Magnetic Orientation in Migratory Songbirds

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Introduction

The navigational challenges faced by migratory songbirds are both immense and complex. Whether migrating short or long distances, within or between continents, or to reach wintering or breeding sites, migratory songbirds must navigate across diverse landscapes, often facing large ecological barriers and adverse weather conditions, to reach habitats appropriate for their needs; indeed, many individuals are capable of migrating to the same breeding site and/or wintering site year after year. Such navigational feats impress amateur birders, naturalists, and scientists alike, and beg for questions about how small birds, often weighing only a few grams or tens of grams, manage to find their way. Moreover, while their final destinations have captured our attention for centuries, scientists have only begun to realize the importance of stopover sites, habitats where birds can rest and 'refuel' to continue migration. The success of the seasonal trips of these birds relies not only on reaching their destination at appropriate times but also by following 'historical' routes that provide adequate habitat along the way.

To find their way, birds require a complement of navigation mechanisms and strategies, which allow them to cope with changing habitats and information as they move between equatorial and polar latitudes. Orientation cues available to songbirds, most of which migrate during the night, include celestial information, such as the stars and sunset (**Figure 1**), as well as the Earth's magnetic field. While the use of the geomagnetic field is the focus of this chapter, birds must integrate or calibrate the direction information they obtain from different cues. Much like humans and other animals that integrate information from their visual and vestibular systems to provide a sense of position and movement, migratory birds must use information from their visual system (about the position of the stars, setting sun, etc.) along with magnetic information in order to obtain their overall 'sense of direction.'

Our goal is to provide an overview of what is currently known about magnetic orientation in songbirds. We will address both physiological mechanism(s) for sensing the Earth's magnetic field, as well as ecological, or functional, uses of magnetic information. While we have known that songbirds are capable of orienting using the Earth's magnetic field for over half a century, there is much more to learn about magnetic sensing, how the nervous system encodes and processes magnetic information, and how birds use magnetic information in different ecological contexts and in combination with other directional cues. We hope this chapter provides an impetus for students of animal behavior to address these mysteries in the decades to come.

A Brief History

Even though the discovery of sensitivity to the geomagnetic field in animals is rather recent, the notion that animals might make use of geomagnetic information for orientation tasks is quite old. As early as the mid-to-late 1800s, scientists suggested that the geomagnetic field might underlie the extraordinary navigational capabilities of birds and insects; Charles Darwin suggested that it might be worth investigating the effect of attaching small magnets to bees to try and manipulate their orientation behavior. However, it was not until the 1960s that Wolfgang Wiltschko, under the tutelage of Friedrich Merkel, was able to demonstrate that the orientation response of a caged migratory bird, the European robin (*Erithacus rubecula*), was affected by the direction of an Earth-strength magnetic field. Although initial evidence for magnetic orientation was met with much skepticism, the body of evidence for magnetoreception in birds and other animals, including many species of invertebrates, fish, amphibians, reptiles, and some mammals, has grown quite rapidly in the past 45 years. Now even a skeptical reviewer of the literature would have to conclude that magnetoreception is a widespread sense among animals.

Wiltschko and Merkel's experimental design to test for magnetic orientation in birds is essentially still the method of choice for examining migratory orientation, although the technique has been modified slightly over the years. The technique is based on observations made by Gustav Kramer in the late 1940s; Kramer observed that captive (i.e., caged) migratory birds exhibit migratory, or nocturnal, restlessness (in German known as 'Zugunruhe'). More importantly, Kramer noticed that the direction of the birds' activity, which is indicated by increased hopping in their cages, corresponds with their seasonal migratory direction. To assess a bird's orientation, Wiltschko and Merkel used radially positioned, recording 'event' perches in an octagonal-shaped cage, which allowed them to monitor each bird's position (i.e., directional preference) and activity. Currently, the most prevalent cage type used by researchers is the circular 'Emlen' funnel (Figure 2), first used by Stephen Emlen to study stellar orientation in indigo buntings (*Passerina cyanea*).

The key to demonstrate magnetic orientation is to show that birds change their absolute, or geographic, direction when the direction of the magnetic field is no longer pointing toward geographic North. 'Magnetic coils' are used to rotate the direction of the magnetic field; these three-dimensional coils are often cubical or octagonal in shape and wrapped with copper wire to which electric current can be applied to create an artificial magnetic field (Figure 3). With proper current and positioning of the coil(s), Earth-strength magnetic fields can be created that differ from the actual Earth's magnetic field only in direction; that is, a magnetic field can be created to point toward geographic East, South, West, or a variety of positions in between. Wiltschko and Merkel used such a magnetic coil to show that European robins, when given access only to magnetic cues, will consistently migrate to the north–north east; when the direction of the magnetic field was rotated, the birds changed their orientation to reflect the position of the magnetic field.

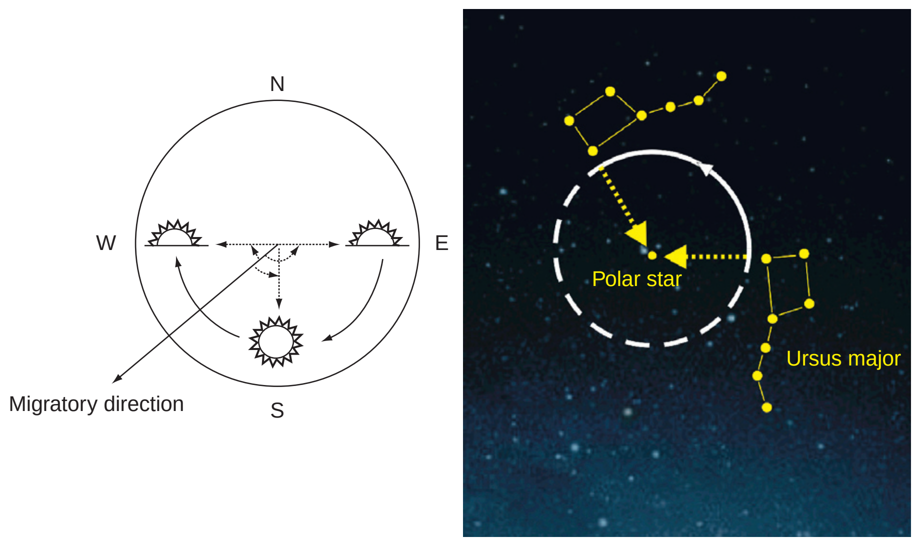

Figure 1 Illustrations of a sun compass (left) and a star, or stellar, compass (right). Celestial compasses each rely on the rotation of the Earth, which causes relative movement of the sun and the stars, to provide information about geographic, or true, North in the northern hemisphere. Left: Although most songbirds migrate at night, some are diurnal (or day) migrants. Diurnal migrants (and homing pigeons) can use the sun's position along with an internal circadian clock to determine a migratory direction. In order to maintain a constant geographic heading, the angle between the migratory direction and the sun's position changes with time of day. Hence, the need to coordinate direction with an internal clock is required to use a sun compass. Nocturnal migrants, which take off and land at sunset and sunrise, can use the position of the sun at sunset or sunrise to determine a direction just before departure or landing, respectively. Right: During the night, the Polar star (in the northern hemisphere) can be used by nocturnal birds to steer a heading. Birds can learn which star is the pole star by the rotation of other constellations around this immobile star in the night sky.

Figure 2 A Savannah sparrow in an Emlen funnel. Inside this funnel-shaped, circular cage, which can either be lined with a recording paper (such as typewriter correction paper or thermal paper) or blank newspaper and an inkpad at the bottom, songbirds will hop. Either method results in marks (scratch marks or ink blotches, respectively) on the paper, which indicate the direction the bird was hopping. During migration, songbirds will tend to hop in the direction in which they would be flying when placed in Emlen funnels during dusk or evening. To test for solely magnetic orientation, visual cues can be blocked by covering the funnel with opaque, white Plexiglas.

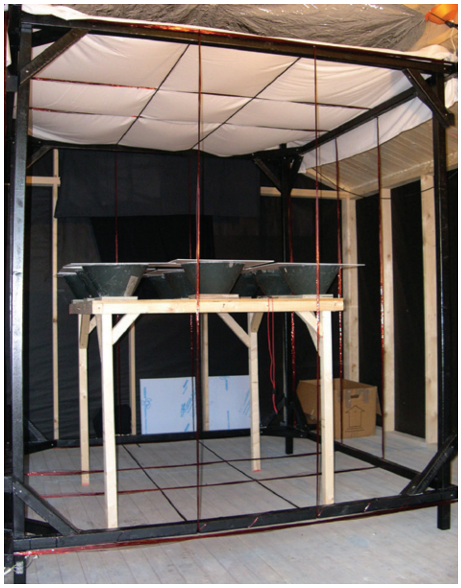

Figure 3 A magnetic cube coil for manipulation of the Earth's magnetic field. On the table in the center of this coil are several Emlen funnels for testing bird orientation. Each is covered with opaque, translucent Plexiglas, which will block out visual cues but allow some light to enter the funnel. The coil is doubly wrapped with copper wires, which allow two magnetic vectors to be created in order to change the magnetic field so that it can point toward geographic north, east, south, or west depending on which wire(s) electric current is applied to.

Since these earliest experiments, researchers have not only demonstrated that the ability to use geomagnetic cues for orientation is widespread in songbirds (over 20 species have been examined to date), but similar methods have been used to provide the evidence for most of the ideas we present in this chapter. While technological advances in tracking devices (such as miniaturized telemetry devices and geolocators) are providing new methods to explore orientation choices in free-flying migrants, experiments on caged migrants have provided the bulk of our current knowledge about magnetic orientation. Indeed, Wolfgang Wiltschko, along with his wife Roswitha, have continued to explore magnetic orientation since the first experiments on European robins, providing a wealth of hypotheses, experiments, and data that have always been at the forefront of research on magnetic orientation in birds. No review of magnetic orientation would be complete without acknowledging their lifetime achievements and their clear influence on their own students, their collaborators, and all of us who have worked on magnetic orientation.

The Geomagnetic Field

The Earth's magnetic field is analogous to a field produced by a bar magnet. However, the geomagnetic field is actually produced by a self-generating geodynamo, where fluid motion in the core of the Earth moves electrically conducting material across an existing field. The magnetic field lines leave the Earth in the southern hemisphere and enter the Earth in the northern hemisphere (**Figure 4**). The intensity of the geomagnetic field ranges from about 68 μT at the magnetic poles, where the field lines stand vertically (known as an inclination, or dip, angle of 90°), to about 23 μT around the magnetic equator, where the field lines are parallel to the Earth's surface (inclination angle is 0°). The two magnetic poles are not static; rather they constantly drift or 'wander.' Moreover, the magnetic poles do not coincide with the geographic poles, which are defined by the axis of rotation of the Earth. The difference between a magnetic pole and its corresponding geographic pole (known as 'declination') is measured as an angle from any reference point on the Earth. Currently, the poles are wandering several tenths of a degree annually, which is called 'secular' variation, and the total intensity of the Earth's magnetic field has decreased by about 10% since 1900.

Functions of the Earth's Magnetic Field for Avian Migration

The Avian Magnetic Inclination Compass

The magnetic compass of migratory birds functions differently from the industrial compasses that humans use for orienteering. The needle of most commercially available compasses points toward the magnetic North pole, which is why this type of compass is called a 'polarity compass.' The magnetic compass of birds is insensitive to the polarity of the magnetic field. Rather birds sense only the axis of the magnetic field and they must rely on magnetic inclination, or the dip angle, to determine direction. Therefore, the avian magnetic compass is called an 'inclination compass.' Birds use the inclination of the magnetic field lines to determine which of the two sides of the magnetic axis leads toward the magnetic equator or toward the closer of the two magnetic poles (**Figure 4**). The side of the magnetic axis where the magnetic field lines meet with the horizon always leads polewards, in both the northern and the southern hemispheres, and the side where the field lines and the horizon diverge always leads toward the magnetic equator.

An experimental method to determine the type of compass (inclination compass or polarity compass) that an animal possesses is to artificially invert only the vertical component of the magnetic field with a magnetic coil surrounding a testing apparatus (such as birds placed in an Emlen funnel). Inverting the vertical component flips the magnetic field vector, that is, reverses inclination, but leaves polarity unchanged. Consequently, animals, such as birds, that possess an inclination compass will reverse their direction of orientation when the vertical component of the magnetic field is inverted, even though the polarity (i.e., N–S axis) of the magnetic field is

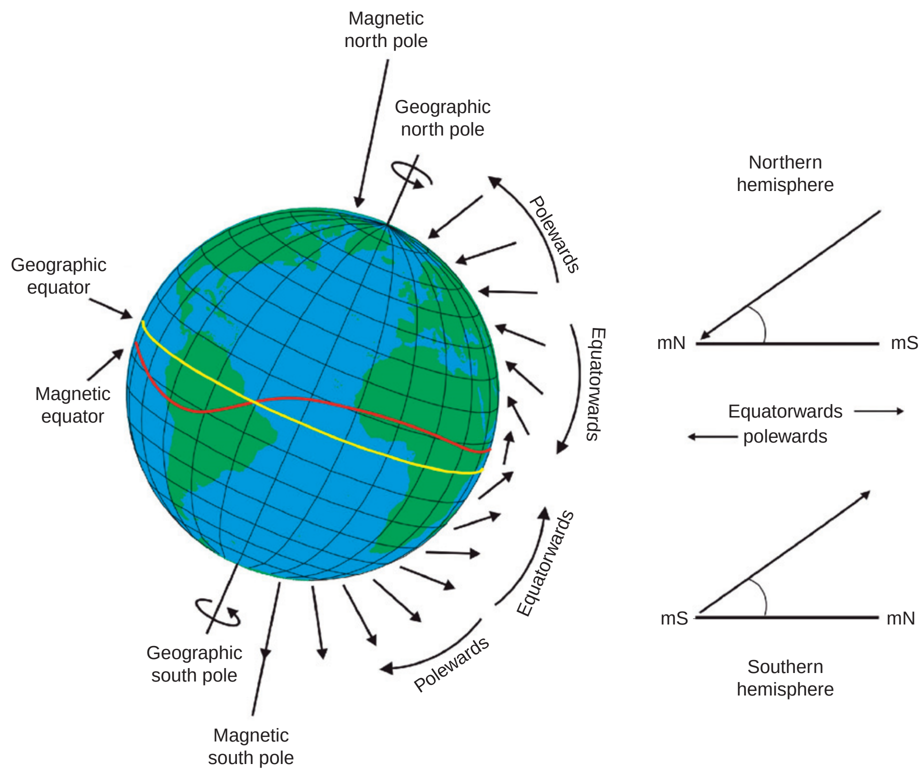

Figure 4 The Earth's magnetic field (left) and function of the avian inclination compass (right). Left: The arrows near the Earth's surface indicate the intensity (lengths of arrows), direction (direction of arrowhead), and angle of inclination (steepness of the arrows in relation to the surface of the Earth) of the magnetic field at a particular site. Right: The birds' inclination compass is not sensitive to the direction of the magnetic field, but rather its alignment and sign of inclination. Birds do not distinguish between 'north' and 'south,' but between 'equatorwards' and 'polewards.' The side of the magnetic axis where the magnetic field lines meet with the horizon always leads toward the pole, in both the northern and the southern hemispheres, and the side where the field lines and the horizon diverge always leads toward the magnetic equator.

unchanged. A polarity-based magnetic compass, such as the one commonly used by humans for orienteering, will not respond to an inversion of the vertical field (i.e., it would continue to point toward magnetic North).

Similar to other sensory systems (such as the visual system), the functional range of the avian magnetic inclination compass also appears to be adaptable to different magnetic field intensities. Experiments with European robins demonstrated that birds are disoriented when tested in artificial magnetic fields weaker (16 and 34 μT) or stronger (60–105 μT) than the Earth's magnetic field. However, preexposure to such unnatural magnetic fields for 1 h resulted in seasonally appropriate orientation, implying that the functional range of the magnetoreceptor is flexible and allows adjustment (although relatively slowly compared to other senses) to new magnetic conditions.

Determining direction: a flexible migratory compass program

Possessing a physiological magnetic compass provides birds only with a directional reference. Determining which direction to migrate (such as 'equatorwards' during autumn migration) requires birds to 'know' the appropriate direction to fly for their species. Andreas Helbig, Peter Berthold, Eberhard Gwinner, and others have shown that the general direction and distance (or length) of migration is, at least in part, determined by an inherited (i.e., genetic) migratory program in birds. Because this genetic program, available to juvenile songbirds on their first migration, encodes information about length of migration and direction, it is called a 'clock and compass' migration strategy.

The migratory programs of songbirds are similar in both hemispheres; species that breed toward the poles migrate 'equatorwards' after the breeding season in autumn when day length decreases, and 'polewards' in spring when day length increases. However, some species (or even populations within a species) may fly in one direction for part of their migration (such as southwest) and then change to a different direction for the remaining part of their migration (such as more southerly directions). Therefore, determining the correct direction for successful migration can be more complicated than just to fly 'equatorwards' or 'polewards,' and even slight species-specific or population-specific differences in migratory direction appear to be at least partially determined by genetic information. For example, when Helbig crossbred male and female blackcaps (*Sylvia atricapilla*) from two populations with different autumn migratory directions in Europe, the offspring oriented in a direction intermediate to the two population-specific directions.

Crossing the magnetic equator using an inclination compass is a challenging task for extremely long-distance migrants, such as bobolinks (*Dolichonyx oryzivorus*) and garden warblers (*Sylvia borin*). The horizontal alignment of magnetic field lines at the magnetic equator prevents the determination of direction with an axial, inclination compass. While crossing the magnetic equator, birds would thus have to rely on other compass cues, such as stellar patterns. Moreover, transequatorial migrants have to change their migratory program from 'fly equatorwards' to 'fly polewards' during fall migration, while at the same time the inclination compass information is ambiguous. Experimental evidence indeed suggests that exposure to the horizontal magnetic field at the magnetic equator triggers this change in migratory program.

Energetic condition and local geography can influence orientation

The migratory program of songbirds can be quite flexible during a single migratory journey. For example, birds can and will adjust their migratory direction to reflect their own energetic condition and/or local ecological features. Songbirds must be physically prepared for migration, which takes enormous amounts of energy, which they store largely as fat. Rather than carry excessive fat loads during migration, birds optimize migration speed and time, at least in part, by periodically arresting migration to replenish fat stores at suitable stopover sites *en route*. Especially important stopover sites are located just prior to or after crossing expansive ecological barriers, such as large bodies of water or deserts, where feeding and refueling are difficult or impossible. At stopover sites near these ecological barriers, birds can gain significant fat to prepare for, or recover from, crossing the barrier. Orientation preferences of individual birds at these sites are dependent on both season and energetic condition of the birds. For example, upon encountering a large body of water (such as the Gulf of Mexico, one of the Great Lakes, or the Baltic Sea), fat migrants usually cross the barrier by exhibiting 'forward' migration in a seasonally appropriate direction. In contrast, lean birds often orient in opposite directions (i.e., reverse orientation) of fat birds when they encounter these same barriers, or they at least discontinue migration temporarily until their energy reserves are sufficient enough to continue migration. Reverse orientation may lead leaner individuals to more suitable stopover areas for refueling, with better food sources, less competition for food, and/or less predation pressure.

Comparing compasses – cue calibration

Migratory songbirds use both celestial and geomagnetic information for compass orientation. Celestial patterns, such as a stellar compass, provide birds with information about true or geographic North or South (**Figure 1**). Having multiple compass mechanisms during migration can be advantageous. Under overcast weather, for example, birds cannot use their sun and star compasses, but need to rely on the magnetic compass. Likewise, the wandering of the magnetic poles makes magnetic information less reliable than geographically based compass mechanisms. The directional information from these two types of compass systems changes during migration because of the spatially changing relationship between geographic and magnetic North (i.e., magnetic declination). Birds migrating at high arctic areas close to the magnetic North pole are exposed to particularly large changes in magnetic declination, because the differences between magnetic and geographic North are maximal there (**Figure 5**).

Both before the start and during the migratory journey, birds can correct for magnetic declination by calibrating their magnetic compass with a celestial compass, thus prioritizing the information from the celestial compass (i.e., geographic, or true, North) over magnetic compass information. Although a controversial idea, polarization patterns of skylight near the horizon at sunrise and sunset may serve as the primary calibration reference for the magnetic compass in many migrants, such as Savannah sparrows (*Passerculus sandwichensis*) and white-throated sparrows (*Zonotrichia albicollis*). These are the two times of day when the skylight polarization pattern is seen as a band of maximum polarization (BMP) across the zenith at a 90° angle relative to the position of the sun (**Figure 6**). The BMP intersects the horizon vertically; thus, detection is independent of horizon height.

Geographic Positioning and Use of Magnetic Information for Noncompass Behaviors

The occurrence of global geomagnetic gradients has led to several hypotheses for a magnetic 'map,' or geographic-positioning, sense. From the equator, both the intensity and the angle of inclination of the geomagnetic field increase toward the poles (as mentioned previously, see **Figures 4–7**). Map-based (or 'true') navigation requires nonparallel gradients of two or more geophysical features to determine one's position relative to a goal in order to return to a familiar area following displacement. A bicoordinate map (one that would provide the equivalent of latitude and longitude) based on the geomagnetic field would require that an animal perceives at least two components of the magnetic field that vary geographically, such as intensity and inclination, and that the two gradients be nonparallel. Geomagnetic intensity and

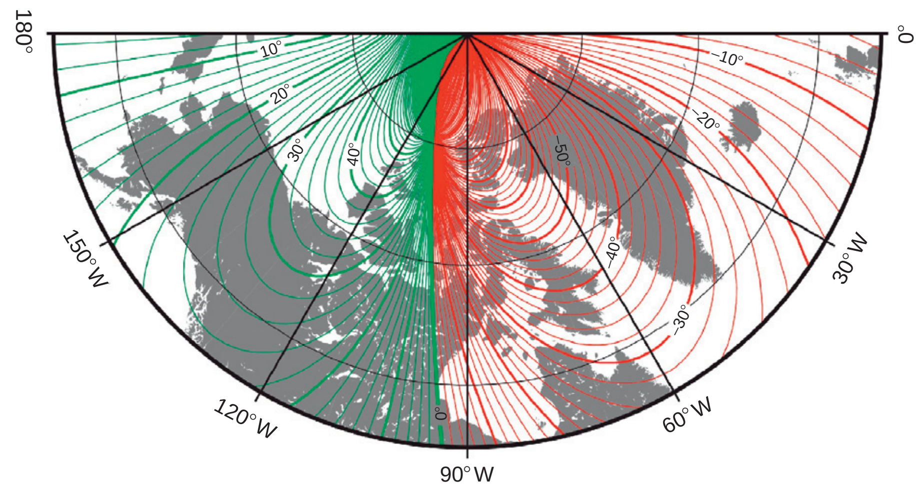

Figure 5 Illustration of magnetic declination at high Northern latitudes according to the World Magnetic Model of the Epoch 2000 (http://geomag.usgs.gov/). Declination isolines in green and red denote positive (deviations to the east of geographic North) and negative values (deviations to the west of geographic North), respectively. Note that in some areas a magnetic compass and a celestial compass could be more than 50° off. Therefore, calibration at high latitudes is essential for birds to make use of their magnetic compass.

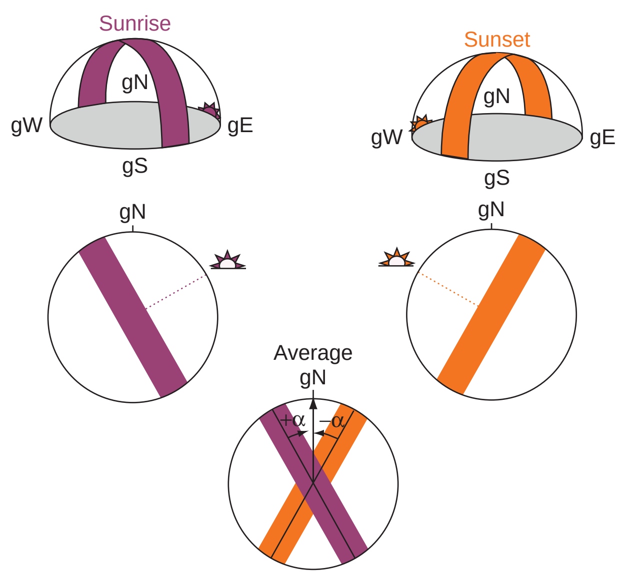

Figure 6 The band of maximum polarization (BMP) of skylight at sunrise and sunset. Top: Three-dimensional view of the BMP that intersects the horizon at a 90° angle at sunrise and sunset. Middle: This pattern is always symmetrical to geographic North, independent of time of year and latitude. Bottom: Averaging of the BMP vectors available at sunrise and sunset would provide birds with a true geographic reference for calibration of the magnetic compass and corrections of magnetic declination.

inclination mostly vary concomitantly along a north-south axis in the Americas and Europe and Africa and may provide only a unicoordinate map limited to latitudinal information for migrants on these continents. However, in several regions (e.g., the Indian and South Atlantic Oceans, and parts of Europe), these two gradients are not parallel to each other, making bicoordinate geomagnetic navigation theoretically feasible (**Figure 7**).

Because of local, regional variation in the alignment and steepness of geomagnetic gradients and temporal (such as daily or annual) geomagnetic variation, most hypotheses about map-based navigation presume that animals would have to learn the pattern of magnetic gradients within their home range or along their migratory route. Juveniles, that have not yet learned these gradients, would have to rely on other orientation strategies (i.e., the inherited, clock and compass strategy for migration as mentioned earlier). Displacement and recovery experiments with free-flying migrants, as well as laboratory experiments, consistently support a purely compass-based orientation strategy in juvenile birds. Age-dependent recoveries of geographically displaced

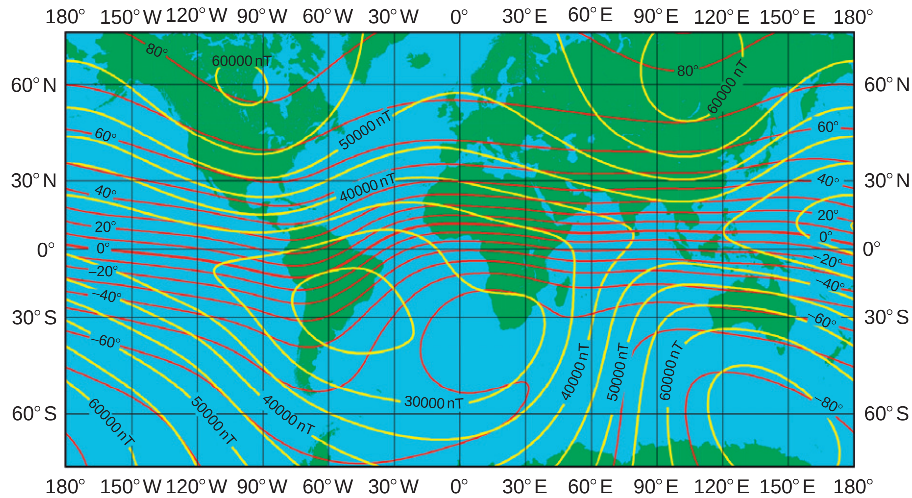

Figure 7 Total intensity (yellow lines) and inclination (red lines) of the Earth's magnetic field according to the World Magnetic Model (WMM) 2000 (http://geomag.usgs.gov/). The total intensity is shown in 5000 nT steps and the inclination is shown in 10° steps.

migratory European starlings (*Sturnus vulgaris*) by Albert Perdeck first suggested that adults use a different orientation strategy than do juveniles. After displacing thousands of banded starlings to the southwest of their autumn migratory route, adults were recovered in their usual population-specific wintering areas. However, juvenile birds, which had never migrated before, were recovered to the southwest of their population-specific wintering grounds. In other words, adults compensated for the geographic displacement, whereas juveniles continued to orient in a fixed compass direction without compensation.

Direct tests of magnetic map hypotheses, where geographic displacements are simulated by altering the intensity and/or inclination of the geomagnetic field, are few and in most cases involve 'homing behavior' in species other than songbirds. Eastern red-spotted newts (*Notophthalmus viridescens*), spiny lobsters (*Panulirus argus*), and green sea turtles (*Chelonia mydas*) orient toward a home or capture site when exposed to magnetic field values that simulate disparate geographical locations. Also consistent with map-based geomagnetic navigation, temporal variation and spatial anomalies in the geomagnetic field also affect homing orientation in pigeons (*Columba livia*) and alligators (*Alligator mississippiensis*). In songbirds, only Australian silvereyes (*Zosterops l. lateralis*) have been directly tested for a magnetic map sense by examining their orientation responses to magnetically simulated geographic displacements. Silvereyes that breed in Tasmania migrate northwards to wintering sites on the Australian mainland and then southwards to Tasmania during spring migration. Fischer and others (including the authors of this article, in unpublished studies) have found that adult silvereyes, but not juveniles, became disoriented or reoriented during autumn migration when exposed to magnetic field values that simulate a northerly displacement (i.e., beyond their normal wintering range). Although other explanations are possible for the orientation behavior observed in these experiments, silvereyes may learn to use gradients in the geomagnetic field for at least a unicoordinate geomagnetic 'map' sense, which provides latitudinal information (see Freake et al., 2006).

Although it is unclear whether songbirds possess a magnetic 'map' sense, specific values of the geomagnetic field have been shown to serve as innate 'sign posts' (or sign stimuli) for locations along a migratory route. Genetically encoded geomagnetic values may stimulate an 'innate releasing mechanism,' causing migrants to change migratory behavior at appropriate locations, such as at stopover sites or migratory boundaries. When exposed to gradually decreasing values of magnetic intensity and inclination, juvenile pied flycatchers (*Ficedula hypoleuca*) shift their autumn orientation from southwest to southeast in magnetic fields that simulate those of southern Spain, as would freely migrating birds. Southeast reorientation toward Africa prevents the birds from migrating over the Atlantic Ocean. This example does not require birds to determine their position; instead, specific geomagnetic field values elicit an appropriate 'programmed' change in the bird's behavior, orientation, or otherwise. Likewise, juvenile thrush nightingales (*Luscinia luscinia*) increase feeding rates in a magnetic field simulating a known stopover site in northern Egypt.

Identifying the Avian Magnetoreceptor(s)

Early hypothetical biophysical models for magnetoreception have led to the discovery of two candidate magnetoreception systems in birds: (1) a light-dependent mechanism located in the eye and (2) an iron-based mechanism associated with the trigeminal nerve. Magnetic compass orientation of both juvenile and adult birds is light dependent, affected by both wavelength and intensity, and in at least two species, it is lateralized to the right eye. In addition, pulse remagnetization experiments and neurophysiological studies suggest that an iron-based mechanism innervated by the trigeminal nerve provides adult birds with magnetic information other than simply compass direction, possibly geomagnetic-positioning information.

Light-Dependent Magnetoreception and Compass Orientation

Magnetic compass orientation of migratory songbirds and homing pigeons is influenced when they are tested under different wavelengths (i.e., colors) of light. Experiments with songbirds, both adults and juveniles, in Emlen funnels illuminated with monochromatic lights demonstrate that birds tested under nearly monochromatic blue, turquoise, or green light (all relatively short wavelengths) were well oriented toward their seasonally expected migratory direction. Birds tested under longer wavelengths (i.e., yellow and red), however, either became disoriented or showed approximately 90° shifted orientation. Experiments with European robins tested under green and green-yellow lights, which differed by only 8 nm, showed that the transition from oriented behavior to disorientation occurred very abruptly. Light-dependent magnetoreception varies in birds not only with wavelength, but also with light intensity (i.e., brightness) at the same wavelength, leading to shifts in orientation, disorientation, or axial alignment along the migratory direction. The interactions of wavelength and intensity of light on compass orientation are complex and still not well understood.

Peter Semm demonstrated some of the first neurophysiological recordings on magnetically sensitive neurons in bird brains. In the nucleus of the basal optic root (nBOR) and the optic tectum, Semm showed a clear involvement of the visual system in light-dependent magnetoreception. His recordings demonstrated magnetic responsiveness to changes in the direction of a magnetic field and to slow inversions of the vertical component of the magnetic field, and thus strongly implied that light-dependent magnetoreception takes place at locations innervated by the optic nerve, with the eyes as likely candidates for the locations of receptor cells. Experiments testing the magnetic orientation of birds (i.e., European robins and Australian silvereyes) with one eye covered with light-proof caps suggest that light-sensitive magnetoreception is actually lateralized; mainly the right eye is involved in magnetoreception. Birds were well oriented and reacted to an inversion of the magnetic field when tested with the right eye open, but were disoriented when tested with the right eye covered.

Currently, the most accepted magnetoreception model for the light-dependent magnetic compass, originally proposed by Klaus Schulten, suggests that an external magnetic field can modulate photon-induced processes in specialized photoreceptors. In this process, radical pairs of light-sensitive molecules are formed by photon excitation through light absorption similar to the photosynthetic reactions. The interconversion between the two excited state products can be modified by an external magnetic field, resulting in the formation of different yields of singlet and triplet products (the triplet products being the signaling state). Cryptochromes, candidates for such a magnetoreception molecule, have been found in retinas of two migratory bird species, European robins and garden warblers. Photoreceptors containing such magnetosensitive molecules arranged in an ordered array in the eye would respond differently, depending on their relative alignment to the magnetic field. Birds would be able to 'see' the magnetic field lines as a three-dimensional pattern of light irradiance (i.e., brightness) or color variation in their visual field or through a dedicated parallel pathway in the brain (**Figure 8**).

The use of low-intensity oscillating radiofrequency magnetic fields (RF fields) in the lower MHz range (0.1–100 MHz) has been established as an important tool to test whether a radical pair mechanism is involved in the primary magnetoreception process of an orientation response. RF fields of distinct frequencies interfere with the interconversion between the excited states of the molecule(s) and can mask or alter the magnetic field effects produced by the Earth's magnetic field. RF interferences can lead to either disorientation or change in orientation, depending on the amount and type of change, and how the animals integrate the information into a migratory direction. Experiments with European robins exposed to such RF showed that birds become disoriented

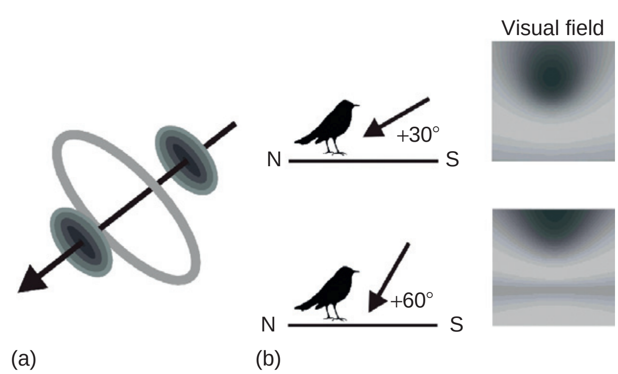

Figure 8 Illustration of light-dependent magnetic compass perception through magnetosensitive photoreceptors. (a) Magnetic field vector (arrow) and three-dimensional pattern which birds are thought to perceive, consisting of a dark area on each side of the magnetic field axis and a ring in the center. (b) Visual pattern perceived by a bird, depending on the relative alignment of the magnetoreceptors and the magnetic field; in this example, the bird is facing toward magnetic North with the eyes horizontally aligned at two different latitudes (i.e., magnetic field inclinations of 30° and 60°, respectively).

when tested under either a broadband RF field or distinct single frequencies in the lower MHz range. Iron-based magnetoreceptors, in contrast, would not be affected by RF fields, because the rotation of iron oxide particles, such as magnetite, would be too slow and the ferromagnetic resonance frequency is expected to be in the GHz rather than MHz range.

Iron-Based Magnetoreception

A magnetoreceptor based on a direct interaction with the magnetic field is fairly easy to imagine if one considers coupling a tiny biological 'bar magnet' with a sensory neuron; pull on or rotation of such a biological 'micromagnet' could, in theory, be detected by a mechanoreceptor-like neuron. Magnetite (Fe_3O_4) is a biogenically produced compound that exhibits ferromagnetic properties, which could give rise to such a 'bar magnet' based magnetoreceptor. In fact, particles of magnetite have been shown to be responsible for geomagnetic alignment of some anaerobic bacteria. In the mid-1970s, Richard Blakemore and Richard Frankel found that both living and dead marine bacteria from the North Atlantic passively oriented parallel to the magnetic field lines; the anterior end of each bacterium was pointed northward and downward (as are the lines of inclination in the northern hemisphere; **Figure 4**). In living bacteria, flagellar motion at the posterior end of the organism results in movement of the organism along the field lines toward the anaerobic areas of sediment at the water–substrate boundary. A variety of magnetotactic bacteria and algae have been found in both fresh and marine waters of the northern and southern hemispheres. In each case, long chains of (single domain) magnetite particles or, in some cases, greigite (an iron sulfide) are present within the bacteria and cause passive alignment with the geomagnetic field lines.

To confirm the role of magnetite in the orientation of these microorganisms, Blakemore (and his colleague, Adrianus Kalmijn) remagnetized the chains of magnetite in bacteria with a strong magnetic pulse oriented antiparallel to the orientation of the bacteria. This technique, known as 'pulse remagnetization,' will remagnetize (i.e., reverse the polarity of) any permanently magnetic particles; however, paramagnetic particles such as radical pairs will not be permanently affected. After pulse remagnetization, the magnetotactic bacteria oriented in the opposite direction showing that the magnetic pulse had reversed their 'behavior' by reversing the polarity of their magnetite chains.

The findings in bacteria triggered the search for a magnetite-based magnetoreception mechanism in animals. Magnetite is a fairly ubiquitous biogenic compound in animals and has been reported in insects, birds, fish, and mammals; it occurs in a variety of tissue types including the nervous system. In order to be useful for magnetic orientation, however, a magnetite-based magnetoreceptor would need to be associated with a directionally selective sensory system. Physiological, anatomical, and behavioral studies have all provided evidence for an iron-based mechanism associated with the ethmoid, or nasal, region in birds and fish. Using traditional neurophysiological techniques, Robert Beason and Peter Semm first demonstrated that the ophthalmic branch of the trigeminal nerve, which innervates the ethmoid region of songbirds, is sensitive to changes in Earth-strength magnetic fields.

Recently, Gerta and Guenther Fleissner and others more fully described iron-containing structures in the dendrites of the ophthalmic branch of the trigeminal nerve in the upper beak of homing pigeons. The complex structures were found to contain both platelets of maghemite (another ferromagnetic iron oxide) and small round intracellular 'bullets' of magnetite, which are influenced by local magnetic fields around the sensors to detect the magnetic field and likely also amplify it so that sensory transduction can take place. Thus, geomagnetic transduction may work similar to other senses such as hearing, where the stimulus is amplified to increase detection. These iron-containing sensory neurons were found in three pairs, bilaterally arranged within the upper beak. Each pair is aligned along a different axis, so that when taken together, they could act as a three-dimensional magnetometer to detect multiple components of the magnetic field, analogous to a human-made three-axis magnetometer. With this structure, birds could sense both the direction and the intensity of the surrounding magnetic field.

Pulse remagnetization experiments similar to those conducted on magnetotactic bacteria have provided evidence that some aspect of magnetic orientation in birds is mediated by an iron-based magnetoreception mechanism. However, the characteristics of this trigeminal magnetic system suggest that it may mediate a magnetic 'map' sense rather than a magnetic compass sense. When birds are exposed to a strong magnetic pulse designed to remagnetize magnetite particles, a change in the direction of migratory orientation is observed in adult birds, but only when the trigeminal nerve is intact. If information from the trigeminal nerve is blocked with anesthesia, bobolinks can still show magnetic orientation, but the effect of the pulse (i.e., a shift in their orientation) is no longer evident. In other words, pulse remagnetization does not influence the adult's compass sense. Likewise, juvenile songbirds captured prior to their first migration, which should not have a map sense, are unaffected by pulse remagnetization. Interestingly, trigeminal neurons exhibit the requisite sensitivity to extremely small magnetic field changes that would be expected for precise geographic positioning.

Conclusion

Since the discovery of magnetic orientation in the European robin and other songbirds, researchers have begun to investigate many proximate questions about the genetics and development of magnetic orientation and the sensory 'rules' and processing of magnetic information. Despite almost 50 years of research, we still do not understand many of the basic rules of operation of this sensory system or its ecological functions; even the elusive magnetoreceptor(s) and magnetoreception mechanism(s) in birds have yet to be conclusively identified. Like many other senses, however, magnetoreception appears predisposed to be 'tuned' to Earth-strength magnetic fields, able to adapt to changes in the magnetic field, and to provide more than one type of information (e.g., birds appear to be able to detect both quantity, or magnetic field strength, and quality, such as magnetic inclination). Moreover, magnetoreception is not used alone for navigation. Rather, songbirds are capable of multimodal processing (i.e., combining magnetic and visual cues) in order to determine a direction for orientation during migration. However, how birds combine information from different compass types in their nervous system is still largely unknown. Furthermore, the functional role of geographic variation in the geomagnetic field for map-based navigation, geographic positioning, or sign post navigation needs to be more fully explored in species with different migratory pathways and constraints. Another 50 years of research on avian magnetoreception, including behavioral studies on caged and free-flying migrants, physiological and anatomical investigations of neurological mechanisms, and collaborations of biologist and physicists will likely lead to some of these answers and to the inclusion of this important sensory system in textbooks on animal behavior, physiology, and sensory systems, where it has largely been ignored.

See also: Amphibia: Orientation and Migration; Bird Migration; Magnetic Compasses in Insects; Maps and Compasses; Sea Turtles: Navigation and Orientation.

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