

The magnetic sense and its use in long-distance navigation by animals

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True navigation by animals is likely to depend on events occurring in the individual cells that detect magnetic fields. Minimum thresholds of detection, perception and 'interpretation' of magnetic field stimuli must be met if animals are to use a magnetic sense to navigate. Recent technological advances in animal tracking devices now make it possible to test predictions from models of navigation based on the use of variations in magnetic intensity.

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Abbreviations

T	Tesla
T	absolute temperature
μ	magnetic moment

Introduction

How animals navigate through apparently featureless environments with pinpoint accuracy, often over very long distances, remains one of the great, unsolved mysteries in biology. Until the past few decades, the mystery was compounded by the absence of robust experimental evidence for the existence of the 'magnetic sense' [1], which, for a long time, has been considered to be one of the primary environmental cues used for navigation (e.g. see [2]). Research concerning magnetic and other methods of long-distance navigation has been influenced greatly by the 'map and compass' hypothesis of Kramer [3], which states that animals must first determine their position relative to their goal (the 'map' step) and then set a course for the goal (the 'compass' step).

In this review, we focus on the use of the Earth's magnetic field to determine position, as the magnetic compasses of animals are relatively well understood [4]. First, we define minimum requirements for the use of any stimulus in position determination and identify position information in the Earth's magnetic field that meets these requirements. We then explore how such information is likely to be detected, analysed and subsequently used to determine position during navigation. In closing, we note that new animal tracking devices will greatly contribute to the experimental testing of hypotheses about magnetic navigation by animals.

What are the minimum requirements of environmental cues for position determination?

Two well-known experiments with homing pigeons demonstrate several fundamental elements of position determination by animals [5••]. First, pigeons wearing frosted contact lenses, which prevent form vision, return to within 0.5–2 km of their loft but do not enter it, presumably because they cannot see it [6]. Second, the initial orientation and homing performance of pigeons transported to release sites under general anaesthesia cannot be distinguished from that of untreated control birds [7].

These two experiments show that homing pigeons can determine their positions at release sites without needing to see landmarks and without any knowledge of their outward journeys to the release sites. The experiments also show that the birds can recognise when they are near their lofts without needing to see landmarks associated with them. The simplest explanation for these results is that, whenever they need to determine their current position, pigeons compare the values of environmental variables at their current position with the values of the same variables at the loft. Similar navigation strategies—whatever they may be—are presumably used by other homing and migrating animals and might have evolved at a relatively early stage in the evolution of the animal phyla.

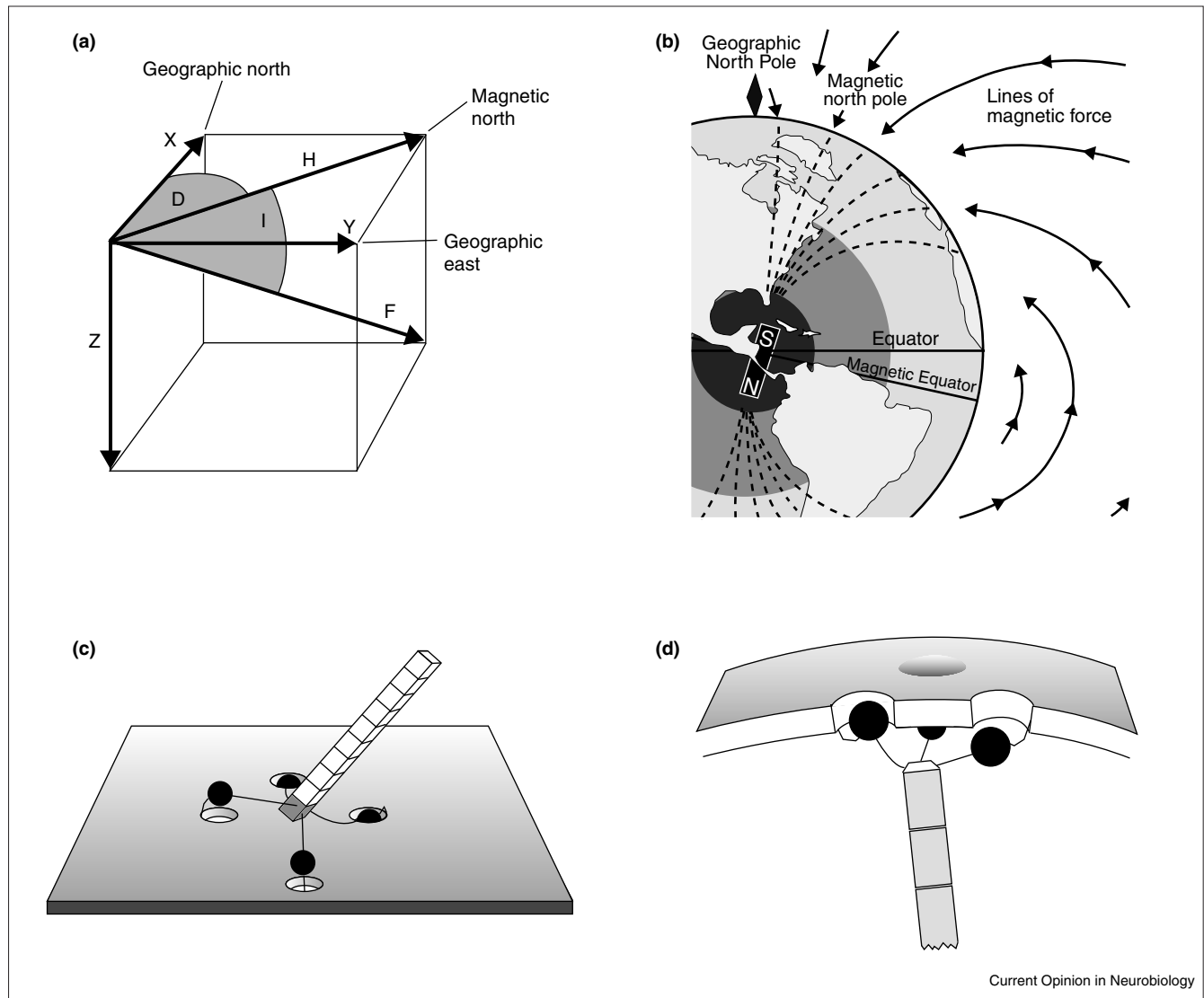
Thus, under the above experimental conditions, any environmental stimulus used to determine position within the portion of the biosphere used by a given species must provide consistent information, must vary systematically such that single points on the surface of the Earth can be identified uniquely, must be sufficiently stable over time to permit selection for the ability to detect and use the stimulus for navigation, and must be detected and used to determine position with sufficient resolution to meet the needs of the animal (e.g. about 1 km for homing pigeons).

How can the Earth's magnetic field environment be characterised?

Although no environmental stimulus is known to meet the first three criteria above absolutely, the Earth's magnetic field meets all of them subject to the constraint that an animal's ability to identify points on the surface of the Earth may be limited to very large areas rather than covering the whole surface of the Earth. (For a detailed discussion of the Earth's magnetic field and its relevance to life, see [8••].) Thus, the magnetic field provides consistent information about position throughout the biosphere.

At any point on the Earth's surface, the magnetic field can be described as a vector in three-dimensional space (Figure 1a). The field is derived from sources in the core and crust of the Earth. Dipole and non-dipole fields (the

Figure 1



The magnetic sense and its input stimulus, the Earth's magnetic field. **(a)** The elements of the total magnetic field vector (F) at the surface of the Earth. The total field vector can be resolved into components (arrows) in the X (north), Y (east) and Z (vertical) axes. The vector component in the horizontal plane (H) points in the direction of a handheld compass needle. The declination (D) is the angle between the H and X elements whereas the inclination (I) is the angle between the H and F elements of the field. **(b)** The main field of the Earth (produced in the core) contains both dipole and non-dipole components. The dipole component (represented by the bar magnet in the core of the Earth) is much greater than the non-dipole component (not shown). The field attributable to the magnetic dipole in the core is represented by field lines, which show how the intensity and inclination

of the field increase systematically between the magnetic equator and the magnetic poles. **(c,d)** Representations of possible magnetic field detection elements based on a chain of single-domain particles such as that found in the rainbow trout. In **(c)**, the chain is attached to a pivot embedded in the cell membrane and is linked by microtubule-like strands to mechanically gated ion channels in the membrane of the receptor cell. In **(d)**, the last few magnetosomes (membrane-enclosed crystals of magnetite) of the chain are shown linked by microtubule-like strands to mechanically gated ion channels on the membrane of the receptor cell. In both cases, the movement of the chain in response to the external magnetic field will cause the chain to pull one or more of the channels open, allowing ions to cross the membrane and change the receptor potential of the cell.

main field; Figure 1b) are produced by convection and eddy currents flowing in the molten core, whereas localised fields (also known as *anomalies*) result from magnetised rocks in the crust. The dipole in the core dominates (>90%) the observed field and causes the magnitude (intensity) and direction of the vector to vary systematically between the magnetic equator and pole (Figure 1b). Its

intensity varies from 25 to 65 micro-Tesla (μT), and the direction of the resulting vector varies between being parallel and perpendicular to the Earth's surface at the magnetic equator and poles, respectively. Variations in the dipole and non-dipole fields in the core therefore produce variations in the observable vector over distances that are mostly greater than 3000 km, whereas variations in the

vector produced by crustal rocks mostly occur over distances of less than 100 km.

Although the variations in the Earth's magnetic field described above provide very stable information about location that animals might use to navigate, extraction and use of that information is complicated by variations in the field that occur over a range of timescales. Slight variations in the field vector are caused over short timescales (milliseconds to hours) by electric currents in the ionosphere and in the Earth itself. These variations include both regular diurnal variation and magnetic 'storms' associated with the solar wind and solar flares, respectively, as well as short, erratic bursts produced by lightning. The components of the field produced in the core are also not fixed: they vary over a range of timescales to produce the secular variation (which is sufficient to require revision of magnetic maps at 5-year intervals) [8**].

Over much longer timescales (10^5 – 10^6 years), the dipole field may undergo polarity reversals, in which the magnetic poles switch hemispheres completely with the dipole component of the field vanishing for short periods (10^3 – 10^4 years). The fields produced by non-dipole components also wander over time but do not disappear when the dipole field reverses. Below, we address issues concerning how animals can detect, extract and use information about location from the external magnetic field stimulus.

How can animals detect magnetic field stimuli? Physical considerations

We have previously argued that only a magnetic field detection system that is based on chains of single-domain crystals of magnetite [9,10,11**,12**,13] can achieve the necessary sensitivity to determine position with the resolution shown by pigeons. The chains will have an energy of interaction with the external magnetic field of μB where μ is the magnetic moment of the chain and B is the intensity of the external field [9,10,11**]. This interaction energy will be opposed at the cellular level by the randomising effects of background thermal energy (kT), where k is the Boltzmann constant.

The behaviour of the chains in the external field obeys the Langevin function, which describes the alignment of extremely small magnetic particles in terms of the ratio of their magnetic energy to thermal energy ($\mu B/kT$). If a magnetic particle is free to rotate in all directions, its mean alignment will be in the direction of the external field vector, whereas the variance around the mean alignment will depend on the intensity of the external field. For example, in a weak or zero magnetic field, the axis of the chains will try to wander through all solid angles, whereas a strong external field will hold them fixed with little dispersion along the field direction. The dispersion, or variance in motion, therefore depends only on the scalar magnitude of the field intensity.

The magnetite chains in animals can thus be used to detect both the intensity and the direction of the magnetic field vector. Theoretical analyses show that the optimum magnetic-to-thermal energy ratios for determining direction and intensity are 2 and 6, respectively [11**], which leads to the prediction that magnetoreceptors specialised for detecting direction and intensity of the magnetic field should have different structures.

Possible magnetoreceptor structures

Figure 1c and d shows our conception of some simple receptor structures specialised for determining magnetic direction and intensity, respectively. In each structure, a chain of magnetite particles (such as that found in the rainbow trout [12**,13]) is linked by microtubule-like strands to a few mechanically gated ion channels in the membrane of a receptor cell.

The chain in the structure specialised for detection of magnetic field direction (Figure 1c) will be about 1.5 μm long and will measure the orientation of the chain axis relative to a fixed plane in the body. In response to the external field, the chain in Figure 1c will rotate around the pivot at its base within the range permitted by the microtubule-like strands. As it rotates, the chain will measure the angle between the axis of the chain and the plane of the membrane by pulling on the strands to open some of the ion channels to which the chain is coupled. The accuracy of the measurement of this angle will increase with the number of ion channels connected to the chain. As few as six such cells (one oriented in each of the principal directions relative to the three body axes [up, down, left, right, anterior, posterior]) would be needed to resolve the direction of the external field. Although a few such cells could provide anything from a flea to a whale with an accurate magnetic compass sense, the actual cells would be extraordinarily difficult to locate by histology (truly, a magnetic 'needle in the haystack').

In contrast, the chain in the structure specialised for detection of magnetic field intensity (Figure 1d) is not fixed to the membrane but is free to move over a limited range in any direction. Attachment of the microtubule-like strands to the tip of the chain means they will track the movement of the tip of the chain as it vibrates under the competing forces of the external field and thermal agitation. When the external field, the axis of the chain and the centre of the range of movement of the chain are closely aligned, the channels connected to the chain will be closed. Movement of the chain out of the centre of its range will be detected by one or more of the channels opening, as for the chain in Figure 1c.

In Figure 1d, however, the cell is sensitive to the vibration of the chain caused by thermal agitation. The variance of the opening and closing of the channels will be determined by the intensity of the external field. If the intensity of the external field is large, the variance of the chain's motion will be small, whereas if the intensity is low, the

Figure 2

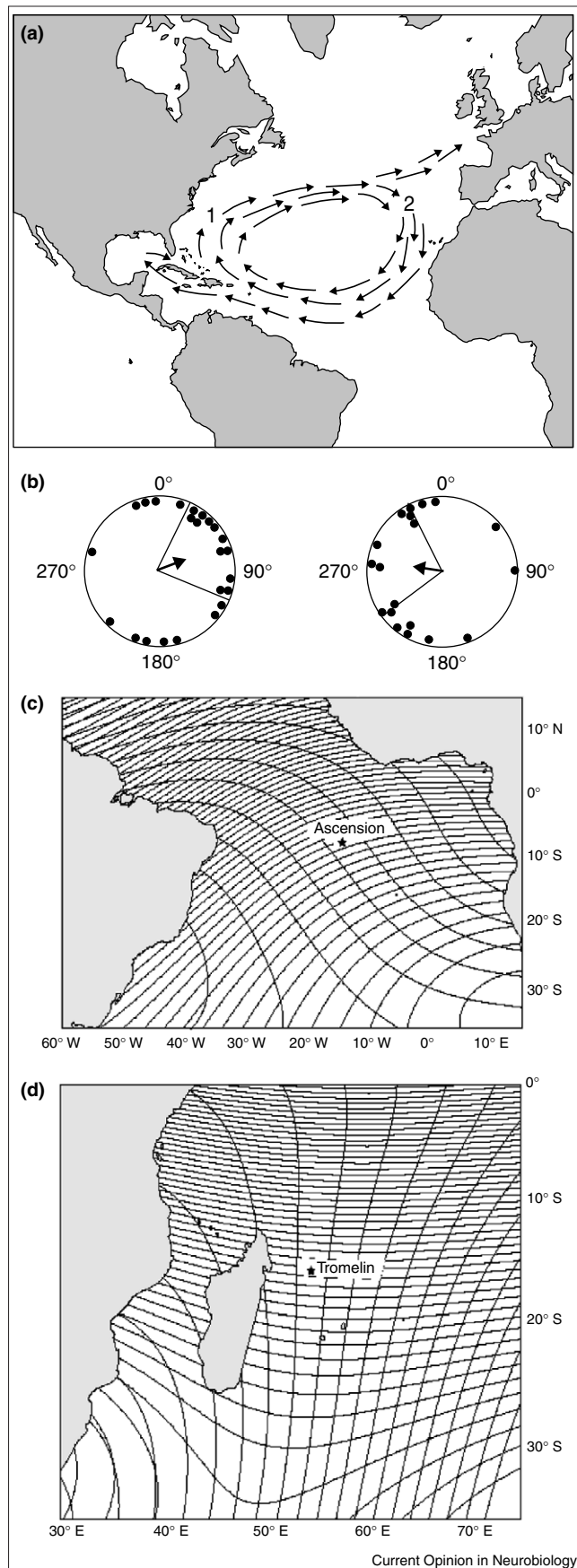


Figure 2 legend

Bicoordinate model of position determination in marine turtles (based on [37]; see also [32*,33–36]). **(a)** Generalised diagram of the North Atlantic gyre indicating locations (marked by '1' and '2') for which the magnetic field was simulated for the tests of orientation of hatchling loggerhead turtles shown in the orientation diagrams in (b). **(b)** Orientation of hatchling loggerheads placed in featureless arenas and presented with magnetic field intensities and inclinations simulating the locations shown in (a). Each dot at the periphery of the orientation diagrams represents the mean direction chosen by a single hatchling, whereas the arrow in each diagram gives the mean direction for each group of animals tested. The length of each arrow reflects the concentration of the directions chosen by individual animals around the mean direction. The two radial lines on either side of each arrow indicate confidence intervals for the mean vectors. **(c)** Contours of equal magnetic intensity and inclination in the oceanic region surrounding Ascension Island. The two parameters of the Earth's magnetic field form a grid that might, in principle, provide Ascension Island turtles with a bicoordinate position-finding system as they migrate between Ascension and the Brazilian coast. The contours of equal intensity are separated by 1000 nT and are aligned roughly northwest–southeast. The contours of equal inclination are separated by 2° and are aligned roughly northeast–southwest. **(d)** Contours of equal magnetic intensity and inclination in the Indian Ocean surrounding Tromelin Island plotted as in (c). The contours of equal intensity are separated by 1000 nT and the contours of equal inclination are separated by 1°.

variance of the chain's motion will be high. The resolution with which the detector can measure the variance of the chain's motion will increase with the number of ion channels connected to the chain. (Note that the translational force on the chain depends on the field gradient [not the intensity] and, for the geomagnetic field, the translational force is many orders of magnitude smaller than other forces acting in a cell.)

The hypothetical detector structures shown in Figure 1 are simple conjectures based on what we have now learnt about the arrangement of magnetite crystals in the candidate magnetoreceptor cells of the rainbow trout [12**,13]. The structures are only two of many different models (e.g. see [9,10]) for transducing the magnetic signal from single-domain magnetite into a mechanical signal. However, the receptor structures shown in Figure 1 would provide incomplete information about the direction and magnitude of the external field. The magnetite chains within individual receptor cells would be unable to align perfectly with fields outside their prescribed range of movements, which are defined by the lengths of the microtubule-like strands connecting the chains to the cell membranes. The direction and intensity of the external field could be determined, however, by integrating signals from many cells oriented in different directions. (For more detailed biophysical analyses of such structures in a viscous medium, see [14,15].)

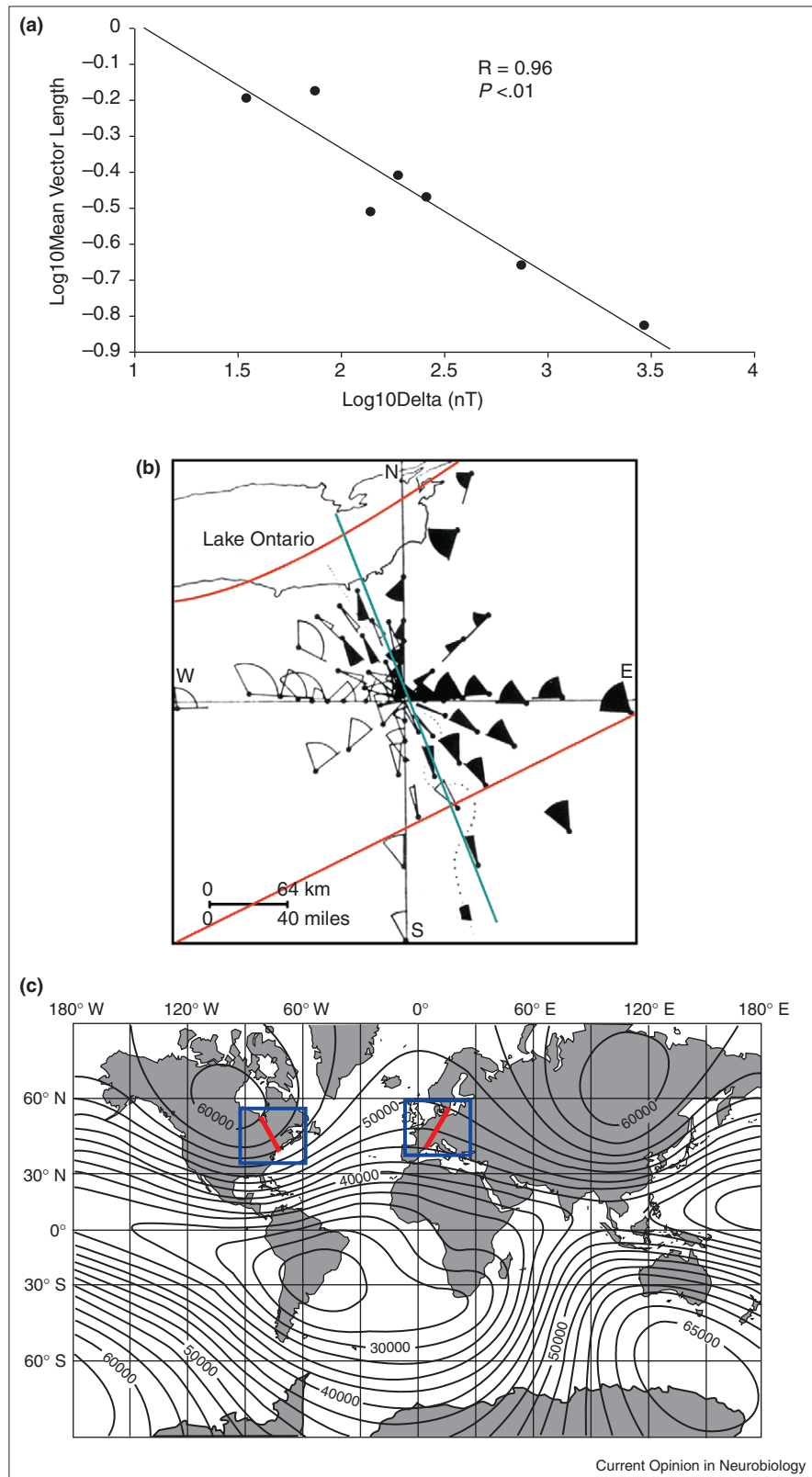
How might animals perceive the Earth's magnetic field?

A magnetoreceptor system using an array of magnetite-based magnetoreceptor cells oriented over all possible

Figure 3

Bi-coordinate model of position determination in homing pigeons on the basis of analyses of patterns of initial orientation errors made by homing pigeons. **(a)** Correlation between the accuracy of orientation of homing pigeons and the magnitude of disturbance caused by magnetic anomalies at release sites around lofts in Lincoln, Massachusetts USA (plotted from data in [26]). The graph plots the logarithm of the mean vector of vanishing bearings (values range between 0 [= $\log_{10}1.0$] and -1 [= $\log_{10}0.1$]) against the logarithm of the maximum change in the total intensity along a 1 km line from the release site in the direction towards the loft.

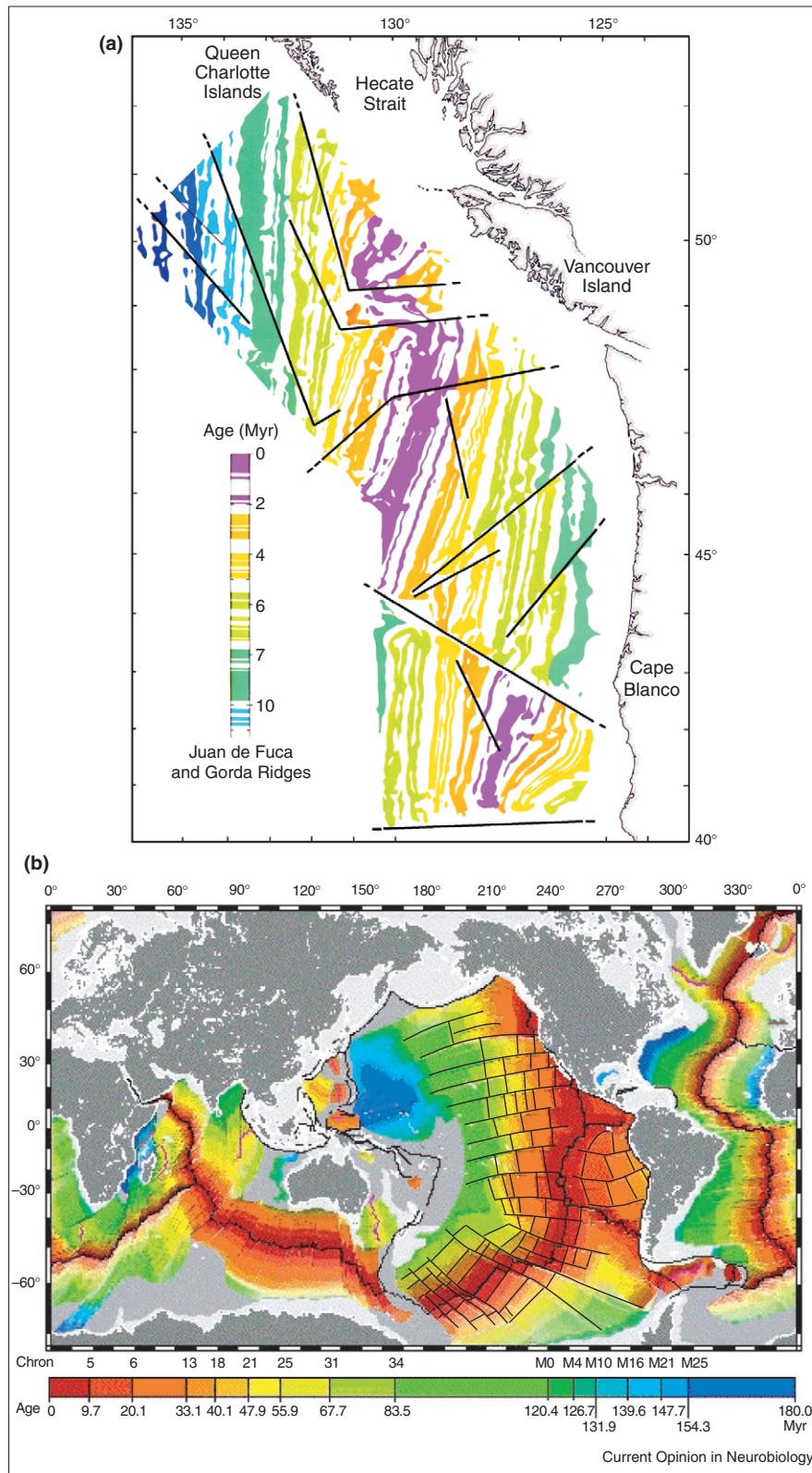
(b) Region-wide pattern of orientation errors made by pigeons homing to a loft at Cornell University, Ithaca, NY, USA. For each release site, a unit vector, which indicates the true direction to the loft (located at the intersection of the grid lines), and the actual mean vector bound an arc indicating the magnitude and the direction of the deviation of the mean vector for the birds from the true home direction. Clockwise and counter-clockwise errors are indicated by filled and open arcs respectively. The red lines show contours of equal intensity of the main magnetic field of the Earth and the blue line shows the direction of magnetic intensity slope of the main field through the loft. The blue line is correlated with the dashed line separating the clockwise and counter-clockwise errors made by the birds (Data from [50], figure modified from [40]). **(c)** Intensity of the main magnetic field of the Earth. Isodynamics (contours of equal intensity) show the pattern of change in magnetic intensity between the magnetic equatorial region and the magnetic poles. The lines separating the clockwise and counter-clockwise errors made by pigeons in the regions around the lofts at Cornell University (and also to Frankfurt University) are superimposed on the map to indicate the relationship between the direction of intensity slope and the contours of equal intensity. Inspection of the map shows that the direction of intensity slope varies systematically along isodynamics over very large areas (up to half a hemisphere) of the globe (Redrawn from [40]).



directions would permit a 'snapshot' reconstruction of the external magnetic field vector. The array could comprise

either detectors specialised for measuring direction (as in Figure 1c) and intensity (as in Figure 1d) separately, or

Figure 4



Systematic intersecting patterns of magnetic anomalies in the deep ocean that could be used to guide movement over long distances. (a) In the eastern north Pacific Ocean, magnetic lineations formed by seafloor spreading are shown in colour with different colours representing seafloor produced at different times (i.e. of different ages; From [47]). The magnetic lineations are intersected by many fracture zones (indicated by straight black lines) crossing the lineations. (b) Large-scale view of magnetic lineations, indicated by the ages (isochrons) of seafloor produced by spreading ridges in the North and South Pacific. The isochrons (which reflect the magnetic lineations) are oriented predominantly north-south and are aligned with the mid-ocean spreading ridges. These anomalies, which are called magnetic lineations, are intersected by anomalies aligned roughly east-west that are produced at fracture zones across the spreading ridges. The black lines superimposed on the isochrons show how the north-south trending isochrons are intersected by fracture zones to produce a block pattern of magnetic field information that could be detected and monitored by animals travelling long distances. (M numbers are the M-series magnetic lineations) Modified, with permission, from [51].

detectors that would allow extraction of both direction and intensity signals. The central tendency of the detected

signals from any of these possible detector systems would be a point estimate of the external field vector (direction

and magnitude, with the variance of the signals from the receptor cells depending on the intensity of the external field).

Measurement of the whole vector in this way would provide maximum sensitivity to changes in either of its components, that is, the direction and intensity of the external magnetic field. The sensitivity achieved by the system would depend on the inverse square root of both the length of time over which signals were integrated and on the number of receptor cells in the array [10,11••]. Depending on the integration time, relatively few receptor cells ($\ll 10^3$) would be required to measure magnetic field direction accurately, whereas a much larger number (10^4 – 10^6) of cells would be required to measure magnetic field intensity with the sensitivities that have been observed in different animals (see below). The amounts of single-domain magnetite that have been found in animals are more than enough to support the latter number of receptor cells and would permit sensitivities to changes in intensity as low as a few nanoTesla (nT) [10,11••].

From the magnetite-based magnetoreception hypothesis the testable predictions that can be made are that: first, the magnetic sense can be impaired by magnets attached near the location of the magnetoreceptors; and second, magnetoreceptor systems are sensitive enough to be used for accurate navigation over long distances [11••]. Attached magnets will impair magnetite-based magnetoreceptors by greatly increasing their magnetic to thermal energy ratios and by reducing the variance about the mean alignment of the magnetite chains. Attaching magnets near the location of the magnetoreceptors should therefore greatly reduce if not abolish the sensitivity of the magnetoreceptor system to changes in magnetic intensity and possibly direction. Orientation and conditioned responses to magnetic fields in the laboratory have been abolished by attaching magnets to hatchling sea turtles and honeybees [16,17]. A variety of less clear-cut effects of attached magnets have also been reported in field experiments with homing pigeons [18–22].

Experimental evidence is accumulating that the threshold sensitivity of some animals to magnetic fields is less than a few tens of nT, a shift of no more than a few parts in 10^4 in the background field of the Earth (approximately $50 \mu\text{T}$). Threshold sensitivities of about 25 nT and 200 nT respectively have been measured behaviourally in honeybees [23,24] and electrophysiologically in the bobolink, a bird that migrates between the northern and southern hemispheres [24]. Estimated sensitivities on the basis of field studies range between 10 nT and about 50 nT in homing pigeons [5••,25,26], sharks [27] and whales [28•–30]. These sensitivities are consistent with the possible use of the magnetic field for navigation over long distances that we consider next.

How might animals behaviourally 'interpret' magnetic stimuli?

The simplest mechanism for determining location on the surface of the Earth is a system of paired coordinates in

which two dimensions of one or more environmental stimuli vary systematically relative to each other. The ideal situation in which the stimulus dimensions vary at right angles to each other over the whole surface of the Earth, as do geographic latitude and longitude, has so far proved impossible to find. Here we focus on magnetic field parameters that are at least aligned at high angles to each other and could be used potentially to determine position over large areas of the Earth.

Although a variety of magnetic field parameters that might be used by animals to determine position have been suggested, none have yet found experimental support in field studies. Paired combinations of magnetic inclination, declination and intensity are based on laboratory responses by animals to magnetic field stimuli [31,32•,33–37]. For example, in separate tests Lohmann and his colleagues evaluated the responses in orientation arenas of hatchling sea turtles to both magnetic intensity and inclination. From these experiments, Lohmann proposed that inclination and intensity act as independent coordinates that could be used for position determination (Figure 2c). The models described above have been challenged on the grounds that the pairs of coordinates only vary at high angles to each other over areas that are both relatively small and ephemeral over evolutionary time [38,39]. The non-dipole anomalies that cause intensity, inclination and declination to be aligned at high angles to each other cover relatively small areas. These anomalies are also an important component of the secular variation and are quite mobile over evolutionary time [39]. Outside the non-dipole anomalies, the inclination and intensity of the Earth's magnetic field are highly correlated with each other because the dipole field is the dominant component of the observed magnetic field. Consequently, these aspects of the Earth's magnetic field are most unlikely to provide consistent information for position determination.

A second model of position determination (Figure 3) is based on systematic variations in the intensity and in the direction of intensity slope (the direction of maximum gradient in intensity) of the Earth's main field [40•,41]. The suggestion that intensity might form part of a bi-coordinate navigation system comes from the observation that homing pigeons are consistently disoriented when released at magnetic anomalies [26]. The degree of disorientation that occurs is also correlated with the magnitude of the localised disturbance in the Earth's magnetic field caused by the magnetic anomaly (Figure 3a). The suggestion that intensity slope might be a second coordinate comes from the observation that region-wide distributions of clockwise and counter-clockwise orientation errors made by homing pigeons are symmetrical about the line of intensity slope through the loft (Figure 3b; [5••,40•]). Total field intensity (a scalar not a vector quantity) can be measured at a point but measurement of the direction of intensity slope requires the animal to move over a spatial domain while keeping accurate track of observed field parameters

and its relative orientation (using other spatial reference systems such as the sun or star compasses) [42].

These two coordinates have the advantage that they are usually orthogonal, avoiding the temporal problems noted by Courtillot *et al.* [39], and so satisfy the first three criteria above for use of the magnetic field in position determination. In addition, these parameters will always be available, because non-dipole components of the field will produce systematic variations in the observed field even during periods where the dipole field of the Earth is reversing.

This model has been challenged [43] on the basis of the required accuracy of measurement of the two parameters (the fourth criterion above): variations in the coordinates are very small along both the temporal and spatial scales of movements made by individual animals [8••]; and the magnitudes of such variations are also embedded in magnetic noise resulting from fields produced by crustal rocks. It turns out, however, that extraction of an accurate, main-field vector signal from the total detected signal should not place unreasonable demands on magnetite-based magnetoreceptor systems.

For example, the rotation time of the magnetite chains observed in trout and illustrated in Figure 1 would be no more than a few tens of milliseconds, which means that an animal could essentially monitor the total field continuously. As an animal moves, it exposes itself to variations in the total magnetic field resulting from the fields produced in the core and crustal rocks. The field variations caused by crustal rocks are localised and comprise only a very small percentage of the total field observed at any point [8••]. Integrating measurements of the field over an area will therefore permit an animal to filter out signals produced by crustal rocks and to estimate the intensity of the underlying main field [42].

The accuracy of the estimate of the main field will then depend on the size of the area over which the sample is taken, together with areal extent and the amplitude of the variations in the magnetic field produced by the crustal rocks. It follows that position determination will require integration over a larger area and so a longer time at magnetically 'noisy' than at magnetically 'quiet' locations. Similarly, the variance in mean vanishing bearings of pigeons will be expected to increase under magnetically 'noisy' conditions during solar flares and the diurnal peak of the solar wind as compared with magnetically 'quiet' periods. All of these effects on pigeon orientation have been observed [21,22,25,26,44].

Another model for magnetic navigation exploits a regular pattern of magnetic anomalies originating from rocks in the deep ocean crust [28•,29] (Figure 4). Oceanic basalts become magnetised in the direction of the Earth's magnetic field at the time that they form from cooling magma rising to the surface of the deep ocean crust [8••]. These basalts

are produced continuously at mid-ocean spreading ridges and show an alternating pattern of linear magnetic anomalies, as the basalts are magnetised in opposing directions over successive magnetic field reversals. A second, systematic pattern of magnetic anomalies is aligned at high angles to the axes of the magnetic lineations. These anomalies are produced by the magnetisation of cooling magma that arose through fracture zones across the new crust produced by the spreading ridges (Figure 4a, b; [45–47]). In the Atlantic Ocean and the Pacific Ocean, the magnetic lineations are aligned roughly along a north–south axis and the fracture zones are aligned roughly east–west (Figure 4b).

Although these intersecting anomaly patterns are not present throughout the biosphere, they are distributed over the whole of the deep ocean, are stable over very long periods and remain present during reversals of the dipole field. Thus, these anomaly patterns could be used to guide migration over long distances [28•,29]. Such a system would require only that the magnetic sense is sensitive to small changes in the total intensity of the Earth's magnetic field. If animals use the anomalies as proposed, the model predicts that they should preferentially follow linear features that are consistent with their direction of migration.

Conclusions and prospects

True navigation by animals occurs over distances of up to thousands of kilometres, but it must be explained, first, in terms of the events that occur in sensory receptor cells (roughly 10 μm in diameter) and, second, in terms of the neural processing of signals originating from those receptor cells. At the level of the detector cell, the only information instantaneously available from the magnetic field at any point on the surface of the Earth is the total field vector.

Although we cannot determine as yet whether animals have separate magnetite-based magnetoreceptor cells that are specialised for magnetic field direction and intensity, we can predict that animals should be able to reconstruct the total field vector accurately and with high sensitivity. The hypothesised magnetoreceptors should also permit animals to derive information about other magnetic field parameters (such as field gradient) both through movement and by reference to other stable geophysical stimuli, such as gravity and the rotation axis of the Earth.

These predictions about the operation of the magnetoreceptor system can be tested electrophysiologically by searching for sensitivity to the total field vector and its components in the magnetoreceptor system. Intensity-dependent but not direction-dependent signals have been reported in primary afferent cells of the trigeminal nerve system of trout and bobolinks [12••,24]. The absence of direction-dependent signals might reflect the larger numbers of receptor cells needed for accurate measurement of magnetic intensity compared with magnetic direction. We suggest that much can be learned by locating and investigating responses to magnetic field parameters in the

centres of the brain that receive magnetic field information transmitted by the trigeminal nerve in vertebrates.

We would like to stress that up to now there is no experimental evidence directly supporting any of the models of position determination discussed above. However, our ability to make and test increasingly detailed predictions concerning the form and function of the magnetic sense from the primary properties of the Earth's magnetic field and from models of the use of the sense in navigation suggests we are at last beginning to understand this most mysterious of senses. The development of global positioning devices small enough to be carried by pigeons now makes it possible to construct detailed flight tracks during homing experiments [48,49]. Integration of the resulting flight-track data with geographical information systems now permits detailed analyses of the navigation behaviour of pigeons in relation to spatial variations in the Earth's magnetic field, as well as a variety of geophysical and other environmental variables. Exciting developments in the study of the magnetic sense and its use in navigation can be expected in the years ahead.

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