

Phototaxis in the magnetotactic bacterium *Magnetospirillum magneticum* strain AMB-1 is independent of magnetic fields

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Abstract Magnetotactic bacteria (MTB) can rapidly relocate to optimal habitats by magneto-aerotaxis. Little is known about MTB phototaxis, a response that might also aid navigation. In this study, we analyzed the relationship between phototaxis and magnetotaxis in *Magnetospirillum magneticum* strain AMB-1. Magnetotactic AMB-1 cells migrated toward light, and migration increased with higher light intensity. This response was independent of wavelength, as AMB-1 cells migrated equally toward light from 400 to 750 nm. When AMB-1 cells were exposed to zero magnetic fields or to 0.2 mT magnetic fields that were opposite or orthogonal to the light beam, cells still migrated toward the light, indicating that phototaxis was independent of magnetotaxis. The R_{mag} value and coercive force (H_c) of AMB-1 increased when the bacteria were illuminated for 20 h, consistent with an increase in magnetosome synthesis or in magnetosome-containing cells. These results demonstrated that the *M. magneticum* AMB-1 responded to light as well as other environmental factors. To our knowledge, this is the first report of phototactic behavior in the bacteria of *Magnetospirillum*.

Keywords Magnetotactic bacteria · Phototaxis · *Magnetospirillum magneticum* AMB-1

Introduction

Most motile microorganisms actively search for an optimal environment by responding to photic, magnetic, mechanical, chemical, thermal, galvanic, and gravitational stimuli that provide directional cues (Hader 1987). Magnetotactic bacteria (MTB) were first described by Bellini in 1963 (Bellini 1963; Frankel 2009) and first reported in a peer-reviewed journal by Blakemore in 1975 (Blakemore 1975). MTB are characterized by the presence of the magnetosome, which allows the bacteria to align and to swim downward along an inclined geomagnetic field in both hemispheres. Genomic analysis revealed that MTB may have unusually high numbers of chemoreceptor-like proteins that are known to be important for bacterial responses to chemical and physical stimuli (Matsunaga et al. 2005; Philippe and Wu 2010). Hence, the MTB might exploit multiple-taxis methods like chemotaxis, aerotaxis, and even phototaxis in conjunction with magnetotaxis to find a more suitable environment (Frankel et al. 1997; Frankel et al. 2007; Richter et al. 2007).

The phototactic response has been shown to be related to magnetoreception in some animals (Deutschlander et al. 1999; Gegeer et al. 2008; Zapka et al. 2009). Frankel et al. (1997) found that magnetococcus strain MC-1 responded to short-wavelength light ($\lambda \leq 500$ nm), but little is known about phototactic behavior in *Magnetospirillum*. It has been reported that light irradiation did not affect the colony formation of *Magnetospirillum* strain AMB-1 (Matsunaga et al. 1991). Whether *Magnetospirillum* can react to light, and the relationship between phototaxis and magneto-

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areotaxis, remain to be elucidated. In this study, we developed a mobile spectrophotometer to observe the migratory light response of AMB-1 cells. In addition, we have performed detailed analysis of phototaxis in strain AMB-1 cells under multiple magnetic environments.

Materials and methods

Bacterial strain and culture

Magnetospirillum magneticum AMB-1 (ATCC 700264) was used in all experiments. Cells were grown microaerobically in enriched magnetic spirillum growth medium (EMSGM; Yang et al. 2001) in a dark room at $28 \pm 1^\circ\text{C}$.

The light source and action spectrum

The light used was a pseudo-solar continuous spectrum produced by an incandescent lamp (Fig. 1a). Three special lights with different wavelengths (400–530, 530–645, and 640–750 nm) were produced by coating the light with optical filters (Beijing HZXD Optical Technology, Beijing, China; Fig. 1b–d). Light spectra were measured using a spectrometer (USB-4000 UV–VIS, Ocean Optics, Ostfildern, Germany). The light intensity was measured with a Field Scout® Quantum Light Meter (Spectrum Technologies, Plainfield, IL, USA).

Mobile spectrophotometer

The light response of AMB-1 cells under the microscope is technically difficult to observe, so we developed a mobile spectrophotometer to assay the spatial distribution of AMB-1 cells directly. As shown in Fig. 2, the mobile spectrophotometer included an optical path system which was fixed on a sliding rail, a power supply, and a signal processing system. The optical path system was composed of a 595 nm light-emitting diode (LED) as the light source and a photodetector which integrated a photodiode and an amplifier–receiver that was placed in a dark box. The glass bottle with AMB-1 cells were placed between the light source and receiver unit and kept immobile. When the optical path system was moved along the sliding rail, the absorbance of the AMB-1 cell suspension in the glass bottles was measured along horizontal lines.

Phototactic behavior of AMB-1 cells

The redox indicator resazurin was added to the medium at final concentration of 2 mg/l to better visualize AMB-1 cells using the distribution of oxygen in the media. Resazurin alone did not affect the growth or viability of bacteria.

Cells at the logarithmic growth phase were poured into glass bottles to ~85% of the maximum volume, and grown in the dark for 3 h. This resulted in an oxic–anoxic interface (OAI) between the oxidized (pink) and the reduced (colorless) resazurin. The bottle was illuminated from one side (Fig. 2), and the light intensity was adjusted from 1 to $16 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The temperature of the medium nearest the light source (and opposite) did not change during 10 min of illumination. The distribution of the cells was measured using the mobile spectrophotometer and the bottles were photographed every 60 s.

Thermotactic behavior of AMB-1 cells

The effects of ambient temperature were investigated by changing the medium temperature using a separate square bottle filled with water at $32 \pm 0.1^\circ\text{C}$ connected to a temperature-controlled water bath (Chongqin Yinhe Experimental Equipment, Chongqin, China). Two Pt-100 temperature sensors were placed inside the bottle on opposite sides about 3 cm apart. When the medium was illuminated at $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from the left side of the bottle and heated by the water-filled bottle at right, the temperature of the medium near the heat source increased to 28.1°C within 10 min and the opposite side remained at 28.0°C , indicating a temperature difference of $\sim 0.1^\circ\text{C}$ from the heat source side to the lighted side.

The phototactic response of AMB-1 cells at different magnetic field

The magnetic field apparatus was composed of three perpendicular pairs of Helmholtz coils (890, 820, and 750 mm in diameter, for X, Y, and Z axes) and three sources of high-precision direct current power. The coil system consisted of an aluminium framework surrounded by a 1.2-mm-diameter copper wire. The three directional components could be adjusted by the three current sources individually.

Bacterial migration was studied under three magnetic conditions: zero field, 0.2 mT magnetic field opposite to the direction of the light beam and 0.2 mT magnetic field perpendicular to the light beam. The zero field with intensity of $<150 \text{ nT}$ in a volume of 100 mm^3 was formed by adjusting the electric currents. The light beam was along the Y-axis. A 0.2 mT magnetic field with its direction opposite to the direction of the light beam was generated by increasing the electric current of the Y-axis coils. When the electric current of the Z-axis coils increased, a 0.2 mT magnetic field perpendicular to the direction of the light beam was generated. The instrument was kept at $28 \pm 1^\circ\text{C}$ in a temperature-controlled chamber, and the magnetic field was measured by a fluxgate magnetometer (National Institute of Metrology, Beijing, China).

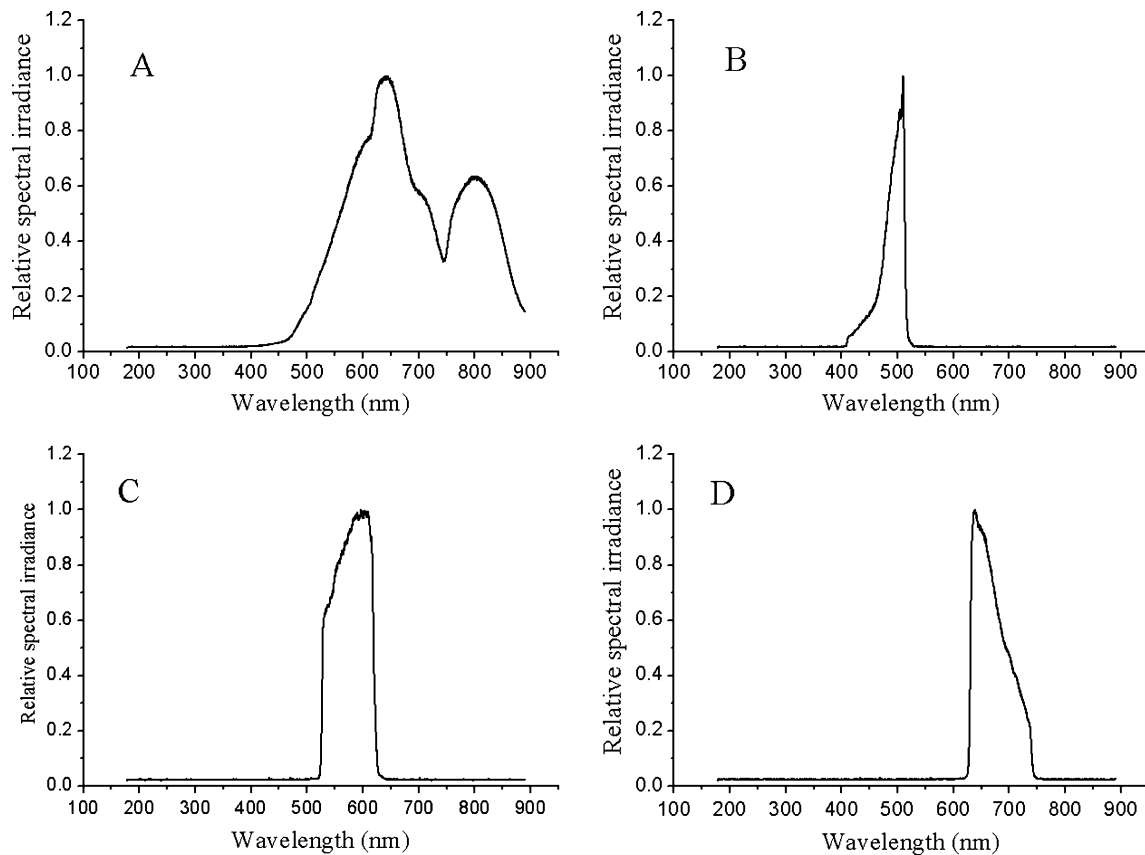


Fig. 1 The spectra of the light sources. The light used was a pseudo-solar continuous spectrum produced by an incandescent lamp. Light spectra were measured using a spectrometer (USB-4000 UV-VIS,

Ocean Optics,). Four kinds of light spectra were produced by the coated optical filters. **a** White light, **b** blue light (400–530 nm), **c** yellow light (530–645 nm), **d** red light (640–750 nm)

Effects of light on growth and R_{mag} of AMB-1 cells

Cells at the logarithmic growth phase were inoculated into 12 bottles filled to ~85% volume and cultured at 28 °C. These bottles were divided at random into an illumination test group ($n=6$) and a control group ($n=6$). All sides of the bottles were masked, except the base of those in the test group. All bottles were kept with the opening facing down and illuminated simultaneously for 20 h with light intensity

of $8 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The temperature in the medium increased to 28.2 °C from 28 °C within 20 h. The experiments were repeated three times. The OD_{600} values were analyzed using a UV-VIS spectrophotometer (Hitachi U 2800, Tokyo, Japan). The R_{mag} values were measured as described previously (Zhao et al. 2007).

Measurement of the magnetic hysteresis loop of AMB-1 cells

The AMB-1 cells (50 ml) were centrifuged at $12,000\times g$ for 10 min and the supernatant was discarded. The precipitate was dried by nitrogen for 10 min, weighed, and kept under nitrogen. The magnetic hysteresis loop of AMB-1 was measured with an alternating gradient magnetometer (AGM model 2900, Princeton Measurements, Princeton, NJ, USA).

Statistical analysis

All statistical analysis was performed with the two-tailed version of Student's *t*-test (SPSS, Chicago, IL, USA). Data were expressed as mean \pm SD and the level of statistical significance was set at $P<0.05$.

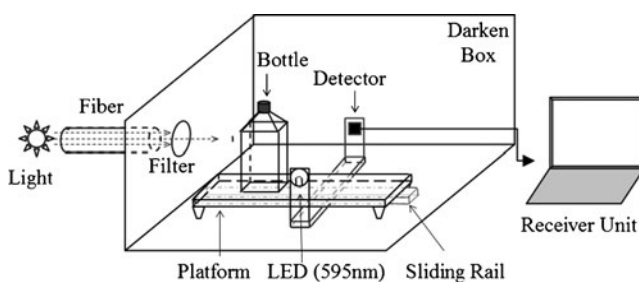


Fig. 2 The schematic figure of the mobile spectrophotometer. It included an optical path system, a power supply, and a signal processing system. The optical path system which was composed of a 595 nm light-emitting diode (LED) and a photodetector could be moved to measure the absorbance of the cells

Results

The OD_{595} values and color of the resazurin indicated the distribution of AMB-1 cells and migration to light

The redox indicator resazurin was added to the medium to better visualize the distribution of the oxygen and AMB-1 cells. When the oxygen of the medium was reduced, the absorbance at OD_{595} of blank medium decreased only slightly (0.05 ± 0.01) as the color of resazurin changed from pink to clear and colorless. This indicates that the color change will not interfere with the absorbance readings for cell density.

After 65 ml of AMB-1 cells at the logarithmic growth phase were poured into glass bottles and grown in the dark for 3 h, an OAI between the oxidized (pink) and reduced (colorless) resazurin formed (Fig. 3a). The distributions of AMB-1 cells in the pink area (line a) and colorless area (line b) were measured by a mobile spectrophotometer (Fig. 3c). From the data shown in Fig. 3c, we determined that the OD_{595} value in the pink area (line a) was only ~ 0.03 , and in the colorless area (line b) ~ 0.18 . When AMB-1 cells were illuminated for 6 min with light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, they formed another distribution similar to that illustrated in Fig. 3b; the color of the resazurin at the OAI changed and the OD_{595} value at the left of line a increased to ~ 0.15 and that at the right of line b decreased to ~ 0.06 (Fig. 3d). It is interesting that the OD_{595} value at the left of line b did not increase. The cells at the left of line a seem to come from cells at the right of line b.

Thus the OD_{595} values indicated the spatial distribution of AMB-1 cells. The AMB-1 cells were found mainly at the colorless OAI, and more importantly, these results proved that AMB-1 cells migrated toward a light source.

The light response of AMB-1 cells could be repeated

The AMB-1 cells were illuminated with a light of intensity 1, 2, 4, 8, and $16 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from one side of the bottle for 6 min. The color of resazurin revealed that the AMB-1 cells could migrate toward the light source within 6 min and that the phototactic response was enhanced by increasing of the light intensity. In particular, the response increased considerably when the light intensity increased from 0 to $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, but increased little above that. There was little difference in response between 8 and $16 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, so light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ was used for all other experiments.

When the AMB-1 cells were illuminated for 6 min with light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, phototaxis was observed (Fig. 4). The AMB-1 cells migrated gradually toward the light source (Fig. 4a). When the light was

removed, they migrated back very slowly (Fig. 4b). When the cells were illuminated again, they migrated back toward the light source. This behavior could be repeated several times.

AMB-1 cells respond to the light and heat simultaneously

Our pilot studies demonstrated that AMB-1 cells migrated rapidly toward a heat source once a small temperature gradient developed ($\sim 0.1 \text{ }^\circ\text{C}$). We asked whether the AMB-1 cell response to light was really due to the heat. There was no temperature difference between the lighted side and the other side, however, even when the medium in the bottle was illuminated for 10 min with a light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. When the cells were illuminated from the left and were heated from the opposite side to create a temperature gradient of $0.1 \text{ }^\circ\text{C}$, the OD_{595} values and the variations in resazurin color indicated that AMB-1 cells migrated toward both the light and heat simultaneously (Fig. 5). Thus, while AMB-1 cells do show a thermotactic response, the response to light was not the result of a temperature change.

Action spectrum

We then investigated whether AMB-1 cells, like Strain MC-1, possess an action spectrum of preferred wavelengths. White light spectra and three light bands of 400–530, 530–645, and 640–750 nm were used to establish the frequency response of phototaxis. The AMB-1 cells migrated toward all three lights and the phototactic response was always enhanced by increased light intensity, so AMB-1 cells have no special action spectrum.

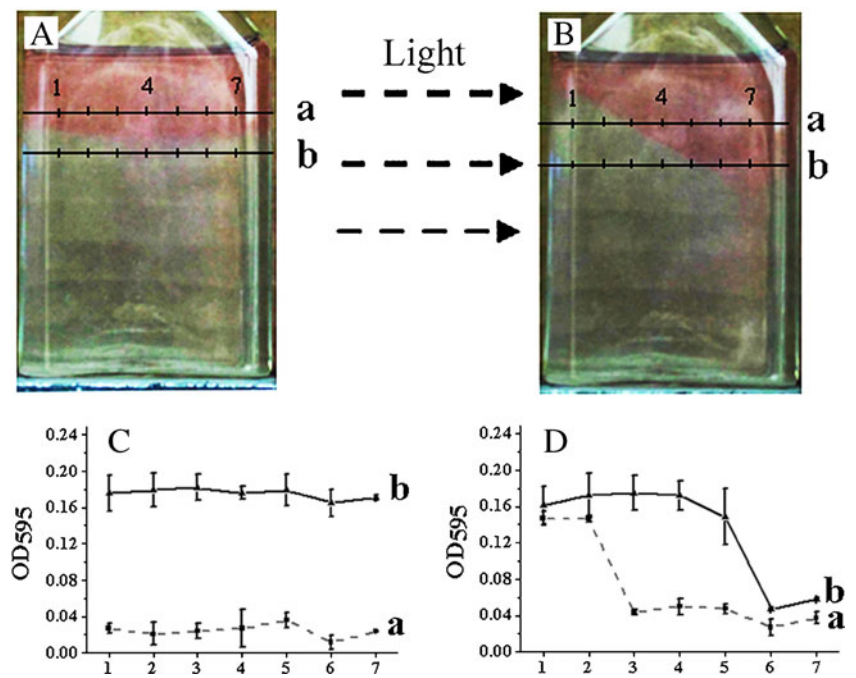
The response of AMB-1 cells to light is independent of magnetic field

In a zero magnetic field, AMB-1 cells would migrate toward the light source. Even when they were exposed to a magnetic field of 0.2 mT that was opposite or perpendicular to the light beam direction, AMB-1 cells still migrated toward the light source, indicating that the phototactic response was not affected by a magnetic field.

Effect of light on the growth and magnetosomes of AMB-1 cells

The illuminated test group and the control group cells were grown at $28 \text{ }^\circ\text{C}$ for 20 h in $8 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ light, and then the OD_{600} and R_{mag} values were measured. When the cells were illuminated, the R_{mag} value was significantly higher ($P < 0.01$, $n = 6$), while the OD_{600} value showed no obvious change ($P > 0.05$, $n = 6$; Table 1).

Fig. 3 AMB-1 cells migrated toward the light source. **a** An OAI was formed as indicated by the oxidized pink and reduced colorless resazurin. **b** AMB-1 cells were illuminated. **c, d** The OD_{595} values along the lines *a* and *b* of **a** and **b**. The interface area was illuminated for 6 min at a light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The blank control was pink growth medium with 2 mg/l resazurin



The magnetic hysteresis loop of AMB-1 cells illuminated for 20 h was measured immediately after the OD_{600} , and R_{mag} were measured. The data given in Table 1 shows that the coercive force (H_c) increased when the AMB-1 cells were illuminated for 20 h ($P < 0.05$, $n = 6$) compared with the control group. The mass-specific remnant magnetization (M_r) calculated by the gram weight of dried AMB-1 cells was increased when the AMB-1 cells were illuminated for 20 h ($P < 0.05$, $n = 6$; Table 1). However, the remanent magnetization (M_r) to saturation magnetization (M_s) ratios were not changed significantly ($P > 0.05$, $n = 6$; Table 1).

Discussion

The *M. magneticum* strain AMB-1 migrated toward pure white light sources and toward multiple spectral bands. Cells also migrated along a thermal gradient but the two responses were independent, indicating that these bacterial are both phototactic and thermotactic in addition to magnetotactic. It is puzzling that the response to light was not observed before during microscopic examinations (just as magneto-aerotaxis has). It is possible that AMB-1 cells migrated toward light, but they do not amass to such an extent that it would be visible to the naked eye. From the results shown in Fig. 3, it could be found that the AMB-1 cells did not mass serious to a higher concentration when they were illuminated. Another possibility is that the cells swim to the bottom of the droplets under a microscope since they are illuminated from the bottom and horizontal swimming of cells along the magnetic field lines might mask the vertical phototaxis.

Magnetotactic coccus strain MC-1 was reported to respond only to short-wavelength light ($\lambda \leq 500 \text{ nm}$; Frankel et al. 1997). Here, the response to light of AMB-1 cells was shown to be independent of a particular wavelength, as cells migrated toward light sources from 400 to 750 nm (even wavelengths as short as 350–400 nm and wavelengths as long as 750–1,100 nm caused phototaxis, data not shown).

It is a puzzle that the phototactic response of AMB-1 cells is independent of particular wavelength. It has been shown that the bacteriophytochromes are photoreceptors that help bacteria sense changes in light wavelength and intensity (Li et al.

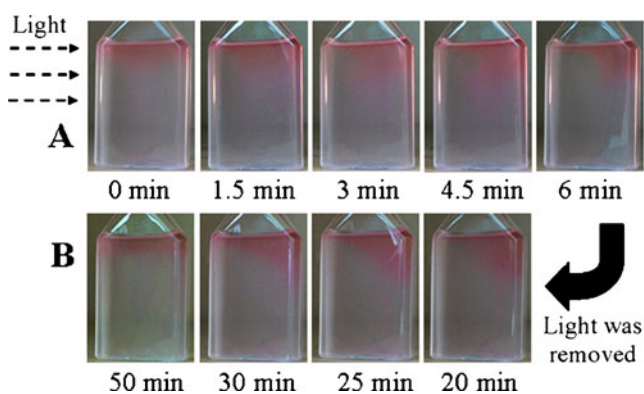


Fig. 4 The phototactic response of the AMB-1 cells. **a** The AMB-1 cells migrated gradually toward the light source when the interface area was illuminated for 6 min with light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. **b** When the light was removed, they migrated back very slowly. This behavior could be repeated several times

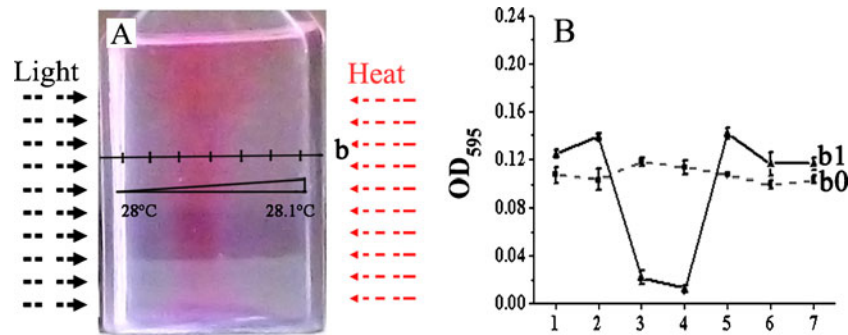


Fig. 5 AMB-1 cells migrated to light and heat simultaneously. **a** The interface area was illuminated for 6 min with light intensity of $4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. **b** The OD_{595} values measured along the line in **a**.

Line *b0* showed the OD_{595} values before illumination and thermostimulation, line *b1* after illumination and thermostimulation. The blank control was pink growth medium with 2 mg/l of resazurin

2010). Gegear et al. (2008) also reported that cryptochromes mediated light-dependent magnetosensitivity in *Drosophila*. A homology gene (*amb2928*) to bacteriophytochrome was also found in AMB-1 (Matsunaga et al. 2005). In general, the conformation of bacteriophytochromes can be changed by light of a particular wavelength light. This would confer wavelength-dependent phototaxis. Perhaps there is more than one kind of bacteriophytochrome in AMB-1 cells, but confirmation will require further research.

Magnetosensitivity has been shown to be light-dependent in some animal experiments (Deutschlander et al. 1999). Gegear et al. (2008) reported cryptochrome-mediated light-dependent magnetosensitivity in *Drosophila*, while Zapka et al. (2009) reported that European robins were able to navigate using either the sun or stars as a compass. The relationship between phototaxis and magneto-aerotaxis in MTB is of great interest. It is well known that MTB can migrate to and remain at positions with a preferred concentration of oxygen. Magnetotactic coccus strain MC-1 can swim away light parallel to a magnetic field (Frankel et al. 1997). In this study, when the AMB-1 cells were illuminated in a zero magnetic field or 0.2 mT magnetic fields that were opposite or perpendicular to the light beam, the cells still migrated toward the light source. These results demonstrate that the response to light of AMB-1 cells does not depend on the geomagnetic field.

Faivre et al. (2008) reported that the biological control of magnetite biomineralization by MTB could be disturbed by environmental parameters (Deutschlander et al. 1999). When AMB-1 cells were illuminated for 20 h, the R_{mag} value increased significantly. The R_{mag} value was correlated linearly with the number of magnetosomes and the percentage of magnetosome-containing bacteria (Nultsch

1991). The magnetic hysteresis loop of AMB-1 cells also showed an increased coercive force and remanent magnetization when the cells were illuminated for 20 h. Light is, perhaps, an important environmental factor for the biological control of magnetite biomineralization by MTB.

To our knowledge, no evidence has been found indicating that the MTB can use light as an energy source like photosynthetic bacteria. The function of phototaxis in AMB-1 is still not known. MTB mainly inhabit water columns or sediments with vertical chemical concentration gradients. They live predominantly at the OAI and in the anoxic regions of the habitat (Bazylinski and Moskowitz 1997; Bazylinski et al. 1995; Frankel et al. 1997; Simmons et al. 2004). In addition, chemical concentration, oxygen, geomagnetic field, and light may be important factors that allow MTB to explore and find a superior habitat. Light gradient in the water columns and sediments change over the day/night cycle and over the seasons. All of these changes affect the distribution of other environmental factors surrounding the cells. Magneto-aerotaxis, chemotaxis, phototaxis, and other taxises could help magnetic bacteria search for nutrients or move away from toxic substances and dangerous physical conditions. It is ultimately cellular metabolism and microenvironment that will determine which mode is dominant at any given time (Taylor et al. 1999). The reason that MTB have evolved so many modes may be related on the high number of methyl-accepting chemotaxis proteins (MCP) expressed. It was reported that the genomes of MTB have more than 40 MCP genes; in contrast *Escherichia coli* has only 5 MCP genes (Philippe and Wu 2010). Indeed, multiple modes of navigation may have helped MTB survive more than 700 million years (Chang and Kirschvink 1989).

Table 1 The effects of the illumination on AMB-1 cells

	OD_{600}	R_{mag}	H_c (Oe)	M_r (emu g^{-1})	M_r/M_s
Illuminated ($n=6$)	0.086 ± 0.004	$0.62 \pm 0.02^*$	$94.32 \pm 5.95^*$	$0.083 \pm 0.025^*$	0.61 ± 0.01
Control ($n=6$)	0.086 ± 0.002	0.68 ± 0.04	86.48 ± 4.81	0.068 ± 0.013	0.59 ± 0.03

* $P < 0.05$ vs. control

In conclusion, AMB-1 cells were observed responding to light. This response proved to be independent of wavelength and the geomagnetic field. Chronic light stimulation affected the formation of magnetosome.

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