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Directional matching of swimming polarity provides a competitive advantage during bacterial magneto-aerotaxis

Carina Weigel¹ and Daniel Pfeiffer^{1*}

Abstract

Background Magnetotactic bacteria (MTB) utilize magnetosomes to align passively with Earth's magnetic field. Magnetic alignment, coupled with flagellar motility and aerotaxis, enables MTB to perform magneto-aerotaxis—a strategy that constrains their movement to a one-dimensional trajectory along geomagnetic field lines, which is believed to optimize their search for low-oxygen niches in aquatic environments. Beyond axially constrained movement, environmental MTB isolates exhibit a hemispherically determined swimming polarity—favoring either magnetic north or south—that has been suggested to facilitate descent into oxygen-depleted zones. However, a systematic and quantitative evaluation of how matching swimming polarity influences navigation toward low-oxygen environments has remained elusive. Here, we employed microcapillary assays to assess the functional significance of polar magneto-aerotaxis in the model organism *Magnetospirillum gryphiswaldense*.

Results We found that a magnetic field configuration matching the predominant swimming polarity of the population results in an up to fourfold increased peak intensity of the aerotactic band compared to populations with non-matching polarity. Competition assays using fluorescently labeled north- and south-seeking populations confirmed that congruence between swimming polarity and magnetic field orientation markedly improves aerotactic band formation in oxygen gradients. Alongside our main findings, we noted biomagnetism-independent light-induced behavioral responses integrated with aerotaxis, driving collective unidirectional migration along the oxygen gradient.

Conclusions Our results provide quantitative evidence that matching swimming polarity with the magnetic field confers a clear competitive advantage over cells with an incorrect polarity when navigating oxygen gradients. These findings reinforce the role of the geomagnetic field in shaping MTB behavior and highlight the adaptive value of magnetotactic swimming polarity in environmental navigation. Our observation of light-triggered behavior further suggests the presence of an additional sensing modality complementing magneto-aerotactic behavior, highlighting the sophisticated sensory capabilities of *M. gryphiswaldense*.

Keywords Magnetospirillum, Magnetotactic bacteria, Magnetosome, Magnetotaxis, Aerotaxis, Magneto-aerotaxis, Photoresponse, Polarity, Geomagnetic, Flagella

*Correspondence:

Daniel Pfeiffer
daniel.pfeiffer@uni-bayreuth.de

¹Department of Microbiology, University of Bayreuth, Bayreuth
95447, Germany



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Background

Organisms across diverse life forms are known to perceive and respond to the Earth's magnetic field [1, 2]. The most ancient and experimentally accessible magnetosensitive organisms are magnetotactic bacteria (MTB) [3, 4]. They orient along geomagnetic field lines using specialized intracellular organelles called magnetosomes [1–3]. Passive magnetic alignment is complemented by flagella-driven motility and chemotactic responses—most notably aerotaxis, which plays a dominant role by guiding movement toward favorable oxygen concentrations [4]. This combined strategy was termed magnetotaxis, emphasizing a magnetically assisted form of aerotaxis [5–7]. It is assumed that by constraining movement along geomagnetic field lines, MTB reduce a three-dimensional random walk to a one-dimensional search, thereby enhancing their ability to locate micro- or anoxic niches that support growth and magnetosome formation [4, 5, 7]. This preference for low-oxygen conditions is reflected in the characteristic aerotactic band formation by cultured MTB in oxygen gradients, aligning with their microaerophilic lifestyle [5–9].

Beyond geomagnetic alignment, MTB populations from natural environments typically show a directional preference for one magnetic pole—referred to as “polar magnetotaxis” or “swimming polarity” [1, 5–8, 10]. Polar magnetotaxis is commonly investigated using the “hanging drop assay,” where a droplet of cell suspension is placed on an inverted coverslip positioned on an O-ring adjacent to a bar magnet and exposed to air [5, 6]. Using this assay, MTB from the Northern and Southern Hemispheres were found to exhibit north- and south-seeking swimming polarities, respectively, as indicated by their predominant accumulation at the edge of the drop facing the south or north pole of the magnet [6]. This directional behavior aligns with current Earth's magnetic field orientation (where the North Magnetic Pole corresponds to the south pole of a physical magnet) and likely facilitates a downward-directed response into less oxygenated or anoxic regions in both hemispheres, away from zones with potentially detrimental oxygen levels [6]. In natural MTB populations, upward geomagnetic field inclinations greater than 6° were associated with an enrichment of south-seeking cells over north-seeking cells by more than an order of magnitude, suggesting that polar magnetotaxis offers an advantage even at relatively shallow inclinations [11, 12]. In contrast, MTB populations from samples collected near the magnetic equator exhibited approximately equal proportions of north- and south-seeking cells [1, 11–14]. Although the mechanisms and relevance of magnetotaxis in environments with near-zero inclination are unclear, these findings indicate that the vertical component of the Earth's magnetic field plays a key role in selecting

the predominant swimming polarity in natural habitats [12, 13]. This conclusion is further supported by laboratory experiments, where sediment samples were exposed to magnetic fields opposing the geomagnetic polarity of their original sampling sites, leading to an inversion of swimming polarity within several weeks [1, 12]. By contrast, the selective mechanisms and ecological significance of swimming polarity have been challenged by occasional observations of both north- and south-seeking MTB coexisting within the Northern and Southern Hemispheres [15, 16].

Studies on axenic cultures of magnetotactic cocci support environmental assessments of swimming polarity. These studies demonstrated that the magnetic field orientation influences individual polarity fractions and the overall abundance of cells during cultivation in oxygen gradient media [10], as well as the ability of polar cells to form aerotactic bands in microcapillaries [5, 6, 17]. Along similar lines, in the laboratory model *Magnetospirillum gryphiswaldense* MSR-1, one of the few genetically tractable MTB, swimming polarity is closely linked to aerotaxis [7]. Strikingly, in *M. gryphiswaldense*, north- or south-seeking swimming polarity was rapidly reestablished within a few generations at single-cell and population levels when magnetic fields were applied parallel or antiparallel to the oxygen gradient, respectively, but was lost when cultures were grown under uniform oxygen conditions with agitation, resulting in equal proportions of both cell types in the hanging drop assay [7]. These observations suggest that the previously reported “axial” magnetotaxis—the apparent lack of swimming polarity in magnetospirilla [5, 17]—might be an artifact of laboratory cultivation [7]. In addition to its selection during growth, the polar response of *M. gryphiswaldense* was inverted when the hanging drop assay was performed under anaerobic conditions [7]. Upon oxygen exposure, cells immediately swam to the opposite side of the drop (and thus to the opposite magnetic pole), suggesting that their immediate directional bias is determined by whether they experience oxygen levels above or below their optimal range [7]. Further evidence for the relevance of magnetic field polarity in navigation by *M. gryphiswaldense* was provided by microcapillary assay studies, which demonstrated that the orientation of the magnetic field relative to the oxygen gradient affects both aerotactic band formation efficiency and band stability [8, 9, 18]. In cell populations derived from oxygen gradient media, inverting the magnetic field resulted in an immediate, partial dispersal of the band, suggesting that polar subpopulations were directed toward regions above and below their preferred oxygen concentration [8]. Overall, these findings show that aerotaxis and swimming polarity are tightly linked, yet mismatches between magnetic-field

and oxygen-gradient orientations can steer cells into otherwise non-preferred regimes.

While the studies discussed above suggest that matching swimming polarity is crucial for magneto-aerotaxis, a quantitative assessment of its role in navigating toward low-oxygen environments, as well as a systematic analysis of how magnetic-field precultivation conditions affect magneto-aerotaxis performance in different field settings, has not yet been performed. To address this gap, we performed microcapillary assays on *M. gryphiswaldense* populations grown under distinct, controlled magnetic field conditions, complemented by quantitative analyses and competition assays between north- and south-seeking cells. Prior to microcapillary experiments, the polarity bias of cell populations was assessed using the hanging drop assay, allowing us to directly link observations across both assays. Thereby, we found that the relative abundance of north- and south-seeking cells in the hanging drop assay is mirrored in their distribution within aerotactic bands formed under magnetic fields aligned parallel or antiparallel to the oxygen gradient. Importantly, we demonstrate that swimming polarity matching the magnetic field orientation substantially enhances migration toward microoxic zones and confers a competitive advantage during magneto-aerotaxis. We further confirm that swimming polarity is selected within just a few generations according to the orientation of the magnetic field relative to the oxygen gradient. Additionally, we identify light-dependent motility responses that drive collective, unidirectional migration along the oxygen gradient. Finally, we discuss our findings not only within the context of existing literature, but also through illustrative models exploring potential mechanisms underlying swimming polarity determination and selection.

Results

Swimming polarity is influenced by magnetic field orientation and intensity

Prior to analyzing swimming polarity using the capillary assay, we aimed to obtain cultures enriched in either north- or south-seeking cells through a cultivation-dependent approach described previously [7]. Therefore, cultivation was performed in non-agitated culture tubes (to establish a vertical oxygen gradient), superimposed with a homogeneous 0.6 mT magnetic field produced by coils oriented either parallel (northern field, NF) or antiparallel (southern field, SF) to the oxygen gradient (Additional file 1: Fig. S1A), simulating Northern and Southern-Hemisphere geomagnetic field polarity, respectively. Consistent with prior results [7], swimming polarity typically developed after ~10 generations of incubation. Hanging drop assays demonstrated a strong enrichment of the respective polarity type; however,

cultures never contained exclusively one type (Fig. 1A,B). In addition to artificially generated vertical magnetic fields, cultures were incubated in the local geomagnetic field (GMF) and in a zero field (ZF) with the GMF cancelled (Additional file 1: Fig. S1A). Although previous studies indicate that magnetospirilla exhibit only moderate alignment in physiologically relevant magnetic fields [19, 20], incubation in the GMF (see Methods for field parameters) led to a subtle yet detectable enrichment of north-seeking cells relative to south-seeking cells, suggesting that the GMF is sufficient for swimming polarity selection (Fig. 1C). Nevertheless, enrichment for one polarity type was notably lower compared to artificially imposed magnetic fields. As expected, incubation in a ZF environment did not promote preferential enrichment of one polarity type (Fig. 1D).

Matching swimming polarity improves navigation to microoxic conditions

To identify the benefits of swimming polarity on magneto-aerotaxis, culture samples were transferred into flat glass capillaries. Two capillaries, each filled with the sample and sealed at one end to establish a unidirectional oxygen gradient, were inverted relative to each other (Additional file 1: Fig. S1B) and monitored in parallel to observe aerotactic band formation (Additional file 1: Fig. S2) under magnetic fields resembling Northern- and Southern-Hemisphere geomagnetic field polarity, hereafter referred to as NF and SF settings, respectively. In agreement with prior work showing preferential accumulation of *M. gryphiswaldense* in regions containing 2–4 μM oxygen compared to the 216 μM present at the liquid–air interface [9], aerotactic band formation was observed a few millimeters below the meniscus. As assessed by dark-field micrographs acquired under identical illumination, the distribution of cells in the aerotactic band under the two magnetic field polarities (Fig. 2; see also Additional file 1: Fig. S2 for the time-course of band formation and Additional file 1: Fig. S3 for overlaid intensity distributions) reflected the proportions of north- and south-seeking cells observed in the hanging-drop assay (Fig. 1). However, while quantification in the hanging-drop assay is limited by the curved geometry of the drop, rectangular flat glass capillaries enabled precise measurement of aerotactic band characteristics, including distance from the meniscus, band width, and band peak intensity.

Analysis of aerotactic band intensity profiles revealed that, under the NF setting, SF cultures exhibited a 75% reduction in peak band intensity compared to NF cultures (Fig. 2A), indicating substantially reduced accumulation of south-seeking cells. Conversely, under the SF setting, NF cultures exhibited a marked decrease in band intensity, with the peak reduced by ~70% relative to SF

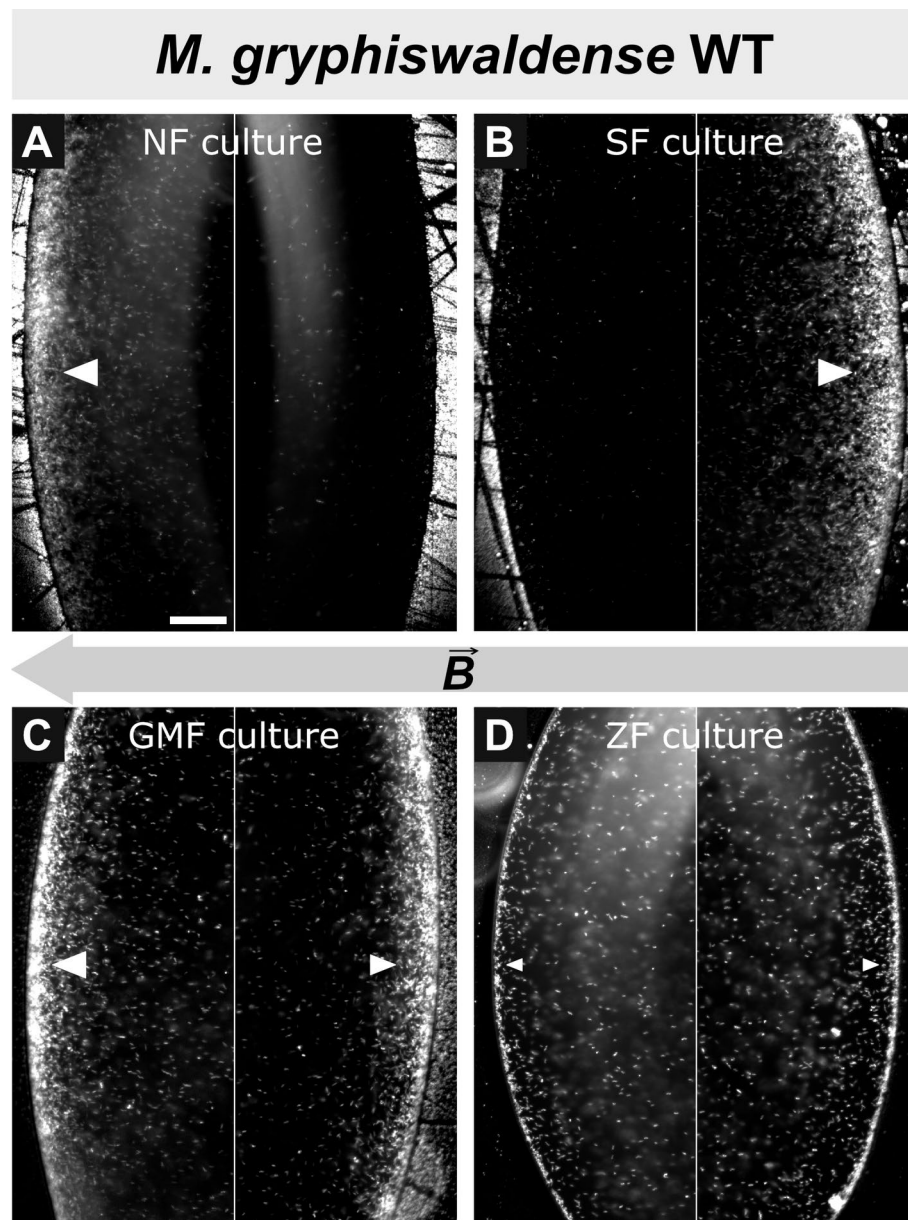


Fig. 1 Cultivation-dependent selection of swimming polarity in *M. gryphiswaldense* wild-type cells. Swimming polarity was analyzed using hanging-drop assays. Cells accumulating at the drop edges corresponding to the north and south magnetic poles are classified as south-seeking and north-seeking, respectively. Representative images of both edges of the same drop are shown for each sample. Cultures were grown for at least 10 generations in vertical oxygen gradients under the following magnetic field configurations: **A** NF: uniform magnetic field applied parallel to the oxygen gradient, enriching north-seeking cells. **B** SF: uniform magnetic field applied antiparallel to the oxygen gradient, enriching south-seeking cells. **C** GMF: growth under the ambient geomagnetic field (Bayreuth, Germany). **D** ZF: ambient magnetic fields were eliminated. The gray arrow indicates the magnetic field ($\vec{B}$) direction, with the arrowhead marking the magnetic south pole direction. White arrowheads indicate enrichment of cells; arrowhead size reflects its extent. Scale bar: 50 μ m (applies to all images; shown in **A**)

cultures (Fig. 2B). Furthermore, intensity profile analysis confirmed that growth under relatively weak GMF conditions (GMF cultures) was sufficient to select for north-seeking cells, as the peak aerotactic band intensity under the NF setting reached ~99% of that observed for NF cultures (Fig. 2A). In contrast, under the SF setting, GMF cultures reached nearly 80% of the peak band intensity of SF cultures (Fig. 2B), indicating that they still contained

a substantial number of south-seeking cells (consistent with hanging-drop results, Fig. 1) and that the artificially imposed field on NF cultures exerted stronger selective pressure. A balanced coexistence of north- and south-seeking cells in ZF cultures, as seen in the hanging-drop assay (Fig. 1), was reflected by aerotactic band peak intensities of ~50% relative to NF and SF cultures under both NF and SF settings (Fig. 2A,B).

M. gryphiswaldense WT

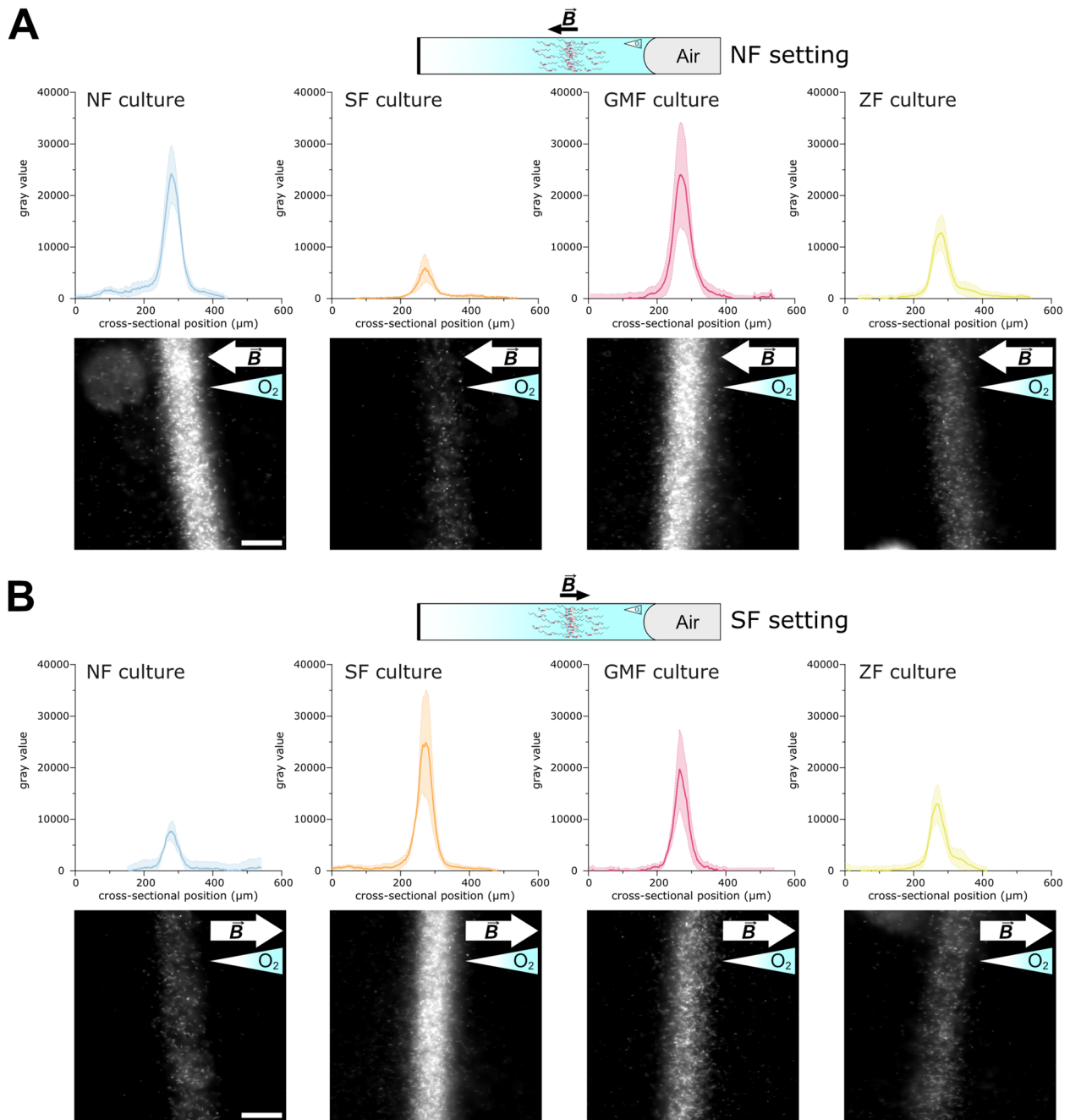


Fig. 2 Intensity profile analysis of aerotactic bands of *M. gryphiswaldense* wild-type cultures. To study aerotactic band formation, cultures were adjusted to the same optical density and loaded into glass microcapillaries. Capillaries were sealed at one end to establish a unidirectional oxygen gradient and examined by dark-field microscopy under both NF (**A**) and SF (**B**) settings. NF and SF cultures were precultured in uniform magnetic fields oriented parallel and antiparallel to the oxygen gradient, respectively. GMF cultures were incubated in the ambient geomagnetic field, ZF cultures in zero field. Aerotactic band intensity profiles and dark-field micrographs shown correspond to the 180-min time point, when aerotactic bands had stabilized; imaging settings were kept constant across experiments. Black and white arrows indicate magnetic field ($\vec{B}$) directions; gradient-filled triangles indicate oxygen gradient directions. Peak intensity (from intensity profiles) was used as a proxy for the number of cells within the aerotactic band. Intensity profiles represent the mean $\pm$ standard error of the mean (SEM) from $n = 3$ independent experiments. Scale bars: 50 μm (apply to all images; shown only in the leftmost images)

The distance of the aerotactic band to the air–liquid interface was monitored throughout the capillary assay, with no notable differences in dynamics observed between the four culture conditions (Additional file 1: Fig. S4). Moreover, after 180 min in the microcapillary, the distance of the aerotactic band from the meniscus did not significantly differ among cultures (Fig. 3A). However, cells from NF cultures accumulated slightly closer to the meniscus under the NF setting, while SF-culture cells displayed the same behavior under the SF setting. This observation may reflect accelerated oxygen depletion due to higher cell density, which could lead to faster migration of the aerotactic band toward the meniscus. Finally, measurements of the full width at half maximum of aerotactic bands revealed no significant differences among the culture conditions (Additional file 1: Fig. S5A).

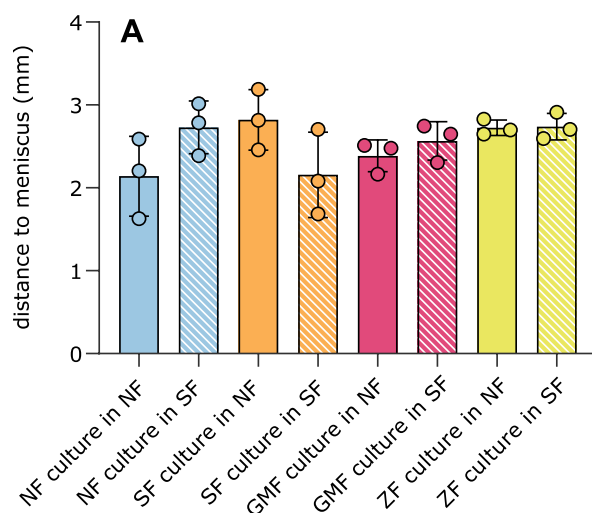
To confirm that the differences observed among wild-type cultures in the capillary assay are due to differences in swimming polarity, we performed equivalent cultivation and capillary experiments using the non-magnetic $\Delta mamAB$ strain, which lacks the entire *mamAB* operon essential for magnetosome formation [21] and is therefore unable to develop swimming polarity (Additional file 1: Fig. S6) [7]. Compared to wild-type cells (Additional file 1: Fig. S4, S5A), $\Delta mamAB$ cells showed only minor differences in aerotactic band morphology and in the spatiotemporal dynamics of its formation under magnetic field influence (Additional file 1: Fig. S5B, S7), indicating that aerotaxis alone is sufficiently efficient under the given experimental conditions. However, unlike the

wild type, the $\Delta mamAB$ strain showed no differences in aerotactic band intensity distributions between cultures grown under different magnetic fields or between fields applied parallel versus antiparallel during the capillary assay (Fig. 4). This confirms that the differences observed among wild-type samples (Fig. 2) are attributable to the biomagnetism-dependent selection of swimming polarity during preceding culture growth.

A matching swimming polarity bias confers competitive advantage in magneto-aerotaxis

To directly assess the competitive advantage conferred by a matching swimming polarity, we conducted competition experiments between fluorescently labeled north- and south-seeking cells. To this end, we introduced genes encoding soluble green (monomeric NeonGreen, mNG) and red (monomeric Cherry, mCherry) fluorescent proteins into both wild-type and $\Delta mamAB$ strains. Cultures of the resulting strains were then incubated again under conditions permissive for swimming polarity selection. In cultures of fluorescently labeled wild-type cells, this resulted in a notable enrichment of cells exhibiting the expected swimming polarity based on the applied magnetic field orientation during cultivation, as revealed by hanging drop assays (Additional file 1: Fig. S8). In contrast, fluorescent $\Delta mamAB$ cells grown under conditions permissive for swimming polarity selection showed no preferential accumulation on either side of the drop (Additional file 1: Fig. S8). Subsequently, green- and red-labeled wild-type cells grown under opposite

M. gryphiswaldense WT



M. gryphiswaldense $\Delta mamAB$

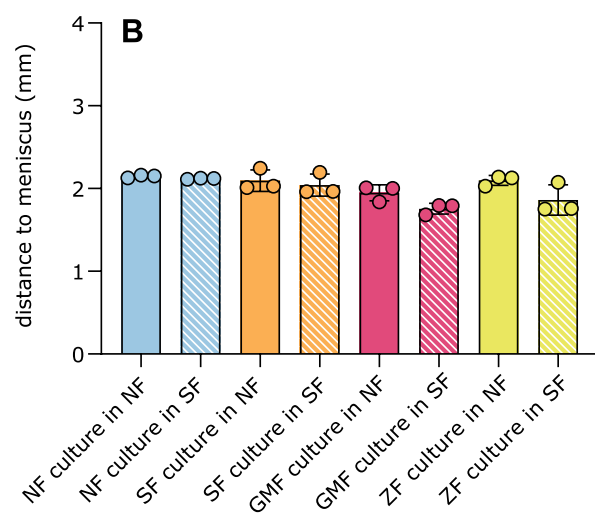


Fig. 3 Distance of the aerotactic band to the air–liquid interface within the microcapillary after 180 min for *M. gryphiswaldense* wild-type (**A**) and $\Delta mamAB$ (**B**) cultures. Overall, no statistically significant differences were found between samples and magnetic field conditions (Kruskal–Wallis test with Dunn's multiple comparison test, $p \geq 0.05$). However, aerotactic bands of NF cultures stabilized slightly closer to the meniscus under the NF setting, while SF-culture bands were similarly positioned under the SF setting (**A**). These positional differences were not observable in $\Delta mamAB$ cultures (**B**). Bars represent the mean and error bars the standard deviation (SD) from $n = 3$ independent experiments. Individual measurements are shown as dots

M. gryphiswaldense $\Delta mamAB$

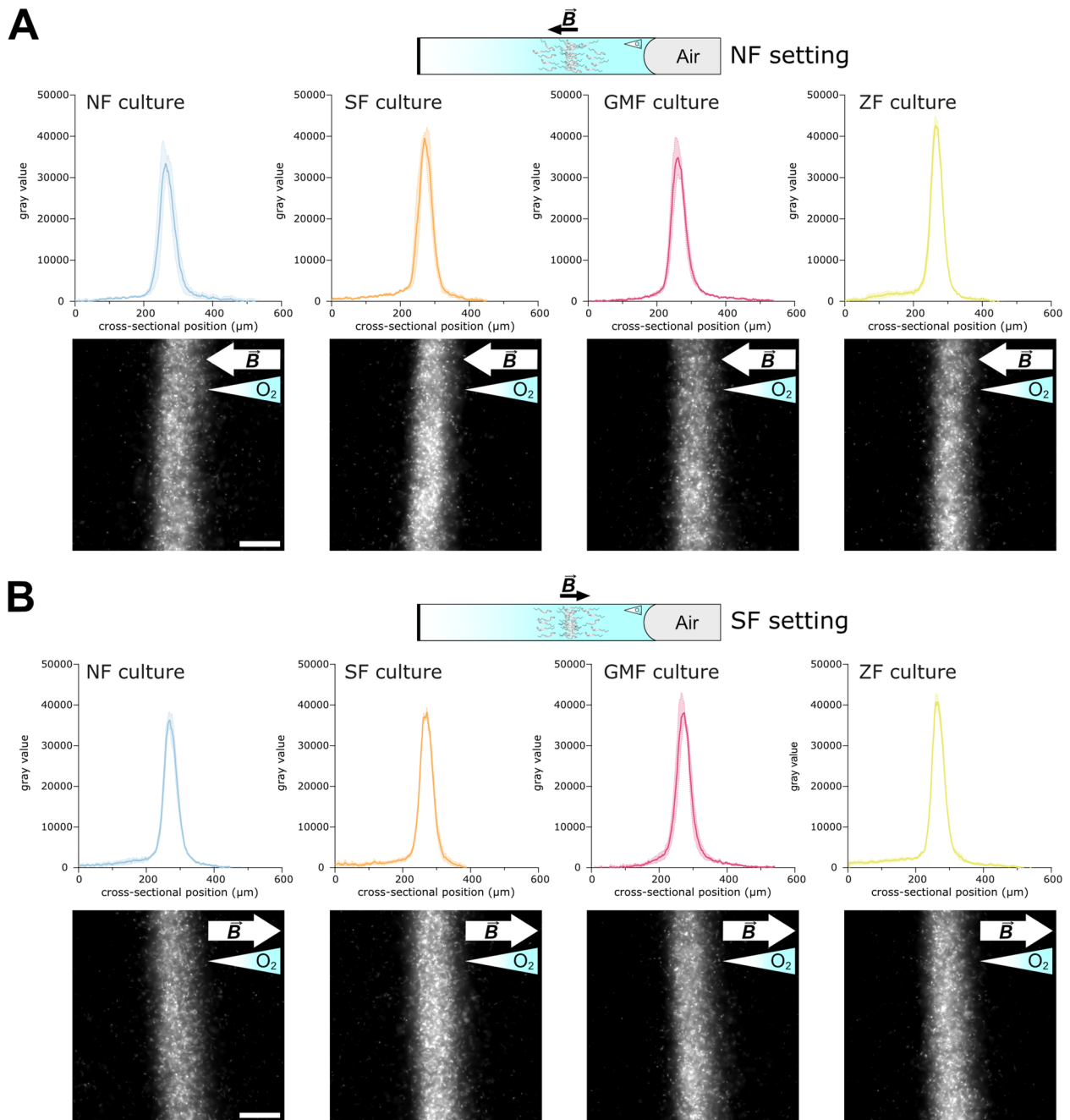


Fig. 4 Aerotactic band intensity profile analysis of *M. gryphiswaldense* $\Delta mamAB$ cultures. $\Delta mamAB$ cells were pre-cultured and analyzed in microcapillaries using procedures identical to those applied to the wild-type strain. Band intensity profiles (mean $\pm$ SEM, $n = 3$) were determined from dark-field micrographs after 180 min. Unlike the wild type, $\Delta mamAB$ cultures showed consistent aerotactic band intensity profiles across all precultivation conditions, and independent of whether the NF (**A**) or SF (**B**) setting was applied during the capillary assay. Black and white arrows denote magnetic field directions ($\vec{B}$), while gradient-filled triangles indicate oxygen gradient directions. Scale bars: 50 μm (apply to all images; shown only in the leftmost images)

polarity-selection conditions were mixed at a 1:1 ratio and examined again by the hanging drop assay, confirming that cells of each fluorescence predominantly migrated to opposite sides of the drop (Fig. 5).

Mixed populations—comprising approximately equal numbers of green-labeled north-seeking and red-labeled south-seeking wild-type cells—were then subjected to capillary assays under NF and SF settings (Fig. 6). Aerotactic bands were imaged using sequential exposure with

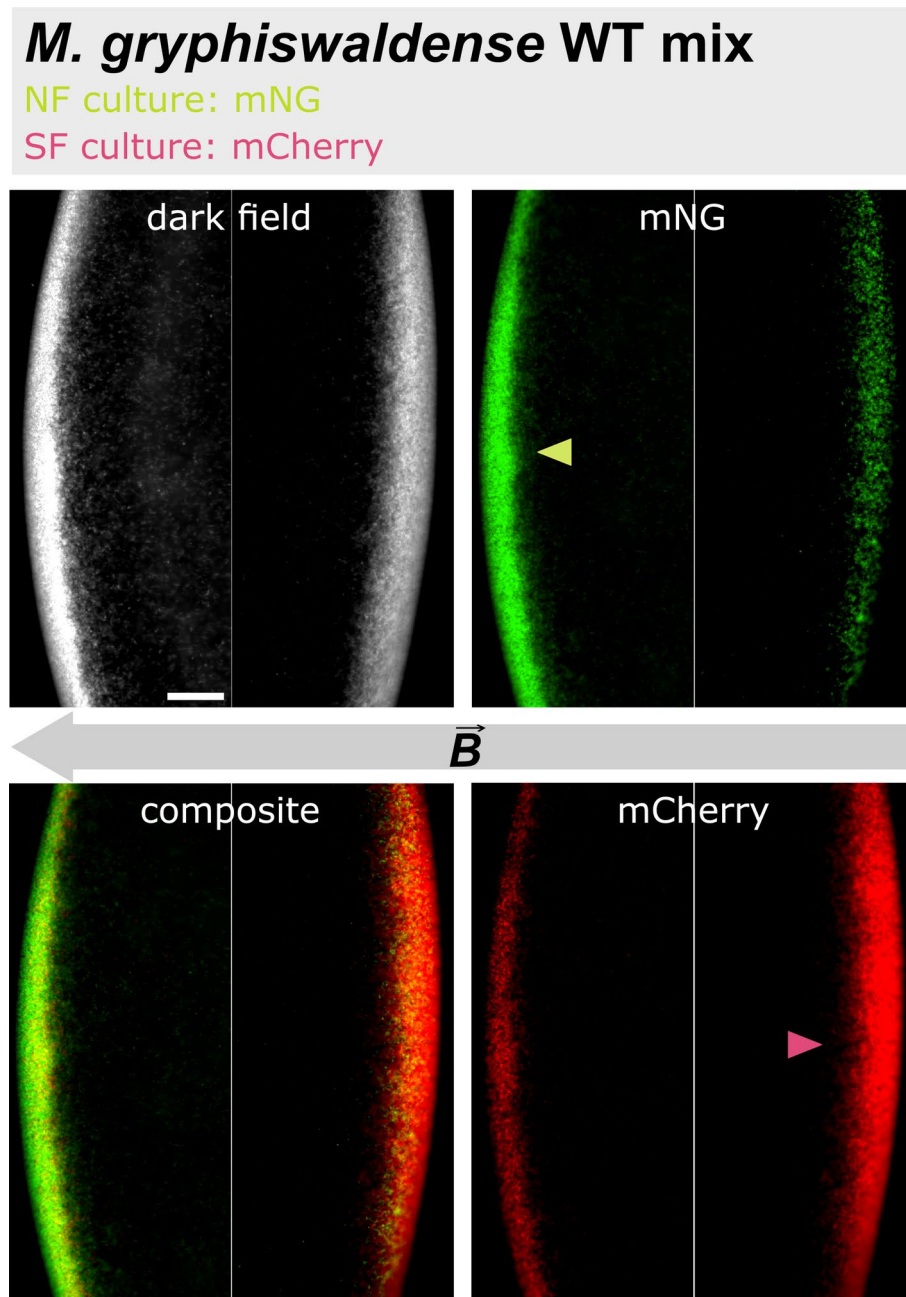
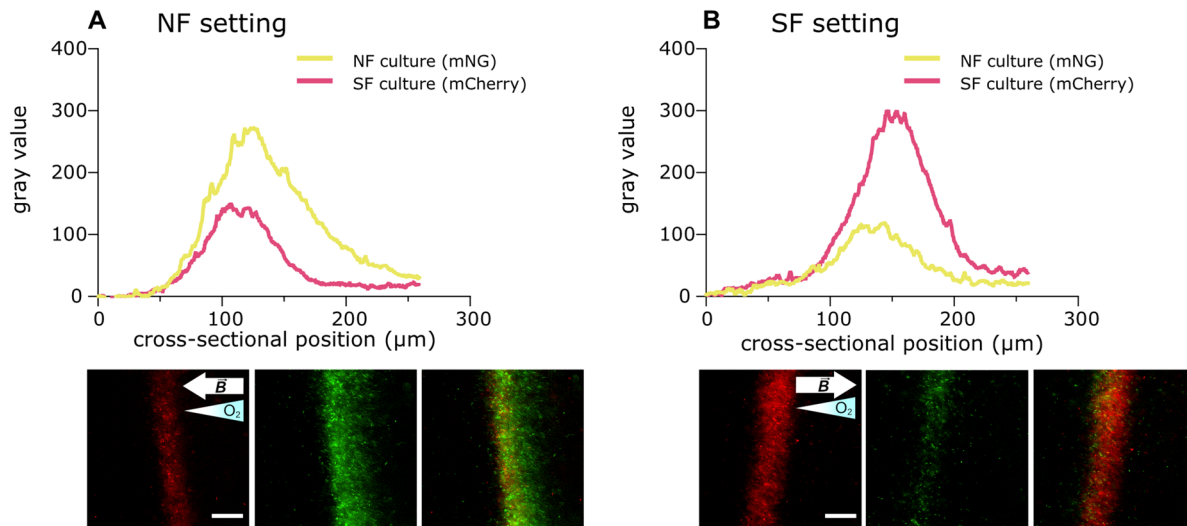


Fig. 5 Swimming polarity-based separation of fluorescently labeled north- and south-seeking wild-type cells in the hanging drop assay. Predominantly north-seeking cells (NF culture), expressing mNG, and predominantly south-seeking cells (SF culture), expressing mCherry, were mixed in equal numbers. Green, north-seeking cells predominantly swam parallel to the applied magnetic field, whereas red-labeled south-seeking cells primarily moved in the opposite, antiparallel direction. Dark-field image (upper row, left), mNG channel (upper row, right), composite of the mNG and mCherry channels (bottom row, left), and mCherry channel (bottom row, right) are shown. The gray arrow indicates the direction of the magnetic field ($\vec{B}$); colored arrowheads indicate preferential enrichment of cells with the respective fluorescence label in the individual fluorescence channels. Scale bar: 50 μm (applies to all images; shown in the upper left image)

both fluorescence channels to quantify the abundance of green and red cells. When the NF setting was applied during the assay, green-fluorescent wild-type cells predominated within the aerotactic band, as evidenced by a stronger mNG signal compared to mCherry (Fig. 6A). In contrast, when the same mixed culture was analyzed

under the SF settings, the opposite pattern emerged, and red-fluorescent wild-type cells accumulated at higher intensities within the band (Fig. 6B). These findings are consistent with capillary assays performed on non-fluorescent cells and confirm that correct swimming polarity confers a direct competitive advantage under matching

M. gryphiswaldense WT mix



M. gryphiswaldense $\Delta mamAB$ mix

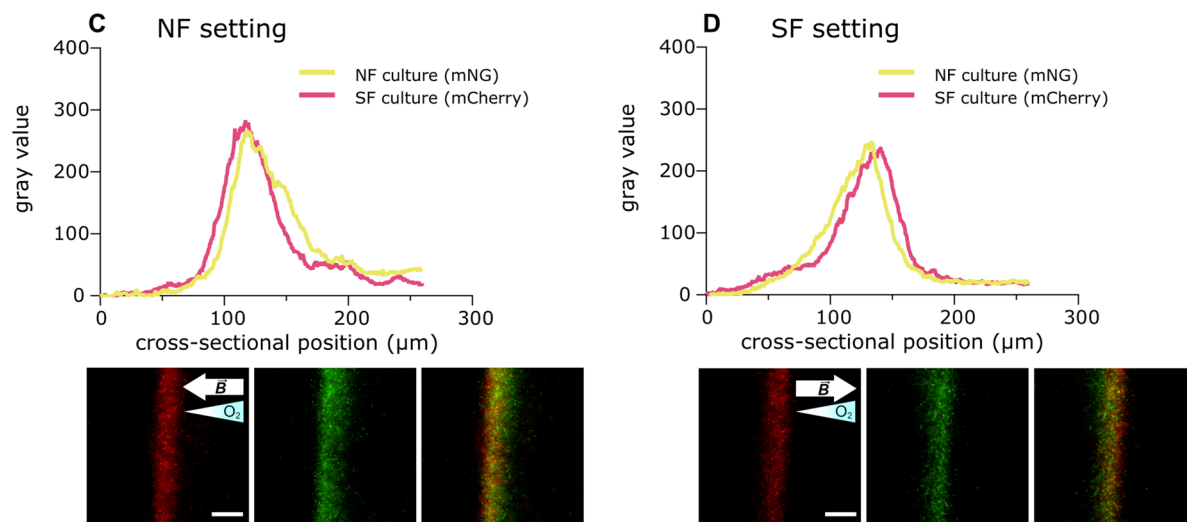


Fig. 6 Correct swimming polarity confers a competitive advantage in mixed populations of north- and south-seeking cells. Equal proportions of green-fluorescent (mNG-expressing, predominantly north-seeking) and red-fluorescent (mCherry-expressing, predominantly south-seeking) wild-type cells were mixed and subjected to capillary assays under NF and SF settings. After 120 min, under the NF setting, green-fluorescent wild-type cells predominated in the aerotactic band (**A**), whereas under the SF setting, red-fluorescent cells outcompeted green-fluorescent cells (**B**). In contrast, the abundance of red and green $\Delta mamAB$ cells did not differ with respect to the applied magnetic field (**C, D**). Shown are representative intensity profiles and fluorescence micrographs (left to right: mCherry, mNG, composite) of aerotactic bands obtained from a total of $n=6$ experiments. White arrows indicate magnetic field directions ($\vec{B}$), while gradient-filled triangles indicate the direction of oxygen gradients. Scale bars: 50 μm (apply to all images; shown only in the leftmost images)

magnetic field conditions. Consistent with this, no such effect was observed in corresponding assays with fluorescently labeled, non-magnetic $\Delta mamAB$ cells lacking a defined swimming polarity (Fig. S9). In these experiments, red and green fluorescence intensities—and thus cell abundances—were comparable within the aerotactic band, regardless of the applied magnetic field orientation

(Fig. 6C,D). The congruent fluorescence profiles of the $\Delta mamAB$ strain (with comparable numbers of red- and green-fluorescent cells loaded into the capillary) further confirmed that the differences observed in mixed wild-type populations reflect genuine differences in cell accumulation rather than variations in fluorescent protein expression, brightness, or imaging-related artifacts.

This is further supported by the additive peaks in mixed wild-type populations, which become apparent when the peaks for one culture are summed across the NF and SF settings, yielding comparable total intensities for both fluorescent labels.

M. gryphiswaldense exhibits light-driven behavioral responses

Several studies suggested that responses to light play an important role in MTB navigation, complementing magneto-aerotaxis [5, 22–24]. However, to our knowledge, until now, such behavior in *M. gryphiswaldense* had not been reported. Experiments with fluorescence illumination revealed an interesting side finding: the aerotactic band shifted by more than 100 μm toward the meniscus upon activation of the fluorescence light source using a green fluorescent protein (GFP) filter set (i.e., blue light). Migration of the band toward the meniscus occurred rapidly, irrespective of whether the NF or SF setting was applied during the experiment, with a change in position within a few seconds, after which movement slowed. This behavior was observed not only in wild-type populations (Fig. 7, Additional file 4: Movie S1) but also in non-magnetic ΔmamAB cells (Additional file 5: Movie S2), further indicating that it is independent of biomagnetism (legends for all Supplementary Movies are provided in Additional file 3). Notably, the blue-light response was only partially reversible—when the fluorescence illumination was switched off, the aerotactic band returned within a few seconds to a position closer to, but not identical with its original location (Fig. 7, Additional files 4–5: Movies S1–S2). No band shift was observed when green light (mCherry filter set) was switched on; however, subsequent switching off the green light caused a slight shift of the band away from the meniscus (Additional file 6: Movie S3). During continuous blue-light exposure (~ 12 min), the aerotactic band steadily migrated toward the meniscus, but its movement slowed over time and stabilized at ~ 5 min (Additional file 7: Movie S4), indicating adaptation to constant blue-light stimulation. It should

be noted, however, that after prolonged blue light exposure, the band also partially dissipated, suggesting potential harmful effects on the cells that prevented further migration of the band.

Discussion

The ability of organisms to respond to Earth's magnetic field, known as magnetosensation, was likely shaped by evolutionary pressures arising from the dynamic geomagnetic field, which varies in intensity and undergoes complete polarity reversals over geological time scales [4, 14, 25, 26]. MTB not only align with magnetic fields of a given strength but also respond to field polarity—a behavior closely linked to their chemosensory abilities that allow for temporal perception of oxygen gradients [4, 7–9, 20]. Here, we examined the impact of this polar response on magneto-aerotaxis. We show that matching swimming polarity is crucial for directing cells toward low-oxygen environments, as evidenced by their predominant accumulation within the aerotactic band only when the magnetic field orientation relative to the oxygen gradient in the capillary matches that experienced during prior culture incubation (Figs. 2, 6). Together with magnetic field inversion experiments [5, 8], these findings suggest that cells with a non-matching polarity bias are redirected into regions above or below their microaerophilic optimum. The faint aerotactic bands that appear when the magnetic-field polarity opposes the prior cultivation condition (Fig. 2) likely arise from the small fraction of cells whose swimming polarity remains consistent with the applied field, as polarity selection did not yield completely uniform populations (Fig. 1). Unlike the oxygen gradients observed in microcapillaries [9], the hanging drop assay likely creates an environment where oxygen levels exceed the physiological optimum [6, 17]. While local oxygen depletion may occur depending on cell density and droplet geometry, in small droplets exposed to air, continuous and rapid oxygen replenishment from the atmosphere prevents the establishment of stable microoxic conditions [6, 17]. Consistent with our

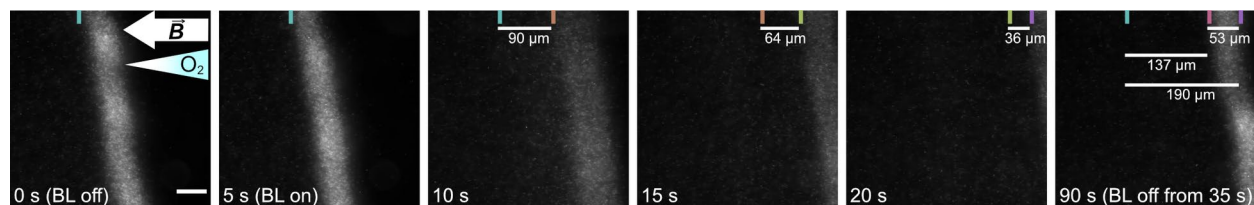


Fig. 7 Response to blue light in *M. gryphiswaldense*. Individual frames from a representative time-lapse recording of wild-type cells using dark-field illumination are shown. The excitation light source for fluorescence imaging (GFP filter set) was activated at 5 s and switched off at 35 s. Blue light (BL) induced a unidirectional movement of cells toward the meniscus, suggesting that light-induced behavior is mechanistically coordinated with aerotaxis. Colored bars indicate the position of the aerotactic band, with each color assigned to a specific location. When the band shifts between time points, the bar color changes accordingly. The movement of the band between two images is visualized by the spatial separation of bars of different colors in the respective frames. Time stamps are indicated in each image. The white arrow shows the direction of the magnetic field ($\vec{B}$), while the colored triangle indicates oxygen gradient direction. Scale bar, 50 μm , in the leftmost image applies to all images

experimental observations, cells do not accumulate in the droplet center but instead localize near the droplet edges—preferentially on the side facing magnetic north or south, depending on their polarity bias—suggesting that oxygen levels remain above their optimal range and trigger a repellent response. Our results further show that combining microcapillary assays with intensity profile analysis allows quantification of north- and south-seeking subpopulations (Fig. 2). In contrast, the hanging drop assay is, at best, semi-quantitative, as pixel intensity measurements at the drop edge are prone to error due to the curvature of the droplet, making results sensitive to the focal plane. Whereas the peak height (or, alternatively, the area) of the aerotactic band intensity profile is well suited for quantifying swimming polarity (Fig. 2), the band width (Fig. S5) and the distance to the meniscus appear less suitable (Fig. 3). In particular, the latter is influenced by the steepness of the oxygen gradient, which in turn depends on the number of cells present in the band and their respiratory activity [9, 18]. The resulting altered spatiotemporal dynamics of band formation may explain the—rather small and statistically non-significant—differences in band distance to the meniscus between wild-type populations with non-matching swimming polarity, those with matching swimming polarity, and $\Delta mamAB$ cells (Fig. 3).

Despite general agreement with previous studies, some unclarity remains. For instance, our analysis suggests that zero-field-grown *M. gryphiswaldense* populations contain equal fractions of north- and south-seeking cells (Figs. 1, 2). This implies that, in the presence of a magnetic field, half of the cells—those with non-matching polarity—are guided away from the aerotactic band and do not contribute to its formation, as reflected by reduced peak intensities in aerotactic band profiles (Fig. 2). Consistent with our observations, early studies reported equal numbers of MTB of each swimming polarity in mud samples maintained in a zero-field environment for extended periods [1, 12]. Moreover, this distribution is consistent with what has been observed in hanging drop assays of (GMF-exposed) *M. gryphiswaldense* cultures grown under homogenous oxygen concentration [7]. However, field inversion experiments on *M. gryphiswaldense* populations grown under homogeneous oxygen concentrations—as well as similar experiments with “axial” *Magnetospirillum magnetotacticum* populations, which form aerotactic bands at both ends of a capillary opened at both ends (unlike polar magnetotactic cocci that formed bands only at one end of the capillary)—showed that cells rotated by 180° upon field inversion but remained within the band [5, 6, 8, 17]. Thus, different results provide conflicting information about whether a genuine “axial” state exists, or if “axial” merely refers to populations containing equal

numbers of north- and south-seeking cells. Since our study design did not include field inversion experiments, we cannot comment on whether the polarity bias of cells among different cultivation samples after band establishment differed from their initial bias prior to aerotactic band formation. Furthermore, comparing results across studies is challenging due to variations in growth conditions and sample preparation. Nevertheless, the previous simultaneous observation of *M. gryphiswaldense* cells swimming away from the band in both directions, alongside cells that rotate by 180° and remain within the band upon field reversal, indicates the coexistence of subpopulations of “polar” and truly “axial” cells [8]. Previous single-cell analyses further suggest that non-polarized *M. gryphiswaldense* populations are not simply a mixture of north- and south-seeking cells, even though hanging-drop assays indicated approximately equal proportions of both swimming polarities [7].

Another important point to consider is that, although previous capillary experiments with wild-type cells under zero-field conditions and magnetic fields (anti) parallel to the oxygen gradient indicated a general benefit of magnetic alignment for aerotactic band formation [9, 18, 27], we did not observe pronounced differences between wild-type cells with matching swimming polarity and non-magnetic $\Delta mamAB$ cells in the capillary assay (Figs. 2–4, Additional file 1: Figs. S3–5, S7). These findings suggest that aerotaxis alone is sufficiently effective under the given experimental conditions. Notably, the navigational benefit of magnetic alignment may be greater in structured environments that resemble natural MTB habitats (where movement is spatially constrained) [28, 29] compared to bulk liquid conditions in capillary assays, in systems subject to perturbations [5], or in long-term cultivation experiments [30]. Moreover, it must be considered that even within our polarity-selected wild-type populations, a certain fraction of cells consistently exhibited non-matching swimming polarity (Figs. 1–2). Therefore, to draw definitive conclusions, similar experiments—including direct competition assays—should be conducted using not just comparable overall numbers of wild-type and $\Delta mamAB$ cells, but specifically wild-type cells of a single polarity type. Achieving such populations through a cultivation-dependent approach is experimentally challenging (Figs. 1 and 2), but could potentially be accomplished via magnetic enrichment of cells with one polarity type following selective growth [8]. Nonetheless, although capillary assays revealed no overarching advantage of magneto-aerotaxis over aerotaxis alone, a clear conclusion can be drawn: without prior cultivation under matching magnetic-field conditions, the aerotactic performance of *M. gryphiswaldense* is substantially reduced—such that non-magnetic cells unequivocally outperform magnetic wild-type cells precultured under

non-matching magnetic-field or zero-field conditions (Figs. 2, 4).

Additionally, our results provide evidence that a stronger, artificial magnetic field imposes a more pronounced selective pressure on swimming polarity (Fig. 1). While these laboratory fields (600 μ T) exceed natural geomagnetic intensities (25–65 μ T depending on location [31]), they were historically used to accelerate swimming polarity selection [7]. Nonetheless, our data show that the local GMF is sufficient to drive north-seeking polarity selection in *M. gryphiswaldense* (Figs. 1C, and 2), consistent with observations that fresh environmental magnetospirilla isolates display swimming polarity [6, 32–34]. Given that redox gradients in natural sediments are more stable than in our GMF-exposed laboratory cultures, the selective pressure in natural environments is likely stronger. In accordance with prior work [7, 27], we also observed that swimming polarity in *M. gryphiswaldense* lab cultures is selected within relatively few generations (Fig. 1), although even extended cultivation did not yield populations consisting exclusively of a single polarity type. Compared to the rapid adaptation of swimming polarity in *M. gryphiswaldense* within several days, in cultures of other MTB it took several weeks of incubation for the inversion of the population-wide swimming polarity bias to occur [1, 6, 12, 17]; however, this process is still extremely rapid when considered on geological time scales. Given that geomagnetic field reversals take thousands of years to complete, these findings raise questions about the selective mechanisms driving such rapid adaptive behavior [25, 26].

Currently, the molecular mechanisms governing swimming polarity determination and inheritance in single cells, as well as the selection of the prevailing polarity type at the population level, are poorly understood. Swimming polarity determination has been proposed to possibly involve both genetic determinants and epigenetically inherited information [4, 7, 12]. In *M. gryphiswaldense*, it is known that swimming polarity is closely tied to aerotaxis and the chemosensory pathway encoded by the major chemotaxis operon 1 [7]. Moreover, swimming polarity may depend on motility-related cellular asymmetries (cellular polarity) and on how corresponding structures align with the overall magnetic dipole (magnetic polarity) generated by the combined magnetosome dipoles [7]. In monopolarly flagellated MTB, it has been suggested that swimming polarity might be maintained by a constant positioning of the flagellum relative to the magnetic polarity (see, e.g., Figs. 1 and 3 in ref. [6]; see also refs. [1, 12, 17, 25, 35, 36]). However, no such cellular polarity is found in bipolarly flagellated magnetospirilla, which swim with a pushing lagging flagellum and a leading flagellum oriented toward and rotating around the cell body (ref. [37] in *Paramagnetospirillum*

magneticum AMB-1; and unpublished data from us in *M. gryphiswaldense*). Structural asymmetry of opposing flagellar motors has been discussed as a possible mechanism to control their counterrotation and to be regulated by multiple paralogous chemotaxis and flagellar genes present in magnetospirilla [7, 37, 38], such as, for example, two copies of the flagellar switch protein FliN or the three copies of putative MotAB stators in *M. gryphiswaldense*. Fig. 8 provides a hypothetical conceptual model of how swimming polarity might be achieved in bipolarly flagellated magnetospirilla, based on the positioning of two structurally distinct subtypes of counter-rotating flagellar motors relative to magnetic polarity and opposite switching behaviors of these motors in response to oxygen changes. While observations of polar *M. gryphiswaldense* cells at both the population and single-cell levels in response to atmospheric changes support such a model [7], it remains to be demonstrated whether structural differences of opposing flagellar motors exist and whether motor subtypes respond differently to external stimuli. Moreover, at present, no published experimental data unambiguously demonstrate motor counterrotation in magnetospirilla [38].

Also, the mechanisms underlying the inheritance of swimming polarity are largely unresolved. In cells where the orientation of cellular polarity relative to magnetic polarity is inherited to daughter cells during division (Fig. S10i), inversion of swimming polarity might be initiated by random loss of magnetosomes due to magnetosome missegregation and inversion of magnetic polarity by de novo formation of magnetosomes (Fig. S10ii), with a 50% probability of magnetic polarity inversion upon magnetosome loss [12, 17, 25]. However, magnetosome chain distribution to daughter cells is tightly regulated in *M. gryphiswaldense* [39, 40]. Apart from a loss of magnetosomes, remagnetization and swimming polarity inversion can be triggered by strong magnetic pulses (in the range of several tens of millitesla) [1, 41]. Although this may be relevant when permanent magnets are used to investigate or enrich MTB [42], such field intensities are unlikely in natural environments. Alternatively, swimming polarity inversion might occur as a result of the production of heterogeneous offspring caused by an inversion of cellular polarity in individual cells following cell division as a bet-hedging strategy (Fig. S10iii). It has been suggested that cells of the opposite non-matching swimming polarity (as also observed in our experiments, Fig. 1) might serve as progenitors and enable rapid swimming polarity inversion at the population level upon a field reversal [1]. Subsequently, the dominant swimming-polarity type could be selected by the prevailing orientation of the magnetic field relative to the oxygen gradient. However, this strategy may be energetically costly, as a fraction of the population would be consistently directed into

Swimming bias of north-seeking cells in the...

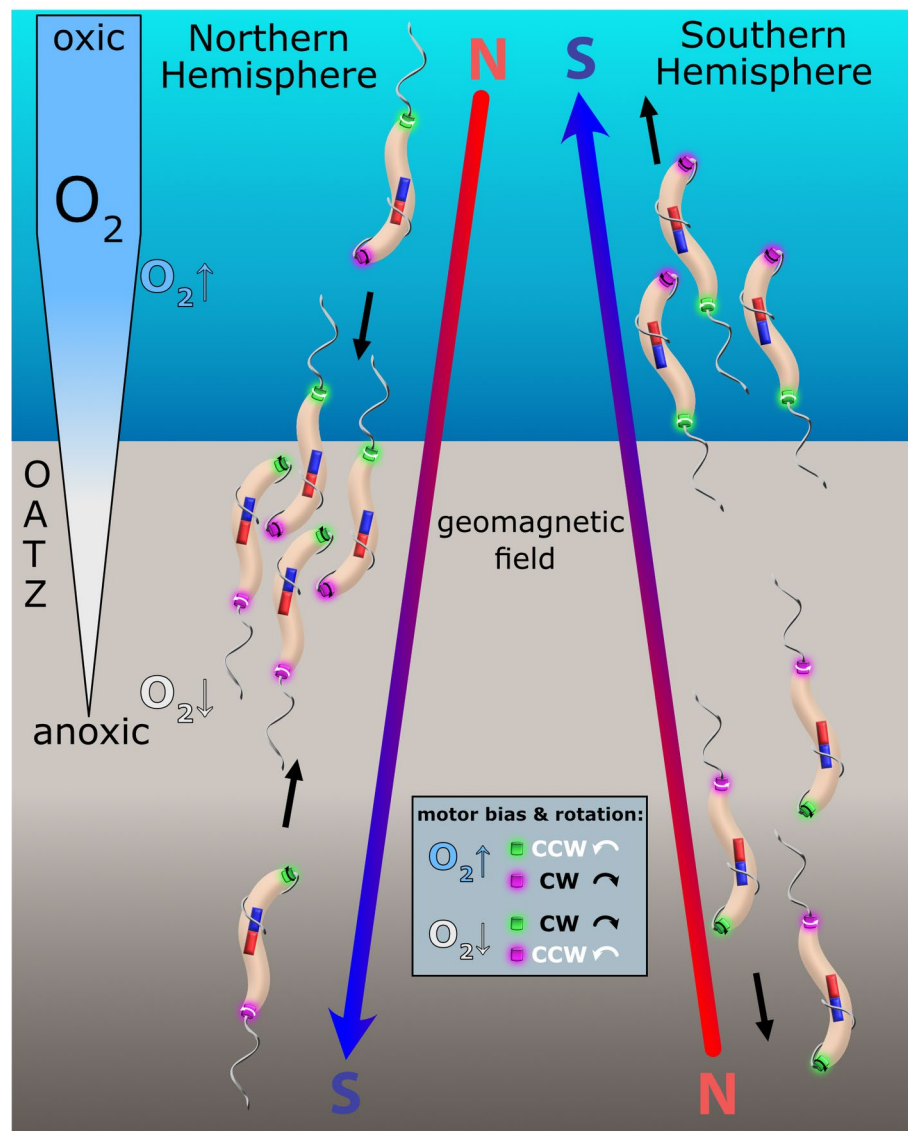


Fig. 8 Hypothetical model of swimming polarity determination in bipolarly flagellated magnetospirilla. In the illustrated model, swimming polarity is governed by the spatial positioning of two structurally distinct, counterrotating flagellar motor subtypes relative to the net magnetic moment of the magnetosome chain (represented by bar magnets). The two motors (shown in green and purple) exhibit opposing switching behavior when cells encounter oxygen concentrations deviating from their microaerophilic optimum. Exposure to oxygen levels exceeding the optimum ($O_2 \uparrow$) increases the probability of switching—the purple motor tends to switch to clockwise (CW) rotation, while the green motor switches to counterclockwise (CCW) rotation. Under suboxic conditions ($O_2 \downarrow$), the opposite switching behavior occurs. CW motor rotation is consistently associated with a flagellum rotating around the cell body at the leading cell pole, whereas CCW motor rotation corresponds to a lagging pushing flagellum. As a result, north-seeking polarity cells (only these are depicted) swim toward the oxic–anoxic transition zone (OATZ) under Northern Hemisphere magnetic field conditions, but away from the OATZ under Southern Hemisphere conditions. The model defines swimming polarity solely by the orientation of magnetic polarity relative to cellular polarity. North- and south-seeking cells respond similarly to temporal changes in oxygen levels, and the model does not incorporate magnetoreceptive mechanisms that involve sensing magnetic field intensity or polarity. Moreover, here, north- and south-seeking refers to the overarching swimming-polarity type characteristic of the cells, rather than merely the immediate swimming direction observed (as in some studies), which depends on whether cells encounter oxygen levels above or below their optimum. Note that this hypothetical model represents an extension of a previous model developed for monopolarly flagellated cells [6] and is primarily intended to provide potential explanations for how our observations at the population level may be explained at the level of individual cells. Although several features are supported by experimental findings—such as the responses of polar cells to oxygen fluctuations [7], as well as the orientation of leading and lagging flagella and the potential counterrotation of flagellar motors (ref. [37]; and unpublished data from us on *M. gryphiswaldense*)—other components, including individual motor responses to oxygen changes and the structural asymmetry of motors relative to magnetic polarity, currently lack experimental validation

hypo- or hyperoxic regions unfavorable for growth. The simultaneous occurrence of MTB with opposing swimming polarities in environmental samples and laboratory cultures [1, 8, 10, 15, 16] could also be an indicator that swimming polarity selection is influenced by multiple environmental cues, including redox and oxygen gradients (both downward and inverted), light (see below), or geomagnetic anomalies from magnetic grains or rocks [1, 5, 6, 8, 27, 43–45]. As discussed above, swimming polarity may also arise gradually within individual cells from a currently undefined intermediate non-polar (or genuine axial) molecular state, either in a selective manner or controlled by a dedicated, switchable molecular mechanism that regulates cellular polarity [7]. Potential mechanisms underlying swimming polarity determination are currently under investigation in our laboratory.

Notably, we also discovered a biomagnetism-independent, partially reversible, photobehavioral response in *M. gryphiswaldense*, characterized by the unidirectional collective movement of cells toward higher oxygen concentrations upon blue-light exposure (Fig. 7, Additional files 4–5, 7: Movies S1–S2, S4). The collective upward movement of *M. gryphiswaldense* cells in an oxygen gradient indicates that the light-dependent response is linked to aerotactic behavior. Similar observations were made in capillary experiments with *Magnetococcus* strain MC-1, but not when using *Magnetospirillum magnetotacticum* [5]. However, in this study, a migration of polar MC-1 cells away from the meniscus was observed upon blue-light exposure [5]. A blue-light response was also recently identified in the *M. gryphiswaldense*-related strain *P. magneticum* (via U-turn analysis) and attributed to the LOV-domain protein Amb2291 and the methyl-accepting chemotaxis protein Amb0994 [24]. Since the *M. gryphiswaldense* genome encodes similar proteins [27, 46], it will be important in the future to analyze their role in light-responsive behavior. It will also be crucial to understand the physiological relevance of this response in natural habitats and how it integrates with aerotaxis. Given the large penetration depth of blue light in water, it remains unclear why cells would swim toward higher oxygen levels upon blue light exposure—potentially exposing themselves to even higher doses of blue light. Also, the band shift observed after cessation of green light exposure (Additional file 6: Movie S3) may indicate additional mechanisms underlying light-driven spatial environmental orientation, warranting further investigation.

Conclusions

Our study underscores the importance of the GMF in magnetic-pole-dependent directional motility and highlights the adaptive nature of polar magneto-aerotaxis. We demonstrate that this behavioral response is tightly coupled with aerotaxis, offering a quantitative measure of

its role in navigating toward low-oxygen environments. Moreover, we show that *M. gryphiswaldense* integrates light-dependent stimuli into its aerotactic responses. Collectively, these findings advance our understanding of bacterial motility and emphasize the sophisticated sensing and integration of environmental cues in *M. gryphiswaldense*. They may also inform bioengineering strategies that exploit MTB as microrobots guided by oxygen, magnetic fields, and light-based (opto) cues, enabling precise spatiotemporal control of their movement for applications in microscale transport, targeted delivery, or environmental sensing.

Methods

Cultivation of bacterial strains

M. gryphiswaldense was cultivated in modified flask standard medium (FSM) [47] at 28 °C. Selection of swimming polarity was carried out according to established protocols [7]. This involved exposing non-agitated cultures (over subsequent culture passages) in glass screw-cap tubes with caps loosened by half a turn for at least 10 and up to 30 generations, to either a uniform 0.6 mT magnetic field (~12-fold stronger compared to the GMF) applied parallel or antiparallel to the oxygen gradient (simulating Northern or Southern Hemisphere geomagnetic field polarity, respectively) using coils, the local GMF (Bayreuth, Germany with north, east, and vertical components of 20.0 μ T, 1.5 μ T, and 45.0 μ T, respectively), or a zero-field generated by triaxial pairs of coils as a control (Additional file 1: Fig. S1A). The optical density and magnetic response (C_{mag}) of *M. gryphiswaldense* cultures were measured at 565 nm as described previously [27]. *Escherichia coli* was grown in lysogeny broth (LB) at 37 °C with shaking at 180 rpm. For the cultivation of *E. coli* WM3064 (W. Metcalf, unpublished), 0.1 mM DL- α , ϵ -diaminopimelic acid (DAP) was added. Media were solidified by adding 1.5% (w/v) agar. Selective growth was achieved using kanamycin at a concentration of 5 μ g/ml for *M. gryphiswaldense* and 25 μ g/ml for *E. coli*. All strains are listed in Additional file 2: Table S1.

Molecular and genetic techniques

Oligonucleotides (listed in Additional file 2: Table S2) were obtained from Sigma-Aldrich (Steinheim, Germany). Genes of interest were amplified using Q5 (NEB) proofreading DNA polymerase. Plasmids (Additional file 2: Table S1) were constructed using standard molecular biology techniques, incorporating FastDigest™ restriction enzymes and T4 DNA Ligase (Thermo Scientific). Constructs were sequenced by MacroGen Europe (Amsterdam, Netherlands). For the construction of mNG- and mCherry-producing *M. gryphiswaldense* strains, a *M. gryphiswaldense* codon-optimized *mNeonGreen* gene (*omNG100*) and the *mCherry* gene, each

under the control of the constitutive $P_{mamDC45}$ promoter, were amplified using primer pairs 717/718 and 717/719, respectively, and cloned into the Tn7 vector pBAMII, which enables site-specific genomic insertion [27]. The resulting constructs were transferred from *E. coli* WM3064 into the *M. gryphiswaldense* wild-type and $\Delta mamAB$ strains via conjugation. Successful transconjugants were verified by PCR screening using primers 558/559.

Hanging drop assay

Swimming polarity of *M. gryphiswaldense* populations was assessed using a modified version of the classical hanging-drop assay. Following cultivation, microdroplets (0.8 μ L) of cell suspension were transferred onto a coverslip, which was placed upside down on a stack of five layers of laboratory tape and imaged by dark-field illumination and/or fluorescence using the same microscope [20] used for the microcapillary assays (see below). To assess swimming polarity, a homogeneous 400 μ T horizontal magnetic field was applied using electromagnetic coils [20], and images of the droplet edges facing magnetic north and south were taken after ~ 5 min.

Microcapillary assays

Analysis of aerotactic band formation under defined magnetic field conditions was performed using custom-made triaxial magnetic coils mounted on a Nikon Eclipse FN1 upright microscope at room temperature. The microscope was equipped with a Nikon S Plan Fluor ELWD 20 $\times$ DIC N1 objective (NA 0.45), a Nikon dark-field condenser (NA dry 0.80–0.95), and a pco.edge 4.2 sCMOS camera (PCO). For the experiments, culture samples were adjusted to an OD₅₆₅ of 0.1 (corresponding to 8.7×10^6 cells/ml), and 1 ml of the diluted suspension was purged with N₂ for 15 min. Samples were transferred into rectangular glass capillaries (0.1 $\times$ 1 $\times$ 50 mm; Vitro Tubes #5010–050) by capillary forces, filling $\sim 2/3$ of the capillary with cell suspension. Capillaries were sealed at one end with vacuum grease to establish a unidirectional oxygen gradient. To study cell behavior under homogeneous 400 μ T magnetic fields mimicking Northern- and Southern-Hemisphere geomagnetic field polarity relative to the oxygen gradient, two capillaries were filled with the same cell suspension and positioned adjacent to each other, with one capillary inverted by 180° so that the aerotactic bands were at approximately similar positions along the microscope stage x-axis (Additional file 1: Fig. S1B). Images and/or videos were captured at various time points to document the spatiotemporal dynamics of aerotactic band formation. Images were acquired in dark-field illumination with a camera exposure of 40 ms, a readout speed of 95 MHz, and the manual light source intensity set to 11 o'clock to prevent overexposure. Band

distances from the meniscus and intensity profiles were measured using the line length and profile tools in ImageJ Fiji [48]. For competition experiments, equal numbers of fluorescently labeled wild-type and $\Delta mamAB$ cells were mixed, and the $\sim 1:1$ ratio was verified by fluorescence microscopy. Capillaries were filled with mixtures, and the capillary assay was performed as described above. Fluorescence illumination and acquisition were performed using a SOLA SE II light source (Lumencor) set to 100% intensity with 200 ms exposure time. The following filter sets were used: GFP (excitation 482/18 nm, dichroic 495 nm, emission 520/28 nm) and mCherry (excitation 562/40 nm, dichroic 593 nm, emission 640/75 nm). To minimize both the blue-light-dependent aerotactic band shift and photobleaching, images of the aerotactic band in fluorescence mode were acquired immediately after activation of the excitation illumination. Intensity profiles were derived from unprocessed images, whereas the depicted fluorescence micrographs of aerotactic bands were adjusted in ImageJ using identical minimum and maximum gray values across all channels to enhance overall contrast.

Statistical analysis

Statistical analyses were conducted using GraphPad Prism 10.1.1. Details on sample sizes (n), statistical tests, and p -value definitions are provided in the figure legends.

Abbreviations

MTB	Magnetotactic bacteria
NF	Northern field
SF	Southern field
GMF	Geomagnetic field
ZF	Zero field
WT	Wild type
mNG	Monomeric NeonGreen
mCherry	Monomeric Cherry
GFP	Green fluorescent protein
BL	Blue light
SEM	Standard error of the mean
SD	Standard deviation

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12866-026-05067-8>.

Supplementary Material 1.
Supplementary Material 2.
Supplementary Material 3.
Supplementary Material 4.
Supplementary Material 5.
Supplementary Material 6.
Supplementary Material 7.

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Authors' contributions

D.P. designed the study. C.W. performed experiments. C.W. and D.P. analyzed data. C.W. and D.P. wrote the manuscript.

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Data availability

All data supporting the findings of this study are available within the article and its Supplementary Information. The raw datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

1. Blakemore RP. Magnetotactic bacteria. *Annu Rev Microbiol.* 1982;36:217–38. <https://doi.org/10.1146/annurev.mi.36.100182.001245>.
2. Monteil CL, Lefèvre CT. Magnetoreception in microorganisms. *Trends Microbiol.* 2020;28:266–75. <https://doi.org/10.1016/j.tim.2019.10.012>.
3. Amor M, Mathon FP, Monteil CL, Busigny V, Lefèvre CT. Iron-biomineralizing organelle in magnetotactic bacteria: function, synthesis and preservation in ancient rock samples. *Environ Microbiol.* 2020;22:3611–32. <https://doi.org/10.1111/1462-2920.15098>.
4. Schüler D, Dziuba M, Pfeiffer D, Uebe R. Biosynthesis and function of magnetic organelles in magnetotactic bacteria. *Nat Rev Microbiol.* 2025. <https://doi.org/10.1038/s41579-025-01234-2>.
5. Frankel RB, Bazylinski DA, Johnson MS, Taylor BL. Magneto-aerotaxis in marine coccoid bacteria. *Biophys J.* 1997;73:994–1000. [https://doi.org/10.1016/S0006-3495\(97\)78132-3](https://doi.org/10.1016/S0006-3495(97)78132-3).
6. Frankel RB, Williams TJ, Bazylinski DA. Magneto-Aerotaxis. In: Schüler D, editor. *Magnetoreception and Magnetosomes in Bacteria*. Berlin, Heidelberg: Springer; 2007. p. 1–24. https://doi.org/10.1007/7171_2006_036.
7. Popp F, Armitage JP, Schüler D. Polarity of bacterial magnetotaxis is controlled by aerotaxis through a common sensory pathway. *Nat Commun.* 2014;5:5398. <https://doi.org/10.1038/ncomms6398>.
8. Lefèvre CT, Bennet M, Landau L, Vach P, Pignol D, Bazylinski DA, et al. Diversity of magneto-aerotactic behaviors and oxygen sensing mechanisms in cultured magnetotactic bacteria. *Biophys J.* 2014;107:527–38. <https://doi.org/10.1016/j.bpj.2014.05.043>.
9. Bennet M, McCarthy A, Fix D, Edwards MR, Repp F, Vach P, et al. Influence of magnetic fields on magneto-aerotaxis. *PLoS ONE.* 2014;9:e101150. <https://doi.org/10.1371/journal.pone.0101150>.
10. Zhang WJ, Chen C, Li Y, Song T, Wu LF. Configuration of redox gradient determines magnetotactic polarity of the marine bacteria MO-1. *Environ Microbiol Rep.* 2010;2:646–50. <https://doi.org/10.1111/j.1758-2229.2010.00150.x>.
11. de Araujo FFT, Germano FA, Gonçalves LL, Pires MA, Frankel RB. Magnetic polarity fractions in magnetotactic bacterial populations near the geomagnetic equator. *Biophys J.* 1990;58:549–55. [https://doi.org/10.1016/S0006-3495\(90\)82398-5](https://doi.org/10.1016/S0006-3495(90)82398-5).
12. Frankel RB. Magnetic guidance of organisms. *Annu Rev Biophys Bioeng.* 1984;13:85–103. <https://doi.org/10.1146/annurev.bb.13.060184.000505>.
13. Frankel RB, Blakemore RP, Torres de Araujo FF, Esquivel DMS, Danon J. Magnetotactic bacteria at the geomagnetic equator. *Science.* 1981;212:1269–70. <https://doi.org/10.1126/science.212.4500.1269>.
14. Chang SBR, Kirschvink JL. Magnetofossils, the magnetization of sediments, and the evolution of magnetite biomineralization. *Annu Rev Earth Planet Sci.* 1989;17:169–95. <https://doi.org/10.1146/annurev.ea.17.050189.001125>.
15. Simmons SL, Bazylinski DA, Edwards KJ. South-seeking magnetotactic bacteria in the Northern Hemisphere. *Science.* 2006;311:371–4. <https://doi.org/10.1126/science.1122843>.
16. Leão P, Teixeira LCRS, Cypriano J, Farina M, Abreu F, Bazylinski DA, et al. North-seeking magnetotactic Gammaproteobacteria in the Southern Hemisphere. *Appl Environ Microbiol.* 2016;82:5595–602. <https://doi.org/10.1128/AEM.0154-5-16>.
17. Frankel RB, Bazylinski DA. Magnetotaxis: Microbial. In: John Wiley & Sons, Ltd, editor. *eLS.* 1st edition. Wiley; 2002. <https://doi.org/10.1038/npg.els.0000397>.
18. Codutti A, Bente K, Faivre D, Klumpp S. Chemotaxis in external fields: simulations for active magnetic biological matter. *PLoS Comput Biol.* 2019;15:e1007548. <https://doi.org/10.1371/journal.pcbi.1007548>.
19. Klumpp S, Lefèvre CT, Bennet M, Faivre D. Swimming with magnets: from biological organisms to synthetic devices. *Phys Rep.* 2019;789:1–54. <https://doi.org/10.1016/j.physrep.2018.10.007>.
20. Pfeiffer D, Schüler D. Quantifying the benefit of a dedicated "magnetoskeleton" in bacterial magnetotaxis by live-cell motility tracking and soft agar swimming assay. *Appl Environ Microbiol.* 2020;86:e01976-19. <https://doi.org/10.1128/AEM.01976-19>.
21. Ullrich S, Schüler D. Cre-lox-based method for generation of large deletions within the genomic magnetosome island of *Magnetospirillum gryphiswaldense*. *Appl Environ Microbiol.* 2010;76:2439–44. <https://doi.org/10.1128/AEM.02805-09>.
22. Chen C, Ma Q, Jiang W, Song T. Phototaxis in the magnetotactic bacterium *Magnetospirillum magneticum* strain AMB-1 is independent of magnetic fields. *Appl Microbiol Biotechnol.* 2011;90:269–75. <https://doi.org/10.1007/s00253-010-3017-1>.
23. Wettstadt S. Some have it all: multicellularity, magnetotaxis and photokinesis in one bacterium. *Environ Microbiol.* 2020;22:2993–5. <https://doi.org/10.1111/1462-2920.15157>.
24. Chen H, Chen C, Zhao H, Wei Y, Wang P, Wu L-F, et al. Synergistic mechanism of magneto-optical sensing mediated by magnetic response protein Amb0994 and Lov-like protein Amb2291 in *Magnetospirillum magneticum* AMB-1. *J Photochem Photobiol B.* 2025;265:113124. <https://doi.org/10.1016/j.jphotobiol.2025.113124>.
25. Lumsden CJ. Dual inheritance in haploid organisms: a model of magnetotactic bacteria. *J Theor Biol.* 1984;111:1–16. [https://doi.org/10.1016/S0022-5193\(84\)80192-7](https://doi.org/10.1016/S0022-5193(84)80192-7).
26. Glassmeier K-H, Vogt J. Magnetic polarity transitions and biospheric effects: historical perspective and current developments. *Space Sci Rev.* 2010;155:387–410. <https://doi.org/10.1007/s11214-010-9659-6>.
27. Herz J, Weigel C, Scheder L, Zarivach R, Algov I, Chemla Y, et al. A two-protein chemoreceptor complex regulates oxygen thresholds in bacterial magneto-aerotaxis. *Adv Sci.* 2025;12:e17315. <https://doi.org/10.1002/adv.202417315>.
28. Rismani Yazdi S, Nosrati R, Stevens CA, Vogel D, Escobedo C. Migration of magnetotactic bacteria in porous media. *Biomicrofluidics.* 2018;12:011101. <https://doi.org/10.1063/1.5024508>.
29. Codutti A, Charsooghi MA, Marx K, Cerdá-Doñate E, Muñoz O, Zaslansky P, et al. Physiological magnetic field strengths help magnetotactic bacteria navigate in simulated sediments. *eLife.* 2025;13:RP98001. <https://doi.org/10.7554/eLife.98001>.
30. Mao X, Egli R, Liu X, Zhao L. Magnetotactic advantage in stable sediment by long-term observations of magnetotactic bacteria in Earth's field, zero field

- and alternating field. *PLoS ONE*. 2022;17:e0263593. <https://doi.org/10.1371/journal.pone.0263593>.
31. Alken P, Thébault E, Beggan CD, Amit H, Aubert J, Baerenzung J, et al. International geomagnetic reference field: the thirteenth generation. *Earth Planets Space*. 2021;73:49. <https://doi.org/10.1186/s40623-020-01288-x>.
 32. Schüler D, Spring S, Bazylinski DA. Improved technique for the isolation of magnetotactic spirilla from a freshwater sediment and their phylogenetic characterization. *Syst Appl Microbiol*. 1999;22:466–71. [https://doi.org/10.1016/S0723-2020\(99\)80056-3](https://doi.org/10.1016/S0723-2020(99)80056-3).
 33. Flies CB, Jonkers HM, de Beer D, Bosselmann K, Böttcher ME, Schüler D. Diversity and vertical distribution of magnetotactic bacteria along chemical gradients in freshwater microcosms. *FEMS Microbiol Ecol*. 2005;52:185–95. <https://doi.org/10.1016/j.femsec.2004.11.006>.
 34. Lefèvre CT, Schmidt ML, Vilorio N, Trubitsyn D, Schüler D, Bazylinski DA. Insight into the evolution of magnetotaxis in *Magnetospirillum* spp., based on *mam* gene phylogeny. *Appl Environ Microbiol*. 2012;78:7238–48. <https://doi.org/10.1128/AEM.01951-12>.
 35. Lefèvre CT, Bennet M, Klumpp S, Faivre D. Positioning the flagellum at the center of a dividing cell to combine bacterial division with magnetic polarity. *mBio*. 2015;6:e02286-14. <https://doi.org/10.1128/mBio.02286-14>.
 36. Müller FD, Schüler D, Pfeiffer D. A Compass to Boost Navigation: Cell Biology of Bacterial Magnetotaxis. *J Bacteriol*. 2020;202. <https://doi.org/10.1128/JB.00398-20>.
 37. Murat D, Hérisse M, Espinosa L, Bossa A, Alberto F, Wu L-F. Opposite and coordinated rotation of amphitrichous flagella governs oriented swimming and reversals in a magnetotactic spirillum. *J Bacteriol*. 2015;197:3275–82. <https://doi.org/10.1128/JB.00172-15>.
 38. Cohen EJ, Nakane D, Kabata Y, Hendrixson DR, Nishizaka T, Beeby M. *Campylobacter jejuni* motility integrates specialized cell shape, flagellar filament, and motor, to coordinate action of its opposed flagella. *PLoS Pathog*. 2020;16:e1008620. <https://doi.org/10.1371/journal.ppat.1008620>.
 39. Katzmann E, Müller FD, Lang C, Messerer M, Winklhofer M, Pitzko JM, et al. Magnetosome chains are recruited to cellular division sites and split by asymmetric septation. *Mol Microbiol*. 2011;82:1316–29. <https://doi.org/10.1111/j.1365-2958.2011.07874.x>.
 40. Toro-Nahuelpan M, Müller FD, Klumpp S, Pitzko JM, Bramkamp M, Schüler D. Segregation of prokaryotic magnetosomes organelles is driven by treadmilling of a dynamic actin-like MamK filament. *BMC Biol*. 2016;14:88. <https://doi.org/10.1186/s12915-016-0290-1>.
 41. Blakemore RP, Frankel RB, Kalmijn AJ. South-seeking magnetotactic bacteria in the Southern Hemisphere. *Nature*. 1980;286:384–5. <https://doi.org/10.1038/286384a0>.
 42. de Melo RD, Acosta-Avalos D. The swimming polarity of multicellular magnetotactic prokaryotes can change during an isolation process employing magnets: evidence of a relation between swimming polarity and magnetic moment intensity. *Eur Biophys J*. 2017;46:533–9. <https://doi.org/10.1007/s00249-017-1199-5>.
 43. Mao X, Egli R, Petersen N, Hanzlik M, Liu X. Magneto-chemotaxis in sediment: first insights. *PLoS ONE*. 2014;9:e102810. <https://doi.org/10.1371/journal.pone.0102810>.
 44. Mao X, Egli R, Petersen N, Liu X. Combined response of polar magnetotaxis to oxygen and Ph: insights from hanging drop assays and microcosm experiments. *Sci Rep*. 2024;14:27331. <https://doi.org/10.1038/s41598-024-78946-7>.
 45. Höfken AF, von Döbeneck T, Winklhofer M, Kuhn T, Kasten S. Life in a benthic mirror-world: evidence for deep-living magnetotactic bacteria in hydrothermally bottom-up oxygenated Pacific Ridge flank sediments. *Geophys Res Lett*. 2025;52:e2024GL113606. <https://doi.org/10.1029/2024GL113606>.
 46. Uebe R, Schüler D, Jogler C, Wiegand S. Reevaluation of the complete genome sequence of *Magnetospirillum gryphiswaldense* MSR-1 with single-molecule real-time sequencing data. *Genome Announc*. 2018;6:e00309-18. <https://doi.org/10.1128/genomeA.00309-18>.
 47. Heyen U, Schüler D. Growth and magnetosome formation by microaerophilic *Magnetospirillum* strains in an oxygen-controlled fermentor. *Appl Microbiol Biotechnol*. 2003;61:536–44. <https://doi.org/10.1007/s00253-002-1219-x>.
 48. Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, et al. Fiji: an open-source platform for biological-image analysis. *Nat Methods*. 2012;9:676–82. <https://doi.org/10.1038/nmeth.2019>.

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