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Swimming Behavior of Selected Species of *Archaea*

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The swimming behavior of *Bacteria* has been studied extensively, at least for some species like *Escherichia coli*. In contrast, almost no data have been published for *Archaea* on this topic. In a systematic study we asked how the archaeal model organisms *Halobacterium salinarum*, *Methanococcus voltae*, *Methanococcus maripaludis*, *Methanocaldococcus jannaschii*, *Methanocaldococcus villosus*, *Pyrococcus furiosus*, and *Sulfolobus acidocaldarius* swim and which swimming behavior they exhibit. The two *Euryarchaeota M. jannaschii* and *M. villosus* were found to be, by far, the fastest organisms reported up to now, if speed is measured in bodies per second (bps). Their swimming speeds, at close to 400 and 500 bps, are much higher than the speed of the bacterium *E. coli* or of a very fast animal, like the cheetah, each with a speed of ca. 20 bps. In addition, we observed that two different swimming modes are used by some *Archaea*. They either swim very rapidly, in a more or less straight line, or they exhibit a slower kind of zigzag swimming behavior if cells are in close proximity to the surface of the glass capillary used for observation. We argue that such a "relocate-and-seek" behavior enables the organisms to stay in their natural habitat.

The ability to move is of pivotal importance for most organisms; this is especially true for microorganisms which experience many, often dramatic, changes in their natural habitats. A translocation of just 1 cm in water current translates into 10,000 body lengths for a bacterium of 1 μm in size (for human, a corresponding translocation would be close to 20 km). Within such a distance, concentrations of potential food sources may differ dramatically in open water bodies, but also temperature differences of >50°C can occur within 1 cm, e.g., within black smoker vent systems. Therefore, microorganisms able to react to such differences by moving to optimal surroundings have a distinct advantage over bacteria that are immotile. Swimming in liquid medium is by far the best-characterized motility mechanism in *Bacteria*, but various other mechanisms of movement on surfaces have been defined for them (see, e.g., references 10, 12, and 16).

Rotation of flagella was identified early on as the mechanism of swimming in the bacterial model organisms *Escherichia coli* and *Salmonella enterica* serovar Typhimurium (5). It also has been known for a long time that switching between "runs" and "tumbles" is the mechanism underlying bacterial chemotaxis (14). Today, the bacterial motility system using flagella for swimming has been studied to a great extent, and very many aspects are known, not only down to molecular details but also with respect to regulation (for a review, see references 3, 20, and 25 and references therein). In principle, signals are sensed by arrays of chemoreceptors; a phosphorelay then transmits the signal to the flagellar motor. The sensitivity of the chemoreceptors can be modulated by their methylation, resulting in the possibility of adaptation to stimuli. The presence of chemoattractants leads to longer-lasting runs (linear movement) by counterclockwise rotation of the peritrichously located flagella, which themselves are combined in one bundle. Runs, typically at a speed of ca. 20 μm/s, are interrupted by tumbles (new, accidental orientation in space by disintegration of the flagellar bundle), which are induced by short clockwise rotation of flagella. *E. coli*, therefore, reacts to attractant/repellent sources by integrating signal intensity over time and not cell length. It also was found that variations of the standard *E. coli* swimming mode system exist. In the case of *Rhizobium meliloti*, the new swimming direction is not accomplished by tumbling; rather, a short stop of flagellar rotation reorients this bacterium.

In the case of *Archaea* much less data were reported about the swimming mode of these organisms. Only in the case of the rod-shaped species *Halobacterium salinarum* (formerly *Halobacterium halobium*) and quadratic-shaped halobacteria has the mechanism of swimming been shown, by dark-field microscopy, to be due to rotation of flagella (1, 2). For these *Archaea* a simple back and forth movement was observed, and cells were relatively slow (2 μm/s). The movement of *Methanococcus voltae* has been described to consist of incomplete circles (90 to 270°), interrupted by short stops (K. Jarrell, personal communication; also data not shown); it has to be mentioned, however, that this holds true only if cells are observed at room temperature under aerobic conditions. Direct measurements of the swimming speeds of hyperthermophilic microorganisms have not been reported up to now; the archaeon *Pyrococcus furiosus*, for example, was named "rushing fireball," but no comment on its actual swimming speed was given (9). In addition to the limited data on their swimming speed and mode, only limited data are available for the synthesis, motor components, hook structures, interaction with the chemotaxis system, and other aspects of archaeal flagella (for a review, see references 7 and 19, e.g.). One problem for studies of archaeal flagella clearly relates to the extremophilic nature of archaeal model organisms. Although halobacteria can be grown aerobically at ambient temperatures, studies of their proteins are difficult due to their salt dependence. Some members of the *Sulfolobales* are aerobic, too; in their case, however, the dependence on very low pH and high growth temperatures complicates studies. In the case of many hyperthermophilic *Archaea*, their growth under anaerobic conditions at temperatures above 80°C hinders analyses of their swim-

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ming modes. In addition, the technique of observing flagella by direct staining with fluorescent dyes, originally developed for *in situ* analyses of swimming *E. coli* (23), is not applicable to a great variety of *Archaea* (24).

Here, we present the first systematic analysis of the swimming mode of selected archaeal model organisms making use of our so-called "thermo-microscope" (11). We asked which swimming patterns these microorganisms exhibit under their optimal growth conditions and determined their swimming speeds. Remarkably, the motility of two species of methanocaldococci is the highest relative speed of any organism on earth.

MATERIALS AND METHODS

Growth of microorganisms. The following microorganisms (species, medium, gas phase, and optimal growth temperature, respectively) were included in this study: *Escherichia coli* (fresh fecal isolate), LB, air, 37°C; *Halobacterium salinarum* DSM 3754^T, DSM medium 97, air, 50°C; *Methanococcus maripaludis* DSM 2067^T, DSM medium 141, H_2/CO_2 (80/20%), 37°C; *Methanococcus voltae* DSM 1224^T, MGG (4), H_2/CO_2 (80/20%), 37°C; *Methanocaldococcus jannaschii* DSM 2661^T, MJ (4), H_2/CO_2 (80/20%), 85°C; *Methanocaldococcus villosus* DSM 22612^T, MGG (4), H_2/CO_2 (80/20%), 80°C; *Methanothermobacter thermoautotrophicus* DSM 1053^T, DSM medium 119, H_2/CO_2 (80/20%), 65°C; *Pyrococcus furiosus* DSM 3638^T, [1/2] SME (containing 0.1% yeast extract and 0.1% peptone) (9), N_2/CO_2 (80/20%), 95°C; and *Sulfolobus acidocaldarius* DSM 639^T, DSM medium 88, air, 70°C. Cells were grown with shaking aerobically in Erlenmeyer flasks filled to a maximum of 1/10 of their nominal volume (*E. coli* and *H. salinarum*) or semiaerobically in Erlenmeyer flasks filled to one-third of the nominal volume (*S. acidocaldarius*). The other species were grown in 120-ml serum bottles filled with 20 ml of medium under the gas phase given above, again with shaking. Growth was in all cases close to stationary phase, a condition under which optimal motility was observed.

Cells were transferred into rectangular glass capillaries (interior dimensions, 1 by 0.1 mm) by capillary action, and the capillaries were closed on both ends by use of instant Super Glue. Thereafter, the capillaries were immediately transferred onto an electrically heated stage which was placed on the microscope table. Since the capillaries had a length of ca. 3 cm and since observations were confined to the centers of capillaries, potential toxic effects of Super Glue were avoided.

Microscopic analyses of swimming behavior. Analyses were done by use of our thermo-microscope (see reference 11 for a detailed description), which in principle consists of a normal phase-contrast light microscope (Olympus BX50) located inside a Plexiglas housing. Heating fans inside this housing were used to heat the system up to ca. 55°C. To obtain higher temperatures, the phase-contrast objectives were heated electrically, as were the glass capillaries (containing cells) located on the electrically heated stage. Objectives and stage were equipped with temperature sensors to ensure that the desired temperature, which could be raised to a maximum of 95°C, had been obtained. All operation elements like focus, shutters, etc., were extended outside the Plexiglas housing to allow operation of the microscope at up to 95°C. After the desired temperature was reached (monitored via the heat sensors on the objectives and stage), motility was recorded using a charge-coupled-device (CCD) camera (pco.1600; PCO Company, Kelheim, Germany). Movies of swimming microorganisms were analyzed using the software ImageJ (version 1.41o with Java, version 1.6.0) with the add-on modules particle tracker and manual tracking. For each movie, the diameter of the particles to be analyzed had to be defined; a certain threshold of gray values (maximal deviation of 50%) was used to avoid analyses of microorganisms deviating in the *z*-plane by more than 2 μm. In some of the movies in the supplemental material, tracks which were used for analyses are indicated by coloration. Tracks that consisted of at least five continuous frames were used for determination of maximum swimming speed. Data are reported only for measurements for which the speed calculations for the five frames varied by less than 10%. The average speed was determined by measuring the speed of at least 10 different cells (tracks) of one sample. To further eliminate experimental variations cells were observed in at least five independent experiments under the same conditions, especially growth/observation temperature. Therefore, at least 50 tracks were combined for determination of the average speed. For recording the swimming tracks of the fastest organisms, a high-speed CCD camera (pco.1200 hs) with a resolution of 100 frames per second had to be used. Calibration for swimming distances was accomplished by photographing a micrometer scale with the standard equipment used.

RESULTS AND DISCUSSION

The species we analyzed were selected for the following reasons. The bacterium *E. coli* was chosen as a positive control because many data are available for this standard bacterium. The archaeon *M. thermoautotrophicus* was chosen as a negative control because we knew from earlier analyses (22) that this species is not motile. The other *Archaea* species were chosen because of their known motility and the fact that they represent model systems for various factors: *H. salinarum* for salt dependence; *M. maripaludis* and *M. voltae* for mesophilic, genetically manipulable methanogens; *M. jannaschii* for hyperthermophilic methanogens; *M. villosus* as a control for the data obtained with *M. jannaschii*; *P. furiosus* for heterotrophic hyperthermophilic anaerobic *Archaea*; and *S. acidocaldarius* for thermoacidophilic *Archaea*.

Control experiments (data not shown) indicated that no difference in swimming behaviors was observed if cells were transferred into the rectangular glass capillaries under anaerobic or aerobic conditions. For ease of operation, glass capillaries therefore were filled under aerobic conditions and closed on both ends by Super Glue. This procedure took less than 1 min, and the medium was still anaerobic inside the glass capillaries, as indicated by a lack of coloration of the redox indicator resazurin used in the anaerobic medium. Table 1 gives a summary of the results obtained, which we interpret as follows.

Swimming speeds. We observed an extensive range of swimming speeds for the various species analyzed, with absolute values for maximal speeds ranging from 10 to ~590 μm/s; average speeds varied from 3 to ~380 μm/s. The average swimming speed we observed for our *E. coli* fecal isolate exceeded that reported for *E. coli* AW405, with ~45 μm/s versus 21 μm/s (6). It has to be emphasized that the experimental setups differ markedly between these two data sets: we did analyses at 37°C, enhancing swimming speed by approximately a factor of 1.5 compared with swimming at room temperature (data not shown) and in rich medium, which clearly shifts runs to longer times (6; also data not shown). An absolute average swimming speed of 45 μm/s translates into a relative swimming speed of ca. 20 bodies per second (bps) for *E. coli*. The maximum speed of the sulfur bacterium *Thiovulum majus* was reported to be approximately 600 μm/s, but because of its size of ~7 μm, this is equivalent to ca. 85 bps (8). In contrast, the bacterium *Bdellovibrio bacteriovorus* swims at approximately 100 μm/s which, due to its small size, is equivalent to a maximum of approximately 150 bps (8).

The average absolute swimming speeds we have measured here for the various archaeal model species are in the range of very slow swimming (3 μm/s for *H. salinarum*, corroborated by earlier data [1]) to very fast swimming (380 μm/s for *M. jannaschii*). There was no correlation between swimming speed and growth temperature: *M. voltae* grown at 37°C swam faster than *P. furiosus* ob-

TABLE 1 Swimming characteristics of various species of *Archaea*

Species	Shape (size [μm])	Optimal growth temp (°C)[a]	Avg velocity (μm/s)[b]	Maximal velocity (μm/s)	Zigzag movement observed	Velocity in zigzag movement (μm/s)[c]	Temp range of swimming (°C)	Mode of swimming and/or remarks
Escherichia coli	Rod (2 by 0.7)	37	45 ± 5.0	66	–		20–60	Smooth curves and smooth lines, interrupted by tumbles
Halobacterium salinarum	Rod (10 by 1)	50	3 ± 0.5	10	–		20–65	Slow smooth lines; swimming speed markedly dependent on temp
Methanococcus voltae	Coccus (2)	37	80 ± 8.5	128	+	ND	20–55	Rapid and long notched tracks; shearing has no big influence on swimming capacity
Methanococcus maripaludis	Coccus (1.5)	37	25 ± 3.4	45	+	<10	20–60	Short, notched tracks; extremely sensitive to shearing
Methanocaldococcus jannaschii	Coccus (1.5)	85	380 ± 40	589	+	50–100	20–90	Extremely fast, directional swimming or slower zigzag movement; very slow swimming at room temp
Methanocaldococcus villosus	Coccus (1)	80	287 ± 36	468	+	80–120	50–90	Very fast directional swimming or slower zigzag movement
Pyrococcus furiosus	Coccus (2.5)	100	62 ± 7.0	110	+	30–50	70–95	Swimming markedly dependent on temp; directional swimming and slower zigzag movement
Sulfolobus acidocaldarius	Coccus (1.5)	70	45 ± 4.2	60	–		30–80	Swimming speed markedly dependent on temp; notched tracks with zigzag elements

[a] The data given for average velocity and maximal velocity were determined for this temperature.

[b] The values represent the mean of at least 50 independent swimming tracks from at least 10 cells measured in five independent experiments (see Materials and Methods). The given standard deviation is derived from tracks that differed by not more than 10% from each other. Also included in the standard deviation values are experimental setup-related error sources, like the tracking of diving cells, or problems with program calibration.

[c] ND, not determined.

served at 95°C but slower than *M. villosus* grown at 80°C. The maximal swimming speed of *M. jannaschii* at 589 μm/s is similar to that of *T. majus*; however, due to the marked difference in sizes of these two microorganisms, their relative swimming speeds differ drastically, with ca. 390 bps versus ca. 85 bps. Because of its smaller size *M. villosus* has an even higher maximal relative swimming speed of ~470 bps. These two archaeal species therefore possess the highest relative speed measured to date for any organism on earth (data available at http://www.pbrc.hawaii.edu/~petra/animal_olympians.html).

Mode of swimming. The fresh fecal isolate of *E. coli* was used here for comparisons and showed the mode of swimming reported earlier: runs were interrupted by tumbles. We noted that the swimming speed (45 μm/s) and length of runs (up to 250 to 300 μm and up to 8 to 10 s) of this fresh isolate exceeded those reported for *E. coli* AW405 (21 μm/s and ~1 s) (6). This very probably is due not only to different experimental setups (see above) but also to the fact that *E. coli* K-12 strains have a lab history of >50 years, a period in which physiological alterations might have accumulated. We have deliberately chosen to compare the fresh fecal *E. coli* isolate with the archaeal species tested because all of the latter were type strains, representing wild types.

Very interestingly, the *Archaea Methanococcus maripaludis*, *Methanococcus voltae*, *Methanocaldococcus jannaschii*, *Methanocaldococcus villosus*, and *Sulfolobus solfataricus* exhibited a swimming behavior that we observed also for *P. furiosus*, which is in stark contrast to that of, for example, *E. coli*. *E. coli* swims in more or less smooth runs, disrupted by tumbles to alter the swimming direction. The hyperthermophilic *Archaea*, on the other hand, exhibit a swimming behavior best characterized as a "relocate-and-seek" strategy; for relocation they swim in more or less straight lines, covering a (relatively) long distance due to their high swimming speed (see the movies in the supplemental material). In this fast-swimming mode some smaller changes in direction are observed but not abrupt ones; thus, tumbles observed in *E. coli* are not observed in these *Archaea*. For comparative reasons the movies in the supplemental material show the following: swimming of *E. coli* (two movies at medium velocity, one without and one with indications of tracks used for analyses), swimming of *H. salinarum* (slow velocity) and swimming of *H. salinarum* at a 10-fold time lapse, swimming of *P. furiosus* (fast swimming), swimming of *M. voltae* (fast swimming), swimming of *M. villosus* (very high velocity), and swimming of *M. jannaschii* (highest velocity). This type of swimming behavior was observed especially for cells swimming parallel to the observation plane in the middle of the capillary. Most of these cells, therefore, did not experience contact of their flagella with the glass capillary wall; on average, they were at a distance of ca. 50 μm from the glass capillary wall.

In addition, the fast-swimming coccoid *Archaea*, however, also exhibited another mode of swimming, namely, a much slower kind of zigzag movement (see, e.g., movies for *M. jannaschii*, *M. villosus*, and *P. furiosus* in the supplemental material). Such swimming behavior was very rarely observed for cells swimming in the middle plane of the capillary but was much more often seen in cells swimming near the glass capillary wall, especially if the focal plane was <10 μm from the glass capillary wall. We argue that in these cells the zigzag "seek" movement is triggered by close contact with the capillary surface. Taken together, this behavior indicates to us that swimming in these *Archaea* can alternate between very rapid relocation movements to bring cells into another surround-

ing and much slower seek movements that result in the cells staying in a locally restricted area. The fast linear movements are thought to result in a rapid change of location to avoid conditions detrimental for growth. The slow zigzag movements are thought to represent a seek strategy, followed by attachment to a surface. Indeed, such attachments were observed in our experiments only for cells exhibiting the slow zigzag movement though not every zigzag movement resulted in adhesion. The zigzag movements reduced the overall swimming speed of the *Archaea* drastically: for *M. jannaschii*, the reduction was from 500 μm/s for fast linear relocation swimming to 80 to 100 μm/s, in some cases even down to 50 μm/s, for the zigzag seek movement; for *M. villosus* the reduction was from 400 μm/s down to 100 to 120 μm/s; for *P. furiosus* the reduction was from 110 μm/s to 35 to 45 μm/s; and in the case of *M. maripaludis* the reduction was from 25 μm/s to below 10 μm/s.

We want to stress that we have shown *P. furiosus* (18) and *M. villosus* (4) to be ideally adapted for this relocate-and-seek strategy of motility because we have proven that their flagella are used not only for swimming but also for adhesion; the same very recently was shown to be true for *M. maripaludis* (13). It has to be noted that all our experiments were done under conditions in which cells did not experience any gradient with respect to temperature, attractant/repellent concentrations, O_2 tension, etc. Further experiments will address the question of the distribution of relocation and seek movements of cells experiencing such gradients; this, however, will need the construction of special swimming chambers in which such gradients can be established.

Conclusions. A beetle obviously cannot move as fast as a human, who, on the other hand, runs much more slowly than a cheetah. The question of which of these organisms is the fastest should, for a fair comparison, take into account body size. Therefore, the relative measurement of speed as bodies per second (i.e., translocation of body sizes per second [bps]) has been introduced. Via this definition the following absolute and relative speeds have been measured (data available from http://www.pbrc.hawaii.edu/~petra/animal_olympians.html): the maximal speed of a cheetah is 113 km/h or 20 bps, the maximal speed of a human is 45 km/h or 11 bps, but the tiger beetle can run at up to 3 km/h, equaling 150 bps. Peregrine falcons can dive in the air at up to 300 bps; this, however, does not represent an active movement. Clearly, size matters very much in this respect, and, therefore, microorganisms come into play here. The swimming speed of *Escherichia coli* was reported to be 20 to 25 μm/s, or approximately 20 bps (17). As Table 1 shows, two species of the genus *Methanocaldococcus*, namely, *M. jannaschii* and *M. villosus*, turned out to be the fastest organisms observed to date, with maximal speeds of close to 400 and 500 bps, respectively. Our data not only disproved the idea that *Archaea* in general might swim more slowly than *Bacteria* (15) but also identified the hyperthermophilic archaeal species *M. jannaschii* and *M. villosus* as the fastest organisms observed to date.

The relocate-and-seek strategy of motility we observed for the hyperthermophilic *Archaea* very well could be explained by the conditions these microorganisms are confronted with in their biotope, namely, very steep gradients of temperature, for example. A passive translocation for only 1 s by a water flow of only 10 cm/s would transport the cells (having a diameter of approximately 1 μm) 10^5 cell diameters away. Even if they were able to swim at 100 μm/s in a continuously unidirectional motion—which has not been observed in microorganisms up to now (17)—it would take them 1,000 s (16.6 min) to relocate into their original habitat. Direct water flows in black smokers at 1 to 2 m/s are indeed much higher; water emanating through the chimney wall, however, flows at reduced velocity. Nevertheless, a translocation of 10 cm would confront the cells with aerobic conditions and low temperature, a situation detrimental to their swimming ability. A repeated change between relocation and adhesion would enable the cells to seek for and remain in a favorable surrounding and would, therefore, be of great advantage for them. We argue that the ability to use one and the same surface structure, namely, flagella, to move within a certain surrounding and to adhere to this surrounding is a remarkably clever strategy for living in such extreme habitats like black smokers. In the case of black smokers, cells would adhere in a region of the porous chimney walls that has the optimal growth temperature, i.e., between the outer surface (close to 4°C) and the inner surface (300 to 400°C). The distribution of extremophiles in different microhabitats—surface, porous layer, hard layer, etc.— of black smoker chimneys, indeed, has been reported to vary (21).

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