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11. Some antibiotics, for example the β-lactams, show a decrease in their bactericidal activity toward slow-growing cells (*25*). In our system, the rate of killing is independent of growth rate.
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17. It is thought that the bactericidal action of antibiotics in *Streptococcus pneumoniae* is related to the autolysin LytA (*29*). Recently, it was suggested that a two-component signaling system controls death in this organism (*30*). Other lysis pathways are also possible (*31*).
18. We do not think that YfgL is a lytic transglycosylase itself because it has no homology to any known lytic transglycosylase (*32*).
19. Incorporation of ^{14}C-labeled uridine diphosphate–*N*-acetylglucosamine (UDP-GlcNAc) into the peptidoglycan in membrane preparations of BE100 and the mutants was measured as described (*33*). The mutant strains were able to incorporate about 18% of the radiolabeled UDP-GlcNAc, whereas the wild-type strain incorporated only 5%. This could be due to increased activity of the transglycosylase enzymes or failure of the lytic transglycosylases to degrade peptidoglycan.
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Regional Magnetic Fields as Navigational Markers for Sea Turtles

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Young loggerhead sea turtles (*Caretta caretta*) from eastern Florida undertake a transoceanic migration in which they gradually circle the north Atlantic Ocean before returning to the North American coast. Here we report that hatchling loggerheads, when exposed to magnetic fields replicating those found in three widely separated oceanic regions, responded by swimming in directions that would, in each case, help keep turtles within the currents of the North Atlantic gyre and facilitate movement along the migratory pathway. These results imply 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.

Hatchling loggerhead sea turtles (*Caretta caretta*) from eastern Florida begin a long-distance migration immediately after entering the sea (*1*). Turtles swim from the Florida coast to the North Atlantic gyre, the circular current system surrounding the Sargasso Sea, and remain within the gyre for a period of years (*2–4*). During this time, they gradually migrate around the Atlantic before returning to the North American coast (*5, 6*).

For young loggerheads, conditions within the North Atlantic gyre are favorable for survival and growth, but straying beyond the latitudinal extremes of the gyre is often fatal (*2, 3*). As the northern edge of the gyre approaches Portugal, the east-flowing current divides. The northern branch continues past Great Britain and the water temperature decreases rapidly. Loggerheads swept north in this current soon die from the cold (*2–4*). Similarly, turtles that venture south of the gyre risk being swept into the South Atlantic current system and carried far from their normal range. An ability to recognize the latitudinal extremes of the gyre, and to respond by orienting in an appropriate direction, might therefore have adaptive value.

Previous experiments have shown that hatchling loggerheads can detect magnetic inclination angle (*7*) and field intensity (*8*), two geomagnetic features that vary across Earth's surface and could, in principle, provide positional information to a migrating turtle (*9, 10*). In these initial experiments, one of the two parameters was held constant while the other was varied. This approach was necessary to demonstrate that turtles can detect each field element. In nature, however, these field elements vary together across Earth's surface. Most pairings of inclination and intensity used in previous studies resulted in fields with combinations of parameters that do not naturally occur in the North Atlantic (*7*).

To determine whether hatchlings can distinguish among the magnetic fields actually found in different oceanic regions, we subjected hatchling loggerheads to fields replicating those found in three widely separated

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locations along their migratory route in the North Atlantic gyre. Turtles were tested in a circular, water-filled arena that was surrounded by a computerized coil system (*11*), which was used to control the magnetic field in which each turtle swam. Each hatchling was tethered to an electronic tracking unit that relayed the position of the turtle to a computer in an adjacent room (*11, 12*).

Turtles exposed to a field replicating one that exists offshore near northern Florida swam east-southeast (Fig. 1). Those exposed to a field like one found near the northeastern edge of the gyre swam approximately south. Turtles exposed to a field like one found near the southernmost part of the gyre swam west-northwest. All three groups were significantly oriented at $P < 0.05$ or less (Fig. 1). The Mardia-Watson-Williams test (*13*) indicated that significant differences existed between the three distributions ($W = 19.5$, $P < 0.001$). Thus, the results show that loggerhead turtles can distinguish among magnetic fields that exist in widely separated oceanic regions.

In addition, the orientation behavior elicited by each of the three fields is consistent with the interpretation that these responses have functional significance in the migration. Near northern Florida, orientation toward the east-southeast would lead turtles away from the North American coast and farther into the Gulf Stream. The Gulf Stream veers eastward soon after passing Florida; when it does, turtles positioned safely away from the gyre perimeter are presumably less likely to stray into fatally cold water that lies to the north. In the northeastern region of the gyre, the Gulf Stream divides. Southward orientation in this area is likely to help turtles remain in the gyre and avoid the North Atlantic Drift, the north-flowing current that can carry turtles into the cold oceanic regions of Great Britain and Scandinavia (*2–4*). Near the southernmost boundary of the gyre, orientation to the west-northwest is consistent with the migratory route of the turtles. Such orientation may prevent turtles from straying too far south and may also help them to remain in favorable currents that facilitate movement back toward the North American coast, where most Florida loggerheads spend their late juvenile years (*6*). We conclude that specific magnetic fields characteristic of widely separated oceanic regions elicit orientation responses that are likely to help turtles remain safely within the gyre and progress along the migratory route.

The hatchlings that we tested had never been in the ocean. Thus, our results also indicate that specific magnetic fields elicit orientation responses in turtles that have not had previous migratory experience. The ability to express a response upon the first encounter with a given field may be critical to young turtles, because those swept out of the gyre usually die before they can regain entry (*2–4*). Turtles probably cannot learn to recognize dangerous geographic areas, because entering such regions is in itself fatal.

One possible interpretation of the results is that hatchlings inherit a large-scale magnetic map (*14–16*) that enables them to continuously approximate their position anywhere in the North Atlantic. However, hatchlings might instead emerge from their nests programmed only to swim in specific directions if and when they encounter magnetic fields resembling those in a few crucial oceanic regions where the risk of displacement from the gyre is high. Thus, young turtles might remain within the gyre and advance blindly along their migratory route without any real conception of their geographic position and without the ability to determine their position relative to a goal. Such a system would not preclude the development of more sophisticated navigational abilities as the turtles mature or the possible involvement of additional cues and mechanisms in guiding the first migration.

From an evolutionary perspective, the responses that we have reported are not incompatible with either secular variation (*17*) or magnetic polarity reversals. As Earth's field gradually changes, strong selective pressure presumably acts to maintain an approximate match between the responses of hatchlings and the fields that mark critical geographic boundaries at any point in time (*18–20*). Although responses to regional fields might be rendered useless during occasional periods of rapid field change associated with magnetic polarity reversals or excursions (*21*), these sporadic events do not preclude the evolution of magnetic responses during the intervening and usually much longer intervals when Earth's field changes more slowly and is relatively stable (*22*).

Irrespective of these considerations, our results provide direct evidence that young sea turtles can in effect exploit regional magnetic fields as open-ocean navigational markers. The turtles emerge from their nests ready to respond to specific fields with directed movement; these responses are appropriate for keeping young turtles within the gyre system and facilitating movement along the migratory route. Such couplings of directional swimming to a regional field may provide the building blocks or "subroutines" (*23*) from which natural selection can sculpt a sequence of responses capable of guiding first-time ocean migrants along complex migratory routes. Similar mechanisms might function not only in sea turtles but in diverse ocean migrants such as fish and marine mammals, as well as in some migratory birds (*24, 25*).

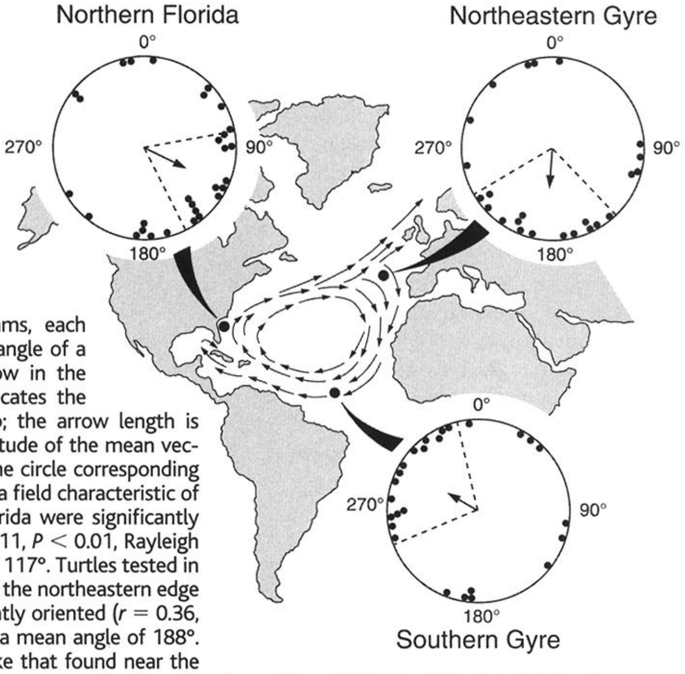

Fig. 1. Orientation of hatchling loggerheads in magnetic fields characteristic of three widely separated locations (marked by black dots) along the migratory route. Generalized main currents of the North Atlantic gyre are represented on the map by arrows [modified from (*2, 30, 31*)]. In the orientation 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 arrow length is proportional to the magnitude of the mean vector **r**, with the radius of the circle corresponding to $\mathbf{r} = 1$. Turtles tested in a field characteristic of the coast of northern Florida were significantly oriented ($r = 0.42$, $Z = 5.11$, $P < 0.01$, Rayleigh test) with a mean angle of 117°. Turtles tested in a field like that found near the northeastern edge of the gyre were significantly oriented ($r = 0.36$, $Z = 3.13$, $P < 0.05$) with a mean angle of 188°. Turtles tested in a field like that found near the southern boundary of the gyre were significantly oriented ($r = 0.35$, $Z = 3.20$, $P < 0.05$) with a mean angle of 297°. Dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north.

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11. The coil system consisted of two different coils arranged orthogonally (*7*). Each coil measured 2.27 m on a side and was constructed in accordance with the four-coil design of Merritt *et al.* (*26*). Turtles were restricted to an area in the center of the coil defined by a horizontal circle of radius 25 cm and a vertical area of about 5 cm; in this region, calculated (*26, 27*) and measured deviations from perfect field uniformity were less than 1%. For details about the coil, arena, and tracking system, see *Science* Online (www.sciencemag.org/cgi/content/full/294/5541/364/DC1).
12. Methods were described in detail in (*7*). Briefly, hatchlings were collected from their nests on the night when they would otherwise have emerged. Each was tethered in the arena and permitted to swim for 10 to 30 min in the field of the natal beach (inclination 57.5°, intensity 47 μT) toward a dim light in the east, a process that serves to set the initial offshore magnetic heading of the turtles (*28*). The light was then turned off and the field immediately changed to one of the three experimental fields (see below). After an acclimation period of 3 min, a computer monitored the direction toward which each turtle swam in darkness under the new field condition (*7*). Each turtle was tested only once under one of the three field conditions; no more than four turtles from the same nest were tested in any given field. The field used to approximate magnetic conditions near northern Florida had an inclination of 59.3° and a total intensity of 49.1 μT (as assessed by five independent measurements with a Schoenstedt digital fluxgate magnetometer, model DM-2220 R). The field used to approximate conditions in the northeastern gyre had an inclination of 59.1° and an intensity of 45.2 μT; the field simulating the southern border of the gyre had an inclination of 16.7° and an intensity of 31.0 μT. The experimental fields were selected on the basis of estimates provided by the International Geomagnetic Reference Field (IGRF) model, 1995 revision, for July and August 1995 (when the data were collected) using latitude 29.0°N, longitude 80.0°W for northern Florida; 43.0°N, 20.0°W for the northeastern gyre region; and 10.0°N, 39.0°W for the southern gyre boundary. The field measured within the arena was within ±0.4° (inclination) and ±0.4 μT (intensity) of the IGRF estimates for each target location. The IGRF declination estimates for the target locations were −5.2° for northern Florida, −10.4° for the northeastern gyre, and −18.7° for the southern gyre. Experiments were conducted in Boca Raton, Florida (declination estimate = −4.6°).
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Neuroanatomy of Magnetoreception: The Superior Colliculus Involved in Magnetic Orientation in a Mammal

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The neural substrate subserving magnetic orientation is largely unknown in vertebrates and unstudied in mammals. We combined a behavioral test for magnetic compass orientation in mole rats and immunocytochemical visualization of the transcription factor c-Fos as a marker of neuronal activity. We found that the superior colliculus of the Zambian mole rat (*Cryptomys anselli*) contains neurons that are responsive to magnetic stimuli. These neurons are directionally selective and organized within a discrete sublayer. Our results constitute evidence for the involvement of a specific mammalian brain structure in magnetoreception.

Behavioral studies have provided abundant evidence for magnetic compass orientation among vertebrates, but its sensory and neural basis remains enigmatic (*1, 2*). A few electrophysiological studies have addressed the involvement of a specific brain structure in the processing of magnetic information (*3–9*). This method, however, has a particular drawback: It does not allow systematic screening of neuronal activities in the central nervous system. Therefore, well-aimed electrophysiological studies cannot be conducted in the absence of a known receptor site. Here, we investigated magnetoreception by combining two established methodological approaches: a behavioral test designed to assess magnetic compass orientation in mole rats (*10, 11*) and immunocytochemical visualization of the transcriptional regulatory protein c-Fos as a marker of neuronal activity, a neuroanatomical technique used extensively in sensory research (*12–14*).

We detected the evoked expression of c-Fos in order to map neuronal activities that had been entrained either by active orientation via the magnetic compass or by changes in the ambient magnetic field. Experimental animals built nests in an unfamiliar arena [i.e., performed a magnetically based spatial orientation task (*15*)] under different test conditions (*16*). Controls (used also to assess basal levels of c-Fos expression) were of two types: (i) untreated animals freely moving within a familiar home area, and (ii) animals resting or sleeping in a shielded magnetic field. We focused on neuronal activities in the superior colliculus (SC), a prominent subcortical sensorimotor integrator that plays an important role in orientation to diverse stimuli (*17–19*). The unique intrinsic circuitry of the SC (*20*) may serve to integrate magnetic information with multimodal sensory and motor information. Magnetic stimuli thus may directly elicit orientation responses via initiation of activity in the premotor efferent collicular pathways.

The SC in all of the experimental and control animals displayed a symmetrical

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