Magnetosensation

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Anyone who observes animals with even cursory interest is likely to reach the conclusion that their movements are frequently directed, as if they had a sense of where they were going. Of course, for any mobile organism directing movement is of considerable adaptive value. Heterogeneity in the environment necessarily means that some places are better to be than others. Movements to avoid less favorable places (or at least quickly transit through them) and movements to target more favorable places (and remain within them) have clearly been favored by natural selection. The possibility that animals could use Earth's magnetic field to direct their movements has been discussed in the scientific literature at least since the mid-1800s, notably in Alexander von Middendorf's treatise on Russian birds, stating "...the astonishing single-mindedness of the migratory birds—in spite of wind and weather, in spite of night and fog—may be due to the fact that the fowl is always aware of the direction of the magnetic pole, and consequently also knows how to keep exactly its direction" (translated by the author) (von Middendorf 1855). More than a century passed between this insightful intuition and the conclusive evidence of such an ability in birds (Wiltschko and Merkel 1966; Wiltschko 1968). In the 50 years that followed these landmark studies, an impressive list of species that are sensitive to magnetic fields has been compiled across diverse taxa that include bacteria, mollusks, nematodes, arthropods, fishes, amphibians, reptiles, birds, and mammals.

Information extracted from Earth's magnetic field

The Earth's magnetic field is formed in the outer core, where swirling, molten iron and nickel create a self-exciting geodynamo driven by thermal convection (for an accessible

review, see Hermann and Vorbach 2020). The magnetic field that is produced extends outward from the southern hemisphere and re-enters the northern hemisphere. This feature of the field provides a way for animals to extract directional information—either from the polarity of the field lines (i.e., detecting north and south) or from the angle of field lines relative to the gravity vector (i.e., detecting poleward and equatorward) (Wiltschko and Wiltschko 2005). It is possible that some animals are only capable of detecting the axis of magnetic field lines, rather than their directionality (Begall et al. 2013). The directional information from the magnetic field can be used to set a heading in the horizontal plane (e.g., 30° clockwise from magnetic north) and, in some instances, the vertical component of the magnetic field allows for oriented movement upward or downward (Blakemore 1982; Vidal-Gadea et al. 2015; Putman et al. 2018). This "compass-like" information has adaptive value over any scale at which organisms move, from bacteria zip-ping through μm of mud to birds migrating from the arctic to the tropics.

Positional information from the magnetic field is also available to animals, owing to spatial gradients in several different parameters. Moving from the equator towards the poles, the strength (intensity) of the magnetic field increases and the inclination angle of magnetic field lines relative to Earth's surface becomes steeper (Freake et al. 2006; Lohmann et al. 2007). Across much of the globe these two gradients are not entirely parallel, and thus form a bicoordinate grid from which both latitudinal and longitudinal information can be extracted (Putman et al. 2011). For animals that can detect geographic north, declination (the angular difference between geographic and magnetic north) may also be a component of this magnetic grid (Chernetsov et al. 2017; Putman 2021). In some situations, magnetic "anomalies" resulting from deposits of magnetic minerals in the Earth's crust could serve as a source of more fine-scale positional information (Klimley 1993) or, in other situations, may cause disruptions to animals attempting to navigate across them (Alerstam 1987). Most researchers feel comfortable with the idea that the "map-like" information of Earth's

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magnetic field could allow animals to resolve position on the order of 10–30 km, because the amount of magnetic change at smaller spatial scales is similar to the amount of magnetic change that occurs due to temporal variations (such as atmospheric tides) (Mouritsen 2018). However, there are indications that resolving position at < 1–2 km could be possible if animals had a way to average the magnetic field values they detected or more strongly weighted detections at twilight when the magnetic field is most stable (Diego-Rasilla and Phillips 2021).

Studying magnetic navigation

Part of the attraction of this line of research is that the work lends itself to very specific predictions as to how animals should behave in response to magnetic fields. Techniques to produce magnetic fields are well established; systems of coiled wires through which electric current runs can be used to change the direction and strength of the magnetic field in three dimensions and measurements with a tri-axial magnetometer can confirm the values that a test subject will experience (Kirschvink 1992). With such an apparatus, it is possible to rotate the direction of magnetic north, precisely changing compass information, or to slightly alter the inclination and total field intensity, so as to shift map information. If an animal is using the magnetic field as a compass to maintain its heading, then rotating the magnetic field should result in a corresponding shift in the animal's orientation. If an animal is using the magnetic field to determine its location, then shifting map information should be perceived in much the same way as a physical displacement and the animal should orient accordingly. With such assays, researchers can then ask, “what disrupts this magnetic orientation?” to investigate a wide-range of questions related to how the magnetic field is detected (Wiltschko et al. 1998; Naisbett-Jones et al. 2020), how is magnetic information integrated with other cues (Stapput et al. 2010), and whether specific human activities inhibit the ability of animals to use magnetic information (Engles et al. 2014; Klimley et al. 2021). While conceptually straightforward, I would be remiss if I did not note that there are all sorts of ways to produce equivocal results from such experiments and, at the heart of clear findings is good experimental design, with well-controlled and appropriately paired treatments (Kirschvink et al. 2010; Putman et al. 2017).

In addition to experimental approaches for investigating magnetic orientation in animals, scientists have long made use of idiosyncrasies in aspects of the magnetic field to explore whether they were predictive of variability in animal movements. For instance, some of the earliest indications that animals might use Earth's magnetic field for map-like information was to compare the headings adopted

by homing pigeons at release sites with and without strong magnetic anomalies or on days with varying levels of magnetic disruption from space weather (Gould 1982; Walcott 1991). Over the course of years and decades, Earth's magnetic field gradually drifts—the magnetic poles move as do specific values of the declination angle, inclination angle, and total field intensity. This process is known as secular variation (i.e., longer term non-periodic variability), as the change is not predictable nor consistent across the globe (Putman 2020). For animals relying on a magnetic map to assess position along their migratory route, drift of the magnetic field might be expected to result in shifts in individual and population-level movements of similar magnitude and direction (Putman et al. 2014; Wynn et al. 2020). Likewise, spatial variation in the magnetic field is related to the genetic structure of populations that display reproductive philopatry; locations that are more magnetically different may be easier for animals to distinguish and thus have a greater level of reproductive isolation than locations that are more magnetically similar (Brothers and Lohmann 2018; Keller et al. 2021). Much of the current work in this area is not so much to indirectly infer whether animals might be magnetosensitive, but to investigate the implications of magnetic navigation, to account for observed ecological patterns, and to predict how species respond to environmental change (Putman 2018).

Magnetic field detection

While there is definitive evidence for animals using Earth's magnetic field as a map and compass and there are exciting indications of the importance of magnetic navigation from ecological and evolutionary perspectives, the hunt for a definitive mechanism of magnetosensation in animals has been proved more difficult (Mouritsen 2018). There are three primary hypotheses associated with magnetoreception in animals: (1) biogenic magnetite, (2) chemical magnetoreception, and (3) electromagnetic induction (Johnsen and Lohmann 2005). The magnetite hypothesis suggests that crystals of the magnetic mineral magnetite transduce magnetic field energy into mechanical forces that can be detected by the nervous system (Kirschvink et al. 2001). In the present framing of the chemical-based magnetoreception hypothesis, cryptochromes form radical pairs (pairs of unpaired electrons) that, when provided additional energy from visible light, can react with Earth's magnetic field (Hore and Mouritsen 2016). Depending on the arrangement of cryptochromes across an animal's retina, it is conceivable that the magnetic field could be visually detected (Hore and Mouritsen 2016). Electromagnetic induction involves detecting small electrical currents that are generated when an animal moves through the Earth's

magnetic field. Over the past several decades, this hypothesis was largely relegated to marine animals such as sharks (which are highly sensitive to electric fields and live in the conductive medium of seawater) (Johnsen and Lohmann 2005). Recent evidence suggests that electromagnetic induction might occur within the endolymph of the semi-circular canals of bird ears, with hair cells functioning as electroreceptors (Nimpf et al. 2019; Winklehoff 2019). While there is evidence in support of each of these hypotheses, there is certainly evidence to refute or question some of the more definitive claims. To the extent that there is consensus, it is that there is not yet reason to dismiss or accept any of these as mechanisms of magnetosensation in animals (Johnsen and Lohmann 2005; Kirschvink et al. 2010; Nordmann et al. 2017; Mouritsen 2018).

The special issue on magnetosensation

In organizing this special issue, I have thought often of my dear friend and post-doctoral mentor, David Noakes, who passed away December 1, 2020. He began studying magnetic orientation rather late in his career, after one retirement and at the age of 70. He was a fish biologist, above all, and he thought that something should be done to understand whether salmon use the magnetic field to return to their natal streams from the open sea. When speaking of our work he would often paraphrase U.S. President, John Kennedy's 1962 speech setting the goal for humans to explore the Moon, saying that we choose to study questions on magnetic orientation "...not because they are easy, but because they are hard, because that goal will serve to organize and measure the best of our energies and skills, because that challenge is one that we are willing to accept, one we are unwilling to postpone, and one which we intend to win..." In this special issue, authors were invited who have risen to the challenge and used the best of their energies and skills to bring better resolution to how magnetic fields are used and detected by organisms. Magnetic orientation research seems to have an attractive pull on a variety of scientists, and the contributors here include those trained as ethologists, neurobiologists, taxonomic specialists, geologists, chemists, physicists, and engineers. In this special issue, papers were invited that fit broadly into five categories: (1) perspectives on the history of magnetic navigation research, (2) the role of radical pairs in magnetic field detection, (3) experimental approaches investigating how organisms use magnetic fields, (4) modeling and correlational approaches investigating how organisms use magnetic fields, and (5) perspectives on overcoming the challenges associated with studying magnetic field detection and orientation.

Milestones of magnetic navigation research

The first three papers detail important aspects of the history of magnetosensation research. The lead paper is by the scientists who have profoundly shaped this field of research, Wolfgang and Roswitha Wiltschko, retired professors from the University of Frankfurt. As mentioned above, this duo was the first to demonstrate that any animal used the magnetic field for a compass. They discuss their discovery of the use of magnetic navigational information in birds and how this research has progressed to present (Wiltschko and Wiltschko 2022). The second paper is led by Lewis Naisbett-Jones, a Ph.D. student at the University of North Carolina who, as a master's student, demonstrated that European eels (*Anguilla anguilla*) use the magnetic field for map-like information (Naisbett-Jones et al. 2017). While much attention is given to birds in the history of magnetic navigation research, fishes have served as important model systems in the hunt for magnetoreceptors and for understanding how the ability to detect magnetic fields functions in the ecology of animals. Naisbett-Jones and Lohmann (2022) present an overview of research on magnetoreception and magnetic navigation in fishes that has occurred over the past 50 years and highlight promising avenues for future work. The third article is from the lab of Kenneth and Catherine Lohmann, from the University of North Carolina. This pair were the first to experimentally demonstrate map-like use of the magnetic field in vertebrates (sea turtles) and invertebrates (lobsters) (Lohmann and Lohmann 1994; 1996; Lohmann et al. 2001; Boles and Lohmann 2003). Their paper reviews the original work on magnetic maps, the flurry of new findings on magnetic maps across a variety of species over the past few years, and the perplexing questions still to be answered (Lohmann et al. 2022).

Radical pairs in magnetic field detection

The second set of articles bring the reader to questions associated with the role of radical pairs in magnetic field detection, a topic that has maintained considerable momentum (Ritz et al. 2000). One major arm of this research is related to investigating the role of cryptochromes in magnetosensation (Liedvogel and Mouritsen 2010). The fourth paper is led by Angelika Einwich, a Ph.D. student in Henrik Mouritsen's lab at the University of Oldenburg, who discovered a new isoform of cryptochrome in the retina of European robins (Einwich et al. 2020). Here, she and her colleagues present a detailed neuroanatomical analysis of the protein cryptochrome 2 within the retina of several bird species to investigate whether locations are consistent with a role in magnetoreception (Einwich et al. 2022). Another important research track has been to use radio frequency electromagnetic noise (RF) (which can disrupt chemical

reactions associated with radical pair formation) to examine under what frequency ranges magnetic orientation in animals ceases to function, thus providing insight into the nature of the responsible magnetic sensor. The fifth paper is led by Jesse Granger, a Ph.D. student in Sönke Johnsen's lab at Duke University, who showed whale strandings are associated with atmospheric RF, presumably due to its impact on whales' ability to navigate (Granger et al. 2020). In the special issue, she discusses how to quantify RF, the natural sources of RF and its potential to affect magnetosensitive animals by comparing environmental values to a meta-analysis of behavioral experiments in which RF has been shown to disrupt orientation (Granger et al. 2022). The sixth paper comes from another Ph.D. student in the lab of Henrik Mouritsen, Bo Leberecht, who, with a distinguished team including Michael Winklhofer and Peter Hore, examines the disruptive effect of RF with a range of 75–85 MHz on Eurasian blackcaps (*Sylvia atricapilla*) and provides new information on the possible radical pair associated with magnetic field detection (Leberecht et al. 2022).

Experiments investigating the use of magnetic fields

The third set of articles are experimental approaches investigating how organisms use magnetic cues. In the seventh paper, Casey Barr and Manuel Bedrossian in the lab of Kenneth Nealson at the University of Southern California provide an overview of the recent work in magnetotactic bacteria. This area of research has seen major advances (and changes) from the oft cited work of the early 1980s (Blakemore 1982) and this article is an accessible way for non-specialists to get up to speed on the present state. Barr and Bedrossian also include a novel set of experiments using digital holographic microscopy to examine the movements of bacteria in response to Earth-strength magnetic fields within a realistic environment (Barr et al. 2022). In the eighth paper, Pauline Fleischmann a post-doc at the University of Würzburg examines the role of magnetic cues in desert ants (*Cataglyphis nodus*) when learning the panorama to relocate their nest entrance after forays to forage (Fleischmann et al. 2022). She has numerous contributions to the recent work on desert ant navigation, notably demonstrating desert ants use the magnetic field as a compass (Fleischmann et al. 2018). The ninth article is from a team led by Giuseppe Bianco and Susanne Åkesson of Lund University, who have been at the forefront of major advances in the understanding of behavior and physiology of bird migration (Åkesson et al. 2005; 2017; Bianco et al. 2019). Here, they use long-term observations under controlled conditions and a machine learning technique to examine whether spontaneous magnetic alignment might play a role in the calibration

of the magnetic compass at sunset in Eurasian reed warblers (*Acrocephalus scirpaceus*) (Bianco et al. 2022).

Modeling the use of magnetic fields

The fourth set of articles use geomagnetic models, computational models, and correlation analyses to explore the use of magnetic cues by animals. The tenth article is led by Joe Wynn, a Ph.D. student of Tim Guilford, who recently used 80 years of ringing recoveries and records from magnetic observatories to show that Manx shearwater (*Puffinus puffinus*) likely imprint on the magnetic inclination angle at their natal site and use that information to return to from their first transequatorial migration (Wynn et al. 2020). In the special issue, Wynn and colleagues use a global geomagnetic model to examine how drift (secular variation) of the magnetic field might influence homing precision in migratory birds of North America, Europe, and Asia (Wynn et al. 2022). In the eleventh article, Susan Pizzuti, an undergraduate in Brian Taylor's lab at the University of North Carolina presents a perspective piece on the use of computational and robotic simulations to investigate the waypoint navigation based on "magnetic signatures" as has been hypothesized from behavioral experiments in marine migrants (Pizzuti et al. 2022). The twelfth article is led by another undergraduate student in Brian Taylor's lab, Sebastian Nichols. They develop a magnetic navigation model inspired by the mechanoreceptor system in leeches and test whether a distributed sensory system and simplifying assumptions of neural processing could be a plausible way for animals to detect and use magnetic information (Nichols et al. 2022). The twelfth paper is led by Petr Jandačka along with Hynek Burda, at Czech University of Life Sciences who demonstrated magnetic alignment and compass use in a variety of mammals and other taxa (Burda et al. 1990, 2009). In this paper, they examine whether weak geomagnetic fluctuations caused by solar winds have a measurable impact on the performance of pigeon races (Jandačka et al. 2022).

Challenges associated with studying magnetic field detection and orientation

In our final set of articles, we have review/perspective pieces that provide insight into some of the challenges in conducting research on magnetosensation and magnetic orientation. The fourteenth article is led by Georgina Fenton, a post-doctoral student in the lab of Pascal Malkemper at the Center of Advanced European Studies and Research. They discuss some of the logistical challenges and best practices for using electrophysiological techniques to study the neural processing of magnetic cues (Fenton et al. 2022). The final paper is led by John Phillips, who demonstrated amphibians use a magnetic compass and map (Phillips 1986; Phillips

et al. 2002) and has made important theoretical contributions to how directional and positional information in the magnetic field may be detected and integrated by animals (Phillips et al. 2010). This paper focuses on why it has been so difficult to elicit magnetic compass orientation in rats and mice, owing to the difficulty of controlling for confounding factors associated with scientific laboratories (Phillips et al. 2022). This paper deserves a careful read irrespective of the taxa one is studying and the lessons learned should likely be applied broadly.

Final thoughts

I appreciate the contributions of all of the authors, reviewers, and the journal production team to this special issue. I especially thank Editor-in-Chief Friedrich Barth for his generous invitation for me to serve as Guest Editor and his guidance and patience along the way. I dedicate my introduction of this special issue to David Noakes. He would often say that good science is predictive: it makes a prediction, it tests that prediction, and thus science is usually driven by the desire to say, “I told you so.” In that spirit, I predict you will enjoy the articles that follow. It is my hope that this special issue will communicate the excitement of using a magnetic lens to search for answers to fundamental questions in biology—ranging from how animals perceive direction and space to the evolutionary diversification of species. I also hope that the articles here will inspire experiments that are both careful and bold and that are able to further uncover the magnetic mysteries of animals.

Declarations

Conflict of interest The author declares that he has no conflict of interest.

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