

10

Mechanisms of Orientation and Navigation

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Many of us have been moved by a crisp autumn day, enveloped in the reds, yellows, and browns of the season and watching formations of ducks or geese fly against a steely sky. We might have noticed that if it is early in the day, the flocks may be heading almost due south. If it is nearing dusk or if fields of grain are nearby, they may be temporarily diverted to resting or feeding areas. But when they resume their flight, they will head southward again.

In the following spring, we may stand beside a swift-moving river in the Pacific Northwest and watch salmon below a dam or a fish ladder. As they lie in deeper pools, resting before the next powerful drive that will carry them one step nearer the spawning ground, they all face one way—upstream.

Both the birds and the fish are responding to a complex and changing environment by positioning themselves correctly in it and by moving from one part of it to another. Although the feats of migration are astounding, they are no more crucial to survival than are mundane daily activities such as seeking a suitable habitat, looking for food and returning home again, searching for a mate, or identifying offspring. These actions also depend on the proper orientation to key aspects of the environment. Indeed, an animal's life depends on oriented movements both within and between habitats.

In this chapter we will explore some of the *mechanisms* by which animals orient themselves in space. (The costs and benefits of dispersal, habitat selection, and migration are covered in Chapter 11.)

LEVELS OF NAVIGATIONAL ABILITY

Many animals often travel between home and a goal, but they do not all accomplish this feat in the same manner. We group animal strategies for finding their way into three levels of ability (Bingman and Cheng 2005; Ronacher 2008).

PILOTING

One level is **piloting**, the ability to find a goal by referring to familiar landmarks. The animal may search either randomly or systematically for the relevant landmarks.

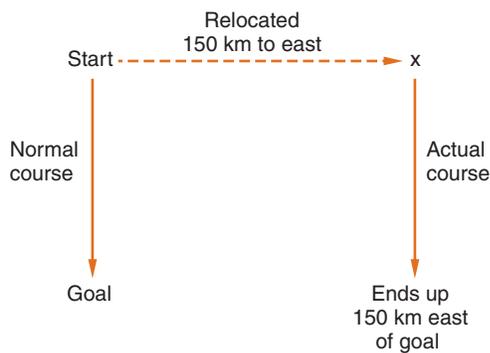


FIGURE 10.1 Experimental relocation of an animal that is using compass orientation causes it to miss the goal by the amount of its displacement.

Although we usually think of landmarks as visual, the guidepost may be in any sensory modality. As we will see shortly, magnetic cues guide sea turtles during their oceanic travels, and olfactory cues guide salmon during their upstream migration.

COMPASS ORIENTATION

A second level, called **compass orientation**, is the ability to head in a geographical direction without the use of landmarks. The sun, the stars, and even the earth's magnetic field may be used as compasses by many different species. One way to demonstrate that an animal is using compass orientation is to move it to a distant location and determine whether it continues in the same direction or compensates for the displacement. If it does not compensate for the relocation, compass orientation is indicated (Figure 10.1). When immature birds of certain migratory species, such as European starlings, were displaced experimentally, they flew in the same direction as the parent group that had not been moved, and they flew for the same distance (Perdeck 1967). In other words, they migrated in a path parallel to their original migratory direction. However, because they had been experimentally displaced before beginning their migration, they did not reach their normal destination. In some cases, this meant that they ended up in ecologically unsatisfactory places (Figure 10.2).

Uses for Compass Orientation

Compass orientation can be used in different ways—in both short-distance and long-distance navigation.

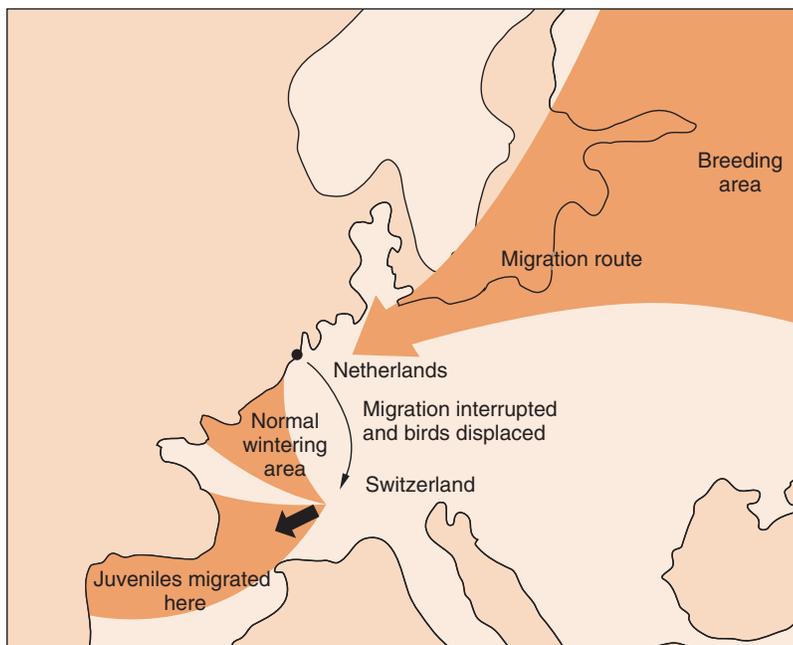


FIGURE 10.2 Immature starlings captured in the Netherlands and released in Switzerland did not compensate for the relocation during their autumn migration. Instead, they traveled southwest, their normal migratory direction, and ended up in incorrect wintering areas. (Modified from Perdeck 1958.)

Migratory Direction of Juvenile Birds Most first time migrant birds reach their destination without knowing where that goal is located. They are guided by an inherited program that tells the juveniles in which direction to fly and how long to fly. This innate program is sometimes called **vector navigation** (Berthold 2001; Bingman et al. 2006).

What observations have supported the idea of vector navigation? Individual birds held in the laboratory flutter in the direction in which they would be flying if they were free. When their cousins in nature have completed their migratory journey, the captive birds also cease their directional activity. Furthermore, many species, particularly those that fly from Central Europe to Africa, change compass bearing during their flight. Garden warblers (*Sylvia borin*) and blackcaps (*S. atricapilla*) held in the laboratory change the direction in which they flutter in their cages at the time that free-flying members of their population change direction (Gwinner and Wiltschko 1978; Helbig et al. 1989). Cross-breeding studies have also shown the inheritance of migratory direction. Andreas Helbig (1991) cross-bred members of two populations of blackcaps that had very different migratory directions. The orientation of the offspring was intermediate between those of the parents. Indeed, migratory direction is inherited by the additive effects of a number of genes (Berthold 2001).

Path Integration Besides their use in long-distance navigation, compasses can be used to improve in another type of navigation, called **path integration** or **dead reckoning**. In path integration, the animal integrates information on the sequence of direction and distance traveled during each leg of the outward journey (Figure 10.3). Then, knowing its location relative to home, the animal can head directly there, using its compass(es). A compass may also be used to determine the direction traveled on each leg of the outward journey, or the direction may be estimated from the twists and turns taken, sounds, smells, or even the earth's magnetic field. Information from the outward journey is used to calculate the homeward direction (vector). (Thus, some authors consider path integration to be a type of vector

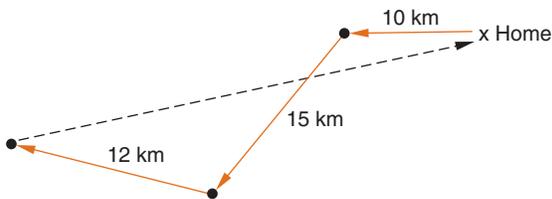


FIGURE 10.3 Navigation by path integration. This involves determining one's position by using the direction and distance of each successive leg of the outward trip. A compass can then be used to steer a course directly toward home.

navigation [Ronacher 2008].) The estimates of distance and direction are often adjusted for any displacement due to current or wind. Once close to home, landmarks may be used to pinpoint the exact location of home.

Many types of animals use path integration to find their way around. Consider, for example, the desert ant (*Cataglyphis bicolor*). During its foraging forays, this insect wanders far from its nest over almost featureless terrain. After prey is located, sometimes 100 meters away from the nest, roughly the distance of a football field, the ant turns and heads directly toward home. It appears that the ant knows its position relative to its nest by taking into account each turn and the distance traveled on each leg of its outward trip. If a researcher captures an ant as it is leaving a feeding station headed for home and relocates the ant to a distant site, the ant's path is in a direction that would have led it home if it had not been experimentally moved (Wehner and Srinivasan 1981).

How does a desert ant determine the direction and distance of its outward route? The direction is determined using the pattern of polarization of skylight. Ants determine their direction by using the pattern of skylight polarization, which is caused by the sun's position (discussed shortly) (Müller and Wehner 2007). Desert ants determine the distance they travel using a mechanism that integrates the number of strides required to reach the goal with stride length. Matthias Wittlinger and colleagues (2007) demonstrated this internal pedometer in a very clever way. As we all know, a person with longer legs requires fewer steps to reach a goal than does a person with short legs. Therefore, the researchers predicted that manipulating the length of ant's legs would cause the ants to misestimate the distance to the nest. The researchers collected ants at an experimental feeder and manipulated the length of the ants' legs. They lengthened the legs of some ants by attaching pig's bristles to the ant's legs, creating stilts. They shortened the legs of other ants by partial amputation. The ants walking on stilts overestimated the distance to the nest, whereas the ants with stubby legs underestimated the distance. An added complication to this means of calculating the distance traveled from home is that stride length varies with rate of travel. Thus, as remarkable as this stride counting might seem, the actual mechanism of distance determination also includes an estimation of stride length. Once at home, cues from inside the nest reset the path integrator to zero, so that it can be set again by the next outward journey (Knaden and Wehner 2006).

Map and Compass A compass may also be used with a map to calculate a homeward path. Imagine yourself abandoned in an unfamiliar place with only a compass to guide your homeward journey. Before you could head home, you would also need a map so that you could know where you were relative to home. Only then could you use your compass and orient yourself correctly.

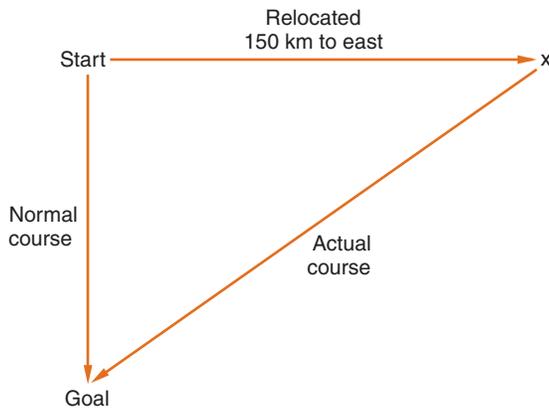


FIGURE 10.4 An animal that finds its way by using true navigation can compensate for experimental relocation and travel toward the goal. This implies that the animal cannot directly sense its goal and that it is not using familiar landmarks to direct its journey.

TRUE NAVIGATION

A third level of orientation, sometimes called true navigation¹ is the ability to maintain or establish reference to a goal, regardless of its location, without the use of landmarks (Bingman and Cheng 2005; Ronacher 2008). Generally, this implies that the animal cannot directly sense its goal and that if it is displaced while en route, it compensates by changing direction, thereby heading once again toward the goal (Figure 10.4).

Only a few species, most notably the homing pigeon (*Columba livia*), have been shown to have true navigational ability. Certain other groups of birds, including oceanic seabirds and swallows, are also known to home with great accuracy (Able 1980; Emlen 1975), as do sea turtles (Lohmann and Lohmann 2006). Interestingly, an invertebrate, the spiny lobster (*Panulirus argus*), also seems to have true navigation abilities (Boles and Lohmann 2003).

MULTIPLICITY OF ORIENTATION CUES

The feats of migration are indeed astounding—an arctic tern circumnavigating the globe, a monarch butterfly fluttering thousands of miles to winter in Mexico, a salmon returning to the stream in which it hatched after years in the open sea. How do they do it? There is no simple answer. Different species may use differ-

¹True navigation is an unfortunate term since it carries with it the implication that other means of finding one's way from place to place are not real methods of navigating. This is certainly not true. Nevertheless, we will use the term simply to distinguish this method of maintaining a course from the others.

ent mechanisms, and any given species usually has several navigational mechanisms available. Indeed, common themes in orientation systems are the use of multiple cues, a hierarchy of systems, and transfer of information among various systems (Berthold 2001; Bingman and Cheng 2005; Walcott 2005). When one mechanism becomes temporarily inoperative, a backup is used. Furthermore, a navigational system may involve more than one sensory system. These interactions can be quite complex, but we will simplify matters by considering each sensory mechanism separately.

VISUAL CUES

Visual mechanisms of orientation include the use of visual landmarks and celestial cues such as the sun, stars, and polarized light.

LANDMARKS

A **landmark** is an easily recognizable cue along a route that can be quickly stored in memory to guide a later journey. Although landmarks can be based on any sensory modality, we most commonly think of visual landmarks. Indeed, landmark recognition is perhaps the most obvious way that vision may be used for orientation or navigation. Humans use landmarks frequently when giving directions: “turn left before the bank” or “make a right just after the gas station.” Because the use of landmarks is so familiar to us, it is probably not too surprising to learn that many animals also use them to find their way.

Demonstrating Landmark Use

There are various ways to show that landmarks play a role in orientation. One way is to move the landmark and see whether this alters the orientation of the animal. In a classic study, Niko Tinbergen demonstrated that the digger wasp, *Philanthus triangulum*, relies on landmarks to relocate its nest after a foraging flight. While a female wasp was inside the nest, a ring of 20 pine cones was placed around the opening. When she left the nest, she flew around the area, apparently noting local landmarks, and then flew off in search of prey. During her absence, the ring of pine cones was moved a short distance (1 foot) away. On each of 13 observed trips, the returning wasp searched the middle of the pine cone ring for the nest opening. However, she did not find it until the pine cones were returned to their original position (Tinbergen and Kruyt 1938).

Animals can also be prevented from using landmarks by clouding their vision. Consider, for example, the ingenious way that Klaus Schmidt-Koenig and Hans Schlichte (1972) demonstrated that homing pigeons do



FIGURE 10.5 Homing pigeons that are wearing frosted contact lenses are unable to use landmarks for navigation. However, these pigeons head home just as accurately as those with normal vision do. Therefore, although pigeons may use landmarks if they are available, they do not require them to home.

not require landmarks to return to the vicinity of their home loft: they created frosted contact lenses for the pigeons (Figure 10.5). Through these lenses, pigeons could only vaguely see nearby objects and distant ones not at all. Nonetheless, the flight paths of these pigeons were oriented toward home just as accurately as those of control pigeons. Thus, the pigeons cannot be depending on familiar landmarks to guide their journey home. Note that this does not mean that they do not use landmarks when they are available, just that they can determine the homeward direction without them. Also, although pigeons with frosted lenses get to the general area of their home loft, they often cannot find the loft itself. Landmarks, then, may be important in pinpointing the exact loft location but are not necessary for determining the direction of home.

Models of Landmark Use

Knowing that an animal uses landmarks to find its way does not tell us *how* those landmarks are used. Do other animals use landmarks as humans do, as part of a mental map of the area? Perhaps some species do, but others might use landmarks in different ways. A simple model of landmark use is that the animal stores the image of a group of landmarks in its memory, almost like a photograph of the scene. Then it moves about the environment until its view of nearby objects matches the remembered “snapshot” (Emery and Clayton 2005). Rüdiger Wehner (1981) suggested that a whole series of memory snapshots might be filed in the order in which they are encountered. He added that invertebrates might be able to use landmarks by comparing the successive



FIGURE 10.6 The desert ant uses a remembered sequence of landmark images to find its way home in a familiar area.

images of surrounding objects with a series of memory snapshots of the landmarks along a familiar route.

One animal that appears to use memory snapshots of landmarks is the desert ant (Figure 10.6). As previously mentioned, desert ants are able to plot a course back to the nest by path integration; that is, they integrate the directions and distances traveled on all legs of the journey away from the nest to plot a direct course back. However, they also use landmarks, especially when they have almost reached the nest on their return from the foraging site (Åkesson and Wehner 2002). Once the ants are close to the nest entrance, they use a systematic search to find the opening of the burrow. The search strategy varies with the species of desert ant and the number of natural landmarks in their native habitat (Narendra et al. 2008). Desert ants tend to follow familiar routes. In fact, if landmarks are available, desert ants often use landmarks instead of path integration. If the most direct path is an unfamiliar route, it could lead over rocks or be blocked by scrub, and so landmarks are favored. Nonetheless, if the ant comes across a clearing, it can use path integration to take the most direct course home (Collett et al. 1998).

SUN COMPASS

Many animals use the sun as a celestial compass. In other words, these animals can determine compass direction from the position of the sun. Because of the earth’s rotation, the sun appears to move through the sky at an average rate of 15° per hour. The sun rises in the east and moves across the sky to set on the western horizon. The specific course that the sun appears to take varies with

the latitude of the observer and the season of the year, but it is predictable (Figure 10.7). Therefore, if the sun's path and the time of day are known, the sun can be used as a compass.

Knowledge of one compass bearing is all that is necessary for orientation in any direction. Consider this simplified example. Suppose you decided to camp in the woods a short distance north of your home. As you headed for your campsite at 9 A.M., the sun would be in the east, so you would keep the sun on your right to travel north. However, during your homeward trek the next morning, you would keep the sun on your left to travel south.

The use of the sun for orientation is complicated by its apparent motion through the sky. The sun appears to

move at an average rate of 15° an hour. Therefore, an animal heading straight for its goal and navigating by keeping a constant angle between its path and the sun would, after one hour, be following a path that would be off by 15° . Some species take only short trips, so errors due to the sun's apparent motion are inconsequential. These species do not adjust their course with the sun's. But if the sun is to be used as an orientation cue for a prolonged period, the animal must compensate for the sun's movement. To do so, it must be able to measure the passage of time and correctly adjust its angle with the position of the sun. At 9 A.M. an animal wishing to travel south might keep the sun at an angle of 45° to its left. By 3 P.M., however, the sun will have moved approximately 90° at an average rate of 15° an hour. To maintain the same southward bearing,

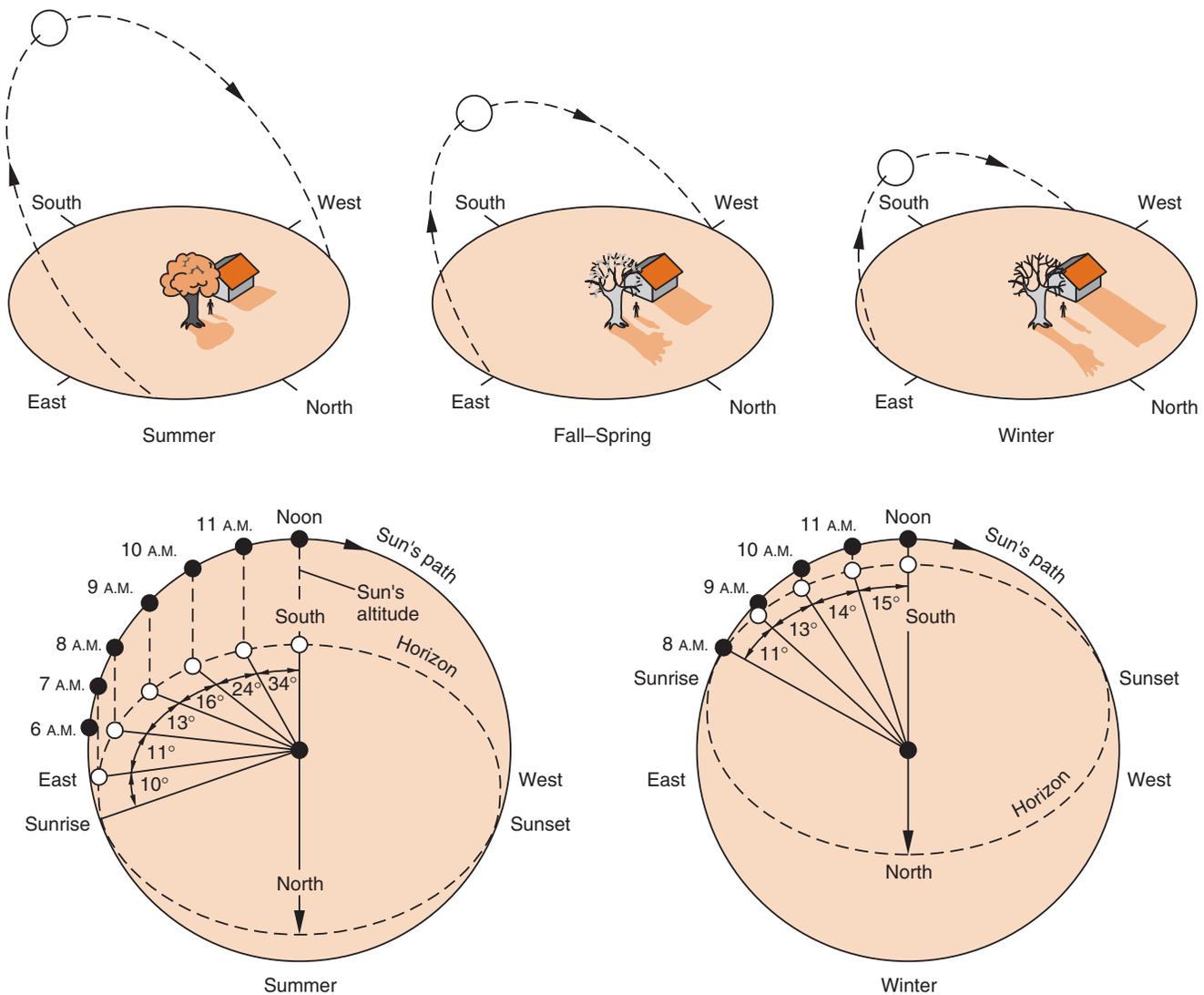


FIGURE 10.7 The sun follows a predictable path through the sky that varies with latitude and season. If the sun's course and the time of day are known, the sun's bearing (azimuth) provides a compass bearing. The sun appears to move across the sky at an average rate of 15° an hour. Therefore, if the sun is to be used as a compass for a long time, the animal must compensate for its movement.

the animal must now assume a 45° angle, with the sun on its right. Time is measured by using a biological clock (discussed in Chapter 9; time-compensated orientation of bee dances is discussed in Chapter 16).

The first work on sun compass orientation was done on birds and bees in the laboratories of Gustav Kramer (1950) and Karl von Frisch (1950), respectively. Although these two investigative groups worked at the same time, neither knew of the other's work. Nevertheless, they often used similar experimental designs to reveal the details of sun compass orientation. We will take a closer look at the experiments of Gustav Kramer here, but if you want to compare these studies to those of von Frisch, consult von Frisch's (1967) fascinating book, *The Dance Language and Orientation of Bees* or the discussion of bee dances in Chapter 16.

Gustav Kramer (1949) began his studies by trapping migrant birds and caring for them in cages. He then noticed that they became restless during their normal migration season. Furthermore, most of their activity took place on the side of the cage corresponding to the direction in which the birds would be flying if they were free to migrate. This activity has been aptly named migratory restlessness. In noting these tendencies, Kramer set the stage for a series of experiments that would yield valuable evidence in the quest for the navigational mechanisms of birds.

The indication that birds migrating during the day use the sun as a navigational cue was that the orientation (directionality) of migratory restlessness was lost



FIGURE 10.8 Starlings are daytime migrators and were the subject of Gustav Kramer's pioneering work on bird navigation.

when the sun was blocked from view. Kramer (1951) set up outdoor experiments with caged starlings, *Sturnus vulgaris* (Figure 10.8), which are daytime migrators, and found that they oriented in the normal migratory direction unless the sky was overcast, in which case they lost their directional ability and moved about randomly. When the sun reappeared, they oriented correctly again, suggesting that they were using the sun as a compass. Then Kramer devised experiments in which the sun was blocked from view and a mirror was used to change the *apparent* position of the sun. The birds reoriented according to the direction of the new "sun."

Because migration occurs during limited periods in the fall and spring, experiments using migratory restlessness to study orientation mechanisms are limited to two brief intervals a year. To eliminate this problem, Kramer (1951) devised an orientation cage in which there were 12 identical food boxes encircling a central birdcage (Figure 10.9). Kramer and his students trained birds to expect food in a box that lay in a particular compass direction. This ring of food boxes could be rotated so that a bird trained to get food in a given compass direction would not always be going to the same food box. This eliminated the possibility that the bird might learn to recognize the food dish by some characteristic,

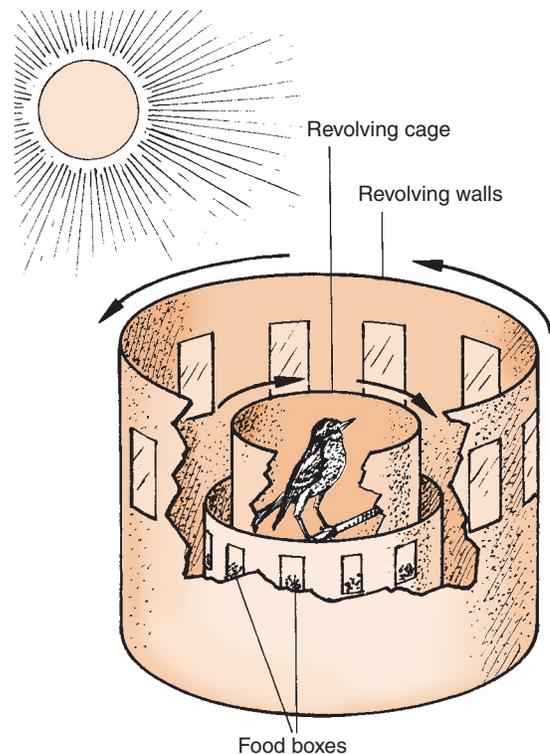


FIGURE 10.9 Kramer's orientation cage. The bird can see the sky through the glass roof but is prevented from seeing the surrounding landscape. It is trained to look for food in a food box that is placed in a particular compass direction.

such as a dent. As long as the birds could see the sun, they would approach the proper food box. However, on overcast days the birds were often disoriented, as would be expected if they were using a sun compass.

The results of experiments with birds in Kramer's orientation cages not only confirm those on migratory restlessness (Kramer 1951), but also indicate that the birds compensate for the movement of the sun. Actually, the idea of time-compensated sun compass orientation began when Kramer noticed that the birds in his orientation cages were able to orient in the proper direction even as the sun moved across the sky. When the real sun was replaced with a stationary light source, the birds continually adjusted their orientation with the stationary sun as though it were moving. The orientation with the artificial sun changed at a rate of about 15° an hour, just as it would to maintain a constant compass bearing using the real sun.

The birds are able to compensate for the sun's apparent movement; therefore, they must possess some sort of independent timing mechanism. As we saw in Chapter 9, the biological clock that allows birds to compensate for the movement of the sun can be reset by artificially altering the light–dark regime. Initially, the birds are placed in an artificial light–dark cycle that corresponds to the natural lighting conditions outside; the lights are on from 6 A.M. to 6 P.M. The light period is then shifted so that it begins earlier or later than the actual time of dawn. For example, if the animal is exposed to a light–dark cycle that is shifted so that the lights come on at noon instead of 6 A.M., the animal's biological clock is gradually reset. In this case, the animal's body time would be set six hours later than real time. Therefore, if the biological clock is used to compensate for the movement of the sun, orientation

should be off by the amount that the sun had moved during that interval. In this example, orientation should be shifted 90° ($6 \times 15^\circ$) clockwise, for example, west instead of south (Figure 10.10).

STOP AND THINK

How would orientation change if the light–dark cycle was changed so that the lights came on at midnight instead of 6 A.M.?

One of Kramer's students, Klaus Hoffmann (1954), was the first to use the clock-shift experiment to demonstrate the involvement of the biological clock in sun compass orientation. After resetting the internal clock of starlings by keeping them in an artificial light–dark cycle for several days, the birds' orientation was shifted by the predicted amount.

Using experiments similar to the classic studies described above, we have confirmed that a time-compensated sun compass exists in a wide variety of organisms (Åkesson and Hedenström 2007, Bingman 2005; Rozhok 2008). We also know more details about time-compensated sun orientation. For example, even with limited exposure to the sun (experience with a partial arc), many animals develop a sun compass that can be used all day (discussed in Rozhok 2008). Furthermore, the apparent movement of the sun through the sky varies with the time of day; it appears to move faster at noon than at sunrise or sunset. The internal clock of birds compensates for daily variation in the rate of the sun's apparent movement (Wiltschcko et al. 2000). Importantly, the compasses used by animals—sun, the stars, and the earth's magnetic field—interact in some interesting ways, as we will see shortly.

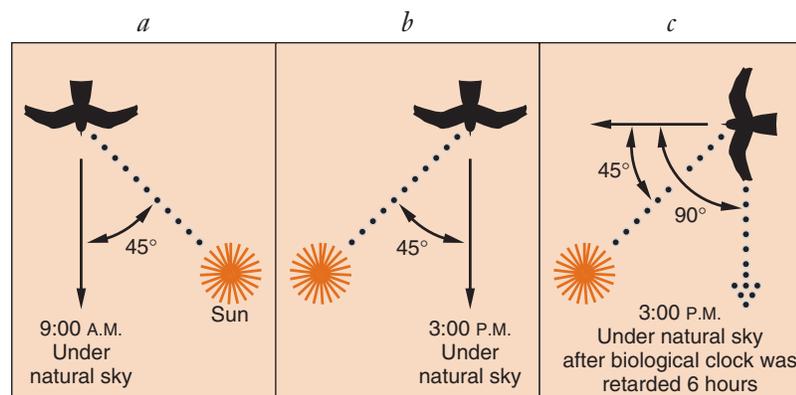


FIGURE 10.10 A clock-shift experiment demonstrates time-compensated sun compass orientation. (a) The flight path of a bird flying south at 9 A.M. might be at an angle of 45° to the right of the sun. (b) By 3 P.M., the sun would have moved roughly 90° , so to continue flying in the same direction, the bird's flight path might be at an angle of 45° to the left of the sun. (c) If the bird's biological clock were delayed by six hours and the bird's orientation tested at 3 P.M. (when the bird's body time was 9 A.M.), it would orient to the west. The flight path of the bird would be determined by the bird's biological clock. The flight path would, therefore, be appropriate for 9 A.M., and orientation would be shifted by 90° clockwise. (From Palmer 1966.)

STAR COMPASS

Many species of bird migrants travel at night. Even if they set their bearings by the position of the setting sun, how do they steer their course throughout the night? One important cue is the stars. This was first demonstrated by Franz and Eleonore Sauer (Sauer 1957, 1961; Sauer and Sauer 1960). Using several species of sylviid warblers, they performed a series of experiments aimed at discovering just which objects in the nighttime sky the birds use as cues. The Sauers kept their caged warblers inside a planetarium so that the nighttime sky could be controlled. They first lined up the planetarium sky with the sky outside and found that the birds oriented themselves in the proper migratory direction for that time of year. Then the lights were turned out, and the star pattern of the sky was rotated. The birds continued to orient according to the new direction of the planetarium sky. When the dome was diffusely lit, the birds were disoriented and moved about randomly. In some experiments, even though the moon and planets were not projected, the birds oriented correctly, apparently taking their bearings from the stars.

We know the most about the mechanism of star compass orientation in the indigo bunting (*Passerina cyanea*). Our knowledge has been gained primarily through Stephen Emlen's systematic planetarium studies. These indicate that the indigo bunting relies on the region of the sky within 35° of Polaris (Figure 10.11). Since Polaris is the pole star, it shows little apparent movement and, therefore, provides the most stationary reference point in the northern sky. The other constellations rotate around this point (Figure 10.12). The stars nearer Polaris move through smaller arcs than do those farther away, closer to the celestial equator. The birds learn that the center of rotation of the stars is in the north, information that is used to guide their migration either northward or southward. The major constellations in this region are the Big Dipper, the Little Dipper, Draco, Cepheus, and Cassiopeia. Experiments have



FIGURE 10.11 (a) Star compass orientation was explored by exposing nocturnal migrants, indigo buntings, to a planetarium sky. During the normal time of migration, caged birds will flutter in the proper migratory direction if the stars are visible. (b) In some studies, a bird's feet were inked, thus creating a record of its activity on the sides of a funnel-shaped cage.

shown that it is not necessary for all these constellations to be visible at once. If one constellation is blocked by cloud cover, the bird simply relies on an alternative constellation (Emlen 1967a, b).

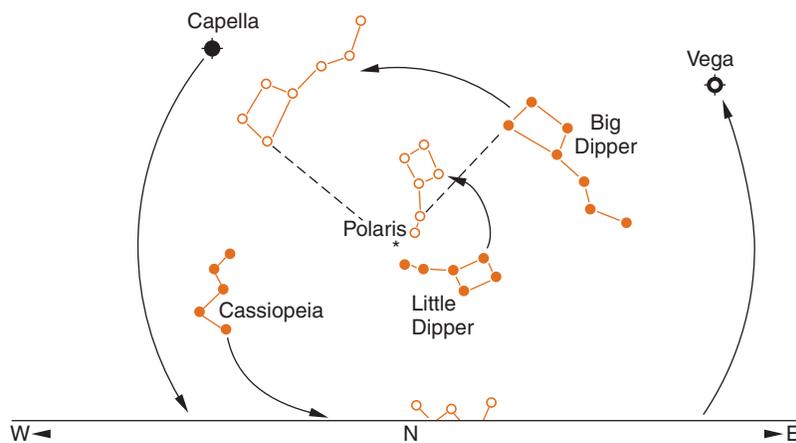


FIGURE 10.12 The stars rotate around Polaris, the North Star. The center of rotation of the stars tells birds which way is north. The positions of stars in the northern sky during the spring are shown here. The closed circles indicate star positions during the early evening, and the open circles indicate the positions of the same stars six hours later.

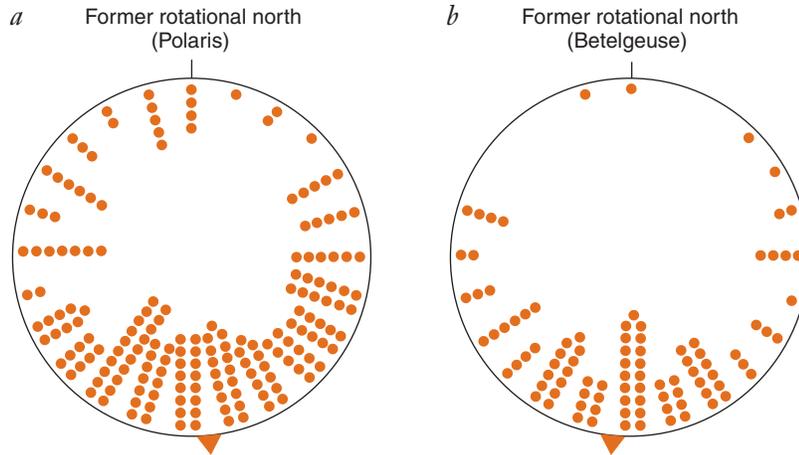


FIGURE 10.13 The orientation of indigo buntings to a stationary planetarium sky after exposure to different celestial rotations. During their first summer, indigo buntings learn that the center of celestial rotation is north. This was demonstrated by exposing a group of young birds to a planetarium sky that rotated (a) around Polaris (the North Star) or (b) around Betelgeuse. During their first autumn, when they would be migrating south, they were exposed to a stationary planetarium sky. Each dot is the mean direction of activity for a single test. The arrow on the periphery of the circle is the overall mean direction of activity. Each group oriented away from the star that had been the center of rotation. (Modified from data of Able and Bingman 1987; Emlen 1970.)

Young birds learn that the center of rotation of stars is north. The axis of rotation then gives directional meaning to the configuration of constellations. Once their star compass has been set in this way, the birds do not need to see the constellations rotate. Simply viewing certain constellations is sufficient for orientation. This was first demonstrated by exposing groups of young indigo buntings to normal star patterns in a planetarium sky. One group saw a normal pattern of rotation, one that rotated around Polaris. The other group viewed the normal pattern of stars, but instead of rotating around Polaris, these stars rotated around Betelgeuse, a bright star closer to the equator. When the birds came into a migratory condition, their orientation was tested under a stationary sky. Although each group was headed in a different geographic direction, both groups were well oriented in the appropriate migratory direction relative to the center of rotation they had experienced, either Betelgeuse or Polaris (Figure 10.13). In other words, in the autumn, when the birds would be heading south for the winter, those that had experienced Betelgeuse as the center of rotation interpreted the position of that star as north and headed away from it (Emlen 1969, 1970, 1972).

The development of the star compass has been studied in only a few species other than the indigo bunting. Garden warblers (Wiltschko 1982; Wiltschko et al. 1987) and pied flycatchers, *Ficedula hypoleuca* (Bingman 1984) also learn that the center of celestial rotation indicates north.

POLARIZED LIGHT AND ORIENTATION

One of the puzzling facets of sun compass orientation is that many animals continue to orient correctly even

when their view of most of the sky is blocked. How is this possible? For at least some of these animals, another celestial orientation cue is available in patches of blue sky—polarized light. Before considering how animals orient to polarized light, let's examine the nature of polarized light and how the pattern of skylight polarization depends on the position of the sun.

The Nature of Polarized Light

Light consists of many electromagnetic waves, all vibrating perpendicularly to the direction of propagation (Figure 10.14). As a crude analogy, think of a rope held loosely between two people as a light beam. The rope itself would define the direction of propagation of the light beam. If one person repeatedly flicked his or her wrist, the rope would begin to wave or oscillate. These oscillations would also be perpendicular to the length of the rope, but they could be vertical, horizontal, or any angle in between, depending on how she flicked her wrist. The same is true of light waves. Most light con-

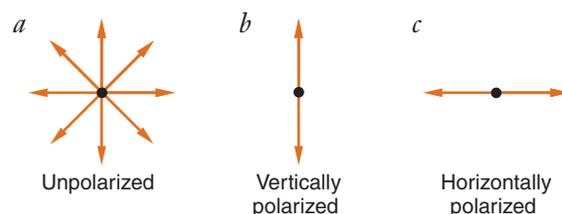


FIGURE 10.14 Unpolarized and polarized light. The arrows show the planes of vibration of a light beam that is coming straight out of the page.

sists of a great many waves that are vibrating in all possible planes perpendicular to the direction in which the wave is traveling. Such light is described as unpolarized. In fully polarized light, however, all waves vibrate in only one plane. Our rope light beam, for instance, would become vertically polarized if the person's wrist were flicked only up and down. In this case, the rope might oscillate vertically in the spaces between the boards of a picket fence.

As sunlight passes through the atmosphere, it becomes polarized by air molecules and particles in the air, but the degree and direction of polarization in a given region of the sky depend on the position of the sun. In other words, there is a pattern of polarized light in the sky that is directly related to the sun's position (Figure 10.15). One aspect of this pattern is the degree of polarization. To picture the pattern of polarization, think of the sky as a celestial sphere with the sun at one pole and an "antisun" at the other. The light at the poles is unpolarized, but it becomes gradually more strongly polarized with increasing distance from the poles. Thus, between the sun and the antisun, there is a band where the light in the sky is more highly polarized than in other regions. This region is described as the band of maximum polarization. But there is more to the pattern than this: the direction of the plane of polarization (called the e-vector) also varies according to the position of the sun. The plane of polarization of sunlight is always perpen-

dicular to the direction in which the light beam is traveling. If you were to draw imaginary lines of latitude around the sun and antisun, these lines would indicate the plane of polarization at any point in the sky. Since the entire pattern of polarization of light in the sky is determined by the sun's position, the pattern moves westward as the sun moves through the sky (Waterman 1989).

Uses of Polarized Light in Orientation

Polarized light reflected from shiny surfaces, such as water or a moist substrate, is used by some aquatic insects to detect suitable habitat. Indeed, polarized light may actually attract them (Schwind 1991). For the backswimmer, *Notonecta glauca* (Figure 10.16), not only is the horizontally polarized light that is reflected from the surface of a pond a beacon that helps the insect, as it flies overhead, locate a new body of water during dispersal, but it also triggers a plunge reaction that brings the insect closer to a new home (Schwind 1983).

The plane of polarization of the light in the sky is used as an orientation cue in two possible ways. First, polarized light is used as an axis for orientation. In other words, an animal might move at some angle with respect to the plane of polarization. Many animals use polarized light in this way. Salamanders living near a shoreline, for instance, can use the plane of polarization to direct their

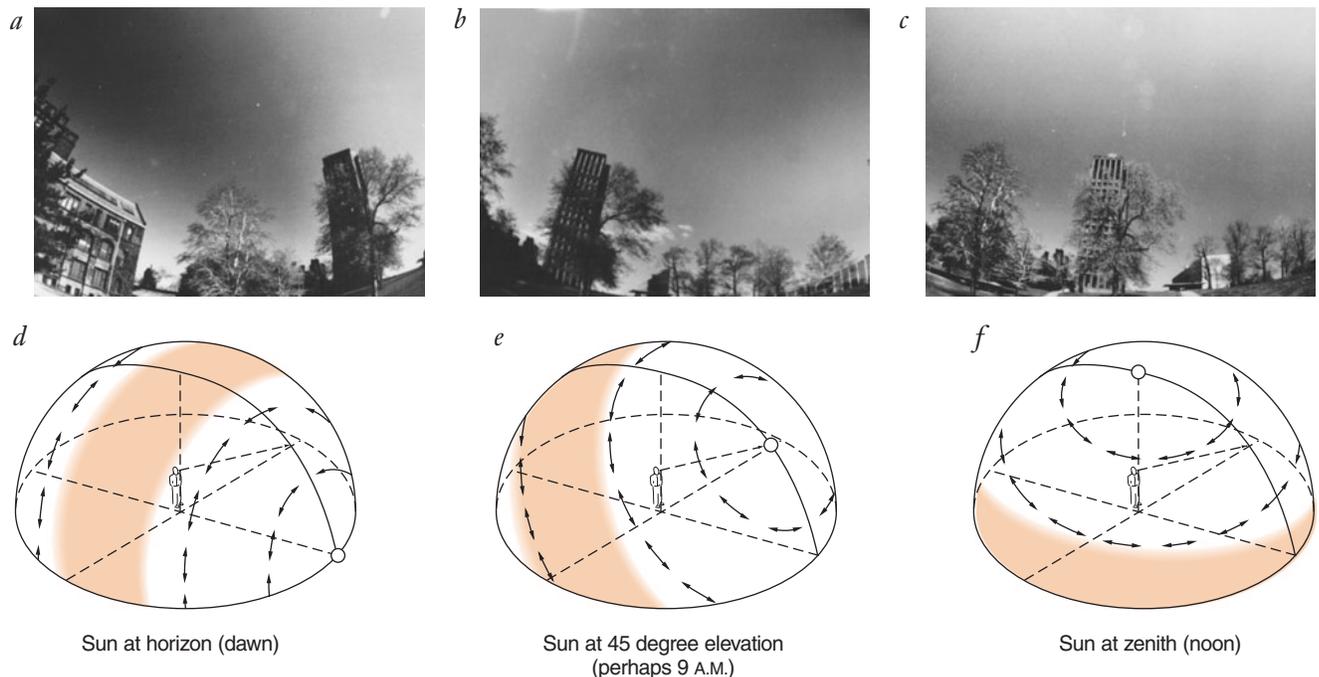


FIGURE 10.15 The sky viewed through a polarizing filter to show the pattern of skylight polarization at (a) 9 A.M., (b) noon, and (c) 3 P.M. The darker region of the sky is the band of maximum polarization. The diagrams below show the pattern of polarization (d) with the sun on the horizon, (e) at 45° elevation, and (f) at zenith. The arrows indicate the direction of the plane of polarization. The small circle denotes the position of the sun. The pattern of polarization depends on the position of the sun. The blue sky provides an orientation cue for animals that can perceive the plane of polarization.



FIGURE 10.16 Many aquatic insects, such as this backswimmer, use polarized light reflected from water or a moist surface to locate an appropriate habitat. A backswimmer spends almost its entire life underwater. These insects are commonly seen in ponds, suspended beneath the water surface, as this one is. Adults can fly, however, and may disperse to a new pond before laying the second batch of eggs of the season.

movements toward land or water (Adler 1976). Second, the pattern of polarization of sunlight might be used to determine the sun's position when it is blocked from view. The polarization of light in the sky could also provide an orientation cue at dawn and dusk, when the sun is below the horizon. Many birds that migrate at night set their bearings at sunset. Apparently, the pattern of skylight polarization at sunset (Able 1982) and at sunrise (Moore 1986) assists the orientation of birds migrating at these times because some experiments have shown that the birds' directional tendencies are altered when the plane of polarized light to which they are exposed is experimentally shifted by rotating polarizing filters. Indeed, when a bird is setting its bearings for the night, polarized light is a more important orientation cue than the sun's position along the horizon at dusk or the geomagnetic field (Able 1993; Able and Able 1996).

MAGNETIC CUES

Many organisms, ranging from bacteria to certain vertebrates, orient their activities relative to the earth's magnetic field. These activities include direction finding and navigation over long and short distances—the long-distance migrations of birds (reviewed in Wiltschko and Wiltschko 2005) to the nightly foraging forays of spiny lobsters (Lohmann et al. 2007). Magnetic sense may also help an organism locate a preferred direction, as when bacteria swim downward, toward the muddy bottom they call home (Blakemore and Frankel 1981). The earth's magnetic field may also orient nest building, as in the Ansell's mole rat, a rodent that lives underground (Marhold et al. 1997), or roosting place of bats (Wang et al. 2007). Indeed, Wolfgang and Roswitha Wiltschko (Wiltschko and Wiltschko 2007) suggest that, in birds at least, a magnetic compass evolved in nonmigratory species first. These species probably used the magnetic compass for optimizing paths to and from various goals, such as nest sites, feeding sites, and drinking sites. Later, when some species began to migrate, the migrants use the magnetic compass to orient during migration.

The ability to use the earth's magnetic field as a compass has its advantages. It can be used in places where visual

cues are limited or absent, such as a roosting cave, underground tunnel, or the depths of an ocean. And, unlike celestial cues, it is constant year round, night and day.

CUES FROM THE EARTH'S MAGNETIC FIELD

To picture the geomagnetic field around the earth, imagine an immense bar magnet through the earth's core from north to south. However, this bar magnet is tilted slightly from the geographic north-south axis, and the magnetic poles are shifted slightly from the geographic, or rotational, poles (Figure 10.17). The difference

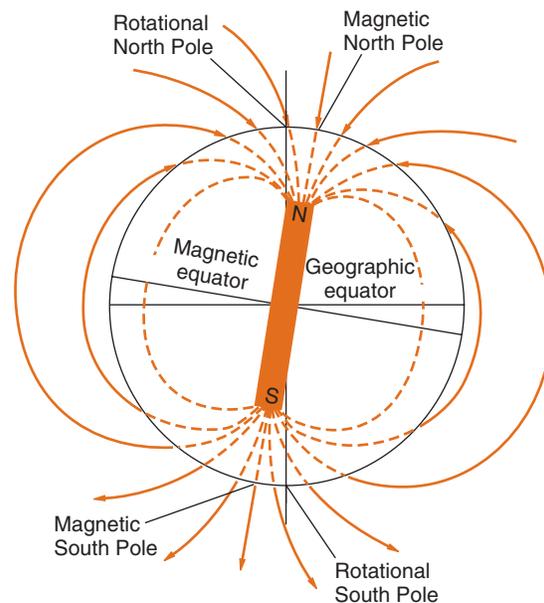


FIGURE 10.17 The earth's magnetic field. The lines of force leave magnetic south vertically; curve around the earth's surface; and enter magnetic north, heading straight down. The geomagnetic field provides several possible cues for navigation: polarity, the north-south axis of the lines of force, and the inclination of the lines of force. The magnetic compass of most animals appears to be an inclination compass. They determine the north-south axis from the orientation of the lines of force but assign direction to this by the inclination of the force lines. In the northern hemisphere, north is the direction in which the force lines dip toward the earth.

between the magnetic pole and the geographic pole is called the declination of the earth's magnetic field. Because the declination is small in most places, usually less than 20°, magnetic north is usually a reasonably good indicator of geographic north. (On maps and nautical charts used for precise navigation, both geographic north and magnetic north are indicated, so that a navigator or backpacker can adjust her compass readings for declination.) The declination is, of course, greatest near the poles.

Several aspects of the earth's magnetic field vary in a predictable manner and could, therefore, provide directional cues. One aspect is polarity. The magnetic north pole is called the positive pole, and the magnetic south, the negative pole. The second aspect is the angle of the lines of force with respect to earth's surface. These leave the magnetic south pole vertically; curve around the surface of the earth; become level with the surface at the magnetic equator; and reenter the magnetic north pole, going straight down. The angle of inclination, or dip, of the magnetic field is the angle that the line of force makes with the horizon. The angle of inclination is steepest (vertical) near the poles and near zero (horizontal) near the equator. The third aspect that varies predictably is the intensity (or strength) of the geomagnetic field. It is greatest at the poles and least at the equator.

Thus, we see that the polarity, inclination, and intensity of the earth's magnetic field vary systematically with latitude, providing three potential orientation cues. Which of these are used? Our own experience with compasses immediately brings polarity to mind. When the needle on a compass points north, it is responding to the polarity of the earth's field. Indeed, some species of animals seem to respond to polarity (Table 10.1). This list includes invertebrates, the spiny lobster, for instance, as

well as vertebrates, including some fish and birds; the mole rat, a rodent that lives underground (Wiltschko and Wiltschko 2006); and a bat (Wang et al. 2007). We know that an animal responds to polarity when its orientation changes in response to an experimental shift in the direction of magnetic north.

Other animals, including most birds and sea turtles, appear to use the magnetic field inclination. Instead of north or south, they distinguish between "poleward," where the lines of force are steepest, and "equatorward," where the lines of force are parallel to the earth's surface. Although the horizontal component of the earth's field (the direction of magnetic north), which runs between magnetic north and magnetic south, indicates to the animal the north-south axis, the vertical component of the earth's magnetic field (the inclination of the field) is the cue that tells the animal whether it is going toward the pole or toward the equator (Wiltschko and Wiltschko 2006).

We can determine whether an animal is using the polarity or the angle of inclination of the pole by separately altering the horizontal and the vertical components of the experimental magnetic field and observing the effect of the animal's orientation. If an animal uses a polarity compass, it will shift its orientation when the horizontal component of the field is shifted. In contrast, an animal using an inclination compass will shift its orientation when the vertical component of the experimental field is altered.

Ansell's mole rats (*Cryptomys anselli*) orient using the polarity of the magnetic field. These small rodents normally live in darkness in subterranean colonies. When housed in circular arenas in captivity, they reliably and spontaneously build their nests in the southeastern region of the arena. Researchers placed mole rats of the

TABLE 10.1 Animals Demonstrated to Use a Magnetic Compass

Systematic group					Type of compass
Molluscs					
Snails	1 order	1 family	1 species		???
Arthropods					
Crustaceans	3 orders	3 families	5 species		Polarity compass
Insects	6 orders	7 families	9 species		Polarity compass
Vertebrata					
Cartilaginous fish	1 order	1 family	1 species		???
Bony fish	2 orders	2 families	4 species		Polarity compass
Amphibians	1 order	2 families	2 species		Inclination compass
Reptilians	1 order	2 families	2 species		Inclination compass
Birds	4 orders	12 families	21 species		Inclination compass
Mammals	2 orders	2 families	3 species		Polarity compass

same family group into a circular test arena. Within hours, the animals gathered nesting materials and built a nest in the southeast sector of the arena. Then researchers used a Helmholtz coil, a device that generates a magnetic field when an electric current runs through it, to alter the magnetic field experienced by the mole rats. The magnetic field experienced by the birds can be altered by reversing the direction of current flow through the coil. When researchers reversed the horizontal component (the polarity) of the magnetic field, the mole rats began to build nests in the northwest sector of the arena. However, when researchers inverted the vertical component (the angle of inclination) of the magnetic field, the mole rats continued nesting in the southeast sector (Figure 10.18*a*) (Marthold et al. 1997).

In contrast, birds use the inclination angle of the earth's magnetic field for orientation. For example, in the laboratory the migratory restlessness of European robins remains oriented in the proper direction even when the birds have no visual cues. When the magnetic world that the birds experienced was reversed by switching the polarity of an experimental field, there was no effect on their orientation. However, the birds reori-

ented if the inclination in the experimental field was altered (Figure 10.18*b*). It is interesting that these birds were not able to orient according to magnetic field lines that were horizontal to the earth's surface. Horizontal field lines occur around the equator. A bird could determine the north-south axis in a horizontal field, but without the inclination it would not know which direction is north or south (Wiltschko and Wiltschko 1972).

The results of an experiment on free-flying homing pigeons are also consistent with the idea that a bird's magnetic compass is based on the inclination of the magnetic lines of force. Small Helmholtz coil hats were fitted onto the heads of homing pigeons (Figure 10.19*a*). A Helmholtz coil is a device that generates a magnetic field when an electric current runs through it. The magnetic field experienced by the birds can be altered by reversing the direction of current flow through the coil. On cloudy days, when the pigeons relied on magnetic cues rather than their sun compass, they oriented as if they considered north to be the direction in which the magnetic lines of force dip into the earth. Those birds that experienced the greatest dip in the magnetic field in the north, as it is in the nor-

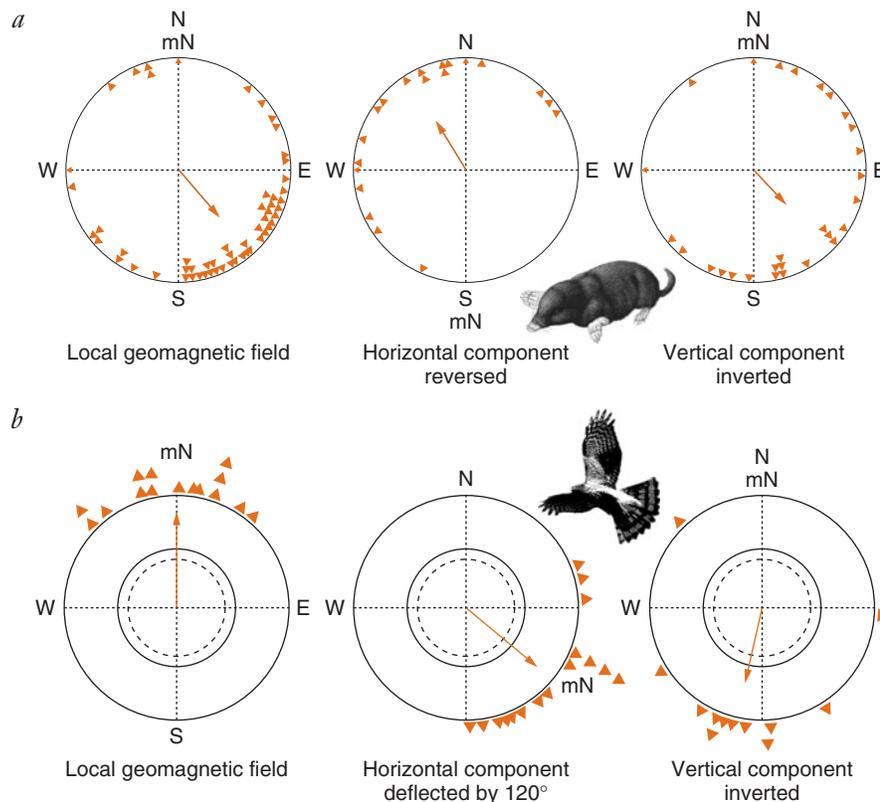


FIGURE 10.18 The earth's magnetic field can serve as a compass. (a) Mole rats respond to the polarity (horizontal component) of the ambient magnetic field. They build their nests in the southeast portion of a circular arena. If the magnetic field is experimentally reversed, mole rats build their nests in the northwest portion of the arena. However, if the vertical component of the ambient magnetic field is reversed, mole rats do not change their orientation. (b) Birds use the inclination of the lines of force (vertical component of the earth's magnetic field) as a compass. The lines of force are steepest at the poles and horizontal at the equator. Birds reverse their orientation when the inclination of the magnetic field is reversed, but they do not alter their orientation if the polarity of the magnetic field is changed. (From Wiltschko and Wiltschko 2005.)

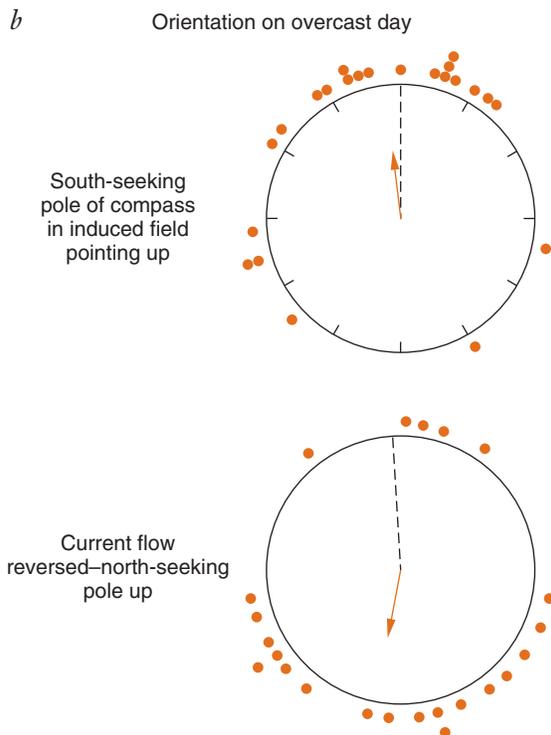
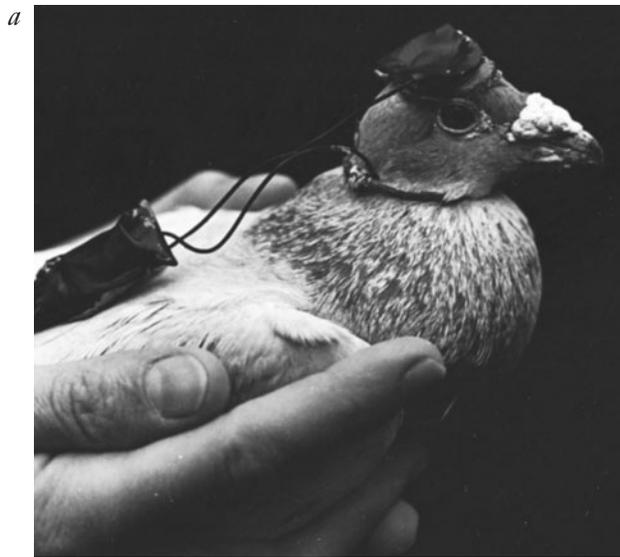


FIGURE 10.19 (a) A pigeon with a Helmholtz coil, a device that generates a magnetic field, on its head. (b) The magnetic field experienced by the pigeon can be altered by changing the direction in which the electric current runs through the coil. On overcast days, when the birds could not use the sun as a compass, the magnetic field influenced their orientation. They oriented as if they interpreted north as the direction in which the magnetic lines of force dip toward the earth. Each dot indicates the direction in which a bird vanished from sight after being released. The arrow in the center indicates the mean vanishing bearing. (Modified from data of Walcott and Green 1974.)

mal geomagnetic field, headed home. In contrast, the birds that experienced the greatest dip in the magnetic field in the south were misdirected by the reversed magnetic information and headed directly away from home (Figure 10.19*b*) (Visalberghi and Alleva 1979; Walcott and Green 1974).

There are also some indications that several species respond to the small differences in the intensity of the geomagnetic field. Among these animals are bees (Kirschvink et al. 1997; Walker and Bitterman 1989), homing pigeons (Dennis et al. 2007; Keeton et al. 1974; Kowalski et al. 1988), sea turtles (Lohmann and Lohmann 1996a), and the American alligator (Rodda 1984). If changes in magnetic intensity can be sensed, the gradual increase in strength between the equator and the poles could also serve as a crude compass.

DIRECTIONAL INFORMATION FROM THE EARTH'S MAGNETIC FIELD: A MAGNETIC COMPASS

If we keep in mind that orientation is essential to the survival of migrating or homing animals, it should not come as a surprise that orientation is affected by the interaction of many cues, as well as many variables, including experience, species differences, and amount of stored energy. We will separate some of these interacting variables to try to understand just how animals remain oriented when faced with the real problems of navigating. Many animals can obtain directional information from the earth's magnetic field; that is, the earth's magnetic field can serve as a **magnetic compass**.

The Magnetic Compass and Bird Navigation

As we have seen, birds use the earth's magnetic field as a compass. They determine whether they are headed toward the pole or the equator by the angle of inclination of the magnetic lines of force.

Inherited Migratory Program Migratory birds inherit a program that tells them to travel in a certain geographical direction, based on magnetic cues, for a certain amount of time. Because the magnetic compass of birds is an inclination compass, migrants from either the northern or the southern hemisphere might use the same migratory program—fly toward the equator (where the lines of force are more horizontal) in the fall and toward the pole (where the lines of force are more vertical) in the spring (Wiltschko and Wiltschko 1996).

Some birds, however, cross the equator during migration and then keep going. We might wonder, then, how a bird from northern regions that crosses the equator can continue to fly south in the southern hemisphere. To continue flying in the same geographical direction when the equator is crossed, the birds must reverse their migratory direction with respect to the inclination

compass: they must now fly “poleward” instead of “equatorward.” Experience with the horizontal magnetic field around the equator is the switch that causes the birds to begin flying “poleward” (Wiltschko and Wiltschko 1996).

The sensitivity of the magnetic compass of birds corresponds to the strength of the earth’s magnetic field. A bird generally does not respond to magnetic fields that are much stronger or weaker than that which is typical in the area where it has been living. In fact, the range of intensities to which a bird may respond on a given day is usually narrower than those that it might experience during migration. However, it seems that the range of sensitivity may be adjusted by exposure to a field of a new strength for a period of time. Thus, responsiveness may be fine-tuned during migration (Wiltschko 1978; Wiltschko and Wiltschko 1999).

The Magnetic Compass of Sea Turtles

Some sea turtles travel tens of thousands of kilometers during their lifetimes, a feat that can require continuous swimming for periods of several weeks, with no land in sight. As a loggerhead sea turtle, *Caretta caretta* (Figure 10.20), makes its way across the featureless Atlantic Ocean from the coast of Florida (perhaps to the Sargasso Sea and back), it is guided by the earth’s magnetic field (Lohmann and Lohmann 1992). The hatchlings swim toward *magnetic* northeast in the normal geomagnetic field and continue to do so when the field is experimentally reversed (Figure 10.21) (Lohmann 1991). And, similar to a bird’s magnetic compass, that of the sea turtle is based on the inclination of the magnetic lines of force (Light et al. 1993). Indeed, the magnetic



FIGURE 10.20 A hatchling loggerhead sea turtle. These turtles may use the earth’s magnetic field to guide their travels through the open ocean.

compass of sea turtles has many of the characteristics of the avian magnetic compass.

A sea turtle begins its journey immediately after hatching. It uses local cues to head toward the ocean. When sea turtle hatchlings first enter the ocean, they simply swim into the waves to maintain an offshore heading. Near the shore, the waves come directly toward land, so swimming into the waves takes the turtles out to sea. The course that is initiated by swimming into the waves is later transferred to the magnetic compass.

In the open ocean, waves can no longer serve as a navigational cue because they can come from any direction. Here, sea turtles maintain the same angle with the magnetic field that they assumed while swimming into the waves. In this way, they stay on course. Simultaneous experience with both cues seems to be important. This was revealed in an experiment in which hatchling loggerhead sea turtles swam into surface waves in tanks for either 15 or 30 minutes. Their orientation was then tested in still water and in a magnetic field. Only those hatchlings with 30 minutes of experience swimming into waves in a magnetic field were able to maintain their orientation in still water (Goff et al. 1998).

POSITIONAL INFORMATION FROM THE EARTH’S MAGNETIC FIELD: A MAGNETIC MAP?

As we have seen, true navigation requires not only a compass but also a map. The map is necessary to know one’s position relative to the goal, and then a compass is needed to guide the journey in a homeward direction. Kenneth and Catherine Lohmann (2006; Lohmann et al. 2007) caution that the magnetic maps of animals have not been fully characterized and may function in a very different way than human maps do. Investigation of magnetic maps has been hampered because there is no standard definition of the term *map* among researchers. For some researchers, a map requires a mental image—an internal spatial representation—of the region, but that view is increasingly giving way to a broader view of a map. For example, by the Lohmanns’ definition, an animal has a **magnetic map** if it can obtain positional information from the earth’s magnetic field, that is, if the animal can use the earth’s magnetic field to determine its position relative to a target or goal. In this construct of a magnetic map, the map may be inherited or learned and specific or very general. We will use the Lohmanns’ definition of a magnetic map in this text.

What features of the earth’s magnetic field could provide positional information? As we have seen, the angle of inclination varies predictably with latitude, so an animal that could detect this feature could determine whether its position is north or south of the goal. If an animal could detect the intensity of the total magnetic field, the horizontal component of the field and/or the vertical component of the field, it could determine its

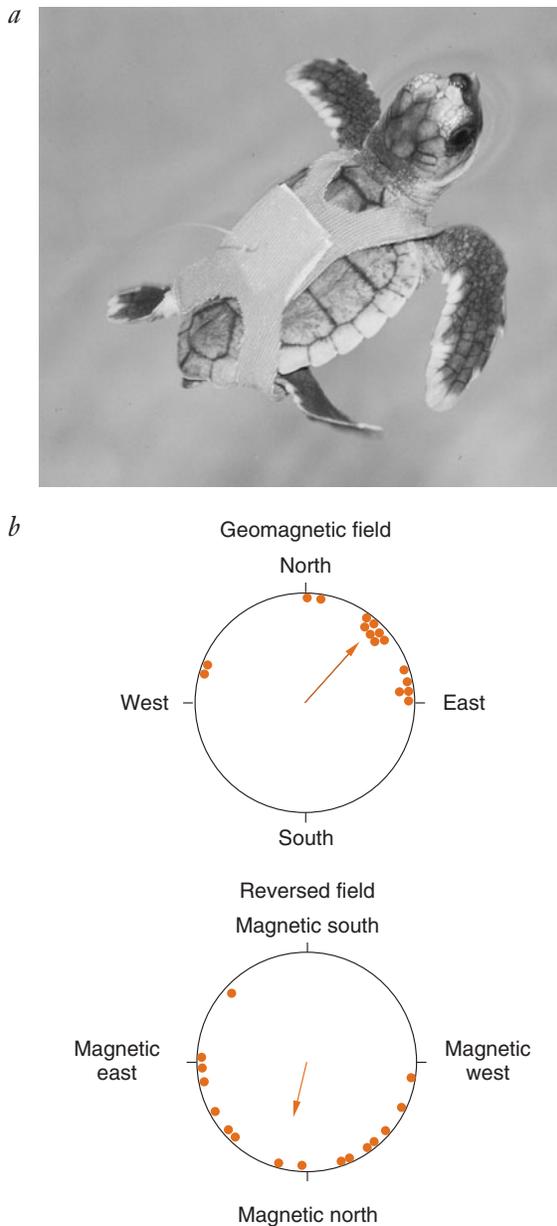


FIGURE 10.21 A demonstration of the ability of loggerhead sea turtle hatchlings to orient to magnetic fields. (a) A sea turtle is harnessed in a small tank so that its swimming direction can be determined. A coil that can alter the magnetic field experienced by the turtles surrounds the tank. (b) When exposed to the earth's magnetic field, the turtles orient toward magnetic northeast. When the field is reversed, the hatchlings still orient to magnetic northeast, even though this is in the opposite geographic direction. (From Lohmann 1991.)

position relative to the goal. Declination (the difference between geographic north and magnetic north) also varies in a regular pattern and could potentially be used as a clue to position. We will see that animals can use cues from the earth's magnetic field to navigate, but the cues used may differ among animals or as an animal ages (Lohmann and Lohmann 2006; Lohmann et al. 2007).

Magnetic Signposts

The magnetic “maps” of some animals may consist of inherited responses to magnetic landmarks, or signposts, that trigger changes in direction. We see such magnetic triggers along the migratory pathways of certain birds, for instance, the pied flycatcher. The Central European population of pied flycatchers first flies southwest to Iberia and then southeast. The change in migratory direction allows the birds to avoid the Alps, Mediterranean Sea, and the central Sahara (Figure 10.22). The birds have an inherited program that causes them to change migratory direction when they experience a magnetic field characteristic of key geographical locations at the appropriate time. Flycatchers held in captivity will flutter their wings and head in the correct migratory direction when they are exposed to a magnetic field characteristic of Frankfurt, Germany, where their free-flying comrades begin their migration. If captive flycatchers are then exposed to the magnetic field characteristic of Iberia, where the migrating flycatchers change direction, the captive flycatchers shift the direction of their fluttering to southeast. Captive flycatchers who continue to experience the same magnetic field throughout the migratory time period or who experience the magnetic field characteristic of the end point do not appropriately shift direction. Thus, the local magnetic field of Iberia acts as a signpost telling the migrating birds to shift flight direction slightly to the left (Beck and Wiltschko 1988; Wiltschko and Wiltschko 2005).

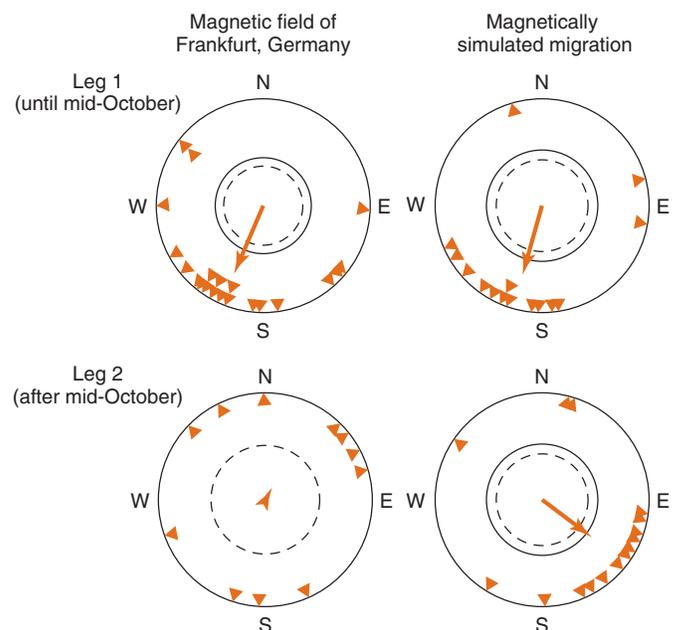


FIGURE 10.22 Orientation of young pied flycatchers held in captivity during their first migration and exposed to magnetic fields typical of those along the route. Only the birds exposed to the correct magnetically simulated journey oriented properly. Each triangle represents the direction in which a bird oriented. The arrow indicates the mean direction of all birds. (Modified from data of Beck and Wiltschko 1988.)

Magnetic signposts also trigger changes in swimming direction during the open-sea navigation of sea turtles. When loggerhead hatchlings are exposed to a magnetic field typical of northern Florida, they swim east-southeast using the earth's magnetic field as a compass. This heading will bring the sea turtles to the Gulf Stream, which will lead them to the North Atlantic gyre, a circular current that flows clockwise around the Sargasso Sea. Young loggerheads remain in the warm, rich water of this gyre for five to ten years.

These inherited orientation responses to magnetic fields help to keep the young loggerheads from straying out of the gyre (reviewed in Lohmann et al. 2008). This was demonstrated by recording the preferred swimming direction of hatchling loggerheads that had never been in the ocean. The turtles were exposed to magnetic fields characteristic of three widely separated regions along the migratory route of the North Atlantic gyre. The young loggerheads oriented to each field by swimming in a direction that would keep them in the favorable waters of the gyre if they had been migrating (Figure 10.23).

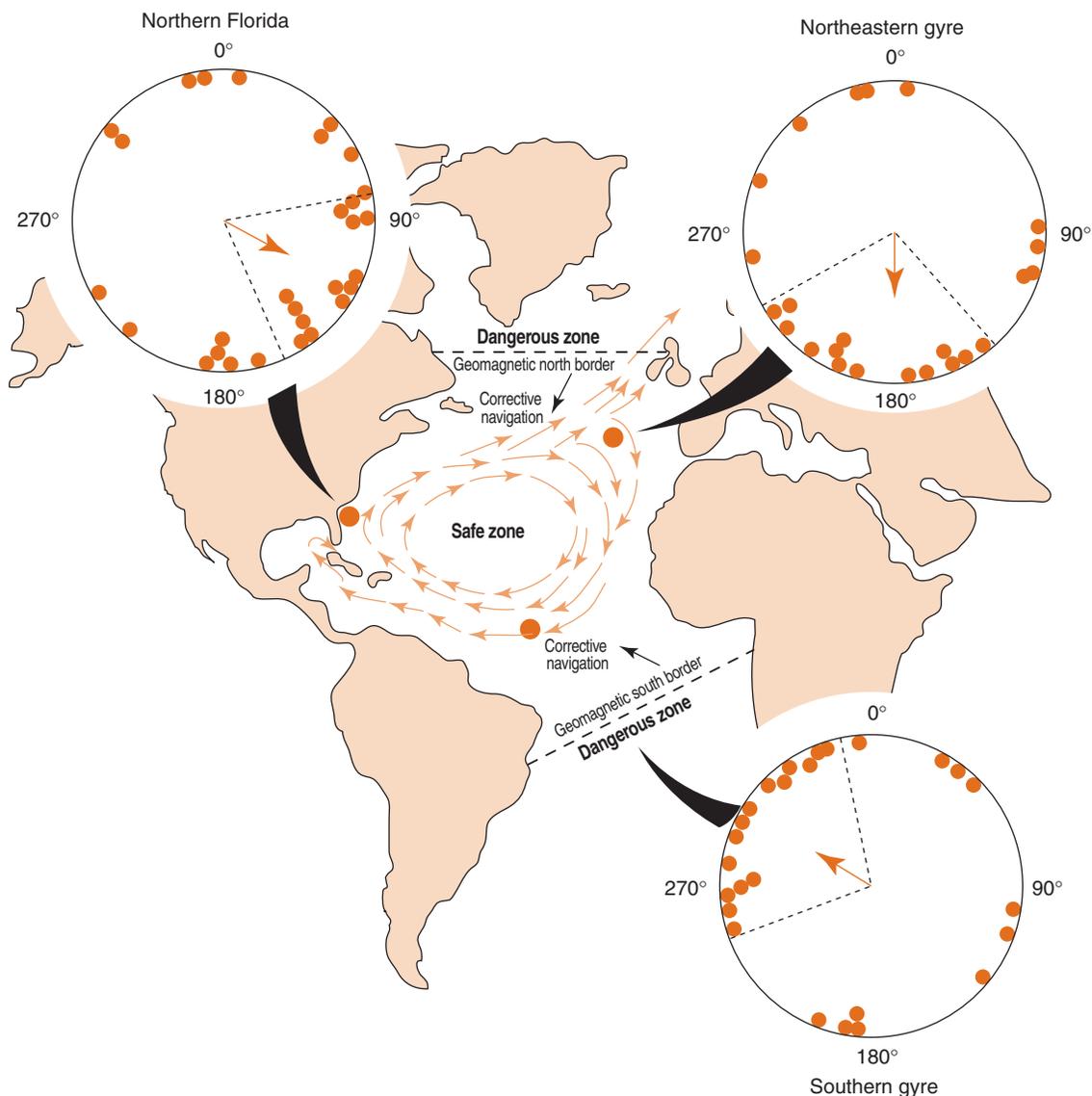


FIGURE 10.23 Magnetic signposts in the earth's magnetic field may direct juvenile sea turtles in the proper direction to remain within the North Atlantic gyre, a circular current in the Sargasso Sea. The arrows in the ocean indicate the direction of the major currents of the gyre. Juvenile sea turtles normally swim within the gyre for several years. In the laboratory, juvenile sea turtles exposed to magnetic fields characteristic of three locations along the migratory route preferred to swim in the direction that would keep them swimming within the gyre if they had been migrating. The arrows leading to each circle show the location of the magnetic field to which the turtles were exposed. Each dot indicates the direction in which a harnessed juvenile sea turtle swam. The arrow in the center indicates the mean swimming bearing. (Modified from Lohmann et al. 2001.)

Thus, hatchling loggerheads are programmed to swim in a particular direction when they encounter magnetic fields found in critical regions of the gyre—places where leaving the gyre would lead the juveniles to unfavorable waters. Regional differences in earth's magnetic field serve as navigational beacons that guide the open-sea migration of young loggerheads, without the turtles having a conception of their geographic position or their position relative to a goal (Lohmann et al. 2001).

Position Relative to Goal

Certain animals may use an aspect or aspects of earth's magnetic field as a map to locate their position relative to a goal. We do know some animals can detect both the inclination and the intensity of earth's magnetic field. Both of these features vary across the earth's surface, and they vary in different directions. Thus, animals could use either of these features to "know" the direction to the goal.

Some of the magnetic effects on pigeon homing seem to be more than interference with the magnetic compass and, therefore, may support the idea of a magnetic map. One example is the disorientation of pigeons released in magnetic anomalies, places where the earth's magnetic field is extremely irregular. Pigeons relying on the predictable changes in the geomagnetic field would become confused in areas where the field is abnormal. Some magnetic anomalies disorient pigeons even under sunny skies, when presumably they would be using the sun as a compass (Frei 1982; Frei and Wagner 1976; Wagner 1976; Walcott 1978). A perfect compass (the sun) cannot help if the map is messed up. This suggests that the geomagnetic field may be more than just a compass. As you can see in Figure 10.24, some birds released at magnetic anomalies appear to follow the magnetic topography, usually preferring the magnetic valleys, where the lower field strength is closer to home values.

In a more recent study, Todd Dennis and his colleagues (2007) equipped homing pigeons with GPS-based tracking devices and tracked their flight paths near places with magnetic anomalies. Regardless of the direction to home, the pigeons flew either parallel or perpendicular to the local lines with similar intensity of the geomagnetic field. The alignment of flight paths with magnetic intensity lines is interpreted as an indication that the pigeons can detect and respond to spatial variability of the geomagnetic field.

As a sea turtle matures, it learns the geomagnetic topography of specific areas and uses that information as at least part of the map it uses to locate an isolated target, such as a nesting beach (Lohmann and Lohmann 1996a, b). After spending several years swimming in the North Atlantic gyre, juvenile loggerhead turtles and green turtles (*Chelonia mydas*) that hatched along the eastern coast of the United States move toward the coastline to feeding sites. Certain sea turtles migrate along the east coast between summer feeding grounds in temperate regions and winter feeding grounds in the south. These juvenile turtles migrate to the same specific feeding locations each autumn and spring (Arens and Lohmann 2004). Every few years, adult sea turtles of nearly all species migrate from their feeding locations to nesting areas and back again. Adults of many populations return to nest on the same beaches where they hatched (reviewed in Lohmann et al. 2008).

How do sea turtles migrate with such precision? The earth's magnetic field provides a global positioning system that tells them their position relative to a goal. Kenneth Lohmann and colleagues (2004) demonstrated that juvenile and adult sea turtles use the geomagnetic field as a navigational map—a more complex use than hatchlings. The researchers captured juvenile green turtles from their feeding grounds located at about the midpoint of the eastern coast of Florida. The swimming

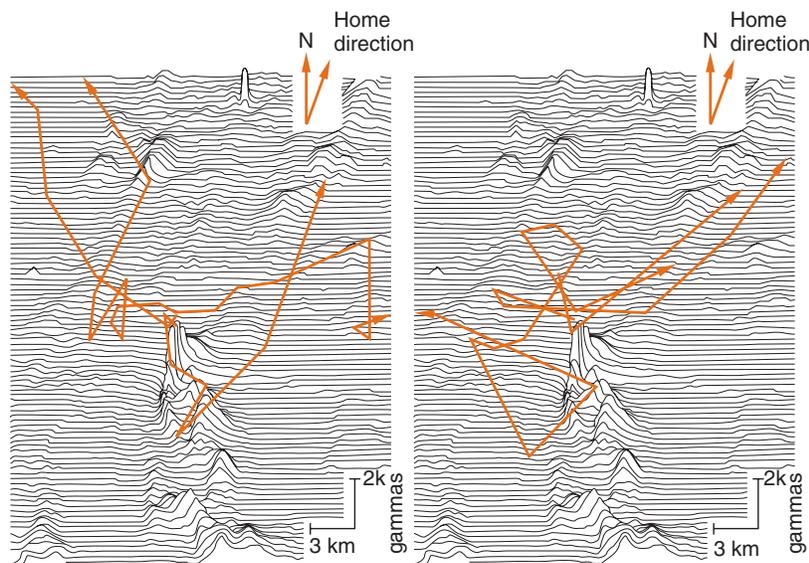


FIGURE 10.24 The flight paths of pigeons in magnetic anomalies. In some places the geomagnetic field is highly irregular. Pigeons released in these areas may be completely disoriented, even on sunny days. The paths of these pigeons seem to follow the magnetic valleys, where the field strength is closer to the value at the home loft. (From Gould 1980.)

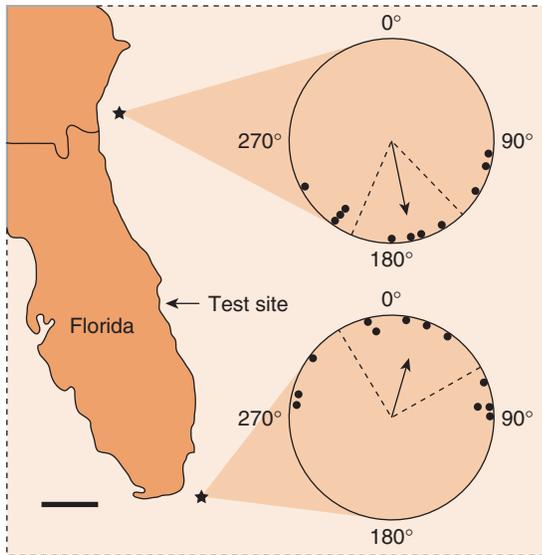


FIGURE 10.25 As sea turtles mature, they use the earth's magnetic field to determine their location relative to home. Sea turtles return to the same feeding grounds every year. Researchers captured sea turtles at their feeding ground along the east coast of Florida. The preferred direction of swimming of each turtle (indicated by a black dot in the circle) was determined as previously described. The turtles were exposed to a magnetic field similar to the field that exists north of the site or to the field that exists south of the site. The sites are indicated by stars. The turtles swam in a direction that would return them to their feeding grounds (the test site) if they actually had been displaced. (From Lohmann et al. 2004.)

direction of tethered turtles was monitored as in previous experiments. Turtles were then exposed to either a geomagnetic field that would be found 337 km north of the test site or a magnetic field that would be found 337 km south of the test site. Turtles exposed to a northern magnetic field swam approximately southward; those exposed to a southern magnetic field swam northward (Figure 10.25). The magnetic field may tell the turtle whether it is north or south of its goal. The turtle might then move in the appropriate direction until it encounters other cues, perhaps chemical, that identify the feeding grounds (reviewed in Lohmann and Lohmann 2006).

MAGNETORECEPTION

Humans do not sense magnetic fields—at least not consciously. We might wonder, then, how animals sense the earth's magnetic field. There are at least two types of magnetoreceptors. One type involves specialized photoreceptors and is light dependent. Thus, certain animals may “see” the earth's magnetic field. The basic idea of this light-dependent model of magnetoreception is that photoreceptor molecules absorb light better under certain magnetic conditions. Thus, the amount of light absorp-

tion also provides information about the local magnetic field. The second hypothesis involves magnetite, a magnetic mineral found in many animals that orient to the earth's magnetic field. In this model, the magnetite responds to the earth's magnetic field. This response could then affect other sensory receptors, perhaps mechanoreceptors, open ion channels, or act on the cell physically.

Light-Dependent Magnetoreception

Because birds are the best-studied group, we will tell their story. We must add, however, that similar observations of a relationship between photoreception and magnetoreception have been discovered in other animals (Rozhok 2008).

What initial observations suggest that photoreception and magnetoreception are linked in birds? First, the magnetoreceptor is located in the eye, specifically the right eye. Second, birds cannot remain oriented to a magnetic field in darkness. Not only is light required, but it must be light of specific wavelengths. Birds usually require blue light to remain oriented to a magnetic field but may be able to orient in red light if they are given time to adjust (Wiltschko and Wiltschko 2006).

Cryptochrome, a photopigment involved in magnetoreception, stimulates the photoreceptors differently depending on the orientation of the magnetic field. Thus, it seems that migratory birds sense the magnetic field as a visual pattern (Figure 10.26) (Ritz et al. 2000). Unlike some photopigments, which change shape when they absorb light, cryptochrome uses photons to transfer electrons forming radical pairs (pairs or triplets of spinning electrons). The radical pairs lead to further reactions in a cascading pathway, and magnetic fields alter the functioning of radical pairs. Cryptochromes absorb blue-green light—the wavelengths important for magnetic orientation. In migratory birds, cryptochromes are pro-

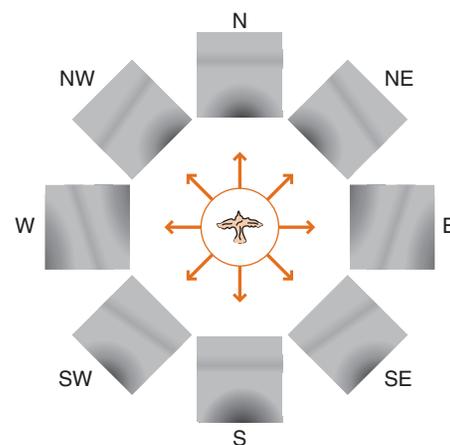


FIGURE 10.26 Seeing the earth's magnetic field. The visual field of a bird flying parallel to the horizon in Urbana-Champaign, Illinois, would be modulated depending on the direction in which the bird was looking. (From Ritz et al. 2000.)

duced (the genes for cryptochromes are active) at night, when many migrants are flying. Nonmigratory birds produce cryptochromes only during the day. The difference in the times of cryptochrome production suggests that all birds may need magnetic information during the day, but only night-flying migrants also need it at night. Notably, cryptochromes are found in the ganglion cells of a migratory garden warbler's retina and in large displaced ganglion cells, which project to brain areas where magnetically sensitive neurons have been reported and these areas show high levels of neuronal activity during magnetic orientation (Mouritsen et al. 2004).

The cryptochrome-containing cells of the retina connect to neurons in a brain region called Cluster N, where neurons are especially active when night-flying migratory birds are orienting to a magnetic field. The retina and Cluster N are connected via pathways through the thalamus, a brain region important for vision. Dominik Heyers and his colleagues (2007) demonstrated this connection using special dyes that can be traced as they travel along nerve fibers. They injected one type of tracer dye into the cryptochrome-containing cells of the retina and another type in the neurons in Cluster N. The tracers met in the thalamus, which supports the hypothesis that birds use their visual system to sense magnetic fields.

Magnetite

Many organisms known to have the ability to sense geomagnetic fields, including honeybees, trout, salmon, birds, and sea turtles, have deposits of magnetic material, magnetite, which often forms chains or clumps. In vertebrates, these deposits are commonly found in the head or skull. The magnetite crystals can twist into alignment with the earth's magnetic field if permitted to do so. Such movement might stimulate a stretch receptor.

If the magnetite deposits function as magnetoreceptors in larger organisms, the information they provide would have to be transmitted to the nervous system. Therefore, associations between magnetite and the nervous system are of particular interest. So far, the closest we have come to identifying the actual magnetoreceptor cells is in the rainbow trout (*Oncorhynchus mykiss*). Michael Walker and his colleagues first confirmed that the ophthalmic branch of the trigeminal nerve (a cranial nerve that carries sensory information from the front of the head) contains fibers that respond to magnetic fields. Then they used a special dye to trace these fibers both to the brain and to cells in the olfactory epithelium in the nose of the trout. These cells, the candidate magnetoreceptor cells, contain small amounts of a material thought to be magnetite (Walker et al. 1997).

In birds, magnetite deposits are found in the area of the upper beak. Interestingly, branches of the bobolink's trigeminal nerve appear to innervate the region in which magnetite deposits are found. These branches respond

to earth-strength changes in the direction of the magnetic field (Semm and Beason 1990).

A popular way to demonstrate a role of magnetite in magnetoreception is to remagnetize the magnetite using a brief, strong magnetic pulse to the region of the animal where magnetite is located. If a strong magnetic pulse alters orientation, the conclusion is that magnetite is a part of the magnetoreceptor. In this way, researchers have demonstrated that the polarity compass of bats is based on magnetite (Holland et al. 2008).

In addition to their light-dependent inclination compass, birds have a magnetite receptor. Experiments on Australian silvereyes (*Zosterops l. lateralis*) provide an example (Holland et al. 2008). When adult silvereyes that were flying northward from Tasmania during their autumn migration were exposed to a strong magnetic pulse, their orientation was shifted clockwise by about 90° toward the east. Similar results were obtained when adult silvereyes were exposed to a strong magnetic pulse during the spring migration. These observations support the idea that a magnetite-based receptor plays a role in orientation, but they don't indicate whether it is involved in the compass sense or the map sense. However, when juvenile silvereyes are exposed to a magnetic pulse shortly after fledging, before they begin to migrate, the pulse had little effect on their orientation. The juveniles continued to orient in their normal autumnal migratory direction. Unlike adult migrants, which have established a navigational map during previous migrations, the juveniles rely on an innate migratory program that heads them in the appropriate compass direction for their first migration. Because a magnetic pulse disrupts orientation in adults but not in juveniles, it is thought that the earth's magnetic field is part of the navigational map of adults (reviewed in Wiltschko et al. 2005; Wiltschko and Wiltschko 2006, 2007).

Two Magnetoreceptor Systems

Recent studies aimed at exploring the physiological basis for magnetoreception support the idea that animals might have more than one type of magnetic sensitivity. As we have seen, there are two proposed mechanisms for magnetoreception, one light-dependent and the other based on magnetite. Table 10.2 presents mechanisms and their proposed functions.

Certain species seem to have both types of magnetoreception systems, each serving a different purpose. For example, the eastern red-spotted newt (*Notophthalmus viridescens*) uses a magnetic compass based on the inclination of the magnetic lines of force when orienting toward the shore. We know this because their orientation was shifted by about 180° when the vertical component of the magnetic field was inverted. These newts are also able to home, that is, to return to the point of origin after being moved to an unfamiliar location. During homing, the newt's orientation is unaffected by an inversion of the vertical component of the magnetic field (Phillips 1986), but is shifted

TABLE 10.2

	Photopigment-dependent magnetoreceptor	Magnetite magnetoreceptor
Feature of geomagnetic field detected	Inclination or polarity	Intensity
Tasks in which it is used in birds	Compass (direction finding)	Map (position, signpost, or trigger)
Site of reception	Retina of right eye	Upper beak and/or ethmoid region
Nerve	Optic nerve	Ophthalmic branch of trigeminal nerve
Brain structures involved	Nucleus of the basal optic root (nBOR); optic tectum	Trigeminal ganglion

by a change in polarity (Phillips 1987). Thus, these initial observations suggest that, in the newt at least, the mechanism(s) for magnetoreception involved in homing differs from the one involved in shoreward compass orientation.

The magnetic compass used by the eastern newt when orienting toward the shore is light-dependent (Phillips and Borland 1992). The orientation of newts during homing is also affected by exposure to different wavelengths of light. However, the effects of long wavelengths on homing are different from those on shoreward orientation. Furthermore, light-dependent processes are not expected to respond to the polarity of a magnetic field, and we know that a newt's homing ability is sensitive to polarity changes. This again suggests two magnetoreception mechanisms in newts (Phillips and Borland 1994).

Migratory birds may also have two mechanisms of magnetoreception that serve different functions. The light-dependent mechanism serves as a magnetic compass (Ritz et al. 2009; Rodgers and Hore 2009). Because a magnetite-based mechanism is theoretically capable of detecting minute variations in the earth's magnetic field, it may be part of the magnetic "map" receptor. To use the geomagnetic field as a map, an animal might merely compare the local intensity of the field with that at the goal. A receptor system used in a map sense, then, would not have to respond to the direction of the field, but it would be expected to respond to slight variations, less than 0.1%, in the intensity of the magnetic field experienced. The amount of magnetic material typically found in pigeons' skulls could comprise a receptor that would provide enough sensitivity to small differences in magnetic field to fit the bill. A comparison of the effects of a strong magnetic pulse on the orientation of juvenile and adult Australian silvereyes supports the idea that a magnetite-based receptor system is part of a "map." It is commonly believed that whereas adult migrants have established a navigational map, juveniles have not. As we have seen, the orientation of adult silvereyes is shifted by a magnetic pulse, presumably because their navigational map was affected. In contrast, the juvenile silvereyes remained oriented in the appropriate migratory direction after a magnetic pulse. The magnetic pulse may not affect the orientation of juveniles because they have not

yet formed a magnetic map. Instead, their orientation was based on an innate migratory program. They use their magnetic compass, which is based on a light-dependent magnetoreception process, to head in the appropriate direction according to their inherited migratory program (reviewed in Wiltschko et al. 2005; Wiltschko and Wiltschko 2006, 2007).

CHEMICAL CUES

In this section, we will focus on the use of olfactory cues for orientation during homing. We will discover that salmon are guided to the stream where they hatched by chemical landmarks, and we will examine the more recent suggestion that pigeons also use olfactory cues when homing.

OLFACTION AND SALMON HOMING

One of the most remarkable stories in the annals of animal behavior concerns the travels of the salmon. Salmon hatch in the cold, clear freshwater of rivers or lakes and then descend from the streams that flow from those areas and swim to sea, fanning out in all directions. Once they reach the ocean, depending on the species, they may spend one to five years there until they reach their breeding condition. Now large, glistening, beautifully colored creatures, they head from their feeding grounds back through the trackless sea to the very river from which they came. When they reach the river, they swim upstream, turning up the correct tributary until they reach the very one where they spent their youth.

Wild salmon return to the specific location of the natal stream in which they were born with remarkable precision. Thomas Quinn and his colleagues (2006) demonstrated this site fidelity by using temperature changes during incubation of pre-hatch sockeye salmon embryos to cause banding patterns on the ear bones of the fish. These banding patterns marked fish for later identification. The researchers chose a pond associated with Hansen Creek in southwestern Alaska as the site where the embryos would emerge and buried the

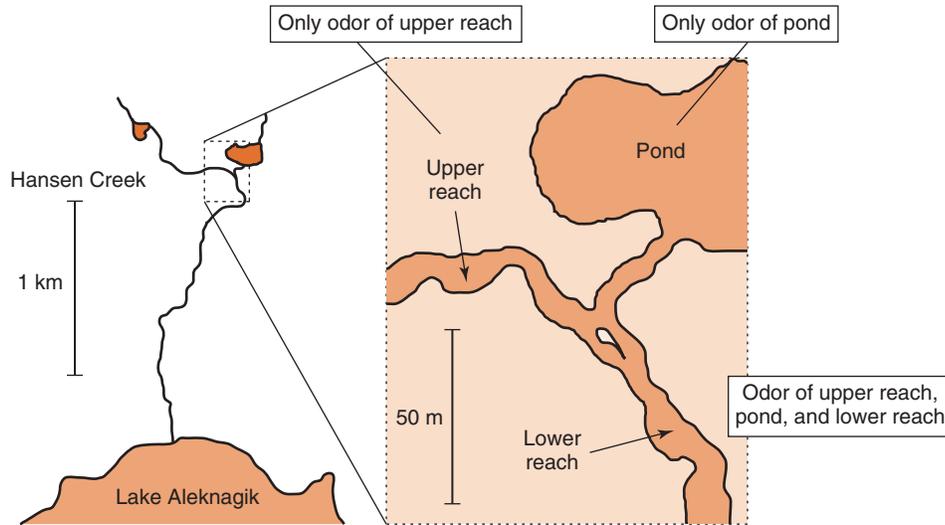


FIGURE 10.27 A map of Hansen Creek, Alaska, showing the distribution of olfactory cues in different regions of the creek area.

embryos at the bottom of the pond (see the map in Figure 10.27). The embryos emerged, migrated to the sea along with unmarked fish from the Hansen Creek area, and then migrated back to the creek. Sockeye salmon die after spawning. The carcasses of salmon along the creek and in the pond were examined for banding patterns on the ear bones. Of the 324 salmon carcasses in the pond, 12 were marked, but none of the 138 carcasses found in the creek were marked. Thus, the marked salmon returned to the site of their incubation—the pond associated with Hansen Creek.

Although navigation in the open seas appears to depend on the integration of several sensory cues, including magnetism (Lohmann et al. 2008), sun compass, polarized light, and perhaps even odors, navigation up the rivers is based primarily on olfactory cues (reviewed in Dittman and Quinn 1996). According to the olfactory hypothesis of salmon homing, young salmon learn the odors of the home stream before they begin their downstream migration (Hasler and Wisby 1951). The odor of the home stream is most likely the particular mixture of amino acids in the water (Shoji et al. 2000; Shoji et al. 2003; Yamamoto and Ueda 2007). After spending time at sea, the salmon return to the coast and use olfactory cues to locate the mouth of the river in which they hatched. During their upstream migration, the salmon follow a chemical trail back to the tributary where they hatched. When they come to a fork in the river, they may swim back and forth across the two branches. If they mistakenly swim up the wrong branch and lose the scent of the home stream, they retreat downstream until the scent is encountered again. Then, they usually take the correct route. Researchers have hypothesized such nondirect homing (choosing the wrong tributary and returning to the fork to choose

another) for many years, but it has only recently been verified. Radio-tagged spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) tracked in the Columbia River system that chose the wrong branch of the river returned to the fork and swam up another branch (Keefer et al. 2008).

Sensory deprivation experiments have demonstrated the importance of olfaction in salmon homing. Blinding the fish had no effect, but plugging their nasal cavities impaired their ability to home correctly. Coho salmon (*Oncorhynchus kisutch*) were trapped shortly after they had made their choice of forks in a Y-shaped stream. The nasal cavities of half of those caught in each branch were plugged. The other half were untreated. All the fish were then released downstream from the fork and allowed to repeat their upstream migration. Whereas 89% of the control fish returned to the branch where they were originally captured, only 60% of the fish with nose plugs made the correct choice (Wisby and Hasler 1954). In another study, a fish with its nose plugged swam with others of its kind to the opening of its home pond. However, unable to smell the special characteristics of its home waters, it did not enter the pond (Cooper et al. 1976).

Olfactory cues, not qualities of the habitat, guide salmon to their birthplace. These conclusions are consistent with a study done on sockeye salmon in Hansen Creek in Alaska. As you can see in Figure 10.27, Hansen Creek has an upper and a lower reach (a reach is the region of a river or creek between two bends). It is also fed by water from a pond (the pond in which marked fish hatched in the study illustrating site fidelity discussed earlier). During the spawning season, salmon were collected and tagged from both reaches of Hansen Creek and from the pond. The olfactory cues available at these sites differed. The upper creek had only the odor of the upper

creek, and the pond had only the odor of the pond. The pond was a better quality area because its characteristics made predation on salmon less likely. The control salmon were released at their capture site, and they remained in that immediate area. The experimental fish were released at a site other than their capture site. Salmon from the pond that were released in the lower reach, where more olfactory cues were available, were more likely to return to the pond than were salmon released in the upper reach. But recall that the pond is a more suitable habitat. How do we know whether the fish displaced from the pond returned because of odor cues or habitat cues? Consider the behavior of fish captured from the upper reach and released either in the lower reach or in the pond. As the displaced upper-reach fish swam upstream, they had olfactory information from the upper reach, as well as from the pond. During the upstream journey, the fish also assessed habitat-quality cues. Most of the homing salmon bypassed the habitat-quality cues from the pond and followed olfactory cues to the upper reach. Most upper-reach fish displaced to the pond stayed in the pond; they did not have olfactory cues to guide them back to the upper reach (Stewart et al. 2004).

STOP AND THINK

What would you have concluded if fish from the upper reach that were released in the pond had stayed in the pond?

OLFACTION AND PIGEON HOMING

No one denies that olfactory cues are of paramount importance during the upstream migration of salmon, but the role olfaction plays in pigeon homing has been controversial (Wallraff 2004, 2005). Let's look at the evidence.

Models of Avian Olfactory Navigation

Two models for olfactory navigation have been suggested. According to Floriani Papi's "mosaic" model, pigeons form a mosaic map of environmental odors within a radius of 70 to 100 km of their home loft. Some of this map would take shape as the young birds experienced odors at specific locations during exercise and training flights. More distant features of the map would be filled in as wind carried faraway odors to the loft. One odor might be brought by wind from the north and another by wind from the east. The bird would associate each odor with the direction of the wind carrying it. When the wind shifted direction, the odors that arrived first would be closer than those that took longer to arrive (Papi et al. 1972). For instance, a hypothetical pigeon might learn that the sea is to the west, an evergreen forest is south, a large city is north, and a garbage dump is east. If the bird in this example smelled pine

needles at its release site, it would assume that it was in the forest south of its loft and would use one of its compasses, perhaps the sun or the earth's magnetic field, to fly north.

Hans G. Wallraff (1980, 1981) has suggested a "gradient" model of olfactory navigation that assumes that there are stable gradients in the intensity of one or more environmental odors. Then, wherever it was, the bird would determine the strength of the odor and compare it to the remembered intensity at the home loft. Unlike the mosaic model, which requires only that the bird make qualitative discriminations among odors, the gradient model demands that the bird make both qualitative and quantitative discriminations. Reconsider the previous example. The smell of the ocean might form an east-west gradient, and the fragrance of the evergreen forest might generate a north-south gradient. If the bird in the previous example smelled the air at a release site and determined that the scent of the sea was stronger but the smell of the forest was weaker than at the home loft, it would determine that its current position was northwest of home.

Tests of the Models

These models of olfactory navigation have stimulated intensive research, and it is becoming clear that odors are important in the navigation of homing pigeons. Let us see how different researchers have approached the question.

Distorting the Olfactory Map A method of testing olfactory hypotheses is to manipulate olfactory information to distort the bird's olfactory map. This has been done by deflecting the natural winds to make it seem that odors are coming from another direction. The deflector lofts used in these experiments typically have wooden baffles that shift wind flow in a predictable manner (Figure 10.28). For instance, wind from the south might be deflected so that it seemed to come from the east. A pigeon in this loft would form an olfactory map that was shifted counterclockwise by 45°. When it was released south of its loft, we would expect it to interpret the local odors as being east of its loft and fly west to get home.

Deflector loft experiments have shown consistent shifts in the orientation of homing pigeons (Baldaccini et al. 1975; Kiepenheuer 1978; Waldvogel et al. 1978). However, there are reasons to believe that the shift in orientation observed in pigeons from deflector lofts might be due to something other than a distorted olfactory map. We would expect pigeons that were temporarily prevented from smelling at the time of their release to be unable to read their olfactory map and to orient randomly. But this is not the case: the orientation of smell-blind (anosmic) pigeons from deflector lofts is

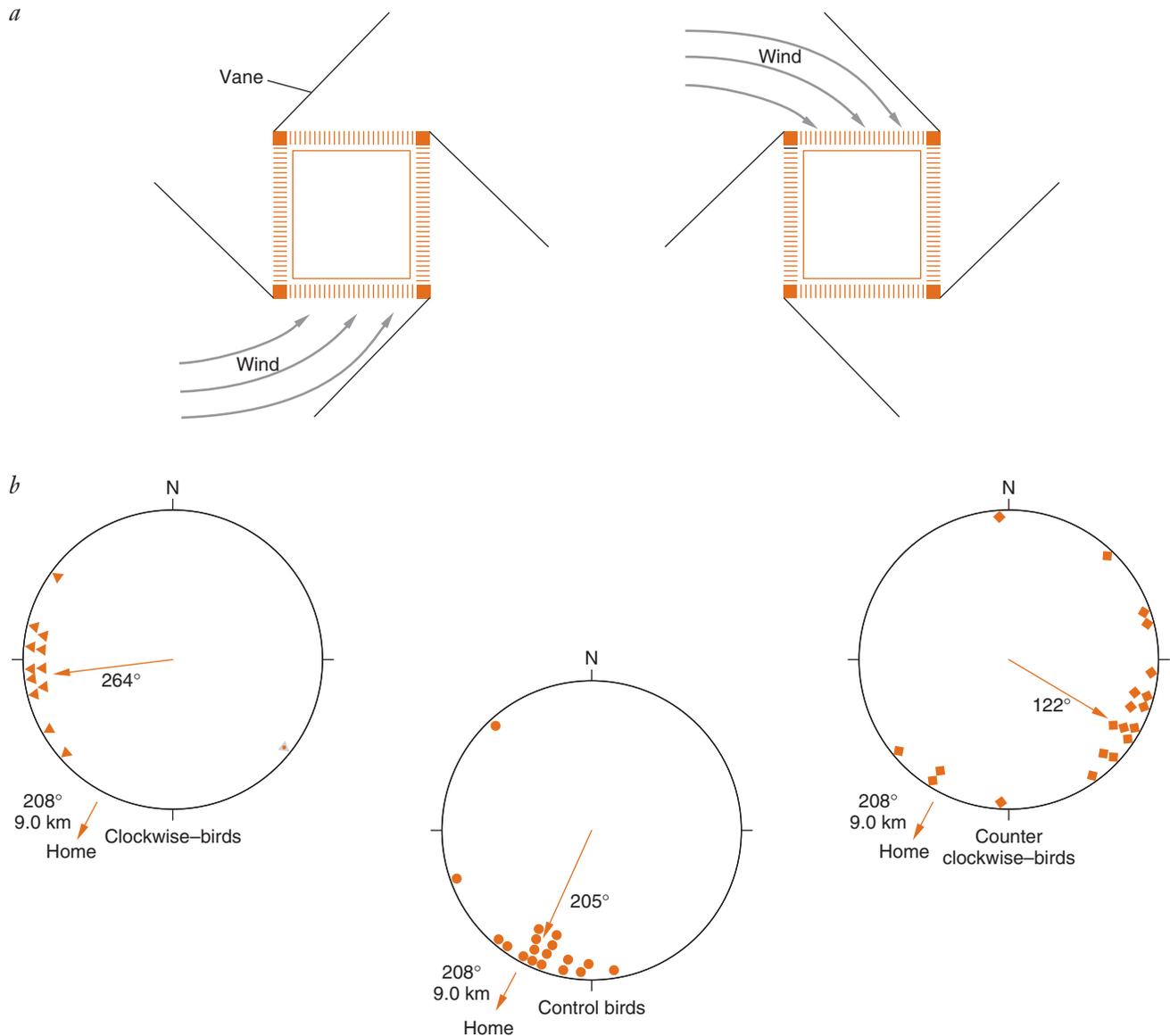


FIGURE 10.28 Deflector lofts shift the orientation of pigeons. (a) Deflector lofts have baffles that shift the apparent direction of the wind by 90°. Pigeons living in deflector lofts should form shifted olfactory maps. (b) The vanishing directions of these pigeons are shifted by about 90°. The dots at the periphery of the circle denote the direction in which the pigeon flew out of sight. The arrow within the circle indicates the mean bearing of all birds. Although a shift in orientation is reported in all deflector loft experiments, it may be due to the deflection of light rather than a shift in the olfactory map. (Data from Baldaccini et al. 1975.)

still shifted (Kiepenheuer 1979). Accordingly, it has been concluded that the baffles in these lofts also deflect sunlight and that the consistent shift in pigeon orientation is caused by an alteration in the sun compass (Phillips et al. 2006).

Manipulating Olfactory Information Although the interpretation of olfactory deprivation and deflector loft experiments is quite controversial, the experiments in which olfactory information predictably alters the orientation of pigeons remain as unshaken support for an

olfactory hypothesis. For example, the orientation of pigeons was influenced by their experience with an unnatural odor, benzaldehyde (Figure 10.29). Pigeons were kept in lofts where they were fully exposed to the wind. The experimental birds were exposed to an air current coming from a specific direction and carrying the odor of benzaldehyde in addition to the natural breezes. We would expect these pigeons to incorporate this information into their olfactory maps. The control birds were exposed to only the natural winds, so they would not have an area with the odor of benzaldehyde

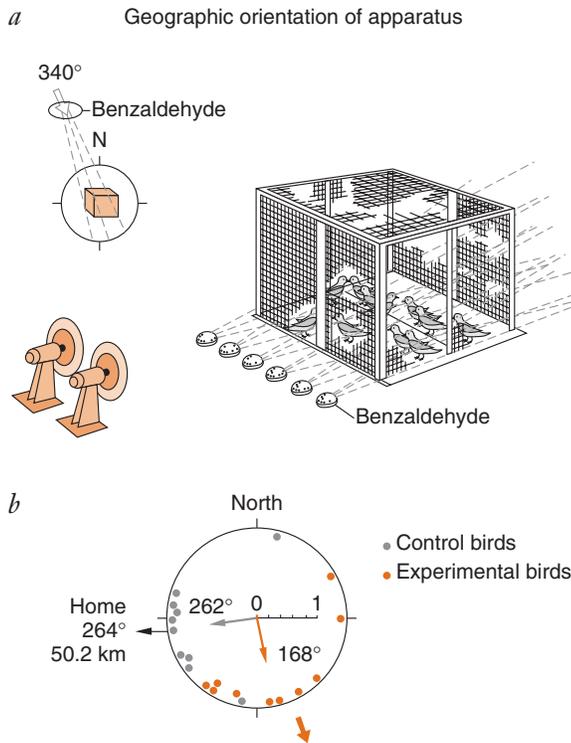


FIGURE 10.29 The results of an experiment that manipulated a pigeon's olfactory information. (a) The experimental pigeons were kept in a loft that was exposed to natural odors, as well as to a breeze carrying the odor of benzaldehyde from a source northwest of the loft. Control birds were exposed to only natural odors. While they were transported to the release site, all birds were exposed to the odor of benzaldehyde. (b) The orientation of the experimental birds, but not the control birds, was altered by exposure to benzaldehyde. The initial orientation of control birds was homeward. However, the initial orientation of experimental birds was toward the southeast, as would be expected if they had interpreted the odor of benzaldehyde as an indication that the release site was northwest of the loft. The experimental birds oriented as if they formed an olfactory map containing an area with the odor of benzaldehyde. (Data from Ioa   et al. 1990.)

in their olfactory map. All the birds were exposed to benzaldehyde while they were transported to the release site and at that site. The experimental birds took off in a direction opposite to that from which they had experienced benzaldehyde at the loft. In other words, they oriented as if they used an olfactory map that contained an area scented with benzaldehyde. If the release site did not smell of benzaldehyde, the experimental birds were homeward oriented. The control birds were not confused by the smell of benzaldehyde at the release site and flew home. Since benzaldehyde was not part of their olfactory map, they did not associate it with a particular direction. They used other cues to guide them home (Ioa   et al. 1990).

Depriving Birds of Their Sense of Smell Another approach in testing olfactory hypotheses is to deprive the pigeon of its sense of smell and observe the effect on its orientation and homing success. These anosmic pigeons are less accurate in their initial orientation, and fewer return home from an unfamiliar, but not from a familiar, release site. Regardless of its effect on orientation, olfactory deprivation always delays the bird's departure from the release site (Able 1996). These results are consistent with the idea that olfaction plays an important role in pigeon homing.

Besides its effect on the pigeon's sense of smell, perhaps olfactory deprivation affects another behavior, one not primarily controlled by olfaction, and this other behavior alters homing performance. Suppose the procedures that impair the sense of smell also affect the pigeons' motivation or their ability to process information. Though possible, the evidence does not support these possibilities. Anosmic pigeons home as well as control pigeons when they are released from familiar sites. Thus, the procedures do not seem to affect the birds' motivation to return home. Furthermore, pigeons whose sense of smell is temporarily blocked by an application of zinc sulfate to the olfactory epithelium have problems in returning home from unfamiliar locations, but they perform as well as controls in a spatial memory task that does not involve homing (Budzynski et al. 1998).

Could it be that some other sense, say sensitivity to magnetism, is blocked along with olfaction? The discovery of magnetite deposits in the beaks of homing pigeons, which are thought to be magnetoreceptors, makes this an intriguing possibility (Tian et al. 2007). Recall that information from the magnetite magnetoreceptors travels to the brain over the trigeminal nerve. Information about odors travels to the brain over the olfactory nerve. To evaluate the relative importance of magnetic and olfactory information, Anna Gagliardo and her colleagues (2006) severed the trigeminal nerves of one group of pigeons to deprive the pigeons of magnetic information and severed the olfactory nerves of another group of pigeons to deprive the pigeons of olfactory information. A control group of pigeons underwent sham surgery, in which the pigeons underwent similar surgical procedures as the experimental birds but the nerves were not severed. None of the pigeons had experience outside of its loft. The pigeons were released more than 50 km from home. As you can see in Figure 10.30, the initial orientation of the released pigeons of the sham-operated control group and the group that had the trigeminal nerve severed was in the general direction of home. In contrast, the initial orientation of pigeons with severed olfactory nerves was in the opposite direction. Furthermore, the number of pigeons that returned home within 24 hours (23 out of 24) was the same in the sham-operated control group and the experimental group without input from their

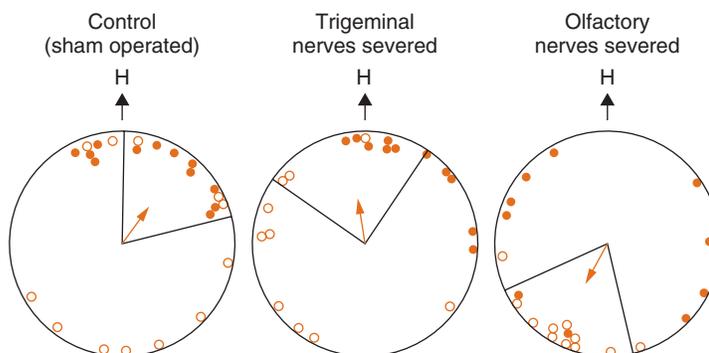


FIGURE 10.30 Information from olfactory receptors is necessary for homing pigeons to return from unfamiliar locations, but input from magnetoreceptors is neither necessary nor sufficient for homing ability. The dots within the circles represent the vanishing direction of each pigeon in each. The arrow within the circle indicates the mean vector of the group's vanishing direction. The arrow outside the circle pointing to H indicates the home direction. Sham-operated pigeons and pigeons with the trigeminal nerve cut headed in the direction of home, but pigeons with the olfactory nerve cut headed away from home. (Gagliardo et al. 2006.)

magnetite receptors. However, only 4 of the 24 pigeons lacking olfactory information made it home. These results are consistent with the hypothesis that olfactory cues are more important than magnetic cues in a homing pigeon's navigational map.

ELECTRICAL CUES AND ELECTROLOCATION

Electrical cues have a variety of potential uses for those organisms that can sense them. As we will see in Chapter 12, certain predators use the electrical cues given off by living organisms to detect their prey. In addition, electrical fields generated by nonliving sources, such as the motion of great ocean currents, waves and tides, and rivers, could provide cues for navigation. Although there is currently no evidence that migrating fish such as salmon, shad, herring, or tuna are electroreceptive, there is some evidence that electrical features of the ocean floor may help guide the movements of bottom-feeding species such as the dogfish shark (Waterman 1989).

Although most living organisms generate weak electrical fields in water, only a few species have electric organs that generate pulses, creating electrical fields that can be used in communication (discussed in Chapter 16) and orientation (reviewed in Caputi and Budell 2006). The electric organs of weak electric fish (mormyriiforms and gymnotidforms), located near their tail, for instance, generate a continuous stream of brief electrical pulses. The result is an electrical field around the fish in which the head acts as the positive pole and the tail as the negative pole. Nearby objects distort the field, and the distortions are detected by

numerous electroreceptors in the lateral lines along the sides of the fish. A weakly electric fish generally keeps its body rigid, a posture that simplifies the analysis of the electrical signals.

These fish examine their surroundings by using their electrical sense. Since they live in muddy water, where vision is limited, and since they are active at night, electrolocation is quite useful. Objects whose electrical conductivity differs from that of water disturb this electrical field. An object with greater conductivity than that of water—another animal, for instance—directs current toward itself. Objects that are less conductive than water, such as a rock jutting into its path, deflect the current (Figure 10.31). Thus, the fish can distinguish between living and nonliving objects in its environment.

The distortions in the electrical field create an electrical image of objects that can tell the fish a great deal about its environment. The distortion varies according to the location of the object relative to the fish, so the location of the image on its skin tells the fish where in relation to its own body the object is located. If the distortion is greatest on the right, the object is located on the right. An object near the fish's head creates the greatest distortion near the head (Caputi et al. 1998). The degree to which the electrical field is distorted by an object (the amplitude of the image) is greater in the center of the image than at the periphery. The fish often performs a series of movements close to the object under investigation. These actions might provide sensory input that helps the fish determine the object's size or shape (von der Emde 1999).

Electric fish can even measure the distance of most objects accurately, regardless of the object's size, shape, or material of which it is composed. In contrast to a visual image, the size (width) of an electrical image

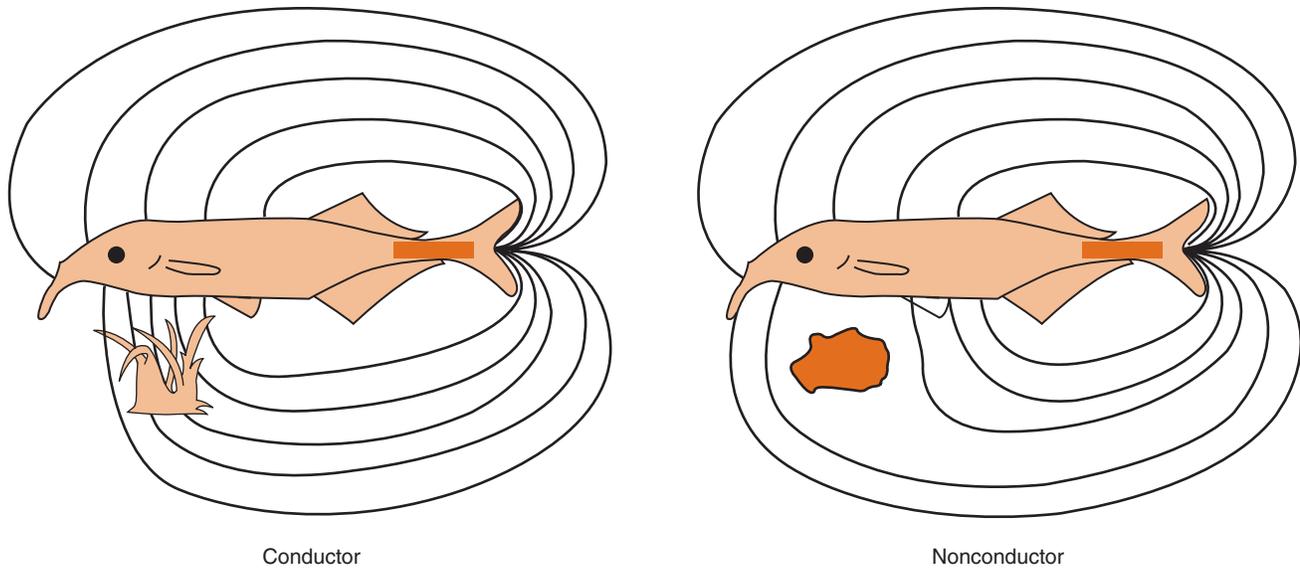


FIGURE 10.31 Electrorception. The electrical field generated by this fish is distorted by nearby objects. A good conductor, such as another living organism, draws the lines of force together. A nonconductor, such as a rock, spreads them out. Using electroreceptors distributed over its body surface, the fish senses the changes in the electrical field to “picture” its environment. (From von der Emde 1999.)

increases with distance. In addition, the amplitude differences between the center and the edges of an electrical image become smaller with the increasing distance of the object (Figure 10.32). The fish uses both of these features—size and amplitude—together to determine the distance of an object. A large, nearby object might cast the same-sized image as a smaller, distant object, but the more distant object would have smaller amplitude differences between the central and outer areas of the

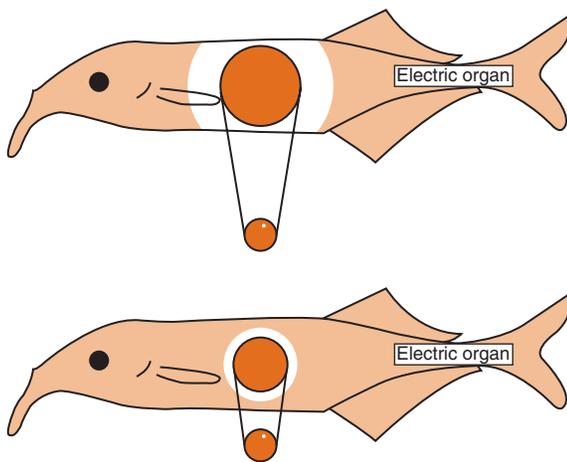


FIGURE 10.32 The electrical image of a metal sphere at different distances from the fish. The size (width) of the electrical image increases with distance. The amplitude differences in the degree of distortion of the electrical field between the center and the periphery of the electrical image decrease with increasing distance. (From von der Emde 1999.)

image. The electrical images of a 2-cm cube of metal or plastic presented at different distances and measured along the midline of an electric fish are shown in Figure 10.33 (von der Emde 1999).

SUMMARY

Navigational strategies can be grouped into three levels. One level of orientation, called piloting, is the ability to locate a goal by referring to landmarks. A second level is compass orientation, in which an animal orients in a particular compass direction without referring to landmarks. This is the type of navigation used by most bird migrants. A young bird migrant uses its compasses for vector navigation, an inherited program that tells the bird to fly in a given direction for a certain length of time. Some animals use a compass in path integration: they memorize the sequence of direction and distance on the outward journey to determine their location relative to home, and then they use a compass to travel directly home. A third level of navigational skill describes an animal's ability to locate the goal without the use of landmarks, even if it is released in an unfamiliar location. True navigation requires a map to determine location and a compass to guide the journey.

Animals have access to and use many different cues for orientation and navigation. The sensory modality of the primary cue varies among species, and many species have a hierarchy of cues. Although the interactions among cues can be complex, we have considered each sensory basis separately.

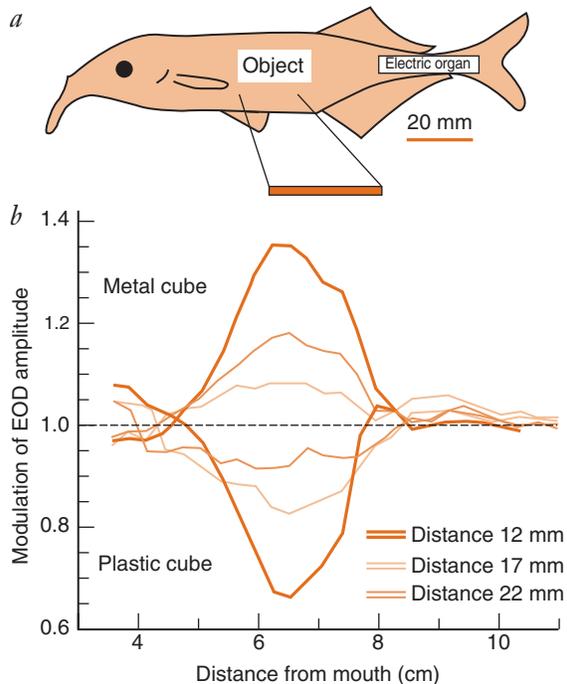


FIGURE 10.33 (a) A weakly electric fish, *Gnathonemus petersii*, with a 2-cm cube positioned for electrical image measurement. (b) The electrical images of a metal or plastic cube at three distances from the fish's surface, measured at the midline. The electrical image of the metal cube is shown as a peak, and the image of the plastic cube is shown as a trough because metal (a conductor) pulls the lines of force together, and plastic (a nonconductor) spreads them out. Regardless of the composition of the cube, the width of the electrical image increases with increasing distance. The difference in amplitude between the center and the periphery of the image gets smaller with increasing distance. The fish uses the ratio of two features of the image—size and the amplitude differences between the core and the rim—to determine the distance of an object. (From von der Emde 1999.)

Visual cues include landmarks; the sun, stars, or moon; and the pattern of skylight polarization. Methods of demonstrating that an animal uses landmarks in navigation include moving the landmark to see whether the animal reorients or becomes disoriented and impairing the animal's vision so that it cannot use landmarks. Some species use landmarks by matching the objects viewed with the remembered image of the array of landmarks. When landmarks are used in this way, the animal must always follow the familiar path. The sun may be used as a point of reference by assuming some angle relative to it during the journey and then reversing the angle to get home. Alternatively, since the sun follows a predictable path through the sky, if the time of day is known, the sun's position provides a compass bearing. If the sun is used as an orientation cue over a long interval of time, the animal must com-

pensate for the sun's movement. Animals must learn to use the sun as a compass. The point of sunset is also an orientation cue that some nocturnal migrants use to select their flight direction, which is then maintained throughout the night by using other cues.

The stars provide an orientation cue for some nocturnal avian migrants. Birds such as the indigo bunting learn that the center of celestial rotation is north. This gives directional meaning to the constellations in the circumpolar area. Since the spatial relationship among these constellations is constant, if one is blocked by cloud cover, the birds can use the others to determine the direction of north.

Sunlight becomes polarized as it passes through the atmosphere. The pattern of polarization of light in the sky varies with the position of the sun. Polarized light may provide an axis for orientation, or it may allow animals to locate the sun from a patch of blue sky even when their view of the sun is blocked.

The earth's magnetic field provides several cues that could be used for orientation: polarity, inclination, and intensity. Some animals use a polarity compass, but most animals use an inclination compass, which distinguishes between equatorward (where the magnetic lines of force are horizontal) and poleward (where the lines of force dip toward the earth's surface).

Birds and sea turtles use an inclination magnetic compass for directional information. Birds use their compass to follow an inherited migratory program based on magnetic cues. Hatchling sea turtles use a magnetic compass while migrating across the Atlantic Ocean. They calibrate their magnetic compass relative to the direction of the surface waves that they experienced as they initially swam offshore.

A magnetic map provides information from earth's magnetic field that an animal can use to determine its position relative to a goal or target. Migrating birds and sea turtles may have a general magnetic map consisting of an inherited program of changes in direction of travel in response to magnetic signposts (magnetic fields characteristic of specific locations). Homing pigeons and sea turtles develop a more detailed magnetic map with experience living in a region. For example, with experience swimming in specific regions, sea turtles form a magnetic map based on the learned topography of the geomagnetic field. This information helps a turtle navigate to a specific target area.

There are (at least) two types of magnetoreceptors. One is light dependent. In birds, the magnetoreceptor, located in the right eye, contains the photopigment cryptochrome. Cryptochrome absorbs light differently depending on the orientation of the magnetic field. Information from these receptors connects to a part of the brain called Cluster N, which connects to a region of the brain that analyzes visual information. A second type of magnetoreceptor contains deposits of a magnetic

material called magnetite. The crystals of magnetite twist in alignment of the magnetic field. This twisting could stimulate a stretch receptor. Salamanders and birds are among the animals that have two magnetoreceptor mechanisms, each serving a different function.

Chemical cues are also used for orientation. Salmon are guided to their natal stream by chemical cues. Young salmon learn (imprint on) the characteristic odors of their natal stream and then follow the odor trail back to that place.

Homing pigeons may also rely on olfactory navigation. Although the results of deflector lofts are consis-

tent, they may not be due to a shifted olfactory map. However, the results of experiments in which olfactory information is manipulated are consistent with an olfactory basis for pigeons' navigation. The role of olfaction in their homing remains controversial.

Some aquatic species can detect electrical fields. These could be of use in navigation. A few species have electric organs that can generate electrical fields, which can be used in communication and navigation. The weak electric fish generate a stream of electrical pulses and then sense objects by the disturbance created in this symmetrical field.