

Multicellular photo-magnetotactic bacteria

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Summary

Multicellular magnetotactic bacteria (MMB) are unique microorganisms typically comprised of 10–40 bacterial cells arranged around a central acellular compartment. Their life cycle has no known unicellular stage and division occurs by separation of a single MMB aggregate into two identical offspring. In this study, South-seeking multicellular magnetotactic bacteria (ssMMB) were enriched from a New England salt marsh. When exposed to light, ssMMB reversed their magnetotactic behaviour to become North-seeking. The exposure time needed to generate the reversal response varied with light wavelength and intensity. Extensive exposure to light appeared to be lethal. This is the first report of a Northern hemisphere MMB displaying South-seeking behaviour and the first time a MMB is found to exhibit photo-magnetotaxis. We suggest that this mechanism enables ssMMB to optimize their location with regard to chemical gradients and light intensities, and propose a model to explain the peculiar balance between photo- and magnetotaxis.

Introduction

Multicellular magnetotactic bacteria (MMB) present a life strategy unique in the microbial world. MMB are typically

comprised of 10–40 bacterial cells arranged around a central acellular compartment, possibly serving inter-cell communication (Keim *et al.*, 2004a). Every cell is multiply flagellated and contains iron sulphide crystals, mostly greigite (cubic Fe₃S₄). These magnetic particles, known as magnetosomes (for a recent review see Schüler, 2008), are typically located inside invaginations of the magnetotactic bacterial cytoplasmic membrane (Komeili *et al.*, 2006). They are arranged in a way as to orient the bacterial movement parallel to the geomagnetic field lines of the Earth. The life cycle of MMB has no known unicellular stage. Division occurs by separation of a single MMB into two identical offspring (Keim *et al.*, 2004b), while disaggregated MMB lose their viability very rapidly (Abreu *et al.*, 2006). While no pure-culture of MMB is currently available, detailed phenotypic characterizations were performed for '*Candidatus Magnetoglobus multicellularis*' aggregates enriched using magnetic fields (Abreu *et al.*, 2007; Silva *et al.*, 2008; Perantoni *et al.*, 2009). All MMB analysed so far are affiliated by 16S rRNA gene sequence to the delta subclass of *Proteobacteria* (Abreu *et al.*, 2007; Simmons and Edwards, 2007; Wenter *et al.*, 2009) and recent findings indicate a potential involvement in sulphate reduction (Wenter *et al.*, 2009). Other than a recent report on a chemotactic response of MMB to acetate and propionate (Wenter *et al.*, 2009) potential carbon sources of MMB remain speculative. Very recently, Lefèvre and co-workers reported on the finding of non-magnetotactic multicellular prokaryotes (Lefèvre *et al.*, 2010), indicating more diverse life strategies for this group of organisms than previously assumed.

Magnetotactic bacteria are globally distributed and can account for ~1% of the bacterial population in marine (Flies *et al.*, 2005; Simmons *et al.*, 2007) and freshwater (Spring *et al.*, 1993) habitats. So far, reports of MMB are restricted to marine environments, including hypersaline coastal lagoons (Abreu *et al.*, 2007), salt marshes (Simmons *et al.*, 2007) and tidal sand flats (Wenter *et al.*, 2009). In a hypersaline lagoon and a meromictic salt pond, MMB have been reported to account for 0.001% (Martins *et al.*, 2009) and 1.9% (Simmons *et al.*, 2007) of the total bacterial community respectively. MMB are typically observed in anoxic environments (Abreu *et al.*, 2007) and die rapidly when in the presence of oxygen (Abreu *et al.*, 2006; Martins *et al.*, 2009; Wenter *et al.*, 2009). The genomes of *Magnetospirillum magnetotacticum*, *Magnetospirillum magneticum* strain AMB-1 and marine coccus strain MC-1 encode several candidate

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genes for aero-, redox- and potentially photo-taxis (Frankel and Bazylinski, 2009). Motility and positioning mechanisms are expected in magnetotactic bacteria as these organisms seem specially adapted for migration along environmental gradients.

Polar magnetotactic bacteria were thought to be North- or South-seeking in the Northern or Southern hemisphere respectively (Blakemore *et al.*, 1980). However, this concept was challenged when single-celled South-seeking magnetotactic bacteria were reported from a marine basin in Falmouth, MA (Simmons *et al.*, 2006).

Herein, we report on the discovery of South-seeking multicellular magnetotactic bacteria (ssMMB) from a New England salt marsh, exhibiting a combination of photo- and magnetotaxis.

Results and discussion

On-site microscopic analysis demonstrated the dominance of South-seekers (estimated at over 90%) in the MMB population in sediment from a shallow mud pond at the Little Sippewissett salt marsh. Following a week of undisturbed incubation in the lab, ssMMB were enriched to become the dominant magnetotactic organisms in the sample. In a hanging droplet, no change in activity was observed following 2 h of incubation, as opposed to decreased activity after 15–90 min of incubation under similar conditions in previous reports (Abreu *et al.*, 2006;

Martins *et al.*, 2009; Wenter *et al.*, 2009). This suggests reduced oxygen sensitivity of ssMMB reported here compared with previously described MMB.

When briefly exposed to UV light (365 nm) at high intensity during observations with a fluorescence microscope, ssMMB changed their magnetotactic behaviour to become North-seeking (Fig. 1; Movie S1), swimming to the opposite side of the droplet. Reversing the magnetic field caused ssMMB to swim back into the light, retaining North-seeking behaviour, with no observed second reversal of swimming direction. Two to five seconds exposure to full-strength UV light at 365 nm appeared to be lethal, with ssMMB losing motility and many becoming disaggregated within minutes following exposure. Heating of the droplet was ruled out as a possible mechanism for the observed response as the light energy was too small to produce a noticeable effect in droplet temperature.

Initial response time as well as the interval between first and last ssMMB to respond (variation) were measured for different light wavelengths and intensities (Table S1). Reversal was observed following 30 s of exposure to approximately 80 W m^{-2} of violet-blue light (395–440 nm; Fig. 1; Table S1). The average energy flux of blue light (400–500 nm) at the Earth's surface at noon, on a clear day, is approximately 170 W m^{-2} (Lee and Downum, 1991; Bell *et al.*, 2000), so that this result is well within the intensity values expected in the pond environment.

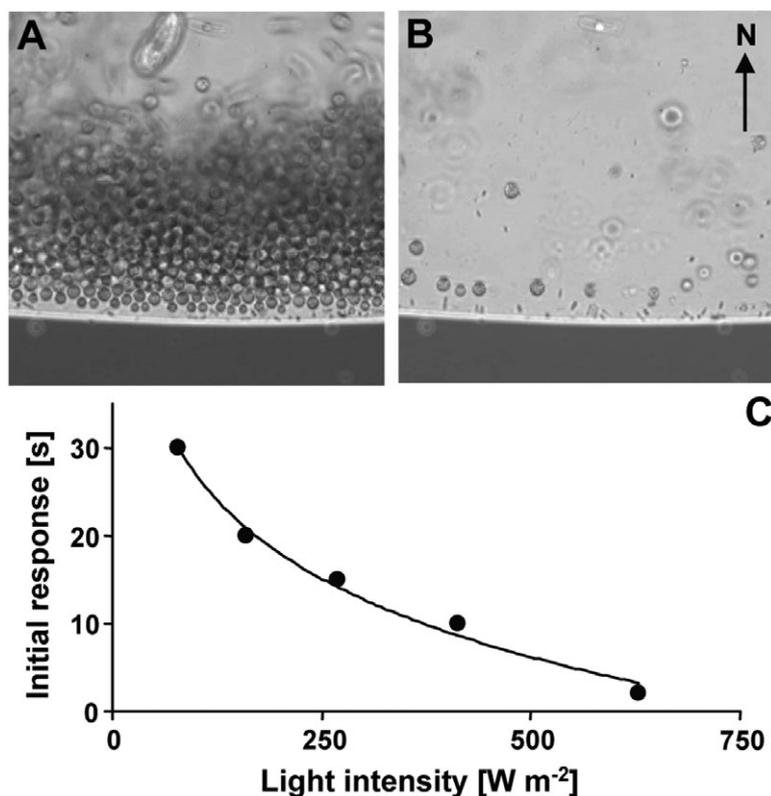


Fig. 1. Photo-magnetotactic behaviour of ssMMB.

A. ssMMB in a hanging droplet.
B. The same field of view after 20 s of exposure to violet-blue light (395–440 nm) at approximately 410 W m^{-2} . The black arrow indicates direction of the applied magnetic field.

C. Initial response time as a function of light intensity (395–440 nm). Black line represents best fit logarithmic curve, $R^2 = 0.99$.

A stronger influence was observed for shorter wavelengths, with the shortest response time at around 2 s. This response time was measured at medium intensities for UV light (365 nm) or high intensities for longer wavelengths (Table S1). Initial response time appeared to be a function of the natural logarithm of light intensity (Fig. 1C), possibly indicating a cumulative mechanism. No response was observed for wavelengths longer than 490 nm (green), but after 5–10 min exposure to green light ssMMB lost motility, eventually undergoing disaggregation. This observation possibly indicates that the photo response mechanism is different from the one responsible for sensitivity to light.

Exposure to blue light (450–490 nm) at approximately 200 W m^{-2} resulted in a reversible response (Movie S2). MMB switched to North-seeking behaviour but appeared to migrate just outside the intense light in the microscope viewing field. Upon turning the blue light off or switching to longer wavelengths, MMB resumed their South-seeking behaviour. This could be repeated several times before MMB lost their motility, possibly because of accumulated light damage. This observation offers a clue to the ecological significance of the photoresponse mechanism. As light intensities at different depths in the pond are expected to gradually change during the day, this type of balanced response may enable ssMMB to maintain their position within a given light intensity range.

A similar photo response was reported by Frankel and colleagues for the magnetotactic marine coccus strain MC-1, while no such response was observed for *M. magnetotacticum* (Frankel *et al.*, 1997). The authors demonstrated that illumination of MC-1 cells with blue (430 nm), yellow (500 nm) or white light triggered a reversible photo response, causing the cells to switch their swimming behaviour. This effect was similar to the cell's response to increased oxygen concentration, overriding their aerotactic response to decreased oxygen concentration (Frankel *et al.*, 1997). No reference was made to a lethal effect of light exposure for strain MC-1, and the purpose for the observed photo response by these organisms remains unclear. No photo response was observed for single-celled magnetotactic bacteria in samples obtained during the present study.

The general, but not exclusively (Simmons *et al.*, 2006), North-seeking behaviour of magnetotactic bacteria in the Northern hemisphere is commonly explained by the adaptation of magnetotactic bacteria to low oxygen concentrations. Previously, it was reported that a fraction of MMB on the Southern hemisphere display North-seeking behaviour (Keim *et al.*, 2007). This is a first report of Northern hemisphere MMB displaying South-seeking behaviour, and the first report of a MMB population dominated by cells behaving opposite to the accepted paradigm.

One possible explanation for a South-seeking life strategy of MMB on the Northern hemisphere (and vice versa) may be that at the respective sites an inverted redox gradient was present at the time of sampling. This could be, e.g. due to oxygenated fresh water input from an underground reservoir into the more oxygen-depleted salty water. Such a situation could lead to the selection of ssMMB over North-seeking MMB.

Recently, it was suggested by Frankel and Bazylinski that an agent of unknown identity obviously prevents South-seeking magnetotactic bacteria in the Northern hemisphere from swimming up to the water surface, because they have not been found in the uppermost water layers (Frankel and Bazylinski, 2009). Based on our findings, we propose that, for some magnetotactic bacteria, light may serve as such a stimulus.

In the Northern hemisphere, a South-seeking magnetotactic organism migrates upwards, towards a more oxygenated layer, in agreement with the apparent low oxygen sensitivity of ssMMB. During daytime, this brings ssMMB towards the sunlit surface. We therefore suggest that the photo-magnetotactic response reported here enables these organisms, for which light appears to be lethal, to optimize their location with regard to chemical gradients and light intensity. Under low-light conditions (e.g. at night) these MMB are thus expected to exhibit South-seeking behaviour, migrating upwards to more favourable conditions. During daytime, MMB reverse their magnetotactic behaviour and seek shelter in the sediment, maintaining their position to avoid excessive light exposure (Fig. 2).

The response described here is different from previously described photophobic behaviour in other bacteria, in which swimming direction is always away from the light. Exposure of ssMMB to light could only trigger the switch from South- to North-seeking polarity, and subsequent exposure did not trigger a switch from North- to South-seeking behaviour. This is appropriate for conditions in their natural environment, where light is always expected to come from above, i.e. from the magnetic South pole. The observed response is most similar to the magneto-aerotaxis exhibited by strain MC-1, with the cells migrating between threshold oxygen concentrations. MC-1 cells respond to light in a fashion similar to ssMMB by reversing their swimming direction (Frankel *et al.*, 1997). This could serve as a mechanism to avoid exposure to light when oxygen concentrations in the photic layer are too low to trigger a reversal. However, as ssMMB do not appear to exhibit aerotaxis, they may be migrating between threshold light intensities. ssMMB thus represent an adaptation to life along photon gradients. The advantage derived by ssMMB from migrating towards the water surface, opposite to all previously described MMB, remains to be explored.

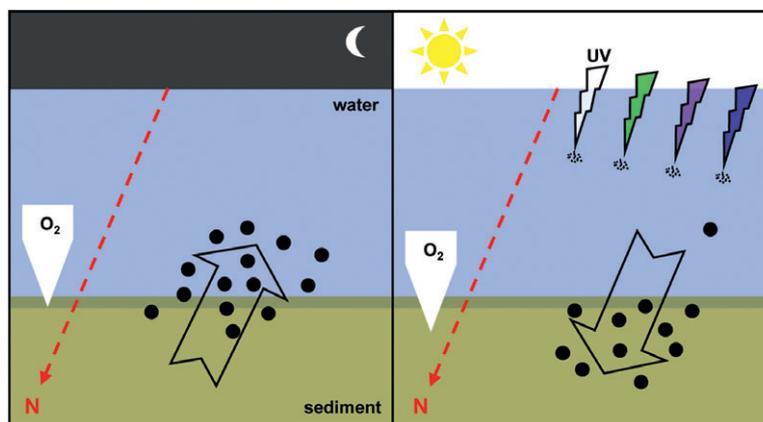


Fig. 2. Diagram of the proposed migration behaviour of ssMMB in the Northern hemisphere. During low-light conditions (e.g. at night) MMB are proposed to exhibit South-seeking behaviour, migrating upwards towards the water–sediment interface or into the overlying water column. During light conditions (day) ssMMB reverse their polarity and move into deeper layers of the sediment as a phobic response to low wavelength light. Big black dots represent viable, motile MMB. Small black dots represent non-motile, presumably dead (Abreu *et al.*, 2006) MMB. Black and red arrows indicate general direction of migration of MMB, and direction of Earth's geomagnetic field (Northern hemisphere) respectively. Lightening bolts are colour-coded to indicate the different wavelengths of light. Penetration depths are not to scale.

The discovery of reversal of magnetotactic behaviour in response to a light stimulus in both multicellular (this study) and single-celled magnetotactic bacteria (Frankel *et al.*, 1997; and discussed in Frankel and Bazylinski, 2009) demonstrates this behaviour to be more widespread than previously assumed. The term photo-magnetotaxis is proposed to describe this behaviour. The recent report of multicellular non-magnetotactic bacteria exhibiting a similar photoresponse to that reported here (Lefèvre *et al.*, 2010) further supports the existence of multiple life strategies for multicellular bacteria and their apparent sensitivity to light. Further study is needed to find and compare the mechanisms enabling light detection and response of these organisms. It appears now, that some magnetotactic bacteria exercise a fine balance between chemo- and phototaxis to determine their position in environmental gradients. Only by the detailed analysis of these response mechanisms on the genetic, biochemical and phenotypic level will researchers be able to understand how these intriguing microorganisms interact with their complex habitats.

Experimental procedures

Sample collection

Samples were collected at low tide from 10 different sites at the Little Sippewissett salt marsh, Falmouth, MA. To sample ssMMB, a magnetic stirring bar was placed at the water–sediment interface with the North magnetic pole facing the bucket. The sediment was stirred briefly and allowed to settle for 10–20 min. A small droplet was collected from the point next to the magnetic stirring bar for on-site microscopic analysis. While several samples were tested positive on the presence of MMB, only a sample from a mud pond (coordinates:

41°34'35"N, 70°38'19"W) contained high numbers of these organisms. A 3 l plastic bucket was filled with sediment and water from this pond and maintained at room temperature in the laboratory for 7–14 days.

Microscopy and photo response

Magnetotactic bacteria were viewed using the hanging droplet method (Abreu *et al.*, 2006). 4 µl droplets were collected from the point next to the magnet using a pipette and placed on a glass cover slip. The coverslip was inverted and placed atop a small o-ring, and a magnet was placed next to the coverslip. Magnetotactic bacteria accumulated at one side of the droplet, depending on the orientation of the magnet and the magnetotactic behaviour of the bacteria. ssMMB were viewed using a Zeiss Axioscope phase contrast/epifluorescence microscope at 40× magnification. The microscope was equipped with LED white light and mercury arc UV/visible light sources. Cells were exposed to light at different intensities and wavelengths using six filter sets, as detailed in Table S2. Light intensity was controlled using a light attenuation shutter located between the UV/visible light source and the band-pass filter. The shutter had six positions, numbered 1–6, with level 1 being the highest intensity.

Light intensity measurement

Light intensity was measured using a LI-COR LI 185B quantum radiometer. The light sensor was covered with a microscope cover slip and placed directly under the 40× objective. Intensity levels 1–5 were measured for filter sets 2–5 as listed in Table S2. Intensity values were corrected according to the instrument manual. Results are detailed in Table S3. Intensity values are given in $W\ m^{-2}$. Measurements for UV light were not performed as the quantum radiometer was unsuitable for measurement of light intensities for wavelengths shorter than 400 nm. However, the light emission

spectra of the mercury-arc lamp used (<http://zeiss-campus.magnet.fsu.edu/articles/lightsources/mercuryarc.html>) shows similar values for 365 nm and 405 nm, implying similar light intensities for these wavelengths.

Response time measurement

Time lapse imaging was used for tracking changes in the number of MMB located at the 'Southern end' of a hanging droplet. Images were taken at 0.5–10 s intervals, according to previously observed response times.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Photo response times (s) measured by time lapse image recording.

Table S2. Filter sets used to investigate the phototactic response of South-seeking multicellular magnetotactic bacteria (ssMMB).

Table S3. Light energy flux for different wavelengths and shutter positions ($W\ m^{-2}$).

Movie S1. Photo-magnetotactic response of South-seeking multicellular magnetotactic bacteria (ssMMB).

Movie S2. Reversible photo-magnetotactic response of South-seeking multicellular magnetotactic bacteria (ssMMB).

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Supplementary information

Table 1. Filter sets used to investigate the phototactic response of South-seeking multicellular magnetotactic bacteria (ssMMB).

| | Filter set | Manufacturer | Wave length (nm) |
|----------|-------------------|---------------------|-------------------------|
| 1 | Fs 02 | Zeiss | 365 |
| 2 | Fs 05 | Zeiss | 395-440 |
| 3 | Fs 38 HE | Zeiss | 450-490 |
| 4 | 49003 | Chroma | 490-510 |
| 5 | Fs 14 | Zeiss | 510-560 |
| 6 | Fs 20 HE | Zeiss | 534-558 |

Table 2. Light energy flux for different wavelengths and shutter positions [W m^{-2}].

| Shutter position | 365 nm | 395-440 nm | 450-490 nm | 490-510 nm | 510-560 nm |
|-------------------------|---------------|-------------------|-------------------|-------------------|-------------------|
| 1 | NA | 628.1 | 464.6 | 518.8 | 581.2 |
| 2 | NA | 414.0 | 283.9 | 340.4 | 375.5 |
| 3 | NA | 268.8 | 206.5 | 220.8 | 247.4 |
| 4 | NA | 159.4 | 121.7 | 132.5 | 143.1 |
| 5 | NA | 78.5 | 59.7 | 66.2 | 74.2 |

NA- not available; energy flux calculated for average wavelength of each filter set.

Table 3. Photo-response times [sec] measured by time lapse image recording. Initial response presents the time interval after which the first MMB started reversing their swimming behaviour. Variation denotes the interval between initial response and the time of departure of the last MMB. Cells remaining in the microscopic field after this time did not show any movement. These presumably dead MMB made up only a very small portion of the population. This is evident from Fig. 1 and Mov. 1. No response was observed for wavelengths longer 490 nm. * denote average of two experiments with standard deviation.

| | 365 nm | | 395-440 nm | | 450-490 nm | |
|------------------------|-------------------------|------------------|-------------------------|------------------|-------------------------|------------------|
| Intensity level | Initial response | Variation | Initial response | Variation | Initial response | Variation |
| 1 | 2 | 2 | 2 | 4 | 2 | 8 |
| 2 | 2 | 2 | * 10 ± 0 | * 10 ± 7.1 | 60 | 70 |
| 3 | 2 | 3 | * 14.5 ± 0.7 | * 15.5 ± 0.7 | 130 | 70 |
| 4 | 10 | 10 | * 20 ± 0 | * 25 ± 7.1 | * 215 ± 21.2 | * 485 ± 21.1 |
| 5 | 60 | 30 | 30 | 60 | 400 | 1,000 |

Movie legends

Movie 1. Photo-magnetotactic response of South-seeking multicellular magnetotactic bacteria (ssMMB). ssMMB are crowded at the “South end” of a hanging droplet. Upon exposure to violet-blue light (395-440 nm; after ~1 sec playing time) at approximately 410 W m^{-2} , MMB switch their polarity and migrate towards the “North end” of the droplet. Due to software processing the frame rate of this movie is slightly different from the original recording.

Movie 2. Reversible photo-magnetotactic response of South-seeking multicellular magnetotactic bacteria (ssMMB). ssMMB are crowded at the “South” end of a hanging droplet. Upon exposure to blue light (450-490 nm; after ~0.5 sec playing time) at approximately 200 W m^{-2} , MMB switch their polarity and migrate towards the “North end” of the droplet. When blue light is replaced by green light (after ~16 sec playing time), the aggregates return to the “South end” of the droplet. Due to software processing the frame rate of this movie is slightly different from the original recording.