The magnetic map of hatchling loggerhead sea turtles
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Young loggerhead sea turtles (Caretta caretta) from eastern Florida, U.S.A., undertake a transoceanic migration in which they gradually circle the North Atlantic Ocean before returning to the North American coast. Hatchlings in the open sea are guided at least partly by a ‘magnetic map’ in which regional magnetic fields function as navigational markers and elicit changes in swimming direction at crucial locations along the migratory route. The magnetic map exists in turtles that have never migrated and thus appears to be inherited. Turtles derive both longitudinal and latitudinal information from the Earth’s field, most likely by exploiting unique combinations of field inclination and intensity that occur in different geographic areas. Similar mechanisms may function in the migrations of diverse animals.

Introduction
The ability of animals to guide themselves unerringly during long-distance migrations has inspired both awe and envy in humans, a species that has only recently, through global positioning technology, achieved a measure of parity with the skills of elite animal navigators. Nowhere are the navigational abilities of animals more stunning than in the marine environment, where various fish [1–3], reptiles [4,5], birds [6,7], and mammals [8,9] routinely traverse vast expanses of seemingly featureless sea. Understanding how these migrations are accomplished has posed a daunting challenge for biologists who have long struggled to explain navigational mechanisms that appear to border on magic.

One of the longest and most spectacular marine migrations is that of the loggerhead turtle (Caretta caretta). Hatchling loggerheads from Florida, U.S.A., emerge from underground nests on oceanic beaches, scramble to the sea, and then migrate offshore to the Gulf Stream current. These young turtles become entrained in the North Atlantic Subtropical Gyre, the circular current system that flows around the Sargasso Sea [10]. Many loggerheads gradually migrate around the entire North Atlantic basin before eventually returning to the North American coast [11,12].

During the past decade, evidence has accumulated that young loggerheads guide their open-sea movements, at least in part, by exploiting positional or ‘map’ information inherent in the Earth’s magnetic field [13,14,15,16]. In this review, we summarize what is known about the magnetic map of loggerheads.

Magnetic compasses and maps
Among the various sensory cues that ocean migrants exploit while navigating, the Earth’s magnetic field is particularly pervasive [17,18]. Unlike most potential sources of directional and positional information, the geomagnetic field is present day and night, remains unaffected by weather and season, and exists throughout the ocean, regardless of depth. By the late 1980s, when studies on sea turtle navigation began in earnest, it was known that diverse animals ranging from molluscs to birds use the Earth’s field as a compass for maintaining direction (e.g. toward north or south) [19]. Experiments soon revealed that a magnetic compass exists in hatchling sea turtles [20,21] and, in combination with visual cues and ocean wave direction, guides hatchlings as they swim offshore from the Florida coast to the Gulf Stream current [22,23].

Once in the Gulf Stream, turtles undertake a transoceanic migration that requires more than just a compass to complete; turtles also need positional information to know where to change swimming direction. For example, the North Atlantic Subtropical Gyre provides an ideal warm-water nursery habitat for growing loggerheads, but turtles along the northern boundary are at risk of being carried by currents into fatally cold waters that lie to the north [10,23]. Similarly, turtles that stray south of the gyre may be swept into South Atlantic currents and transported far from their normal range. An ability to determine geographic position, and to adjust swimming direction at crucial locations along the migratory route, might therefore have considerable adaptive value.

Information about geographic position can potentially be derived from the predictable geographic variation of Earth’s magnetic field [24–26]. For example, magnetic
field lines intersect Earth’s surface at specific inclination angles, which become progressively steeper as one moves from the magnetic equator toward the magnetic poles. Similarly, field intensity (strength) varies predictably across the Earth’s surface, but in a direction that differs from that of inclination. As a consequence, most open-sea regions have a unique magnetic signature comprised of a combination of inclination and intensity that exists nowhere else in the ocean basin [14**,27].

**The magnetic map of loggerheads**

To investigate whether young loggerheads can exploit positional information in Earth’s magnetic field, hatchlings have been tested in various magnetic fields matching those that exist in different locations along their migratory route [13,14**,15**]. In all of these experiments, turtles were collected from nests a few hours before they would otherwise have emerged naturally. Hatchlings were tested singly in a circular, water-filled arena surrounded by a computerized coil system (Figure 1), which controlled the magnetic field in which each turtle swam. Orientation was monitored by tethering the turtle to an electronic tracking unit that relayed swimming direction to a computer in an adjacent room.

In the first of these studies [13], hatchlings were exposed to three magnetic fields that exist at widely separated locations along the migratory route. Two of the fields replicated ones along the northern boundary of the gyre, while the third was like one near the southernmost gyre edge. Turtles responded to the fields by swimming in directions that would, in each case, help them remain within the gyre and advance along the migratory pathway. These results demonstrated that young loggerheads have a guidance system in which regional magnetic fields function as navigational markers and elicit changes in swimming direction at crucial geographic boundaries.

Because the fields tested initially replicated ones along the latitudinal extremes of the migratory route, the results left open the question of whether turtles can also use the Earth’s field to distinguish among geographic areas that differ in longitude. To investigate, hatchling loggerheads were exposed to magnetic fields that exist at two locations with the same latitude but on opposite sides of the Atlantic Ocean [14**].

Turtles exposed to a field that exists on the east side of the Atlantic, near the Cape Verde Islands, responded by swimming southwest. In contrast, turtles exposed to a field that exists on the west side of the Atlantic, near Puerto Rico, swam approximately northeast. Both orientation responses appear likely to have functional significance in the migration. Near the Cape Verde Islands, southwesterly orientation coincides with the southwest-flowing Canary current and the migratory pathway. Swimming southwest might also help turtles avoid the southeast-flowing Guinea Current, which can potentially displace turtles from the gyre. Near Puerto Rico, northerly orientation is likely to direct turtles into the Antilles Current [14**]. This current flows swiftly toward the US coast, where most Florida loggerheads spend their late juvenile years [23].

These results demonstrated, for the first time, that longitudinal information can be encoded into the magnetic map of an animal. Before the study, a common view among many animal navigation researchers was that magnetic

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**Figure 1**

Experimental apparatus used to monitor orientation responses of hatchling loggerhead turtles to regional magnetic fields. (A) A hatchling loggerhead swimming in a cloth harness. (B) Turtles were tethered to a rotatable tracker arm attached to a digital encoder, which relayed the direction of swimming to a computer in a nearby building. The arena was enclosed by a magnetic coil system capable of replicating magnetic fields found at different locations along the turtles’ migratory route. Modified from Lohmann and Lohmann [23].
cues, which typically vary more in a north–south rather than an east–west direction, are likely used by animals as a surrogate for latitude but not for longitude [28–31]. The new findings indicate, however, that young loggerheads exploit the Earth’s field as a kind of bicoordinate magnetic map from which both longitudinal and latitudinal information can be extracted. This in turn implies that turtles perceive at least two different geomagnetic features that vary in different directions across the Atlantic [14**].

The precise organization of the loggerhead magnetic map is not known. Given that turtles detect both field inclination [32] and intensity [27], a reasonable hypothesis is that the map is structured around magnetic signatures comprising unique combinations of these two parameters ([13,14**]; see also magnetic compasses and maps). Because isolines of inclination and intensity do not coincide with either latitude or longitude, and because they intersect at different angles in different oceanic regions [24], the geographic areas defined by different magnetic signatures are not of a uniform size or shape. They also depend at least partly on the sensitivity of turtles to each magnetic parameter.

The difficulty in relating magnetic signatures to latitude and longitude raises questions about the conceptual framework that has guided recent discussions of animal navigation. Although much attention has focused on identifying environmental cues that might serve as surrogates for latitude and longitude [29,31,33], sea turtles appear to have evolved a navigational system largely independent of these concepts, relying instead on recognition of ecologically important geographic areas defined by distinctive magnetic fields.

Regardless of how the map is organized, growing evidence suggests that a surprising amount of information is encoded into it. At present, turtles have been shown to respond with oriented swimming to fields that exist in at least 8 different locations along the migratory pathway (Figure 2). In each case, the direction of orientation is suitable for helping turtles remain in the gyre and advance along the migratory route.

Active swimming versus passive drifting

When evidence was first presented that Florida loggerheads undertake a transoceanic migration, it was assumed that turtles drift passively in the gyre currents until they return to the North American coast [10]. The existence of an elaborate set of responses to regional magnetic fields in hatchling loggerheads suggests a very different paradigm: that turtles actively direct their migration.

With an increased understanding of ocean currents, it has become evident that passive drifting alone cannot account for the migration of Florida loggerheads. For example, analyses combining ocean circulation models and particle tracking techniques (Figure 3) reveal that, if turtles were to drift passively in geographic areas with magnetic fields known to elicit oriented swimming, they would often disperse in highly variable directions or, in some cases, be carried by currents to locations where survival is unlikely. An interesting example of the latter occurs near the coast of north Florida, where turtles drifting passively are likely to linger for weeks in a shallow region along the southeastern U.S. coast where predatory fish and birds are abundant. Similarly, turtles that drift along the northern boundary of the gyre may fail to pass reliably through ocean regions where temperatures drop to lethal levels in winter (Figure 3) [34]. Simulations of passive drifting at other points in the gyre currents have also failed to produce appropriate paths, implying that active swimming is essential to completing the migratory route.

A versatile navigation system

A remarkable aspect of the orientation responses elicited by regional magnetic fields is that they are expressed by hatchlings that have never been in the ocean. Thus, turtles do not need migratory experience to recognize and respond to fields that mark the migratory pathway. In addition, hatchlings do not need to pass through a specific sequence of locations or magnetic fields before responding to fields that they would not, under natural conditions, encounter for weeks, months, or sometimes even years after entering the sea.

The ability of young turtles to respond to a variety of fields independently of when they encounter them may have evolved because ocean currents exert a strong but unpredictable influence on the path that a young turtle follows. For example, a hatchling that reaches the center of the Gulf Stream may be carried rapidly across the Atlantic, whereas one on the periphery of the current may be spun off into an eddy and lag far behind. As a result, the time that it takes to complete the transoceanic migration, or to arrive at a particular region along the way, probably varies greatly among individuals. Moreover, analyses of ocean currents indicate that a range of migratory trajectories is possible, suggesting that there is no single, uniform migratory route that all turtles follow and thus no reliable sequence of fields encountered along the way (NF Putman, PhD thesis, University of North Carolina, 2011). Given these uncertainties, there are clear advantages to a system comprised of location-dependent responses, in which turtles respond to specific regional fields that exist in particular geographic areas if and when they encounter them.

An interesting question is how turtles can evolve a navigational system based on magnetic fields that exist in different geographic areas, even though the Earth’s field gradually changes over time [23]. Because poor navigation in young turtles often equates to death, a likely answer is that strong selective pressure acts to maintain an appropriate coupling between the turtles’ directional swimming responses and the magnetic fields that exist at crucial geographic locations.
Orientation of hatchling loggerheads in magnetic fields characteristic of widely separated locations along the migratory route. The fields used in experiments replicated ones that exist at the locations on the map marked by black dots; data are from [13,14**,15**], and (NF Putman, PhD thesis, University of North Carolina, 2011). Generalized main currents of the North Atlantic subtropical gyre are represented on the map by arrows. In the orientation diagrams, each dot represents the mean angle of a single hatchling. The arrow in the center of each circle indicates the mean angle of the group. The shaded sector represents the 95% confidence interval for the mean angle. Each group of turtles was significantly oriented at \( P < 0.05 \) or better (see [13,14**,15**] for statistical details). In each case, the direction of orientation was suitable for helping turtles remain in the gyre and advance along the migratory route. Near the coast of northern Florida, southeasterly orientation presumably moves turtles farther into the Gulf Stream, reducing chances of straying into cold water north of the gyre [13]. Midway across the Atlantic in the northern part of the gyre, east-northeast orientation is likely to help turtles cross the Atlantic and avoid lingering in oceanic regions that become cold during part of the year [15**]. Near northern Portugal, swimming south presumably helps turtles remain in the warm gyre currents [15**]. Near southern Portugal, swimming southwest may help turtles move offshore and distance themselves from the shallow, predator-rich coastal waters of northern Africa [15**]. Near the Cape Verde Islands, southwesterly orientation presumably helps turtles start back toward the west side of the Atlantic [14**]. Near the southernmost boundary of the gyre, northwesterly orientation coincides with the migratory route back toward North America [13]. Near Barbados, swimming north may help turtles remain in the gyre and avoid being carried into the Caribbean (NF Putman, PhD thesis, University of North Carolina, 2011). Near Puerto Rico, northeasterly orientation is likely to guide turtles toward the main gyre currents moving back toward North America [14**].
Likely trajectories of passively drifting turtles derived from an ocean circulation model. In this simulation, virtual turtles (particles) were released from 8 points (black dots) in the North Atlantic that correspond to the locations of regional magnetic fields used in laboratory experiments (Figure 2). Ocean circulation was modeled using the Global Hybrid Coordinate Ocean Model [48], which is based in part on oceanographic measurements compiled over a period of years. To accommodate seasonal and annual variation in ocean circulation, one virtual turtle was released from each point on the first day of the month for the period of 2005–2008. The particle-tracking program iChiHyop (v. 2) was used to calculate the daily positions of virtual turtles [49]. Gray lines indicate the paths of turtles drifting passively for 60 days in the surface layer. These simulations, and others like them, imply that loggerheads are unlikely to migrate successfully around the gyre by drifting passively as proposed by Carr [10]. Instead, directed swimming at various locations along the migratory pathway appears essential.

along the migratory route [13,14**,15**]. For example, under present conditions, turtles that stray out of the gyre are probably eliminated from the population, whereas those with orientation responses that keep them safely within are favored by natural selection. Similarly, as the field that exists in a specific region of the migratory pathway changes, only those turtles that respond to the new field in a way that allows them to migrate successfully will survive to pass on their genes.

**Mechanism of magnetic field detection**

The neural mechanisms that underlie magnetic field detection have not been clearly established in any animal [26]. The status of sea turtles as threatened species limits their utility in neurobiological research. In other animals, however, three main mechanisms of magnetoreception have been proposed: electromagnetic induction, magnetite, and chemical magnetoreception [35,36].

Mechanisms based on electromagnetic induction appear unlikely for turtles. Marine animals swimming through the Earth’s field induce small electrical currents in the surrounding water, so it may be possible for sharks or other animals with a highly sensitive electric sense to detect magnetic fields indirectly [36,37]. Sea turtles, however, appear to lack electroreceptors.

A second hypothesis is that crystals of the magnetic mineral magnetite function in magnetic field detection [38*]. Possible magnetite-based receptors have been identified in rainbow trout [39] and pigeons [40]. Preliminary evidence for magnetite in sea turtles has also been obtained [41], but whether magnetite underlies magnetoreception in turtles is not known.

A third hypothesis is that magnetoreception is accomplished through a complex set of chemical reactions associated with the visual system [42,43]. Some evidence consistent with this hypothesis has been obtained in birds, flies, and other animals [44*], [Mouriksen, in this issue], but the idea has not yet been investigated in turtles.
An interesting possibility is that two different mechanisms [25,26,45]. In birds, it has been proposed that a compass sense based on chemical magnetoreception exists in the eye, while a map sense based on magnetic fields exists in the beak. According to this idea, two different mechanisms evolved, each to detect different aspects of the field: the compass receptors detect field direction, whereas the map receptors detect field intensity, inclination, or both. Whether dual magnetoreceptor systems exist in turtles is not known.

Conclusions

Loggerhead sea turtles embarking on their first migration possess a magnetic map in which regional magnetic fields characteristic of specific oceanic areas elicit orientation responses that help steer turtles along the migratory route. Couplings of regional fields with directional swimming appear to provide the building blocks from which natural selection can sculpt responses that guide first-time migrants along complex migratory pathways. Because the direction that a young turtle travels depends both on the direction that it swims and the direction that it is carried by ocean currents, a thorough understanding of sea turtle navigation probably requires integration of behavioral findings with oceanographic analyses.

The magnetic map of young loggerheads is most likely based on magnetic signatures (unique combinations of magnetic inclination angle and intensity that exist in different oceanic regions), rather than on natural proxies for latitude and longitude. Stepping outside of our own deeply ingrained human spatial system appears essential to understanding sea turtle navigation.

Finally, the mechanisms that guide young sea turtles on their first transoceanic migration may function in diverse migratory animals. The use of regional magnetic fields as a system of navigational markers appears particularly plausible for migrations of salmon [1] and other marine fishes [2,3], but is also worth considering for other long-distance migrants such as marine mammals [9] and birds [46,47*].

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

• of special interest

•• of outstanding interest


This study demonstrated that longitudinal information is encoded into the magnetic map of hatching loggerheads. The findings showed for the first time that animals with magnetic maps are not restricted to using Earth’s magnetic field exclusively as a source of latitudinal information, contrary to what many researchers had assumed previously.


This paper reports on orientation responses elicited by three different magnetic fields that exist along the northern portion of the turtles’ transoceanic migratory pathway. It also reports on the failure of hatchlings to respond to a field that exists in a location far outside of the migratory route.


This review discusses the physics of magnetite-based magnetoreception and speculates about how magnetite crystals might be coupled to the nervous system.


This study provides some of the strongest and most direct experimental evidence for chemical magnetoreception. Using genetic techniques, the authors build a case that photoreceptive proteins known as cryptochromes are involved in magnetoreception in Drosophila.


This study presents data consistent with the possibility that some migratory birds also have a kind of magnetic map, although alternative possibilities cannot yet be ruled out.
