

in the central brain to allow color discrimination. In *Drosophila*, the integration of sensory information coming from randomly distributed receptor neurons into the visual system's topographic organization has not been analyzed. Although most of the cellular components and their projection patterns in the fly visual system have been described [13], our understanding of how the brain 'sees' the colorful world is still in its beginnings.

References

1. Mombaerts, P. (2004). Odorant receptor gene choice in olfactory sensory neurons: the one receptor-one neuron hypothesis revisited. *Curr. Opin. Neurobiol.* 14, 31–36.
2. Mazzoni, E.O., Desplan, C., and Celik, A. (2004). 'One receptor' rules in sensory neurons. *Dev. Neurosci.* 26, 388–395.
3. Wernet, M.F., Mazzoni, E.O., Celik, A., Duncan, D.M., Duncan, I., and Desplan, C. (2006). Stochastic spineless expression creates the retinal mosaic for colour vision. *Nature* 440, 174–180.
4. Voas, M.G., and Rebay, I. (2004). Signal integration during development: insights from the *Drosophila* eye. *Dev. Dyn.* 229, 162–175.
5. Reifegerste, R., and Moses, K. (1999). Genetics of epithelial polarity and pattern in the *Drosophila* retina. *Bioessays* 21, 275–285.
6. Heisenberg, M., and Buchner, E. (1977). The role of retinula cell types in visual behavior of *Drosophila melanogaster*. *J. Comp. Physiol.* 117, 127–162.
7. Chou, W.H., Hall, K.J., Wilson, D.B., Wideman, C.L., Townson, S.M., Chadwell, L.V., and Britt, S.G. (1996). Identification of a novel *Drosophila* opsin reveals specific patterning of the R7 and R8 photoreceptor cells. *Neuron* 17, 1101–1115.
8. Franceschini, N., Kirschfeld, K., and Minke, B. (1981). Fluorescence of photoreceptor cells observed *in vivo*. *Science* 213, 1264–1267.
9. Mollereau, B., Dominguez, M., Webel, R., Colley, N.J., Keung, B., de Celis, J.F., and Desplan, C. (2001). Two-step process for photoreceptor formation in *Drosophila*. *Nature* 412, 911–913.
10. Chou, W.H., Huber, A., Bentreop, J., Schulz, S., Schwab, K., Chadwell, L.V., Paulsen, R., and Britt, S.G. (1999). Patterning of the R7 and R8 photoreceptor cells of *Drosophila*: evidence for induced and default cell-fate specification. *Development* 126, 607–616.
11. Mikeladze-Dvali, T., Wernet, M.F., Pistillo, D., Mazzoni, E.O., Teleman, A.A., Chen, Y.W., Cohen, S., and Desplan, C. (2005). The growth regulators warts/lats and melted interact in a bistable loop to specify opposite fates in *Drosophila* R8 photoreceptors. *Cell* 122, 775–787.
12. Crews, S.T. (1998). Control of cell lineage-specific development and transcription by bHLH-PAS proteins. *Genes Dev.* 12, 607–620.
13. Fischbach, K.F., and Dittrich, A.P. (1989). The optic lobe of *Drosophila melanogaster*. I. A Golgi analysis of wild-type structures. *Cell Tissue Res.* 258, 441–475.

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Bacterial Cell Biology: Managing Magnetosomes

Sensing of magnetic fields by living organisms – magnetosensing – is best understood in magnetotactic bacteria. Recently work has provided new insight into the biogenesis of bacterial magnetosomes, and links these organelles to a newly recognized prokaryotic cytoskeletal filament which organizes magnetosomes into a sensory structure capable of aligning cells with the geomagnetic field.

Craig Stephens

Several centuries ago, humans learned to construct navigational compasses that could sense the earth's magnetic field [1]. By that time, the living world was millions of years ahead of us in geomagnetic sensing technology. While the significance and mechanisms of magnetosensing in animals, such as migratory birds, fish and insects, that execute remarkable global navigational feats have been debated for years, the biological compass mechanism we know the most about at the cellular level is found in magnetotactic bacteria. These aquatic microbes are thought to use their internal magnets for the relatively mundane task of pointing themselves downward, toward their preferred homes in oxygen-depleted sediments [2]. We will

discuss here recent insights into how 'magnetosomes', the membrane-enclosed magnetite crystals central to bacterial magnetosensing, are produced and organized [3,4]. Magnetosome-like structures have been observed in many animals, and the work discussed here may provide insight into the development, function and evolution of magnetosomes in eukaryotes.

Experimental work on bacterial magnetotaxis began over 30 years ago, when Richard Blakemore made the curious observation that a population of motile bacteria from salt marsh mud responded dramatically to magnetic manipulation [2]. Since Blakemore's initial discovery, magnetotactic bacteria have been found in freshwater and marine sediments around the world [5].

Most magnetotactic bacteria seen in the Northern hemisphere are north-seeking, and most in the Southern hemisphere are south-seeking [6,7]. Why is this? Blakemore hypothesized that, because of the significant vertical component of the geomagnetic field at latitudes away from the equator, alignment of a bacterial cell with the geomagnetic field would facilitate downward migration by north-seeking bacteria in the northern hemisphere (and conversely in the south) [2]. Since the magnetotactic bacteria isolated so far prefer anaerobic or microaerobic conditions, if they find themselves in an O₂-rich environment, such as the water column above the sediment, following the geomagnetic field downward — and supplementing magnetotaxis with O₂ and/or redox sensing and taxis — should help them to find more anoxic sediments [2,8].

The cell biology of magnetotaxis is under active investigation [9,10]. Magnetosomes contain crystalline particles of magnetite (Fe₃O₄) or greigite (Fe₃S₄). The individual crystals are generally 35–100 nm in size, and constitute a permanent single magnetic domain [11,12]. To generate a sufficiently large

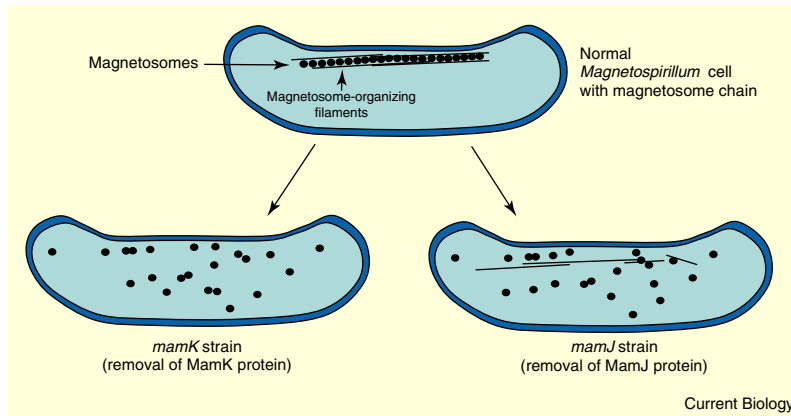


Figure 1. Cellular organization of bacterial magnetosomes.

Komeili *et al.* [3] and Scheffel *et al.* [4] used electron cryotomography to visualize magnetosome organization in *Magnetospirillum*, shown here diagrammatically. Magnetosome vesicles were closely associated with the inner membrane, and fine filaments (4–6 nm thick) were seen running parallel and in close proximity to the magnetosome chain. Both MamK and MamJ were similarly localized to these magnetosome-associated filaments, and genetic disruption of either *mamJ* or *mamK* caused magnetosomes to become disorganized; the Δ *mamK* mutant, however, lost its cytoskeletal filaments, while the Δ *mamJ* strain still exhibited filaments.

magnetic moment to align a bacterial cell with the geomagnetic field, magnetosomes are organized into a linear chain of 20–40 units (Figure 1), with the total dipole moment for the chain being the sum of the individual units. Our understanding of how the magnetite crystals are generated and organized is still fairly rudimentary, though it is known that magnetosome vesicles are generated before magnetite crystals appear inside [13]. The vesicles are derived from the inner membrane, and acquire a subset of proteins presumably dedicated to magnetosome functions, such as iron uptake and magnetic crystal formation [14,15]. Because magnetosomes are one of the few examples of an internal membrane-enclosed organelle in a prokaryotic cell, their biogenesis could speak to the evolution of organelles in primitive cells [9,10].

The ability of the magnetosome chain to physically align a bacterial cell in a magnetic field depends on the structure being relatively fixed within the cell. Komeili *et al.* [3] now present evidence that magnetosomes do not float freely in the cytoplasm. Using electron cryotomography (ECT) to peer inside flash-frozen *Magnetospirillum magnetotacticum* cells retaining much of their native structure, the ‘vesicles’ enclosing

magnetosomes appear to be invaginations of the cytoplasmic membrane. Three-dimensional reconstructions from their stacked ECT images strongly suggest that magnetosomes remain associated with the cytoplasmic membrane.

Once magnetosomes form, how are they organized into coherent chains? Komeili *et al.*'s [3] ECT imaging of *M. magnetotacticum* revealed fine filaments alongside the magnetosomes, reminiscent of cytoskeletal elements in eukaryotic cells (Figure 1). In fact, there is ample precedent for prokaryotic cytoskeletal structures. FtsZ, a key player in bacterial cell division, strikingly resembles eukaryotic tubulins in both structure and polymerization properties [16]. Two bacterial actin homologs, MreB and ParM, form filaments that direct cell wall synthesis and plasmid segregation, respectively [17,18], and a third, unrelated family of ATPases forms dynamic filaments involved in plasmid positioning and segregation [19]. So, the notion of a cytoskeletal structure organizing magnetosomes is not terribly far fetched.

The magnetosome-associated filaments in *M. magnetotacticum* are comparable in size to other bacterial actin-type filaments. Komeili *et al.* [3] noted that the

mamK gene, which is located within a genomic region implicated in magnetotactic behavior, encodes a protein related to MreB and ParM. When they knocked out *mamK*, the magnetosome-associated filaments disappeared and magnetosomes were distributed randomly rather than in chains (Figure 1). When cells producing a fusion of MamK to green fluorescent protein (GFP) were examined by fluorescence microscopy, the magnetosome-associated filaments glowed green. These observations are consistent with MamK assembling into filaments that organize and position the magnetosome chain, allowing the bacterium to be aligned appropriately in the geomagnetic field.

Scheffel *et al.* [4] also observed magnetosome-associated filaments in the closely related magnetotactic bacterium *Magnetospirillum gryphiswaldense*. Their work focused on MamJ, an acidic, repetitive protein that they initially suspected to be involved in magnetite crystallization. When *mamJ* was deleted, magnetite-filled magnetosomes still formed, ruling out a significant role in crystal formation. But magnetosomes were disorganized in the *mamJ* mutant, as in the *mamK* mutant strain (Figure 1). Although a MamJ–GFP fusion protein is targeted to the magnetosome-associated filaments in normal cells, ECT images still showed filaments in the *mamJ* mutant, unlike in the *mamK* strain (Figure 1). Thus, MamJ is not an essential structural component of the magnetosome-organizing filament. Scheffel *et al.* [4] speculate that MamJ is arranged along the filaments to attach magnetosomes, perhaps as an interface between MamK and receptors in the magnetosome membrane.

There is still much to be learned about the cell biology of magnetosomes and magnetotaxis. What is the composition and structure of these filaments, and how are they placed appropriately within the cell? Do they interact with the membrane? What happens to them during cell

division, or when environmental conditions change? When and how are magnetosomes attached? Does this relate to magnetite crystallization and orientation? How does the position and polarity of the magnetosome chain relate to other important cellular structures, such as flagella? And finally, how did this structure evolve? Magnetotactic bacteria are somewhat scattered in phylogenetic terms, but how likely is it that magnetosomes evolved independently more than once? Indeed, genes for magnetosome synthesis and organization are clustered on the *M. gryphiswaldense* genome and contain numerous insertion elements that facilitate recombination, so lateral transfer of this gene set between species may be fairly easy [20]. More genetic and genomic analysis will be needed to address this issue.

We'll close this foray into magnetotaxis with one last twist. Simmons *et al.* [6] recently reported substantial populations of south-seeking magnetotactic bacteria co-existing with north-seeking bacteria at a site in the northern hemisphere (Falmouth, Massachusetts, USA), not far from where Blakemore's samples first revealed magnetotaxis. The north and south-seeking bacteria were significantly stratified, with the south-seekers most abundant in more highly oxidized locations. The south-seekers Simmons *et al.* [6] observed are morphologically distinct from known magnetotactic species, but have not yet been isolated and cultured for laboratory investigation. How and why these bacteria have adapted magnetotaxis to generate a distinct behavioral response is as yet unknown. Future investigations should yield more insight into mechanisms by which microbes coordinate magnetotaxis with other sensory systems to find their way home — and perhaps provide clues as to how macroscopic creatures generate and utilize cellular-scale magnetic structures for their own ends.

References

1. Aczel, A. (2002). *The Riddle of the Compass: The Invention that Changed the World* (New York: Harcourt, Inc.).

2. Blakemore, R. (1975). Magnetotactic bacteria. *Science* 190, 377–379.
3. Komeili, A., Li, Z., Newman, D.K., and Jensenm, G.J. (2006). Magnetosomes are cell membrane invaginations organized by the actin-like protein MamK. *Science* 311, 242–245.
4. Scheffel, A., Gruska, M., Faivre, D., Linaroudis, A., Plietzko, J.M., and Schuler, D. (2006). An acidic protein aligns magnetosomes along a filamentous structure in magnetotactic bacteria. *Nature* 440, 110–114.
5. Blakemore, R. (1982). Magnetotactic bacteria. *Annu. Rev. Microbiol.* 36, 217–238.
6. Simmons, S.L., Bazylinski, D.A., and Edwards, K.J. (2006). South-seeking magnetotactic bacteria in the Northern Hemisphere. *Science* 311, 371–374.
7. Blakemore, R.P., Frankel, R.B., and Kalmijn, A.J. (1980). South-seeking magnetotactic bacteria in the Southern Hemisphere. *Nature* 286, 384–385.
8. Frankel, R.B., Bazylinski, D.A., Johnson, M.S., and Taylor, B.L. (1997). Magneto-aerotaxis in marine coccoid bacteria. *Biophys. J.* 73, 994–1000.
9. Bazylinski, D.A., and Frankel, R.B. (2004). Magnetosome formation in prokaryotes. *Nat. Rev. Microbiol.* 2, 217–230.
10. Matsunaga, T., and Okamura, Y. (2003). Genes and proteins involved in bacterial magnetic particle formation. *Trends Microbiol.* 11, 536–541.
11. Bazylinski, D.A., Garratt-Reed, A.J., and Frankel, R.B. (1994). Electron microscopic studies of magnetosomes in magnetotactic bacteria. *Microsc. Res. Tech.* 27, 389–401.
12. Dunin-Borkowski, R.E., McCartney, M.R., Frankel, R.B., Bazylinski, D.A., Posfai, M., and Buseck, P.R. (1998). Magnetic microstructure of magnetotactic bacteria by electron holography. *Science* 282, 1868–1870.
13. Komeili, A., Vali, H., Beveridge, T.J., and Newman, D.K. (2004). Magnetosome vesicles are present before magnetite formation, and MamA is required for their activation. *Proc. Natl. Acad. Sci. USA* 101, 3839–3844.
14. Gorby, Y.A., Beveridge, T.J., and Blakemore, R.P. (1988). Characterization of the bacterial magnetosome membrane. *J. Bacteriol.* 170, 834–841.
15. Grunberg, K., Muller, E.C., Otto, A., Reszka, R., Linder, D., Kube, M., Reinhardt, R., and Schuler, D. (2004). Biochemical and proteomic analysis of the magnetosome membrane in *Magnetospirillum gryphiswaldense*. *Appl. Environ. Microbiol.* 70, 1040–1050.
16. Lowe, J., and Amos, L.A. (1998). Crystal structure of the bacterial cell-division protein FtsZ. *Nature* 391, 203–206.
17. van den Ent, F., Amos, L.A., and Lowe, J. (2001). Prokaryotic origin of the actin cytoskeleton. *Nature* 413, 39–44.
18. Garner, E.C., Campbell, C.S., and Mullins, R.D. (2004). Dynamic instability in a DNA-segregating prokaryotic actin homolog. *Science* 306, 1021–1025.
19. Lim, G.E., Derman, A.I., and Pogliano, J. (2005). Bacterial DNA segregation by dynamic SopA polymers. *Proc. Natl. Acad. Sci. USA* 102, 17658–17663.
20. Ullrich, S., Kube, M., Schubbe, S., Reinhardt, R., and Schuler, D. (2005). A hypervariable 130-kilobase genomic region of *Magnetospirillum gryphiswaldense* comprises a magnetosome island which undergoes frequent rearrangements during stationary growth. *J. Bacteriol.* 187, 7176–7184.

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Social Evolution: Cooperation by Conflict

A recent study suggests that aggression between wasps depends upon the costs and benefits of fighting, as determined by the position of individuals in a dominance hierarchy.

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In a world where individuals are destined to be selfish, conflict seems likely. As described by Darwin's 'survival of the fittest', all individuals are motivated by the need to survive and reproduce, passing their genes on to future generations. Each individual acts upon their own best interests, but what is best for one individual will not necessarily be ideal for another. Thus individuals can prefer different outcomes, and

inevitably, this often leads to a conflict of interests. Conflict ranges from the peacefully resolved competition amongst male lion coalitions, for access to oestrus females [1], to the aggressive and often lethal fighting observed between wingless male fig wasps [2].

Whilst conflict is inevitable, aggression is less easily explained. In general, animals avoid fighting — and thus avoid serious injury — through ritualistic assessment of opponents [3]. In most species this 'conflict