Magnetoreception, the neurobiology of

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The magnetic field of the Earth provides a pervasive and reliable source of directional information that certain animals can use as an orientation cue while migrating, homing, or moving around their habitat. Behavioral experiments have demonstrated that a surprising number of diverse organisms can orient magnetically, including certain species of bacteria, molluscs, insects, fishes, amphibians, reptiles, birds, and mammals. Relatively little is known, however, about the neural mechanism or mechanisms that underlie magnetic field detection and geomagnetic orientation in animals. This article briefly describes the difference between a magnetic compass and a magnetic map sense, reviews the three major hypothesized transduction mechanisms for magnetic field detection, and concludes with an overview of recent neurophysiologic advances.

1. Magnetic compasses and magnetic maps

An animal with the ability to orient its movements with respect to the Earth's magnetic field is said to have a *magnetic compass sense*. Some animals, however, are able not only to maintain consistent headings, but also to return to a home area after being displaced to unfamiliar areas by researchers. To accomplish such a navigational feat, an animal needs more than a compass. It also needs to know where it is with respect to its goal, so that it can set an appropriate course. For this reason, certain animals have been hypothesized to possess an additional sense, called a *map sense*, which provides the ability to determine position relative to a destination.

In principle, the Earth's magnetic field provides a potential source of positional information that might be used in such a map sense. Several geomagnetic parameters, such as field intensity and the inclination of field lines relative to the Earth's surface (dip angle), vary across the Earth's surface (Figure 1). During the past decade, evidence has accumulated steadily that some animals can, indeed, derive positional information from features of the Earth's field. Sea turtles, newts, and honeybees have been shown to distinguish between different magnetic inclination angles or field strengths. Electrophysiologic recordings from birds and trout have also provided evidence for the presence of cells that respond to changes in field intensity (see below). An interesting possibility is that some species possess two separate magnetosensory systems: one for a magnetic compass, the other for a magnetic map. Each system may detect a different feature of the Earth's field, and each may have a different underlying physiologic mechanism.

2. Transduction hypotheses

Although diverse mechanisms have been proposed that might provide the physical basis for a magnetic sense in animals, most recent research has focused on three possibilities: magnetoreception mediated by (1) induction, (2) magnetic field-dependent chemical reactions, and (3) magnetite. The last possibility generally is divided into two cases: (a) the use of single-domain magnetite crystals and (b) superparamagnetism.

Electromagnetic induction. An electron moving through a uniform magnetic field experiences a force perpendicular to both its motion and the direction of the field. The magnitude of this force is proportional to the product of the charge, the velocity, and the sine of the angle between the motion and field vectors. Thus, if an electrically conductive bar moves through a magnetic field in any direction except parallel to the field lines, then electrons will migrate to one side of the bar. If the two sides of the bar are connected by a conducting medium that is stationary relative to the field, then the bar and the medium will form an electrical circuit, with the intensity and polarity of the current dependent on the speed and direction of the bar relative to the magnetic field. This principle, known as *electromagnetic induction*, has been invoked to explain how elasmobranch fish (sharks, skates, and rays) detect the Earth's magnetic field.

According to this hypothesis, structures on elasmobranchs known as *ampullae of Lorenzini* function as the conducting bar; the surrounding sea water functions as the motionless conducting medium, and the highly resistive and sensitive electroreceptors found at the end of the ampullae detect the voltage drop of the induced current. However, the electric fields induced by ocean currents complicate this simple model considerably, because the animal would have to determine which portion of the total field it experiences is attributable to its own motion and which is due to the motion of water. It has been suggested, but not proven, that this problem might be overcome if the critical directional information is derived instead from the oscillating electric field that results as the ampullae on the head move back and forth during the swimming movement of the fish.

Direct evidence that animals use electromagnetic induction to detect the Earth's magnetic field has not yet been obtained. Rays and sharks clearly possess an electric sense that is, in principle, sensitive enough to permit detection of the Earth's field, and rays have been conditioned successfully to move toward a specific magnetic direction within an enclosure. However, whether these rays actually relied on induction for magnetoreception, or instead used an alternative mechanism, remains to be determined.

Although sea water is highly conductive, fresh water and air are not. Thus, animals that inhabit fresh water or terrestrial environments cannot accomplish magnetoreception by induction in the same way that has been hypothesized for electrosensitive marine fish. While an induction-based system using an internal current loop (a closed circuit inside an animal) is theoretically possible, such a loop would need to rotate relative to the Earth's field and would also probably require a specialized internal transduction organ several millimeters in diameter. The semicircular canals have some of the necessary features, but no evidence exists that magnetoreception occurs in the inner ear, and no likely alternative structure or site has been found in any animal.

Chemical magnetoreception. Another hypothesized mechanism of magnetoreception involves chemical reactions that are affected by Earth-strength magnetic fields. Magnetic fields are known to influence particular types of chemical reactions by exerting a subtle influence on nuclear and electron spins. However, no biologic reactions have been identified that completely fulfill the special properties required. Among these are that the reactions must be slow (at least 1 microsecond duration) for a significant magnetic effect to be observed. In addition, the speed of the reaction and the interaction of the nuclear and electron spins involved must be related in specific ways. Finally, the initial reaction step must not affect the electron spin relationships, which is not true in general, but often occurs in photoexcitation (photon absorption). This last consideration suggests that if chemical magnetoreceptors exist, they may also be photoreceptors. Photoreceptors are an appealing location for chemical magnetoreception for another reason. In order for chemical magnetoreception to yield directional (compass) information, reactions must vary with the direction an animal faces. Thus, the molecules affected must presumably be held in a fixed orientation relative to the animal. The retina, with its numerous photoreceptors, provides an ordered array of receptor molecules that might potentially be exploited for this purpose.

Indirect support for a link between magnetoreception and photoreceptors has come from behavioral experiments indicating that the magnetic orientation behavior of birds, newts, and flies changed when the animals were tested under different wavelengths of light. No consistent pattern has yet emerged among species, but wavelength-dependent effects reported so far include random orientation and shifts of about 90 degrees in orientation direction. Although certain results, such as random orientation, might conceivably be explained as an effect of wavelength on an animal's motivation, 90-degree shifts in direction elicited by specific wavelengths are more challenging to explain as anything other than an effect on a magnetoreceptor system. Several studies have also suggested a link between magnetoreception and the pineal gland. A recent study with newts has revealed that a 90-degree shift in magnetic orientation direction that occurs when newts are tested under a specific wavelength of light can be elicited if the pineal complex, but not the eyes, are illuminated with light of the same wavelength.

If magnetoreception involves a modulation of the response of retinal photoreceptors to light, then magnetic orientation should not be able to occur in darkness. Birds and newts do, indeed, fail to orient magnetically in the dark, but several other animals, including sea turtles, mole rats, and certain insects, are capable of magnetic orientation in darkness. Thus, light dependence is not a universal feature of magnetic compasses.

Biogenic magnetite. The magnetic mineral magnetite (Fe_3O_4) has been detected in honeybees, salmon, trout, sea turtles, birds, and several other animals known to orient to the Earth's magnetic field. Most magnetite isolated from animals has been in the form of single-domain crystals. Such crystals are minute (~50 nm diameter), permanently magnetized bar magnets that twist into alignment with the Earth's magnetic field if allowed to rotate freely. This rotation could then exert pressure on secondary receptors (such as stretch receptors, hair cells, or mechanoreceptors), open ion channels, or act physically on the cell in some other fashion.

For magnetite crystals to function as magnetoreceptors in animals, the magnetite presumably needs to contact the nervous system. Although such a linkage has been hypothesized for more than two decades, direct anatomic evidence remains scarce. Trout olfactory cells containing magnetite are innervated by the ros V nerve, which has units that respond to magnetic stimuli. Magnetite has also been found in a region of the upper beak of the bobolink that is innervated by the ophthalmic nerve, which also responds to magnetic stimuli (Figure 2).

In some animals, magnetite crystals exist in a form that differs from that of single-domain crystals. Crystals of this second type are said to be *superparamagnetic*. They are smaller than single-domain particles and have different magnetic properties. One characteristic is that the magnetic axis of a superparamagnetic crystal tends to track the direction of a weak (Earth-strength) external field, whereas the magnetic axis of a single-domain crystal is fixed and stable under the same conditions. Superparamagnetic crystals generate fields strong enough to attract or repel adjacent crystals. Such intercristal interactions provide the basis for another possible transduction mechanism (Figure 3).

3. Neurobiologic research

Electrophysiologic and neuroanatomic research into the mechanisms underlying magnetic field detection has lagged behind behavioral work on magnetic orientation and theoretic considerations of possible transduction modes. One difficulty is that magnetic field lines permeate biologic tissue. Thus, primary magnetoreceptors need not contact the external environment and might plausibly exist almost anywhere within an animal's body. Magnetoreceptors might also be tiny and dispersed throughout a large volume of tissue, or the transduction process might occur as a set of chemical reactions, so that no obvious organ or structure devoted to magnetoreception necessarily exists. Moreover, accessory structures such as lenses, which focus sensory stimuli on receptors and are often conspicuous, are unlikely to have evolved for the magnetic sense because few biomaterials affect field lines. Identifying even the approximate locus of magnetoreception has thus proven challenging in many animals, and in no case have primary magnetoreceptors been identified with certainty. Nevertheless, significant progress toward understanding the neural mechanisms that underlie magnetic field detection has been made in several animals. Some of the most important advances are summarized below.

3.1. Birds

In the bobolink, a transequatorial migrant known to orient magnetically, magnetite exists in an area in the upper beak that is innervated by the ophthalmic branch of the trigeminal nerve. Specific neurons in the trigeminal ganglion, to which the ophthalmic nerve projects, respond to changes in vertical field intensity as small as about 0.5% of the Earth's field (see Figure 2). These cells have been hypothesized to function in a magnetic map sense system.

Additional electrophysiologic responses to magnetic fields have been detected in several parts of the avian nervous system that receive projections from the visual system. The nucleus of the basal optic root (nBOR) receives projections from retinal ganglion cells, and some neurons in the nBOR respond to directional changes in ambient magnetic fields. Similar responses have been observed in certain cells within the optic tectum. Responses to magnetic fields in both locations disappeared when the optic nerves were cut. These results suggest that one locus of magnetoreception in birds is in the visual system (perhaps in the photoreceptors).

Because responses to magnetic fields in the trigeminal system are apparently independent of those in the nBOR and optic tectum, however, the data also imply that two separate magnetoreceptor systems coexist in birds. Although the role that each system plays in bird navigation has not been clearly established, one possibility is that the system associated with the visual system provides directional (compass) information and might be based on chemical reactions similar to those previously described. A second set of receptors, based on magnetite and associated with branches of the trigeminal nerve, might be involved in detecting features of the Earth's field that can be used in assessing geographic (map) information.

3.2. Fishes

Several species of fishes can orient to the Earth's magnetic field. Single-domain magnetite crystals have been isolated from the ethmoid region of the skull in sockeye salmon; as in birds, this area is innervated by branches from the trigeminal nerve. Analyses of the trout olfactory lamellae using confocal microscopy have revealed cells that appear to contain magnetite, and the region of the trout nose containing these cells is innervated by the ros V nerve. Electrophysiologic recordings from the ros V have revealed units that respond to magnetic stimuli consisting of abrupt changes in field intensity. These findings have led to the hypothesis that magnetite-containing cells in the trout nose function as magnetoreceptors and relay information to the brain through the ros V nerve. Because reversals of field direction did not elicit responses in the magnetically responsive units of the ros V, the putative magnetite receptors have been hypothesized to detect field intensity, a parameter potentially useful in position-finding or "map" information.

3.3. Mole rats

Behavioral experiments have indicated that subterranean rodents known as *mole rats* have a magnetic compass sense and are able to orient magnetically in the dark. In addition, strong, pulsed magnetic fields have been shown to alter the magnetic direction toward which the rats orient. This finding is consistent with the hypothesis that single-domain magnetite crystals function in mole rat magnetoreception, because a strong magnetic field of very brief duration alters the direction of magnetization in such particles but would not be expected to have a lasting effect on chemical magnetoreception. Recent studies using the transcription factor c-Fos as a marker of neuronal activity have suggested that the superior colliculus of the mole rat contains neurons that are responsive to magnetic stimuli, although the locus of the primary magnetoreceptors has not yet been determined.

3.4. Molluscs

The marine mollusc *Tritonia diomedea* can orient to the Earth's magnetic field. This animal has large, individually identifiable neurons and a simple nervous system accessible to electrophysiologic studies. Intracellular recordings from two identifiable neurons (LPd5 and RPd5) in the brain of *Tritonia* indicate that these cells respond with enhanced electrical activity to changes in ambient Earth-strength magnetic fields. Although recent experiments suggest that the Pd5 neurons control or modulate the motor output of the magnetic orientation circuitry, these cells nevertheless represent the first individually identifiable neurons known to respond to Earth-strength magnetic stimuli. Thus, they provide a potential gateway into a neural circuit containing magnetoreceptors, and the relative simplicity of the *Tritonia* nervous system makes this mollusc a promising neuroethologic model animal for studies on the neural mechanisms underlying magnetic field detection.

4. See also

Animal migration: orientation and navigation

The magnetic sense in animal navigation

5. Further reading

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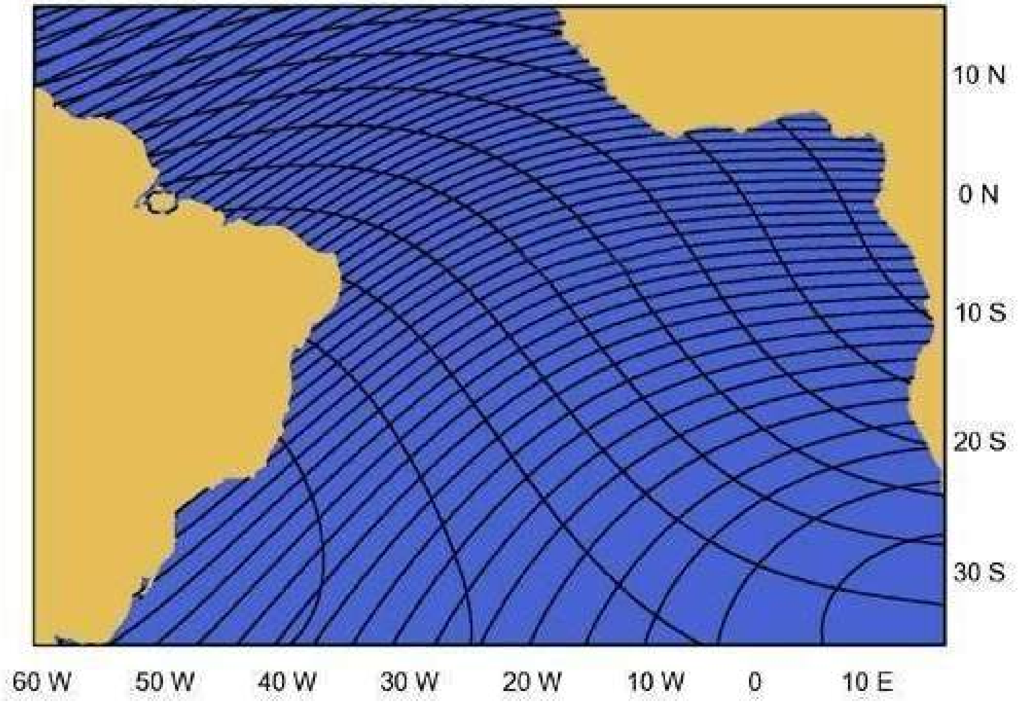

Figure 1. Lines of constant inclination (isoclinics) and constant field strength (isodynamics) in the southern Atlantic Ocean. Isoclinics in this region are aligned approximately northeast-southwest and represent differences in inclination of 2 degrees. Isodynamics in this region are aligned approximately northwest-southeast and represent differences in intensity of 1000 nanoTeslas (nT). The two geomagnetic features form a nonorthogonal grid that might, in principle, be used as a magnetic map by magneto-sensitive animals. Isoclinics and isodynamics were derived from the IGRF 1995 model.

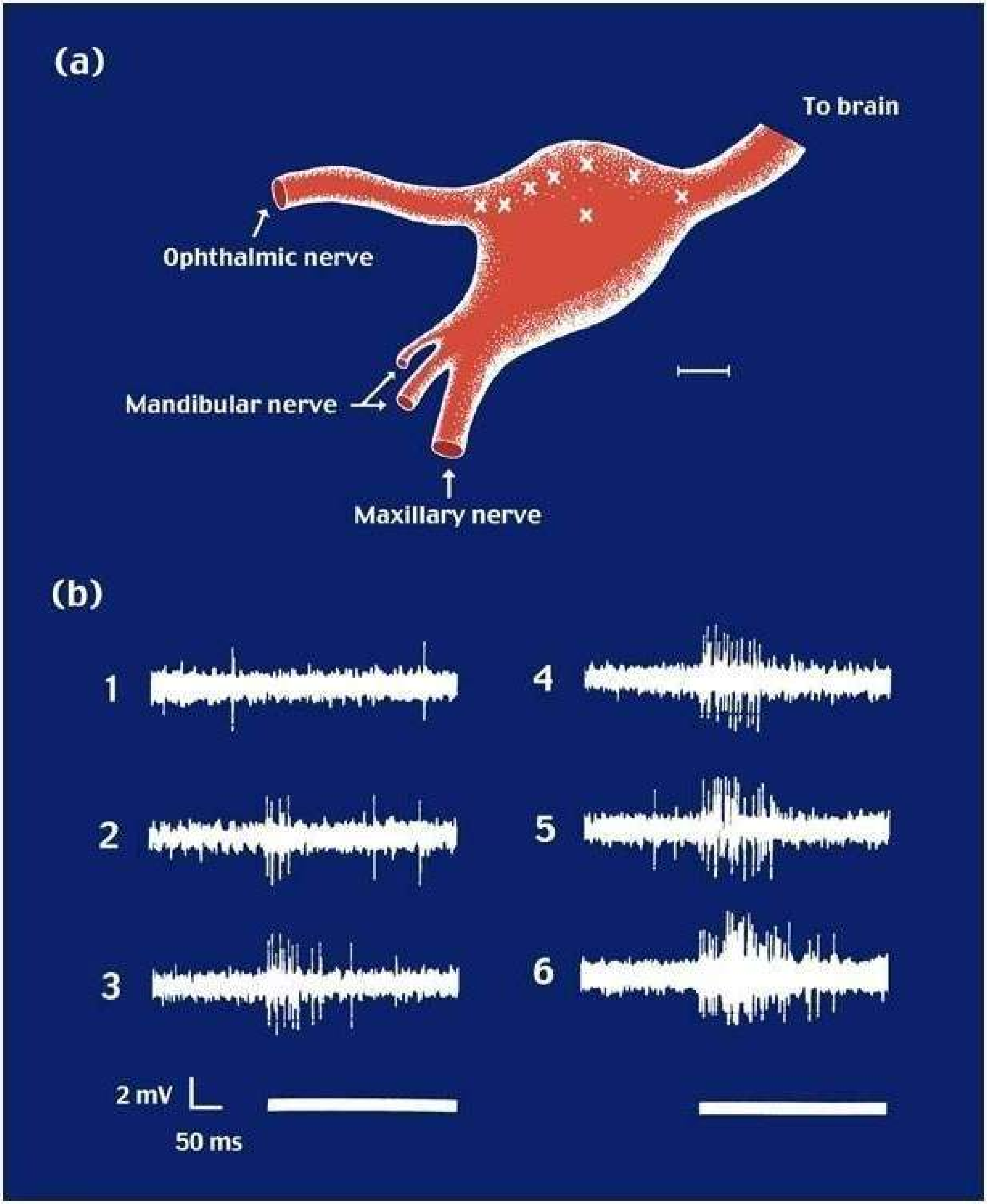

Figure 2. *Top*: A schematic drawing of the trigeminal ganglion of the bird *Dolichonyx oryzivorus* (the bobolink), showing the nerves and locations (marked by x's) of neurons responding to changes in ambient magnetic fields. *Bottom:* Recordings from one such ganglion cell in response to different changes in vertical magnetic field intensity. (1) Spontaneous activity. (2) Response to 200-nanoTesla (nT) change. (3) Response to 5000-nT change. (4) Response to 15,000-nT change. (5) Response to 25,000-nT change. (6) Response to 100,000-nT change. The Earth's field is approximately 50,000 nT. The stimulus onset is indicated by the bar below each series. Horizontal scale = 50 ms, vertical scale = 2 mv. From Semm and Beason (1991).

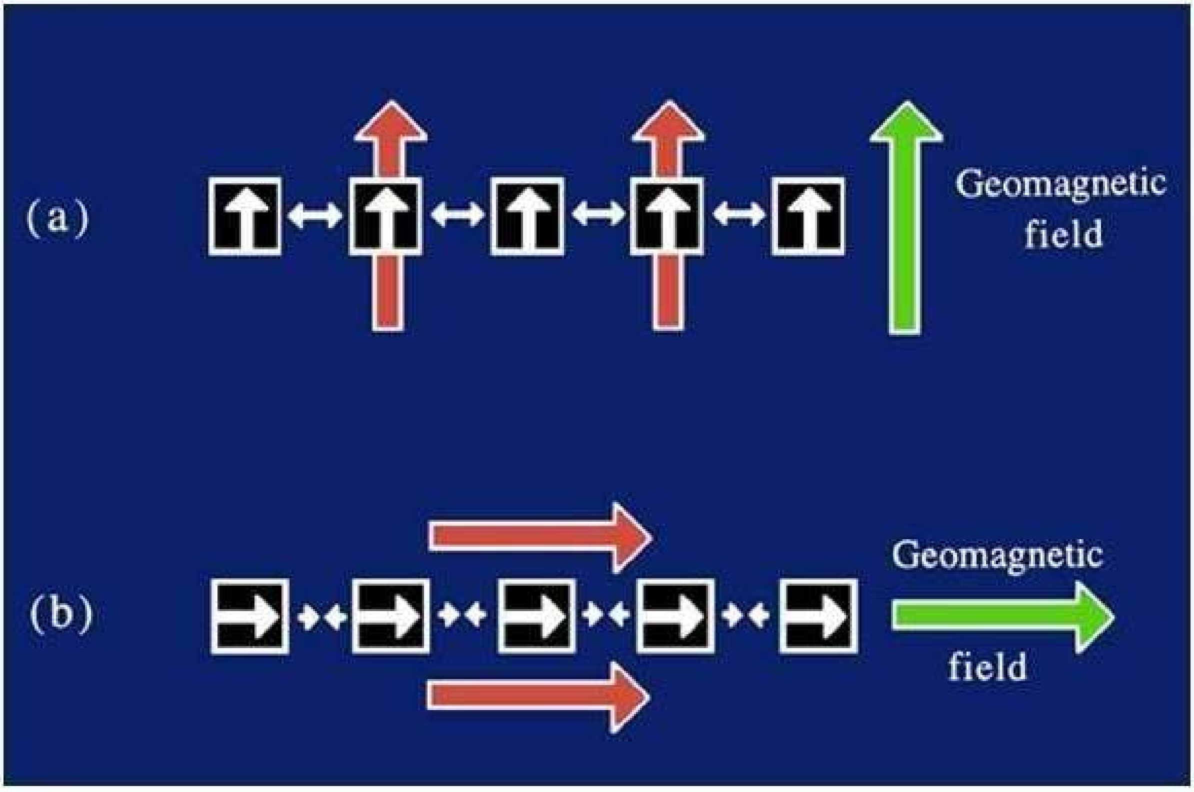

Figure 3. Diagram of a possible transduction process based on an array of interacting superparamagnetic magnetite crystals. Each box represents a crystal; the *arrow* inside it represents the direction of the field the crystal generates. Each crystal field tracks the direction of the Earth's field. In the top figure, the orientation of the geomagnetic field and consequent orientation of the crystal fields results in a configuration in which adjacent crystals repel each other. The crystals behave like a row of bar magnets aligned side by side; the resulting interactions stretch the tissue or membrane in which the crystals are embedded. When the animal (and the superparamagnetic array inside it) is oriented differently relative to the Earth's field, different interactions arise. A 90-degree change in ambient field direction relative to the array (*bottom figure*), for example, results in adjacent crystals attracting each other like a row of bar magnets aligned end-to-end. The supporting material is compressed. Expansion and contraction of this type could be detected by stretch receptors or mechanoreceptors, or could directly activate stretch-sensitive ion channels in cell membranes if the crystals existed there.