RESEARCH ARTICLE

Positioning the Flagellum at the Center of a Dividing Cell To Combine Bacterial Division with Magnetic Polarity

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ABSTRACT Faithful replication of all structural features is a *sine qua non* condition for the success of bacterial reproduction by binary fission. For some species, a key challenge is to replicate and organize structures with multiple polarities. Polarly flagellated magnetotactic bacteria are the prime example of organisms dealing with such a dichotomy; they have the challenge of bequeathing two types of polarities to their daughter cells: magnetic and flagellar polarities. Indeed, these microorganisms align and move in the Earth's magnetic field using an intracellular chain of nano-magnets that imparts a magnetic dipole to the cell. The paradox is that, after division occurs in cells, if the new flagellum is positioned opposite to the old pole devoid of a flagellum during cell division, the two daughter cells will have opposite magnetic polarities with respect to the positions of their flagella. Here we show that magnetotactic bacteria of the class *Gammaproteobacteria* pragmatically solve this problem by synthesizing a new flagellum at the division site. In addition, we model this particular structural inheritance during cell division. This finding opens up new questions regarding the molecular aspects of the new division mechanism, the way other polarly flagellated magnetotactic bacteria control the rotational direction of their flagella, and the positioning of organelles.

IMPORTANCE Magnetotactic bacteria produce chains of magnetic nanoparticles that endow the cells with a magnetic dipole, a "compass" used for navigation. This feature, however, also drastically complicates cellular division in the case of polarly flagellated bacteria. In this case, the bacteria have to pass on to their daughter cells two types of cellular polarities simultaneously, their magnetic polarity and the polarity of their motility apparatus. We show here that magnetotactic bacteria of the *Gammaproteobacteria* class pragmatically solve this problem by synthesizing the new flagellum at the division site, a division scheme never observed so far in bacteria. Even though the molecular mechanisms behind this scheme cannot be resolved at the moment due to the lack of genetic tools, this discovery provides a new window into the organizational complexity of simple organisms.

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The complexity of cellular organization and dynamics has long been recognized in eukaryotes. However, it is only in the last decade that such complexity has started to be documented for bacteria (1). One example for such organization is cellular polarity with concomitant anisotropic cell division, which has been observed specifically for monotrichous bacteria, i.e., cells with one polar flagellum, such as *Caulobacter crescentus* (2), *Vibrio cholerae* (3), and *Pseudomonas aeruginosa* (4). These microorganisms are known to divide according to a scheme whereby the newly synthesized flagellum emerges from the old pole devoid of a flagellum, opposite the flagellated pole. In addition, subcellular compartmentalization has been observed in some bacteria (5, 6) that form intracellular organelles with dedicated functions, such as carboxysomes for enhancement of carbon fixation (7) or magnetosomes in magnetotactic bacteria responsible for cellular orientation in the Earth's magnetic field (8).

In the latter case, the magnetic nanoparticles formed in the magnetosome vesicles are arranged in chains to produce a single magnetic dipole (9). This compass-needle-like actuator passively orients the cells in the Earth's magnetic field, whereas active swimming is achieved by the flagellar system, a behavior called magnetotaxis (9). Magnetotaxis supposedly helps the microorganisms to more efficiently find the oxic-anoxic transition zone in the water column (10) since the Earth's magnetic field is inclined with respect to the surfaces of aquatic environments. Thus, each bacterium needs a magnetic dipole with the appropriate magnetic polarity to find the microaerobic zone and to remain there. An inversion of the polarity of the chain with respect to the magnetic field indeed causes the cells to swim away from the microaerobic zone toward the oxic and anoxic zones (11).

The magnetic polarity of magnetotactic bacteria imposes particular challenges during cell division. When magnetotactic bacteria divide, the magnetosome chain is split into two parts that are inherited by the two daughter cells (12–14). In this way, the magnetic polarity is passed on to both daughter cells, but the cells need to overcome the attractive magnetic force between the two parts of the magnetosome chain (14). Magnetotactic bacteria are a diverse group with respect to their physiology, taxonomy, and morphol-

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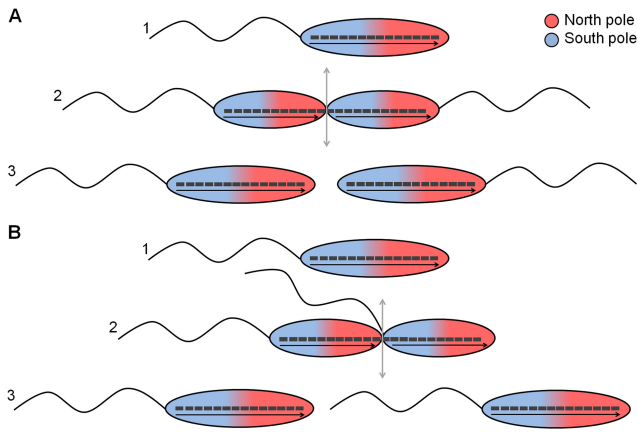
FIG 1 Two possible schemes for dividing monotrichous bacteria. (A) Established model for anisotropically dividing cells (2). Such a scheme results in two daughter cells with opposite magnetic polarities with respect to the localization of the flagellum. (B) Alternative scheme in which the newly formed flagellum emerges at the new pole, i.e., at the septum. In this scheme, the two daughter cells exhibit the same positioning of their flagella relative to the magnetic polarity of the magnetosome chain.

ogy (15), and among the different morphologies observed are those of vibrios or rod-shaped cells with a single polar flagellum (15). These bacteria encounter an additional dilemma with respect to the localization of the new flagellum; during cell division, all monotrichous bacteria studied so far synthesize the new flagel-

lum at the pole opposite to the flagellum (2, 3). If monotrichous magnetotactic microorganisms divide based on this mechanism, the flagella are placed at opposite magnetic poles in the two daughter cells (Fig. 1A). For a given direction of flagellar rotation, the two daughter cells would swim away from each other (in opposite directions) in a magnetic field. Therefore, in order to swim in the same direction as the cell that has inherited the old flagellum, the other daughter cell would have to adapt its sensory apparatus to reverse the flagellar rotation. In this article, we show that magnetotactic bacteria of the *Gammaproteobacteria* class use an alternative division scheme to cope with this challenge: they place the new flagellum at the septum (Fig. 1B), thus passing on to both daughter cells an orientation of magnetic polarity that is the same as that of the polarity of the motility apparatus.

In this study, we used strain SS-5 as a model organism that has a combination of magnetic and cellular polarity. SS-5 is a rod-shaped magnetotactic bacterium (16) with a single chain of magnetosomes and a single polar flagellum (Fig. 2A). We show that SS-5 divides according to the strategy depicted in Fig. 1B, i.e., by placing the new flagellum at the division site. We discuss how widespread this scheme is and propose a model that generates such a mechanism through the formation of a double protein concentration gradient within the cell.

RESULTS AND DISCUSSION

Cells of strain SS-5 synthesize the new flagellum at the septum. If monotrichous magnetotactic bacteria divide according to the same scheme as described for other monotrichous bacteria, with
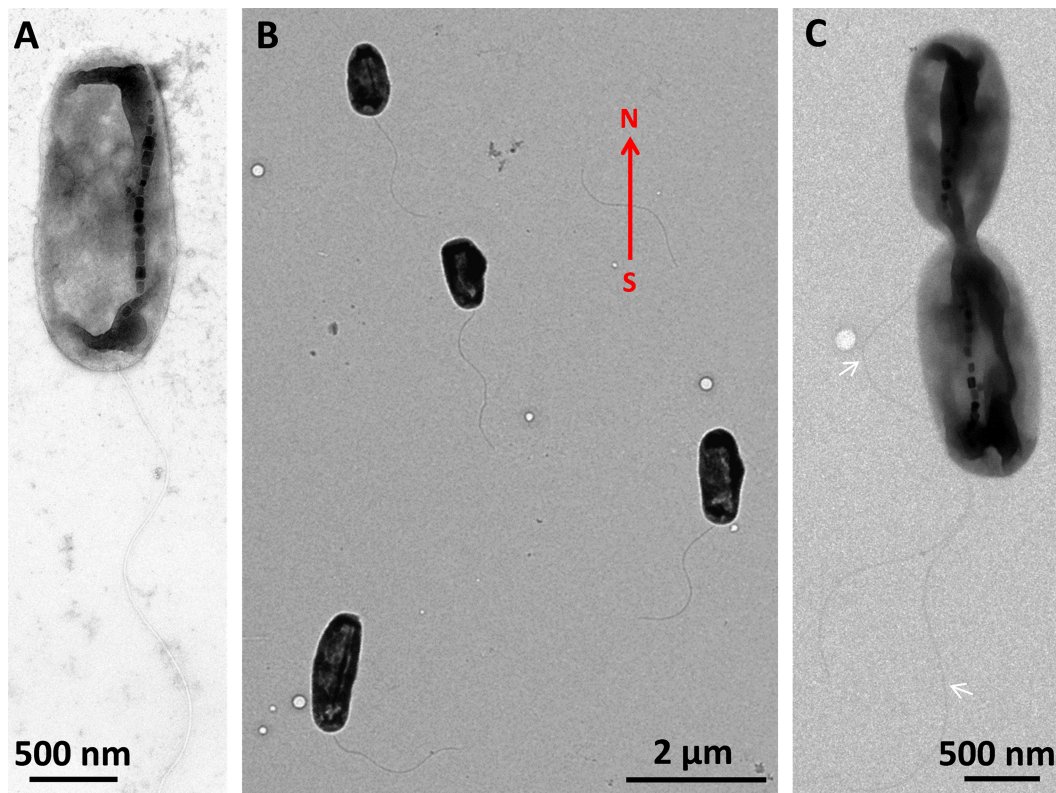
FIG 2 Transmission electron microscope (TEM) images of the north-seeking magnetotactic bacterium SS-5. (A) Cells stained with 1% uranyl acetate for visualization of the polar flagellum. (B) Cells magnetically aligned on a TEM grid. The applied magnetic field is shown by the red arrow. (C) Dividing cell of strain SS-5. The two flagella are indicated with white arrows.

the new flagellum emerging from the pole opposite that of the old flagellum, after cell division, the two daughter cells will have their flagella positioned at different magnetic poles (Fig. 1A). Thus, when a population of these bacteria is aligned in a sufficiently strong magnetic field, this model predicts that half of the population will have the flagellum positioned adjacent to the cellular north magnetic pole and that the other half will have the flagellum positioned adjacent to the cellular south magnetic pole. To test this prediction, magnetotactic cells were grown and magnetically separated in order to select only north-seeking bacteria. They were then magnetically aligned while they were swimming toward north in a medium containing a homogeneous concentration of atmospheric oxygen. Once the cells were fixed on a transmission electron microscope (TEM) grid or a light microscope slide, they were stained for observation of their flagella. Microscopy analyses revealed that the individual flagella of cells of strain SS-5 are always positioned at the south pole of the cellular magnetic dipole (Fig. 2B and see Fig. S1 in the supplemental material), in contrast to the prediction based on the classical division scheme. Since the bacteria were swimming north, this orientation also means that the flagella were pushing the bacteria rather than pulling them under these conditions. As a control, we grew strain SS-5 under Southern Hemisphere-like conditions (with a magnetic field parallel to that of the oxygen gradient) to obtain south-seeking cells. In this case, the cells swimming toward the south had their flagellum positioned adjacent to the cellular north magnetic pole, i.e., opposite the leading pole of the swimming cell (Fig. S2).

Finally, since the observed orientation of the flagella did not agree with the classical division scheme, we imaged dividing cells using light and electron microscopy. Surprisingly, we observed that in SS-5, the new flagellum emerges at the septum (Fig. 2C and see Fig. S1 in the supplemental material). To our knowledge, this new division scheme has never been observed for any other bacteria. It was hypothesized and depicted long ago (see Fig. 2.24a in reference 17) but has, to our knowledge, never been observed. The question of how such localization is controlled is intriguing, as it requires the placement of the flagellum not only close to the septum but also on the correct side of the septum.

Two division strategies are found in polarly flagellated magnetotactic bacteria. Next, we analyzed division in other magnetotactic bacteria to see how widespread this division mechanism is. For several strains of monotrichous magnetotactic bacteria, the new flagellum was found to emerge from the pole opposite to the old flagellum, as in the classical scheme of polar division; examples are *Magnetovibrio blakemorei* strain MV-1, a magnetic vibrio of the *Alphaproteobacteria* class (18), strain LM-1, another *Alphaproteobacterium* (19), and magnetotactic bacteria of the *Deltaproteobacteria* class, namely, *Desulfovibrio magneticus* strain RS-1 (20), "*Candidatus* Desulfamplus magnetomortis" strain BW-1 (21), and the alkaliphilic strain ZZ-1 (22) (Fig. 3A to C). We thus subsequently investigated the strategy used by bacteria phylogenetically related to strain SS-5 from the *Gammaproteobacteria* class. We found that another magnetotactic bacterium, strain BW-2 (16), has its bundle of seven flagella emerging at the septum during cell division, as for SS-5 (Fig. 3D), while nonmagnetotactic bacteria, such as *Pseudomonas brassicacearum* (23) and *Allochromatium vinosum* (24), form a new polar bundle of flagella at the old pole opposite the old flagella (Fig. 3E), similarly to their previously described relatives *Vibrio cholerae* (3) and *Pseudomonas*

aeruginosa (4). Thus, the new division mechanism described here appears to be specific to the magnetotactic *Gammaproteobacteria*.

The observation of different division schemes in monotrichous magnetotactic bacteria also means that these bacteria must control the rotation of their flagellar motors differently. Indeed, after division of an MV-1 cell (or a cell of any strain with the new flagellum emerging from the pole opposite the old flagellum), the two daughter cells have to rotate their flagellum differently to obtain the same direction of movement. Thus, these cells must possess a regulatory mechanism for adjusting the direction of flagellar rotation to the location of the flagellum relative to its magnetic polarity (see Fig. S3A in the supplemental material). No such control is needed for the cells dividing according to the new scheme (SS-5 and BW-2), as in these cells, the correct relative orientation of magnetic movement and of the motility apparatus is inherited from one generation to the next. Moreover, the different senses of flagellar rotation in MV-1 cells that swim in the same direction also mean that the flagellum pushes the cell body in one half of the population (cells that swim with the nonflagellated pole ahead) but pulls it in the other half of the population (cells that swim with the flagellated pole ahead) (Fig. S3A). In contrast, for SS-5 cells, the position of the flagellum relative to the swimming direction is the same in all cells but will depend on the oxygen concentration; in the Northern Hemisphere, where in the natural environment the magnetic field of the Earth is antiparallel to the oxygen gradient in layered aquatic environments, these bacteria swim north under oxic conditions but south under anoxic conditions to navigate to the oxic-anoxic transition zone (11). Due to the magnetic alignment of the cell body, the change in swimming direction must be accomplished by a change in the direction of flagellar rotation, with the flagellum pushing the cell body under oxic conditions but pulling it under anoxic conditions (Fig. S3B).

Model for the division strategy of the monotrichous magnetotactic bacterium SS-5. To explore the mechanistic basis of the observed division scenario, we formulated a mathematical model (Fig. 4). In general, cellular polarity is established and inherited via intracellular protein gradients (5, 6, 25). Due to their small cell size, gradients in bacterial cells are typically gradients of the active form of a protein rather than the concentration of a protein, e.g., due to localized phosphorylation or dephosphorylation, which is more rapid than protein degradation. The characteristic length scale of such a gradient depends on the diffusion coefficient (D) and the rate of inactivation (k) and is given by the formula $L = \sqrt{D/k}$. For inactivation by phosphorylation or dephosphorylation, this length scale can be in the submicron range (25), corresponding to a fraction of the cell size. In the classical scheme of polar division, the localization of a flagellum at the pole opposite that of the old flagellum can thus be accomplished by the localized activation of a negative regulator or inhibitor of flagellar assembly near the old flagellum (or the localized inactivation of a positive regulator) (Fig. 4A). Evidence for such a gradient has been reported for *C. crescentus*, where, however, the developmental program is more complex due to the presence of the stalked stage (25). In turn, positioning the new flagellum in the cell center close to the septum requires a double gradient from both poles, e.g., by activation of the inhibitor both at the old flagellum and at the opposite pole. An example of such a gradient is the bipolar gradient distribution of MipZ in *C. crescentus* (26), which organizes cell division and localization of cellular components, including the
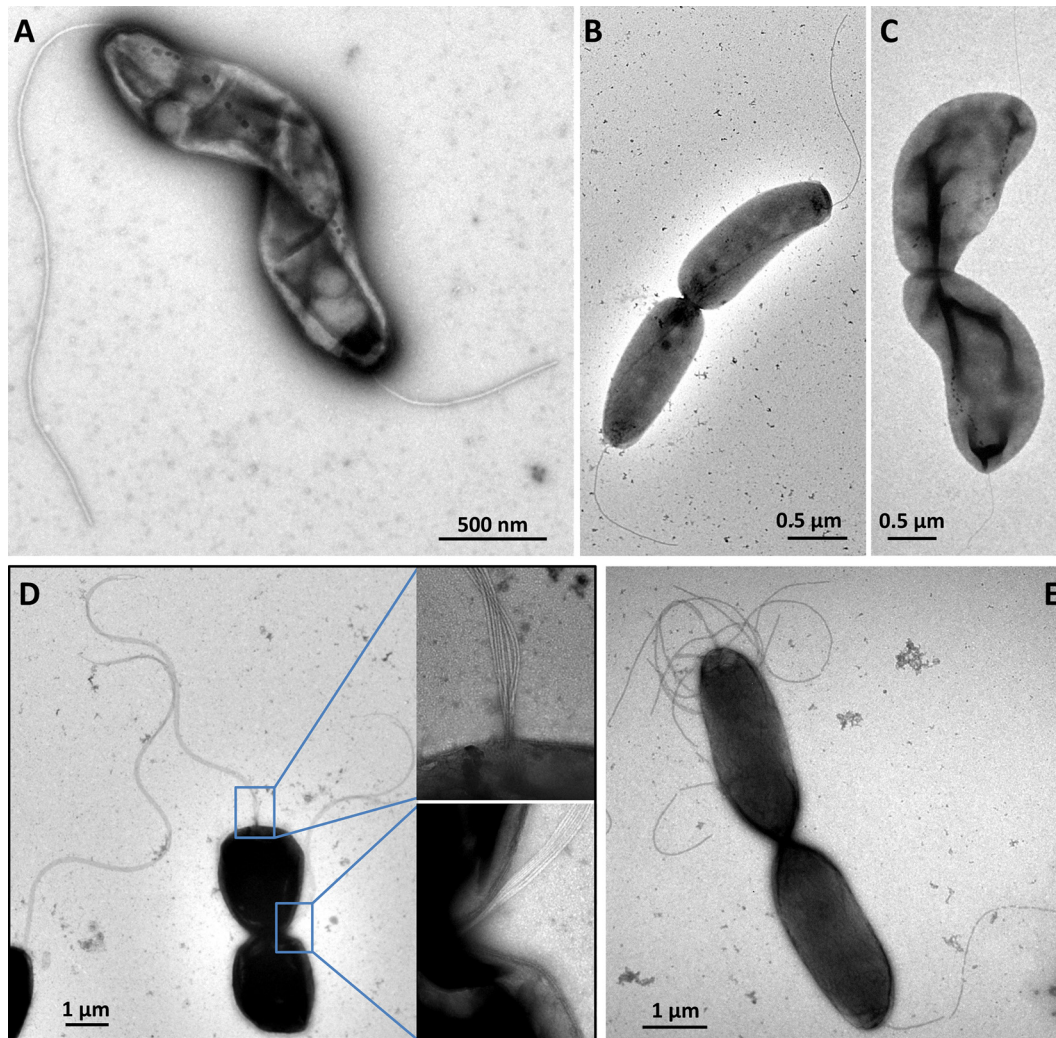
FIG 3 Structural inheritance of asymmetric magnetotactic bacteria and related organisms during cell division. Transmission electron micrographs of dividing cells of *Magnetovibrio blakemorei* strains MV-1 (A) and LM-1 (B) of the *Alphaproteobacteria* class, strain ZZ-1 of the *deltaproteobacteria* class (C), and strain BW-2 (D) and *Pseudomonas brassicacearum* (E) of the *Gammaproteobacteria* class. All these bacteria but *P. brassicacearum* are magnetotactic. Cells are stained with 1% uranyl acetate to show the positions of their flagella.

flagellar apparatus. Likewise, the MinCD oscillations in *Escherichia coli* effectively result in a bipolar double gradient (27). Such a double gradient is naturally obtained in bipolarly flagellated bacteria if the negative regulator is activated at both flagella and, thus, results in the localization of the new flagella at the cell center, as observed for the bipolarly flagellated magnetotactic bacterium *Magnetospirillum gryphiswaldense* strain MSR-1 (14).

In the new division mechanism (strain SS-5), however, the new flagellum needs to be positioned not only in the center of a cell but also such that, upon cell division, it is not erroneously located in the same daughter cell as the old flagellum. For positioning in the center without an additional control mechanism, this scenario should occur in 50% of divisions. Positioning on the side of the septum opposite the old flagellum thus requires an asymmetry between the inhibitors emanating from the old flagellum and from the opposite nonflagellated pole. In our model, we implemented such an asymmetry by using a second inhibitor of flagellar assembly that is activated at the nonflagellated pole and that has a weaker inhibitory effect than that of the inhibitor arising from the

flagellated pole. As a consequence, the initiation of flagellar assembly is biased toward the nonflagellated side of the cell center (Fig. 4B). Nevertheless, the spatial distribution of the flagellar position still has a significant tail on the flagellated side as well. Robust positioning on the correct side requires a stable gradient over the short distance across the septation site, which is virtually impossible as long as there is diffusive exchange between the two daughter cells, as it would require an extremely high rate of inactivation. The correct positioning of the flagellum is obtained if its assembly is delayed until septation or the closing of a diffusion barrier between the daughter cells, as observed in *C. crescentus* (28). Upon closing of such a diffusion barrier, our double gradient model naturally splits into two independent gradients, as only one inhibitor is now activated in each daughter cell and robustly predicts correct positioning of the new flagellum at the side of the septum belonging to the nonflagellated daughter cell (Fig. 4C).

Concluding remarks. We have reported a new cell division strategy for monotrichously flagellated bacteria in which the new flagellum is synthetized at the septum. This strategy avoids the
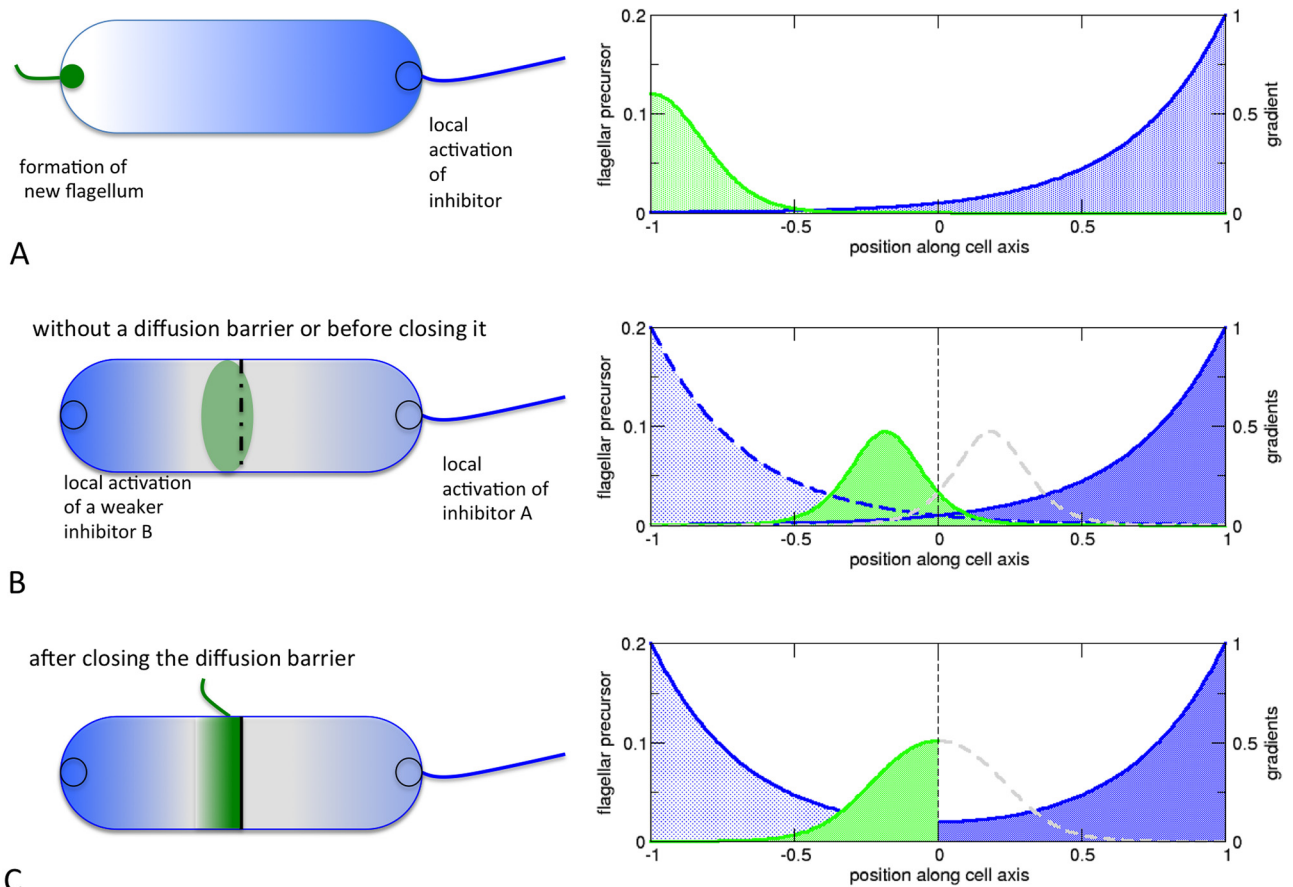
FIG 4 Theoretical models for the positioning of bacterial flagella during cell division. Models are according to the classical mechanism based on a single gradient (A) and for the new mechanism observed for strain SS-5 (B and C).

need for a regulatory mechanism to adjust the direction of flagellar rotation to the relative orientation of the flagellum and the magnetic polarity of the cell, but our results suggest that this strategy is specific to magnetotactic bacteria of the *Gammaproteobacteria* class.

We expect the observation of different cell division strategies in different magnetotactic bacteria to also be of evolutionary significance, providing a clue toward explaining the polyphyletic distribution of magnetotactic bacteria in the domain *Bacteria*. Indeed, magnetotaxis is sustainable only in conjunction with a specific flagellar and sensory apparatus and a cell division mechanism adapted to it.

Our study confirms the organizational complexity of bacteria, not only with respect to the adaptation of their chemotactic and motility apparatus but also with respect to the diversity of division strategies. We believe that the discovery of the division mechanism of the magnetotactic *Gammaproteobacteria* that passes on two types of cellular polarities to both daughter cells provides a new window into the principles of how proteins and larger complexes are localized in cells, but further studies will require the establishment of genetic tools for those strains in order to decipher the molecular mechanisms underlying this strategy.

MATERIALS AND METHODS

Bacterial growth. Strain SS-5 was used as model monotrichous magnetotactic bacterium for its ability to be magnetically oriented on a surface

and for the ease with which its flagellum can be visualized under transmission and optical microscopes. Moreover, when exposed to a magnetic field of 35 to 40 mT, the magnetosome chain conserves its orientation, i.e., it is not remagnetized (Fig. S4) (29). Cells of strains SS-5 and BW-2 were grown in a semisolid, oxygen gradient medium under autotrophic conditions as previously described (16). Cells of strain MV-1 were also grown in a semisolid, oxygen gradient medium but under heterotrophic conditions, as previously described (18). Cells of strains LM-1, ML-1, "*Candidatus* Desulfamplus magnetomortis" strain BW-1, and *Desulfovibrio magneticus* strain RS-1 were grown in semisolid media as previously described (21, 22, 30). Cells of *Pseudomonas brassicacearum* were grown in 10-fold-diluted tryptic soy broth (Difco) medium at 28°C (23) and cells of *Allochromatium vinosum* in modified *Rhodospirillaceae medium* (24).

To generate south-seeking cells of strain SS-5, a 0.4-T magnet was applied to the culture tube a few millimeters below the oxic-anoxic transition zone, with the north pole in contact with the tube (31). In this case, the artificial magnetic field had the orientation opposite that of the geomagnetic field. Therefore, the north-seeking cells were induced to swim toward the surface of the medium, away from the oxic-anoxic interface located in the growth medium. After several subsequent inoculations, the cells obtained displayed south-seeking behavior when analyzed in droplets by light microscopy.

Light and electron microscopy. Light microscopy was performed with a custom-made microscope platform (32), and images were obtained with a camera (2,560- by 2,160-pixel NeosCMOS camera; Andor Technology plc.). Samples were adsorbed on microscope slides and stained as previously described (33). Electron microscopy was performed with a Zeiss 912 Omega EM with 120-kV acceleration voltage and a Tecnai 12 G²

TABLE 1 Parameters used in the gradient model

Parameter	Value used
Length scale of gradient (λ)	$L/3$
Concn scale for strong inhibition (K_1)	$r_1(x = L)/30$
Concn scale for weak inhibition (K_2)	$r_1(x = L)/10$
Hill coefficient of inhibition (n)	4

BioTwin TEM (FEI Company, Eindhoven, Netherlands) with 100-kV acceleration voltage. Samples were adsorbed on carbon film-coated Cu TEM grids. After removal of the liquid with Kimwipe paper, grids were negatively stained with a drop of 1% uranyl acetate for 1 min.

Gradient model. The concentrations of the active forms of the negative regulators are denoted by r_1 and r_2 and follow the differential equation

$$\frac{\partial}{\partial t} r_{1,2} = D \frac{\partial^2}{\partial x^2} r_{1,2} - k r_{1,2}$$

where D is the diffusion coefficient and k is the inactivation rate, taken to be the same for both regulators. Activation of the inhibitors at one of the poles is described by a constant concentration, r_o, at the appropriate boundary ($x = +L$ or $x = -L$, where L is the cell length). The second boundary condition is that the diffusive flux vanishes at the other pole (or, upon closing of a diffusion barrier, at the septum). The steady-state solution is given by the equations

$$r_1(x) = r_0\left(e^{\frac{x}{\lambda}} + e^{-\frac{2L+x}{\lambda}}\right), \qquad r_2(x) = r_0\left(e^{-\frac{x}{\lambda}} + e^{-\frac{2L-x}{\lambda}}\right)$$

where λ is equal to $\sqrt{D/k}$.

The profile $f(x)$ of the flagellar precursor or positioning marker is then obtained via a Hill function of the inhibitors, as follows:

$$f(x) = \frac{f_0}{1 + \left[\frac{r_1(x)}{K_1}\right]^2 + \left[\frac{r_2(x)}{K_2}\right]^n}$$

For the asymmetric positioning of the new flagellum, inhibition by the inhibitor activated at the old flagellum needs to be stronger than that by the inhibitor from the nonflagellated pole, i.e., K_2 is $>K_1$. A profile for a precursor directing the location of the activation of the weaker inhibitor to the new nonflagellated pole is obtained by exchanging the roles of the weak and strong inhibitors. This profile is shown as the gray lines in Fig. 4. The parameters that we used are summarized in Table 1. In the plots, all concentrations are normalized to the maximal values, $r_1(x = L)$, $r_2(x = -L)$, and f_0, and the spatial coordinate x is normalized to the cell length (L).

SUPPLEMENTAL MATERIAL

Supplemental material for this article may be found at http://mbio.asm.org/lookup/suppl/doi:10.1128/mBio.02286-14/-/DCSupplemental.

Figure S1, TIF file, 2.8 MB.
Figure S2, TIF file, 2.6 MB.
Figure S3, TIF file, 1.6 MB.
Figure S4, TIF file, 2.5 MB.

ACKNOWLEDGMENTS

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