

BACTERIUM SWIMMING MOTION CLOSE TO A WALL

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Summary The mechanism of some characteristics about swimming motion of the marine bacterium, *Vibrio alginolyticus*, close to a boundary was investigated. The motion of the microorganism that possesses single polar-flagellum propelling the cell body was dealt with as an outer flow problem from a bio-fluid dynamics viewpoint. Numerical analyses based on the boundary element method in addition to the resistive force theory were applied to elucidate the effects of the boundary on the swimming motion.

The boundary reduces the swimming speed when a bacterium moves along it. Forward swimming is stable in pitching motion and backward swimming is unstable. The swimming speed varies depending on the attitude of the bacterium. When the flagellum is closer to the boundary, the trajectory of the bacterium draws a curve. These results qualitatively agree with the observed motions and have potential to explain the mechanism of the phenomena.

INTRODUCTION

Bacteria can swim by use of rotating flagella, each of which is driven by a rotary motor embedded in the cell bodies. The flagellum is like a helix and its rotation produces a force that pushes the cell body forward as a screw propels a ship. The bacteria can also change the swimming direction or swim backward by rotating the flagella in the opposite direction. Monotrichous bacteria each of which possesses only one flagellum swim forward and backward by changing the direction of motor rotation. The swimming direction changes slightly in every turn because of thermal fluctuation or bending of the flagellum.

Recently, Magariyama *et al.* found on the swimming of cells of *Vibrio alginolyticus*, YM4, that the forward swimming speed is slower than the backward swimming speed [1]. Ramia *et al.* calculated the motion of an imaginary microorganism, and the trajectory near a wall became a circular curve and the speed of the microorganism close to the wall was higher than the speed at a distance from the wall [2]. Berg & Turner observed that smooth swimming mutant of *E. coli* swam along the surface of a chamber in circles [3].

According to our recent observation, these interesting phenomena occur only when a bacterium swims in the vicinity of a boundary. When the swimming motion of bacteria is observed through a microscope, the suspension containing bacteria is usually sealed between a glass-cover-slip and a glass-slide. Some of the bacteria swim so close to either glasses that their swimming speeds and tracks are noticeably changed by the presence of those of rigid boundaries. The tracks tend to draw curved lines rather than straight lines as observed when a bacterium swims at a long distance from a boundary.

In this study, the effect of the boundaries on the swimming motion of bacteria was investigated. The resistive force theory and the boundary element method were applied to elucidate the difference between forward and backward motions of bacteria swimming near a wall. We found that the distance from a wall and the attitude of the bacterium are influential in the swimming motion.

SUMMARY OF OBSERVATION

In this paper, mainly analytical results will be presented. However, as background information to them, some of observational results related to the analyses are summarized below.

The suspension including the bacteria, YM4, was sealed in a chamber of almost 150 μ m depth. When the microscope was focused near a wall, bacteria swimming in the range of about 10 μ m from the wall were observed. And when the microscope was focused in the middle of the chamber, observed bacteria swam at least 50 μ m apart from the walls. Unfortunately, by the phase-contrast microscopy we could not see the flagella, which means we could not judge whether the bacterium swam forward or it swam backward. Nevertheless, we treated two speeds as a set, one of which was just before a turn and the other was after the turn, and compared the speeds in several dozens of sets. The observation revealed the following:

(a) When bacteria swim in the middle of the chamber, there is no significant difference in the speed before a turn and the speed after the turn. On the other hand, when bacteria swim near a boundary, the difference is obvious.

(b) The tracks are also different. When a bacterium swims at a long distance from a boundary, it moves straight, switching the direction back and forth. On the contrary, near a wall, the track becomes a combination of curves whose radii of curvature are in the order of 10mm and straight lines. The direction of the curve is counter-clockwise when it is seen from above.

These facts reveal that the swimming motion of bacteria is considerably influenced by the presence of boundaries.

RESULTS AND DISCUSSIONS

Analysis

The present analysis by use of the boundary element method and the resistive force theory is based on the fact that the size of a bacterium is very small. The typical size of bacteria is approximately $1\mu\text{m}$ and their swimming speed is $10\text{--}100\mu\text{m/s}$. Because of the smallness, the viscous force surpasses the inertial force, that is, the Reynolds number is very small. Therefore, at any instant, the net force and the net torque exerted on a bacterium by the surrounding fluid flow should be zero. We can calculate the swimming speed from this condition.

Calculations were carried out for two bacterium models, the size of one was determined according to an averaged cell body size and an averaged flagellum size observed for dozens of cells of YM4 [4], [5] (average cell). The other had a small cell body and had the same flagellum (small cell).

Swimming motion parallel to the wall

According to our calculations by use of the boundary element method, the swimming speed of the average cell decreases when the cell swims closer to the wall. On the other hand, the speed of the small cell increases. Ramia *et al.* [2] carried out boundary element analyses on the swimming motion of an imaginary microorganism similar to a bacterium and reported that when the microorganism of bacterium type swims close to a wall, the swimming speed increases by about 10%. Their microorganism has a relatively small cell body and corresponds to the small cell in the present study.

We investigated the reason of the difference between the averaged cell and the small cell by use of the resistive force theory dividing the wall effects into terms; translational and rotational drag increases of the cell body, translational and rotational drag increases of the flagellum, and propulsive force increase of the flagellum.

As for the average cell, the drag of the cell increases more than the propulsive force when the cell swims near a wall and consequently the speed decreases. As for the small cell, on the contrary, the additional resistance of the flagellum causes additional propulsive force and drag of the flagellum. The former exceeds the latter in the case of the small cell.

The small cell is an imaginary one introduced to indicate the difference from the average cell. According to the results on the average cell of YM4, the cells move slower when they swim in the presence of a boundary than they move in a free space. This has a connection with a reason of the difference in swimming speeds between forward and backward motions that has been confirmed by observations.

Swimming motion at a pitch angle to the wall

Next, we dealt with the attitude of a bacterium relative to a wall. If the bacterium swims towards or apart from the wall, the swimming speed may change because the degree of the interaction varies.

Our numerical results were qualitatively consistent with the observed data. According to the results, we have been able to build up an image explaining the swimming speed difference and the circular track that have been observed:

- (a) A bacterium swims slower when it swims closely along a wall than when it swims in free space.
- (b) When the bacterium swims forward, it tends to move stably parallel to the boundary keeping a certain distance from the wall.
- (c) When the bacterium swims backward, its motion is unstable. It continuously leaves from the wall or gets close to the wall.
- (d) The backward swimming bacterium swims faster than the forward swimming bacterium because the bacterium swims at a distance from the wall or the flagellum is close to the wall.
- (e) Since the pitch angle of the bacterium swimming backward is greater than that of the bacterium swimming forward, the backward swimming bacterium interacts more with the boundary. Consequently, the yaw direction change of the former is greater than that of the latter. Therefore, the track of the swimming backward bacterium is observed as to be bent in a counter-clockwise manner rather than to be straight.

CONCLUSIONS

The cause of the swimming speed difference between forward and backward motion and the cause of the circular trajectory of bacteria was investigated. Since the phenomena were observed in the presence of boundaries, analyses based on the boundary element method and on the resistive force theory were carried out taking a plane wall into account. Numerical results being qualitatively consistent with the observation were obtained. These results showed that considering the distance from the wall and the attitude of the bacterium was crucial to explain the phenomena.

References

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