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Detection and Use of the Earth's Magnetic Field by Aquatic Vertebrates

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Abstract

Although the hypothesis that animals use a magnetic sense to navigate over long distances in the sea is intuitively appealing, evidence that aquatic vertebrates respond to the magnetic field in nature has been difficult to obtain until recent years. Aquatic vertebrates have, however, been prominent in laboratory-based demonstration and analysis of the magnetic sense and its mechanism. The key conclusions of these studies have been that the magnetic sense exhibits fundamental properties found in other specialized sensory systems and that the magnetic senses of aquatic vertebrates and birds exhibit substantial similarities. In particular, the magnetic sense appears to be *selective* for the magnetic field stimulus; that is, it responds only to the magnetic field stimulus and does not extract magnetic field information from interactions of the magnetic field with the detector components in other specialized sensory systems. The magnetic sense of aquatic vertebrates is also likely to be *highly sensitive* to small changes in magnetic fields, with its detector cells operating at close to the limit set by background thermal energy. Finally, it seems likely that the magnetic senses of birds and aquatic vertebrates exhibit substantial similarities in their structure and function.

Laboratory experiments have demonstrated behavioral and neural responses to magnetic direction and intensity in species from four classes of aquatic vertebrates. Magnetic impairment experiments also strongly imply that magnetic field detection in both sea turtles and elasmobranchs is based on single-domain particles of magnetite. At the receptor level, an array of new imaging and microscopic techniques has identified magnetoreceptor cells that contain 1- μ m-long chains of single-domain magnetite crystals within the olfactory lamellae of rainbow trout. These chains of magnetite crystals will respond only to magnetic fields and appear to have been selected for high sensitivity to small changes in magnetic field stimuli. Recent experiments have demonstrated that the magnetic sense of birds is also based on magnetite located in the nasal

region and that the same nerve carries magnetic field information to the brain in both fishes and birds. It therefore seems likely that magnetite is the basis of magnetic field detection in a wide range of vertebrate groups. We conclude that, in the aquatic vertebrates, the magnetic sense can now be demonstrated and analyzed in the laboratory using experimental approaches developed for the study of other sensory modalities. Careful selection of experimental subjects will be required, however, to overcome the challenge of applying insights gained in the laboratory to experimental analysis of the use of the magnetic field in the aquatic environment.

1. Introduction

How animals navigate over long distances is one of the great, unsolved mysteries in biology today. Nowhere is this more true than in aquatic environments, where swimming animals are subject to passive displacement by water currents that may be very difficult to detect, particularly in deep water. There are, however, abundant examples that pelagic animals traveling in deep water (e.g., Holland et al., 1990; Klimley, 1993; Papi et al., 1997, 2000) know where they are and can travel direct routes between important locations in their environment even when traveling within major current systems. What such studies do not provide is answers to questions about the external stimuli used by animals to navigate over these long distances.

The hypothesis that animals navigate using the earth's magnetic field was first proposed in the nineteenth century (Viguier, 1882), and has an abiding intuitive appeal. This appeal serves only to add to the mystery of animal navigation, however, because the difficulty of achieving reproducible behavioral responses to magnetic field stimuli in the laboratory and the lack of an identifiable magnetic sense "organ" led instead to widespread skepticism about the existence of the magnetic sense (e.g., Griffin, 1982). It was not until the early 1970s that the first experimental evidence was obtained for detection of magnetic fields by birds (Keeton, 1971; Wiltschko, 1972) and it was some years before the first reproducible responses to magnetic fields by aquatic species were reported

(Phillips, 1977; Quinn, 1980). These results were not sufficient to dispel skepticism entirely, however, because the locus and mechanism of magnetic field detection and the neural pathway transmitting magnetic field information to the brain remained unidentified.

In this chapter, we summarize the evidence from field studies suggesting that sharks and whales use the magnetic field to guide long-distance movements. We then focus on experimental demonstration and analysis of the magnetic sense and its mechanism. Our central thesis is that the magnetic sense will share key properties with other sensory systems. In particular, the cells that detect magnetic fields should be selective for and have high sensitivity to magnetic fields (Block, 1992). That is, the receptor cells should respond only to magnetic fields (their adequate stimulus) and their sensitivity to changes in magnetic fields should approach the limit set by the background thermal energy, kT . Experimental results suggest that the magnetic sense of aquatic vertebrates does indeed respond only to its adequate stimulus, but it remains to be demonstrated experimentally that the magnetic sense also shares the property of being highly sensitive to magnetic fields. We conclude that a coherent picture is emerging but that much more work is required to elucidate the structure, function, and use of the magnetic sense in aquatic vertebrates. Of particular importance will be demonstration of the links among the components of the magnetic sense and experimental testing of the use of the sense in nature.

3. Detection and Use of the Earth's Magnetic Field

2. The Magnetic Field as a Stimulus

2.1. Sources of the Observed Magnetic Field

By far the bulk of the magnetic field that can be observed within the biosphere is generated through heat convection currents flowing within the molten core of the Earth. These produce the well-known magnetic dipole (represented schematically in Fig. 3.1) that attracts the north-seeking pole of a hand-held compass. The magnetic dipole is responsible for systematic increases in the *intensity* (the force the magnetic field exerts on a unit dipole) and *inclination* (the angle formed between the magnetic field vector and the local horizontal) between the equator and the poles of the Earth's magnetic field. A mathematical model of the dipole and non-dipole components of the field produced in the Earth's core permits calculation of the systematic variation in the observed field. The model does not account for all of the fields due to crustal rocks, which constitute the residual field (sometimes termed magnetic anomalies). The *declination* of the Earth's field is defined as the angle between magnetic and geographic north and arises because the axes of the earth's rotation and its magnetic dipole are not aligned. Magnetic declination varies rapidly near the magnetic poles and relatively slowly near the magnetic equator (see Skiles, 1985, for a comprehensive review of the Earth's magnetic field relevant to living organisms).

In addition to the dipole field produced in the Earth's core, non-dipole components of the field produced in the core and crustal rocks produce magnetic fields (magnetic anomalies) that add to or subtract from the dipole field produced in the core. The fields due to crustal rocks are generally small (<5% of the total field) but can vary rapidly over short distances relative to the field produced in the core. The non-dipole components of the core field produce magnetic anomalies that vary more slowly and spread over much larger areas than those normally produced by crustal rocks. Figure 3.1 shows in schematic form a magnetic anomaly caused by the interaction between the

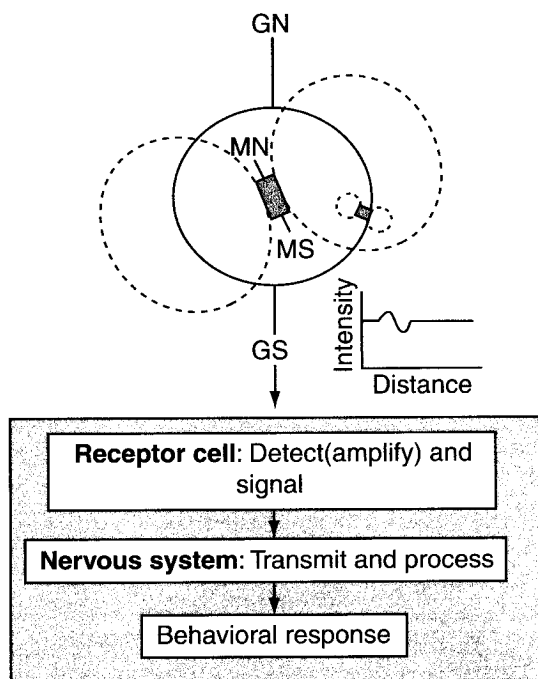


FIGURE 3.1. Schematic of the dipole magnetic field produced in the Earth's core, its interaction with a simple dipole source in the Earth's crust, and hypothesized locations and interactions with key components (boxes) of the magnetic sensory system. MN, MS: magnetic north and south poles; GN, GS: geographic north and south poles; solid circle: surface of the Earth; broken lines: magnetic field lines around magnetic dipole sources (filled bars) in the core and crust of the Earth. (Inset: schematic plot of intensity as a function of distance along a transect through a simple dipole anomaly arising from the interaction of a magnetic source in the crust with the dipole produced in the Earth's core.) The magnetic field stimulus enters the body (shaded box) unchanged where it interacts with the detector element in a receptor cell. The transduced magnetic signal may then be amplified before conversion into a change in the membrane potential of the receptor cell that transmits the transformed signal to the afferent nerve. The peripheral afferent nerve then transmits the signal to the brain where it is processed and a behavioral output is produced.

Earth's magnetic dipole and a dipole magnetic source (such as a volcanic or iron deposit) in the Earth's crust. The inset graph in Figure 3.1 is a simplified illustration of the field that would

be recorded by a magnetometer along a transect across the source of the anomaly. The intensity measured by the magnetometer is constant outside the anomaly and represents the field produced in the Earth's core. The interaction between the dipole fields from the core and the source of the anomaly produces the sinusoidal section of the intensity plot in Figure 3.1.

The Earth's dipole magnetic field thus provides consistent information about direction and latitude throughout the biosphere. In particular, the polarity of the field provides information about absolute direction, whereas the inclination of the field identifies the Earth's magnetic axis together with the directions to the magnetic equator and nearest magnetic pole. Animals sensitive enough to magnetic fields to detect the systematic variations in the inclination and intensity of the field could obtain information about their location relative to the magnetic equator and pole (a magnetic latitude akin to geographic latitude). Note, however, that the information about latitude from the intensity of the Earth's field is embedded in considerable noise due to the non-dipole fields produced in the core, fields produced by crustal rocks, and short-term variations in the field produced by the solar wind and solar flares (Skiles, 1985). Over longer time periods, secular variation can cause considerable variations in total intensity at any given site while the dipole field can reverse completely at time intervals of from tens of thousands to hundreds of thousands of years (Skiles, 1985; Courtillot et al., 1997).

2.2. Implications for Detection and Use of the Earth's Magnetic Field

Magnetic fields are relatively simple stimuli that have only the two dimensions of intensity and direction. The magnetic field observed at a point on the surface of the Earth includes stable components that vary systematically over very long distances (thousands of km) and randomly over much shorter distances (meters to tens of km; Fig. 3.1). Systematic variations in intensity due to the field in the Earth's core range from 2 to 5 nanoTesla (nT) per km between the mag-

netic equator and the magnetic poles, whereas the intensity variations due to crustal rocks range from 10^1 to 10^2 nT per km with extremes on the order of 10^3 nT per km.

If we consider only the above stable components of the Earth's magnetic field, we can see that animals will only experience change in the magnetic field they observe when they move. Because the Earth's magnetic field varies over different scales, the separate components of the observed field will change at different rates. As animals move around their environment, they will thus be exposed to field changes over a range of frequencies. The lowest frequencies will spring from the systematic variation due to the dipole produced in the Earth's core, whereas the highest frequencies will be those experienced when animals move through areas where there are strong magnetic anomalies.

Based on our central thesis above, we present in schematic form (Fig. 3.1) the entry of the magnetic field stimulus into the body of the animal and its interactions with the key components of the magnetic sensory system. Because tissues are transparent to magnetic fields, the magnetic field stimulus potentially can enter the receptor cell directly, where it will impinge on a detector element that responds only to magnetic fields. The transduced magnetic field signal is likely to be amplified after detection (Block, 1992) and to result in a change in the membrane potential of the receptor cell. The change in the membrane potential of the receptor cell is transmitted across the afferent synapse to the afferent nerve, which then transmits the encoded information about the magnetic field stimulus to the central nervous system. This information is then processed by the brain and a behavioral output specified if necessary.

The hypothesis that animals use the Earth's magnetic field for navigation predicts that animals should be differentially associated with particular features of the field. The fields produced in the Earth's core and in crustal rocks both potentially contain navigational information that animals might use to guide movement. It has proven difficult, however, to determine what might be the respective roles of the two components in navigation by animals. The sys-

tematic variation produced in the Earth's core provides information about location between the magnetic equator and pole (a latitude), but a second coordinate (a longitude) that might be used with the latitudinal information to determine position has not yet been clearly identified. The fields produced in the crustal rocks produce a magnetic topography that animals might use as landmarks or guides during homing and migration (e.g., Kirschvink et al., 1986). Results presented in the next section are consistent with the hypothesis that both sharks and whales respond to features of the magnetic environment associated with magnetic anomalies. Note, however, that there is as yet no direct experimental evidence outside the laboratory for response by aquatic animals to magnetic fields.

3. Evidence for Response to the Earth's Magnetic Field in the Aquatic Environment

Differential association with magnetic field parameters of the positions where whales strand themselves alive (Klinowska, 1985; Kirschvink et al., 1986), where fin whales are sighted at sea (Walker et al., 1992), and of the tracks of hammerhead sharks (Klimley, 1993) are consistent with the hypothesis that aquatic animals respond to the magnetic intensity topography produced by crustal rocks. Thus Klinowska (1985) hypothesized that whales that strand themselves alive have made a significant orientation error and that examination of geophysical variables at such stranding sites should give clues to the nature of the sensory information that was being used when the mistake was made. When she superimposed the locations of live stranding sites on magnetic anomaly maps of the United Kingdom, Klinowska (1985) observed an association between the locations of live stranding sites and areas where minima (or valleys) in the magnetic topography intersected the coast. This pattern was confirmed and extended for the coast of the eastern United States by Kirschvink et al. (1986), who used Monte Carlo simulations to show that the

observed patterns of live strandings could not have occurred by chance. These results were consistent with the ability of the whales to detect geomagnetic topography (Kirschvink et al., 1986) as suggested by Klinowska (1985).

It must be acknowledged, however, that live strandings of whales are, first, rare events that in no way reflect the normal behavior of whales and, second, subject to significant sampling biases associated with unrelated phenomena such as human population density (Mead, 1979). These problems were overcome in an analysis of associations between the sighting positions at sea of fin whales collected by the Cetacean and Turtle Assessment Programme (CETAP) run by the Bureau of Land Management during the late 1970s and early 1980s. The CETAP surveys collected systematic sighting data to assess the abundance of large marine animals over the continental shelf between Cape Hatteras and the Gulf of Maine.

Sighting positions for fin whales from the CETAP data set were superimposed on geophysical data for the continental shelf obtained from the NOAA Geophysical Data Center (Fig. 3.2). Monte Carlo simulations showed that the sighting positions were preferentially associated with areas of low magnetic intensity and gradient at times when the whales were migrating (spring and fall but also with low intensity in winter), but not in summer when the whales were at their summer feeding areas in the Gulf of Maine (Table 3.1). These results were consistent with the hypothesis that the whales traveled in the magnetic valleys, which will be characterized by low values of intensity and gradient. Kirschvink et al. (1986) suggested that use of magnetic topography would permit whales, and perhaps other animals, to guide north-south migrations in the deep ocean using the marine magnetic lineations produced by seafloor spreading.

Differential associations with magnetic topography have also been reported for scalloped hammerhead sharks tracked during nocturnal homing movements between Las Animas Island and the Espiritu Santo seamount in the Gulf of California. Klimley (1993) found that the sharks were highly oriented. They swam in the same directions for extended periods while

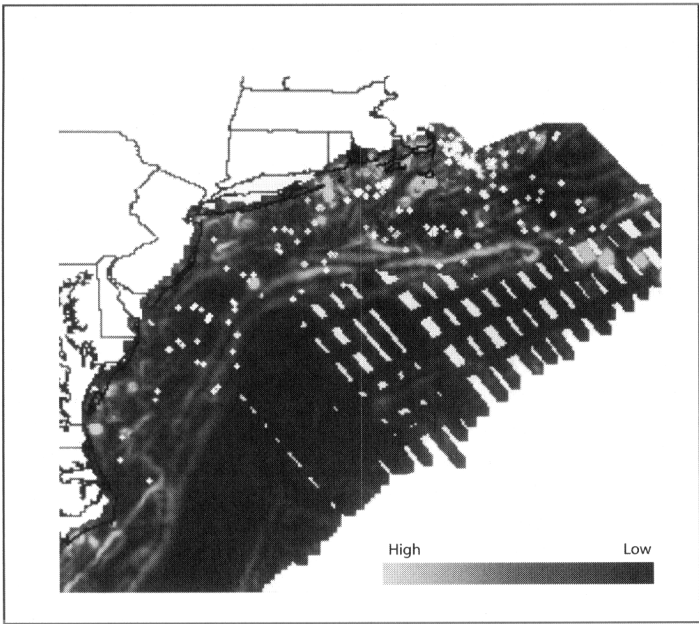


FIGURE 3.2. Sighting positions (all seasons) for fin whales superimposed on an image of magnetic field intensity gradients over the outer continental shelf off the northeastern United States. Magnetic data are from the Decade of North American Geology data set. Sighting positions from the CETAP dedicated aerial surveys are indicated by white crosses. Magnetic field gradients are indicated by shades of gray, with 256 steps between minimum (dark) and maximum (light) gradients. (Adapted from Walker et al., 1992.)

remaining at depths out of sight of both the surface and the seafloor as they traveled between the island and the seamount. The movements could not be correlated with bathymetric features but were associated with areas of high intensity slope (37nT/km) in the Earth’s magnetic field. On the basis of these results, Klimley (1993) proposed that the sharks navigate using geomagnetic topotaxis in which they actively track features of the magnetic topography, such as magnetic intensity ridges and valleys.

4. Behavioral Responses to Magnetic Fields in the Laboratory

Over the last two decades, a variety of experiments have provided experimental confirmation of the above evidence that aquatic vertebrates from different classes respond to magnetic fields in nature. Amphibians, salmonid fishes, and sea turtles have been

TABLE 3.1. Results of Monte Carlo simulations used in two-tailed tests of the hypothesis that mean values of geophysical parameters at positions where fin whales were sighted in different seasons were significantly different from the mean values at simulated sighting positions on the CETAP flight tracks.

| | All | Spring | Summer | Fall | Winter |
|------------------|-----|--------|--------|------|--------|
| No. of sightings | 82 | 31 | 29 | 7 | 15 |
| Bottom depth | >.1 | >.1 | >.1 | >.1 | >.1 |
| Bottom slope | >.1 | >.1 | >.1 | >.1 | >.1 |
| Field intensity | >.1 | >.1 | >.1 | >.1 | .034 |
| Field gradient | >.1 | .024 | >.1 | .008 | .038 |

Note: Animals observed feeding or engaged in behavior associated with feeding were excluded from the analysis on the grounds that their sighting positions would have been determined by the location of food. Cells in the table contain estimates of the probabilities that the mean values of the geophysical parameters for the simulated positions that are equal to or lower than the mean values for the parameters at sighting positions could be obtained by chance.

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 laboratory. In the paragraphs that follow, we examine key results from these experiments with amphibians, sea turtles, and fishes.

4.1. Orientation Responses to Magnetic Direction and Intensity

The critical assumption of orientation arena 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, during their migration seasons, many birds become active at night, and orient in the same directions when placed in a featureless arena as their migrating conspecifics are flying. In the laboratory setting, animals can be induced to establish an orientation direction to a key feature of their living environment such as a water flow direction or a shore. The animals are then tested for that orientation direction when placed in a featureless arena.

The first experimental evidence of magnetic orientation by aquatic vertebrates came in cave salamanders (Phillips, 1977) and in two salmon species (Quinn, 1980; Taylor, 1986, 1987). The cave salamanders were trained to move either parallel or perpendicular to the direction of the magnetic field present in training corridors (Phillips, 1977). When released in a cross-shaped testing assembly in which corridors were aligned parallel and perpendicular to the direction of the magnetic field, the salamanders were significantly oriented along the axes in which they had been trained. In ongoing work with amphibians by Phillips and his colleagues (e.g., Fischer et al., 2001; see also Deutschlander et al., 1999), eastern red spotted newts are trained to escape sudden temperature changes in their living tank by swimming toward an artificial shore. The newts subsequently swim in the training direction when they are placed in an orientation arena without a shore. Similarly, juvenile chinook salmon were allowed to establish an orientation facing into a current that carried their food and flowed from west to east in their living tank. When placed in a feature-

less arena where there was a radial current flow, the fishes oriented in the east–west axis (Taylor, 1986, 1987).

In contrast with the above examples, Quinn (1980) tested the orientation of sockeye salmon fry during their migration to the lakes in which they would disperse to live. Newly hatched sockeye salmon fry leave the gravel beds where they hatch and swim upstream to lakes where they live until their seaward migration (Quinn, 1980). Migrating fry were captured as they swam toward the lake in which they would live until they migrated downstream to the sea. The fishes were then placed in an orientation arena. The directions chosen by the fry in the arena were consistent with the hypothesis that the fishes 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.

More recently, Lohmann and colleagues (1996, 2000, 2001) have demonstrated orientation to both magnetic inclination and intensity by hatchling loggerhead turtles. When placed in an orientation arena, the hatchling turtles oriented in the offshore direction as indicated by the magnetic field to which they were exposed (Fig. 3.3A). When presented with fields of inclinations and intensities found at several different locations around the central North Atlantic Ocean, the hatchlings oriented in directions that would have caused them to move toward the center of the North Atlantic gyre (Lohmann and Lohmann, 1996; Lohmann et al., 2001). Such a pattern would be expected to keep the turtles entrained within the North Atlantic gyre and prevent them from being carried into colder waters to the north of the gyre (Lohmann and Lohmann, 1996; Lohmann et al., 2001).

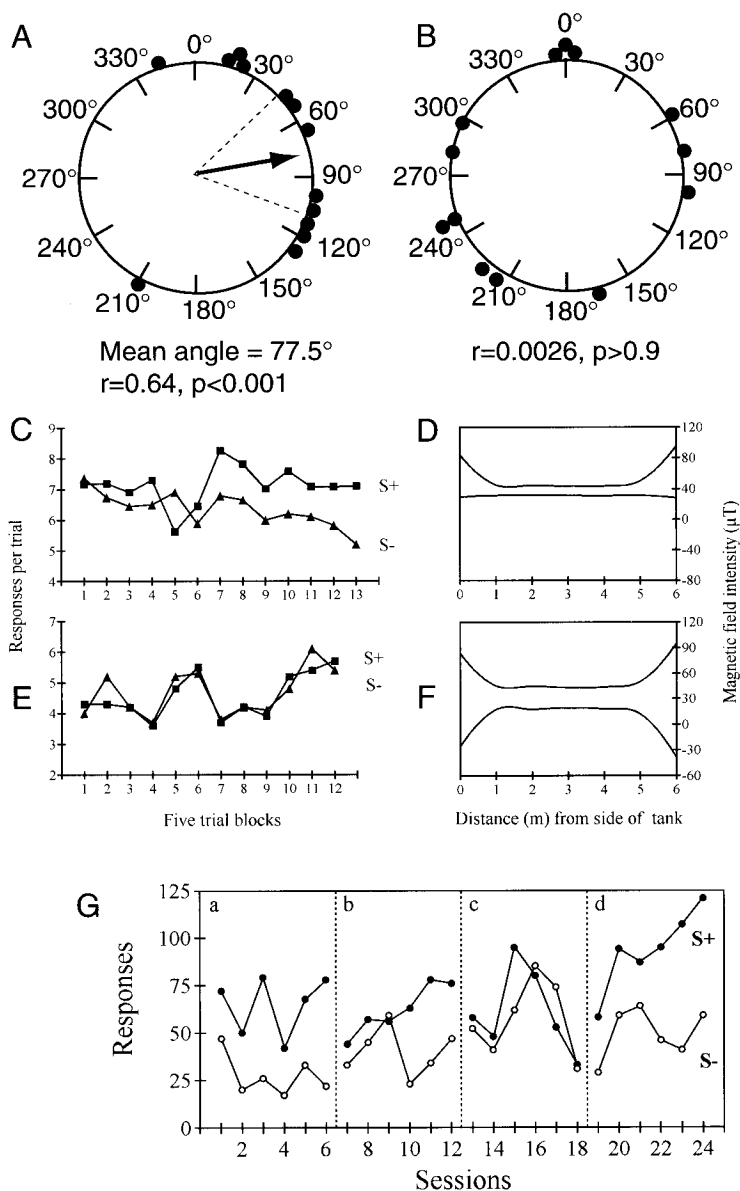
4.2. Conditioned Responses to Magnetic Intensity

Although it is difficult to change magnetic intensity without also changing magnetic field direction, it appears that animals can discriminate changes in magnetic intensity in conditioning experiments subject to two constraints. These constraints are that (1) the fields to be discriminated are spatially distinctive and (2)

the subjects must be moving. 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 is thus asked to 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). Nonuniform fields (produced by passing direct current through vertically oriented coils) added localized fields of varying intensities to the uniform Earth's field within



the tanks in which fishes were trained. 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. Individually-trained yellowfin tuna swam repeatedly through a hoop lowered into an experimental tank for a 30-second trial period. At the end of each trial and depending on the presence or absence of the magnetic field produced by the coil, the fishes were rewarded or not rewarded with food for swimming through the hoop. Discrimination learning was then detected as a change over time in the rates of response during reinforced (S+) and nonreinforced (S-) trials.

The fishes readily learned to discriminate the presence and absence of the nonuniform field but not between the two nonuniform fields produced by reversing the polarity of the current to the coils. For fishes tested with the presence and absence of the nonuniform field due to the coil (Fig. 3.3E), response rates during both S+ and S- trials remained similar over the first 6 five-trial blocks (Fig. 3.3C). After 6 five-trial blocks, however, response rates were consistently higher in the presence of S+ than in the

presence of S- (Fig. 3.3C). For fishes trained with two nonuniform fields produced by reversing the polarity of the current to the coils (Fig. 3.3F), there was no separation of response rates to S+ or S- at any stage of the experiment (Fig. 3.3D).

The basic result with the tuna has now been replicated in two other fish species, a teleost and an elasmobranch. Rainbow trout (*Oncorhynchus mykiss*; Walker et al., 1997) and the short-tailed stingray (*Dasyatis brevicaudata*; Hodson, 2000) discriminated between the presence and absence of magnetic anomalies superimposed on the background field in experimental tanks. The pattern of discrimination learning by these two species and the yellowfin tuna was remarkably similar despite variations among the three species in the number of trials required for discrimination to appear. In the case of the trout, reversal learning, a well-known learning phenomenon, has also been demonstrated (Haugh and Walker, 1998). Taken together, these results demonstrate that the magnetic sense can be analyzed using conditioning approaches in the same manner as better-known sensory systems.

FIGURE 3.3. Behavioral responses to magnetic fields (A, B) Distributions of mean bearings for hatchling loggerhead turtles in an orientation arena. The animals wore a nylon lycra harness into which brass weights (controls) or stirring bar magnets (experimentals) were placed. Distributions of bearings in A and B are for control and experimental animals respectively. (C, D) Magnetic discrimination learning in individually trained yellowfin tuna ($n = 7$ in C; $n = 2$ in D). Each point is the mean of five trials in which responding was reinforced with food (S+; filled squares) given at the end of each trial or five trials in which responding was not reinforced no matter how often the fish responded. (E, F) Variations in magnetic intensity (in microTesla; μT) with distance from the edge of the experimental tanks used in the experiments plotted in C and E. In D, the background field of the Earth is a uniform $37\mu\text{T}$, whereas the field produced by a coil wrapped around the tank wall adds between $10\mu\text{T}$ and $60\mu\text{T}$ respectively to the Earth's field at the center and edge of the tank. In F, the field produced by the coil is added to (upper

trace) or subtracted from (lower trace) the background field of the Earth in the tank. The fields shown in D and F were used in the experiments presented in C and E respectively. (G) Impairment of learned magnetic discrimination by short-tailed stingrays. The experimental procedure differed little from the procedure used for the experiments with the tuna in C and D. Each point represents the mean number of responses per session made by the experimental animals in the presence of the reinforced stimulus (S+; filled circles) and the nonreinforced stimulus (S-; open circles). Panels A and B show the discrimination performance before and after the insertion of brass weights into the nasal cavities of the animals. Panel C shows impairment of discrimination by replacement of the brass weights by neodymium-iron-boron magnets of the same size as the brass weights. Panel D shows the recovery of discrimination after removal of the magnets. (A, B: redrawn from Irwin and Lohmann, 2000; C-F: adapted from Walker, 1984; G: Hodson, 2000.)

5. Implications for Magnetoreceptor Mechanisms

These behavioral experiments have wider implications for the mechanism of magnetic field detection in other aquatic vertebrates. Hypotheses concerning the magnetoreceptor mechanism have proposed that the magnetic field signal is either (1) extracted from interactions of the magnetic field with the detector components in other specialized sensory systems (Leask, 1977; Kalmijn, 1978); or (2) detected directly using magnetite that is linked somehow to the nervous system (Kirschvink and Gould, 1981). Three hypotheses have been proposed. The "light-dependent" (also known as the "optical pumping") hypothesis proposes that electrons from visual pigments that have been excited by light will interact with the external magnetic field to produce a signal that could be detected by the visual system (Leask, 1977; Deutschlander et al., 1999). The electrical induction hypothesis proposes that the electroreceptor systems of the elasmobranchs (sharks and rays) detect electric current flows induced as the animals, and/or the water mass in which they are swimming, move through the Earth's magnetic field (Kalmijn, 1978, 1981, 1982). In contrast, the magnetite hypothesis proposes that the motion of single-domain crystals of magnetite, a magnetic mineral, converts the force exerted on the crystals by an external magnetic field into a mechanical signal that can be detected by the nervous system. Kirschvink and Gould (1981) suggested several mechanisms that might be used to convert the magnetic signal from the movement of the magnetite into an electrical signal at the membrane of a receptor cell.

The competing hypotheses of electrical induction-based and magnetite-based magnetoreception can be distinguished on the basis of the predictions they make concerning the effect of attached magnets on magnetic field detection. Because attached magnets impose a constant field relative to the body, they will make no contribution to the electrical signal induced by an elasmobranch fish as it swims. Magnets should therefore not affect magnetic field

detection using electroreceptors but they should impair magnetite-based magnetoreception provided they are placed close enough to the magnetite to interfere with its use in magnetic field detection.

We have tested the magnetite-based magnetoreception hypothesis in an elasmobranch, the short-tailed stingray, *Dasyatis brevicaudata*. We assumed that, if magnetite located in the nose of the rainbow trout (Diebel et al., 2000; see below) is to form the basis of a general mechanism of magnetic field detection in the vertebrates, then magnetite-based magnetoreceptors are likely to occur in similar locations in representatives of major vertebrate taxa. We therefore sought to impair magnetite-based magnetoreceptors by attaching magnets over the noses of stingrays that had been trained to discriminate the presence and absence of a magnetic intensity anomaly in an experimental tank (Fig. 3.3G(a)). When the rays carried brass weights (3 mm × 2 mm cylinders) implanted in the nasal cavity, they were still able to discriminate the presence and absence of the anomaly (Fig. 3.3G(b)). The rays could no longer discriminate the anomaly, however, when the brass weights were replaced with rare-earth (neodymium-iron-boron) magnets of the same dimensions (Fig. 3.3G(c)). The rays were able to make the discrimination again immediately after the magnets were removed (Fig. 3.3G(d)). Although use of the ampullary electroreceptors to detect magnetic fields is not excluded by this finding, it seems likely that magnetite-based magnetoreception is at least the primary means of magnetic field detection in the stingray and perhaps also in other elasmobranchs.

A similar experiment has been carried out with sea turtles. In orientation experiments, hatchling loggerhead turtles wore a harness to which a stirring bar magnet or a brass weight of equivalent size and weight could be attached (Irwin and Lohmann, 2000). Figure 3.3A shows that turtles with a brass bar attached to the harness were significantly oriented with a mean heading of 77.5° ($r = 0.64$, $n = 15$, $p < 0.001$, Rayleigh test). The 95% confidence interval for the mean bearing included the expected orientation direction (90°) for the hatchlings. Turtles with a bar magnet attached to the harness were

not significantly oriented as a group ($r = 0.0026$, $n = 13$, $p > 0.9$, Rayleigh test; Fig. 3.3B). Experimental data consistent with the magnetite-based magnetoreception have thus been obtained in aquatic species from three vertebrate classes.

6. Neural Transmission

The discovery of magnetite suitable for use in magnetoreception in the front of the head in a variety of teleost fishes (Walker et al., 1984; Kirschvink et al., 1985; 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 that, in rats, is known to innervate the olfactory epithelium (Finger et al., 1990). The ALLN innervates the highly sensitive mechanoreceptors of the lateral line and, in the elasmobranchs, innervates mechanoreceptors that have been adapted for electroreception.

Responses to magnetic field stimuli were found to occur in the superficial ophthalmic branch (SO) 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 transient responses to a trebling of magnetic intensity presented as square waves at frequencies of 0.5 and 1 Hz (Fig. 3.4A–D). Both excitatory and inhibitory responses were observed but the units responded only to either the onset or the offset of a stimulus (Fig. 3.4D). Surprisingly, no unit responded when magnetic field direction was reversed without a simultaneous change in intensity (Fig. 3.4B). The response of the units could also be modulated by varying the presentation rate of a change in magnetic intensity.

The latency and time-course (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) of the responses by the two units exposed to both stimulation frequencies were similar but the peak amplitudes of the responses decreased and increased, respectively, when the rate at which intensity changed was presented increased from 0.5 to 1 Hz (Fig. 3.4C).

The neural responses to magnetic fields in the trout have not been localized to any branch of the TN, 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 the front of the head of the trout and led to a search for detector cells associated with the TN.

7. The Search for the Site of Magnetic Field Detection

The behavioral and electrophysiological experiments led us to search for candidate magnetite-based magnetoreceptor cells in the rainbow trout. This search was complicated by the transparency of tissues to magnetic field stimuli, the nature of the Earth's magnetic field as a stimulus, and the extremely small size of the magnetite crystals themselves. New techniques, and combinations of techniques, have had to be developed to overcome these obstacles.

7.1. The Magnetoreceptor Cells

We have used the crystal and magnetic properties of single-domain magnetite to identify magnetoreceptor cells in the nose of the rainbow trout despite the small size (<50 nm) and extreme rarity (<5 p.p.b. by volume) of the crystals. We first used reflection mode confocal laser scanning microscopy (CLSM) to demonstrate detection of the chains of magnetite crystals present in magnetotactic bacteria (Walker et al., 1997). We then searched for similar

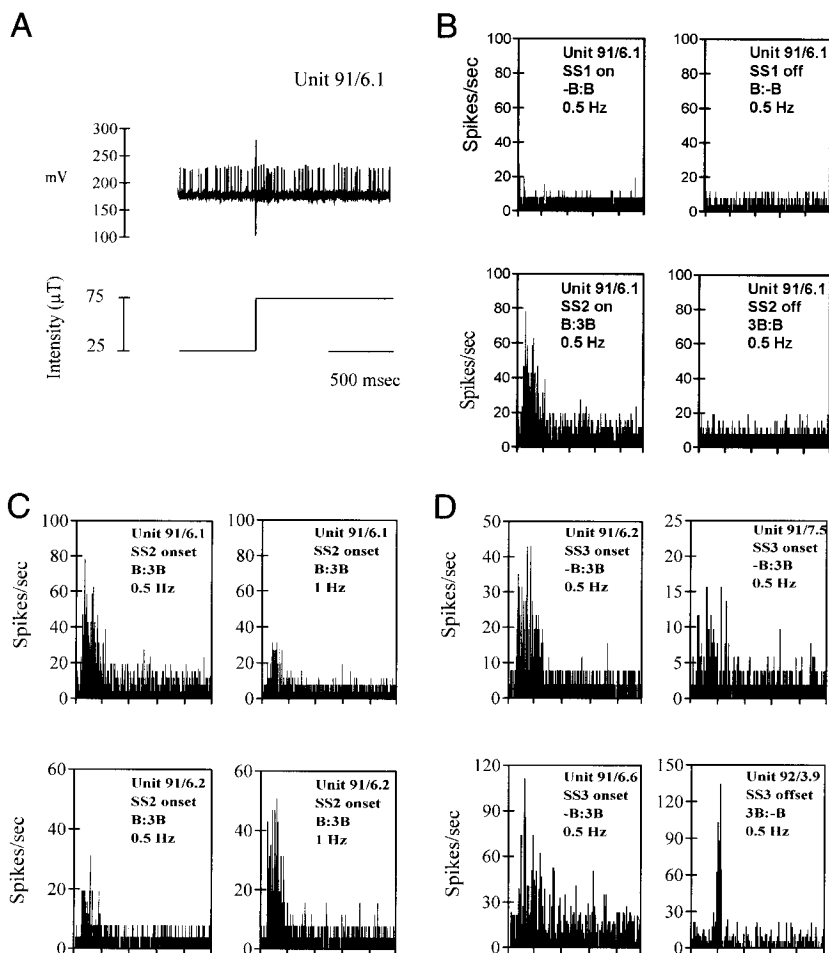


FIGURE 3.4. Neural responses to magnetic field stimuli in rainbow trout (adapted from Walker et al., 1997). (A) Peristimulus activity of a single unit (91/6.1) in the SO branch of the TN in the rainbow trout. The onset of a standard search stimulus (labeled SS2; bottom trace) that trebled the intensity without changing the direction of the magnetic field in the experimental situation is aligned with the associated stimulus artifacts (clipped for clarity) in the top trace. To the left of the artifact, the unit is spontaneously active in the background magnetic field. To the right of the artifact, the trace shows the activity of the unit for 1 s after the onset of SS2. Acceleration of the firing rate of the unit is evident for the first 100 ms after the stimulus step. (B) Poststimulus time histograms (PSTHs) of responses by the unit shown in A to SS1 (a search stimulus that reversed the direction without changing the intensity of the field

in the experimental situation) and SS2 presented 128 times at 0.5 Hz (on for 1 s then off for 1 s). (C) PSTHs of responses by two spontaneously active units to the onsets of SS2 presented 128 times at 0.5 and 1 Hz. (D) PSTHs of responses by four spontaneously active units to SS3 (a search stimulus whose onsets reversed the direction and trebled the intensity of the magnetic field in the experimental situation and whose offsets reversed the effect of the onsets). The stimuli were presented 128 times in each case. Each plot in B–D begins at the step change in the field and is of duration 500 ms. The magnetic field remained constant throughout the period. Unit identification number, search stimulus number, stimulus step, and presentation rates are listed. Sampling bin widths are 2 ms in B, C, and in the upper-left panel of D, and 4 ms in the remaining panels of D. Tick marks on the abscissae are at 100 ms intervals.

reflections in heads of rainbow trout that had been embedded in plastic (Fig. 3.5A,B). Mapping the reflections in three dimensions then permitted us to image single crystals in thin sections in the transmission electron microscope (Fig. 3.5C,D) and to identify the crystals uniquely as magnetite using atomic and magnetic force microscopy (Fig. 3.5E; 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 (Fig. 3.5A,B). The cells are relatively rare and were found only 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) that help delineate the basal layer (Fig. 3.5B). The chain of magnetite crystals in each cell is about 1 μm long (range 0.5 μm –1.5 μm , $n = 4$; estimated from the CLSM; Diebel et al., 2000) and we estimate each chain will have a magnetic-to-thermal-energy ratio of about 4. The location of the chain of magnetite crystals within each cell suggests that 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.

7.2. Neuroanatomy

In the first step toward testing the hypothesis that the magnetite-containing cells may be functionally linked to the TN, we sought to trace the superficial ophthalmic branch of the TN from the site where electrophysiological recordings of responses to magnetic field stimulation were made, to the endings of the individual nerve cells (Fig. 3.6). We used serial histological sections and DiI, a fluorescent lipophilic dye, placed on the cut ends of the TN 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 gan-

glion (Fig. 3.6C). From the ganglion, the labeled nerve tracts entered the anterior dorsal area of the medulla oblongata. Anterior to the orbit, the SO branch has branches that innervate the skin, surround the olfactory nerve and olfactory capsule (processes 1–3 in Fig. 3.6C), and also penetrate the olfactory lamellae within the olfactory capsule itself (Fig. 3.6C). Fine branches of the TN penetrate the olfactory lamellae both from the top and from the base before terminating in finer processes within the olfactory lamellae, where the magnetite-containing cells are most often found (Fig. 3.6A).

Although we can propose a link from the candidate magnetoreceptor cells in the lamina propria of the olfactory lamellae 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 nerves. In addition, it has been impossible so far 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. There is thus only indirect evidence from the magnetic impairment experiments and the magnetic-to-thermal-energy ratio of the magnetite chains that the magnetoreceptor cells are functionally linked to the nervous system.

8. Discussion

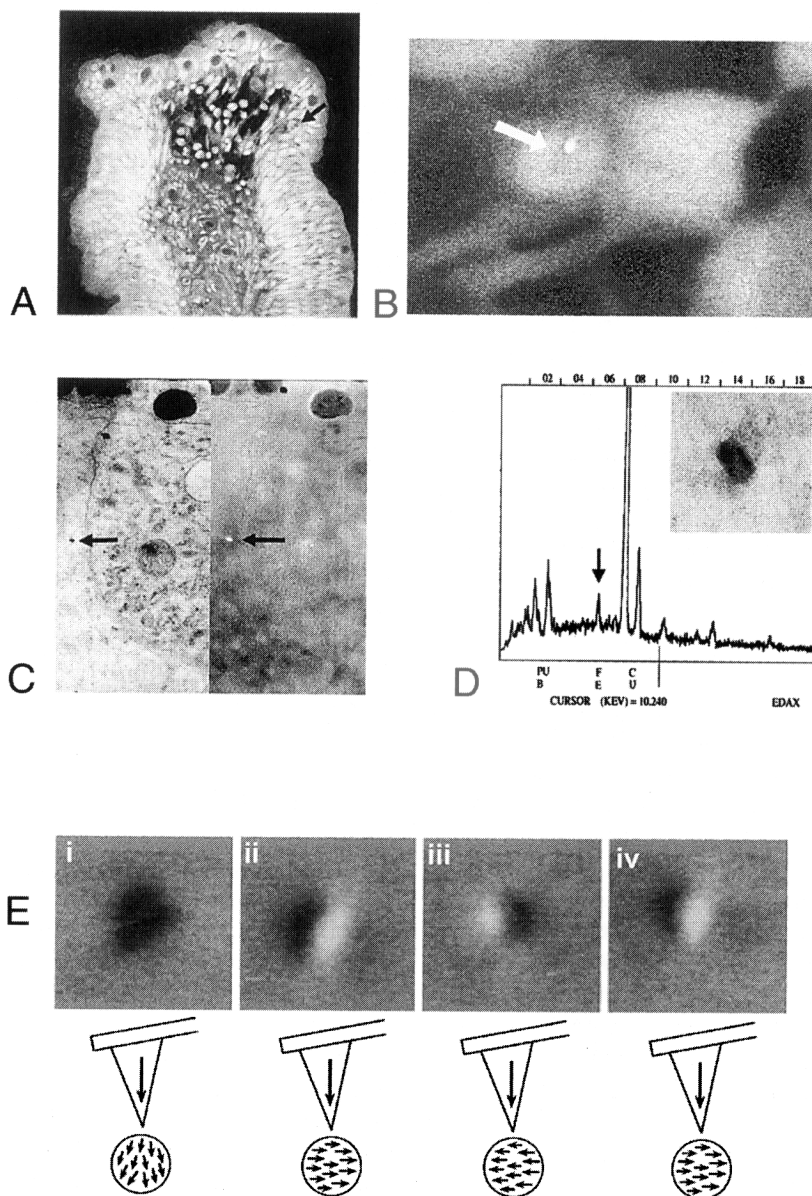
We conclude first that the mystery surrounding the magnetic sense is well on the way to being dispelled. Experimental results now demonstrate that the magnetic sense has key properties, in particular selectivity and sensitivity, in common with other senses (Block, 1992). Although behavioral and electrophysiological results from aquatic species bear directly only on the issue of selectivity, their similarity with results from terrestrial species is consistent with the widespread use of magnetite in magnetic

field detection. Second, there is now some evidence to underpin the intuitive appeal of the hypothesis that aquatic animals use a magnetic sense to navigate over long distances. Much remains to be learned, however, because the results so far permit no more than an outline description of the structure and function of the magnetic sense in a single species and there is as yet no direct experimental evidence for use

of the magnetic field for any purpose by aquatic species.

8.1. How Magnetic Fields Are Detected

Although we have focused on magnetite, it cannot yet be determined whether there is a single common mechanism or multiple, inde-



pently derived mechanisms of magnetic field detection in aquatic vertebrates. Magnetic field detection has been proposed to occur in the visual system of amphibians (Deutschlander et al., 1999) and the electroreceptor system of elasmobranchs (Kalmijn, 1981) as well as in specialized cells that contain magnetite in the teleost fishes (Walker et al., 1984, 1997; Diebel et al., 2000). The number of species studied so far in each of these vertebrate classes is small and no more than two of the proposed mechanisms for magnetic field detection have been investigated in any of them. The small number of species and variation in experimental techniques used to date make it difficult to evaluate the detection hypotheses by comparing experimental results from among the different taxa that have been studied.

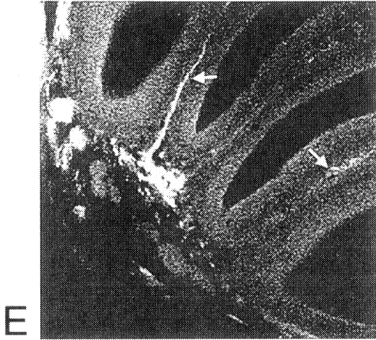
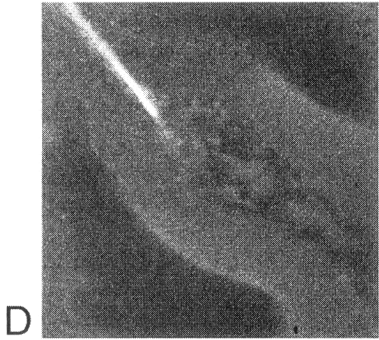
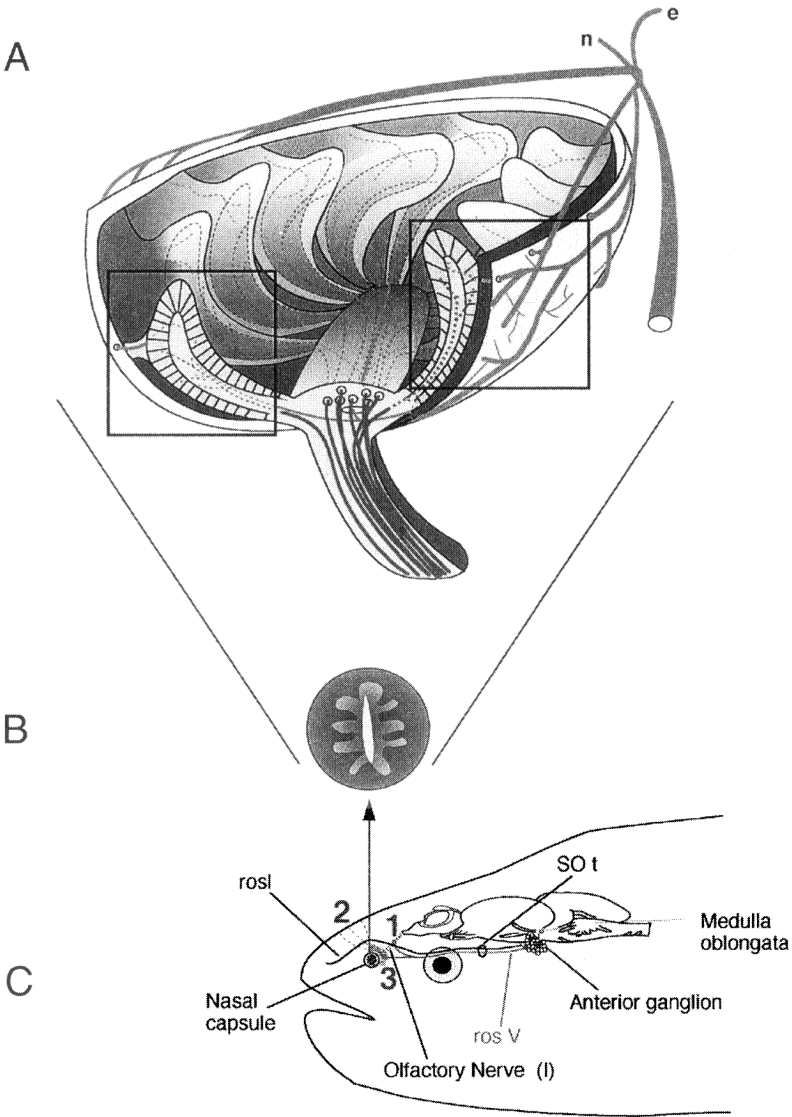
Block's (1992) argument that evolutionary pressures should produce highly specialized

sensory systems does, however, provide a theoretical basis for evaluation of magnetic field detection hypotheses. The magnetite hypothesis assumes that magnetite will form the basis of a sensory system that specializes in detecting magnetic fields. If, on the other hand, magnetic fields are detected secondarily in other sensory systems, then subsets of receptor cells in those sensory systems should be specialized for magnetic field detection. In both cases, the detector cells should be both *selective for* and *highly sensitive to* magnetic field stimuli (Block, 1992).

The magnetite-based magnetoreceptor cells in the nose of rainbow trout will be clearly selective for magnetic field stimuli (Walker et al., 1997; Diebel et al., 2000). The magnetoreceptor cells in the trout could respond only to pervasive stimuli, such as magnetic fields, gravity, and temperature variations, that pass through tissue because the cells do not contact

FIGURE 3.5. Detection of intracellular magnetite. (A) Magnetite detected using a confocal laser scanning microscope (CLSM) in reflection mode shows as a spot (arrow) and has been overlaid onto an autofluorescence image of the olfactory lamella taken at the same depth and magnification ($\times 190$). (B) Autofluorescence image of a magnetite-containing cell viewed using transmission mode CLSM. The white spot (arrow) shows where the reflection due to magnetite has prevented light passing through the cell. (C) Bright-field (left) and dark-field (right) transmission electron micrograph (TEM) of a crystal associated with a reflectance in the trout olfactory lamellae. 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 (magnification 12,500). (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. (E) Magnetic force microscopy (MFM) images that show the response of a putative single magnetic particle (within trout olfactory tissue) in

the presence of an applied magnetic field. The magnetic field applied in the plane of the sample was +1.4, +150, -150 and +130 milliTesla (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 particle 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. (Ei.) Image shows a dark patch at the location of the particle. This dark patch indicates an attractive reaction between the tip and sample, consistent with the magnetic field from the MFM tip weakly magnetizing the particle and causing an attractive interaction. (Eii-iv.) MFM images show the nearly dipolar responses of the magnetic particle under a strong applied magnetic field. These are consistent with an MFM image of a single-domain particle magnetized along the direction of the applied field. Note that the reversal of the field and dipolar response in C are consistent with the particle magnetization flipping in the reversed applied field. In images B-D, the applied field was large enough to completely align the magnetic moment of the crystals within the field. (A, C, D: adapted from Walker et al., 1997; B, E: adapted from Diebel et al., 2000.)



the external environment directly. The magnetite crystals in the receptor cells are too small to be affected by gravity but their motion will be affected by external temperature variations (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985). Poikilotherms such as fishes may therefore require processes that compensate for temperature effects on magnetic field detection.

The magnetite-based magnetoreceptor cells in the nose of rainbow trout are also likely to achieve high sensitivity to magnetic field stimuli (Diebel et al., 2000). Theoretical analyses (Kirschvink and Walker, 1985) predicted the existence of such arrays. These analyses also predicted that the energy of interaction of these arrays with the Earth's magnetic field would be two and six times the background thermal energy, kT , in arrays specialized for detecting the intensity and direction respectively of the Earth's magnetic field (Kirschvink and Walker, 1985). We have estimated the energy of interaction of the chains of magnetite in the trout with the Earth's magnetic field to be about $4kT$ (Diebel et al., 2000).

Although we cannot yet explain why this magnetic interaction energy should be inter-

mediate between the values predicted by Kirschvink and Walker (1985), we note that these magnetite chains will respond only to magnetic fields and, if present in sufficient numbers, will permit high sensitivity to changes in magnetic field stimuli.

In contrast with magnetite-based magnetoreceptors, there is as yet no evidence for specialized receptors that are selective for magnetic fields in either the visual or the electroreceptor systems respectively of amphibians and elasmobranchs. In the absence of specialized subsets of receptors, it also seems unlikely that these sensory systems could achieve the high sensitivity necessary to explain the close associations of hammerhead sharks with magnetic topography (Klimley, 1993) or the sensitivity to small changes in magnetic field inclination proposed for amphibians (Fischer et al., 2001). In the elasmobranchs, high sensitivity would require extremely long ampullary canals in the electroreceptor system (Kirschvink et al., 2001). Similarly, the eyes of amphibians would require either much greater numbers of receptor cells or receptor cells with much greater volumes of visual pigments than are necessary for vision (Kirschvink et al., 2001).

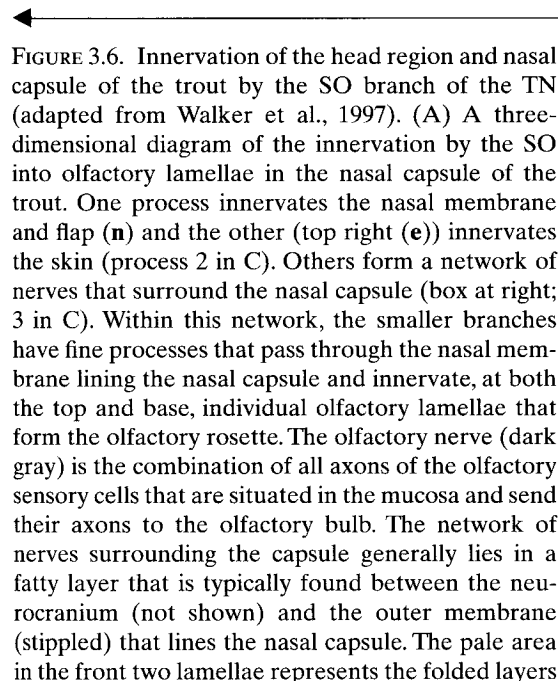


FIGURE 3.6. Innervation of the head region and nasal capsule of the trout by the SO branch of the TN (adapted from Walker et al., 1997). (A) A three-dimensional diagram of the innervation by the SO into olfactory lamellae in the nasal capsule of the trout. One process innervates the nasal membrane and flap (**n**) and the other (top right (**e**)) innervates the skin (process 2 in C). Others form a network of nerves that surround the nasal capsule (box at right; 3 in C). 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 (dark gray) is the combination of all axons of the olfactory sensory cells that 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 that is typically found between the neurocranium (not shown) and the outer membrane (stippled) 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 box at left outlines the areas where the TN enters the olfactory lamellae from the top (shown in D) and the bottom (shown in E). (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) Schematic of the innervation of the SO (labeled SO t) in the head region of the trout. (D, E) Optical slices showing two different branching patterns of DiI-labeled nerve processes entering trout olfactory lamellae. In D, a labeled fine process from a branch of the SO ramus of the TN can be seen entering a single lamella through the top (magnification $\times 135$). In E, fine processes can also be seen entering the lamina propria of several lamellae (arrows) from their bases (magnification $\times 55$). These processes originate from a different branch of the SO than the one that innervates the top area in D.

Such elaboration of the sensory cells and associated structures in these sensory systems has yet to be reported.

In the two vertebrate groups where current experimental results bear on more than one of the magnetic field detection hypotheses, we suggest that the evidence favors the magnetite hypothesis. Hatchling sea turtles orient in complete darkness (Lohmann and Lohmann, 1996; Irwin and Lohmann, 2000; Lohmann et al., 2001) when there will be no photons to excite the electrons in visual pigments as required by the optical pumping hypothesis (Leask, 1977). They cannot orient, however, when they are carrying magnets in a harness on their backs. Similarly, magnetic field discrimination in short-tailed stingrays is abolished by magnets attached over the likely location of magnetite used in magnetoreception. Because the electroreceptor system would still have been stimulated in these latter experiments, the failure to respond in the presence of the magnets suggests that the stingrays do not normally attend to signals in the electroreceptor system that are derived from the external magnetic field. The similarity of these experimental results in the elasmobranchs and the turtles, combined with the results from the teleost fishes, suggests that a single common mechanism is more likely than multiple, independently derived mechanisms of magnetic field detection in the aquatic vertebrates.

8.2. Use of the Magnetic Sense in the Aquatic Environment

Our developing ability to study the structure and function of the magnetic sense in aquatic vertebrates using orthodox approaches to the study of sensory systems is not matched by our ability to test experimentally for use of the Earth's magnetic field by aquatic animals. Travel paths and positions of sharks and whales can be correlated with minute variations in magnetic intensity (Kirschvink et al., 1986; Walker et al., 1992; Klimley, 1993). These results are consistent with the hypothesis that sharks and whales may navigate using the magnetic topography produced by magnetic anomalies but are contradicted by the apparent disorient-

ing effect of magnetic anomalies on homing pigeons (Walcott, 1977).

Significant issues of scale and experimental control explain why the few attempts to test experimentally for use of the Earth's magnetic field in navigation by aquatic animals have been inconclusive (e.g., Papi et al., 1997, 2000; Yano et al., 1997). First, sensory systems operate over short time scales (milliseconds to minutes) but long-distance movements can take from hours to months. Detection of magnetic effects on behavior are therefore likely to require that activity be monitored on the temporal and spatial scales over which the magnetic sense will operate. Second, because free-living animals will frequently carry out other normal functions such as feeding, resting, and avoiding predators during long-distance journeys, it will be difficult to predict the direction an animal will travel on short time scales and so to predict the effects of experimental manipulations on the direction of travel. Greater experimental control than has been achieved so far is likely to come through careful selection of subjects for which a direction of travel can be predicted in advance. We suggest seabirds that roost on land at night and feed well away from land during the day could be studied experimentally in much the same way as homing pigeons. An exciting new development that would support such experiments is the development of global positioning devices small enough to be carried by birds as small as homing pigeons (Steiner et al., 2000).

8.3. Comparison with Results from Birds

The far greater volume of research that has been done on the magnetic sense in birds has produced a number of similarities and differences from the results obtained so far with aquatic vertebrates. There is experimental evidence for both selectivity and high sensitivity of the magnetic sense in birds to go with the evidence for selectivity obtained from the aquatic vertebrates. Recordings from the superficial ophthalmic branch of the trigeminal nerve and the trigeminal ganglion in the bobolink, *Dolichonyx oryzivorus*, demonstrated sensitiv-

ity to changes in magnetic intensity of 200 nT (Semm and Beason, 1990), whereas studies of the effects of magnetic anomalies on the initial orientation of homing pigeons suggested that the behavioral threshold for changes in magnetic intensity may be as low as 10 nT (Gould, 1982). These results are consistent with the sensitivities to intensity changes estimated for whales (Kirschvink et al., 1986; Walker et al., 1992). Recent impairment experiments have demonstrated the likely dependence of magnetic field detection on magnetite located in the front of the head in homing pigeons (Haugh et al., 2001). Although there are still major gaps in our knowledge, the similarities in the results from laboratory studies of the magnetic sense in birds and aquatic vertebrates give us confidence in the hypothesis that magnetite provides the basis for a general mechanism of magnetic field detection in the vertebrates.

Although use of the Earth's magnetic field by birds has been difficult to demonstrate reliably and the results of experiments have sometimes been difficult to interpret (Walcott, 1992), several consistent results now permit a sketch of how birds such as homing pigeons may use the magnetic field to navigate. First, magnetic coils and attached magnets disrupt the initial orientation of homing pigeons on cloudy but not on sunny days, apparently by preventing the birds from using their magnetic compass on cloudy days (Keeton, 1972; Walcott and Green, 1974). Recent experiments using rare-earth magnets attached over the olfactory cavity of pigeons have demonstrated a highly reproducible effect on the initial orientation of homing pigeons on sunny days (Haugh et al., 2001). This result is consistent with the hypothesis that the magnets interfered with determination by the birds of their position rather than of direction because the birds use the sun compass in preference to the magnetic compass when the sun is available to them (Keeton, 1971). Finally, pigeon orientation errors associated with magnetic storms and anomalies have been interpreted to be errors in position determination (the "map step" of Kramer, 1953; Gould, 1982). This interpretation is consistent with the hypothesis that magnetic anomalies affect pigeon orientation by disrupting the

ability of the birds to determine position using systematic variations in the intensity of the Earth's magnetic field (Gould, 1982).

8.4. Future Research

A key conclusion from our work is that the structure and function of the magnetic sense can now be studied in the laboratory using orthodox approaches for the study of sensory systems. Skepticism that the magnetic sense exists was reasonable in the absence of a clearly identified detector system and afferent nerves. In the last five years, it has been possible to identify candidate detector cells that meet the criterion of selectivity for the magnetic field stimulus and permit high sensitivity of the magnetic sense (Diebel et al., 2000). Psychophysical studies using electrophysiological and conditioning techniques have confirmed the high sensitivity of the magnetic sense and its dependence on magnetite in birds (Semm and Beason, 1990), bees (Walker and Bitterman, 1988, 1989), and fishes (Walker, 1984; Walker et al., 1997; Hodson, 2000). The magnetic sense thus shares key properties of all specialized sensory systems (Block, 1992).

What the above studies of the magnetic sense have not achieved has been demonstration that the separate components of the sense are functionally linked. Thus, there is no ultrastructural evidence that the magnetic chains in the trout are linked to the candidate magnetoreceptor cells in a way that will produce changes in the membrane potential of the cells due to movements of the chains in response to the external magnetic field. Nor has any histological or cytological evidence been obtained that demonstrates the existence of afferent synaptic contacts between the magnetite-containing cells and the trigeminal nerve. There is also a complete lack of knowledge of both the central projections of the magnetic sensory nerves and how the stimulus is processed in the brain.

There are even greater challenges to be had in the study of the use of the magnetic sense by animals in nature. The case for use of magnetic compasses by homing pigeons is reasonably clear but there is no experimental evidence yet that clearly identifies how animals might

determine their position using the Earth's magnetic field. We suggest that experimental designs for field experiments could be usefully informed by the results of sensory studies that have been published over the last two decades or so. We suggest also that field experiments will benefit from careful selection of experimental subjects and from the availability of new tracking technologies that permit reconstruction with high resolution of the paths traveled by animals. In summary, there are many exciting opportunities for experimental study of the magnetic sense in both the laboratory and the field and we eagerly await the results of research over the years to come.

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