Structure, function, and use of the magnetic sense in animals (invited)

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The hypothesis that animals navigate magnetically is attractive because the earth’s magnetic field provides consistent information about position and direction in all environments through which animals travel. However, the hypothesis has been difficult to test because (i) the structure and function of the sense could not readily be analyzed in the laboratory and (ii) the effects of experimental treatments on behavior in the laboratory and field could not be reliably predicted. Our research is focused on the structure and function of the sense in rainbow trout and on applying the understanding gained in the laboratory to studies of navigation by homing pigeons. We have found iron-rich crystals (most likely single-domain magnetite) in candidate magnetoreceptor cells located within a discrete layer of sensory tissue in the nose of rainbow trout. The candidate receptor cells are closely associated with a branch of the trigeminal nerve that responds to changes in intensity but not direction of magnetic fields. In parallel work, we have developed a model of magnetic position determination in which pigeons derive magnetic analogues of geographic latitude and longitude from (i) the total intensity and (ii) the direction of the intensity slope of the earth’s magnetic field. Taken together with our other results, the model gives us confidence that a coherent understanding of the structure, function, and use of the magnetic sense in animals is now developing. © 2000 American Institute of Physics.

I. INTRODUCTION

The idea that animals use a magnetic sense to navigate was first proposed well over 100 years ago (e.g., Ref. 1). Animals are presumed to navigate over long distances by first determining their position with respect to a goal and then setting a course towards that goal. How animals determine direction when setting a course is well understood but how they might determine position has caused vigorous debate (e.g., Refs. 3–5). The geomagnetic field provides consistent directional and positional information in all environments through which animals travel but attempts to demonstrate use of the geomagnetic field to navigate have largely been inconclusive. Similarly, laboratory studies of the structure and function of the magnetic sense have achieved only limited success.

We have been studying the magnetic field detection system of rainbow trout and the potential use of the earth’s magnetic field for position determination by homing pigeons. We have found that single neurons in the trigeminal nerve (TN) respond to changes in the intensity of an imposed magnetic field and that fine branches of the nerve closely approach candidate magnetite-based magnetoreceptor cells in the nose of the trout. Responses by the trout to changes in magnetic intensity are consistent with a model of magnetic position determination derived from analyses of pigeon homing data. The model proposes that pigeons determine position using two coordinates based on the intensity of the earth’s magnetic field. These exciting results provide substantial support for the hypothesis that many animals have a magnetic sense that they use to navigate over long distances.

II. NEURAL RESPONSES TO MAGNETIC FIELD INTENSITY

We recorded from both sensory nerves and the brain of the rainbow trout but found positive responses to magnetic field stimuli only in the branch of the TN that passes behind the eye to innervate the nose and anterior skull. We used a series of search stimuli presented as uniform square waves that changed direction, intensity, or both direction and intensity of the magnetic field [represented by B in Fig. 1(b)] around the head of experimental fish. The stimuli were produced by (i) subtracting, (ii) adding, and (iii) switching between subtracting and adding 50 μT to the background field (25 μT) in the experimental tank. Thus, the first search stimulus (designated SS1) reversed the magnetic field direction in the tank but did not change intensity whereas the second stimulus (SS2) trebled the intensity [represented as B:3B in Fig. 1(b)] without changing field direction in the tank. Our third stimulus (SS3) switched between a field with...
the same intensity but reversed direction relative to the background field and a field with the same direction but three times the intensity of the background field.

The responsive nerve fibers (or units) in the TN exhibited regular firing patterns except during the transient responses to a change in intensity but not direction of the magnetic field around the head of the fish. The top trace in Fig. 1(a) shows the pattern of action potentials (or spikes) traveling along the nerve toward the brain in the period around the onset of a step change in magnetic intensity (SS2), which is shown in the bottom trace and reflected in the electrical artifacts induced in the record of the nerve’s activity.

The top left panel in Fig. 1(b) shows a post-stimulus time histogram (PSTH) produced by binning the responses of the unit in Fig. 1(a) to 128 presentations of SS2. The PSTH gives a picture of the average activity of the unit over time immediately following the onset of the stimulus. The transient increase in firing rate has a latency and duration (the first point following the stimulus step and the time period during which the firing rate was more than two standard deviations above the mean for the unit) of 20 and 100 ms, respectively, reaching a peak firing rate about seven times the average firing rate in the period just before the stimulus onset [Fig. 1(a)]. Response by this and a second unit to the same change in intensity presented at 0.5 and 1 Hz is shown in Fig. 1(b). The latency and time course of the responses by the units were similar but the peak amplitudes of the responses decreased and increased respectively when the rate at which SS2 was presented increased from 0.5 to 1 Hz. In addition to these responses to the onsets of SS2, we also observed responses to the onsets and offsets of SS3 but never to either the onsets or the offsets of SS1.

The short latency of the responses recorded here implies that the recording site (behind the eye) is located very close to the site of magnetic field detection. The conduction velocity for action potentials in sensory nerve fibers such as those recorded here is on the order of 0.5–1 m/s, which suggests the recording site is no more than about 0.5 cm from the detector. There remains, however, the possibility that the electrical artifact due to induction in the recording circuit may be stimulating the nerves directly. This possibility can be excluded because the artifact due, for example, to the onset of SS1 was identical to the artifact due to the offset of SS2 and vice versa. Thus, because the units responded to the onset of SS2 but not to the offset of SS1, we were able to distinguish between response to the magnetic stimulus and response to the associated artifact. In addition, only a very small proportion of the units responded whereas electrical induction should affect all units in the TN in the same way. We can therefore be confident that we have recorded from magnetically responsive units that are located close to the site of magnetic field detection in the trout.

III. CANDIDATE MAGNETORECEPTOR CELLS

Demonstrating a magnetite-based detection mechanism depends first on identification of magnetite associated with candidate magnetoreceptor cells. We have used the crystal properties of magnetite to detect the particles in the confocal laser scanning microscope (CLSM) despite their extremely small size (50 nm) and in the transmission electron microscope (TEM), where they will not be obvious amongst the large variety of electron dense material in cells treated with heavy metal stains.
showed that the crystal was iron-rich and almost identical in size and shape to the magnetite in the bacteria. Bright spots observed in reflection mode coincide with the location of the magnetotactic bacteria cells viewed in transmitted light modes. Bright spots in the CLSM study revealed intensity and dimensions to the magnetite in the bacteria. The crystals gave reflections of similar or three being detected at a time within the volume containing the reflecting particles are 10–15 \( \mu \text{m} \) in length, have a distinctive shape and are consistently located near the basal lamina of the olfactory epithelium [Fig. 2(b)]. Cells containing reflections are relatively rare, with never more than two or three being detected at a time within the volume \((\approx 250 \mu \text{m}^3)\) sampled by the CLSM at the magnification required to detect the reflections. The crystals gave reflections of similar intensity and dimensions to the magnetite in the bacteria. Serial thin sections through one of the reflections revealed the crystal shown in Fig. 2(c) in bright field (left arrow) and dark field (center arrow) TEM. Further TEM analysis showed that the crystal was iron-rich [right arrow in Fig. 2(d)] and almost identical in size (length 50 nm) and shape to single-domain magnetite extracted from sockeye salmon.

The distinctive shape and consistent location of the cells that contain the reflectances together with the similarity of the reflectances in the trout to magnetite reflectances in the bacteria lead us to view the reflectance-containing cells as candidate magnetoreceptors. We are encouraged that the TEM study showed the similarity (size, shape, and presence of iron) of the crystal shown in Fig. 2(c) and 2(d) to magnetite extracted from sockeye salmon. The crystal was likely to be part of a larger group such as a chain of crystals, as is the case in the magnetotactic bacteria, because it was too small on its own to produce a reflection that could be detected at the light microscope level.

### IV. ASSOCIATION BETWEEN THE NERVE AND CANDIDATE MAGNETORECEPTOR CELLS

In the CLSM, the chains of magnetite in locally collected magnetotactic bacteria reflected the laser light to produce bright spots that are clearly associated with the bacterial cells when viewed in transmitted light [Fig. 2(a)]. A search through rainbow trout heads embedded in both JB4 and Epon resins using the CLSM revealed crystalline material in a discrete cell layer within the nose of the trout. The cells containing the reflecting particles are 10–15 \( \mu \text{m} \) in length, have a distinctive shape and are consistently located near the basal lamina of the olfactory lamella (see Ref. 24). The crystal was likely to be part of a larger group such as a chain of crystals, as is the case in the magnetotactic bacteria, because it was too small on its own to produce a reflection that could be detected at the light microscope level.

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If the cells in the olfactory lamellae do indeed contain magnetite used in magnetoreception, it is reasonable to predict that the magnetically responsive nerve should be linked to the candidate receptor cells. We have used serial histological sections and Di-I, a fluorescent lipophilic dye, to trace branches of the TN from the site where electrophysiological recordings of responses to magnetic field stimulation were made to the endings of the individual nerve cells (see Fig. 3). Di-I migrated in both anterograde and retrograde directions along both myelinated and unmyelinated fibres in the TN. En route to the brain, it joined other branches of the TN and ended in cell bodies that make up part of the anterior ganglion. From the ganglion, the labeled nerve tracts entered the anterior dorsal area of the medulla oblongata. Anterior to the eye, the TN coalesces with the anterior lateral line nerve
treated as a point detector capable of detecting only the direction and magnitude (intensity) of the magnetic field vector at any point in space. If we ignore time-varying components, the intensity of the field \( B_{\text{OBS}} \) as observed by the bird can be expressed as

\[
B_{\text{OBS}} = B_{\text{TOT}} + B_{\text{ANOM}} + \epsilon,
\]

where \( B_{\text{TOT}} \) is the field produced in the earth’s core, \( B_{\text{ANOM}} \) is the residual field due to crustal rocks, and \( \epsilon \) is the measurement error due to the bird’s detector.

Among the components of \( B_{\text{OBS}} \) in Eq. (1), \( B_{\text{TOT}} \) is relatively large but slowly varying whereas \( B_{\text{ANOM}} \) is relatively small but rapidly varying. \( B_{\text{TOT}} \) increases by 1–10 nT/km from about 25 to 60–70 \( \mu \text{T} \) between the magnetic equator and the magnetic poles, respectively. Contours of equal intensity for \( B_{\text{TOT}} \) mostly course approximately east-west, particularly in the mid-latitudes. \( B_{\text{ANOM}} \) varies over a much smaller range (generally less than 1000 nT) but can vary rapidly over short distances (tens to hundreds of nT/km) compared with \( B_{\text{TOT}} \). The error, \( \epsilon \), in Eq. (1) is likely to be small (perhaps one to a few tens of nT; 7, 14) and to vary at random.

Thus, \( B_{\text{TOT}} \) varies systematically over the surface of the earth and could act as an analogue of geographic latitude in a bicoordinate navigation system. The second coordinate in a bicoordinate navigation system using \( B_{\text{TOT}} \) should ideally vary systematically along the isodynamics for \( B_{\text{TOT}} \). The nature of such a coordinate has hitherto been the key obstacle to understanding the potential contribution of \( B_{\text{TOT}} \) to pigeon navigation. One possible source of the second coordinate is considered next.

C. Identifying the second coordinate

Region-wide patterns in departure directions are evident for pigeons homing to lofts in both the USA and Europe. Figures 4(a) and 4(b) show that clockwise and counterclockwise release site biases (deviations of mean departure directions from the true home directions) are symmetrically distributed around lofts at Ithaca, New York, USA, and Frankfurt am Main, Germany (indicated by the heavy lines running approximately NNW-SSE and NNE-SSW through the lofts at Ithaca in the U.S.A. and Frankfurt in Germany).

The similarity of these regional patterns in release site biases suggests they reflect large scale variations in the environment rather than the effects of local variables such as visual landmarks. The axes separating clockwise and counterclockwise release site biases for Ithaca and Frankfurt intersect isodynamics (dashed lines) in \( B_{\text{TOT}} \) in the regions surrounding the lofts at angles approaching 90°, or close to the lines of intensity slope (the normal to the isodynamics) on the scale of these maps. The similar association between the directions of the axes through the lofts and the lines of intensity slope in the regions around the lofts suggests that the distribution of release site biases around a loft is systematically related to the direction of intensity slope.

It turns out that the isodynamics in \( B_{\text{TOT}} \) rotate systematically around the magnetic poles in the mid-latitudes and the direction in which the steepest intensity slope lies...
therefore varies systematically as the isodynamics rotate. Points on the surface of the earth can thus be defined by vectors comprising $B_{TOT}$ and the direction in which the field slope lies. It is therefore proposed that homing pigeons use $B_{OBS}$ in Eq. (1) and the direction of intensity slope $\text{DIR}(B'_{OBS})_{\text{MAX}}$ as vector coordinates for determining position.

The model requires that pigeons have vector coordinate information specific to both the loft and release site. The birds have ample opportunity to learn the vector coordinates for the loft and any patterns of variation in the vector components over the distances from the loft covered during exercise and training flights. The model then proposes that the pigeons determine the vector for a release site in the few

FIG. 4. Region-wide patterns of release-site biases in the homing orientation of pigeons. (a) Ithaca, New York. For each release site, a unit vector indicates the true direction to the loft (located at the intersection of the grid lines) while the actual mean vector for the birds is shown. An arc connects the two vectors, indicating the direction of the release-site bias at each site. Clockwise biases are shown in black, counterclockwise biases in white. The heavy solid line running through the loft indicates the approximate axis of symmetry for the distribution of release site biases about the loft as well as the axis along which orientation is most accurate (modified from 22). (b) Distributions of release-site biases for pigeons homing to a loft (located at the intersection of the heavy lines) at Frankfurt a.M., Germany. Stippled circles indicate clockwise biases, hatched circles indicate counterclockwise biases. Circles with dashed outlines indicate mean vectors in the semicircle away from home. Circles with heavy outlines indicate sites where birds were not significantly oriented. The heavy solid line running NNE-SSW through the loft indicates the approximate axis of symmetry for the distribution of release site biases about the loft (modified from 22). The dashed lines in (a) and (b) are isodynamics for the magnetic field produced in the earth’s core in the vicinity of the loft. (c) Geometric subtraction of position vectors for a loft and release site located in an area of uniformly varying magnetic field. The release site (RS) and “home” (H) are located at the origins of two vectors (arrows) that intersect at I. Subtracting the home vector from the release site vector permits estimation of the length and direction of the unknown vector (labeled ‘?’) for the direct course from the release site to the home loft. (d) Example of how the effect of a magnetic anomaly on $B_{OBS}$ might affect position determination by homing pigeons and produce a release site bias. For clarity, the arrows indicate the directions but not the magnitudes of the position vectors. The true release site (TRS) is located within the positive anomaly. The contribution to $B_{OBS}$ due to the anomaly leads to the apparent release site (ARS) being located some distance from the true location. The anomaly thus causes a difference between the apparent home course (broken line labeled AHC) and the true home course (dotted line labeled THC). $\text{DIR}(B'_{OBS})_{\text{MAX}}$ is assumed to be unchanged. Curved lines indicate isodynamics in (c) and (d).
minutes they spend flying around at the site before setting off for home. Subtraction of the vectors for the release site and the loft will determine their positions relative to each other and permit the birds to set a compass course from the release site to the loft.

Figures 4(c) and 4(d) illustrate how the model might operate under conditions where $B_{\text{OBS}}$ is controlled by either $B_{\text{TOT}}$ or $B_{\text{ANOM}}$ in Eq. (1). Figure 4(c) shows a loft ($H$) and a release site ($RS$) located at points with different values of $B_{\text{TOT}}$ and $\text{DIR}(B_{\text{OBS}}')_{\text{MAX}}$ in a uniformly varying field. Also shown is a geometric treatment in which the release site vector is compounded with the vector at $I$. Negation of the vector for the loft followed by summation with the vector for the release site will provide a course vector for the distance and direction [vector labeled ‘?’ in Fig. 4(c)] from the release site to the loft.

Figure 4(d) illustrates the case where a loft is located in a magnetically quiet region while a release site is located in a positive anomaly. When only $B_{\text{OBS}}$ at the release site differs from the surrounding region, the release site will appear to be displaced up the region-wide intensity slope to an apparent release site with an apparent home direction (a release site bias) that is different from the true home direction. When both $B_{\text{OBS}}$ and $\text{DIR}(B_{\text{OBS}}')_{\text{MAX}}$ for a release site differ from their values in the surrounding region, the release site will appear to have been displaced along both the intensity slope and the isodynamic. These conditions will make position determination more difficult and may be responsible for the disorientation observed at strong anomalies (e.g., Refs. 13 and 15).

V. DISCUSSION

We suggest that a magnetite-based magnetoreceptor system provides a general mechanism for navigation over long distances by animals. The environmental heterogeneity and seasonal variations in incident solar radiation that create the conditions for homing and migration, and so of accurate navigation, to occur have existed throughout the history of life on earth. The earth’s magnetic field alone provides consistent information about both position and direction in all environments through which animals travel, particularly in the marine environments in which homing and migration probably first occurred. It therefore seems reasonable to hypothesise that consistent selection has resulted in a general mechanism used by widely divergent taxa to navigate over long distances and that a magnetic sense is perhaps the most likely sense to be used for such a purpose.

A magnetite-based magnetoreceptor mechanism is certainly likely to be widespread among animals. Our discovery of the detector, neural and behavioral components of the magnetic sense in the trout suggests that the magnetic sense of vertebrates depends on magnetite located in the nose. Similar results have been obtained for honeybees, which cannot respond to magnetic fields when magnetic wires are placed over magnetite located in their upper abdomen. What cannot be resolved is whether magnetite-based magnetoreception was present in the last common ancestor or has since evolved independently in the different animal groups that respond to magnetic fields.

The accuracy with which some animals navigate requires sensitivity to changes in magnetic intensity that seemed extremely unlikely until the discovery of magnetite in animals. Theoretical analyses then quickly showed that a magnetite-based magnetoreceptor mechanism could readily account for a threshold as low as 10 nT, equivalent to a change of about 2–5 km in magnetic ‘latitude.’ Our model for the use of the earth’s magnetic field in navigation is consistent with both the observed behavioral responses to magnetic fields by animals and with the models of magnetic field detection based on single-domain magnetite. Thus, it now appears that a coherent understanding of the structure, function and use of the magnetic sense in navigation is developing and exciting results can be expected as the details of magnetite-based magnetoreception are explored.

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