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This is the way – The mystery of magnetoreception and its use in long-distance migration in sea turtles.

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Abstract

Magnetoreception has been theorized since the 19th century and is now known to be used as a guidance system among a wide array of animals. It relies on the geomagnetic field that englobes planet earth and provides a globe-wide compass for migrating animals. Among them, sea turtles are the most studied, and yet little is known about the internal mechanisms allowing them to exploit such magnetic information and use it for navigation. How do animals find their way when they rely on magnetoreception? In this essay, I first discuss the three main current hypotheses regarding the way animals may detect magnetic field parameters. I then relate this to the puzzling case of sea turtles, whilst also exploring the novel symbiotic magnetoactic hypothesis that may bridge the gaps in our understanding. Finally, I discuss the difficulties in studying magnetoreception and what are in my view the biggest challenges faced by scientists when looking for answers. I find that although each of the three main theories, namely the magnetite-particle-based magnetoreception theory, electromagnetic induction or light-dependent radical-pair theory offer convincing arguments when it comes to specific individual species, none currently explain the mechanics of magnetoreception in all animals. I discuss that it is likely that these mechanics are not exclusive but instead occur simultaneously in individuals, and I show through the example of sea turtles and magnetitic bacteria, that there may even be entirely new mechanism we are yet to unravel. I finally describe how our biases based on our human senses as well as the difficulties we encounter when measuring magnetic activity may lead to errors, and how research needs to take this into account in order to yield convincing results that will shed light on what is still unknown.

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I Introduction

Magnetoreception, or the ability of animals to detect the earth's magnetic field and use it for orientation and navigation, has been theorized since the 19th century and is yet seldom included in literature as part of the classical senses (Middendorff, 1859; Wiltschko and Wiltschko, 2006; Viguier, 1882). Many animals, among which molluscs, arthropods and members of all major vertebrates' groups have nonetheless been shown to perceive the magnetic field of the earth and often to use it as a guidance system (Mouritsen, 2018; Wiltschko and Wiltschko, 2005). Unlike other well-studied senses used for migration, including sight, olfaction, and hearing, magnetoreception represents a reliable, omnipresent source of navigational information and is therefore a vital parameter to consider when studying long-distance migrants (Wiltschko and Wiltschko, 2005). Interestingly, it is also the only sense that is not used for communication, but rather for navigation (Yong, 2022).

Magnetoreception and earth's magnetic field

Magnetoreception relies on the geomagnetic field that englobes planet earth and can therefore guide animals migrating over the span of several continents. This is due to earth's core, composed of a solid iron sphere surrounded by molten iron and nickel, which, through its agitation, essentially turns the planet into a giant magnet (Lohmann and Lohmann, 2019; Yong, 2022). The geomagnetic field of earth therefore compares to the dipole field of a bar magnet, with field lines emerging from the southern hemisphere, curving around the planet, and re-entering the Earth in the northern hemisphere (see Fig. 1). Although the physical aspects on which magnetoreception rely are well understood, with each point on earth corresponding to a unique geomagnetic field direction, *how* individuals are able to harness this information and use it for navigation remains mostly a mystery.

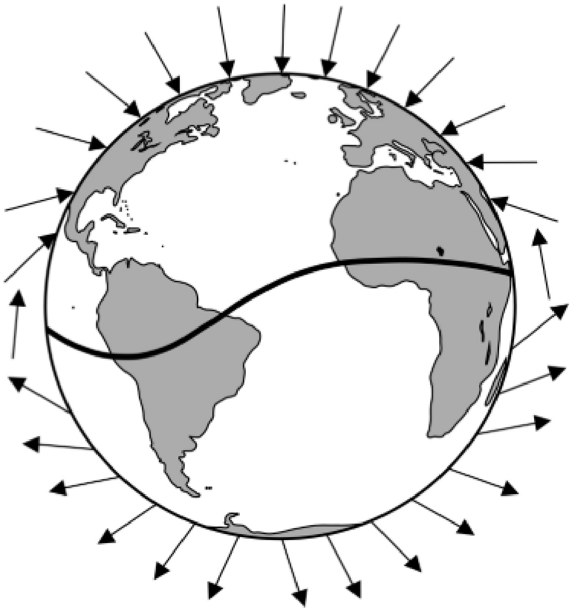


Fig. 1: Earth's magnetic field. Magnetic field lines (arrows) intersect Earth's surface, forming an inclination angle which varies with latitude. At the magnetic equator (the curving line across the planet), field lines are parallel to Earth's surface and the inclination angle is 0 degrees. Field lines become progressively steeper as one moves toward the magnetic poles, where the field lines are perpendicular to Earth's surface and the inclination angle is 90 degrees (Lohmann and Lohmann, 2019).

Magnetoreception and migration

Magnetic information as a tool for orientation in animals was first observed by Merkel and Wiltschko (1965) during behavioural experiment with the migratory European robin, *Erithacus rubecula* (Turdidae). They robins they captured in the fall showed pre-migratory behabviour, i.e. were about to start migrating southward. Their experiment was simple: they used a setup known as the Emlen funnel; they placed the birds in a closed funnel (so stars could not be perceived) with at its base an ink pad and blotting paper on its sides. They were then able to count the inky footprints left by the birds as they tried to jump out, showing clear quantitative evidence that the robins were heading south-west. When later flipping the magnetic fields around them using Helmholtz coils, thereby altering the magnetic north, the birds were shown to shift the direction of their heading accordingly. This demonstrated that they oriented with respect to the magnetic field, and it proved the presence of an internal compass (Wiltschko, 1968). Since Merkel and Wiltschko's pioneering work, scientists have uncovered evidence of magnetoreception throughout the animal kingdom, including among marine animals.

Magnetoreception in sea turtles

Diverse marine species are known to migrate across vast stretches of apparently featureless ocean, to then return in their birth area once adult (Meylan *et al.,* 1990; Baker *et al.,* 2013; Feldheim *et al.,* 2014). The mechanisms of this impressive journey of natal homing, where individuals leave their geographic area of origin when young, migrate considerable distances, and then return to reproduce, were until recently a mystery (Lohmann *et al.,* 2008; Rooker *et al.,* 2008). Among the marine species exhibiting natal homing, the migration undertaken by sea turtles are of the most treacherous (Groot and Margolis, 1991; van Buskirk and Crowder, 1994). Sea turtles are iconic long-distance ocean migrants, know to exploit chemical cues to complete reproductive migrations in the same way salmons famously do (Grassman et al., 1984; Endres et al., 2016). However, because such chemical cues cannot extend over the thousand kilometres span of open sea that these migrations represent, other mechanisms must be at play here (Lohmann *et al.,* 2013). In 1991, Lohmann showed that sea turtles could determine their magnetic heading through the use of their internal magnetic compass sense; later, it was shown they could assess their geographic position using a magnetic map sense by differentiating among locations on earth based on the different magnetic field features present (Lohmann and Lohmann, 1993; Lohmann et al., 2001, 2004, 2012; Putman et al., 2011). Importantly, however, much is yet unknown about the internal mechanisms allowing them to exploit such magnetic information and use it for navigation.

Research aim

In this essay, I will investigate how animals are able to find their way when they rely on magnetoreception. To do so, I will firstly discuss the three main current hypotheses regarding the way animals may detect magnetic field parameters: (1) induced electrical fields detected by highly sensitive electroreceptors; (2) magnetic-particle-based magnetoreception; and (3) radical-pair-based magnetoreception. I will then relate this to the puzzling case of sea turtles, whilst also exploring the novel theories put forth that may bridge the gaps in our understanding, through the example of the symbiotic magnetotactic hypothesis. Finally, I will discuss the difficulties with studying magnetoreception and what are in my view the biggest challenges faced by scientists when looking for answers.

II The mystery of magnetoreception - How does it work, really?

A wide array of organisms, from magnetotactic bacteria (Bazylinski and Frankel, 2004) to mammals (Begall *et al.,* 2013), are now known to align themselves with the magnetic field. We therefore know that many species are able to detect and use the geomagnetic field to orient themselves and navigate in space, but the exact way in which they detect magnetic field parameters is not as clear. Because the geomagnetic field can pass unimpeded through biological matter, the sensors used for magnetoreception – magnetoreceptors – could be present anywhere in an individual's body. This is especially abstruse considering the anatomical constraints and structures present within small species, as they are still able to reliably detect the 25,000–65,000 nT geomagnetic field (Mouritsen, 2018). Nonetheless, three mechanisms are currently theorised: (1) magnetic-particle-based magnetoreception; (2) induced electrical fields detected by highly sensitive electroreceptors; and (3) radical-pair-based magnetoreception.

Magnetic-particle-based magnetoreception

This first hypothesis involves a magnetite iron mineral known as magnetite. Magnetotactic bacteria, a diverse group of prokaryotes, were discovered in the 1970s and shown to build intracellular chains of magnetite (Fe_3O_4) particles called magnetosomes, used to direct themselves using a magnetic field (Natan *et al.,* 2020). These chains are necessary for magnetoreception, as individual crystals are too small to contribute effectively and react to the earth's magnetic field (Walker *et al.,* 1984). Magnetotactic bacteria were the first example which suggested that organisms could synthesize magnetic crystals, that could then act as internal compass needles (Blakemore, 1975; Uebe and Schüler, 2016). The Magnetic-particle-based theory is based on the principle of cell depolarization and neuronal activation, following a deflection of magnetite particles anchored to specialized neural cells (Caiou and McNaughton, 2010; Kirschvink and Goud, 1981; Kirschvink *et al.,* 2001; Walker, 2008). In other words, it is as though individuals have a magnetite needle tied to a sensory cell, which can trigger a nervous signal when the individual moves and as the needle tugs upon its tether (Yong, 2022, Shaw *et al*., 2015) (see Fig. 2).

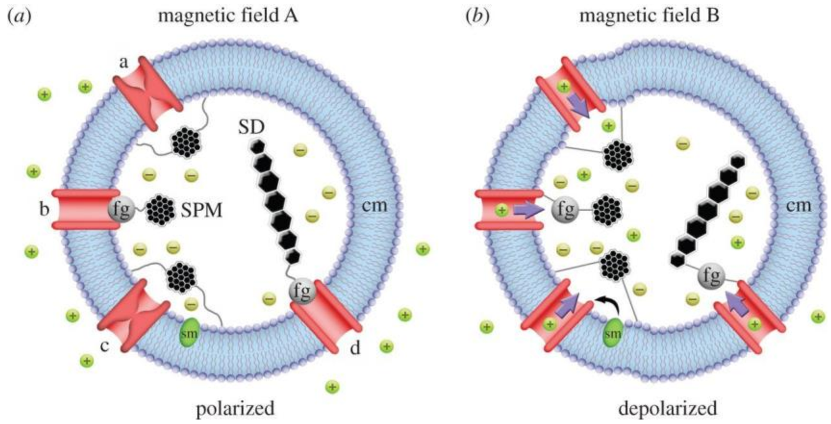


Fig. 2. (*a*,*b*) Diagrammatic representation of various hypothesized magnetite particle-based magnetoreceptor systems under two differing magnetic field conditions. Three separate magnetoreceptor systems based on clusters of superparamagnetic (SPM) particles are shown on the left hemisphere of each cell (a, b and c) and an example of a single domain system is provided on the right hemisphere (d). Under magnetic field condition A, all systems are shown in the resting, polarized state, where particles are connected to closed mechanosensitive ion channels via cytoskeletal filaments to the cell membrane (cm) or to force-gated ion channels (fg). The change to magnetic field condition B, results in movement of the SPM clusters, which distorts the cell membrane in example a and opens a force-gated ion channel in example b. Example c is similar to a, but in this case ion channel

activation is mediated by a secondary messenger (sm). In the single domain system (d), shown as a chain of single crystals, the change from magnetic field condition A to B applies torque on the chain and again results in the opening of a force-gated ion channel. In all cases, cell depolarization leads to an action potential, which, travelling via afferent nerves, leads to neuronal activation in the brain (Shaw *et al.*, 2015).

Following this discovery, magnetite and/or iron oxides have successfully been detected in virtually every species carefully investigated (Mouritsen, 2018). In vertebrates, they were mostly found in the ethmoid region of the head (Kirschvink *et al.,* 1985); in birds, in the orbital and nasal cavities (Beason and Nichols, 1984; Beason and Brennon, 1986; Williams and Wild, 2001) (see Fig. 3). However, the exact position of these magnetite-based receptors remains unclear. For decades, researchers were confident to have found magnetite-loaded neurons in the beaks of several bird species (e.g., Hanzlik et al. 2000; Fleissner et al. 2003, 2007; Falkenberg et al. 2010), but this was strongly challenged by the histological study by Treiber *et al.,* (2012), where it was shown that the previously alleged magnetite neurons were in fact a certain type of white blood cells called macrophages. In essence, unless these magnetic particles are found to be consistently located inside cells at specific locations, in many individuals of the same species, and are found to be associated with the nervous system, their presence could serve other purpose than magneto-sensors (Winklhofer and Kirschvink, 2010; Hore and Mouritsen, 2016). For example, because iron homeostasis is vital for organism function, iron oxides may just be a way for organisms to deposit excess iron (Galizia and Lledo, 2013; Treiber *et al.,* 2012). Additionally, research carried out on baby loggerhead turtles, *Caretta caretta* (Cheloniidae), showed that following a series of five strong magnetic field pulses applied perpendicular to each other, hatchlings were still oriented towards a light, but were disoriented in the dark when they had to rely on their magnetic compass (Irwin and Lohmann, 2005). The pulses therefore appeared to affect compass responses, and yet, interestingly, magnetite has never been documented in marine turtles. Considerations on magnetite-based compass mechanisms overall and in sea turtles especially, are therefore still rather speculative, and other mechanisms are likely at play.

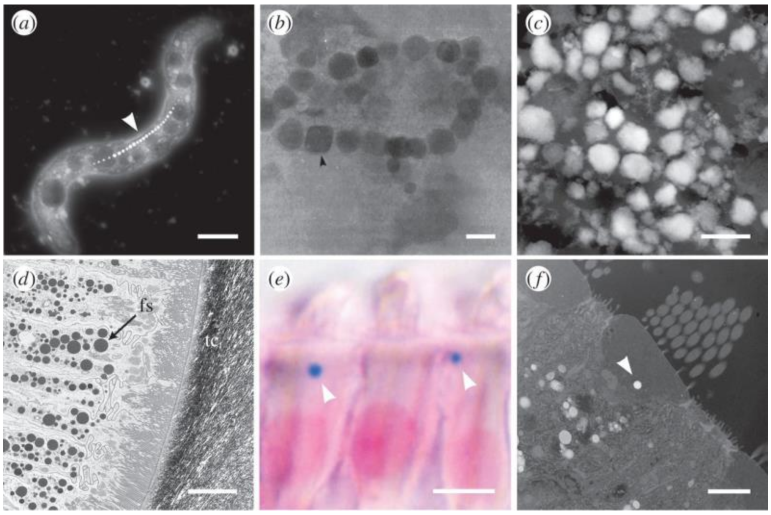


Fig 3. A selection of electron and optical micrographs of biogenic iron minerals formed by organisms. (a) Magnetotactic bacterium *Magnetospirillum magnetotacticum* and the chain of nanoparticulate magnetite forming the magnetosome (arrowhead). (b) Chains of magnetite isolated from ethmoid tissue from the salmon *Oncorhynchus nerka*. (c) Iron granules extracted from trophocyte cells in the abdominal fat layer of the honeybee *Apis mellifera*. (d) Ferritin siderosomes in the epithelial tissue surrounding the magnetite mineralized tooth cusp of the chiton *Acanthopleura hirtosa*. (e) Optical micrograph of a Perls' Prussian blue stained section. (f) Iron-rich cuticulosome in the cuticular plate of inner ear hair cells from the pigeon *Columbia livia*. Scale bars: (a) 1 µm, (b) 50 nm, (c) 500 nm, (d) 5 µm, (e) 5 µm & (f) 2 µm.

Electromagnetic induction

A second hypothesis on magnetoreception involves a mechanism called electromagnetic induction. Any conduction rod moving through a magnetic field develops a nonuniform charge distribution; when a rod is immersed in a conductive medium that is stationary relative to the field, an electrical circuit is formed (Johnsen and Lohmann, 2008). In other words, if an object composed of electrically conductive material moves through a magnetic field, positively and negatively charged particles migrate to opposite sides of the object which results in a constant voltage, which itself depends on the speed and direction of the object's motion relative to the magnetic field. When the moving object is in a conductive medium that is stationary relative to the field, then an electric circuit is formed and a current flows through the medium and the object. This hypothesis therefore suggests that the detection of magnetic fields would rely on accessory structures that convert the magnetic field into another stimulus, here, electric stimulus. A change in electric potential could be detected by cells expressing voltage-sensitive channels, such as electroreceptors in aquatic animals. Elasmobranchs, for example, possess electroreceptors that are sensitive to stimuli as small as 5 nVcm^{-1} (Kalmijn, 1971, 1982; Meyer *et al*., 2005). This is thanks to the several hundred long canals filled with highly conductive 'jelly' that start at tiny pores in the skin and end inside their body, at the ampullae of Lorenzini (see Fig. 4). The latter are collections of highly sensitive cells, capable of detecting the smallest changes in voltage. In essence, as a shark swims, weak electric currents are induced in the surrounding water, the strength of which changes depending on its angle relative to the geomagnetic field; these small changes can be detected and could be used by the shark to determine its heading (Paulin, 1995).

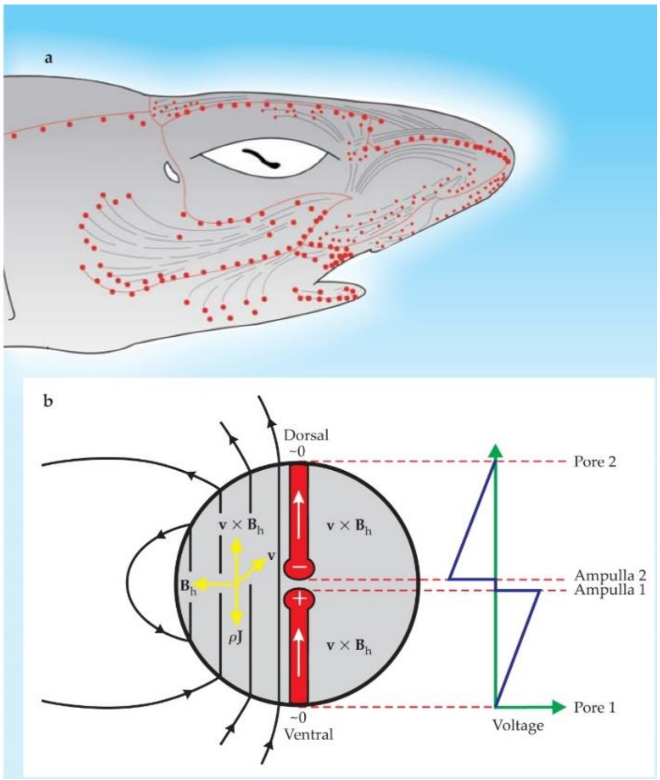


Fig. 4: Inductive magnetoreception. (a) Side view of a shark's head, showing the ampullae of Lorenzini electroreceptors (red dots) and jelly-filled conductive canals (gray lines). The red lines are so-called lateral lines, used to detect vibrations in the surrounding water. (Image courtesy of Chris Huh.) (b) Schematic showing two ampullae with their canals. As the shark swims east and into the page with a velocity **v**, its movement across the horizontal component of Earth's field, $\mathbf{B}_h$, causes a vertical electromotive force of magnitude vB_h. Because the shark's body and especially its skin are highly resistive, the voltage drop due to the current density $_{\rho}J$ results in

no potential difference between the dorsal and ventral surfaces of the animal. The high conductivity of the canals, however, results in a large voltage drop across the ampullae. The thick black lines illustrate the electric field surrounding and permeating the shark. (Johnsen and Lohmann, 2008).

Similar mechanisms have been hypothesised in birds. Indeed, Jungerman and Rosenblum (1980) posed that electromagnetic induction may also occur within the endolymph of the semi-circular canals of birds, with hair cells located on the periphery of the cupula acting as electroreceptors. As a bird's inner ear contains three canals full of conductive fluid, the geomagnetic field could induce a detectable voltage in that fluid when a bird flies and could therefore be used for navigation (Nimpf *et al.*, 2019). Although this theory has therefore shown to be promising for sharks and birds, such electroreceptors have never been found in sea turtles or any other reptile; magnetoreception based on electromagnetic induction is therefore unlikely for these animals.

The light-dependent radical pair theory

This last hypothesis is perhaps the most complex, but it is also the one that has gained the most momentum these past few years. It is based on the theory that the quantum mechanics of electron spins could form the basis of a magnetic compass sense (Hore and Mouritsen, 2016). It gets its name from the two molecules it involves, that form a *radical pair*, and whose chemical reaction is influenced by magnetic fields. The radical pair model states that specialized photopigments absorb a photon and are elevated to the singlet excited state; as light hits the two partner molecules, one donates an electron to the other, leaving both with an unpaired electron: they thus become radicals (Wiltschko and Wiltschko, 2005). Radicals are magnetic because those electrons have a property known as spin angular momentum, or 'spin' (Hore and Mouritsen, 2016). Because spin is a quantum mechanical property, and quantum objects do not behave classically, it is best regarded as an attribute that some particles have and some do not, like mass or charge (Åkesson *et al.,* 2001). Importantly, spin can either be up or down; the radical pair can either have the same spins or opposite ones, and they can flip between these two states several million times per second. The amount of time these flips occur can be governed by the magnetic field, and depending on its nature, the molecules end up in either state which in turn will affect how chemically reactive they are (Hore and Mouritsen, 2016; Yong, 2022) (see Fig 5). In simpler words, it is as though, once triggered by light, the two molecules are dancing and enter an excited state; once in this state, the magnetic field can alter the tempo of their dance as well as its final steps. In that way, one partner's final position offers a record of the magnetic field they were last under. Thanks to this, the radical pair transforms the previously complex magnetic stimulus into a chemical stimulus much simpler to assess (Yong, 2022).

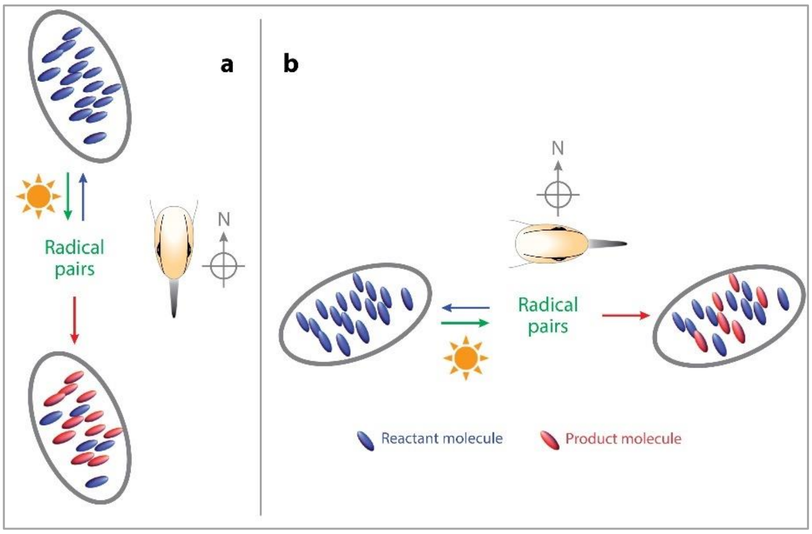


Fig. 5: The principle of a radical-pair compass. Reactant molecules *(blue)* are photochemically converted into product molecules *(red).* This transformation occurs via radical-pair intermediates, which can either proceed forward to the products *(red arrows)* or return to the reactants *(blue arrows*). The reactants and therefore the radical pairs are aligned relative to one another and oriented within the bird's eye so that they experience a change in the direction of the Earth's magnetic field when the bird moves its head. If this change is to form the basis of a magnetic compass, it must affect the probability that the radical pairs proceed along the red and blue pathways. The figure shows, schematically, the case in which more efficient conversion of reactants to products occurs when the bird's head is (a) aligned with the north–south axis than when it is (b) aligned with the east–west axis.

By definition, this theory relies on the primary role of light. The only photoreceptor molecules known to use light energy to form long-lived radical pairs in vertebrates are cryptochrome proteins, which can for example be found in birds' eyes (Ritz *et* al., 2000; Liedvogel *et al.,* 2007). Interestingly, studies have shown the radical-pair chemistry of cryptochromes to be magnetically sensitive (Hore and Mouritsen, 2016; Maeda *et al.,* 2012). Following this, in 2005, Mouritsen *et al.,* identified the magnetic processing centre in bird's brains: 'cluster N'. This region of the brain was shown to be particularly active when migratory birds are orienting with their compass at night when they travel with the stars or moon as a source of light, which is all the more interesting when considering it is also part of the brain's visual centres (Heyers *et al.,* 2007; Zapka *et al.,* 2009). In this way, we can theorise that migrating individuals can actually *see* Earth's magnetic field, over their normal field of view, perhaps as a gradient of shade or as a bright spot indicating north (see Fig. 6) (Mouritsen *et al*., 2005). Surprisingly, marine turtles have been proven to be well oriented in total darkness (Lohmann, 1991; Lohmann and Lohmann, 1993). Therefore, unless there is a yet unknown way that radical pairs could be generated in complete absence of light, magnetoreception as proposed by the radical pair model seems unlikely here (Wiltschko and Wiltschko, 2005).

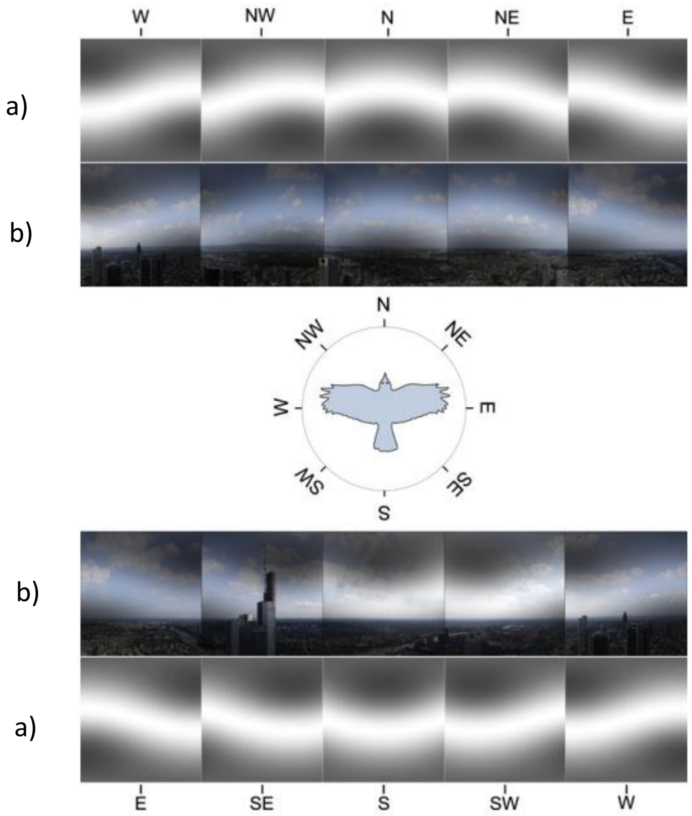


Fig. 6: The image shows the landscape perspective recorded from a bird flight altitude of 200 m above the ground with the cardinal directions indicated (N, NE, E, SE, S, SW, W, and NW) (images of Frankfurt provided by Vita Solovyeva). For the sake of illustration the magnetic field-mediated pattern is in grayscale alone, reflecting the perceived pattern if the magnetic visual pathway is completely separated from the normal visual pathway (rows a). It is then shown added onto the normal visual image the bird would see, if magnetic and normal vision uses the same neuronal pathway in the retina (rows b) (Solov'yov *et al*., 2010).

III Magnetoreception and sea turtles – the mystery continues.

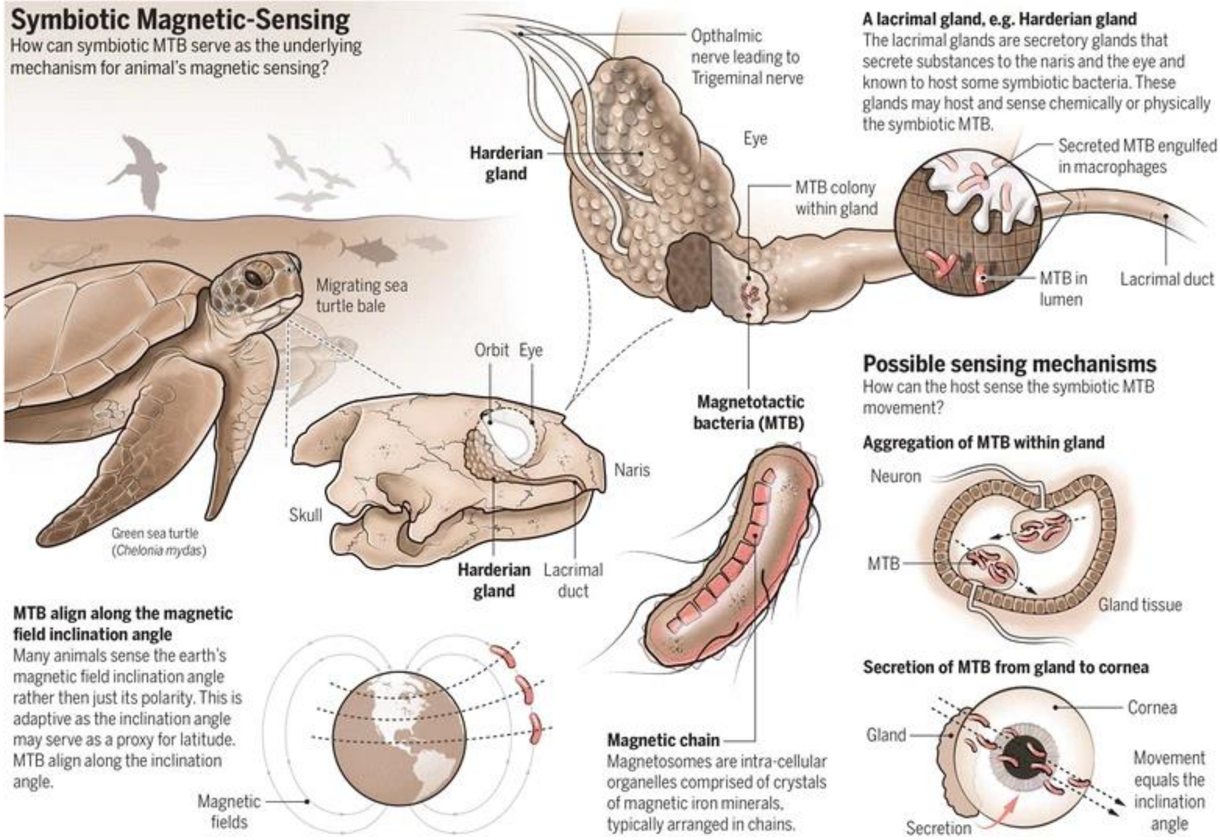
The ability of various taxa of animals to sense and use the earth's magnetic field has been well documented for the past 40 years, and although several theories present convincing evidence, overall, the sensor and sensory mechanisms behind this ability are an enigma to this day. In the second part of this essay, I will use the example of sea turtles to illustrate the gaps in the current hypotheses and discuss possible untested theories that could fill these gaps, all the while illustrating how the current considerations might be too narrow-minded, and the possible limitations in our perception of magnetoreception.

Sea turtles and magnetoreception

As briefly mentioned in the introduction of this essay, sea turtles are among the most iconic long-distance migrants; their involvement with magnetoreception research is therefore not surprising. Although they are among the most studied species within the scope of magnetic navigation, much remains unknown. As I will discuss here, they are therefore a perfect example of the biases and gaps in our understanding of magnetoreception. Most research efforts have been focused on the loggerhead sea turtles *(Caretta caretta)* (Lohmann *et al.,* 2012*).* Their migration is one of the longest and most spectacular, with many individuals migrating around the entire North Atlantic basin before returning to their native beach on the North American coast (Bolten *et al.,* 1998; Bowen and Karl, 2007). Such exploits naturally sparked the extensive research carried out the past few years. First, several experiments revealed that they possess a magnetic compass which, combined with their other senses, can guide them (Lohmann, 1991; Lohmann and Lohmann, 1993, 1996, 2007). Then, importantly, more than a compass, loggerheads need positional information to know when and where to change swimming direction, and avoid being carried by currents into fatally cold waters or far from their normal range (Carr, 1986; Lohmann and Lohmann, 2003). As most open-sea regions have a unique magnetic signature, comprised of a combination of inclination and intensity, being able to read such information poses real evolutionary advantages (Putman *et al.,* 2011; Lohmann and Lohmann, 1996). In order to test whether this was the case, studies were conducted in which hatchlings were collected from the nests before naturally emerging, and were then exposed to different magnetic fields that exist at different locations along their migratory route. They showed that the hatchlings would systematically swim in the directions that would help them stay on course were they to be located at that position (Lohmann *et al.,* 2001). Further, the turtles were then exposed to fields that exist at the same latitude but different longitude, and again, the individuals swam east or west appropriately (Lohmann *et al.,* 2001). These magnetic maps, in which specific magnetic fields characteristic of regional oceanic areas are stored, were therefore also proven to be used by loggerhead sea turtles. Interestingly, although little doubt is left on the fact that they are able to do this, no research thus far has been able to answer *how* they do so.

The puzzling case of sea turtles

As discussed throughout the first part of this essay, although some theories may be fitting to explain magnetoreception in certain specific species, none seem to illuminate the mystery of sea turtles. Electromagnetic induction seems unlikely, as the crucial electroreceptors it relies on have never been found in sea turtles. Then, the light-dependent radical pair theory is put into question by the fact that turtles are known to orient themselves in total darkness. Finally, magnetic-particle-based magnetoreception was considered impossible in sea turtles as no magnetite molecules had ever been found. Recently, however, the latter theory was put back in the running by Natan and Vortman (2017) when they published a paper arguing that such a mechanism could actually be possible, if we imagine a symbiotic relationship between magnetotactic bacteria and a host animal. In that way, magnetite molecules may in fact be present in sea turtles, but not where we were previously looking. Their theory, called symbiotic magnetic sensing, is based on the following: although it is well known that magnetotactic bacteria can move along a magnetic field using nanometric chain-like structures (see the previous 'Magnetic-particle-based magnetoreception' paragraph, page 6), it is still unknown *why* they evolved to do so; for metazoan, the exact opposite is true: we know the *why* but not the *how*. This, alongside the absence of any 'magnetic-sensors' in these species therefore led to the hypothesis that a mutualism between metazoan and magnetotactic bacteria provides an answer (Natan and Vortman, 2017). Furthermore, magnetite crystals, found in a number of organisms, have been described as "strikingly similar to the magnetotactic bacteria crystals" (Kirschvink *et al.,* 2001; Hand, 2016). Remained the question of the possible mechanisms through which symbiotic magnetic-sensing would work in animals. Natan and Vortman (2017) propose such an explanation in their paper. Past research has shown that the magnetic sensing organ is usually located in the ethmoid region of the head; they in turn advance that the magnetotactic bacteria, here the 'magnetic-sensor' for the host, could be located in the lacrimal glands of vertebrates (Hand, 2016; Payne, 1994) (see Fig. 7).



Symbiotic Magnetic-Sensing
How can symbiotic MTB serve as the underlying mechanism for animal's magnetic sensing?

A lacrimal gland, e.g. Harderian gland
The lacrimal glands are secretory glands that secrete substances to the naris and the eye and known to host some symbiotic bacteria. These glands may host and sense chemically or physically the symbiotic MTB.

MTB align along the magnetic field inclination angle
Many animals sense the earth's magnetic field inclination angle rather then just its polarity. This is adaptive as the inclination angle may serve as a proxy for latitude. MTB align along the inclination angle.

Magnetic chain
Magnetosomes are intra-cellular organelles comprised of crystals of magnetic iron minerals, typically arranged in chains.

Possible sensing mechanisms
How can the host sense the symbiotic MTB movement?

Fig. 7: Visual abstract of the symbiotic magnetotactic hypothesis. An example in sea turtles. (Natan and Vortman, 2017)

Although its primary function is lubricating the eye, it also allows photoreception, immunocompetence, as well as secreting hormones, porypherins and symbiotic bacteria to the naris and eye (Payne, 1994; Kugadas, 2016). Interestingly, studies have shown that a complex nerve system associated with the ophthalmic nerve runs through the gland; its exact function is still unknown, but it has been shown that sectioning the ophthalmic nerve in birds impairs magnetic sensing (Walcott and McLean, 1985; Mora *et al.,* 2004).

Perhaps most important to consider if we are to validate this hypothesis is the mechanism by which such bacteria may communicate with its host. Here again, several mechanisms are plausible. The first is that there is cell-to-cell communication, through the bacteria moving, either passively or actively, and accumulating at a certain location on the gland. In this way, their movement and/or accumulation in response to the magnetic field could be detected by a specific nerve and be interpreted by the host (Cryan and Dinan, 2012; Natan and Vortman, 2017) (see Fig. 7). The second mechanism has more to do with the host's visual system: secreted bacteria for the lacrimal glands may move along the cornea depending on the earth's field, which could be perceived by the host. Both mechanisms would be consistent with results found in experiments manipulating conditions for magnetoreception: sectioning of the ophthalmic nerve has been shown to alter magnetic sensing (Walcott and McLean, 1985; Mora *et al.,* 2004) and here may alter both sensing and secretion of bacteria from the gland; lack of light has been shown to alter magnetoreception, and here could make bacteria less detectable or reduce the secretions within the gland (Payne, 1994). Overall, it therefore seems that the proposed theory shows much potential, and if proven correct in future experiments, it could shed light on some of the currently unanswered questions regarding magnetoreception and open a wider discussion regarding what we think we already know.

The limitations of our human perception

It is important to consider that the study of animal behaviour is plagued by human biases in observation and interpretation, and this likely represents a strong limitation in the study of magnetoreception. Magnetic fields and magnetoreception can seem deeply counterintuitive because it is hard to compare it to a familiar sense, the same way we might do for echolocation or electroreception for example. This may in part explain why the radical pair idea has gained so much traction; it translates a sense that is foreign to us into something we can comprehend: sight. Even at its very base, we describe magnetoreception using terms such as compass or magnetic map, which are both human concepts and are likely to not represent the truth accurately (Johnsen *et al.,* 2020) (especially since our own compass acts by pointing north, whereas the magnetoreceptor “compass” apparently measures the inclination of the magnetic field). In actuality, the biological “compass” of animals is likely to be much more noisy, and require several readings over long periods in order to form an average rather than an instant precise read of the earth’s magnetic field. If this is the case, studying it in experimental, repeatable ways can prove highly difficult. In order to overcome this likely noisy compass, many animals have in fact been known to use a multimodal navigational strategy, relying for example on a sun compass alongside the magnetic one (Wiltschko and Wiltschko, 2001); mathematical models have in fact suggested that long-distance navigation may rely on the simultaneous use of at least four or five different factors (Schiffner *et al*., 2011). If we see magnetoreception as a ‘human’ *sense*, the same way we consider sight, olfaction or touch for example, this may appear quite familiar. We ourselves often require several of our senses to interpret information; magnetoreception may very well require the same, especially since it provides animals with both a “compass” and a “map” and likely in different ways (Hore and Mouritsen, 2016). Its noisy and erratic nature perhaps makes it more of a ‘back-up’ sense, used when the more reliable senses cannot be. Loggerheads hatchlings rely instead on the direction of waves when first entering the water, and olfactory cues when close enough to the coast, thereby likely ignoring the less reliable magnetic cues. Finally, the difficulties in defining magnetoreception also lies in our technical limitations. Unlike studying a medium that relies on hearing or vision, where uncalibrated equipment and error may be easily spotted, magnetic fields are imperceptible and correcting error becomes much more complicated, and quickly very expensive (Yong, 2022).

Conclusion

In conclusion, magnetoreception may serve varying functions, and work through different mechanics depending on the specific medium and challenges each species faces. It is becoming apparent that although it may help guide individuals through their long journey, it is best seen as a ‘last-resort” sense which comes into play mostly when other senses cannot be used. Although its use is now clear among several taxa, its mechanics are much less understood. The three theories listed in this essay, namely the magnetite-particle-based magnetoreception theory, electromagnetic induction or light-dependent radical-pair theory all provide convincing arguments, but none can answer all questions that remain within the wide diversity of species using this sense. It is possible that these mechanics are not exclusive but actually occur simultaneously in individuals, and as seen with the example of sea turtles and magnetitic bacteria, there may even be entirely new mechanism we are yet to unravel. In my mind, filling in the gaps in our knowledge will require extensive species-specific research that considers each individual’s environment and internal senses, rather than finding one apparatus common in all species. We must finally be careful not to let our biases based on our own human senses cloud our judgment and expectations, but instead open our considerations to much different systems than those we are familiar with.

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