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Geomagnetic Field and Animal Orientation

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Abstract

A large variety of animals possess a magnetic sense. Migratory birds use magnetic clues to find their way south in fall and north in spring. Salamanders, frogs, use the magnetic field for orientation when they have to find the direction of the nearest shore quickly, e.g., when they sense danger. Behavioral experimentalists have used these natural movement patterns to design experiments that allow them to investigate in which way geomagnetic information is used for orientation. For example, during migratory unrest (Zugunruhe), birds are so eager to migrate that they will assemble even in cages in the direction they want to migrate to, e.g., south in fall. If the magnetic field is changed, so that magnetic south appears in a different direction, birds will assemble in this new direction. This behavioral assay was used in 1966 by Wolfgang Wiltschko of the University of Frankfurt, Germany to demonstrate for the first time that migratory birds indeed use magnetic clues. Although the use of the geomagnetic field for directional information is well established experimentally, it is not known by which biophysical mechanism magnetoreception is achieved. The magnetic sense is perception mechanism for which the nature of the receptors and of the biophysical mechanism remain unknown. Magnetoreception (also magnetoception) is a sense which allows organism to detect a magnetic field to perceive direction, altitude or location. This sensory modality is used by a range of animals for orientation and navigation, and as a method for animals to develop regional maps. For the purpose of navigation, magnetoreception deals with the detection of the Earth's magnetic field. Magnetoreception is present in bacteria, arthropods, molluscs and members of all major taxonomic groups of vertebrates. Humans are not thought to have a magnetic sense, but there is a protein (a cryptochrome) in the eye which could serve this function.

Keywords: Magnetoception; Cryptochrome; Magnetosomes; magnetosensitivity

INTRODUCTION

The perception of Earth's magnetic field is used by many animal species for orientation and navigation. A magnetic sense is found in some insects, fish, reptiles, birds and mammals, whereas humans do not appear to be able to perceive Earth's magnetic field. The magnetic sense in migratory birds has been studied in considerable detail: unlike a boy scout's compass, which shows the compass direction, a bird's compass recognizes the inclination of the magnetic field lines relative to Earth's surface. Surprisingly, this inclination compass in birds is linked to the visual system as the magnetic field activates the light-sensitive molecule cryptochrome 1a in the retina of the bird's eye. Cryptochrome 1a is located in the blue- to UV-sensitive cone photoreceptors and only reacts to the magnetic field if it is simultaneously excited by light (Christine Niessner, *et al*, 2016). In addition to the senses of touch, smell, taste, hearing, and sight, some animals are able to sense Earth's magnetic field. Migratory turtles and birds use this sense to guide them on long journeys. Homing pigeons use it to find their way home. New research suggests that large mammals, such as cows and deer, may also have the ability to sense the direction of magnetic north. The grazing animals are aligned with the local magnetic field (Science Buddies, 2017). It seems that animals that use the magnetic field to navigate may come with a built-in compass, but there may be more than one type of compass. The bodies of animals such as birds and the fruit fly contain proteins called cryptochromes. When these proteins are exposed to blue light, they form molecules with electrons that spin in specific ways depending on the earth's magnetic field. Researchers think that these cryptochromes could help some animals navigate.

ROLE OF CRYPTOCHROMES

Experimental data suggests that cryptochromes in the photoreceptor neurons of birds' eyes are involved in magnetic orientation during migration. Cryptochromes are also thought to be essential for the light-dependent ability of *Drosophila* to sense magnetic fields. Magnetic fields were once reported to affect cryptochromes also in *Arabidopsis thaliana* plants: growth behavior seemed to be affected by magnetic fields in the presence of blue (but not red) light. Nevertheless, these results have later turned out to be irreproducible under strictly controlled conditions in another laboratory, suggesting that plant cryptochromes do not respond to magnetic fields. Cryptochrome forms a pair of radicals with correlated spins when exposed to blue light. Radical pairs can also be generated by the light-independent dark re-oxidation of the flavin cofactor by molecular oxygen through the formation of a spin-correlated FADH-superoxide radical pairs. Magnetoreception is hypothesized to function through the surrounding magnetic field's effect on the correlation (parallel or anti-parallel) of these radicals, which affects the lifetime of the activated form of cryptochrome. Activation of cryptochrome may affect the light-sensitivity of retinal neurons, with the overall result that the animal can "see" the magnetic field. Animal cryptochromes and closely related animal photolyases contain a longer chain of electron-transferring tryptophans than other proteins of the cryptochrome-photolyase superfamily (a tryptophan tetrad instead of a triad). The longer chain leads to a better separation and over 1000× longer lifetimes of the photoinduced flavin-tryptophan radical pairs than in proteins with a mere triad of tryptophans. The absence of spin-selective recombination of these radical pairs on the nanosecond to microsecond timescales seems to be incompatible with the suggestion that magnetoreception by cryptochromes is based on the forward light reaction (Griffin, *et al*, 1999).

Cryptochromes are a class of flavoproteins that are sensitive to blue light. They are found in plants and animals. Cryptochromes are involved in the circadian rhythms of plants and animals, and possibly also in the sensing of magnetic fields in a number of species. The name *cryptochrome* was proposed as a

portmanteau combining the cryptic nature of the photoreceptor, and the cryptogamic organisms on which many blue-light studies were carried out. The two genes *Cry1* and *Cry2* code for the two cryptochrome proteins CRY1 and CRY2. In insects and plants, CRY1 regulates the circadian clock in a light-dependent fashion, whereas, in mammals, CRY1 and CRY2 act as light-independent inhibitors of CLOCK-BMAL1 components of the circadian clock. In plants, blue-light photoreception can be used to cue developmental signals. Besides chlorophylls, cryptochromes are the only proteins known to form photoinduced radical-pairs in vivo (Gressel, 1979). It has been realized that animal cryptochromes (CRYs) fall into two broad groups. Type 1 CRYs, the prototype of which is the “*Drosophila* CRY”, that is known to be a circadian photoreceptor. Type 2 CRYs, the prototypes of which are human being. Both, CRY 1 and CRY 2, are known to function as core clock proteins. The mechanism of photo signaling by the Type 1 CRYs is not well understood. Nuri Ozturk, *et al* (2008) reported that the flavin cofactor of the Type 1 CRY of the monarch butterfly may be in the form of flavin anion radical, FAD. Further, this team (Nuri Ozturk, *et al*, 2008) described the purification and characterization of wild-type and mutant forms of Type 1 CRYs from fruit fly, butterfly, mosquito, and silk moth. Cryptochromes from all four sources contain FAD_{ox}. When purified, and the flavin is readily reduced to FAD by light. Interestingly, mutations that block photo-reduction in vitro do not affect the photoreceptor activities of these CRYs, but mutations that reduce the stability of FAD in vitro abolish the photoreceptor function of Type 1 CRYs in vivo. Collectively, our data provide strong evidence for functional similarities of Type 1 CRYs across insect species and further support the proposal that FAD represents the ground state and not the excited state of the flavin cofactor in Type 1 CRYs (Nuri Ozturk, *et al*, 2008).

POSSIBLE MECHANISM OF RESPONSE OF ANIMALS TO MAGNETIC FIELD

An unequivocal demonstration of the use of magnetic fields for orientation within an organism has been in a class of bacteria known as magnetotactic bacteria. These bacteria demonstrate a behavioural phenomenon known as magnetotaxis, in which the bacterium orients itself and migrates in the direction along the Earth's magnetic field lines. The bacteria contain magnetosomes, which are nanometer-sized particles of magnetite or iron sulfide enclosed within the bacterial cells. The magnetosomes are surrounded by a membrane composed of phospholipids and fatty acids and contain at least 20 different proteins. They form in chains where the magnetic moments of each magnetosome align in parallel, causing each bacterium cell to essentially act as a magnetic dipole, giving the bacteria their permanent-magnet characteristics (Blakemore, 1975).

For animals the mechanism for magnetoreception is unknown, but there exist two main hypotheses to explain the phenomenon. According to one model, magnetoreception is possible via the radical pair mechanism. The radical-pair mechanism is well-established in spin chemistry, and was speculated to apply to magnetoreception in 1978 by Schulten *et al.* In 2000, cryptochrome was proposed as the “magnetic molecule”, so to speak, that could harbor magnetically sensitive radical-pairs. Cryptochrome, a flavoprotein found in the eyes of European robins and other animal species, is the only protein known to form photoinduced radical-pairs in animals. The function of cryptochrome is diverse across species, however, the photoinduction of radical-pairs occurs by exposure to blue light, which excites an electron in a chromophore. The Earth's magnetic field is only 0.5 gauss and so it is difficult to conceive of a mechanism, other than phase shift, by which such a field could lead to any chemical changes other than those affecting the weak magnetic fields between radical pairs. Cryptochromes are therefore thought to be essential for the light-dependent ability of the fruit fly *Drosophila melanogaster* to sense magnetic fields (Wolfgang, *et al*, 2008; Hore, *et al*, 2016). The second proposed model for magnetoreception relies on Fe₃O₄, also referred to as iron (II, III) oxide or magnetite, a natural oxide with strong magnetism. Iron (II, III) oxide remains permanently magnetized when its length is larger than 50 nm and becomes magnetized

when exposed to a magnetic field if its length is less than 50 nm. In both of these situations the Earth's magnetic field leads to a transducible signal via a physical effect on this magnetically sensitive oxide (Cadiou Hervé, *et al*, 2010).

Another less general type of magnetic sensing mechanism in animals that has been described is electromagnetic induction used by sharks, stingrays and chimaeras (cartilaginous fish). These species possess a unique electroreceptive organ known as *ampullae of Lorenzini* which can detect a slight variation in electric potential. These organs are made up of mucus-filled canals that connect from the skin's pores to small sacs within the animal's flesh that are also filled with mucus. The ampullae of Lorenzini are capable of detecting Direct Currents (DC) and have been proposed to be used in the sensing of the weak electric fields of prey and predators. These organs could also possibly sense magnetic fields, by means of Faraday's law: as a conductor moves through a magnetic field an electric potential is generated. In this case the conductor is the animal moving through a magnetic field, and the potential induced depends on the time varying rate of flux through the conductor according to Kalmijn (1971).

These organs detect very small fluctuations in the potential difference between the pore and the base of the electroreceptor sack. An increase in potential results in a decrease in the rate of nerve activity, and a decrease in potential results in an increase in the rate of nerve activity. This is analogous to the behavior of a current carrying conductor; with a fixed channel resistance, an increase in potential would decrease the amount of current detected, and vice versa. These receptors are located along the mouth and nose of sharks and stingrays. Although debated, it has been proposed that in terrestrial animals the semicircular canals of the inner ear could host a magnetosensitive system based on electromagnetic induction (Lohmann, *et al*, 1987).

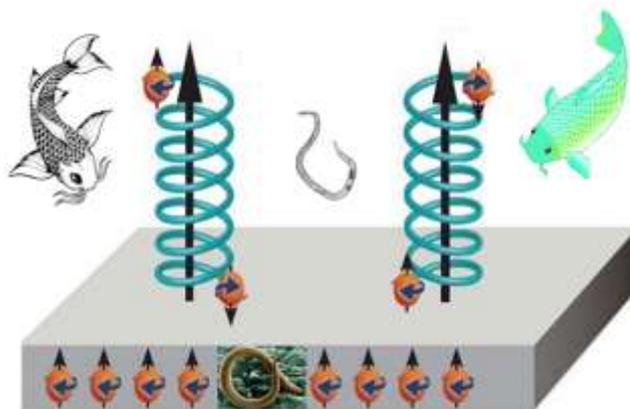


Fig.1: Theoretical diagram explaining the response of invertebrates and fishes.

MAGNETORECEPTION IN INVERTEBRATES ANF FISHES

The nematode *Caenorhabditis elegans* (L) (Family: Rhabditidae) was proposed to orient to the magnetic field of the Earth using the first described set of magnetosensory neurons. Worms appear to use the magnetic field to orient during vertical soil migrations that change in sign depending on their satiation state (with hungry worms burrowing down, and satiated worms burrowing up). However, recent evidence challenges these findings (Vidal-Gadea, *et al*, 2015; Landler, *et al*, 2018).

The mollusk *Tochuina tetraquetra* (formerly *Tritonia diomedea* or *Tritonia gigantea*) has been studied for clues as to the neural mechanism behind magnetoreception in a species. Some of the earliest work with *Tochuina* showed that prior to a full moon *Tochuina* would orient their bodies between magnetic north and east (Lohmann, et al, 1987). A Y-maze was established with a right turn equal to geomagnetic south and a left turn equal to geomagnetic east. Within this geomagnetic field 80% of *Tochuina* made a turn to the left or magnetic east. However, when a reversed magnetic field was applied that rotated magnetic north 180° there was no significant preference for either turn, which now corresponded with magnetic north and magnetic west. These results, though interesting, do not conclusively establish that *Tochuina* uses magnetic fields in magnetoreception. These experiments do not include a control for the activation of the Rubens' coil in the reversed magnetic field experiments. Therefore, it is possible that heat or noise generated by the coil was responsible for the loss of choice preference. Further work with *Tochuina* was unable to identify any neurons that showed rapid changes in firing as a result of magnetic fields (Lohmann, et al, 1991; Wang, 2004). However, pedal 5 neurons, two bisymmetric neurons located within the *Tochuina* pedal ganglion, exhibited gradual changes in firing over time following 30 minutes of magnetic stimulation provided by a Rubens' coil. Further studies showed that pedal 7 neurons in the pedal ganglion were inhibited when exposed to magnetic fields over the course of 30 minutes. The function of both pedal 5 neurons and pedal 7 neurons is currently unknown.

Drosophila melanogaster (L) (Drosophilidae) is another invertebrate which may be able to orient to magnetic fields. Experimental techniques such as gene knockouts have allowed a closer examination of possible magnetoreception in these fruit flies. Various *Drosophila* strains have been trained to respond to magnetic fields (Gegeer, et al, 2008). In a choice test flies were loaded into an apparatus with two arms that were surrounded by electric coils. Current was run through each of the coils, but only one was configured to produce a 5-Gauss magnetic field at a time. The flies in this T-maze were tested on their native ability to recognize the presence of the magnetic field in an arm and on their response following training where the magnetic field was paired with a sucrose reward. Many of the strains of flies showed a learned preference for the magnetic field following training. However, when the only cryptochrome found in *Drosophila*, type 1 Cry, is altered, either through a missense mutation or replacement of the Cry gene, the flies exhibit a loss of magnetosensitivity. Furthermore, when light is filtered to only allow wavelengths greater than 420 nm through, *Drosophila* loses its trained response to magnetic fields. This response to filtered light is likely linked to the action spectrum of fly-cryptochrome which has a range from 350 nm – 400 nm and plateaus from 430-450 nm (VanVickle-Chavez, et al, 2007). Although researchers had believed that a tryptophan triad in cryptochrome was responsible for the free radicals on which magnetic fields could act, recent work with *Drosophila* has shown that tryptophan might not be behind cryptochrome dependent magnetoreception. Alteration of the tryptophan protein does not result in the loss of magnetosensitivity of a fly expressing either type 1 Cry or the cryptochrome found in vertebrates, type 2 Cry (Gegeer, et al, 2010). Therefore, it remains unclear exactly how cryptochrome mediates magnetoreception. These experiments used a 5 gauss magnetic field, 10 times the strength of the Earth's magnetic field). *Drosophila* has not been shown to be able to respond to the Earth's weaker magnetic field. Magnetoreception is well documented in honey bees, ants and termites (Pereira-Bomfim, et al, 2015). In ants and bees, this is used to orient and navigate in areas around their nests and within their migratory paths (Wajnberg, et al, 2010). For example, through the use of magnetoreception, the Brazilian stingless bee *Schwarziana quadripunctata* is able to distinguish differences in altitude, location, and directionality using the thousands of hair-like particles on its antennae. Magnetoreception has also been reported in the European eel by at least one study. (Nunes, et al, 2009).

Experimental data and field observations demonstrate that fish belonging to taxa of different evolutionary levels can use the geomagnetic field for orientation and navigation. Fish possessing special electrosensory

systems can perceive the magnetic fields via electroreceptors. Some teleosts can sense magnetic fields via sensory cells containing chains of biogenic magnetite crystals. Natural fluctuations of the geomagnetic field affect the locomotor activity and spatial distribution of fish, but such an effect is studied to a lesser extent than fish orientation in magnetic fields. The effect of artificial magnetic fields and natural fluctuations of the geomagnetic field (magnetic storms) on fish embryos causes changes in their ontogenesis. In this aspect, Elasmobranchii and Teleostei are studied more thoroughly. Elasmobranchs and some

teleosts are able to perceive magnetic fields via electroreceptors. Some teleosts can sense magnetic fields via sensory cells that contain crystals of biogenic magnetite. Laboratory and field studies demonstrate that magnetic fields affect fish locomotor activity and spatial distribution. The geomagnetic field can be used by fish for navigation. In addition, the effect of artificial magnetic fields and natural fluctuations of the geomagnetic field on fish embryos lead to changes in their development. It is suggested that changes in development can have an aftereffect on fish behavior.

Magnetic shark repellents utilize permanent magnets, which exploit the sensitivity of the Ampullae of Lorenzini in sharks and rays (electrosense). This organ is not found on bony fishes (teleosts), therefore, this type of shark repellent is selective to sharks and rays. Permanent magnets do not require power input, making them ideal for use in fisheries and as bycatch reduction devices. During November 2004, SharkDefense researcher Eric Stroud accidentally dropped a magnet onto a rubber mat near a captive tank at the Oak Ridge Shark Laboratory. He noticed that juvenile nurse sharks (*G. cirratum*) near the tank wall swam away. While the initial event may have been due to vibrations, it led him to test the effects of the magnet on the captive sharks. Placing the magnet within the tank, Eric observed that nurse sharks avoided the region around the magnet. Follow-on tests in 2005 with Michael Herrmann at the laboratory used an acrylic Y-Maze and showed preference towards non-magnetic exits and strong conditioning. During February 2005, Patrick Rice and Eric Stroud conducted tonic immobility trials at the Bimini Biological Field Station, Bahamas, which confirmed that juvenile lemon sharks (*N. brevirostris*) and juvenile nurse sharks (*G. cirratum*) roused when permanent magnets were presented within 50 cm of the sharks nares. Mobility was not terminated when strong electromagnets were placed near the sharks. On January 1, 2009, a peer-reviewed publication described experiments in Australia showing the efficacy of using magnets to deter sharks (Rigg, *et al*, 2009). On January 12, 2010, Craig O'Connell from SharkDefense also published a peer-reviewed paper on the efficacy of magnetic shark repellents (O'Connell, *et al*, 2010).

MAGNETORECEPTION IN HOMING PIGEONS

Homing pigeons can use magnetic fields as part of their complex navigation system (Keeton, 1971; Walcott, 1996). William Keeton showed that time-shifted homing pigeons are unable to orient themselves correctly on a clear, sunny day which is attributed to time-shifted pigeons being unable to compensate accurately for the movement of the sun during the day. Conversely, time-shifted pigeons released on overcast days navigate correctly. This led to the hypothesis that under particular conditions, homing pigeons rely on magnetic fields to orient themselves. Further experiments with magnets attached to the backs of homing pigeons demonstrated that disruption of the bird's ability to sense the Earth's magnetic field leads to a loss of proper orientation behavior under overcast conditions (Gould, 1984). There have been two mechanisms implicated in homing pigeon magnetoreception: the visually mediated free-radical pair mechanism and a magnetite based directional compass or inclination compass (Mora, *et al*, 2004). More recent behavioral tests have shown that pigeons are able to detect magnetic anomalies of 186 microtesla (1.86 Gauss) (Fleissner Gerta, *et al*, 2003).

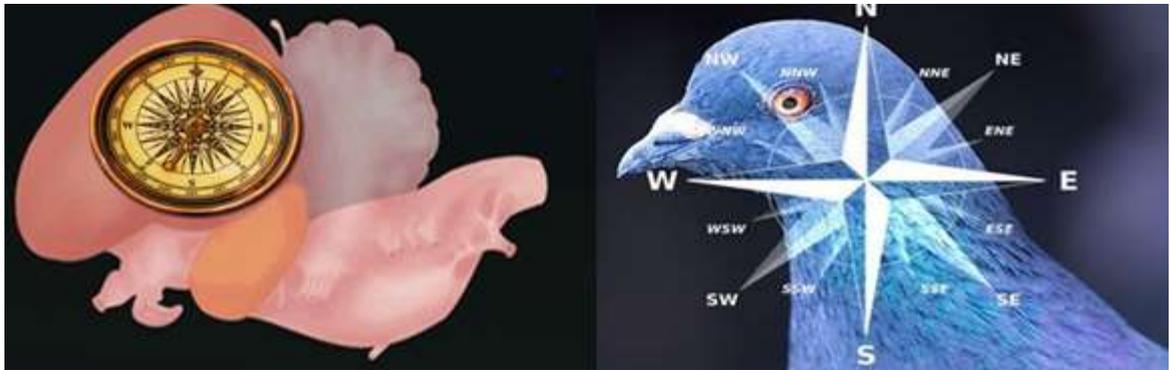


Fig.2: Navigation Map in the brain of pigeon

In a choice test birds were trained to jump onto a platform on one end of a tunnel if there was no magnetic field present and to jump onto a platform on the other end of the tunnel if a magnetic field was present. In this test, birds were rewarded with a food prize and punished with a time penalty. Homing pigeons were able to make the correct choice 55%-65% of the time which is higher than what would be expected if the pigeons were simply guessing.

For a long time the trigeminal system was the suggested location for a magnetite-based magnetoreceptor in the pigeon. This was based on two findings: First, magnetite-containing cells were reported in specific locations in the upper beak (Treiber, *et al*, 2012). Subsequent studies, however, revealed that these cells were macrophages, not magnetosensitive neurons (Engels, Svenja, *et al*, 2018; Wiltschko Roswitha, *et al*, 2010). Second, pigeon magnetic field detection is impaired by sectioning the trigeminal nerve and by application of lidocaine, an anesthetic, to the olfactory mucosa (Engels Svenja, *et al*, 2018). However, lidocaine treatment might lead to unspecific effects and not represent a direct interference with potential magnetoreceptors (Lauwers, Mattias, *et al*, 2013). Therefore, an involvement of the trigeminal system is still debated. In the search for magnetite receptors a large iron containing organelle (the cuticulosome) in the inner ear of pigeons was discovered (Wu and Dickman, 2011; Nimpf, Simon, *et al*, 2017). This organelle might represent part of an alternative magnetosensitive system. Taken together the receptor responsible for magnetosensitivity in homing pigeons remains uncertain. Aside from the sensory receptor for magnetic reception in homing pigeons there has been work on neural regions that are possibly involved in the processing of magnetic information within the brain. Areas of the brain that have shown increases in activity in response to magnetic fields with a strength of 50 or 150 microtesla are the posterior vestibular nuclei, dorsal thalamus, hippocampus, and visual hyperpallium (Falkenberg, *et al*, 2010).

MAGNETORECEPTION IN DOMESTIC HENS

Domestic hens have iron mineral deposits in the dendrites in the upper beak and are capable of magnetoreception (Wiltschko, *et al*, 2007; Freire, *et al*, 2011). Because hens use directional information from the magnetic field of the Earth to orient in relatively small areas, this raises the possibility that beak-trimming (removal of part of the beak, to reduce injurious pecking, frequently performed on egg-laying

hens) impairs the ability of hens to orient in extensive systems, or to move in and out of buildings in free-range systems (Mather and Baker, 1981). The magnetic compass found in chickens and other non-migrants suggests that it is an important mechanism for orientation within the home range. It may have developed to optimize the daily movements between the nest, food sources, water, to save energy, and minimize the chance of predation—here, an efficient navigational system represents a great advantage. A magnetic compass is also demonstrated in a number of animals from other groups (Wiltschko and Wiltschko, 1995) and these are mainly not migratory. When some birds later began to migrate, they could call on their already existing magnetic compass to orient their long flights. Hence chickens have probably inherited their magnetic compass from their ancestors. However, it would be surprising if such a complex mechanism remained intact and functional over such a long time without being maintained by some selective pressure. Today, chickens are domestic animals, living in the care of man. They descended from the Red Jungle Fowl, *Gallus gallus*, and their wild ancestors roamed in the dense jungle of Southeast Asia. In this environment, the magnetic compass would be very helpful: because of the closed canopy and the thick foliage, the birds could not orient with the help of the sun compass. There are numerous landmarks, but tree trunks and bushes are all quite similar, and they change with time, sometimes rapidly because of storms. Using the magnetic compass to keep track of their movements, or using the compass together with some prominent landmarks, as proposed by the concept of the mosaic map, would be a useful, efficient strategy (Denzau, *et al*, 2013).



Fig. 3: Hen responding the magnetic field.

The magnetic technology has been cited in the literature and investigated since the turn of the 19th century, when Lodestones and naturally occurring magnetic mineral formations were used to decrease the formation of scale in cooking and laundry applications. Today, advances in magnetic and electrostatic scale control technologies have led to their becoming reliable energy savers in certain applications (Lin and Yotvat, 1990; Laptev and Tioutine, 1996; Het, 1988; Welder and Partridge, 1954). The magnetic compass found in chickens and other non-migrants suggests that it is an important mechanism for orientation within the home range. It may have developed to optimize the daily movements between the nest, food sources, water, to save energy, and minimize the chance of predation—here, an efficient navigational system represents a great advantage. A magnetic compass is also demonstrated in a number of animals from other groups, and these are mainly not migratory. When some birds later began to migrate, they could call on their already existing magnetic compass to orient their long flights.

MAGNETORECEPTION IN MAMMALS

Work with mice, mole-rats and bats has shown that some mammals are capable of magnetoreception. When woodmice are removed from their home area and deprived of visual and olfactory cues, they orient themselves towards their homes until an inverted magnetic field is applied to their cage (Marhold, *et al*, 1997). However, when the same mice are allowed access to visual cues, they are able to orient themselves towards home despite the presence of inverted magnetic fields. This indicates that when woodmice are displaced, they use magnetic fields to orient themselves if there are no other cues available. However, early studies of these subjects were criticized because of the difficulty of completely removing sensory cues, and in some because the tests were performed out of the natural environment. In others, the results of these experiments do not conclusively show a response to magnetic fields when deprived of other cues, because the magnetic field was artificially changed before the test rather than during it (Nemec, *et al*, 2001). Later research, accounting for those factors, has led to a conclusion that the Zambian mole-rat, a subterranean mammal, uses magnetic fields as a polarity compass to aid in the orientation of their nests (Nemec, *et al*, 2001).

In contrast to work with woodmice, Zambian mole-rats do not exhibit different orientation behavior when a visual cue such as the sun is present, a result that has been suggested is due to their subterranean lifestyle. Further investigation of mole-rat magnetoreception lead to the finding that exposure to magnetic fields leads to an increase in neural activity within the superior colliculus as measured by immediate early gene expression (Holland, *et al*, 2006). The activity level of neurons within two levels of the superior colliculus, the outer sublayer of the intermediate gray layer and the deep gray layer, were elevated in a non-specific manner when exposed to various magnetic fields. However, within the inner sublayer of the intermediate gray layer (InGi) there were two or three clusters of responsive cells. The more time the mole rats were exposed to a magnetic field the greater the immediate early gene expression within the InGi. However, if Zambian mole-rats were placed in a field with a shielded magnetic field only a few scattered cells were active. Therefore, it has been proposed that in mammals, the superior colliculus is an important neural structure in the processing of magnetic information.

Bats may also use magnetic fields to orient themselves. While it is known that bats use echolocation to navigate over short distances, it is unclear how they navigate over longer distances (Wiltschko and Wiltschko, 2006). When *Eptesicus fuscus* are taken from their home roosts and exposed to magnetic fields 90 degrees clockwise or counterclockwise of magnetic north, they are disoriented and set off for their homes in the wrong direction. Therefore, it seems that *Eptesicus fuscus* is capable of magnetoreception. However, the exact use of magnetic fields by *Eptesicus fuscus* is unclear as the magnetic field could be used either as a map, a compass, or a compass calibrator. Recent research with another bat species, *Myotis myotis*, supports the hypothesis that bats use magnetic fields as a compass calibrator and their primary compass is the sun.

Red foxes (*Vulpes vulpes*) may use magnetoreception when preying on small rodents. When foxes perform their high-jumps onto small prey like mice and voles, they tend to jump in a north-eastern compass direction. In addition, successful attacks are "tightly clustered" to the north (Hart, *et al*, 2013). One study has found that when domestic dogs are off the leash and the Earth's magnetic field is calm, they prefer to urinate and defecate with their bodies aligned on a north-south axis (Begall, 2008).

There is also evidence for magnetoreception in large mammals. Resting and grazing cattle as well as roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) tend to align their body axes in the geomagnetic north-south direction (Burda, *et al*, 2009). Because wind, sunshine, and slope could be excluded as common ubiquitous factors in this study, alignment toward the vector of the magnetic field provided the most likely explanation for the observed behaviour. However, because of the descriptive nature of this study, alternative explanations (e.g., the sun compass) could not be excluded. In a follow-up study, researchers analyzed body orientations of ruminants in localities where the geomagnetic field is disturbed by high-voltage power lines to determine how local variation in magnetic fields may affect orientation behaviour. This was done by using satellite and aerial images of herds of cattle and field observations of grazing roe deer. Body orientation of both species was random on pastures under or near power lines. Moreover, cattle exposed to various magnetic fields directly beneath or in the vicinity of power lines trending in various magnetic directions exhibited distinct patterns of alignment. The disturbing effect of the power lines on body alignment diminished with the distance from the conductors. In 2011 a group of Czech researchers, however, reported their failed attempt to replicate the finding using different Google Earth images. (Kirschvink, 1997; Hert, *et al*, 2011).

Humans "are not believed to have a magnetic sense", but humans do have a cryptochrome (a flavoprotein, CRY2) in the retina which has a light-dependent magnetosensitivity. CRY2 "has the molecular capability to function as a light-sensitive magnetosensor", so the area was thought (2011) to be ripe for further study.

CONCLUSION

The largest issue affecting verification of an animal magnetic sense is that despite more than 50 years of work on magnetoreception there has yet to be an identification of a sensory receptor. Given that the entire receptor system could likely fit in a one-millimeter cube and have a magnetic content of less than one ppm, it is difficult to discern the parts of the brain where this information is processed. In various organisms a cryptochrome mediated receptor has been implicated in magnetoreception. At the same time a magnetite-based system has been suggested to be relevant to magnetosensation in birds. The third proposed mechanism (electromagnetic induction) has still not been tested in non-aquatic animals. Furthermore, it is possible that two complementary mechanisms play a role in magnetic field detection in animals. This dual mechanism theory in birds raises the questions: If such a mechanism is actually responsible for magnetoreception, to what degree is each method responsible for stimulus transduction, and how do they lead to a transducible signal given a magnetic field with the Earth's strength? The precise use of magnetoreception in animal navigation is unclear. Some animals appear to use their magnetic sense as a map, compass, or compass calibrator. The compass method allows animals not only to find north, but also to maintain a constant heading in a particular direction. Although the ability to sense direction is important in migratory navigation, many animals also have the ability to sense small fluctuations in earth's magnetic field to compute coordinate maps with a resolution of a few kilometers or better. For example, birds such as the homing pigeon are believed to use the magnetite in their beaks to detect magnetic signposts and thus, the magnetic sense they gain from this pathway is a possible map. Yet, it has also been suggested that homing pigeons and other birds use the visually mediated cryptochrome receptor as a compass. The purpose of magnetoreception in birds and other animals may be varied, but has proved difficult to study. Numerous studies use magnetic fields larger than the Earth's field. Studies such as of *Tritonia* have used electrophysiological recordings from only one or two neurons, and many others have been solely correlative.

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7 November is birthday of Eric Richard Kandel (The second author and nobel prize winning neuroscientist). This review article is wishing his kind self Happy Birthday.

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