta^{-1}, \quad \text{on } |\zeta| = 1 \quad (5.58)$$

The conjugate $\overline{h}(z)$ of an analytic function $h(z)$ is defined by $\overline{h}(z) = \overline{h(\overline{z})}$.

The boundary condition in eq. (5.46) can be written as

$$-F(\zeta) + z(\zeta) \frac{\overline{F'}(\rho^2 \zeta^{-1})}{\overline{z'}(\rho^2 \zeta^{-1})} + \overline{G}(\rho^2 \zeta^{-1}) = U + i\Omega(z(\zeta) - z_a) \quad (5.59)$$

where

$$\bar{\zeta} = \rho^2 \zeta^{-1}, \quad \text{on } |\zeta| = \rho \quad (5.60)$$

Integrating $\zeta \mapsto \rho^2 \zeta$ into eq. (5.59),

$$-F(\rho^2 \zeta) + z(\rho^2 \zeta) \frac{\overline{F'}(\zeta^{-1})}{\overline{z'}(\zeta^{-1})} + \overline{G}(\zeta^{-1}) = U + i\Omega(z(\rho^2 \zeta) - z_a) \quad (5.61)$$

Using eq. (5.57) and (5.61), the functional relation for only $F(\zeta)$ is given as

$$F(\rho^2 \zeta) - F(\zeta) - (z(\rho^2 \zeta) - z(\zeta)) \frac{\overline{F'}(\zeta^{-1})}{\overline{z'}(\zeta^{-1})} = -U - i\Omega(z(\rho^2 \zeta) - z_a) \quad (5.62)$$

Here, the decomposition of $F(\zeta)$ is introduced,

$$F(\zeta) = F_d \log \zeta + \hat{F}(\zeta) \quad (5.63)$$

where F_d is a constant. Integrating this expression into eq. (5.62),

$$F_d \log \rho^2 + \hat{F}(\rho^2 \zeta) - \hat{F}(\zeta) - \left(\frac{z(\rho^2 \zeta) - z(\zeta)}{\overline{z'}(\zeta^{-1})} \right) (\overline{F_d} \zeta + \overline{\hat{F}'}(\zeta^{-1})) \quad (5.64)$$

$$= -U - i\Omega(z(\rho^2 \zeta) - z_a) \quad (5.65)$$

From eq. (5.49),

$$\frac{z(\rho^2 \zeta) - z(\zeta)}{\overline{z'}(\zeta^{-1})} = (1 - \rho^2) \frac{\zeta - 1}{\zeta(\rho^2 \zeta - 1)} \quad (5.66)$$

Thus, integrating this expression into eq. (5.65), we obtain

$$\hat{F}(\rho^2 \zeta) - \hat{F}(\zeta) - (1 - \rho^2) \frac{\zeta - 1}{\zeta(\rho^2 \zeta - 1)} (\overline{F_d} \zeta + \overline{\hat{F}'}(\zeta^{-1})) \quad (5.67)$$

$$= -U - F_d \log \rho^2 - i\Omega(z(\rho^2 \zeta) - z_a) \quad (5.68)$$

After inspection of the singularities in eq. (5.68), finding the rational function as a solution of $\hat{F}(\zeta)$ is possible.

$$\hat{F}(\zeta) = \frac{A}{\zeta - 1} + \frac{B}{\zeta} + C\zeta \quad (5.69)$$

By integrating eq. (5.69) into these equations, we can obtain A, B, C and F_d .

As a result, $F(\zeta)$ and $G(\zeta)$ are expressed as

$$F(\zeta) = F_d \log \zeta + \frac{\rho^2 \overline{C}}{\zeta} + C\zeta \quad (5.70)$$

$$G(\zeta) = -\overline{F_d} \log \zeta + \rho^2 C\zeta + \frac{\overline{C}}{\zeta} + \left(\frac{\zeta^2 - 1}{2} \right) \left(\frac{F_d}{\zeta} - \frac{\rho^2 \overline{C}}{\zeta^2} + C \right) \quad (5.71)$$

where

$$F_d = -\frac{U(1 - \rho^2 + (1 + \rho^2) \log \rho^2) + \bar{U}(1 - \rho^2)}{[2(1 - \rho^2) + (1 + \rho^2) \log \rho^2] \log \rho^2} \quad (5.72)$$

$$C = \frac{\bar{F}_d}{1 - \rho^2} - \frac{\rho^2 \log \rho^2 F_d}{(1 - \rho^2)^2} + \frac{(\Omega R - U + i\Omega z_a) \rho^2}{(1 - \rho^2)^2} \quad (5.73)$$

Rotating torque of the cylinder

If $U = 0, \Omega \neq 0$ and the cylinder is force free, the torque is given as

$$T = 2\mu \operatorname{Re} \left[\oint_{|z-z_a|=r} z g''(z) dz \right] \quad (5.74)$$

Transplanting the integral to the ζ -plane,

$$T = 2\mu \operatorname{Re} \left[\oint_{|\zeta|=\rho} z(\zeta) \frac{dG(\zeta)}{d\zeta} d\zeta \right] \quad (5.75)$$

Therefore,

$$T = -4\pi\mu\Omega r^2 \left(\frac{1 + \rho^2}{1 - \rho^2} \right) = -\frac{4\pi\mu\Omega r^2 d}{(d^2 - r^2)^{1/2}} \quad (5.76)$$

Parallel force to the cylinder

If $\Omega = 0, U = \bar{U}$, the cylinder moves parallel to the wall.

$$F_d = -\frac{U}{\log \rho^2} \quad (5.77)$$

The force on the cylinder is

$$[2\mu i H]_{|\zeta|=\rho} = [2\mu i (2F_d \log \zeta)]_{|\zeta|=\rho} = -8\pi\mu F_d \quad (5.78)$$

Thus,

$$F_x + iF_y = \frac{8\pi\mu U}{\log \rho^2} = -\frac{4\pi\mu U}{\log(1/\rho)} = -\frac{4\pi\mu U}{\log(d/r + \sqrt{(d/r)^2 - 1})} \quad (5.79)$$

Perpendicular force to the cylinder

If $\Omega = 0, U = -\bar{U}$, the cylinder moves perpendicular to the wall.

$$F_d = -\frac{U}{2(1 - \rho^2)(1 + \rho^2) + \log \rho^2} \quad (5.80)$$

Thus,

$$\begin{aligned} F_x + iF_y &= -8\pi\mu F_d = \frac{4\pi\mu U}{(1 - \rho^2)(1 + \rho^2) + \log \rho} \\ &= -\frac{4\pi\mu U}{\log((d+a)/r) - (a/d)} \end{aligned} \quad (5.81)$$

Surface velocity of a neutral swimmer

We calculated a neutral swimmer using hydrodynamic theory. We employed a complex variable formulation. First, we defined the surface velocity of a spherical neutral swimmer.

$$U_s = 2V \sin(\phi - \theta) \frac{dz}{ds} \quad (5.82)$$

In the case of a treadmilling swimmer, which has quadrupole velocity potential,

$$U_s = 2V \sin 2(\phi - \theta) \frac{dz}{ds} \quad (5.83)$$

where z is the complex coordinate, and s is the surface.

$$z = z_d + re^{i\phi}, \quad \frac{dz}{ds} = \frac{i(z - z_d)}{r} \quad (5.84)$$

which implies

$$U_s = V \left\{ \left(\frac{z - z_d}{r} \right)^2 e^{-i\theta} - e^{i\theta} \right\} \quad (5.85)$$

Here, we applied confocal mapping. It is simply Möbius mapping,

$$z(\zeta) = iR \left(\frac{\zeta + 1}{\zeta - 1} \right) \quad (5.86)$$

In the expression of Möbius mapping,

$$U_s = V \left\{ \frac{-1}{\rho^2} \left(\frac{\zeta - \rho^2}{\zeta - 1} \right) e^{-i\theta} - e^{i\theta} \right\} \quad (5.87)$$

$$\tilde{U}_s = V \left\{ \frac{-1}{\rho^2} \left(\frac{\tilde{\zeta} - \rho^2}{\tilde{\zeta} - 1} \right) e^{i\theta} - e^{-i\theta} \right\} \quad (5.88)$$

on $|\zeta| = \rho$, which means that $\tilde{\zeta} = \rho^2 \zeta^{-1}$,

$$\tilde{U}_s = - \left\{ c \rho^2 \left(\frac{\zeta - 1}{\zeta - \rho^2} \right)^2 + \tilde{c} \right\} \quad (5.89)$$

where $c \equiv V e^{i\theta}$.

Reciprocal 2-dimensional neutral swimmer

$$\oint_{|z-z_a|=r} u_i \sigma'_{ij} n_j ds = \oint_{|z-z_a|=r} u'_i \sigma_{ij} n_j ds \quad (5.90)$$

$$u_i = U_i + \epsilon_{imn} \Omega_m (x_n - x_{dn}) \quad (5.91)$$

$$\oint_{|z-z_a|=r} (U_i + \epsilon_{imn} \Omega_m (x_n - x_{dn})) \sigma'_{ij} n_j ds \quad (5.92)$$

$$= \oint_{|z-z_a|=r} (U'_i + \epsilon_{imn} \Omega'_m (x_n - x_{dn}) + U_{si})_i \sigma_{ij} n_j ds \quad (5.93)$$

$$U_i \oint_{|z-z_a|=r} \sigma'_{ij} n_j ds + \Omega_m \oint_{|z-z_a|=r} \epsilon_{mni} (x_n - x_{dn}) \sigma'_{ij} n_j ds = \mathbf{F}' U + \mathbf{T}' \Omega \quad (5.94)$$

where $\mathbf{F}'$ and $\mathbf{T}'$ are the force and torque, respectively, on the swimmer.

Here, the swimmer satisfies the force free condition, which is expressed as $\mathbf{F}' = \mathbf{T}' = \mathbf{0}$. Therefore,

$$0 = \oint_{|z-z_a|=r} (U'_i + \epsilon_{imn} \Omega'_m (x_n - x_{dn}) + U_{si})_i \sigma_{ij} n_j ds \quad (5.95)$$

$$\mathbf{F} U' + \mathbf{T} \Omega' = - \oint_{|z-z_a|=r} U_{si} \sigma_{ij} n_j ds \quad (5.96)$$

Evolution equations

We calculated the evolution equations of a neutral swimmer near a wall from the Jeffrey and Onishi solution and reciprocal theorem.

If the stream function of Stokes flow can be expressed as $\Phi(x, y) = \text{Im}[\tilde{z}f(z) + g(z)]$,

$$u + iv = -f(z) + zf'(\tilde{z}) + g'(\tilde{z}) \quad (5.97)$$

Here, the stress tensor $\sigma_{ij} = -p\delta_{ij} + 2\mu e_{ij}$ is defined,

$$\sigma_{ij} n_j = 2\mu i \frac{dH}{ds} ds, \quad H(z) \equiv f(z) + zf'(\tilde{z}) + g'(\tilde{z}) \quad (5.98)$$

Angular Velocity

When $U = 0$, $\Omega = 1$,

$$\oint_{|\zeta|=\rho} \tilde{U}_s \frac{dH}{d\zeta} d\zeta = \frac{16\pi i R c \rho^4}{(1 - \rho^2)^2} \quad (5.99)$$

Thus, eq. (5.96) is

$$\begin{aligned} T\Omega' &= - \oint_{|z-z_d|=r} U_{si} \sigma_{ij} n_j ds \\ &= -\text{Re} \left[2\mu i \oint_{|\zeta|=\rho} \tilde{U}_s \frac{dH}{d\zeta} d\zeta \right] \\ &= \frac{16\pi\mu R \rho^4 (c + \tilde{c})}{(1 - \rho^2)^2} \end{aligned} \quad (5.100)$$

Using eq. (5.76), we obtain the expression of Ω' .

$$\Omega' = -\frac{2\rho^3(c + \tilde{c})}{r(1 + \rho^2)} \quad (5.101)$$

Velocity u' parallel to wall

When $U = 1$, $\Omega = 0$,

$$\oint_{|\zeta|=\rho} \tilde{U}_s \frac{dH}{d\zeta} d\zeta = -4\pi i F_d (2\rho^4 c - 2\rho^2 c + \tilde{c}) \quad (5.102)$$

Thus, eq. (5.96) is

$$F_x u' = (c + \tilde{c}) \frac{2\pi\mu}{\log \rho^2} (2\rho^4 - 2\rho^2 + 1) \quad (5.103)$$

Using eq. (5.79), we obtain the expression of u' .

$$u' = \frac{(c + \tilde{c})}{4} (2\rho^4 - 2\rho^2 + 1) \quad (5.104)$$

Velocity ν' perpendicular to wall

When $U = i$, $\Omega = 0$,

$$\oint_{|\zeta|=\rho} \tilde{U}_s \frac{dH}{d\zeta} d\zeta = -4\pi i F_d \left[2\rho^2 c \frac{1 + \rho^4}{1 + \rho^2} + \tilde{c} \right] \quad (5.105)$$

Thus, eq. (5.96) is

$$-F_y \nu' = \frac{2\pi\mu i (c - \tilde{c})}{(1 - \rho^2) + (1 + \rho^2) \log \rho} (2\rho^6 + \rho^2 - 1) \quad (5.106)$$

Using eq. (5.81), we obtain the expression of ν' .

$$\nu' = \frac{-i(c - \tilde{c})}{2(1 + \rho^2)} (2\rho^6 + \rho^2 - 1) \quad (5.107)$$

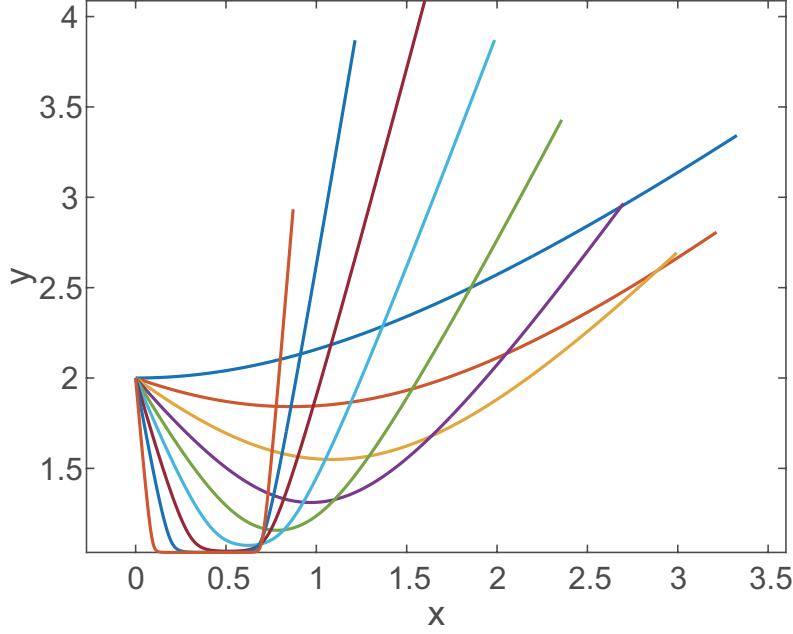


Fig. 5.6 Trajectories of a neutral swimmer near a wall on the XY plane.

Trajectories approaching a non-slip boundary

Summarizing these results, the equations of the swimmer motion are expressed as follows:

$$\frac{dx}{dt} = \frac{(c + \tilde{c})}{4}(2\rho^4 - 2\rho^2 + 1) \quad (5.108)$$

$$\frac{dy}{dt} = \frac{-i(c - \tilde{c})}{2(1 + \rho^2)}(2\rho^6 + \rho^2 - 1) \quad (5.109)$$

$$\frac{d\theta}{dt} = -\frac{2\rho^3(c + \tilde{c})}{r(1 + \rho^2)} \quad (5.110)$$

Solving these equations by the Euler method, the trajectories of a neutral swimmer near a non-slip boundary are obtained (5.6). The colors represent the initial incident angles of the swimmer's direction. As a result, the neutral swimmer must be repelled regardless of the initial angles.

Boundary Element Method

In this section, the Boundary Element Method (BEM) used in Chapters 3 and 4 is exhibited.

Mesh

The method for calculating the coordinates of the mesh points (nodes) on a swimmer is exhibited. The surface of a numerical swimmer in the BEM needs to be discretized into a polygon.

First, calculate the body surface. The method obeys the following process:

1. The coordinates of mesh nodes are defined as 12 vertexes of a regular icosahedron.
2. The middle points of the elements of the regular icosahedron project to the circumscribed sphere.
3. A polygon is defined regarding the first 12 vertexes and the projected points as new nodes.
4. Repeating steps 2 and 3, the detailed polygon, which resembles a sphere, is obtained.

The accuracy of the mesh is dependent on the number of nodes after dividing the polygon. When the shape of the swimmer is ellipsoidal, the nodes are linearly projected from the nodes of a spherical polygon.

Next, calculate the cilia surface and the stress surface. Both nodes of the cilia surface and the stress surface are placed along the normal vector from the nodes of the body surface. The length between the node of the cilia surface and the node of the body surface is fixed at $1/10$ th the minor length of the body, and the length between the node of the stress surface and the node of the body surface is fixed at $2/30$ th the minor length of the body.

In this thesis, the number of nodes is 162 when the swimmer is far from a boundary, and the number of nodes is 2562 when the swimmer touches the boundary.

Governing equation of a swimmer

We establish a governing equation of a swimmer who is swimming in incompressible fluid at a low-Reynolds number according to the method proposed by Ishikawa *et al.*[126].

Boundary integral equation

This system satisfies the continuity equation of an incompressible fluid (eq. (1.13)) and Stokes equation (eq. (1.16)); thus, the Oseen tensor (eq. (1.31)) can be utilized.

The fluid velocity of an arbitrary boundary in the system is analytically expressed by the Oseen tensor[124].

$$\begin{aligned} \mathbf{u}(\mathbf{x}) = & \frac{2}{1+\lambda} \mathbf{u}_\infty(\mathbf{x}) - \frac{1}{4\pi\mu(1+\lambda)} \int_{S_b} \mathbf{q}(\mathbf{y}) \cdot \mathbf{J}(\mathbf{x}, \mathbf{y}) dS(\mathbf{y}) \\ & + \frac{1-\lambda}{4\pi\mu(1+\lambda)} \int_{S_b} \mathbf{u}(\mathbf{y}) \cdot \mathbf{K}(\mathbf{x}, \mathbf{y}) \cdot \mathbf{n}(\mathbf{y}) dS(\mathbf{y}) \end{aligned} \quad (5.111)$$

where $\mathbf{u}_\infty$ is the background flow velocity, $\mathbf{q}(\mathbf{x})$ is the force applied to the boundary surface, λ is the ratio of the inside and outside viscosities, μ is the outside viscosity and S_b represents the surface of the boundary. $\mathbf{J}(\mathbf{x}, \mathbf{y})$ and $\mathbf{K}(\mathbf{x}, \mathbf{y})$ are Green functions defined as

$$\mathbf{J}(\mathbf{x}, \mathbf{y}) = \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3}, \quad \mathbf{K}(\mathbf{x}, \mathbf{y}) = -6 \frac{r_i r_j r_k}{r^5} \quad (5.112)$$

where $\mathbf{r} = \mathbf{y} - \mathbf{x}$ and $r = |\mathbf{r}|$.

In this case, the viscosity inside a swimmer is assumed to be equal to the outside viscosity, which is expressed as $\lambda = 1$. Therefore, the third term in eq. (5.111) vanishes.

$$\mathbf{u}(\mathbf{x}) = \mathbf{u}_\infty(\mathbf{x}) - \frac{1}{8\pi\mu} \int_{S_b} \mathbf{q}(\mathbf{y}) \cdot \mathbf{J}(\mathbf{x}, \mathbf{y}) dS(\mathbf{y}) \quad (5.113)$$

This equation is generally employed for the numerical calculation of a squirmer model.

In our study, the thrust force per unit area $\mathbf{F}$ is located on the second surface at a distance from the boundary surface; thus, the following term needs to be added to the right side of eq. (5.113).

$$\frac{1}{8\pi\mu} \int_{S_c} \mathbf{F}(\mathbf{y}) \cdot \mathbf{J}(\mathbf{x}, \mathbf{y}) dS'(\mathbf{y}) \quad (5.114)$$

Boundary condition on swimmer surface

In this system, there are two types of boundary conditions.

The first boundary condition pertains to the velocity on the surface. Defining the velocity and the angular velocity of a swimmer as $\mathbf{U}$ and $\mathbf{\Omega}$, respectively, the flow velocity on the surface is expressed as

$$\mathbf{u}(\mathbf{x}) = \mathbf{U} + \mathbf{\Omega} \wedge \mathbf{r} + \mathbf{u}_s \quad (5.115)$$

where $\mathbf{u}_s$ is the surface velocity of the swimmer. If the swimmer is a squirmer, the surface velocity obeys eq. (1.43) and (1.44). In our study, $\mathbf{u}_s = \mathbf{0}$.

$$\mathbf{u}(\mathbf{x}) = \mathbf{U} + \mathbf{\Omega} \wedge \mathbf{r} \quad (5.116)$$

The second boundary condition pertains to the force free condition. If a swimmer is moving without any external force, the external force $\mathbf{F}$ and torque $\mathbf{T}$ experienced by the swimmer must be zero, which is referred to as the force free condition. Using $\mathbf{q}$, the force and torque are also expressed as follows:

$$\mathbf{F} = \int \mathbf{q}(\mathbf{y}) dS_b(\mathbf{y}) \quad (5.117)$$

$$\mathbf{T} = \int \mathbf{q}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_b(\mathbf{y}) \quad (5.118)$$

In our study, the reaction force and torque from the thrust force are added to the right side of eq. (5.118).

$$\mathbf{F} = \int \mathbf{q}(\mathbf{y}) dS_b(\mathbf{y}) - \int \mathbf{F}(\mathbf{y}) dS_c(\mathbf{y}) \quad (5.119)$$

$$\mathbf{T} = \int \mathbf{q}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_b(\mathbf{y}) - \int \mathbf{F}(\mathbf{y}) \wedge (\mathbf{y} - \mathbf{X}_0) dS_c(\mathbf{y}) \quad (5.120)$$

This relationship can be regarded as a force free condition $\mathbf{F} = \mathbf{0}, \mathbf{T} = \mathbf{0}$.

Discretization of the dominant equation

Using the matrix, eqs. (5.113), (5.115) and (5.118) can be expressed as

$$[\mathbf{u} - \mathbf{u}_\infty] = [\mathbf{A}] [\mathbf{q}] \quad (5.121)$$

$$[\mathbf{u}] = [\mathbf{B}] [\mathbf{U}, \mathbf{\Omega}] + [\mathbf{u}_s] \quad (5.122)$$

$$[\mathbf{F}, \mathbf{T}] = [\mathbf{C}] [\mathbf{q}] \quad (5.123)$$

Combining these three equations,

$$\begin{bmatrix} \mathbf{u}_s - \mathbf{u}_\infty \\ \mathbf{F}, \mathbf{T} \end{bmatrix} = \begin{bmatrix} \mathbf{A} & -\mathbf{B} \\ \mathbf{C} & \mathbf{0} \end{bmatrix} \begin{bmatrix} \mathbf{q} \\ \mathbf{U}, \mathbf{\Omega} \end{bmatrix} \quad (5.124)$$

Solving this matrix equation, we obtain $\mathbf{q}$, $\mathbf{U}$ and $\mathbf{\Omega}$ from the known parameters $\mathbf{u}_s$, $\mathbf{u}_\infty$, $\mathbf{F}$ and $\mathbf{T}$. In this study, LU factorization is employed as the method to solve a matrix equation.

Gaussian quadrature

As a method for numerically calculating surface integrals, we applied the method referred to as the Gaussian quadrature [153, 154]. In the Gaussian quadrature,

an integral is approximated to a $2N - 1$ -order polynomial by N Gaussian points. First, we discretize the integral of the function $f(x)$ by the weight ω_i .

$$\int_1^1 f(x)dx \approx \sum_{i=0}^N \omega_i f(x_i), \quad (i = 1, 2, \dots, N) \quad (5.125)$$

The Lagrange polynomial $P(x)$ is described as

$$P(x) = \sum_{i=1}^N \frac{f(x_i)}{\phi'(x_i)(x - x_i)} \quad (5.126)$$

where

$$\phi(x) = (x - x_1)(x - x_2) \cdots (x - x_N) = \prod_{i=1}^N (x - x_i) \quad (5.127)$$

From this equation,

$$\omega_i = \int_{-1}^1 \frac{\phi(x)}{\phi'(x)(x - x_i)} dx \quad (5.128)$$

An arbitrary point x_i satisfies

$$f(x_i) - P(x_i) = 0 \quad (5.129)$$

Thus, $f(x) - P(x)$ can be expressed as

$$f(x) - P(x) = q(x)\phi(x) \quad (5.130)$$

where

$$q(x) = a_{n-1}x^{n-1} + a_{n-2}x^{n-2} + \cdots + a_0 \quad (5.131)$$

Integrating eq. (5.130),

$$\begin{aligned} \int_{-1}^1 f(x)dx &= \int_{-1}^1 P(x)dx + \int_{-1}^1 q(x)\phi(x)dx \\ &= \int_{-1}^1 P(x)dx + \sum_{i=0}^{n-1} a_i \int_{-1}^1 x^i \phi(x)dx \end{aligned} \quad (5.132)$$

To obtain high accuracy, the Gaussian points are chosen to satisfy the following equation:

$$\int_{-1}^1 x^i \phi(x)dx = 0 \quad (5.133)$$

Here, the solution of eq. (5.133) is an N th Legendre polynomial.

In this thesis, the surface integral is discretized as follows:

$$\int_S \mathbf{q}(\mathbf{y}) \mathbf{J}(\mathbf{x}, \mathbf{y}) dS \approx \sum_{NGP} \omega_i \mathbf{q}_G \left(\frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right) \Delta S \quad (5.134)$$

where $\mathbf{r} = \mathbf{y}_G - \mathbf{x}$ and $r = |\mathbf{r}|$.

Position update

The velocity and the angular velocity of the swimmer are derived at each time step. Using this velocity and angular velocity, the position and the rotation of the swimmer are updated. We employ the 4th Adams-Bashforth method to calculate the time evolution.

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \Delta t \left(\frac{55\mathbf{u}_n - 59\mathbf{u}_{n-1} + 37\mathbf{u}_{n-2} - 9\mathbf{u}_{n-3}}{24} \right) \quad (5.135)$$

$$\mathbf{\Theta}_{n+1} = \mathbf{\Theta}_n + \Delta t \left(\frac{55\mathbf{\Omega}_n - 59\mathbf{\Omega}_{n-1} + 37\mathbf{\Omega}_{n-2} - 9\mathbf{\Omega}_{n-3}}{24} \right) \quad (5.136)$$

Rotation using quaternions

To calculate the 3-dimensional direction of the swimmer from Euler angles, quaternions are usually employed. Quaternions are defined by one real number t and three imaginary numbers x, y, z .

$$Q = (t; x, y, z) = (t; \mathbf{v}) \quad (5.137)$$

where $\mathbf{v} = xi + yj + zk$. i, j, k obey

$$ii = jj = kk = -1, \quad ij = -ji = k, \quad jk = -kj = i, \quad ki = -ik = j \quad (5.138)$$

Multiplication of quaternions is expressed as

$$AB = (ab - \mathbf{u} \cdot \mathbf{v}; a\mathbf{v} + b\mathbf{u} + \mathbf{u} \times \mathbf{v}) \quad (5.139)$$

where $A = (a; \mathbf{u})$ and $B = (b; \mathbf{v})$.

Here, consider the rotation around the axis vector (α, β, γ) , $(\alpha^2 + \beta^2 + \gamma^2 = 1)$. To rotate the angle of the vector (x, y, z) by θ around the axis vector, three quaternions are needed.

$$P = (0; x, y, z) \quad (5.140)$$

$$Q = \left(\cos \frac{\theta}{2}; \alpha \sin \frac{\theta}{2}, \beta \sin \frac{\theta}{2}, \gamma \sin \frac{\theta}{2} \right)$$

$$R = \left(\cos \frac{\theta}{2}; -\alpha \sin \frac{\theta}{2}, -\beta \sin \frac{\theta}{2}, -\gamma \sin \frac{\theta}{2} \right)$$

Using P, Q, R , the rotated vector (x', y', z') is calculated as follows:

$$RPQ = (0; x', y', z') \quad (5.141)$$

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