

Walker, M.M., Diebel, C.E. & Kirschvink, J.L., "Chapter 8: Magnetoreception". In: Toshiaki Hara and Barbara Zielinski (eds.), *Sensory Systems Neuroscience: Fish Physiology*, v.25, Elsevier Inc, pp.335-374.

8

MAGNETORECEPTION

MICHAEL M. WALKER
CAROL E. DIEBEL
JOSEPH L. KIRSCHVINK

1. Introduction
2. Introduction to Magnetic Field Stimuli
 - 2.1. The Earth's Magnetic Field
 - 2.2. Magnetic Fields as Experimental Stimuli in the Laboratory
3. How Can Magnetic Fields Be Detected?
 - 3.1. Magnetic Field Detection by Electrical Induction
 - 3.2. Magnetic Field Detection Based on Magnetite
4. Structure of Candidate Magnetite-Based Magnetoreceptors
5. Behavioral Responses to Magnetic Fields in the Laboratory
 - 5.1. Orientation Responses to Magnetic Field Direction
 - 5.2. Conditioned Responses to Spatial Variations in Magnetic Field Intensity
 - 5.3. Other Experiments Using Conditioned Responses
6. Neural Responses to Magnetic Fields in the Laboratory
 - 6.1. Induced Electrical Signals in Ampullary Electroreceptors
 - 6.2. Responses in the Trigeminal Nerve of Teleost Fish
7. Neuroanatomy
8. Use of the Magnetic Sense in Navigation
 - 8.1. Constraints on Theory and Experiment in the Study of Navigation by Fish
 - 8.2. Hypotheses on Magnetic Navigation Mechanisms
 - 8.3. Developing Experimental Approaches to Navigation
9. What is Known About the Navigational Abilities of Fish?
10. Concluding Remarks

1. INTRODUCTION

The opportunity to participate in both the discovery and the analysis of the structure, function, and use of a completely new sense is a rare event in the biological sciences (Bullock and Szabo, 1986). In the fishes, such an opportunity has occurred not once but twice in recent decades. The electric

sense was identified in the elasmobranch and teleost fishes during the 1960s (Murray, 1960; Dijkgraaf and Kalmijn, 1962; Kalmijn, 1966; von der Emde, this volume). Despite having been described nearly three centuries earlier, the function of the ampullae of Lorenzini was not conclusively identified until the work of Dijkgraaf and Kalmijn (1962), and Kalmijn (1966, 1982) in particular. Electrophysiological studies subsequently analyzed in detail the detection of electric fields via the electroreceptor cells located in the ampullae of Lorenzini of the elasmobranch fishes (Clusin and Bennett, 1979a,b) and in the tuberous electroreceptors of some freshwater teleost fishes (von der Emde, this volume).

In contrast with the electric sense, the existence of the magnetic sense was proposed a century before there was any experimental evidence for its existence (Wiltschko and Wiltschko, 1995). The original hypothesis that animals would have a magnetic sense was based on recognition that the Earth's magnetic field could be used by animals to navigate over long distances during homing and migration (Viguer, 1882). In contrast with the electric sense, the existence of the magnetic sense proved difficult to demonstrate experimentally and it is only in recent decades that the existence of the magnetic sense has been widely accepted. Thus, the first experimental evidence for the existence of the magnetic sense in the fishes was not reported until the work of Kalmijn (1978) and Quinn (1980), more than a decade after the electrical sense of elasmobranch fishes had been demonstrated at the behavioral and electrophysiological levels.

Vigorous debates continue, however, over the mechanisms for detection of magnetic fields and how animals might actually use the Earth's magnetic field to guide movement. In the fishes, there are at least two mechanisms proposed for magnetic field detection. Proponents of both hypotheses can clearly identify a detector mechanism located in specific receptor cells, afferent nerves that respond to magnetic field stimuli, and behavioral responses that permit psychophysical analysis of the capacities of the sense. Although many students of animal navigation also think the hypothesis that animals use the Earth's magnetic field in navigation is reasonable, there is as yet very little robust evidence in support of the hypothesis. This chapter begins by briefly characterizing the magnetic field as a stimulus in both the field and the laboratory. The central questions about the magnetic sense that are then addressed in the chapter are as follows:

- ! What is the evidence that animals, in this case fish, have a magnetic sense?
- ! What is the evidence that animals use a magnetic sense for navigation?
- ! What are the priorities for future research?

2. INTRODUCTION TO MAGNETIC FIELD STIMULI

2.1. The Earth's Magnetic Field

Along with providing the information about direction with which we are all familiar, the Earth's magnetic field provides two potential sources of information about location. These are as follows:

- ! Systematic variation in the intensity (or strength) and direction of the field generated in the Earth's core that might be translated by an animal's magnetoreceptor system into useful information for navigation over very large areas.
- ! Localized variation in intensity due to magnetic sources in the Earth's crust (e.g., magnetite in basalt, iron ore deposits) that could be used as magnetic landmarks or to identify specific locations such as seamounts.

At any point on the Earth's surface, the observed magnetic field can be described as a vector in three-dimensional space (Figure 8.1) (Skiles, 1985). The total field vector (TFV) is the sum of fields arising from a variety of sources, two of which are most relevant here. The primary source is the main field, which is produced in the core of the Earth and contains both dipole and nondipole components. Geophysicists have developed a periodically updated mathematical model [the International Geomagnetic Reference Field (IGRF)] that calculates the value of the main field at any point in space in and around the Earth. The dipole in the core dominates (generally >90%) the observed field and causes the magnitude (intensity) and direction of the vector to vary systematically between the magnetic equator and poles. Intensity of the main field varies from 25 to 65–70 microTesla (μT) or 2–5 nanoTesla/kilometer (nT/km) between the magnetic equator and poles, respectively. Similarly, the inclination of the Earth's magnetic field (the angle between the vector direction and the horizontal component of the field; Figure 8.1) varies from parallel to perpendicular to the Earth's surface between the magnetic equator and poles. The declination of the Earth's magnetic field is the angle between the directions of geographic and magnetic north and arises from the displacement of the magnetic poles relative to the geographic poles (Figure 8.1).

The second source of the Earth's magnetic field is the residual field (the field remaining after the IGRF has been subtracted from the observed field). The residual field (sometimes called magnetic anomalies) is produced by magnetized rocks in the crust of the Earth and causes slight variations in the observed TFV over a range of spatial scales. When mapped, these

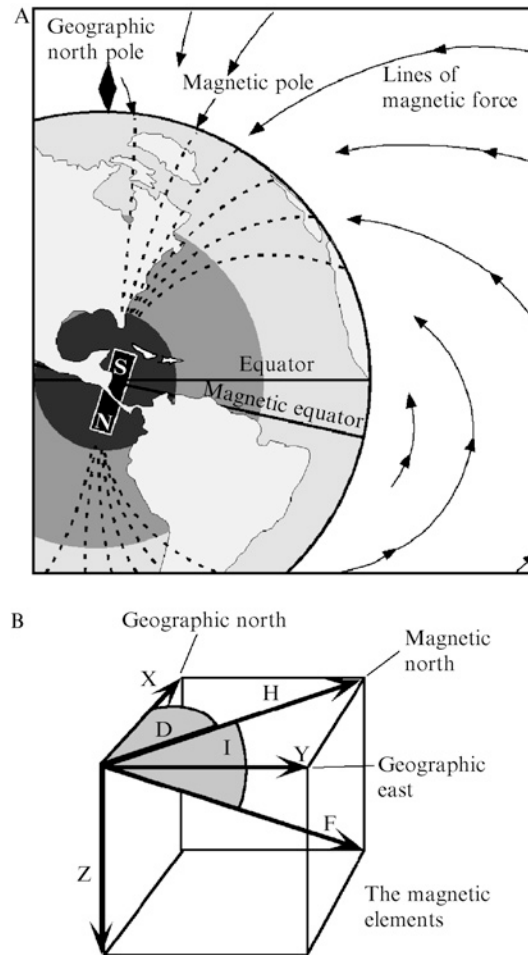


Fig. 8.1. The magnetic field of the Earth. [Adapted from Walker *et al.* (2002).] (A) The main field of the Earth (produced in the core) contains both dipole and nondipole components. The dipole component (represented by the bar magnet in the core of the Earth) is much greater than the nondipole component (not shown). The field due to the magnetic dipole in the core is represented by field lines, which show how the intensity (through increasing proximity of field lines) and inclination (through increasing angles of intersection of field lines with the surface of the Earth) of the field increase systematically between the magnetic equator and the magnetic poles. (B) The elements of the total magnetic field vector (labeled 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 (H) in the horizontal plane 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.

variations can be represented as a surface much like a physical topography. Of particular interest here are the new strips of seafloor produced by volcanic activity at mid-ocean spreading ridges. This seafloor becomes magnetized in the direction of the Earth's magnetic field at the time it cools to the temperature (the Curie temperature) below which magnetite in the magma spontaneously acquires a magnetic field. The magnetic field acquired by the rocks at the time of magnetization then adds to the field produced in the core but will subtract from the total field observed at the surface of the Earth when the polarity of the main field is reversed. Over geological time, successive reversals of the Earth's field result in distinct bands of positively and negatively magnetized seafloor (positive and negative magnetic anomalies) that are symmetrically arranged on opposite sides of spreading ridges (Vine, 1966). Cooling of magma through the Curie temperature is also responsible for the magnetic anomalies associated with the volcanoes that form seamount chains in the deep ocean.

As in space, the Earth's magnetic field varies over time scales ranging from seconds to decades. Short term variations in the TFV are produced by the interaction of the solar wind, a stream of charged particles flowing outwards from the sun with electric currents carried by charged particles flowing in the ionosphere (Skiles, 1985). Variations in the solar wind that cause changes in the magnitude of these currents can be caused by solar flares (magnetic storms), which can be powerful enough to disrupt radio transmissions and electric power systems. Similarly, at any point on the Earth, the observed field varies slightly with a 24-h period (the diurnal variation) because the interaction of the solar wind with electric currents in the ionosphere varies with the rotation of the Earth.

Over longer time periods, the values of the intensity, inclination, and declination of the Earth's field vary (the secular variation) as a consequence of the process of convection within the molten core of the Earth that generates the field. Heat-driven convection cells in the molten core spiral outwards through the molten core toward the boundary between the molten core and the solid mantle of the Earth (Glatzmaier and Roberts, 1995). This cyclonic convection is sufficient to cause the declination of the Earth's field to vary by as much as 30 min of arc per year whereas intensity and inclination of the field may vary by up to 120 nT and 20 min of arc per year, respectively. At much longer intervals (tens of thousands to hundreds of thousands of years), cyclonic convection can become disordered, resulting in substantial reduction of the intensity of the observed field, and can lead to reversal of the polarity of the field when convection becomes orderly again (Glatzmaier and Roberts, 1995). Estimates of the time taken for reversals to occur range from hundreds to a few thousand years and a mathematical

model of cyclonic convection in the core simulated a reversal over about 1000 years (Glatzmaier and Roberts, 1995).

2.2. Magnetic Fields as Experimental Stimuli in the Laboratory

The first consideration in laboratory studies of the magnetic sense is the Earth's magnetic field and its interaction with built structures in the experimental situation. At the scale of a laboratory, the Earth's field is effectively invariant in space. That is, intensity, inclination, and declination of the field are constant apart from the changes (primarily in intensity) induced by temporal variations such as magnetic storms and the diurnal variation in the field. If required, the temporal variations can be controlled to some extent using feedback from a fluxgate magnetometer to programmable power supplies that drive electromagnetic coils which control the background field in an experimental space (see later).

The Earth's magnetic field in a laboratory space will be affected by the presence of iron and other materials in a building and by the constant and time-varying fields produced by laboratory equipment. Thus iron in girders and the bars used to reinforce concrete will result in spatial variations in both magnetic intensity and direction within the laboratory. Experimental spaces in which animals will be studied should therefore be isolated as much as possible from inhomogeneities due to iron in buildings so that the background field is uniform. This isolation can be achieved by locating the experimental space as close as possible to the center of a room or, even better, in a purpose-built structure that is free of magnetic materials such as iron. Once an experimental space has been established, the background field should be mapped in detail with a fluxgate magnetometer, as the values within the building will often be different from those that exist outside the building.

Control of magnetic fields used in laboratory experiments can be required at several levels and is usually achieved using electromagnetic coils. Because coils generate a variety of nonmagnetic artifacts that could interfere with experiments, it has become standard practice to generate experimental fields using double-wrapped coils (Kirschvink, 1992). Such coils have two sets of windings connected so that current flows in either parallel or anti-parallel directions through the windings to generate an experimental field or no field, respectively. Under these conditions, the coils produce constant amounts of heat at constant current and so can have no influence on the outcomes of trials in which the experimental field produced by the coils is present or absent. Switching artifacts cannot be avoided and control tests (for example, with fields that are changed gradually rather than instantly) must be carried out to determine whether or not artifacts could be

influencing the outcomes of experiments. Other nonmagnetic effects, for example, electrical fields and vibration, can be controlled relatively easily using appropriate shielding, isolation, or insulation.

Control of the background field throughout an experimental space, for example, in migratory orientation experiments, requires coil systems that produce a uniform field space. Although it has often been assumed that paired Helmholtz coils produce uniform fields, this is true only for a small space at their center. Substantially better designs for coils that use systems of three to five coils and generate larger uniform field volumes for a given coil size are now available (Kirschvink, 1992). In the simplest case, a single set of coils aligned with the inclination of the Earth's magnetic field can be used to reduce or increase the intensity of the field in an experimental space without changing the direction of the field significantly. To achieve independent control of the direction and intensity of the background field, a minimum of two, and preferably three, orthogonal coil systems are required. If two coil systems are used, the horizontal system must be aligned with the axis of the Earth's magnetic field and the second system must be oriented in the vertical plane. If three coil systems are used, control of the field in an experimental space will be easiest if one of the horizontal coil systems is aligned in the axis of the Earth's field in the laboratory and the other two systems are aligned in the remaining horizontal axis and the vertical axis, respectively.

A productive line of research has been the use of conditioning experiments to analyze the responses of animals to the presence and absence of localized magnetic anomalies superimposed on the uniform background field. The anomalies also introduce significant local variations in magnetic field direction into the experimental spaces so it is not certain which of these dimensions the animals are actually discriminating. The fields are produced by small magnetic coils associated with a response detector such as a micro-switch that the animal activates by pressing on a key or paddle or through some other behavior that can be measured easily and objectively. The magnetic field produced by a coil in an experiment is typically a dipole that interacts with the background field to produce a localized dipole anomaly which increases and decreases the total field on opposite sides of the coil. The magnitude of the anomaly decays with distance from the center of the coil but has diffuse edges that make it difficult to determine the point at which the animal detects the stimulus. Kirschvink and Kobayashi-Kirschvink (1991) describe a coil system that uses two coplanar, concentric coils of equal dipole moment (area · current) but with antiparallel directions and different diameters (e.g., 2 and 10 cm). Close to the center of the coils, the small coil dominates and produces the anomaly. At larger distances, the two fields cancel and confine the anomaly to the area bounded by the larger of the two coils. This coil configuration has been used successfully to measure

a threshold sensitivity to changes in the intensity of the anomaly at different frequencies (Walker and Bitterman, 1989; Kirschvink *et al.*, 1997).

There is now a significant opportunity to combine coil systems that produce uniform field spaces with the coplanar, concentric coil systems to determine the threshold sensitivity as a function of background field intensity. Such an experiment will provide the first test for the magnetic sense of Weber's law, which states that the ratio (the Weber fraction) of the threshold sensitivity to change in the intensity of a stimulus to the magnitude of the background intensity is a constant. The existence of some range of stimulus intensities over which the Weber fraction is constant is a widespread property of sensory systems. Demonstration of a constant value of the Weber fraction for the magnetic sense over a biologically relevant range of magnetic intensities would provide powerful psychophysical evidence that the magnetic sense shares a key sensory property with other senses.

Experiments in which the animal is restrained for electrophysiological recording or does not move from a constant position in behavioral experiments provide better conditions for control of the exposure of the animal to magnetic field stimuli. Such experiments can, however, present other challenges for control of stimulation. Thus, the ground plates used in electrophysiological recording experiments are often made of soft iron. Careful mapping with a fluxgate magnetometer of the magnetic field above the ground plate (at the level of the preparation) can be used to locate a point where the intensity of two of the field elements (typically the vertical and east-west components) approach zero, leaving just the horizontal component of the field. Aligning a coil with the remaining north-south component of the Earth's field makes it possible to change field intensity but not direction or to reverse field direction without changing intensity (Walker *et al.*, 1997). When the animal is restrained or does not move in experiments, a relatively small uniform field space is required simply to allow for slight variations in the position of the animal. Although success in obtaining reproducible behavioral responses to magnetic fields by animals that are not moving has been limited, the enhanced control of magnetic field stimulation under these experimental conditions potentially permits much more powerful psychophysical studies than has been possible with freely moving animals.

3. HOW CAN MAGNETIC FIELDS BE DETECTED?

3.1. Magnetic Field Detection by Electrical Induction

The fishes have been particularly important in the study of the magnetic sense because there are at least two plausible sensory mechanisms by which

fish might detect magnetic fields. The first hypothesis proposed was that the marine elasmobranch fishes detect the electrical fields induced by their own movement and the movement of the saltwater medium through the Earth's magnetic field (Kalmijn, 1978, 1982). Because elasmobranch fishes are almost exclusively marine, they inhabit a medium that is electrically highly conductive. In the elasmobranch electroreceptor system, jelly-filled canals in the ampullae of Lorenzini are connected by a small pore to the external medium. As a consequence, an electrical circuit is formed between the fish and the saltwater medium. Because the jelly in the ampullary canals has a low electrical resistance, the voltage difference between the internal and external media is converted into a voltage drop across the electroreceptor cells located in the ampullae at the ends of the canals. The electroreceptor cells quickly accommodate to constant electrical fields, permitting the cells to operate at close to their threshold and detect electrical field stimuli in the 10–20 nV/cm range (Bodznick *et al.*, 2003). Variations in the membrane potential of the electroreceptor cells in response to variations in electrical field stimuli are then detected by neurons of the anterior lateral line nerve and transmitted to the brain. For a recent review of the structure and function of the electroreceptor system of the elasmobranchs, the reader is referred to Bodznick *et al.* (2003).

Because the fish and the saltwater form an electrical circuit, movement of the fish through the water will induce an electrical field that produces a voltage drop across the electroreceptor cells. Movement of saltwater through the Earth's magnetic field will also produce a voltage drop across the electroreceptor cells, even when the animal is passively moving with the water. The magnitude of the voltage drop depends on the intensity of the external magnetic field, the length of the canal, the orientation of the canal relative to the external magnetic field, and the relative conductivities of the internal and external media. The voltage drops generated by movement of both the fish and the water are sufficient to stimulate the electroreceptors and permit determination of magnetic field direction (Kalmijn, 1978, 1982), independent of whether the animal uses this information. Although the electroreceptors will not detect the constant electrical field signals produced by completely uniform movement of either the water or the fish, further theoretical analysis has shown that the low frequency movements of the body during swimming (side-to-side in sharks or up and down in rays) will still permit extraction of information about magnetic field direction (Paulin, 1995). Experimental evidence consistent with this hypothesis is considered in a later section.

3.2. Magnetic Field Detection Based on Magnetite

In contrast with the elasmobranch fishes, the teleost fishes have been important in the search for a magnetoreceptor system based on the magnetic

mineral, magnetite. This hypothesis proposes that animals use the motion of or torque from chains of single-domain (SD) magnetite crystals to transduce magnetic field stimuli into mechanical signals that can be detected by the nervous system (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985). Theoretical analyses demonstrate that magnetite-based magnetoreceptors should permit detection of both magnetic field direction and intensity, with the threshold sensitivity to changes in magnetic intensity potentially being as low as 10 nT (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985). As discussed later, much of the experimental evidence that is consistent with the magnetite-based magnetoreception hypothesis has been obtained from the teleost fishes, and in particular from taxa that contain well-known migratory species. This evidence is considered in detail in the following sections.

The final hypothesis on the mechanism of detection of magnetic fields that is being investigated is based on the effects of Earth-strength magnetic fields on particular molecules in the retina. This hypothesis has not received significant attention in the fishes and is not considered further here.

4. STRUCTURE OF CANDIDATE MAGNETITE-BASED MAGNETORECEPTORS

The first evidence that animals produce magnetic particles suitable for use in magnetoreception came from studies of the rock magnetic properties of animal tissues. Following the discovery (Blakemore, 1975) of magnetotactic bacteria and their use of chains of SD magnetite for orientation, a search for magnetic material suitable for use in magnetoreception in animals identified magnetite in SD, multidomain (MD), and superparamagnetic (SPM) states in a variety of animals (Kirschvink *et al.*, 1985a). MD magnetite has a low magnetization that renders it unsuitable for use in magnetoreception because its interactions with the external magnetic field are weak (Kirschvink *et al.*, 2001).

In contrast, SPM magnetite has a high magnetization but the small size of the particles means that their moments are not fixed and align with an external magnetic field without physical movement of the particles. Broadly similar models for magnetic field detection using SPM magnetite have been proposed by Kirschvink and Gould (1981) and Davila *et al.* (2003) to explain responses to magnetic fields by honeybees (Gould *et al.*, 1978) and birds (Fleissner *et al.*, 2003). Both models depend on closely spaced SPM particles which are aligned such that their interactions in the external magnetic field exert forces of expansion or contraction within an elastic matrix. A further suggestion for the use of SPM magnetite in magnetoreception is through

amplification of the flux density of the external magnetic field, which should enhance the frequency response and sensitivity of the SD receptors discussed later (Kirschvink *et al.*, 1997).

Models for the use of SD crystals in magnetic field detection are also based on the strength of their interaction with the external magnetic field. SD crystals have the maximum magnetization per unit volume for magnetite but must move if their moments are to align with the external magnetic field because the crystals are permanently magnetized (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985). Thus, single domains have the strongest possible interaction with the relatively weak magnetic field of the Earth. Transduction of the magnetic field of the Earth into a signal that can be detected by the nervous system, however, requires the use of chains of SD magnetite such as those that are observed in the magnetotactic bacteria (Kirschvink and Walker, 1985) and fish (Mann *et al.*, 1988). The motion of these chains in response to the external magnetic field will then convert the magnetic field stimulus into a mechanical stimulus that could readily be detected using mechanically gated ion channels linked to the magnetite chain (Kirschvink, 1992). Thus MD particles are considered unlikely to play any role in magnetoreception whereas critical experimental tests have yet to resolve between models of magnetic field detection using SPM and SD particles.

The crystal and magnetic properties of SD magnetite have been used to identify chains of SD crystals within cells in the nose of the rainbow trout despite the small size (<50 nm) and extreme rarity (<5 ppb by volume) of the crystals. Reflections of laser light off crystal surfaces permitted detection of the chains of magnetite crystals in reflection mode confocal laser scanning microscopy (CLSM) (Figure 8.2A and B). Mapping the reflections in three dimensions then permitted imaging of single crystals in thin sections in the transmission electron microscope (Figure 8.2C and D) and unique identification of the crystals as magnetite using atomic and magnetic force microscopy (Figure 8.2E) (Walker *et al.*, 1997; Diebel *et al.*, 2000).

The cells containing the magnetite particles are 10–12 μm in length, have a distinctive multilobed shape, and are consistently located near the basal lamina of the olfactory epithelium (Figure 8.2A and B). The cells are relatively rare and were only found near the tips of the olfactory lamellae (distal to the cells of the olfactory sensory epithelium). The cells each have several processes that extend out to and are surrounded by tubular-shaped fibroblastic cells (with two processes) which help delineate the basal layer (Figure 8.2B). The chain of magnetite crystals in each cell is about 1- μm long (range 0.5–1.5 μm , $n = 4$; estimated from the CLSM; Diebel *et al.*, 2000) and the chains are estimated to have a magnetic to thermal energy ratio of about 4. The location of the chain of magnetite crystals within each cell suggests that

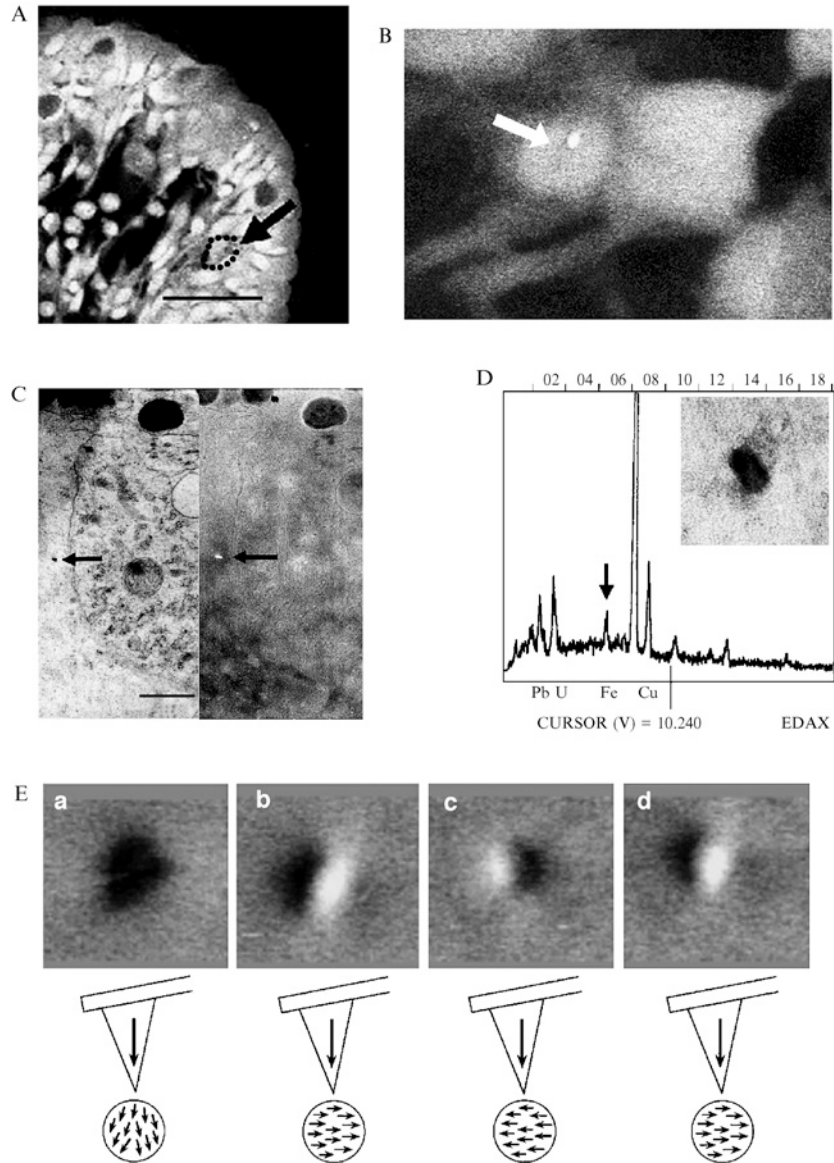


Fig. 8.2. Detection of intracellular magnetite. (A) Autofluorescence image of a magnetite-containing cell (dotted outline) viewed using a confocal laser scanning microscope in transmission mode. The slightly darker area at the lower right of the cell is where the reflection of the laser light by the magnetite has prevented light passing through the cell (scale bar 25 μm). [Adapted from Walker *et al.* (2000).] (B) CLSM optical slice (~30-μm wide) taken through a

a mechanical linkage of the chain to the cell could transduce the movement of the chain in response to the external magnetic field into changes in the membrane potential of the cell.

5. BEHAVIORAL RESPONSES TO MAGNETIC FIELDS IN THE LABORATORY

A variety of laboratory experiments have demonstrated that both teleost and elasmobranch fishes can detect magnetic fields. Fishes from at least two teleost orders have been shown to respond to magnetic field direction in orientation experiments whereas both teleost and elasmobranch fishes have been successfully conditioned to magnetic fields. In the paragraphs that follow, we examine key results from these experiments.

magnetite-containing cell within an olfactory lamella. The arrow points to the reflectance arising from particles contained within the cell. [Adapted from Diebel *et al.* (2000).] (C) Bright-field (left) and dark-field (right) transmission electron micrograph (TEM) of a crystal associated with the reflecting structure in a cell like those shown in **a** and **b**. In bright-field TEM, both the crystal (arrow) and a much larger pigment granule (top center) are electron dense. In dark-field TEM, the crystal (arrow) reflects the electron beam strongly whereas the large pigment granule (upper right) does not (scale bar 1 μm). [Adapted from Walker *et al.* (1997).] (D) Energy dispersive analysis of X-ray emissions (EDAX) of the crystal in **c**. Inset shows the crystal (length 50 nm) at higher magnification. The copper (Cu) peak is due to the copper grid used, and lead (Pb) and uranium (U) peaks are from TEM stains. The peak from iron (Fe) present in the crystal is indicated by an arrow. This peak was absent in control regions of the same section. [Adapted from Walker *et al.* (1997).] (E) MFM images that show the response of a single magnetic field source within a trout olfactory lamella in the presence of an applied field. The magnetic field applied in the plane of the sample was +1.4, +150, -150, and +130 mT for images **a-d**, respectively. MFM images (75-nm squares) are shown on top with a representation of the MFM tip and magnetization of the field source underneath. The MFM tip (inverted triangle) is permanently magnetized with a coercivity of +500 mT at right angles (arrow in inverted triangle) to the applied field. The small arrows within each circle under the tip represent the alignment of the individual magnetic dipole moments that might act as the field source. (a) Image shows a dark patch at the location of the magnetic field source. This dark patch indicates an attractive reaction between the tip and sample, consistent with the magnetic field from the MFM tip weakly magnetizing the field source and causing an attractive interaction. (b-d) MFM images show the nearly dipolar responses of the magnetic field source under a strong applied magnetic field. These are consistent with an MFM image of a field source comprising multiple single-domain particles of magnetite that are magnetized along the direction of the applied field. Note that the reversal of the field and dipolar response in **c** is consistent with the magnetization of the dipole moments in the field source flipping in the reversed applied field. In images **b-d**, the applied field was large enough to align completely the magnetic moments within the field, forming a dipole that interacted with the magnetized MFM tip to produce the light and dark patches in the images. [Adapted from Diebel *et al.* (2000).] Reversing the direction of magnetization of the dipole then resulted in the different locations of the light and dark patches in **b-d**.

5.1. Orientation Responses to Magnetic Field Direction

The critical assumption of orientation experiments is that the spontaneous directional choices made by animals placed in featureless orientation arenas match the directions they would choose in their normal environment (Emlen, 1975). Thus, diurnal birds that migrate at night will become spontaneously active at night as each migration season begins. When placed at night in a featureless orientation arena such as an Emlen funnel, the activity of the birds in the arena is consistent with the hypothesis that they are attempting to fly in the same direction as their flock mates are flying at the same time (Emlen, 1975).

Similar approaches have been used to study the migratory orientation of fish. Quinn (1980) captured sockeye salmon fry migrating from the gravel beds where they hatch to lakes where they spend their early life. The directions chosen by the fish when placed in an orientation arena were consistent with the hypothesis that they were orienting to the axis of the lake in which they would live until they reached the smolt stage and began their migration to the sea. In similar experiments, juvenile chinook salmon established a preferred orientation in which they faced into a current running from east to west in their home tank. When placed in a featureless arena where there was a radial current flow, the fish oriented preferentially in the east-west axis (Taylor, 1986, 1987) despite being able to choose any orientation direction. The orientation directions of the fish in the arenas used in both sets of experiments changed in response to variations in magnetic field direction produced using electromagnetic coils.

5.2. Conditioned Responses to Spatial Variations in Magnetic Field Intensity

Although the evidence to date is indirect, it appears that freely moving fish readily learn to discriminate changes in magnetic intensity in conditioning experiments. Two constraints on these experiments are that (1) the fields to be discriminated must be spatially distinctive and (2) the subjects must be required to move to produce the conditioned response. The simplest pair of spatially distinctive fields is the case where the animal discriminates the presence and absence of a magnetic intensity anomaly induced by an electromagnetic coil. Because the intensity of the Earth's magnetic field is constant within an experimental arena, the animal must therefore discriminate the presence and absence of intensity variations due to the coil. The animal must then move in order to gain exposure to the presence or absence of intensity variations in the experimental situation.

Yellowfin tuna have been trained to discriminate the presence and absence of a nonuniform magnetic field in experimental tanks (Walker, 1984).

8. MAGNETORECEPTION

Passing direct current through vertically oriented coils wound around the outside of the tank imposed localized, nonuniform fields of varying intensities on the uniform Earth's field within the tanks in which fish were trained (Figure 8.3B). Reversing the polarity of the current to the coils caused the nonuniform field to be added to or subtracted from the Earth's magnetic field in the tank (Figure 8.3D). Individually trained yellowfin tuna swam repeatedly through a hoop lowered into an experimental tank for a 30-sec trial period. At the end of each trial and depending on the presence or absence of the magnetic field produced by the coil, the fish were reinforced or unreinforced with food for swimming through the hoop. Discrimination learning was then detected as a change over time in the rates of response

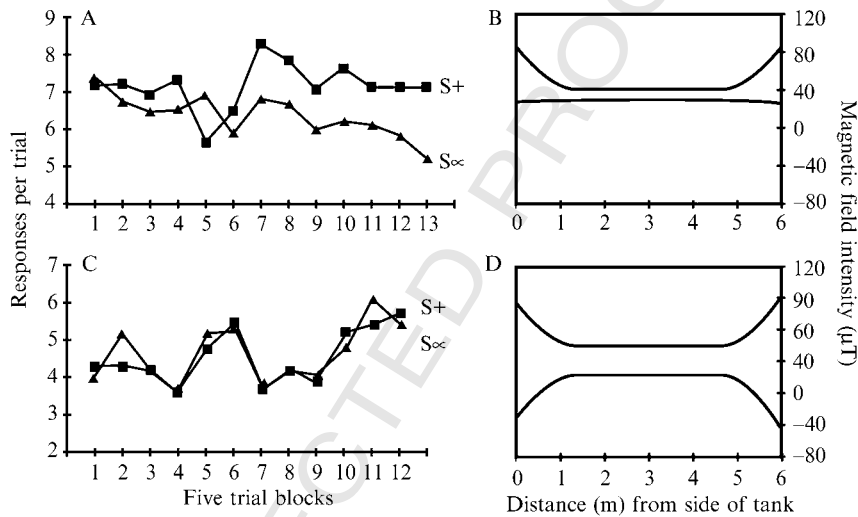


Fig. 8.3. Behavioral responses to magnetic fields by teleost fish. Magnetic discrimination learning in individually trained yellowfin tuna. [Adapted from Walker (1984).] In the training procedure, individual fish swam through a hoop during 30-sec trials. Depending on the magnetic field presented to the fish, response by the fish was reinforced with food (S+) given at the end of each trial or unreinforced (S-; triangles) no matter how often the fish responded. Each point is the mean of five S+ (squares) or S- (triangles) trials. (A) Fish ($n = 7$) were required to discriminate the presence and absence (indicated by varying and constant intensity values across the tank in B) of a localized magnetic field anomaly projected into the experimental tank by a coil through which direct current could be passed. To control for possible generalized effects of the experimental field on behavior, some of the fish were trained with the magnetic field of the Earth as S+ and the localized anomaly as S- whereas for the remaining fish the anomaly was S+ and the Earth's field was S-. (C) Fish ($n = 2$) were required to discriminate between two magnetic anomalies (indicated by the mirror image curves of varying intensity values across the tank in D) produced by reversing the polarity of the current passed through the coil.

during reinforced (S+) and unreinforced (S-) trials. In similar experiments, the pattern of discrimination learning by rainbow trout (*Oncorhynchus mykiss*; Walker *et al.*, 1997) was remarkably similar to the yellowfin tuna despite variations in the number of trials required for discrimination to appear.

Although the tuna learned to discriminate the presence and absence of the nonuniform field, they could not discriminate between the two nonuniform fields produced by reversing the polarity of the current to the coils. For fish tested with the presence and absence of the nonuniform field due to the coil, response rates during both S+ and S- trials remained similar over the first 6 five-trial blocks (Figure 8.3A and B). After 6 five-trial blocks, however, response rates were consistently higher in the presence of S+ than in the presence of S-. For fish trained with two nonuniform fields produced by reversing the polarity of the current to the coils, there was no separation of response rates to S+ or S- at any stage of the experiment (Figure 8.3C and D). The interpretation of these results was that the tuna distinguished the uniform and nonuniform fields based on the presence and absence of changes in intensity but failed to distinguish between the mirror image patterns of variation in intensity of the two nonuniform fields as the fish swam in the tank during trials (Walker, 1984).

Elasmobranch fishes have also been trained to discriminate the presence and absence of magnetic anomalies in experimental tanks. Hodson (2000) used the same approach as that used with the tuna to train short-tailed stingrays (*Dasyatis brevicaudata*) to discriminate the presence and absence of a magnetic intensity anomaly in an experimental tank. Meyer *et al.* (2005) used activity conditioning to demonstrate that a mixed species group of sharks could be trained to search for food when a magnetic intensity anomaly was presented for 1 min at randomized intervals. The animals were required to swim to a target area in the center of the tank where food was only ever delivered if the magnetic anomaly was present. The animals quickly learned to recognize that the anomaly signaled food and entered the target area much more frequently when the anomaly was present than they did during control periods when the anomaly was absent (Figure 8.4). Because the magnetic fields were switched instantaneously in the above-mentioned experiments, there remains the possibility that the animals responded to the electrical transients associated with switching the magnetic field on and off. Reversible impairment of the responses by attachment of magnets adjacent to the olfactory epithelium in the short-tailed stingray suggests, however, that the electroreceptors do not play a significant role in magnetic field detection (Hodson, 2000; Kirschvink *et al.*, 2001).

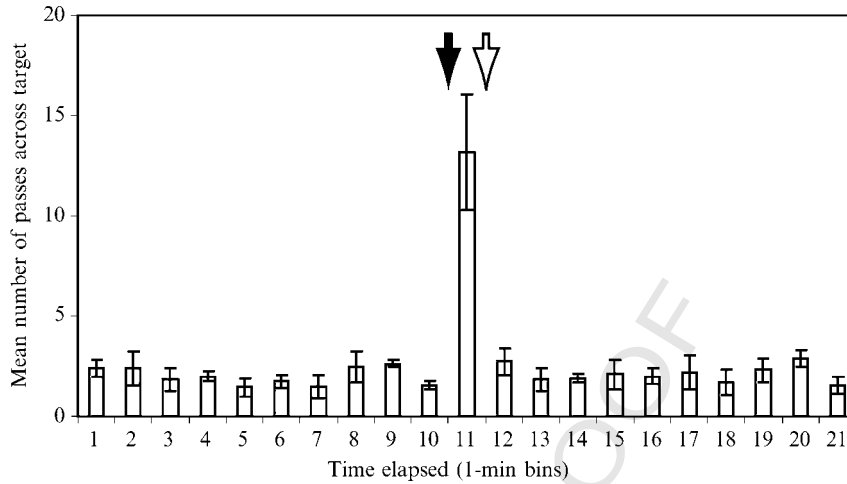


Fig. 8.4. Behavioral responses to magnetic fields by elasmobranch fish. Mean number of passes per minute by sharks across a 1.5 m² target during the 21-min duration of magnetoreception experiments. Means for each 1-min bin are derived from 11 trials. Error bars are 1 S.E.M. Shaded arrow, artificial magnetic field activated; unshaded arrow, artificial field turned off. [Adapted from Meÿer *et al.* (2005) with permission.]

5.3. Other Experiments Using Conditioned Responses

Classical conditioning to magnetic field stimuli has also been attempted with mixed results. Rommel and McCleave (1973) used cardiac conditioning to demonstrate sensitivity to electric field stimuli in American eels (*Anguilla rostrata*) and Atlantic salmon (*Salmo salar*) but obtained only equivocal results concerning the sensitivity of both species to changes in magnetic fields under the same conditions. Nishi and his colleagues (Nishi *et al.*, 2004, 2005; Nishi and Kawamura, 2005) reported cardiac conditioning of Japanese eels (*A. japonica*) to magnetic fields that differed in both magnetic field direction and intensity. Significant reductions in heartbeat rates (Figure 8.5B) occurred in 17 of 19 eels in both the marine and freshwater phases of the life cycle. Responses were recorded across changes in magnetic field intensity and direction ranging from 12,663 to 192,473 nT and from 21° to 80° easterly shift in the direction of the horizontal component of the magnetic field in the experimental tank (Figure 8.5A). The responses appear, however, to have been quite variable and did not exhibit any quantitative relationship between the magnitude of the stimulus and the cardiac response. This outcome could result from use of stimuli that were well above the threshold for detection,

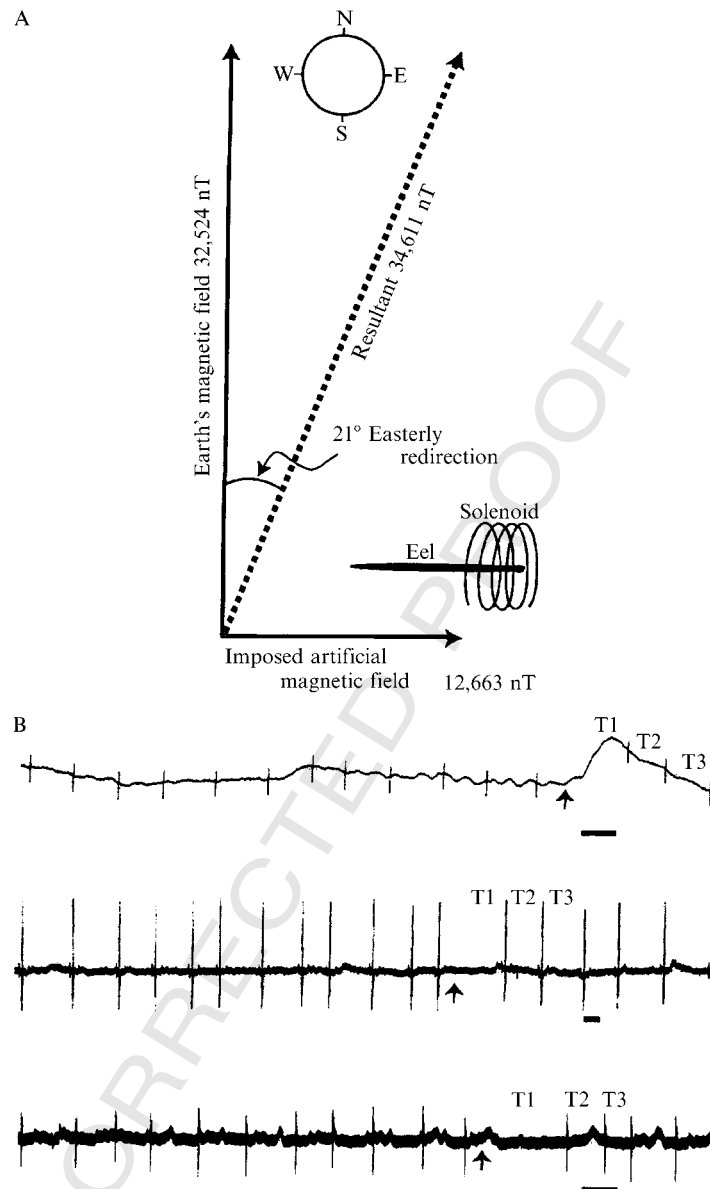


Fig. 8.5. Cardiac conditioning responses to magnetic fields in eels. (A) Experimental apparatus used in cardiac conditioning experiments with Japanese eels. The eel's head lay at the center of a solenoid (35-cm diameter) wrapped around a polyvinyl chloride (PVC) aquarium and oriented in the east-west axis. The solenoid in the apparatus produced a resultant field due to the combination of the geomagnetic field and the imposed magnetic field. The imposed field ranged between

suggesting that the eels discriminated all the magnetic field changes equally easily. In follow-up experiments, Nishi *et al.* (2005) showed that these responses did not occur when the eels had been made anosmic and argued that magnetoreception takes place in or around the nares of the eel. Taken together, these experimental results demonstrate that the magnetic sense can be analyzed using conditioning approaches in the same manner as better-known sensory systems.

6. NEURAL RESPONSES TO MAGNETIC FIELDS IN THE LABORATORY

6.1. Induced Electrical Signals in Ampullary Electoreceptors

As noted earlier, elasmobranch fishes are highly sensitive to electric fields and theoretically should be able to use their ampullary electroreceptors to detect electric current flows induced by their own or the water's movement through the Earth's magnetic field. Evidence consistent with this hypothesis has been obtained by recording responses to electrical and magnetic field stimuli in the Black Sea skate. Afferent nerves from ampullary electroreceptors in the wings (Brown and Ilyinsky, 1978) and primary area acoustico-lateralis in the dorsolateral region of the medulla oblongata of the brain (Andrianov *et al.*, 1974) responded to both electrical and magnetic field stimuli in the skate. A range of excitatory and inhibitory responses were detected in the primary afferent nerves that were tested under conditions of static and time-varying magnetic fields, water flow, and animal movement. Responses were recorded in the afferent nerves so long as the magnetic field was varying continuously and when either the fish or the water were moving, that is, when electrical fields were likely to be induced. The smallest field to which a response was detected was a field that was changing at a rate of 200 $\mu\text{T}/\text{sec}$. These results clearly confirmed that the electroreceptors do detect the electric current flows induced by magnetic field variations and by the movement of either the fish or saltwater through a static magnetic field. Because these experiments did not demonstrate that the induced electrical signals were either necessary or sufficient for use of magnetic fields

12,663 and 192,473 nT with the resultant intensity ranging from 35,611 to 187,298 nT. These intensity changes produced resultant fields whose directions ranged from 21° to 80° to the east of magnetic north. (B) Electrocardiograms showing changes in heartbeat rate in response to magnetic field changes in Japanese eels (scale bars = 1 sec). Arrows indicate the onset of the conditioning stimulus (magnetic field); T1–T3 indicate beats used to compare response to the magnetic field change with heartbeat rate during control tests in the absence of the experimental magnetic field. [A and B adapted from Nishi *et al.* (2004) with permission.]

by elasmobranch fishes, however, the mechanism of magnetic field detection in the elasmobranchs remains an open question.

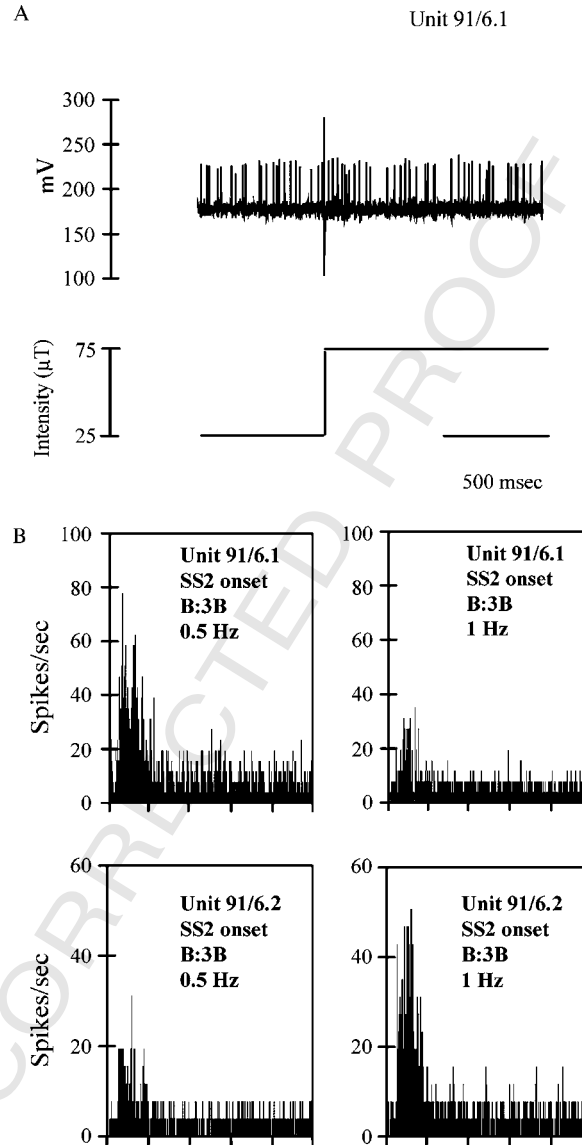
6.2. Responses in the Trigeminal Nerve of Teleost Fish

The discovery of magnetite suitable for use in magnetoreception in front of the head in a variety of teleost fishes (Walker *et al.*, 1984; Kirschvink *et al.*, 1985b; Mann *et al.*, 1988; Diebel *et al.*, 2000) provided a focus for the search for the sensory nerve that might transmit magnetic field information to the brain. The olfactory (ON), trigeminal (TN), and anterior lateral line (ALLN) nerves are sensory nerves that innervate the front of the head and that could each potentially carry magnetic field information to the brain. The ON is the major source of afferent innervation for the olfactory mucosa. The TN is a mixed nerve that, *inter alia*, carries afferent signals from mechanoreceptor cells and is known to innervate the olfactory epithelium in birds and rats (Finger *et al.*, 1990; McKeegan *et al.*, 2005). The ALLN innervates the highly sensitive mechanoreceptors of the lateral line and, in the elasmobranchs, innervates the morphologically and developmentally related electroreceptors.

Responses to magnetic field stimuli were found to occur in the superficial ophthalmic (SO) branch of the TN of the trout (Walker *et al.*, 1997), the same branch of the TN system that responded to magnetic field stimuli in birds (Beason and Semm, 1987; Semm and Beason, 1990). The responsive units in the trout showed regular firing patterns except during phasic (transient) responses to a trebling of magnetic intensity presented as square waves at frequencies of 0.5 and 1 Hz (Figure 8.6A–C). Both excitatory and inhibitory responses were observed but each unit responded only to either the onset or the offset of a stimulus. The responses of the units could also be modulated by varying the presentation rate of the change in magnetic intensity. For the units shown in Figure 8.6B, poststimulus time histograms (PSTHs) showed that the latency (10–15 msec; the first point after the stimulus step and the period during which the firing rate was more than two standard deviations above the mean for each unit) and time course (~100 msec) of the responses by the two units exposed to both stimulation frequencies were similar. The peak amplitudes of the responses in the units in the upper and lower panels of Figure 8.6B decreased and increased, respectively, when the presentation rate of the step change in intensity increased from 0.5 to 1 Hz.

Surprisingly, no unit responded when magnetic field direction was reversed without a simultaneous change in intensity. As described in Section 2.2, the experimental apparatus permitted imposition of a field aligned either parallel or antiparallel to the background field in the experimental situation. Adding 50 μT parallel to the background field trebled intensity

without changing magnetic field direction (upper panels of Figure 8.6C), whereas adding the same field antiparallel to the background field reversed the magnetic field direction without changing intensity (lower panels of Figure 8.6C). The unit presented in Figure 8.6C clearly did not respond to



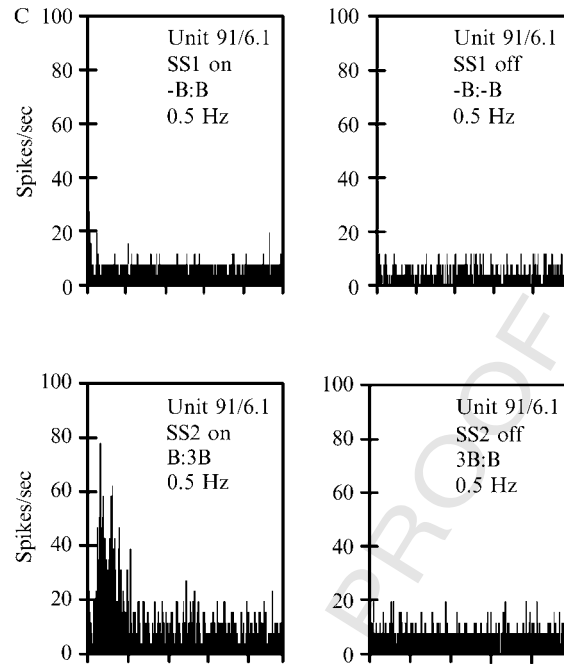


Fig. 8.6. Neural responses to magnetic field stimuli. (A) Spontaneous activity of a single unit (upper trace) in the TN of the rainbow trout in the background magnetic field followed by the activity for 1 sec following the onset of a stimulus (lower trace) that produced a step change in magnetic field intensity from 25 to 75 μ T within the experimental tank. (B) Poststimulus time histograms of responses by two spontaneously active units to the same stimulus presented 128 times each at 0.5 and 1 Hz. Each plot begins at stimulus onset and is of 500-msec duration with the magnetic field remaining constant throughout the period shown in each panel. Sampling bin width is 2 msec in all panels and tick marks on the abscissa are at 100 msec intervals following stimulus onset. The top left panel in B is the same record as the bottom left panel in C. (C) Poststimulus time histograms of responses by one spontaneously active unit to the onsets and offsets of a trebling of magnetic intensity (lower two panels) or a reversal of magnetic field direction in the experimental tank (upper two panels). Each stimulus was presented 128 times at 0.5 Hz. Each plot begins at stimulus onset and is of 500 msec duration with the magnetic field remaining constant throughout the period shown in each panel. [All data adapted from Walker *et al.* (1997).]

reversal of the magnetic field direction and, as in the other units recorded, responded only to one of the two intensity changes (onset and offset of the experimental stimulus) presented to it. Of interest also are the differences in the firing rate of the unit during the last 300 msec of stimulation shown in Figure 8.6C. The mean and variance of the firing rate of the unit not only

increased greatly during the phasic response to the change in intensity but also remained higher while the intensity was high (lower left panel in Figure 8.6C) and remained higher when the field switched back to the lower intensity (lower right panel in Figure 8.6C). In contrast, the mean and variance of the firing rate of the unit were uniformly low throughout the PSTHs when direction but not intensity was changing (upper panels in Figure 8.6C). This observation suggests that there may be sustained differences in firing rate that accommodate only slowly at different levels of magnetic intensity.

The pattern shown in Figure 8.6C is important also because it demonstrates that the units did not respond to the electrical artifacts induced by the sudden changes in magnetic fields in the experimental situation. The stimuli all changed the field by a constant 50 μ T, which was sufficient either to reverse direction or to treble the intensity of the field in the experimental situation. As a consequence, the induced artifacts would have been the same in the top right and lower left panels and in the top left and lower right panels of Figure 8.6C. That is, the units appeared indifferent to the induced artifacts and only responded to one particular step change in the intensity of the magnetic field.

The neural responses to magnetic fields in the trout have neither been localized to any branch of the SO, shown to depend on magnetite such as that found in the cells in the nose, nor to underpin behavioral responses to magnetic fields by the trout. The responses to changes in magnetic intensity found in the TN are, however, consistent with detection of magnetic fields in front of the head of the trout and led to the search for detector cells associated with the TN discussed earlier.

7. NEUROANATOMY

In the first step toward testing the hypothesis that the magnetite-containing cells may be functionally linked to the TN, the SO branch of the TN was traced from the site where electrophysiological recordings of responses to magnetic field stimulation were made to the endings of the individual nerve cells as well as to the brain (Figure 8.7) (Walker *et al.*, 1997). Serial histological sections and DiI, a fluorescent lipophilic dye, placed on the cut ends of the TN were used to trace the nerve in both anterograde and retrograde directions. The dye migrated along both myelinated and unmyelinated fibers in the TN. Posterior to the orbit, the SO branch joined other branches of the TN and ended in cell bodies that make up part of the anterior ganglion (Figure 8.7C). From the ganglion, the labeled nerve tracts entered the anterior dorsal area of the medulla oblongata. Anterior to

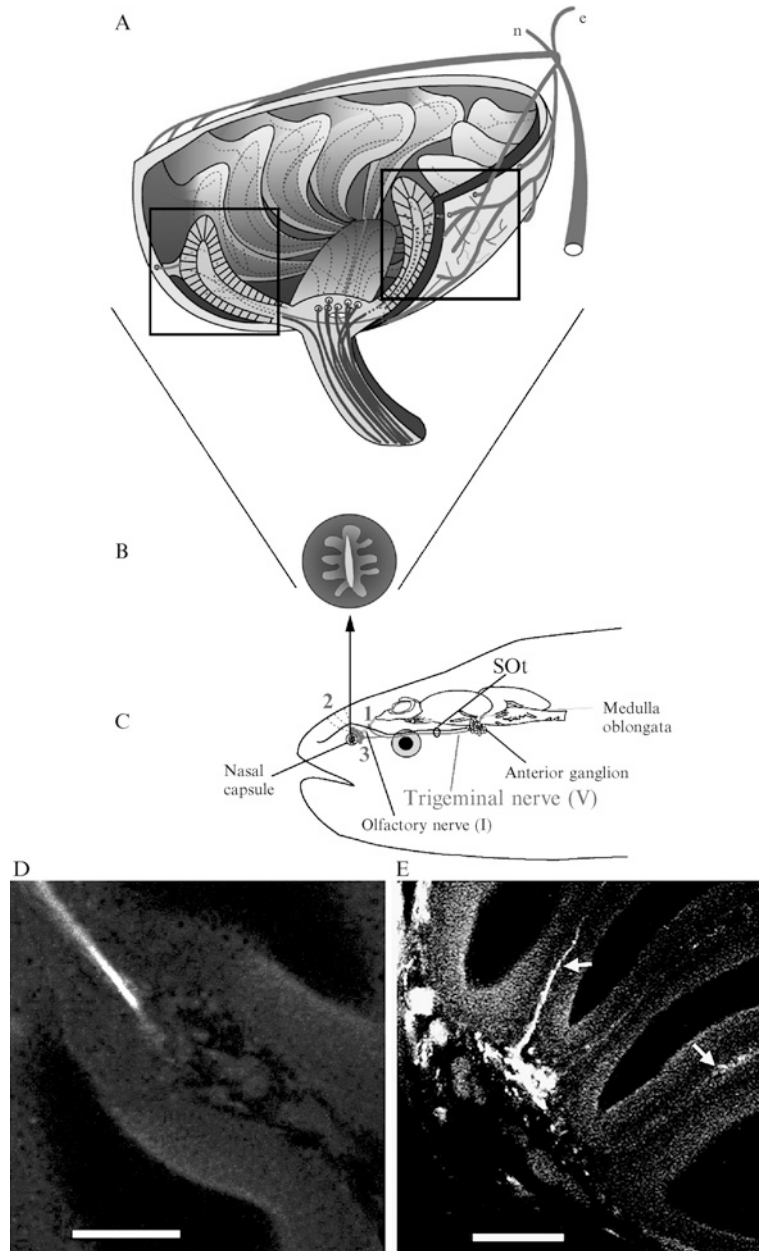


Fig. 8.7. Innervation of the head region and nasal capsule of the trout by the SO branch of the TN. (A–C) Schematic diagram of the innervation of the head region and nasal capsule of

the orbit, the SO branch has branches that innervate the skin, surround the olfactory nerve and olfactory capsule (processes 1–3 in Figure 8.7C), and also penetrate the olfactory lamellae within the olfactory capsule itself (Figure 8.7C). Fine branches of the SO penetrate the olfactory lamellae from both the top and from the base before terminating in finer processes within the olfactory lamellae, where the magnetite-containing cells are most often found (Figure 8.7A, D, and E).

Although it can be proposed that the candidate magnetoreceptor cells in the lamina propria of the olfactory lamellae are linked through the SO branch of the TN to the brain, afferent synaptic contacts between the nerve endings and the magnetoreceptor cells have not yet been identified. Detection of both magnetite and the endings of stained nerves in the confocal microscope has not yet been achieved due to the different media required for best detection of the magnetite and the labeled nerves. It has also been impossible to recognize the chains of magnetite crystals in the transmission electron microscope, at least in part because there is a very low probability that more than one crystal in a chain will fit within one thin section. A further difficulty in visualizing the magnetite in the electron microscope

the trout by the superficial ophthalmic (SO; shown in red in A–C) branch of the trigeminal nerve (TN) [A–C adapted from Walker *et al.* (1997).] (A) A three-dimensional diagram of the innervation by the SO into olfactory lamellae in the nasal capsule of the trout. One process innervates the nasal membrane and flap (n) and the other [top right (e)] is process 2 in C. Others form a network of nerves that surround the nasal capsule (right box). Within this network, the smaller branches have fine processes that pass through the nasal membrane, lining the nasal capsule, and innervate, at both the top and base, individual olfactory lamellae that form the olfactory rosette. The olfactory nerve (blue) is the combination of all axons of the olfactory sensory cells which are situated in the mucosa and send their axons to the olfactory bulb. The network of nerves surrounding the capsule generally lies in a fatty layer (light shading on outside surface of capsule; right box in A), which is typically found between the neurocranium (not shown) and the outer membrane (brown) that lines the nasal capsule. The pale area in the front two lamellae represents the folded layers of the olfactory epithelium that are separated internally by the lamina propria. New lamellae are formed in the area of the nasal capsule (not shown). The left box outlines the area shown in D. (B) Olfactory rosette within the trout nasal capsule (top view). The nasal flap that lies over the top of the olfactory rosette has been removed for clarity. (C) Innervation of the SO in the head region of the trout. The label SOt identifies the SO trunk where the SO branches of the trigeminal (V) and anterior lateral line (VIII) nerves pass together across the top of the eye before diverging to innervate the front of the head. (D) Optical slices showing two different branching patterns of DiI-labeled nerve processes entering trout olfactory lamellae. Optical slice through a single olfactory lamella (scale bar 100 μm). A labeled fine process from a branch of the SO branch can be seen entering the lamella through the top. [D and E adapted from Walker *et al.* (1997).] (E) Fine processes can also be seen entering the lamina propria of several lamellae (arrows) from their bases (scale bar 100 μm). These processes originate from a different branch of the SO than the one that innervates the area in D. (See Color Insert.)

is that the magnetite is very hard and, as a consequence, any crystal that is not completely contained within a thin section will catch the microtome knife and pull out of the section. There is thus only indirect evidence from magnetic impairment experiments in fish (Hodson, 2000) that the magnetoreceptor cells are functionally linked to the nervous system. Evidence that the magnetite will be linked to the SO branch of the TN in the trout has, however, come from conditioning experiments with pigeons, where bilateral sectioning of the SO branch abolished conditioned responses to magnetic fields by the birds (Mora *et al.*, 2004).

8. USE OF THE MAGNETIC SENSE IN NAVIGATION

8.1. Constraints on Theory and Experiment in the Study of Navigation by Fish

The only hypothesis ever proposed to explain the existence of the magnetic sense in animals is that the sense permits use of the Earth's magnetic field for navigation over long distances. Unfortunately, rigorous theoretical and methodological frameworks against which to assess hypotheses and evidence on how animals such as fish use the Earth's magnetic field for navigation have not yet been developed. Such frameworks are necessary because the experiments required to test such hypotheses present significant challenges in experimental design, control, and interpretation over and above the logistical difficulties of studying fish traveling in water. As a consequence, it has been difficult to achieve convincing evidence that fish do indeed use the Earth's magnetic field for navigation.

Developing a theoretical framework begins with the definition of navigation. For our purposes, navigation can be defined as the processes by which an animal first determines its current position relative to some goal that it cannot detect directly, and then sets a course to reach that goal. These two processes are consistent with the "map" and "compass" steps of true navigation originally proposed by Kramer (1953). The above definition excludes cases where fish can detect a goal at a substantial distance. Thus, salmon on their spawning migration that locate their natal river by following its chemical signature upstream are not navigating because they are in direct sensory contact with their goal.

This definition presents challenging problems in understanding how fish navigate. Fish that travel significant distances are likely to lose sensory contact with persistent features (such as visual, auditory, and olfactory landmarks) of the environment. Traveling fish must also overcome the effects of passive displacement during movement through water that may itself be

moving with, against and across the directions taken by the animals as they travel (Figure 8.8). The risk of passive displacement during such movements generates strong selective pressure for the ability to monitor both position and direction, particularly when traveling over long distances to find small targets. These constraints require that external stimuli used in navigation provide consistent information which varies systematically such that locations can be identified uniquely over at least the portion of the biosphere used by a given species (Walker *et al.*, 2002).

As described earlier, the Earth's magnetic field provides consistent information about direction and potentially about location throughout the biosphere. Because this information varies systematically, locations can potentially be identified uniquely over large areas of the Earth (Walker *et al.*, 2002). The Earth's magnetic field will therefore permit animals such as fish to monitor position and direction while traveling at any depth and

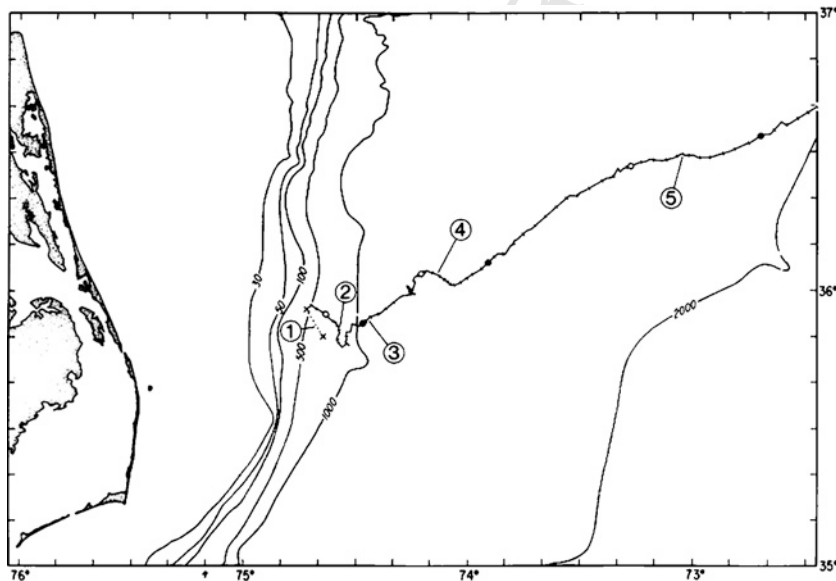


Fig. 8.8. Sustained directional swimming in a swordfish. Path of a swordfish tracked continuously for several days in the Atlantic Ocean near Cape Hatteras, North Carolina. Numbers at points along the track represent the following events: (1) The fish was caught on long-line gear. (2) The fish moved beneath a layer of cold surface water. (3) The fish emerged from beneath the cold surface layer 10 h later. (4) Nine hours later the fish was in the Gulf Stream. (5) By mid-afternoon on the following day, the fish had left the Gulf Stream and entered the Sargasso Sea. Filled circles represent sunset; open circles represent sunrise. [Adapted from Carey and Robison (1981).]

independent of any passive displacement due to water currents. Obtaining such information also depends on the sensory system(s) detecting variations in the stimuli to determine position with sufficient resolution to meet the navigational needs of the animal (Walker *et al.*, 2002).

The physics of proposed magnetoreceptor mechanisms do not exclude the possibility that the Earth's magnetic field is used for navigation, although the psychophysical experiments to determine whether or not fish have the necessary sensitivity have not yet been carried out. The results of sensory studies and field experiments with other vertebrates suggest, however, that the magnetic sense is widespread and that fish are likely to have the sensitivity required for use of the Earth's magnetic field in navigation (Klimley, 1993; Walker *et al.*, 1997; Diebel *et al.*, 2000). Thus, a magnetic sense based on the electroreceptors in the ampullae of Lorenzini could be useful in determining direction when setting a course toward a goal (Kalmijn, 1978; Paulin, 1995). Similarly, a magnetic sense based on SD magnetite would permit determination of direction and provide sufficient sensitivity to determine position with a resolution of a few kilometers (Kirschvink and Gould, 1981).

8.2. Hypotheses on Magnetic Navigation Mechanisms

As noted earlier, navigating animals must first determine their current location relative to a goal and then set and maintain a course for the goal (Kramer, 1953). The magnetic compasses of fish and other animals are well understood from laboratory studies. There is evidence that teleost and elasmobranch fishes respond to both magnetic intensity and direction in laboratory experiments (Wiltschko and Wiltschko, 1995) but almost no evidence that they respond to either of these dimensions of the Earth's magnetic field in nature. The use of magnetic field direction as a reference direction for setting and maintaining courses during long-distance navigation is relatively easy to understand. In contrast, there is no widely accepted model for how the Earth's magnetic field can be used to determine location. Because at least three models for magnetic position determination have been proposed (see later), caution will be required to ensure that the outcomes of experimental tests of predictions derived from any hypothesis on position determination are not ambiguous.

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. Models of bicoordinate position determination using the Earth's magnetic field fall into two classes: one derived from properties of the Earth's magnetic field and the other in which inferences about how the Earth's magnetic field might be

used are made from the results of behavioral experiments. Ideally, such models should be able not only to explain existing observations but also to make testable predictions about navigation behavior. Although several models of position determination using the Earth's magnetic field have been suggested, none have yet found experimental support in field studies.

One model of position determination that is based on properties of the Earth's magnetic field exploits a regular pattern of magnetic anomalies originating from rocks in the deep ocean crust. The process of seafloor spreading in the deep ocean results in linear magnetic anomalies (magnetic lineations) that are symmetrically arranged on opposite sides of spreading ridges. A second pattern of magnetic anomalies, aligned at high angles to the axes of the magnetic lineations, arise from magnetization of cooling magma produced at fracture zones across the new crust produced by the spreading ridges (Vine, 1966). These intersecting anomaly patterns distributed over the whole of the deep ocean are stable over very long periods and remain present during reversals of the dipole field (Kirschvink *et al.*, 1986). The anomaly patterns could be used to guide movement over long distances and would require only that the magnetic sense be able to detect small changes in the total intensity of the Earth's magnetic field. If animals use the anomalies as proposed, the model predicts that animals should preferentially follow linear features that are consistent with their migration direction.

Two further models of navigation under discussion used an alternative approach of deriving models of position determination based on data from behavioral experiments. First, Lohmann and his colleagues (Lohmann and Lohmann, 1996) developed a model of position determination based on responses by hatchling sea turtles to magnetic inclination and intensity in laboratory orientation experiments. This model was challenged on the grounds that inclination and intensity of the Earth's magnetic field are normally highly correlated and are only aligned at high angles to each other over areas that are both comparatively small and ephemeral over evolutionary time (Courtillet *et al.*, 1997).

Although the nature of the second coordinate has yet to be resolved, subsequent laboratory orientation experiments have demonstrated that sea turtles could use magnetic intensity, inclination, or both to determine magnetic "latitude." In experiments, juvenile sea turtles have been exposed to magnetic fields that simulated displacement over several hundred kilometers to the north or south of the location where they had been captured. Under these conditions, the animals oriented in directions that would lead them to return to the location from where they were captured (Lohmann *et al.*, 2004). This result suggests that the turtles could, in effect, use the value of the magnetic field at a single point (the area of a small orientation arena) to determine latitude.

The second model of magnetic position determination based on existing behavioral data arises from systematic variations in the behavior of homing pigeons returning to a loft from release sites distributed across a region (Walker, 1998). The variations in the behavior of the pigeons at release sites were correlated with the systematic variations in the intensity and the direction in which the slope in the intensity of the Earth's main field is oriented (Walcott, 1978). The model proposed that the intensity of the main field, which varies systematically in the magnetic north-south direction, could be treated as a latitude. In contrast, the second coordinate (direction of the slope of the main field) varies at right angles (roughly east-west) to the intensity latitude and so could be treated as a "longitude."

Challenges to this model have been based on physical arguments (Reilly, 2002) and the sensitivity to changes in magnetic fields required for the model to work (Wallraff, 1999). The model does, however, make predictions about the position determination behavior of animals that could be tested experimentally by displacing animals away from their familiar areas in much the same way as occurs in homing pigeon experiments. The model predicts that the behavior of displaced animals should be dominated by the residual magnetic field of the Earth at the release site (Walker, 1998). Testing the prediction will require high-resolution magnetic field information to which the behavior of the animals can be correlated, and higher resolution (more fixes per unit time) data than have been acquired to date in the tracking of the animals.

8.3. Developing Experimental Approaches to Navigation

Efforts to develop a methodological framework for the experimental study of navigation by fish can benefit from the experience of studies with birds. Homing pigeons have been the experimental model of choice for the study of long-distance navigation because they will navigate on demand, returning directly to their loft after displacement to distant, unfamiliar locations. Homing pigeons differ from wild birds (e.g., bank swallows; Keeton, 1973) and the rock dove, the ancestral species of the homing pigeon, in that pigeons have been bred for their homing ability, and also feed, rest, and breed exclusively at the loft. It therefore seems reasonable to hypothesize that the motivation of the pigeons to return directly to their loft is higher than in wild birds which, depending on their needs, may travel to feed in any one of a number of locations as well as returning to their nest after being captured, displaced, and released.

The variable that has been used almost exclusively in studies of pigeon navigation has been the vanishing bearing, the compass bearing from a release site at which an individual bird disappears from view in binoculars. Because

pigeons normally take up to several minutes to disappear from view, the vanishing bearing represents the outcome of the processes by which the bird determines its current location and then sets a course to its loft. It has therefore been very difficult to interpret the effects of experimental treatments on navigation behavior except where the effects can be interpreted as simple effects on the sun compass or the magnetic compass (Schmidt-Koenig, 1958; Keeton, 1971; Walcott and Green, 1974). In the last 5 years or so, high resolution tracks have been obtained from pigeons that have carried devices (Steiner *et al.*, 2000) which record positions taken from the satellites in the global positioning system (GPS). The use of geographical information systems combined with computer-intensive analytical techniques promise rapid advances in the ability to detect and analyze any behavior emitted as the animals seek to determine their current location and set a course for their loft.

The implication of the above-mentioned fact for experimental studies of navigation in fishes is that it will be important to achieve as much experimental control as possible over the behavior of the animals and, in particular, over their motivation to travel directly to a particular location that can be specified in advance. It will also be necessary in future experimental studies of navigation by fishes to develop methods for detecting navigational responses against the background of other behaviors that may be exhibited by free-living wild animals. Although it is not possible to obtain track records using the GPS, acoustic transmitters have long been used to track fish continuously. Maximizing the density and accuracy of position fixes on fish being tracked should therefore assist detection of navigational responses and also the effects of sensory treatments on behavior of fish that have been experimentally displaced.

9. WHAT IS KNOWN ABOUT THE NAVIGATIONAL ABILITIES OF FISH?

Descriptive evidence for the navigational abilities of fishes has come from mark-recapture and tracking studies that described point-to-point movements and continuous tracks recorded over periods from a few days up to years. Early studies demonstrated that representatives of different fish taxa travel over distances from tens to thousands of kilometers in both the shallow and deep water marine environments (Block *et al.*, 2001; Boustany *et al.*, 2002; Bonfil *et al.*, 2005; Weng *et al.*, 2005). During many of these movements, the fish clearly traveled independently of the flow directions of either local or major currents and could stay on the same course for long periods (Figure 8.8) (Carey and Robison, 1981).

Tracking of individual fish using ultrasonic transmitters has also provided clear evidence for the ability to return repeatedly to the same locations (Yuen, 1970; Carey and Robison, 1981; Klimley and Nelson, 1984; Klimley, 1993) and to travel in the same direction for extended periods (Carey and Robison, 1981). The earliest examples of the ability of fish to monitor position during travel include those of Yuen (1970), Carey and Robison (1981), and Klimley and Nelson (1984) who found that skipjack tuna, billfish, and scalloped hammerhead sharks made repeated daily movements to and from feeding or refuge areas. A skipjack tuna tracked over 5 days by Yuen (1970) fed at the Ka'ula Bank in the Hawai'ian Islands by day and made night journeys of 25–206 km away from the bank, returning to the bank at about the same time each morning. Scalloped hammerhead sharks and swordfish showed the same pattern, although the sharks left shallow water each night to feed and returned to shallow water by day (Figure 8.9) (Carey and Robison, 1981; Klimley and Nelson, 1984). The precise timing of these movements and the regular returns to the same locations are consistent with the hypothesis that both teleost and elasmobranch fishes can monitor their position accurately.

More direct evidence that fish can both determine and monitor their position has come from the homing movements made by displacement experiments with juvenile lemon sharks (Sundström *et al.*, 2001). Sharks were transported away from their previously determined activity space to 18 randomly chosen release sites 4–15 km offshore from Bimini Islands. After release, the sharks swam in an oscillating zigzag pattern along a consistent mean direction for 2–10 min before selecting a heading along a new axis (Figure 8.10). After repeating this pattern in several directions, the fish chose a “homeward” direction, much as homing pigeons appear to do (Dennis *et al.*, 2005). The fish then returned rapidly to shallow water areas around the Bimini Islands but did not simply retrace the path over which they were taken during the displacement. These observations are consistent with the ability of fish to navigate but do not tell us how navigation is achieved.

Evidence that fish use the Earth's magnetic field for navigation is, to our knowledge, limited to one study in which scalloped hammerhead sharks were tracked around seamounts in Baja, California (Klimley, 1993). As in the studies with tuna, the tracked fish made repeated round trip journeys each night, traveling away from El Bajo Espiritu Santu seamount into the pelagic area and returning each morning. Monte Carlo simulations demonstrated that the fish responded to features of the residual magnetic field but not to bathymetric features that were associated with the seamount. Klimley (1993) described the pattern of movement by the sharks as a magnetotaxis and suggested that the fish used the Earth's magnetic field in navigation. This conclusion is consistent with the prediction that

8. MAGNETORECEPTION

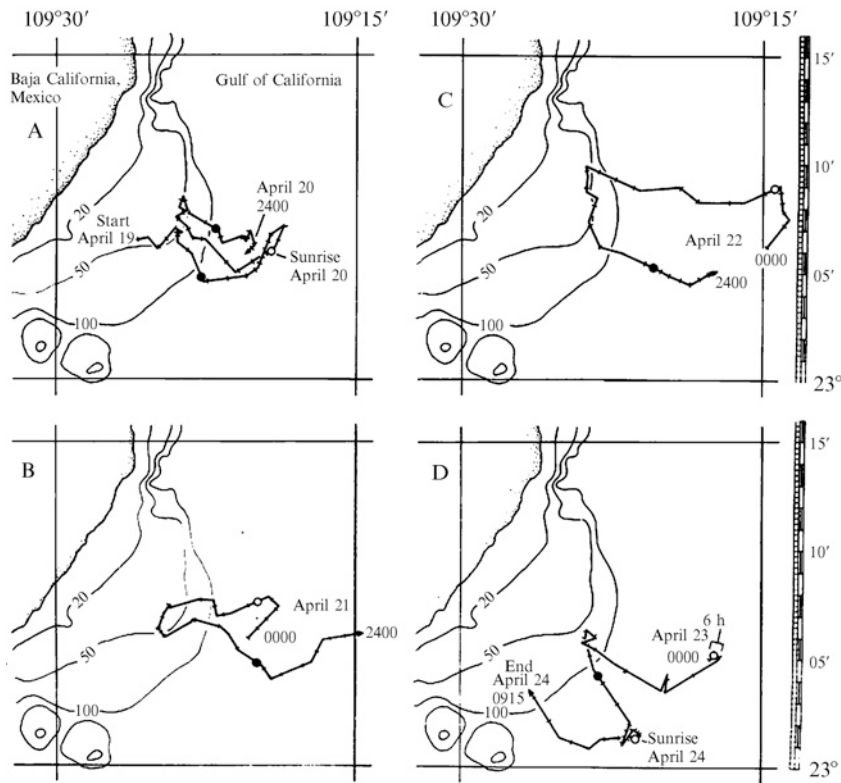


Fig. 8.9. Diurnal movement patterns in swordfish. Track of a swordfish showing repeated return movements over 4 days. Each day the fish moved onshore to the 50 fathom (91 m) depth contour on a bank and then moved out over deep water at night. The move toward shore began about 1 h before dawn and the move offshore began several hours before sunset. Filled circles represent sunset and open circles represent sunrise. [Adapted from Carey and Robison (1981).]

navigating animals might use the topography of the residual magnetic field to construct a familiar area map.

Attempts to manipulate the magnetic sense experimentally during navigation have been inconclusive. Yano *et al.* (1997) tracked salmon fitted with magnetic coils that reversed both the horizontal direction and the inclination of the magnetic field and increased the total intensity 3.5-fold within the heads of the fish. The coils were switched on and off at 11.25-min intervals and the behavior of the animals monitored in the presence and absence of the reversed field produced by the coils. Although the swimming speed of the fish was observed to decrease prior to any changes in swimming

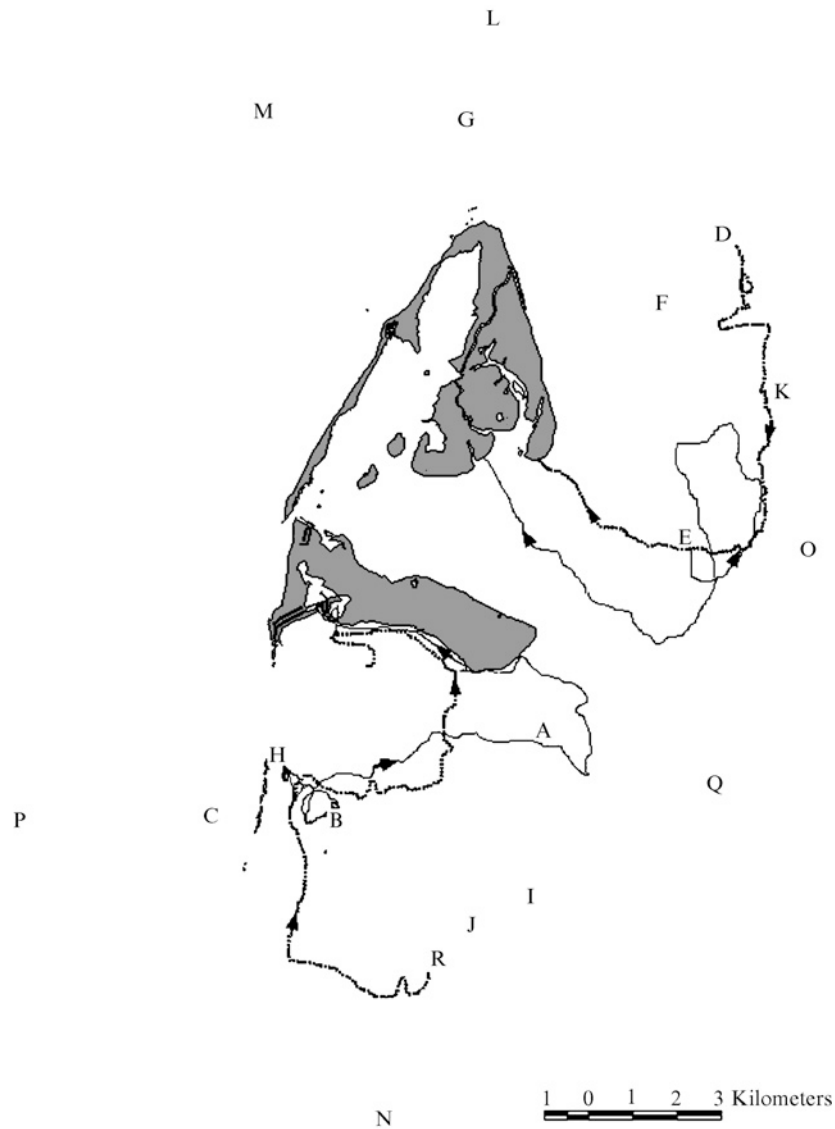


Fig. 8.10. Homing behavior of juvenile lemon sharks. Tracks from 4 (of 41) juvenile lemon sharks, *Negaprion brevirostris*, displaced to release points (A–R) located 4–15 km offshore from Bimini Islands, Bahamas. On release (at points B, D, E, and R), the sharks swam to the bottom and moved in a pattern of oscillating directions for 2–10 min before setting off on sustained, relatively straight courses that quickly brought them back to the islands. [Adapted from Sundström *et al.* (2001) with permission.]

direction, at no stage during the tracks was it possible to detect any effect on behavior of switching the magnetic coils on or off. This result illustrates the need to seek greater experimental control over the behavior of tracked animals, for example, by using animals that will return to a specified location after displacement.

10. CONCLUDING REMARKS

Fish have played a central role in studies of the structure and function of the magnetic sense. More is known about the crystal properties of biogenic magnetite, the candidate magnetite-based magnetoreceptor cells, and the magnetic field detection pathway in the fishes than in any other metazoan group. We are, however, only just beginning the systematic study of the magnetic sense in animals and there is much more yet to be discovered than has been learned to date. Thus, for a magnetite-based magnetoreceptor system, descriptions of the internal structure of candidate magnetoreceptor cells, their synaptic links to afferent nerves, and central projections in the brain are priorities for structural study of the magnetic sense in all animals, including the fishes, which are well suited for such work. Similarly, functional studies of these magnetoreceptor cells, the coding of magnetic field information for transmission to the brain, analysis of the psychophysical properties, and demonstration of dependence of sensory capacity on the structure of the sense are all required if we have to understand the magnetic sense in detail.

Despite no new data having been reported for some time, it is important to resolve the issue of whether or not the elasmobranch fishes detect magnetic fields using their electroreceptor system. Recordings from both peripheral and central neurons demonstrate that the electroreceptor system of elasmobranchs detects the electrical currents induced by fish and water movement through the Earth's magnetic field (Andrianov *et al.*, 1974; Brown and Ilyinsky, 1978). What the recordings do not show is whether the electrical information about the external magnetic field is distinguished from other electrical field information and whether use is made of the magnetic information obtained by the electroreceptor system. It is also not clear how sensitive the electroreceptor system will be to magnetic fields as the threshold sensitivity to magnetic field changes estimated from the recordings was 200 $\mu\text{T}/\text{sec}$ (Andrianov *et al.*, 1974), equivalent to traveling from the magnetic equator to the magnetic pole in 0.25 sec.

Distinguishing between the electrical induction- and magnetite-based magnetoreception mechanisms will require further behavioral experiments

like those in which magnets were attached over the predicted location of magnetite-based magnetoreceptors in the short-tailed stingray (Hodson, 2000; Kirschvink *et al.*, 2001). A further approach to distinguishing these mechanisms is bilateral sectioning of the SO branch of the TN, which abolished magnetic field discrimination in homing pigeons (Mora *et al.*, 2004). Failure to discriminate magnetic fields after bilateral sectioning of the SO of the TN would suggest the conclusion that their electroreceptors provide the elasmobranchs with no useful sensitivity to magnetic field stimuli even though the electroreceptors clearly detect the electrical signals that will frequently be induced in them.

The discovery that juvenile lemon sharks will home rapidly after being experimentally displaced (Sundström *et al.*, 2001) opens the way for more detailed studies of the role of the magnetic sense in navigation. Homing pigeons have been the only organisms that would home reliably after experimental displacement. In contrast with the pigeons, the likely motivation for the lemon sharks to home as rapidly as they did was to escape predation because “numerous large sharks that feed on smaller sharks inhabit the water around the Bimini Islands” (Sundström *et al.*, 2001). There are perhaps other fish species in which juvenile animals inhabit nurseries to which they will return after experimental displacement. Thus, the opportunity exists to begin comparative study of the navigation behavior of fish and homing pigeons. Although there is little powerful experimental evidence for the use of the Earth’s magnetic field in navigation in any major taxonomic group, we suggest that there will be much to learn from such comparative studies just as from comparative studies of the magnetic sense itself in fish and birds. We look forward to exciting advances in our understanding of the properties and use of this most enigmatic of animal senses in the years to come.

REFERENCES

- Andrianov, G. N., Brown, H. R., and Ilyinsky, O. B. (1974). Responses of central neurons to electrical and magnetic stimuli of the Ampullae of Lorenzini in the Black Sea Skate. *J. Comp. Physiol. A*, **93**, 287–299.
- Beason, R. C., and Semm, P. (1987). Magnetic responses of the trigeminal nerve system of the bobolink (*Dolichonyx oryzivorus*). *Neurosci. Lett.* **80**, 229–234.
- Blakemore, R. P. (1975). Magnetotactic bacteria. *Science* **190**, 377–379.
- Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A., and Fudge, D. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic Bluefin Tuna. *Science* **293**, 1310–1314.
- Bodznick, D., Montgomery, J., and Tricas, T. C. (2003). Electroreception: Extracting behaviorally important signals from noise. In “Sensory Processing in Aquatic Environments” (Collin, S. P., and Marshall, N. J., Eds.), pp. 389–403. Springer-Verlag, NY.

- Bonfil, R., Meÿer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D., and Paterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 101–103.
- Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J., and Block, B. A. (2002). Satellite tagging: Expanded niche for white sharks. *Nature* **415**, 35–36.
- Brown, H. R., and Ilyinsky, O. B. (1978). The ampullae of Lorenzini in the magnetic field. *J. Comp. Physiol. A* **125**, 333–341.
- Bullock, T. H., and Szabo, T. (1986). Introduction. In “Electroreception” (Bullock, T. H., and Heiligenberg, W., Eds.), pp. 1–12. Wiley, New York.
- Carey, F. G., and Robison, B. H. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish Bull.* **79**, 277–292.
- Clusin, W. T., and Bennett, M. V. L. (1979a). The oscillatory responses of skate electroreceptors to small voltage stimuli. *J. Gen. Physiol.* **73**, 685–702.
- Clusin, W. T., and Bennett, M. V. L. (1979b). The ionic basis of oscillatory responses of skate electroreceptors. *J. Gen. Physiol.* **73**, 703–723.
- Courtyllot, V., Hulot, G., Alexandrescu, M., le Mouel, J.-L., and Kirschvink, J. L. (1997). Sensitivity and evolution of sea-turtle magnetoreception: Observations, modelling and constraints from geomagnetic secular variation. *Terra Nova* **9**, 203–207.
- Davila, A. F., Fleissner, G., Winklhofer, M., and Petersen, N. (2003). A new model for a magnetoreceptor in homing pigeons based on interacting clusters of superparamagnetic magnetite. *Phys. Chem. Earth* **28**, 647–652.
- Dennis, T. E., Rayner, M. J., and Walker, M. M. (2005). Spatially explicit behavioural response to geomagnetic intensity during homing in pigeons (Abstract). In “Fifth International Conference on Orientation and Navigation: Birds, Humans, and Other Animals,” paper 18. Royal Institute of Navigation, University of Reading, London.
- Diebel, C. E., Proksch, R., Green, C. R., Neilson, P., and Walker, M. M. (2000). Magnetite defines a magnetoreceptor. *Nature* **406**, 299–302.
- Dijkgraaf, S., and Kalmijn, A. J. (1962). Verhaltensversuche zur Funktion der Lorenzischen Ampullen. *Naturwissenschaften* **49**, 400.
- Emlen, S. T. (1975). Migration: Orientation and navigation. In “Avian Biology” (Farner, D. S., and King, J. R., Eds.), Vol. 5, pp. 129–219. Academic Press, New York.
- Finger, T. E., St. Jeor, V. L., Kinnamon, J. C., and Silver, W. L. (1990). Ultrastructure of substance P- and CGRP-immunoreactive nerve fibers in the nasal epithelium of rodents. *J. Comp. Neurol.* **294**, 293–305.
- Fleissner, G., Holtkamp-Rötzler, E., Hanzlik, M., Winklhofer, M., Fleissner, G., Petersen, N., and Wiltshko, W. (2003). Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* **458**, 350–360.
- Glatzmaier, G. A., and Roberts, P. H. (1995). A three-dimensional self-consistent computer simulation of a geomagnetic field reversal. *Nature* **377**, 203–209.
- Gould, J. L., Kirschvink, J. L., and Deffeyes, K. S. (1978). Bees have magnetic remanence. *Science* **201**, 1026–1028.
- Hodson, R. B. (2000). Magnetoreception in the short-tailed stingray, *Dasyatis brevicaudata*. University of Auckland, New Zealand. Unpublished Masters Thesis.
- Kalmijn, A. J. (1966). Electro-perception in sharks and rays. *Nature* **212**, 1232–1233.
- Kalmijn, A. J. (1978). Experimental evidence of geomagnetic orientation in elasmobranch fishes. In “Animal Migration, Navigation and Homing” (Schmidt-Koenig, K., and Keeton, W. T., Eds.), pp. 347–353. Springer-Verlag, Berlin, New York.
- Kalmijn, A. J. (1982). Electric and magnetic field detection in elasmobranch fishes. *Science* **218**, 916–918.
- Keeton, W. T. (1971). Magnets interfere with pigeon homing. *Proc. Natl. Acad. Sci. USA* **68**, 102–106.

- Keeton, W. T. (1973). Release-site bias as a possible guide to the "map" component in pigeon homing. *J. Comp. Physiol. A* **86**, 1–16.
- Kirschvink, J. L. (1992). Uniform magnetic fields and double-wrapped coil systems: Improved techniques for the design of bioelectromagnetic experiments. *Bioelectromagnetics* **13**, 401–412.
- Kirschvink, J. L., and Gould, J. L. (1981). Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems* **13**, 181–201.
- Kirschvink, J. L., and Kobayashi-Kirschvink, A. (1991). Is geomagnetic sensitivity real? Replication of the Walker-Bitterman magnetic conditioning experiment in honey bees. *Am. Zool.* **31**, 169–185.
- Kirschvink, J. L., and Walker, M. M. (1985). Particle-size considerations for magnetite-based magnetoreceptors. In "Magnetite Biomineralization and Magnetoreception by Living Organisms: A New Biomagnetism" (Kirschvink, J. L., Jones, D. S., and MacFadden, B. J., Eds.), pp. 243–254. Plenum Publishing Corporation, New York.
- Kirschvink, J. L., Jones, D. S., and MacFadden, B. J. (Eds.). (1985a). "Magnetite Biomineralization and Magnetoreception by Living Organisms: A New Biomagnetism," Vol. xxi, p. 682. Plenum Publishing Corporation, New York.
- Kirschvink, J. L., Walker, M. M., Chang, S.-B., Dizon, A. E., and Peterson, K. A. (1985b). Chains of single-domain magnetite particles in the chinook salmon, *Oncorhynchus tshawytscha*. *J. Comp. Physiol. A* **157**, 375–381.
- Kirschvink, J. L., Dizon, A. E., and Westphal, J. A. (1986). Evidence from strandings for geomagnetic sensitivity in cetaceans. *J. Exp. Biol.* **120**, 1–24.
- Kirschvink, J. L., Padmanabha, S., Boyce, C. K., and Oglesby, J. (1997). Measurement of the threshold sensitivity of honeybees to weak, extremely low frequency magnetic fields. *J. Exp. Biol.* **200**, 1363–1368.
- Kirschvink, J. L., Walker, M. M., and Diebel, C. E. (2001). Magnetite-based magnetoreception. *Curr. Opin. Neurobiol.* **11**, 462–467.
- Klimley, A. P. (1993). Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and substrate irradiance, temperature, bathymetry and geomagnetic field. *Marine Biol.* **117**, 1–22.
- Klimley, A. P., and Nelson, D. R. (1984). Diel movement patterns of the scalloped shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: A refuging central position social system. *Behav. Ecol. Sociobiol.* **15**, 45–54.
- Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *J. für Ornithologie* **94**, 201–219.
- Lohmann, K. J., and Lohmann, C. M. F. (1996). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61.
- Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A., and Swing, T. (2004). Geomagnetic map used in sea turtle navigation. *Nature* **428**, 909–910.
- Mann, S., Sparks, N. H. C., Walker, M. M., and Kirschvink, J. L. (1988). Ultrastructure, morphology and organization of biogenic magnetite from sockeye salmon, *Oncorhynchus nerka*: Implications for magnetoreception. *J. Exp. Biol.* **140**, 35–49.
- McKeegan, D. E. F., Smith, F. S., Demmers, T. G. M., Wathes, C. M., and Jones, R. B. (2005). Behavioral correlates of olfactory and trigeminal gaseous stimulation in chickens, *Gallus domesticus*. *Physiol. Behav.* **84**, 761–768.
- Meÿer, C. G., Holland, K. N., and Papastamatiou, Y. P. (2005). Sharks can detect changes in the geomagnetic field. *J. R. Soc. Interface* **2**, 129–130.
- Mora, C. V., Davison, M. C., Wild, N. M., and Walker, M. M. (2004). Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature* **432**, 508–511.
- Murray, R. W. (1960). Electrical sensitivity of the ampullae of Lorenzini. *Nature* **187**, 957.

- Nishi, T., and Kawamura, G. (2005). *Anguilla japonica* is already magnetosensitive at the glass eel phase. *Fish. Sci.* **67**, 1213–1224.
- Nishi, T., Kawamura, G., and Matsumoto, K. (2004). Magnetic sense in the Japanese eel, *Anguilla japonica*, as determined by conditioning and electrocardiography. *J. Exp. Biol.* **207**, 2965–2970.
- Nishi, T., Kawamura, G., and Sannomiya, S. (2005). Anosmic Japanese eel *Anguilla japonica* can no longer detect magnetic fields. *Fish. Sci.* **71**, 101–106.
- Paulin, M. G. (1995). Electroreception and the compass sense of sharks. *J. Theor. Biol.* **174**, 325–339.
- Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake-migrating sockeye salmon fry. *J. Comp. Physiol. A* **137**, 243–248.
- Reilly, W. I. (2002). Magnetic position determination by homing pigeons? *J. Theor. Biol.* **218**, 47–54.
- Rommel, S. A., and McCleave, J. D. (1973). Sensitivity of American eels (*Anguilla rostrata*) and Atlantic salmon (*Salmo salar*) to weak electric and magnetic fields. *J. Fish. Res. Board Canada* **30**, 657–663.
- Schmidt-Koenig, K. (1958). Experimentelle Einflußnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unter besonderer Berücksichtigung des Heimfindevermögens. *Zeitschrift für Tierpsychologie* **15**, 301–331.
- Semm, P., and Beason, R. C. (1990). Responses to small magnetic field variations by the trigeminal system of the bobolink. *Brain Res. Bull.* **25**, 735–740.
- Skiles, D. D. (1985). The geomagnetic field: Its nature, history and biological relevance. In “Magnetite Biomineralization and Magnetoreception by Living Organisms: A New Biomagnetism” (Kirschvink, J. L., Jones, D. S., and MacFadden, B. J., Eds.), pp. 43–102. Plenum Publishing Corporation, New York.
- Steiner, I., Bürgi, C., Werffeli, S., Dell’Omo, G., Valenti, P., Tröster, G., Wolfer, D. P., and Lipp, H.-P. (2000). A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol. Behav.* **71**, 589–596.
- Sundström, L. F., Gruber, S. H., Clermont, S. M., Correia, J. P. S., de Marniac, J. R. C., Morrissey, J. F., Lowrance, C. R., Thomassen, L., and Oliveira, M. T. (2001). Review of elasmobranch behavioural studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Env. Biol. Fishes* **60**, 225–250.
- Taylor, P. B. (1986). Experimental evidence for geomagnetic orientation in juvenile salmon, *Oncorhynchus tshawytscha* Walbaum. *J. Fish Biol.* **28**, 607–623.
- Taylor, P. B. (1987). Experimental evidence for juvenile chinook salmon, *Oncorhynchus tshawytscha* Walbaum, orientation at night and in sunlight after a 7° change in latitude. *J. Fish Biol.* **31**, 89–111.
- Viguiier, C. (1882). Le sens d’orientation et ses organes chez les animaux et chez l’homme. *Revue Philosophique de la France et de l’Étranger* **14**, 1–36.
- Vine, F. J. (1966). Spreading of the ocean floor; new evidence. *Science* **154**, 1405–1415.
- Walcott, C. (1978). Anomalies in the Earth’s magnetic field increase the scatter of pigeons’ vanishing bearings. In “Animal Migration, Navigation, and Homing” (Schmidt-Koenig, K., and Keeton, W. T., Eds.), pp. 143–151. Springer-Verlag, Berlin.
- Walcott, C., and Green, R. P. (1974). Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. *Science* **184**, 180–182.
- Walker, M. M. (1984). Learned magnetic field discrimination in the yellowfin tuna, *Thunnus albacares*. *J. Comp. Physiol. A* **155**, 673–679.
- Walker, M. M. (1998). On a wing and a vector: A model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 341–349.
- Walker, M. M., and Bitterman, M. E. (1989). Honeybees can be trained to respond to very small changes in geomagnetic field intensity. *J. Exp. Biol.* **145**, 489–494.

- Walker, M. M., Kirschvink, J. L., Chang, S.-B. R., and Dizon, A. E. (1984). A candidate magnetic sense organ in the yellowfin tuna, *Thunnus albacares*. *Science* **224**, 751–753.
- Walker, M. M., Diebel, C. E., Haugh, C. V., Pankhurst, P. M., Montgomery, J. C., and Green, C. R. (1997). Structure and function of the vertebrate magnetic sense. *Nature* **390**, 371–376.
- Walker, M. M., Diebel, C. E., and Green, C. R. (2000). Structure, function and use of the magnetic sense in vertebrates. *J. Appl. Physics* **87**, 4653–4658.
- Walker, M. M., Dennis, T. E., and Kirschvink, J. L. (2002). The magnetic sense and its use in long-distance navigation by animals. *Curr. Opin. Neurobiol.* **12**, 735–744.
- Wallraff, H. G. (1999). The magnetic map of homing pigeons: An evergreen phantom. *J. Theor. Biol.* **197**, 265–269.
- Weng, K. C., Castilho, P. C., Morrissette, J. M., Landeira-Fernandez, A. M., Holts, D. B., Schallert, R. J., Goldman, K. J., and Block, B. A. (2005). Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* **310**, 104–106.
- Wiltschko, R., and Wiltschko, W. (1995). “Magnetic Orientation in Animals,” Vol. xvii, p. 297. Springer, Berlin, New York.
- Yano, A., Ogura, M., Sato, A., Sakaki, Y., Shimizu, Y., Baba, N., and Nagasawa, K. (1997). Effect of modified magnetic field on the ocean migration of maturing chum salmon. *Marine Biol.* **129**, 523–530.
- Yuen, H. S. H. (1970). Behaviour of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. *J. Fish. Res. Board Canada* **27**, 2071–2079.