



Magnetotactic Bacteria

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Source: *Science*, New Series, Vol. 190, No. 4212 (Oct. 24, 1975), pp. 377-379

Published by: [American Association for the Advancement of Science](#)

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cussion. First, the remarkable precision of size determination at resonance is on a relative basis only. It presumes that m is fixed, and therefore any uncertainty in m degrades the absolute precision. In trials to determine both m and d simultaneously at resonance, the precision of each seems limited to about 0.5 percent. This is also what we find for nonresonant scattering. Second, the relationship of "optical" diameters determined at resonance to "physical" diameters is not entirely clear, particularly when relative precisions of a few angstroms are considered. In polystyrene aerosols ranging from about 1 to 3 μm , diameters determined by our optical method (away from resonances) match those from physical methods and electron microscopy to within a few percent (7, 8).

The sensitivity of scattering to particle parameters at resonance can be either a useful tool or a liability. It is clearly the latter if resonances within the range of aerosol parameters are not recognized. Techniques based on differential scattering in particular may be subject to substantial errors if one is not careful (8). On the other hand, the availability of tunable monochromatic light sources makes these resonances generally accessible for many systems. Since the effects of resonance occur for absorbing as well as nonabsorbing particles, and since they should be seen with cylindrical objects (10) as well as spheres, numerous applications are possible. The phenomenon might be used to detect extremely small changes in the dimensions of a scatterer due to externally applied stress or modifications to its environment, or to changes in its composition. The effect might also be used as a continuous monitor in the manufacturing of wires or optical fibers requiring a precise maintenance of the diameter or refractive index. It is also possible that resonant scattering may be a useful tool for studying regularly shaped nonspherical particles in biological systems.

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4. For example, see pp. 97-127 in (1).
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9. The values $d = 2.956 \mu\text{m}$ and $m = 1.581$ are given by the manufacturer (Dow Chemical Co., Midland, Michigan). The batch number is unknown.
10. W. A. Farone and M. Kerker [*J. Opt. Soc. Am.* **56**, 481 (1966)] and D. Cooke and M. Kerker [*Rev. Sci. Instrum.* **39**, 320 (1968)] have characterized nonresonance differential scattering from in-

finite cylinders. Diameters can be found with precisions better than one-half percent.

11. Contribution No. 2632 from the Chemical Laboratories of Indiana University. Supported by the National Science Foundation. C.S.P. appreciates the help of E. C. Hartman in the formative stages of this work.

16 June 1975

Magnetotactic Bacteria

Abstract. *Bacteria with motility directed by the local geomagnetic field have been observed in marine sediments. These magnetotactic microorganisms possess flagella and contain novel structured particles, rich in iron, within intracytoplasmic membrane vesicles. Conceivably these particles impart to cells a magnetic moment. This could explain the observed migration of these organisms in fields as weak as 0.5 gauss.*

Few studies have unequivocally revealed effects of the earth's magnetic field on living organisms, although recent work indicates that birds (1) and elasmobranchs (2) detect and may use geomagnetism as a cue for orientation. I now describe a bacterial tactic response to magnetic fields, a phenomenon for which the term magnetotaxis is appropriate.

During attempts to isolate *Spirochaeta plicatilis* from marine marsh muds (3), I observed microorganisms which rapidly migrated (4) toward one side of drops of the mud transferred to microscope slides (Fig. 1). I presumed this to be a phototactic response toward light from a northwest laboratory window. It became apparent, however, that light was not the stimulus directing the migration of these organisms as cells aggregated at the same side of mud drops regardless of the distribution of light on the slides, as well as in the dark. The direction in which these organisms moved immediately changed when small magnets were moved about in the vicinity of the microscope preparations. This suggested that geomagnetism was the stimulus for the behavior of the cells. It was experimentally confirmed that the migration of the bacteria was, indeed, directed by the earth's magnetic field (5).

Magnetotactic organisms were present in surface sediments collected from salt marshes of Cape Cod, Massachusetts, and in surface layers of sedimentary cores collected from a depth of 15 m in Buzzards Bay. Population densities in these environments ranged from 200 to 1000 cells per milliliter. Mud samples placed under several centimeters of seawater in glass jars and kept in dim light in the laboratory underwent an ecological succession (3). Populations of magnetotactic organisms increased to hundreds of thousands of cells per milliliter in many such mud samples after several months to several years of storage. Magnetotactic bacteria were evenly distributed in surface layers of the stored muds even though the jars were positioned for long periods in the same geographic orientation. Apparently factors additional to magnetotaxis also determine the distribution of the organisms in natural environments, since larger populations of magnetotactic bacteria were not detected in the northern areas of a marsh as compared to other locations in the marsh.

The organisms have not yet been iso-

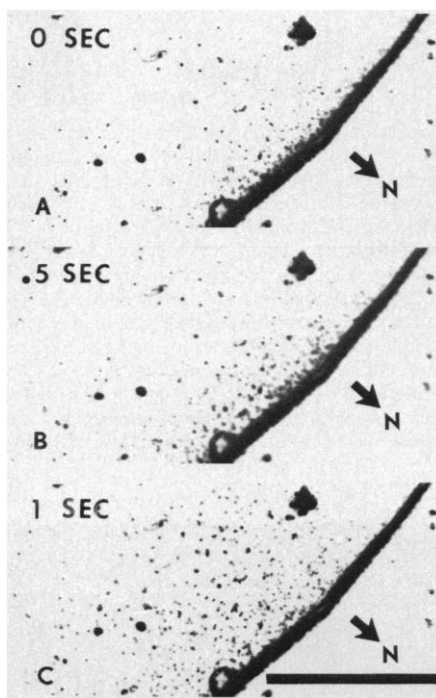


Fig. 1. Cinematographic sequence of bacteria displaying magnetotaxis. Portions of three sequential frames recorded on Kodak Tri-X reversal 16-mm movie film at 18 frames per second, with a Zeiss RA 38 microscope. The images shown were photographically reversed and enlarged. (A) Freely swimming magnetotactic bacteria aggregated at the northern extremity of a water drop by responding to geomagnetism. At the time of recording, a small permanent magnet was used to reverse the magnetic field. The cells then migrated in the opposite direction as recorded in frames (B) (0.5 second or 9 frames later) and (C) (recorded 1 second or 18 frames later). The arrow indicates the direction of the earth's north geomagnetic pole (bar, 100 μm).

lated and grown in pure culture. I obtained purified cell suspensions for electron microscopic examination by taking advantage of the cells' magnetotactic behavior. I placed drops of seawater in contact with the northern edge of drops of mud enrichment material on microscope slides. Orga-

nisms which rapidly migrated to the seawater drop were collected with micropipets and prepared for electron microscopy.

Magnetotactic cells were roughly spherical and averaged 1 μm in diameter (Fig. 2, A to C). Two bundles of flagella were observed at one side of the cell (Fig. 2, A

and B). Each bundle consisted of approximately seven flagella which were inserted in a disk-shaped structure (Fig. 2B, arrows) similar to those present in *Ectothiorhodospira mobilis* (6). Two chains, each consisting of approximately five to ten electron-opaque crystal-like particles, characterized magnetotactic cells (Fig. 2, A to D). In chemically fixed, thin-sectioned magnetotactic bacteria, these chains of particles were found to be internal cell components (Fig. 2C, white arrowheads). The crystal-like particles may exist as relatively thin plates. Apparent variation in the electron opacity of these structures (Fig. 2, A and D) may be due either to variation in thickness or to electrical charging encountered when they were placed in the electron beam of the microscope. In addition to a typical gram-negative type of wall, cells possessed intracytoplasmic unit membranes arranged as vesicles about their periphery (Fig. 2C, black arrows). The crystallike particles were often found within these membrane vesicles (Fig. 2D, arrow). The intravesicular location of the particles suggests that they may be synthesized by the membranes. Clumps of these particles, outside of cells, were also observed by transmission electron microscopy of sediments underlying older enrichments. These observations suggest that intracellular particles synthesized by the magnetotactic bacteria are released after death and lysis of cells, and accumulate in sediments. Mishustina (7) isolated similar particles from sediments of the Barents Sea but did not realize their probable origin or properties. The tendency of these particles to clump when outside of cells is consistent with the possibility that they may be a permanently magnetic substance such as magnetite.

Unstained whole cells and their crystal-like inclusions were subjected to energy dispersive x-ray microanalysis (8). An energy profile of x-rays collected after electron excitation of chains of the particles within a single cell appears in Fig. 3. Iron was the predominant detectable element within the particles. Elemental ratio analysis (8) of the signals obtained from each of several chains of particles indicated that the other elements detected were not present in a constant ratio to iron. These elements were also far less abundant than iron in the crystal-like particles found outside the cells. Thus, these elements were apparently not constituents of the novel cell inclusions and probably represent contamination from areas adjacent to the particles.

The relation between the chains of iron-rich particles and magnetotaxis is probably not coincidental. Recently, I observed in

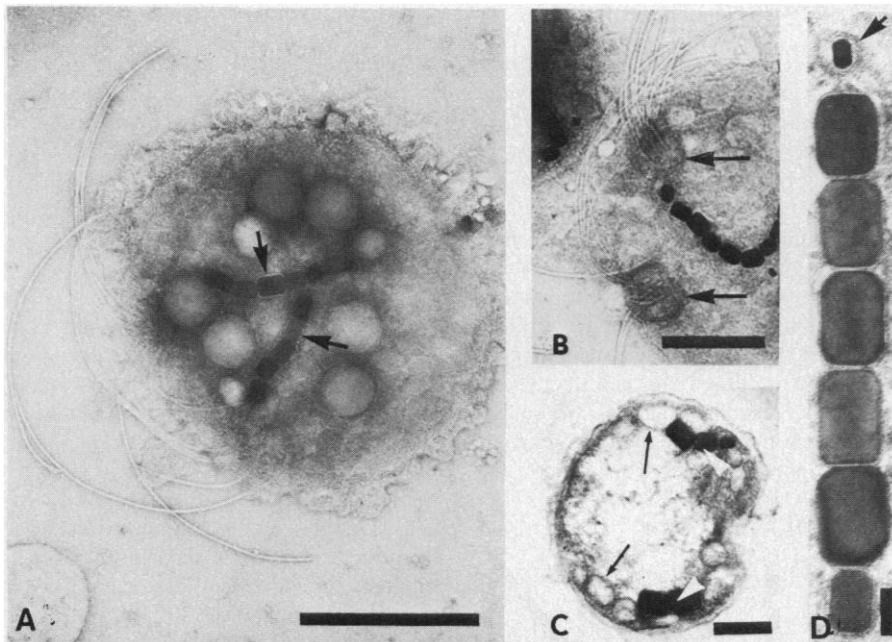
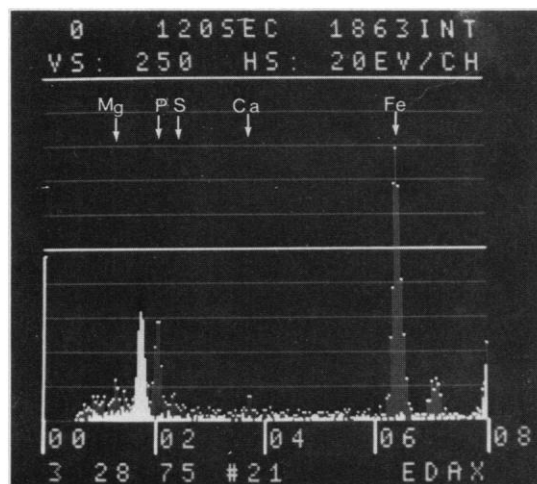


Fig. 2. Transmission electron micrographs recorded on Kodak EM estar thick base film with a Hitachi HU-12 electron microscope operating at 75 kv. (A) Electron micrograph of a magnetotactic bacterium. Two bundles of flagella insert at one side of the cell. Two chains of iron-rich particles are present (arrows). Deposits believed to be polyphosphate are abundant. The outer cell layers appear disrupted. Cell stained with phosphotungstic acid (bar, 0.5 μm). (B) Electron micrograph of a portion of a magnetotactic bacterium showing the two disks (arrows) into which flagella insert. Osmotically lysed cell stained with phosphotungstic acid (bar, 0.25 μm). (C) Electron micrograph of a chemically fixed and thin-sectioned magnetotactic bacterium stained with lead and uranyl salts. The cell has a gram-negative type wall. The iron-rich particles (white arrowheads) have been unintentionally displaced during thin-sectioning revealing intracytoplasmic membranes arranged as vesicles (black arrows) adjacent to the cell plasma membrane. Much of the central portion of the cell appears to have been extracted during chemical preparation (bar, 0.25 μm). (D) Electron micrograph of a single chain of particles containing iron present in a cell prepared as described for (C). The particles are enclosed within vesicles consisting of triple-layered membranes (arrow) (bar, 0.07 μm).

Fig. 3. A portion of an energy profile of x-rays collected after electron excitation of part of an unstained magnetotactic bacterium. The area analyzed contained two chains of the particles similar to those in Fig. 2D. X-rays with energies of 6.4 and 7.0 kev correspond to those for $K\alpha$ and $K\beta$ emission lines of iron, respectively. X-rays from elements present in the sample, but not in a control area from which cells were absent, are indicated by peaks consisting of vertical bars topped with white dots. Silicon (solid white peak, 1.7 kev) was more abundant in the control than in the sample. The unstained specimen was analyzed for 120 seconds on a copper grid in a beryllium holder positioned 36° incident to the 0.25- μm -diameter electron beam. Analysis was performed in the transmission mode at $\times 43,000$ and 60 kv. The electron beam was astigmatized to accommodate the elongated shape of the chains of particles. Large amounts of phosphorus suggest contamination from adjacent granules (see Fig. 2A) believed to be polyphosphate.



marsh muds a larger type or species of magnetotactic bacterium than that described. This organism measures 1.2 by 3.2 μm and differs from the aforementioned in a number of morphological details when viewed by phase contrast microscopy. Both types of magnetotactic bacteria contain chains of iron-rich particles. At least five morphologically distinct types of magnetotactic bacteria are recognizable in samples collected from marshes in the vicinity of Woods Hole. This raises the interesting possibility that several (perhaps previously unrecognized) species of bacteria may be among those organisms which can be separated from their environment by their magnetotactic responses.

Magnetotaxis could not result from a magnetic force tending to "pull" these bacteria northward since, in uniform magnetic fields such as those used to demonstrate cell responses to geomagnetism (5), a dipole would not translocate in any direction as a consequence of magnetism; it would merely rotate to a preferred orientation within the magnetic field. Cells suspended in seawater did not migrate when killed with vapors of osmium tetroxide. Those not stuck to glass surfaces rotated so as to remain aligned with an applied magnetic field when the direction of the field was changed. Thus, cell motility is required for magnetotaxis, and cell orientation is the primary response to magnetism. Freely suspended killed cells also frequently formed chains of up to ten cells. Each chain behaved as a single dipole in response to changes in the position of a nearby permanent magnet. Perhaps the iron-rich cell inclusions serve as magnetic dipoles which convey a magnetic moment upon the cell, thus orienting the cells in magnetic fields. Magnetotaxis would result if, within each cell, a fixed spatial relationship existed between the orienting mechanism and cell propulsion. Studies of the behavior of living and dead cells in uniform and nonuniform fields should contribute to an understanding of the magnetotactic mechanism. It may also be possible to detect a preferred orientation of cells or their flagella and their iron-rich inclusions in magnetic fields. Results of survival experiments indicate that these organisms are either microaerophiles or strict anaerobes. Because the vertical component of the earth's magnetic field has a greater magnitude than the horizontal in the locations where they have been found, magnetotaxis might serve to direct these organisms downward toward sediments and anaerobic areas favorable to their growth.

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24 OCTOBER 1975

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4. In the absence of obvious artificial magnetic fields the organisms migrated downward and northward at about 100 $\mu\text{m}/\text{sec}$.
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lated area free of detectable geomagnetic distortion.

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9. Supported by PHS grant AI-08248 to Dr. E. Canale-Parola at the University of Massachusetts, Amherst, and by a grant from the Sarah Mellon Scaife Foundation to the Woods Hole Oceanographic Institution. I thank Drs. V. T. Bowen, E. Canale-Parola, H. W. Jannasch, and A. J. Kalmijn for stimulating conversations and helpful criticism of the manuscript. I thank L. Surprenant for her contribution to the work reported here and Dr. R. Turner for the use of her cinematographic equipment. Contribution 3581 of the Woods Hole Oceanographic Institution.

9 June 1975; revised 30 July 1975

Mass Measurement: A Study of Anomalies

Abstract. *It has always been assumed that the measurement of the difference in mass between two objects would be the same in all laboratories. Recent National Bureau of Standards measurements involving dissimilar objects (effective density ranging from 2.7 to 16.6 grams per cubic centimeter) at a wide variety of pressures (0.5 to 2 atmospheres) have been made with sufficient precision to test this assumption. The results show unsuspected discrepancies which may approach 1 milligram in a kilogram in the assignment of mass values when dissimilar materials are involved. These discrepancies have not been noted in the past because precision comparisons of both like and unlike materials have nearly always been made in a relatively restricted range of environmental conditions. The worldwide mass measurement system is therefore consistent, because similar materials have been used in the construction of weight sets, but possibly offset with respect to the mass unit as embodied in the platinum-iridium defining artifact.*

The unit of mass of the Syst me International d'Unit s (SI) system of measurement units is defined by an artifact, the International Prototype Kilogram preserved at the Bureau International des Poids et Mesures near Paris. The transfer of a mass value from such a defining artifact to another cannot be done directly in a normal laboratory environment. The mass value assigned to another object must be inferred from the results of a comparison of the artifact and the "unknown" by means of a balance. The balance, in turn, is a force comparator, responding to both the gravitational force and the buoyant force of the atmosphere acting on the object or objects on the balance pan or pans. In a given location, the gravitational force acting on an object is a constant and proportional to the mass of the object. The buoyant force, however, is proportional to the displacement volume of the object and the density of the surrounding air. Although the buoyant force is not large with respect to the gravitational force, being only on the order of 0.015 percent for materials of normal density, it is large with respect to the precision of currently available balances. Commercial kilogram balances are avail-

able with standard deviations of a single weighing on the order of 0.03 mg, and research balances in national laboratories have standard deviations on the order of 0.005 mg. Careful attention must be given to the manner in which the buoyant force is accounted for if this precision is to be utilized in the transfer of the mass unit from one object to another.

In such a transfer the observed difference, as determined by the balance, is adjusted or corrected by the product of the computed air density, D , at the time of the measurement and the difference in the previously measured displacement volumes, V_1 and V_2 , of the objects being compared. In essence, the observed difference, Y , is the difference between the resultant forces acting on the two objects (the gravitational force minus the buoyant force). To determine the gravitational force, one must add a correction of Y for the difference $D(V_1 - V_2)$ in buoyant force; that is, the value for the mass difference, $M_1 - M_2$, is given by

$$M_1 - M_2 = Y + D(V_1 - V_2)$$

One expects the mass difference for any given pair of objects to be constant regardless of location.