

Integrating Systems *at Work*: Animal Navigation

This newly hatched marine turtle crawling toward the sea is beginning an astounding migration during which it will spend up to three decades in the Pacific Ocean before returning to its birth site (Malaysia) to breed. In the South Atlantic Ocean, green turtles (*Chelonia mydas*) feed off the coast of Brazil and then migrate eastward across more than 2200 km of open ocean to nest at Ascension Island, an isolated speck of land in the middle of the South Atlantic. In the Northern Hemisphere, loggerhead turtles (*Caretta caretta*) hatch on Florida beaches, swim out to the Gulf Stream, and spend years circulating around the North Atlantic before returning to U.S. waters.

Because it may take an individual sea turtle 30 years to reach sexual maturity, researchers had been uncertain whether the turtles were returning to their *natal* beaches. Accumulated evidence suggests that they do. For example, no sea turtle tagged at Ascension Island has ever been found to nest elsewhere. Moreover, analysis of mitochondrial DNA indicates that green turtles nesting at different sites are genetically distinct, a fact suggesting that gene exchange between different colonies is relatively rare. The reproductive success of sea turtles is based on their finely tuned sense of place. As breeding season arrives, sea turtles move unerringly toward a precise destination, irrespective of their individual positions at sea.

Sea turtles are masters of animal navigation. As physiologists use the term, **navigation** is the act of moving on a particular course, or toward a specific destination, by using sensory cues to determine direction and position. As sea turtles demonstrate, navigational abilities facilitate specialized locomotor behaviors such as migration and homing. **Migration** is the periodic movement of an animal from one region to another. Migratory periods may be prompted by seasonal changes, as is often the case with migratory birds. A migratory cycle, however, may extend over an animal's lifetime, as is true of Pacific salmon (*Oncorhynchus* sp.), which return from the sea to their natal lakes to spawn and die. Whereas migration may involve movements on a global scale, homing is often a more localized behavior. **Homing** is the ability of an animal to find its way repeatedly to a *specific point*, most often its nesting or dwelling place, although some animals, such as honeybees (*Apis mellifera*), use their homing abilities to pinpoint food sources too.

The dividing line between migration and homing is not always clear, and some navigating animals appear to engage both abilities selectively. Homing performance, however, usually declines as the distance from home or a target increases, and an animal's homing abilities may be disrupted completely if it is passively displaced (e.g., blown off course by a storm or deliberately moved by a researcher) from its path of travel.

It's not surprising that animal navigation has been an object of scientific interest to researchers. Lacking maps, compasses, and other human cultural accoutrements, how do navigating animals gather and interpret cues about their position on the planet? Do they possess physiological (sensory) mechanisms unavailable to humans? Is the ability to navigate mainly a result of learning and memory of past experience? And what is the evolutionary importance for the animal of the ability to navigate?



A newly hatched sea turtle begins a lifetime of navigation.

The Adaptive Significance of Animal Navigation

Physiologists presume that navigational abilities evolved because they represent an adaptive advantage to the animals that possess these skills. Before examining how animals navigate, let's consider *why* it may be advantageous for them to do so.

Navigational abilities promote reproductive success

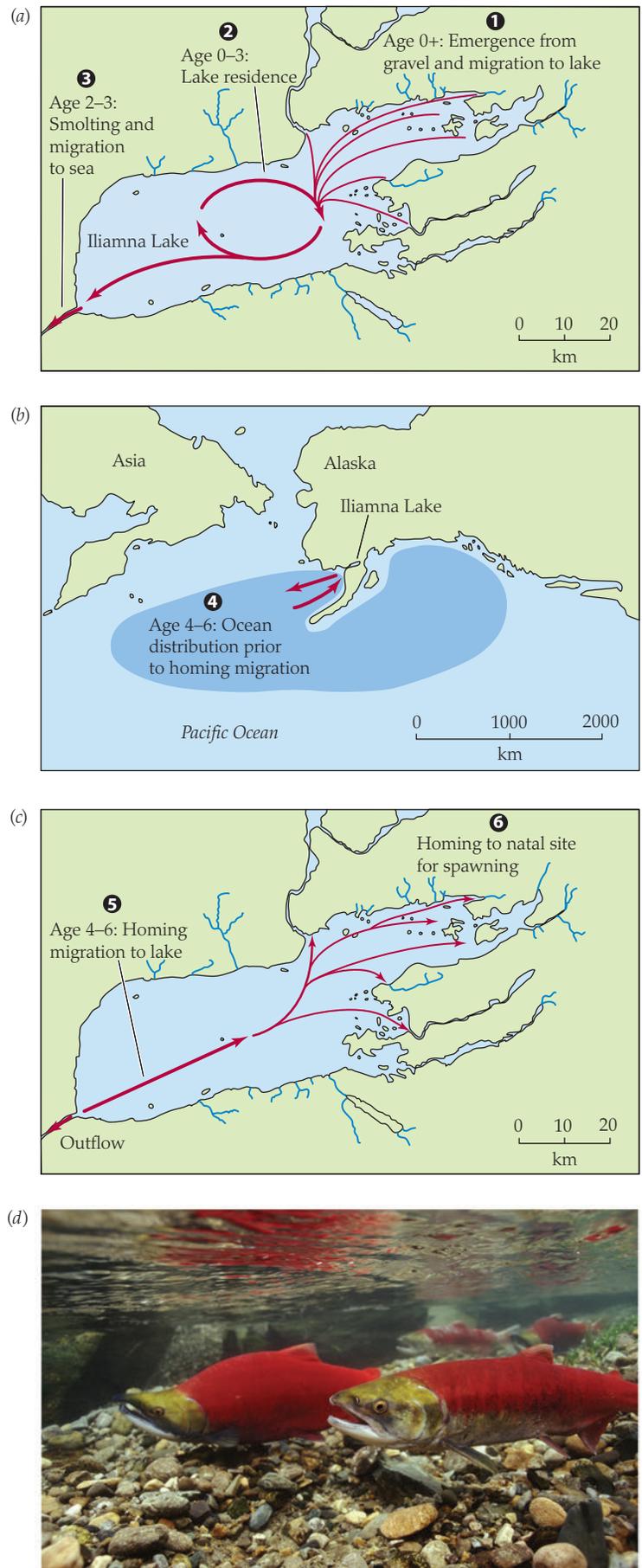
Most (but hardly all) animals reproduce at a time and place that presents the lowest degree of environmental stress to the parents and their offspring. For example, long-distance migrants such as humpback whales (*Megaptera novaeangliae*) spend the summer feeding in the food-rich polar seas of the Northern Hemisphere. In the winter, however, they migrate to more tropical waters to reproduce, often traveling as much as 3200 km. Surprisingly, humpback whales apparently do not eat during the winter breeding season; only one out of 2000 caught in one study had food in the stomach. The winter migration is *not* to areas of high food productivity, but rather to areas of warm water that engender less thermoregulatory stress, especially for the young.

Many animals exhibit *natal philopatry*, the tendency either to stay in the area of their origin or to return to it to reproduce. In many species of migrating birds, such as the wood thrush (*Hylocichla mustelina*), males return every spring to reestablish the same territories each year. In this case, learned familiarity may contribute to the advantage of philopatry, but not in another case. Anadromous fish (i.e., fish that ascend rivers from the sea to breed), such as Pacific salmon, provide the most dramatic example of how animal navigation skills are employed to accomplish this reproductive aim (Figure 18.1).

Several species of salmon (*Oncorhynchus*) hatch in freshwater streams and lakeshores in the North Pacific rim. After spending between 1 and 3 years in downstream waters and lakes as juveniles, they metamorphose into smolts and migrate downstream to the Pacific. The maturing salmon spend a few years in the Alaskan Gyre, a large circulating current that offers plentiful foraging opportunities. The adult salmon of North American species share the gyre with those of Asiatic species. Although the various species feed together, they do not breed in the gyre. Spawning occurs only after adult salmon migrate through the open ocean to their natal river and then, using the imprinted scent of their natal lake or stream, home accurately to it. Here they reproduce once and die.

Presuming that natal philopatry evolved by natural selection, what is its adaptive advantage that has led to such impressive navigation ability in salmon? Probably the most important advantage is that the ability to home to the natal stream returns locally adapted individuals to appropriate environments. Salmon populations are often strongly adapted to local breeding environments, and this

FIGURE 18.1 Salmon life-cycle migration and homing The life cycle of sockeye salmon (*Oncorhynchus nerka*) from Iliamna Lake in Alaska. (a) Newly hatched salmon emerge from gravel of streams and beaches and spend up to 3 years in the lake before transforming to smolts that migrate to the sea. (b) Ocean distribution of maturing salmon prior to their homing migration back to Iliamna Lake. (c) Homing migration back to the lake and to their natal site for spawning. (d) A male in the reproductive phase (left) has red sides, a deep body, and elongated, hooked jaws. (a–c from Dittman and Quinn 1996.)



adaptation reduces the fitness of strays that disperse instead of returning to the natal site.

However, *perfect* site fidelity would be expected to be disadvantageous because conditions change from year to year at a breeding habitat, so there should be some dispersal to adjust to these temporal changes. Salmon populations appear to maximize reproductive fitness by natural selection favoring a balance of a high percentage of return to natal sites and a low percentage of dispersal. By using navigational skills to feed globally but spawn parochially, salmon thus maintain distinct populations that are well adapted to their breeding sites.

Navigational abilities facilitate food acquisition

The examples cited of sea turtles, humpback whales, and Pacific salmon all suggest a common conclusion: The best place to feed isn't always the best place to breed. Using their navigational abilities, migratory animals can position themselves favorably at food sources, accumulating chemical energy until they reach breeding readiness. By spending their summers feeding in polar seas, humpback whales take advantage of mineral-rich upwellings from the ocean floor that support an abundant food chain, as well as long summer days that maximize the time these animals can spend foraging.

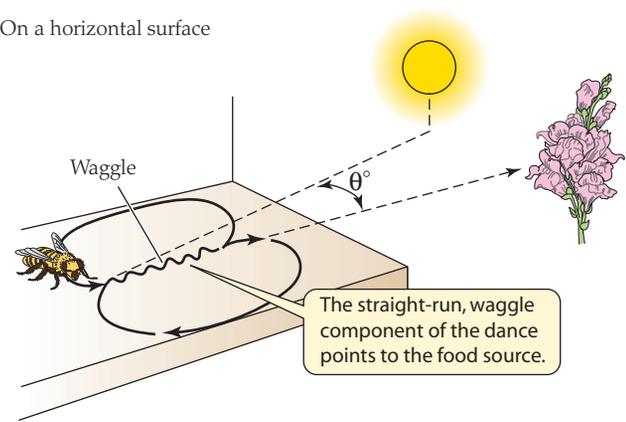
Animal navigators also employ homing skills to acquire food. For example, several species of birds store or cache seeds, hiding them and then retrieving them days or months later. Clark's nutcrackers (*Nucifraga columbiana*) and pinyon jays (*Gymnorhinus cyanocephalus*) dig holes in sandy ground and bury seeds. An individual of either species is able to locate thousands of cache sites and also to remember which sites it has already visited and emptied. A single Clark's nutcracker may hide 33,000 seeds in a season at approximately 6600 locations, and it can remember these locations and retrieve the seeds with a degree of success that is nothing less than astonishing.

In another example of using homing skills to acquire food, foraging honeybees may take hours or days to first locate a new source of nectar, but then new workers will appear at the food source within minutes of the first bee's return to the hive. Karl von Frisch (1886–1982) demonstrated that a returning forager performs a "dance" that conveys information to other bees about the direction and distance of the food source (Figure 18.2). The dance consists of looping turns alternating with a straight-line portion in which the signaling bee waggles her abdomen. Typically the dance is performed in the hive, on the vertical surface of a honeycomb, out of view of the sun. The angle between the sun and the food source is translated into an angle between vertical and the waggle component of the dance, so that other workers leaving the hive know the correct direction of the food source. Food location by honeybees certainly requires navigation, but it is somewhat atypical of homing behavior because it involves social cooperation and communication among individuals.

Migrating animals need navigation

For migrating animals, the adaptive value of navigation is difficult to separate from the adaptive value of the migration itself. If migratory movements have evolved by natural selection, they must convey adaptive advantages that outweigh their energetic and informational costs. Sometimes the adaptive advantages of migration are obvious; for example, birds that feed on flying in-

(a) On a horizontal surface



(b) Inside the hive on a vertical surface

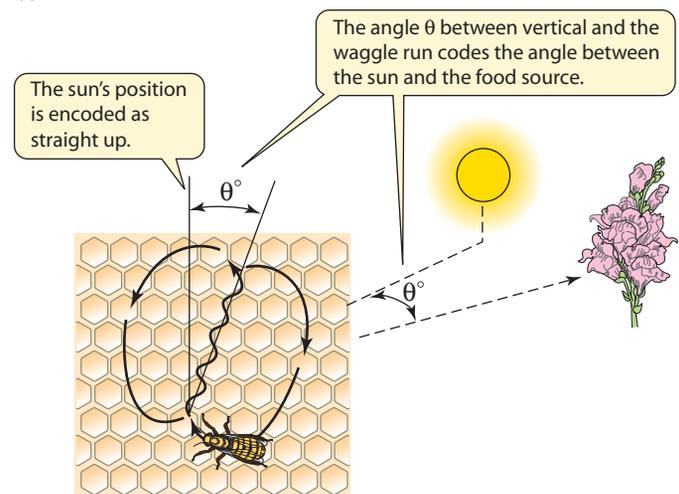


FIGURE 18.2 The waggle dance of honeybees conveys information about the direction and distance of a food source. A returning forager that has discovered a nectar source dances either outside the hive on a horizontal surface (a) or inside the hive on a vertical surface (b). Distance is coded by the duration of the waggle run.

sects in temperate summers must go south in the winter (when the insects at temperate latitudes are dormant), unless they hibernate or find a different winter food. Navigation is clearly important in migration, and not only for knowing which way is south. Most seasonal migrants do not just move south in the fall and north in the spring; instead they travel along defined routes to restricted destinations (more restricted for some than others). Therefore, detailed navigation ability of migrants presumably imparts its own selective advantage, one that is separable (at least in principle) from the migratory journey itself.

Navigational Strategies

In the novel *Something about a Soldier*, Mark Harris describes army inductees in World War II riding a train through New Jersey to the unknown destination of their next training camp:

The men ... engaged in quiet conversation ... devoting themselves, in the main, to speculation concerning their destination. In this they were handicapped, lacking, as they did, the near presence of

streets, avenues, schoolhouses, saloons, subway kiosks marked Uptown and Downtown, and other familiar landmarks by which they ordinarily brought themselves into relationship with the compass. They were now moving (they argued) either south or north or west. They dismissed only the possibility that they were traveling east, into the Atlantic Ocean. Jacob [the protagonist of the novel] observed that they ignored compromises or combinations, and he thought, *the fallacy of absolutes*.

Like Harris's army inductees, animals can use a variety of sensory cues to navigate. Accordingly, when researchers speculate about how animals navigate, and test their hypotheses, they need to avoid the *fallacy of absolutes*. A trip can involve several sequences of direction, and navigating its course can likewise involve combinations of mechanisms. While it is navigating, an animal may use several different sensory cues, and it may use them to implement a variety of navigational strategies—in sequence, in a hierarchy, or in simultaneous combinations.

Navigation is a complex instance of animal behavior, involving sensory integration and motor control, as well as learning and memory. Hence, it is often useful to approach this topic by studying the repertoire of behavioral mechanisms that animals exhibit as they navigate rather than to dive immediately into a search for underlying physiological mechanisms or cellular functions. Biologists who study animal behavior recognize five behavioral strategies that animals use to navigate (Table 18.1): *Trail following, piloting, path integration, compass navigation, and map-and-compass navigation*.

It is noteworthy that the names of these strategies have analogies with human navigational techniques. But because some navigating species have sensory abilities and integrative capacities that humans lack, these named strategies may not actually encompass *all* the navigational techniques that animals employ. Moreover, terms such as *compass* and *map* are metaphors when applied to animals; we cannot know how animals actually experience the compasses and maps that their behavior suggests they possess.

Trail following is the most rudimentary form of animal navigation

Most people are familiar with following a trail through a forest or across a field in which each spot of trampled earth follows in a continuous series from start to finish. Similarly, **trail following** is a navigational strategy that is accomplished by detection of an interconnected series of local sensory cues (i.e., cues that are immediately proximate to an animal). Although humans are used to thinking about trails in visual terms, for many navigating species of arthropods, such as ants, a trail may consist solely of olfactory cues.

Trail-laying ants have an abdominal scent gland that is used to lay a *trail pheromone*, a chemical signal that marks a path to a food source. Each ant senses the olfactory profile of its path of travel and, in turn, deposits olfactory markers that it and other members of the colony can use to travel between a nest and the food source. (As we will discuss shortly, other kinds of ants employ different navigational strategies.)

Piloting animals follow a discontinuous series of learned cues

A person who knows that a hot-dog stand is located at the base of a tower, and who heads toward the tower to find the stand, is employing piloting. Using this navigational strategy, **piloting** animals

TABLE 18.1 A classification of strategies in animal navigation

Strategy	Description and source of information
Trail following, route learning	Continuous cues about trail, landmarks
Piloting	Landmarks (discontinuous)
Path integration	Integrated direction and distance information
Compass navigation	Celestial or magnetic cues, learned or genetic
Map-and-compass navigation	Compass cues, landmark- or gradient-based map

Source: After Papi 1992.

follow a discontinuous series of learned landmarks to determine where they are in their path of travel with respect to their destination. (A **landmark** is a discrete, sensed marker of position, usually but not necessarily visual.) The ability to use learned landmarks to navigate means that sensory cues need not be connected in a relatively unbroken series, as is the case with trail following. Moreover, because piloting is learned behavior, most animals that employ this strategy improve their navigational performance with age and experience. Although landmark-based learning such as piloting is considered relatively simple behavior, we will see that it is difficult to distinguish from more behaviorally sophisticated processes, such as map-and-compass navigation, a topic we cover later in the chapter (see page 494).

As our example of the hot-dog stand suggests, animals often use piloting as a strategy to find their way to a specific destination, a fact that Nikolaas Tinbergen (1907–1988) proved in a classic field experiment with digger wasps (*Philanthus triangulum*). Tinbergen placed a ring of pinecones around the entrance of a wasp's burrow. When the wasp emerged, she flew around the entrance for about 6 s before disappearing to hunt for food. Tinbergen established experimentally that the wasp used the pinecones as a local landmark for navigation by shifting the pinecone ring about 30 cm from the entrance while the wasp was away. On returning, the wasp flew to the center of the pinecone ring and was unable to find the nest. If the pinecone ring was moved farther than 1 or 2 m from the nest, the wasp even failed to locate the ring (and the nest). This latter observation suggests that, for the digger wasp, it is primarily the final moments in navigating to a destination that depend on piloting; the wasp uses other sensory cues to return to the correct neighborhood.

Birds that cache seeds also appear to use local landmarks as a primary mechanism in relocating their food. In one experiment, Clark's nutcrackers in an aviary hid pine seeds in an open arena strewn with landmark objects. After the birds had cached the seeds, the array of objects on one side of the arena was displaced by 20 cm, whereas the array on the other side was untouched. When the nutcrackers returned to search for their caches, they probed the ground at the "correct" places *with respect to the moved objects*, missing the caches by 20 cm on the manipulated side of the arena and retrieving them accurately on the undisturbed side. In the middle of the arena, the birds probed about 10 cm away from the caches, indicating that they were using information from both displaced and undisplaced landmarks.

Piloting is the navigational strategy employed in many instances of localized homing behavior and probably depends on a variety of familiar sensory cues, such as visual landmarks or odor profiles. Bees and other insects use landmarks to compose visual “snapshots” that are stored in memory in learning familiar paths. Like the digger wasps described previously, animals are most likely to pilot by the use of landmarks near home. For example, homing pigeons fitted with translucent contact lenses that obscure visual landmarks can still return to their home *area* (because they are using a different navigational strategy), but once in the area, they have difficulty finding their pigeon loft.

Path integration is a form of dead reckoning

As with piloting, animals that exhibit **path integration** behavior use this navigational strategy to accomplish homing, but unlike animals engaged in piloting, they do *not* refer to landmarks. In path integration, the navigating animal somehow keeps a running tally of its past directions and distances traveled, and it integrates this information in a manner that allows it to set a direct route back to its starting point at any time. Desert ants (*Cataglyphis fortis*) provide an excellent example of path integration behavior: They forage along tortuous, novel paths but can return from any point directly back to their hidden nesting site once they have located food (Figure 18.3).

Path integration in desert ants is equivalent to the method of dead reckoning often used by early mariners. *Dead reckoning* was a way of determining a ship’s position at sea without using landmarks or star positions. The sailors kept a record (the “logbook”) of the ship’s direction and speed, and accumulated this information into an aggregate direction and distance. Mariners used the position of the sun to ascertain their direction, and they assessed speed by throwing overboard a piece of wood (the “log”) attached to a long, knotted line that was cast off or played out as the ship sailed. The number of knots of line that were cast off over a period of time gave the speed and was entered in the logbook.

Ants navigate in a featureless desert rather than a featureless ocean, but their strategy is similar to sailors’ technique of dead reckoning. Ants gather directional information by using the sun’s position (or polarized light) as a compass. The ants measure distance by integrating proprioceptive information while walking, rather like counting steps for humans. Experimenters captured ants that had just found food and were ready to return home. They altered the length of the ant’s legs, cutting them short in some ants and gluing longer “stilts” on others, and displaced them as in Figure 18.3b. The ants made systematic errors in their attempt to return home: The ants with stilts walked too far before beginning their random search of the expected home area, whereas the ants with stumps underestimated the distance and shifted to random search too early.

Other animals use different methods to estimate distance traveled. A honeybee, for example, estimates the distance between its hive and a food source on the basis of **optic flow**, an impression of the speed at which objects sweep through the bee’s visual field as it flies. An object’s apparent distance determines its contribution

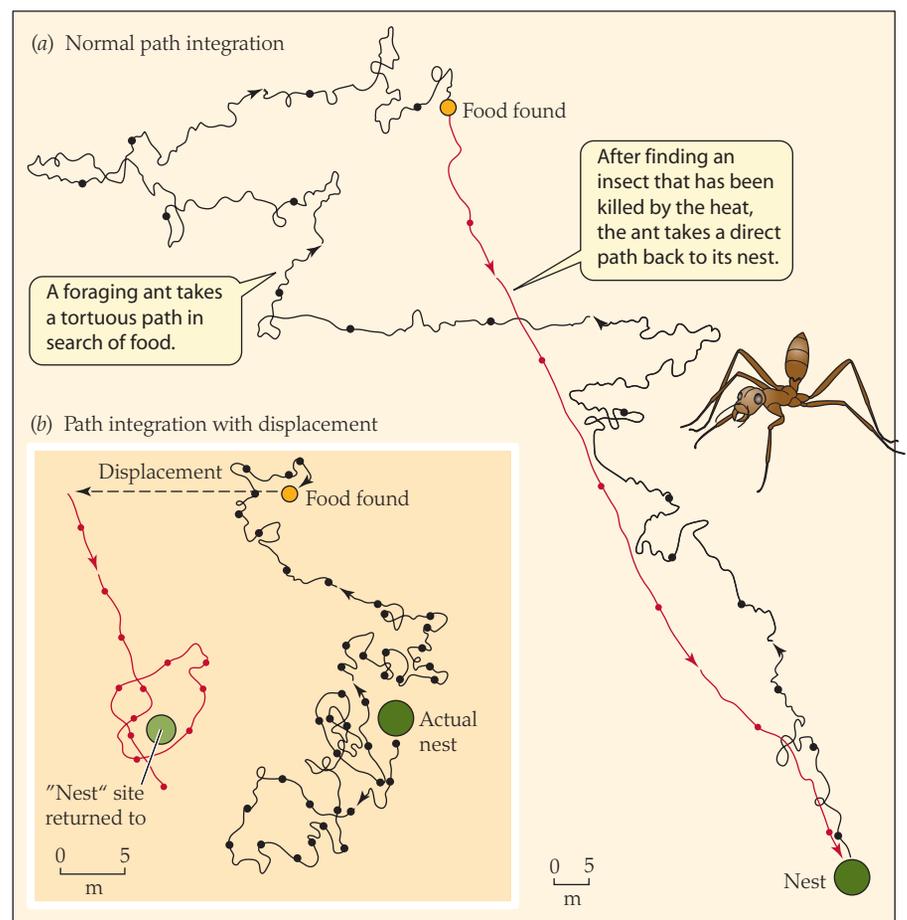


FIGURE 18.3 Path integration in desert ants (a) After finding food via a circuitous path, an ant takes a direct path back to its nest that does not depend on landmarks, but rather on path integration—adding all the direction and distance vectors in the tortuous outward path—and using a sun compass or polarized-sky-light compass to determine the direction back. (b) If an ant is artificially displaced when it has found food, it returns to where home would have been without the displacement, using external compass cues and ignoring local landmarks (except at the presumed nest location). Points mark positions at 1-min intervals. (After Collett and Zeil 1998.)

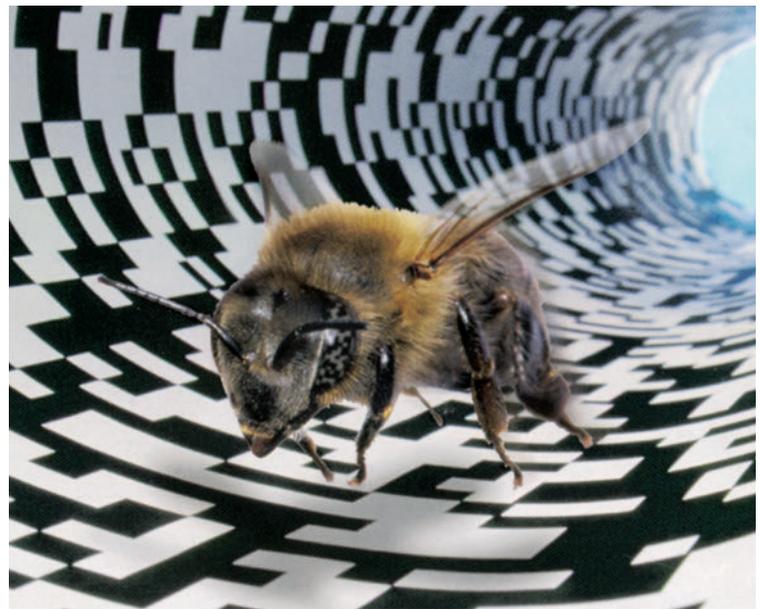
to optic flow. Nearby objects sweep by more quickly than distant ones, so they increase optic flow and heighten the sense of distance traveled.

To confirm that honeybees use optic flow, researchers manipulated the apparent distance of objects along their flight path. When bees were made to fly through a narrow tunnel with finely patterned walls (Figure 18.4), their optic flow increased and they overestimated their travel distances. Moreover, they communicated their overestimate to other bees in their waggle dance (see Figure 18.2), so that other bees (not flying through the tunnel) searched for the food source at too great a distance from the hive.

Animals can derive compass information from environmental cues

A **compass** is a mechanism that indicates geographical direction. Animals use compass information to *orient*—that is, to choose a direction in which to head. Orientation is a necessary component of compass navigation and map-and-compass navigation; no matter how you determine that you are north of your goal and need to go south, you need a mechanism to tell you which way is south. Ani-

FIGURE 18.4 Distance estimation by optic flow Bees assess the distance they travel by the flow of visual images past them as they move. The closer they are to objects they pass, the greater the objects' apparent motion is, and the greater the bees' estimation of distance. Bees that must fly through a narrow tunnel with densely patterned walls (shown in this composite photograph) consistently overestimate the distance they have traveled, because of the greater optic flow. Moreover, using a waggle dance, they signal their overestimate to other bees in the hive, so that the other bees (not flying in tunnels) fly in the correct direction but go too far in search of a food source. (From Srinivasan et al. 2000.)



mals derive compass information for navigation from a variety of environmental cues, such as the position of the sun and stars, the quality of polarized light, or the lines of force in Earth's magnetic field. It is useful to remember that we are using *compass* here as a metaphorical designation: Investigators can only infer the presence of a compass on the basis of an animal's behavior.

To study compass-based navigational strategies, researchers usually manipulate the sensory basis of a suspected animal compass while they measure the animal's *initial orientation*, the direction in which the animal orients its body and movements at the start of an actual or intended journey. In some cases this measurement might consist of observing the flight of a bird to vanishing point—the point at which it moves beyond the observer's viewing horizon. In the case of migratory birds, measuring initial orientation may entail quantifying the direction of *migratory restlessness*.¹ Birds in migratory phase will orient in a cage, facing and hopping in the direction of intended migration. Researchers can alter the suspected compass cues and then observe whether the orientation direction of migratory restlessness changes.

THE SUN COMPASS Many animals use the position of the sun as a source of compass information. In an early example demonstrating the presence of a sun compass, Gustav Kramer (1910–1959) showed that caged songbirds in migratory phase changed the orientation of their migratory restlessness when he altered the apparent position of the sun by using mirrors. The other original demonstration of sun-compass navigation was for foraging bees. The bee's waggle dance (see Figure 18.2) conveys information about the direction of a nectar source as an angle relative to the sun's position. Other worker bees in the hive use this sun-compass information to fly directly to the nectar source.

The sun moves across the sky from east to west at about 15° per hour, so animals must know the time of day to determine a compass heading from the sun's position. (Details of the sun's path also depend on latitude and season.) An animal that navigates using a sun compass must integrate solar position and circadian time information in order to orient its path of travel. The caged birds and the bees described earlier could maintain their sense of direction at different times of the day using their circadian clocks to account for the sun's movement.

Researchers can disrupt a suspected sun compass by resetting the animal's circadian clock, usually by imposing an artificial light–dark cycle that is different from natural sunrise and sunset (see Chapter 15, pages 411–412). If an animal experiences a shifted light–dark cycle, one in which the lights come on at noon and go

off at midnight (rather than at 6:00 AM and 6:00 PM, respectively), the new light–dark cycle will entrain the animal's circadian clock, causing the animal to misinterpret the sun's position.

Consider the following example: Guided by its normal circadian clock, a pigeon flying south at 9:00 AM will orient 45° to the right of the sun, which will be in the southeast (Figure 18.5a). If the pigeon flies south at 3:00 PM, it will orient 45° to the left of the sun, which will be in the southwest. A pigeon whose circadian clock is set ahead 6 h, however, will make predictable errors in sun-compass navigation (Figure 18.5b). If the pigeon thinks it is 3:00 PM when it is really 9:00 AM, the bird will fly due east, 90° from its intended southerly route, because it will fly 45° to the left of the sun. Experiments such as this one show that homing pigeons and most diurnal migrating birds use a sun compass as their primary mechanism of navigation.

THE POLARIZED-LIGHT COMPASS In addition to using a sun compass to navigate, many insects and birds appear to use polarized light as a source of compass information. This means of navigating is helpful on partly cloudy days, after sunset, or whenever the position of the sun is obscured from view.

Atmospheric particles polarize sky light. Recall from physics that white light from the sun is unpolarized; that is, it is a bundle of electromagnetic waves, each with an electrical vector (e-vector) that vibrates at right angles to the line of propagation of the light ray. In unpolarized light the e-vectors of different waves are at an infinite number of planes (Figure 18.6a). **Polarized light**, however, vibrates in only one plane with respect to its line of propagation. A fraction of the energy in a ray of sunlight will become polarized if it is reflected from a particle. Light reflecting from a surface at 90° from the incoming light ray is fully polarized; light reflecting at other angles is incompletely polarized.

Earth's atmosphere contains an abundance of suitably reflective particles—dust, water droplets, and ice crystals—that can polarize sunlight and provide the photic information that is the basis of an animal's polarized-light compass. Sky light in the vicinity of the sun reaches an observer's eye in a direct path, so it is unpolarized (see Figure 18.6a). Light reaching the eye from other parts of the sky, however, is reflected from atmospheric particles. As the reflec-

¹Migratory restlessness is sometimes known by the German term *Zugunruhe*.

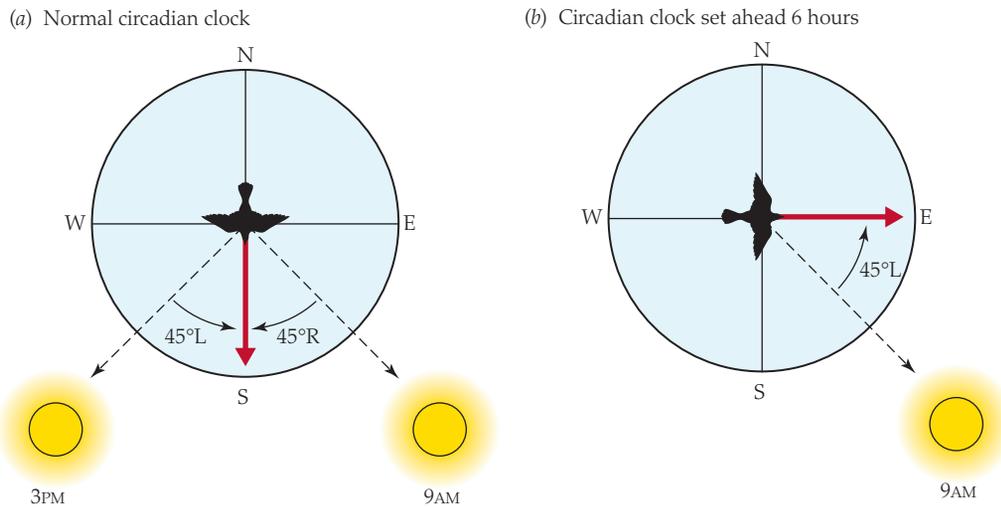


FIGURE 18.5 Homing pigeons use a sun compass on sunny days The direction in which individual pigeons vanished over the horizon from a release point north of home. (a) Control pigeons oriented in the homeward direction (south) when released at any time of day. They used the sun's position and their internal circadian clocks to determine which direction was south. (b) Pigeons whose circadian clocks had been shifted 6 h ahead misinterpreted the sun's position and departed approximately 90° to the left of the homeward direction. If released at 9:00 AM, they thought it was 3:00 PM and departed 45° to the left of the sun's position (appropriate for 3:00 PM).

tion angle (from the sun, to the particles, to the eye) increases up to 90° , the proportion of light reaching the eye becomes increasingly polarized. Sky light, then, is maximally polarized in a band that is 90° away from the sun's position (Figure 18.6b).

Human eyes cannot detect useful differences in the polarization of sky light, but the eyes of many navigating insects (and birds) can. A bee, for example, has eyes that are sensitive to polarized ultraviolet light. As long as a patch of blue sky remains in view, a bee can detect the plane of light polarization and use this information to infer the position of the sun. Researchers cannot say with certainty *how* an animal experiences polarized light, but to extract compass information, it must be able to detect the angle of polarization, as well as gradients in the degree of light polarization (see Figure 18.6b).

The effect of light polarization detected by the bee may not be altogether different from what people experience when they wear polarized sunglasses. The polarizing filter in the lenses absorbs the horizontally polarized components of sunlight and passes the vertically polarized components. By tilting the head, a wearer of polarized glasses will observe that the sky appears to be noticeably darker in a band that is at right angles to the sun. Light reaching the eye from this part of the sky is maximally polarized, and the polarizing filter passes only the fraction of the light that is vertically polarized. The degree of darkness and the tilt angle of the wearer's head provide sensory cues from which the sun's position can be inferred.

How do the photoreceptor cells of insects respond to polarized light? First, an individual rhodopsin molecule must be differentially sensitive to the plane of light polarization. A rhodopsin

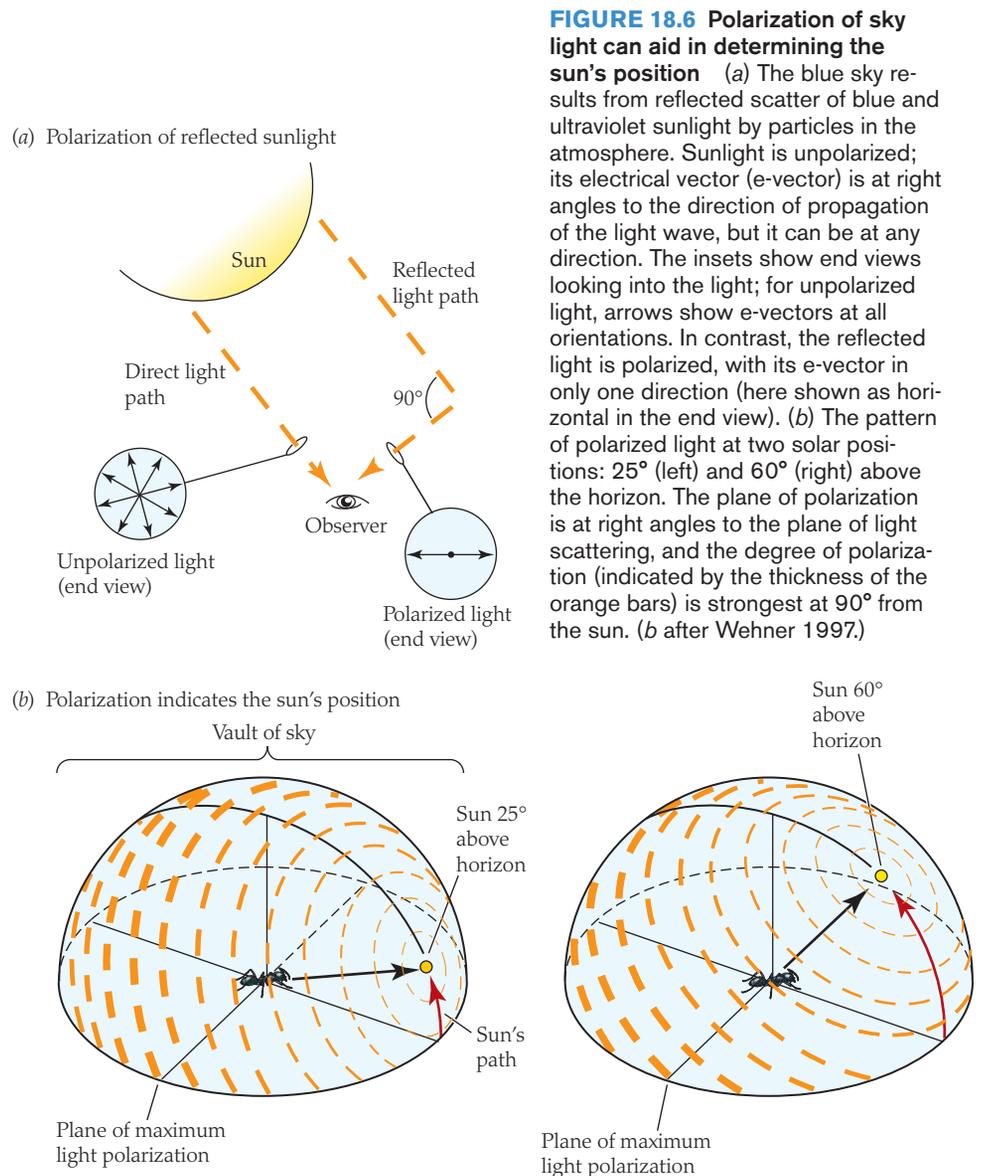


FIGURE 18.6 Polarization of sky light can aid in determining the sun's position (a) The blue sky results from reflected scatter of blue and ultraviolet sunlight by particles in the atmosphere. Sunlight is unpolarized; its electrical vector (e-vector) is at right angles to the direction of propagation of the light wave, but it can be at any direction. The insets show end views looking into the light; for unpolarized light, arrows show e-vectors at all orientations. In contrast, the reflected light is polarized, with its e-vector in only one direction (here shown as horizontal in the end view). (b) The pattern of polarized light at two solar positions: 25° (left) and 60° (right) above the horizon. The plane of polarization is at right angles to the plane of light scattering, and the degree of polarization (indicated by the thickness of the orange bars) is strongest at 90° from the sun. (b after Wehner 1997.)

molecule maximally absorbs light when the e-vector of the light is parallel to the long axis of the retinal chromophore (see Figure 14.23). Second, the many rhodopsin molecules in a photoreceptor must be aligned similarly, so that they all absorb light at the same plane of polarization.

In arthropod eyes, rhodopsin is localized in rhabdomeres, collections of microvilli arrayed at right angles to the long axis of the photoreceptor (retinular) cell (see Figure 14.24). The rhodopsin molecules are preferentially oriented so that the 11-*cis* retinal chromophore of each is parallel to the long axis of the microvillus. Therefore, light with its e-vector parallel to the long axis of the microvilli is preferentially absorbed. Different photoreceptor cells have their microvillar arrays aligned at right angles to each other and thus are differentially responsive to light at different planes of polarization.

THE STAR COMPASS Many species of birds that are normally diurnal migrate at night, perhaps to escape predation. They cannot effectively use the sun as a compass (although some nocturnally migrating birds do use the direction of the setting sun and sky-light polarization for initial nighttime orientation). The moon is an unreliable source of nocturnal directional information; it is visible at night only half the time, and its phases (resulting from a different periodicity than that of the sun) make lunar navigation a complex problem. The stars of the night sky provide more reliable information and are used by nocturnal migrants as a **star compass**. Earth's rotation makes the stars appear to sweep across the sky like the sun, but the region around Polaris (the North Star) provides a stable reference point for north (in the Northern Hemisphere).

Experiments by the behaviorist Stephen Emlen convincingly demonstrated that some nocturnal migrants use star patterns in the night sky as a compass to determine their heading. Emlen raised indigo buntings (*Passerina cyanea*) so that they could see the night sky but not local landmarks. When the birds reached spring migratory phase, he measured their pattern of migratory restlessness. Caged buntings that could see the night sky exhibited the expected north-oriented pattern of restlessness, as did buntings that could see the identical Northern Hemispheric constellations projected in a planetarium (Figure 18.7a). When Emlen projected the same constellations so that they faced south in the planetarium, the buntings reversed their pattern of migratory restlessness by 180° to the south (Figure 18.7b).

To orient successfully, young birds must learn the elements of the night sky during a critical period prior to their first migration. Birds in the Northern Hemisphere learn that the northern sky rotates around Polaris (the North Star), and they learn star patterns within 35° of Polaris. Emlen raised indigo buntings so that they never saw the real night sky, but only artificial night skies in a planetarium. One group saw the normal pattern of stellar rotation around Polaris. The other group saw the normal star pattern, but instead of rotating around Polaris, the constellations rotated around Betelgeuse, a bright star in the constellation Orion. When the birds came into fall migratory condition, Emlen tested their orientation in a planetarium, under a stationary sky. The control birds oriented away from Polaris, that is, away from their stellar north. The experimental birds oriented away from Betelgeuse, indicating that they had learned a star map in which the stationary star (Betelgeuse) was considered north! Apparently rotation of the

star pattern is necessary for learning the location of stellar north, but it is not necessary for using the pattern once that pattern has been learned.

MAGNETIC COMPASSES Earth acts like a gigantic bar magnet; it has north and south poles that are connected by magnetic lines of force (Figure 18.8a). Earth's magnetic field, in principle, provides a reliable source of directional information: The magnetic poles are close to the geographical poles, and they never change during an animal's lifetime. Because humans are quite unaware of magnetic fields, it is surprising to find that many species of animals can detect Earth's magnetic field and can use it to navigate.

Animals can sense the polarity and dip angle of Earth's magnetic field—two qualities that provide the navigational cues that animals use as a **magnetic compass**. Magnetic lines of force have a *polar component*: their north and south polarity. They also have an *inclination component*: the "dip angle" of the lines of force relative to Earth's surface (Figure 18.8b). Magnetic lines of force exit Earth nearly vertically at the south magnetic pole, and their angle of inclination steadily decreases at lower latitudes until they are parallel to Earth's surface at the magnetic equator. From there, their angle of inclination steadily increases until the lines of force are again nearly vertical at the north magnetic pole.

Accordingly, animals may use either a *magnetic polarity compass* (one sensing directional polarity) or an *inclination compass* (one sensing the magnetic inclination angle) to navigate. Experimental

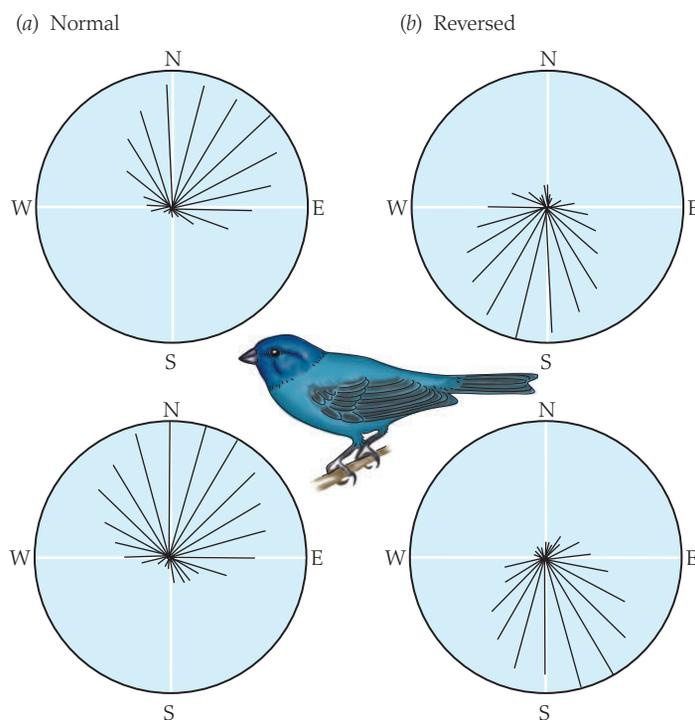


FIGURE 18.7 Planetarium experiments demonstrate that nocturnally migrating birds use star patterns for orientation. Indigo buntings were raised so that they could see the night sky but not local landmarks. The orientation preferences of their migratory restlessness (indicated by the radiating black lines) were then tested in a planetarium with either normal star patterns (a) or star patterns reversed in direction (b). The results for two buntings shown here reveal that the star pattern is the dominant determinant of orientation direction.

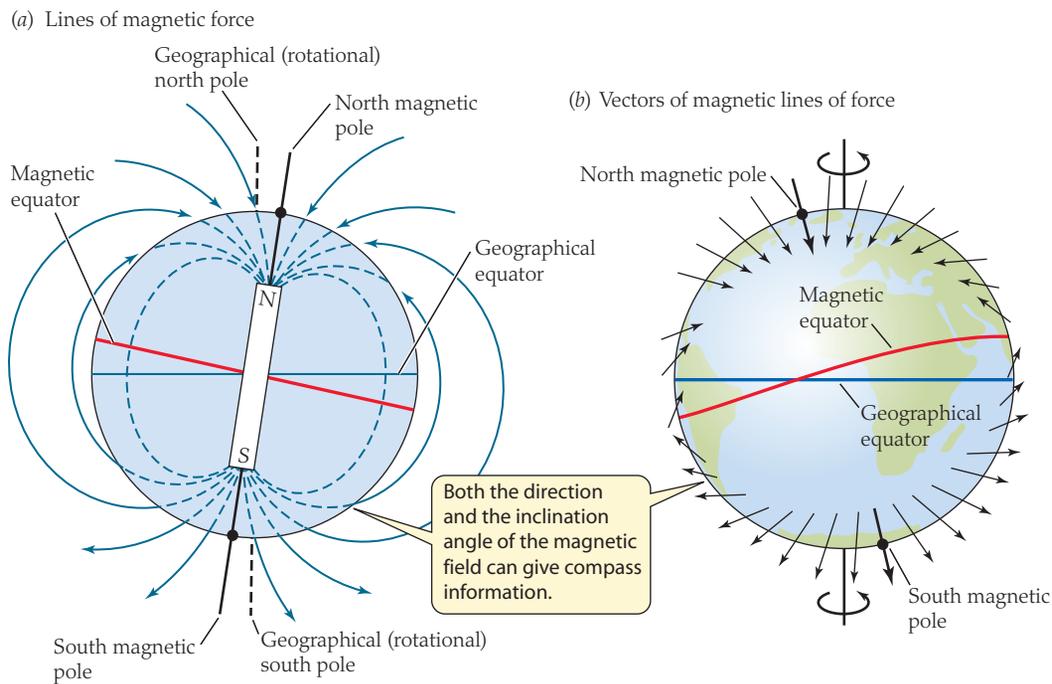


FIGURE 18.8 Earth's magnetic field can provide compass information (a) Lines of magnetic force leave the south magnetic pole vertically, curve around Earth's surface, and reenter vertically over the north magnetic pole. (b) Vectors of magnetic lines of force at different points on Earth's surface. Arthropods and some vertebrates use a directional compass (arrowheads point toward magnetic north), and many vertebrates use an inclination compass (into the ground = toward the nearer pole). (a after Goodenough et al. 2001; b after Wiltschko and Wiltschko 1996.)

evidence shows that arthropods such as bees sense magnetic polarity, whereas birds and other reptiles sense the inclination angle. Using an inclination compass, the direction “downward into Earth” is always poleward, as close inspection of Figure 18.8*b* reveals. Thus the downward inclination is toward magnetic north in the Northern Hemisphere but toward magnetic south in the Southern Hemisphere. At the magnetic equator the lines of force are parallel to Earth's surface, and an animal's inclination compass cannot discriminate between north and south. For this reason, birds that obtain navigational cues from an inclination compass may become disoriented as they migrate past the magnetic equator if they don't have a backup source of navigational information.

Researchers infer the presence of a magnetic compass from animal behavior. To detect an animal's use of a magnetic compass, a researcher may experimentally alter the magnetic sensory cues that the animal receives. One way to do this is to place the test animal in a box made of a type of metal (mu metal) that shields it from Earth's magnetic field. Alternatively, researchers may alter the magnetic field in the animal's vicinity by using permanent magnets or by placing tiny Helmholtz coils around the suspected locations of the animal's magnetic sensory apparatus (Figure 18.9*a*). A Helmholtz coil consists of a pair of ring-shaped electromagnets. When an electrical current is passed through the coils, a magnetic field is established in the space between the coils that can be used to nullify or reverse the effect of Earth's magnetic field. By placing a Helmholtz coil to either side of a homing pigeon's head, for example, researchers can control the bird's perception of magnetic fields.

The ability of animals to sense magnetic fields may be a primitive, relatively widespread mechanism, since it is found in some bacteria as well as many animals. Magnetic orientation is often used as a backup for other forms of compass navigation, as exemplified in homing pigeons. Recall from our discussion earlier that pigeons whose circadian clocks had been shifted forward 6 h flew in the wrong direction when they attempted to navigate south by following their sun compass (see Figure 18.5). However, the clock-shifted

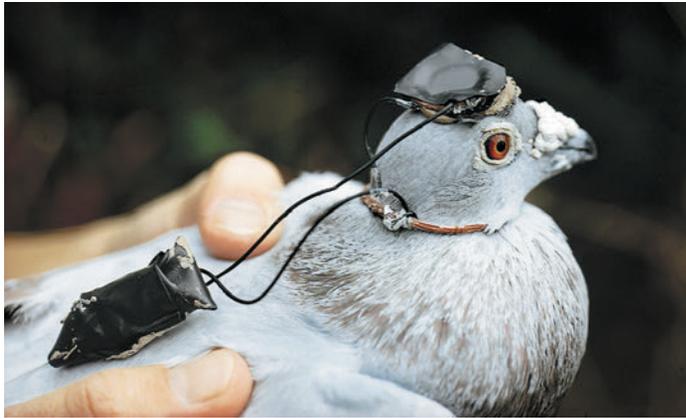
birds had no trouble navigating in the desired direction on *cloudy* days, which suggests they have another navigational mechanism that is not based on solar position.

Evidence demonstrates that this second navigational system in homing pigeons is a magnetic compass. Pigeons with magnets attached to their backs or heads home normally on sunny days but are disoriented on overcast days; control pigeons with brass bars attached to their backs instead of magnets home normally on both sunny and overcast days. What's more, homing pigeons wearing Helmholtz coils (see Figure 18.9*a*) experience similar disruptions of their homing abilities when released on cloudy days. When the inclination angle of the induced field between the coils matches that of Earth's magnetic field, the pigeons orient normally (Figure 18.9*b*). But when the inclination angle of the induced field is reversed, the pigeons fly in the opposite direction from their intended course home (Figure 18.9*c*).

Another line of evidence for animals' use of a magnetic compass comes from studying the effects produced by natural magnetic anomalies (distortions of Earth's magnetic field by geological peculiarities) on a navigating animal's path of travel. On overcast days, pigeons homing in a northeasterly direction toward Boston sometimes become disoriented at a major magnetic anomaly called Iron Mountain, in Rhode Island. The mountain's metallic composition bends the magnetic-field lines in its vicinity, sending the hapless birds off course. In the ocean, magnetic-field lines cluster together to form high-intensity ridges or spread apart to form low-intensity troughs that can be mapped by satellite. Whales and dolphins are more likely to swim ashore and become stranded at locations where troughs in magnetic-field intensity meet the shore. This correlation suggests that whales migrate using a magnetic compass and perhaps follow the path of magnetic troughs.

Other organisms, including salamanders, turtles, salmon, and bacteria, have been shown to orient to magnetic fields. Such orientation is commonly weaker than that to solar or other celestial cues, supporting the idea that magnetic orientation is a primitive,

(a) The experimental setup



(b) Magnet in normal orientation

(c) Magnet in reversed orientation

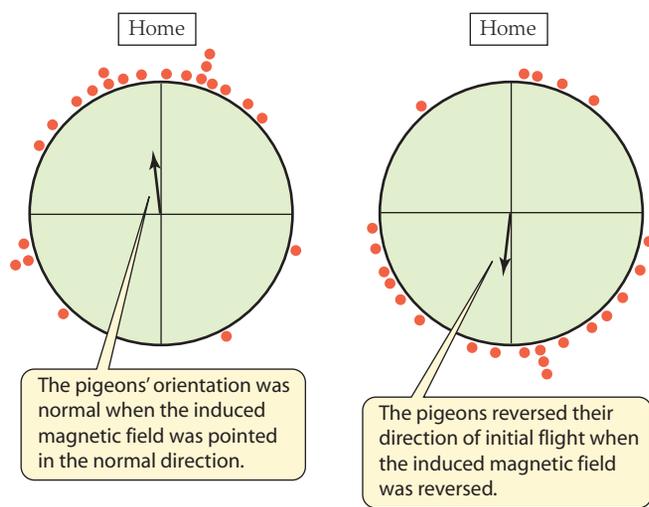


FIGURE 18.9 Changing the magnetic field changes the orientation of released pigeons (a) A small Helmholtz coil is shown attached to a pigeon's head, with a power pack on the pigeon's back. Reversing the direction of electrical current flow through the coil reverses the direction of the magnetic field. (b,c) Pigeons with Helmholtz coils were released south of home on overcast days. They interpreted the direction in which magnetic lines dip into Earth as north. Each dot outside the circle represents the direction in which a released pigeon vanished over the horizon. The arrow at the center of each circle is the mean vanishing bearing for the group. (After Walcott and Green 1974.)

widespread mechanism, often used when other cues are unavailable. Monarch butterflies (*Danaus plexippus*), for example, use a sun compass when the sun is available, but in the absence of celestial cues, they may use magnetic-compass information to orient and navigate. Detection of magnetic fields in monarch butterflies and in *Drosophila* may depend on cryptochrome-based light reception (see **Box 18.1**). Bees are also able to detect magnetic fields, and the orientation of their dances at the hive can be influenced by magnetic fields. However, magnetic information plays little role in ordinary bee navigation.

For any animal that navigates using magnetic-compass cues, the magnetic response is innate and presumably genetically determined. But unlike the star compass—which appears to be fixed

once it has been learned during a critical period in the animal's life—an animal's magnetic compass seems to be subject to at least some degree of recalibration. The ability to recalibrate is important because migrants to Arctic latitudes must resolve conflicts between magnetic and celestial navigational cues. The north magnetic pole and the geographical North Pole are not identical (see Figure 18.8). Magnetic-field information points to a different location than celestial-compass information does, and the disparity between the two increases at higher and higher latitudes. For this reason, migrating Arctic birds must pause in their journey at intervals in order to allow their magnetic compasses to realign with celestial-compass cues such as polarized sky light. If prevented from pausing long enough to recalibrate, the birds may become disoriented.

The physiological mechanisms by which animals detect magnetic fields are discussed in **Box 18.1**.

Some animals appear to possess a map sense

Most animals probably do not use simple compass navigation in migration or homing without also using landmark or map information. In cases of **map-and-compass navigation**, the animal possesses in its brain some sort of representation of its position, and the position of its goal. This is the *map*, and the animal's *compass* provides bearings relative to the map.

For most animals that appear to have a map sense, we do not know the map's basis, although it might be based on various sensory cues. A map could be based on geomagnetic information, since both the vertical angle and the strength of magnetic fields increase near the magnetic poles. The disorientation of homing pigeons and migrating whales in the vicinity of magnetic anomalies suggests that magnetic information is an important basis of their maps. Solar cues could also provide map information; the height of the sun above the horizon varies with the latitude, and the times of sunrise and sunset vary with longitude. For some migrating creatures, infrasounds (very low-frequency sound waves—for example, from waves crashing on a distant shore) may serve as the basis of the map. Even olfactory cues are suspected of forming the basis of the map sense, as appears to be the case with pigeons. Whatever its basis, map construction and use represent a sophisticated instance of animal learning.

DISPLACEMENT EXPERIMENTS TEST FOR A MAP SENSE Displacement experiments show the difference between path integration and compass navigation on the one hand, and complex map-and-compass navigation on the other. If a desert ant is experimentally moved while it is feeding, its return path makes no correction for this passive displacement (see Figure 18.3). Therefore, the ant has no map sense that allows it to detect its displacement relative to its goal.

Birds, in contrast, are more likely to correct for a passive displacement, whether experimental or by natural means such as a storm. If a bird migrating southwest purely by compass navigation became displaced, say, 100 km to the southeast, it would continue to go southwest. If the bird were using map-and-compass navigation, it would realize it had been displaced (apparently without using local, familiar landmarks) and would correct its path to the west or northwest.

Figure 18.10 illustrates the distinction between path integration and compass navigation. European starlings (*Sturnus vulgaris*)

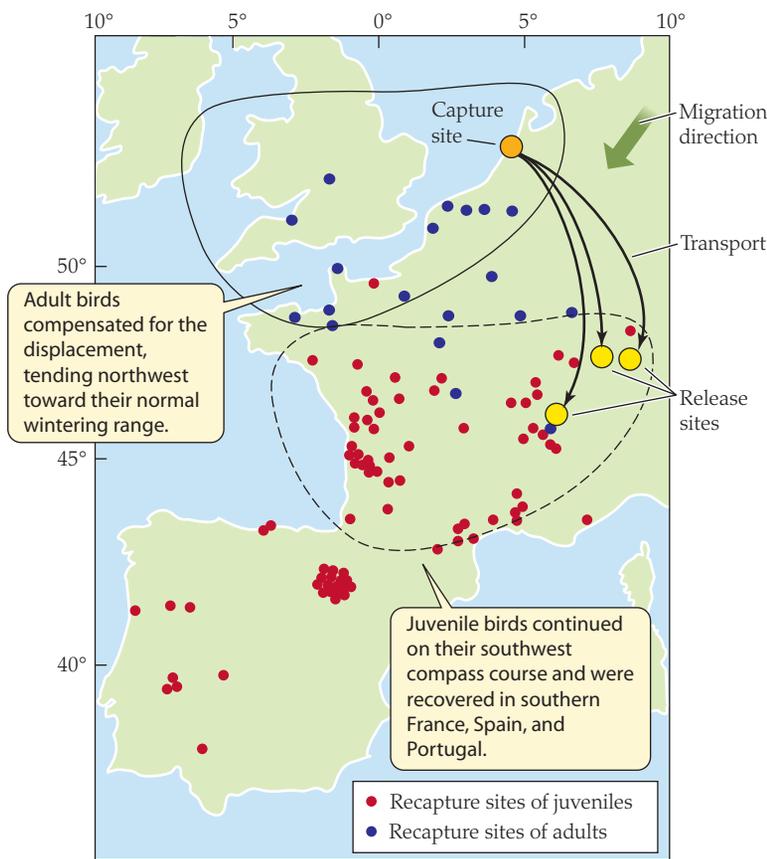


FIGURE 18.10 Migrating adult and juvenile starlings respond differently to displacement European starlings were captured in the Netherlands while in their autumn migration southwest from north-eastern Europe and were transported to release sites in Switzerland. The normal wintering range is bounded by the solid line; a dashed line shows a similar area displaced to the same extent as the displacement of the released birds. The adults' compensation for displacement suggests the use of map-and-compass navigation. (After Perdeck 1958.)

migrate from Baltic breeding grounds to wintering grounds in France and England. Migrants were captured in the Netherlands, transported to Switzerland, and released. The juvenile starlings continued southwest (by compass navigation) and ended up in Spain, but the older, experienced birds that had developed a map sense could detect the displacement and reorient to a new northwestern path. Map-and-compass navigation is sometimes called *true navigation*, an unfortunate term because it (wrongly) suggests that other methods of an animal's finding its way are not really navigation. Because we find that compass orientation is relatively complex, we may expect the basis of the less-understood map sense to be complex as well.

PIGEONS MAY HAVE AN OLFACTORY MAP Some of the clearest studies of map sense have focused on pigeons, and the dominant hypothesis of map sense in pigeons is the *olfactory-map hypothesis*. Displaced pigeons can determine their position relative to home without using visual or proprioceptive information from the outward journey to the release site. Therefore, investigators conclude that the pigeons must have some sort of map sense that, with the compass information previously discussed, allows them to return from more than 700 km away. According to the olfactory-map hypothesis, the pigeon's map sense is based on an odor profile somewhat analogous to the one used by homing salmon. The odor profile could consist of a mosaic of discrete odor sources or a few odor gradients.

Several lines of experimental evidence support the olfactory-map hypothesis. Pigeons are usually housed in somewhat open structures (lofts), often on the roofs of buildings. A pigeon that has its olfactory sense disrupted has difficulty homing to its loft. Manipulations of odors around the home loft can also affect homing performance, perhaps by affecting the learning of an olfactory map. In one example, pigeons were raised in a loft that was exposed to normal odors but also had an odor of benzaldehyde blown in by a fan from the north-northwest. Thus they presumably learned to associate north-northwest wind with benzaldehyde. At the end of the summer they were transported to various distant, unfamiliar release sites, exposed to benzaldehyde, and released. They flew primarily south, regardless of the release site. Control birds raised without benzaldehyde, but exposed to it just prior to release, oriented toward home normally from the release sites. The simplest interpretation of these findings is that the pigeons learned to associate benzaldehyde odor with north-northwest wind, so the experimental pigeons thought they had been released at a benzaldehyde source north-northwest of home, and flew south-southeast.

BOX 18.1 MAGNETORECEPTORS AND MAGNETORECEPTION

Kenneth J. Lohmann

The idea that animals perceive Earth's magnetic field was once dismissed as impossible by physicists and biologists alike. Earth's field is much too weak for an organism to detect, the argument went, and there are no possible biological mechanisms capable of converting magnetic-field information into electrical signals used by the nervous system.

Over time, however, evidence accumulated that animals do indeed perceive magnetic fields, until even the most hardened skeptics came to accept the idea. Today it now seems clear that diverse animals, ranging from invertebrates such as molluscs and insects to vertebrates such as sea turtles and birds, exploit information in Earth's field to guide their movements over distances both large and small. What has remained mysterious is exactly how they do this.

Determining how the magnetic sense functions is an exciting frontier of sensory physiology. For sensory systems such as vision, hearing, and smell, the cells and structures involved in perceiving relevant sensory stimuli have been largely identified, and the basic way in which the sense operates is understood. In contrast, the cells that function as receptors for the magnetic sense have not been identified with certainty in any animal. Even the basic principles around which magnetic sensitivity is organized remain a matter of debate. This box continues on the web in **Box Extension 18.1**. There you will find more information on magnetoreception in animals and on mechanisms that may underlie it.

Other investigators have criticized the olfactory-map hypothesis on several grounds. Olfactory anesthesia or nerve cuts to make pigeons unable to smell may have indirect effects on homing performance that have been mistakenly interpreted as affecting an olfactory map. Some indirect effects can be ruled out; for example, the olfactory manipulations do not simply make the animal sick. Other effects, such as a possible indirect disruption of the pigeons' use of magnetic signals, are harder to rule out. In addition, some experiments have been hard to replicate, perhaps because investigators in different countries raise their birds in different styles of lofts that may affect olfactory-map learning. Overall, however, there is substantial evidence to infer roles of olfactory cues in pigeon homing, and so we can consider the olfactory-map hypothesis to be supported by evidence but not proven.

Sea turtles exemplify the degree of our understanding of navigation

Sea turtles illustrate what we know and don't know about the behavioral mechanisms of navigational control. Turtles use different cues in navigation at different stages in their life cycle, and some of these cues are much easier to analyze than others. New hatchlings starting off the beach appear to engage in a sequence of orienting mechanisms. Loggerhead sea turtles hatching on Florida beaches initially orient toward a lighter sky, which will be toward

water (because the water reflects more sunlight or moonlight and makes the sky lighter). This light orientation and a tendency to move down a slope take the hatchlings to the water, where they swim out continuously for 24 h. The primary orientation cue for this frenzied outward swim is the waves; the turtles head into the waves, which come (with rare exceptions) from the open ocean. (During the exceptions, young turtles swim into the waves even if that orientation takes them back to shore.)

The young turtles can also detect Earth's magnetic field, and magnetic-compass orientation may replace wave orientation after their initial outward swim. This navigational sequence is thought to take the turtles out to the Gulf Stream, one of the currents flowing around the North Atlantic Subtropical Gyre (Figure 18.11). Adult turtles must use map-and-compass navigation to return to their natal beach to nest (in contrast to juveniles, which only have to reach the gyre). Tracking studies indicate that the adults navigate by direct, straight-line routes. Recent evidence indicates that even the younger turtles can use magnetic information as a map component that helps keep them in the gyre as they mature.

Experimental replication of the parameters of the magnetic field at different points in their migration route leads to different swimming orientations that match the turtles' swimming direction at that location (see Figure 18.11). For example, caged turtles in an artificial magnetic field that replicates the natural

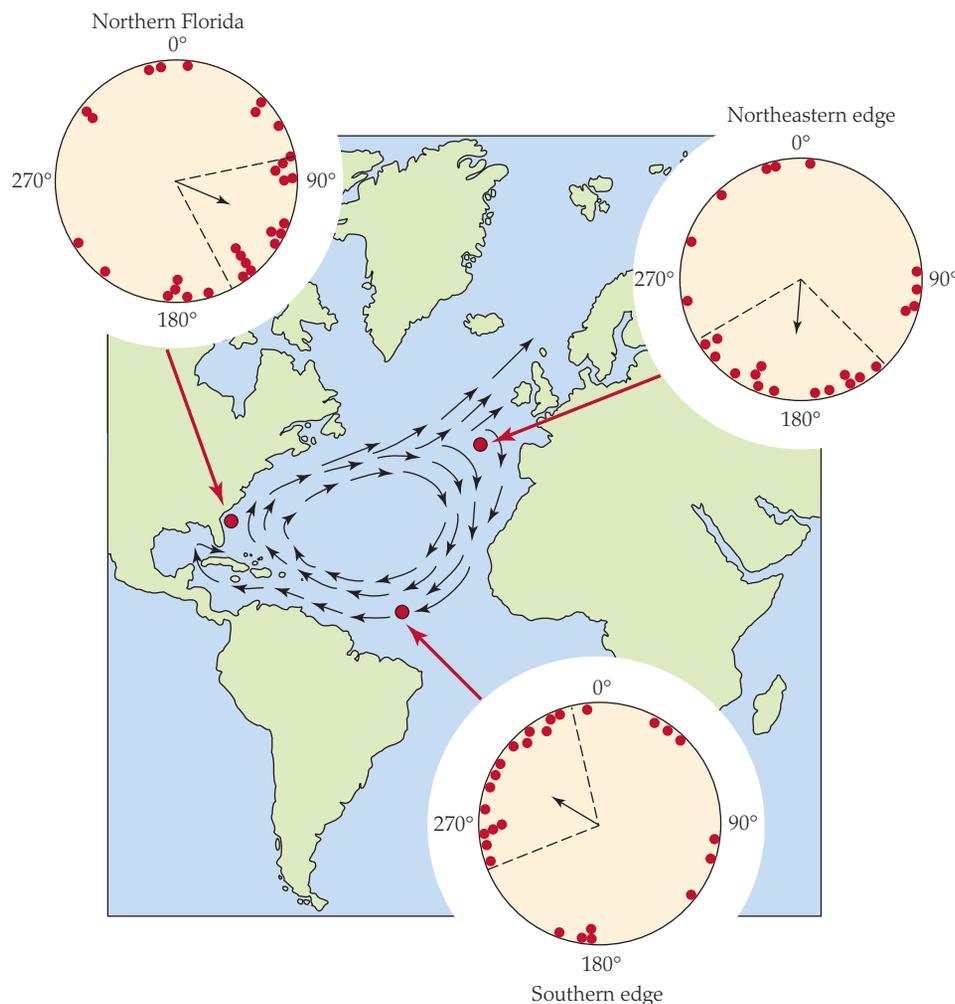


FIGURE 18.11 Hatchling turtles orient to artificial magnetic fields in ways that suggest a magnetic map Newly hatched loggerhead turtles were placed in artificial magnetic fields characteristic of three locations (red dots on map) along their prospective migratory route. Arrows on the map show major currents of the North Atlantic Subtropical Gyre, around which the turtles swim as they mature. Each dot in the orientation diagrams represents the mean angle of oriented swimming of one hatchling. The arrow in the center of an orientation diagram indicates the mean angle of orientation of each group; arrow length shows the statistical degree of orientation of the group. All three groups showed statistically significant orientation to the artificial magnetic fields. The angle of orientation differed greatly for the three groups tested with artificial magnetic fields corresponding to different locations. Moreover, the orientation at each simulated location was appropriate to keep turtles within the gyre, rather than (for example) straying into the fatally cold water of the North Atlantic and North Sea. Dashed lines represent the 95% confidence interval for the mean angle; data are plotted relative to magnetic north. (From Lohmann et al. 2001.)

magnetic field off the coast of Spain swim southward, a direction that keeps them in the North Atlantic Subtropical Gyre rather than washing into northern waters off Scandinavia. Similar experiments with turtles as well as with salamanders, spiny lobsters, and birds all show that experimental replication of the magnetic-field vectors and strengths of a particular location can alter orientation behavior in predictable ways. These studies suggest that animals can use magnetic information as a map (as well as a compass), a finding that may begin to clear up the murkiest area in complex navigation.

Innate and Learned Components of Navigation

We have indicated that many elements of navigation, such as using landmarks, imprinting to a home stream, and constructing a map, are largely learned behaviors. Here we discuss the roles of innate (“hardwired”) behavior and of learning in navigation, and we consider how vertebrates learn their spatial surroundings.

Some forms of navigation have strong innate aspects

Two examples demonstrate innate components of navigation that do not depend on prior learning. Monarch butterflies summer throughout the United States north of the Gulf states. Those east of the Rocky Mountains migrate south every fall to overwintering sites in forested mountains of central Mexico. In the spring the same individuals migrate north to the U.S. Gulf Coast states, where females lay eggs on milkweed and die. A new generation continues the migration to summering grounds in the northern states and produces two or more short-lived generations in a summer. The autumn migrants that return to the same restricted overwintering sites in the following year are thus descendants, three to five generations removed, of ancestors that occupied the sites the previous winter! The navigational performance of the monarch butterfly therefore must have a strong innate, genetic component; the butterflies cannot have learned the overwintering location from previous experience.

Some birds also have innate, apparently genetic components of their migratory navigation. European blackcaps (*Sylvia atricapilla*), for example, migrate from Europe to Africa around the Mediterranean Sea—those in western Europe going southwest via Gibraltar, and those in eastern Europe going southeast via Syria. When birds from the two sides of the divide are raised in isolation, they orient in cages in the correct direction for their area of origin, despite the lack of opportunity to learn their way. Cross-breeding experiments further demonstrate that the difference in orientation between eastern and western strains is genetic.

The hippocampus is a critical brain area for vertebrate spatial learning and memory

As we have discussed, an animal’s ability to navigate often involves learning, such as the recognition of landmarks by some homing animals, or the imprinting of home stream odors by salmon. Spatial learning is crucial for many sorts of navigation, and for vertebrates a major locus of spatial learning is the *hippocampus* of the brain.

By surgically creating hippocampal lesions in test animals and monitoring their performance in mazes, researchers have shown the importance of the hippocampus in spatial learning.

One standard test of spatial learning in laboratory rodents is the *Morris water maze*, which consists of a hidden, submerged escape platform in a pool of turbid water. The test animal must learn the location of the platform from local cues (landmarks) that are situated outside the pool. Mice or rats with hippocampal lesions do not remember the location of the platform, and they continue to swim about randomly, trial after trial. Another means of testing spatial learning is the *radial-arm maze*, which consists of several blind corridors that extend symmetrically from a central chamber. The researcher repeatedly baits the end of one arm (or shifts the bait from arm to arm in a recurring pattern); the test animal must remember which arm is baited to earn the reward. Normal mice and rats remember the arms they have visited and do not reenter them during a test session, but mice and rats with hippocampal lesions repeatedly enter the same arm and often bypass the arms they have not yet visited.

Does spatial learning in the hippocampus explain how food-caching birds such as Clark’s nutcrackers store information about the locations of thousands of cache sites? In fact, birds with bilateral hippocampal lesions continue to hide food normally, but they cannot recover their caches. They can, however, remember simple, nonspatial associative tasks (such as pairing a sound with a reward). Thus the deficit appears to be specific for spatial learning and memory. Also suggesting the importance of this brain region in spatial learning is that researchers have noticed that the hippocampus is significantly larger in food-caching birds than in size-matched species that do not cache. Moreover, for species that cache, preventing caching behavior in immature birds appears to diminish hippocampal growth.

The hippocampus also appears to be involved in homing in pigeons. It is critical for learning two aspects of pigeon navigation: piloting and navigational maps. Inexperienced pigeons with hippocampal lesions are impaired in learning local landmarks for piloting, as might be expected from the studies with seed-caching birds and rodents. They also fail to orient correctly from distant, unfamiliar release sites, indicating that they have failed to learn a navigational map. Experienced pigeons that receive hippocampal lesions *after* learning a navigational map orient correctly from distant release sites, but they still have difficulty with local, landmark-based navigation. Therefore, the hippocampus appears necessary throughout life for landmark-based navigation but not for using a navigational map once that map has been learned. Interestingly, the left hippocampus appears necessary for map learning in pigeons, but not the right.

The two hippocampi may also be used differently in humans. There are two aspects or strategies of spatial learning and memory, called *allocentric* (world-centered) and *egocentric* (body-centered) representations. These are comparable to two kinds of video games: the maplike bird’s-eye-view strategy games and the “first-person shooter” games in which the screen shows the view ahead of the character. Either allocentric or egocentric representations can be used to orient in an environment. A recent human study using fMRI and a virtual radial-arm maze concluded that activation of the right hippocampus predicted the use of an allocentric spatial representation, and activation of the left hippocampus predicted use of a sequential egocentric representation. Thus the right human hippocampus may code places and the left may code temporal sequences of movement.

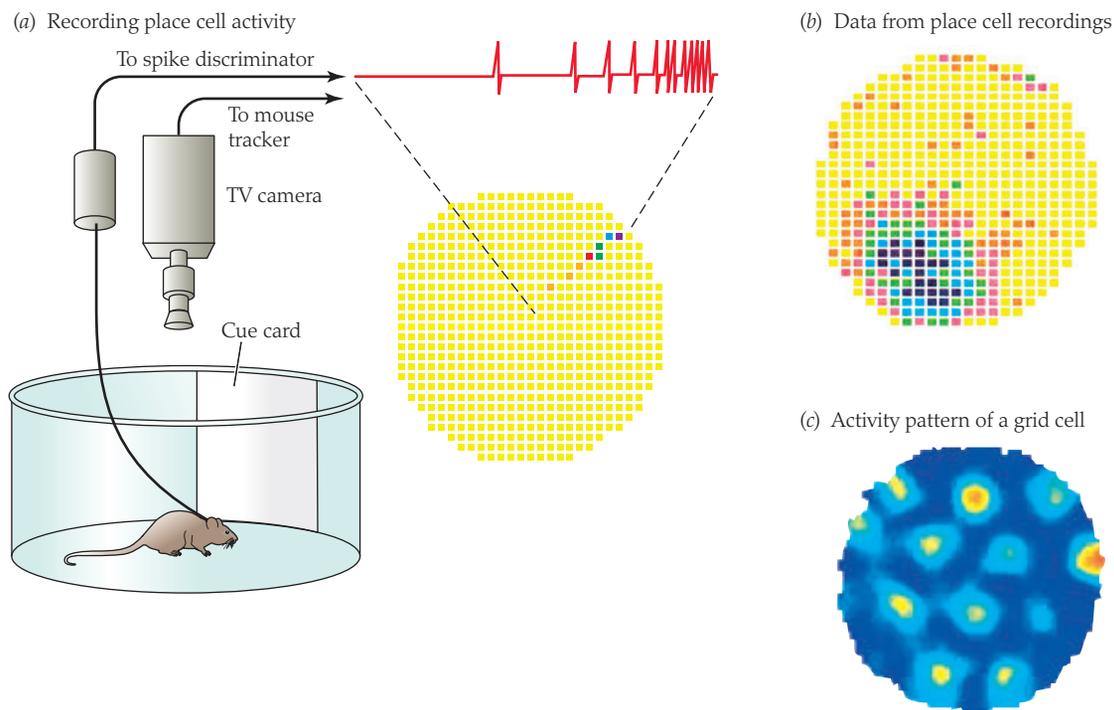


FIGURE 18.12 Place cells suggest how the hippocampus of the brain plays a role in spatial learning (a) A chronically implanted electrode records activity of an individual hippocampal pyramidal neuron while a mouse is moving around an arena. A TV camera records the mouse's position and correlates it with the neuronal activity. The cue card is a landmark to aid the animal in orientation. (b) An individual hippocampal neuron is active (cool colors) when the mouse is in a particu-

lar part of the arena. Such correlations are rather stable from day to day and are learned during exploration of initially unfamiliar environments. The diameter of the circle is 0.76 m. (c) A grid cell in the entorhinal cortex is active (warm colors) when the animal is at any apex of an invisible triangular grid within the environment. The circle's diameter is about 2 m. (b from Muller et al. 1987; c from Hafting et al. 2005.)

Exactly *how* the hippocampus stores and retrieves spatial memory has not been determined, but two interesting findings are relevant. First, the hippocampus is a principal site of long-term potentiation (LTP) (see Chapter 13, page 353). Gene knockouts that disrupt LTP in mice disrupt spatial learning in tests such as the Morris water maze. Overexpressions of genes that enhance LTP improve learning and memory of familiar objects, spatial tasks such as the Morris water maze, and other memory tasks.

Second, chronic electrical recordings from single neurons in the hippocampus of rats or mice show that some neurons generate action potentials only when an animal is in a particular part of a familiar area (Figure 18.12a,b). These hippocampal neurons are termed **place cells** because their activity encodes the spatial position of the animal. The existence of place cells in the hippocampus suggests that this brain area creates some sort of a spatial map of the environment in the brain. The spatial representations of place cell activity are dynamic; as an animal is exposed to new environments, some place cells may change their specification to incorporate new areas.

The hippocampus is not the only brain area that is involved in processing spatial information used in navigation. Investigators have recorded from neurons—termed **head direction cells**—that encode the direction the animal's head is pointing. These neurons occur in a circuit in the rodent forebrain that extends from the dorsal tegmental nucleus to the entorhinal cortex, and are activated by vestibular and other sensory information. Head direction cells are direction-specific but not location-specific, unlike place

cells, which are location-specific but not direction-specific. Other neurons appear to provide distance calibration for a mental map. Neurons in one part of the entorhinal cortex are called **grid cells**, because they are active when the animal is in any of several grid-like locations in its environment (Figure 18.12c). Grid cells do not provide locale information like place cells do; instead, they increase their activity when a rat walks through the vertices of an invisible grid of equilateral triangles that measure off distances within the environment. Different grid cells have somewhat different scales, representing 30-cm grids in the dorsalmost part of the area and 70-cm grids ventrally. The finding of grid neurons is certainly consistent with the idea that animals form a kind of maplike representation of their environment in their brains.

Such studies of the hippocampus and other brain areas are starting to build a physiological basis of navigation. It is not clear just how animals use the neural information these studies describe, but the findings are consistent with what animals would need for complex spatial representation. One can imagine how animals might use place cells that encode landmark-based learning of familiar areas, head direction cells that encode compass-heading information (and receive input from various directional sensors), and grid cells that provide a distance scale. Our increasing ability to relate sensory and brain mechanisms to map functions should provide an important link between brain processes and the complex spatial behaviors of navigation, and ultimately to the navigational basis of migration, homing, and other spatial behaviors.

Study Questions

1. Explain the effect on sun-compass orientation of a circadian-clock shift to a light schedule that is 4 h later (e.g., from lights-on at 6:00 AM to lights-on at 10:00 AM).
2. List the advantages and disadvantages to an animal of using information from magnetic, sun, star, and polarized-light compasses.
3. Experienced homing pigeons were thought not to need any information about the outward journey to a release site in order to home successfully. Much evidence for this conclusion came from depriving the birds of visual, magnetic, and vestibular information that could be used for path integration. What other sorts of studies would you want performed before accepting this conclusion?
4. Outline how a vertebrate might use place cells, head direction cells, and grid cells in different forms of navigation.

Go to sites.sinauer.com/animalphys3e for box extensions, quizzes, flashcards, and other resources.

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See also **Additional References** and *Figure and Table Citations*.