

Magnetic Orientation and Navigation in Marine Turtles, Lobsters, and Molluscs: Concepts and Conundrums¹

SHAUN D. CAIN,² LARRY C. BOLES, JOHN H. WANG, AND KENNETH J. LOHMANN

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599

SYNOPSIS. The Earth's magnetic field provides a pervasive source of directional information used by phylogenetically diverse marine animals. Behavioral experiments with sea turtles, spiny lobsters, and sea slugs have revealed that all have a magnetic compass sense, despite vast differences in the environment each inhabits and the spatial scale over which each moves. For two of these animals, the Earth's field also serves as a source of positional information. Hatchling loggerhead sea turtles from Florida responded to the magnetic fields found in three widely separated regions of the Atlantic Ocean by swimming in directions that would, in each case, facilitate movement along the migratory route. Thus, for young loggerheads, regional magnetic fields function as navigational markers and elicit changes in swimming direction at crucial geographic boundaries. Older turtles, as well as spiny lobsters, apparently acquire a "magnetic map" that enables them to use magnetic topography to determine their position relative to specific goals. Relatively little is known about the neural mechanisms that underlie magnetic orientation and navigation. A promising model system is the marine mollusc *Tritonia diomedea*, which possesses both a magnetic compass and a relatively simple nervous system. Six neurons in the brain of *T. diomedea* have been identified that respond to changes in magnetic fields. At least some of these appear to be ciliary motor neurons that generate or modulate the final behavioral output of the orientation circuitry. These findings represent an encouraging step toward a holistic understanding of the cells and circuitry that underlie magnetic orientation behavior in one model organism.

INTRODUCTION

Perceived through human senses, the environment beneath the ocean's surface is often a murky, disorienting, and nearly featureless realm. Relative to air, visibility in the sea is greatly diminished by turbidity and the increased scattering of light. Visual landmarks are seldom present, and except under unusually clear conditions in shallow areas, celestial cues such as skylight polarization patterns, or the position of the sun and stars, cannot be perceived (Shashar *et al.*, 2004). To humans, the idea of holding a consistent heading under such conditions, let alone navigating with precision from one distant location to another, appears impossible without specialized equipment. Yet more than 70 percent of the Earth's surface is covered by ocean, and numerous marine animals move about from place to place during both day and night, often with remarkable precision and over long distances.

For anyone who has been diving in deep waters, it is tempting to conclude that there are fewer orientation cues available in the ocean than on land. However, although our own senses are not optimized to detect stimuli in the marine environment, it does not follow that animals that have evolved in the sea have the same limitations, or that environmental cues imperceptible to us are not readily detected by other species. Studies have revealed diverse and sometimes unexpected sen-

sory abilities in marine animals. For example, hatchling sea turtles exploit ocean waves as an orientation cue and determine wave propagation direction by detecting sequences of accelerations (Lohmann and Lohmann, 1992; Lohmann *et al.*, 1995b). Sharks have an acute electric sense with which they can detect prey (Kalmijn, 1971), dolphins can detect characteristics of objects from a distance using ultrasonic echolocation (Harley *et al.*, 2003), and crabs perceive water depth by sensing water pressure (Fraser and Macdonald, 1994). Thus, the challenge of investigating orientation and navigation in the ocean is to attempt to perceive the marine environment not through our own sensory systems, but through the sensory modalities of the animals that live there.

Among a number of sensory cues potentially available in the ocean, the Earth's magnetic field is a particularly pervasive environmental feature (Skiles, 1985). In contrast with most other cues, the field is present night and day, is largely unaffected by weather and season, and exists in all parts of the ocean, from shallowest to deepest. Thus, it is perhaps not surprising that a number of ocean animals have evolved the ability to derive useful directional and/or positional information from the Earth's magnetic field (Wiltschko and Wiltschko, 1995a). Here we highlight recent findings about the magnetic orientation, navigation, and neuroethology of three well-studied but phylogenetically diverse marine animals: the loggerhead sea turtle *Caretta caretta*, the spiny lobster *Panulirus argus*, and the sea slug *Tritonia diomedea*. Despite vast differences in behavior, habitat, and the distances over which each travels, all of these animals depend at least partly on the Earth's magnetic field to guide their movements.

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² Present address: Friday Harbor Laboratories, University of Washington, 620 University Rd., Friday Harbor, Washington 98250; E-mail: crabboy@u.washington.edu

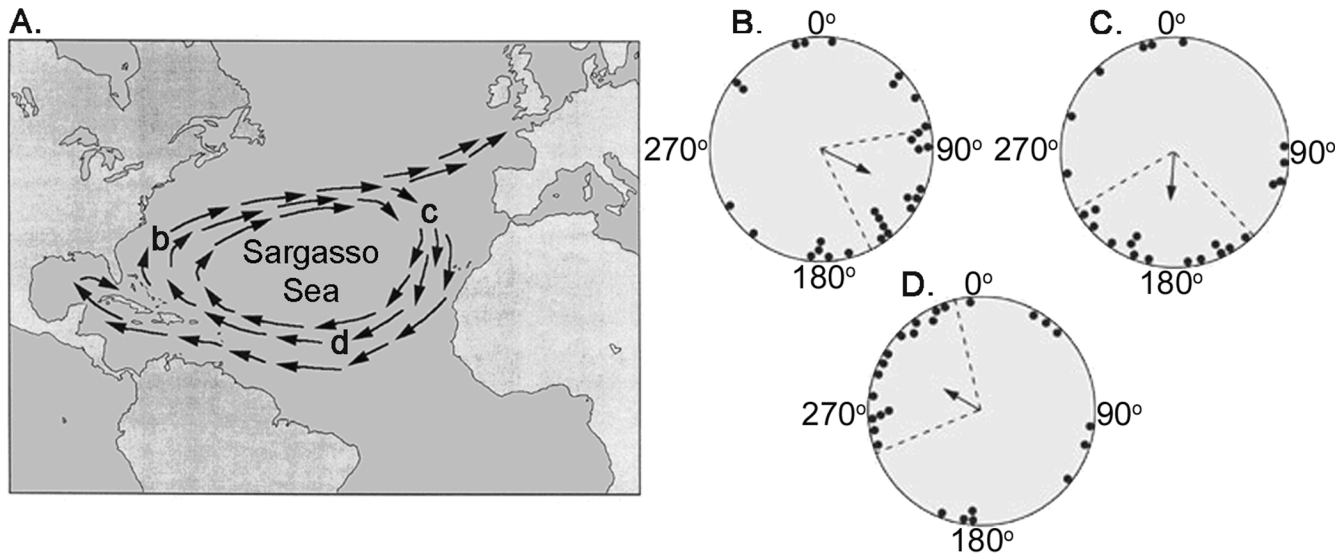


FIG. 1. A. The circum-Atlantic migration of young loggerhead turtles. Dark arrows on the map represent generalized currents of the North Atlantic Gyre. B–D. The orientation of hatchling turtles tested in magnetic fields from the three locations marked by letters on the map. Each dot within the orientation circles represents the average swimming direction of an individual hatchling. The arrow within each circle represents the mean heading of the group and the dashed lines represent the 95% confidence interval for the mean. Adapted from Lohmann *et al.* (2001).

DIRECTIONAL AND POSTIONAL INFORMATION IN THE EARTH'S MAGNETIC FIELD

At least two different types of information can potentially be derived from the Earth's magnetic field. Directional or compass information enables an animal to maintain a consistent heading in a particular direction such as north or east. Positional, or "map" information as it is sometimes called, assists an animal in assessing its geographic position, so that it can move in an appropriate direction along a migratory route or toward a specific destination such as a home area.

Magnetic compasses are known to exist in diverse animals (Wiltschko and Wiltschko, 1995a), and the list of marine animals known to possess such compasses now includes sharks (Kalmijn, 1978), spiny lobsters (Lohmann *et al.*, 1995a), sea turtles (Lohmann, 1991; Lohmann and Lohmann, 1993), isopods (Ugolini and Pezzani, 1995), and salmon (Quinn *et al.*, 1981). Much less is known about the use of magnetic positional or map information. During the past decade, however, evidence has accumulated that at least two marine animals, sea turtles and spiny lobsters, are able to derive positional information from the Earth's field.

Hatchling sea turtles and regional magnetic fields

Young loggerhead sea turtles (*Caretta caretta*) perform one of the longest and most spectacular marine migrations. Hatchlings along beaches of the east coast of Florida, U.S.A., emerge from nests, scramble across the beach to the sea, and migrate offshore to the Gulf Stream and North Atlantic gyre, the circular current system that encircles the Sargasso Sea (Fig. 1a; Carr, 1986; Lohmann and Lohmann, 2003; Musick and Limpus, 1997). Young loggerheads evidently remain for at least several years in the gyre system, during

which time many cross to the eastern side of the Atlantic Ocean (Bolten *et al.*, 1993, 1998) before returning to the waters of the southeastern United States to take up residence in coastal feeding grounds (Carr, 1987; Sears *et al.*, 1995; Musick and Limpus, 1997).

The waters of the North Atlantic gyre provide a favorable, food-rich environment for young turtles, but straying beyond the latitudinal extremes of the gyre is often fatal. 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 (Carr, 1986, 1987; Hays and Marsh, 1997). Similarly, turtles that venture south of the gyre may be swept into the South Atlantic current system and transported 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 considerable adaptive value.

How might a young turtle with no previous experience in the ocean determine when it is approaching the northern and southern boundaries of the gyre? Several features of the Earth's magnetic field vary in a predictable way across the surface of the Earth and might, in principle, be used in position-finding (Skiles, 1985; Lohmann *et al.*, 1999). For example, at each location on the globe, the geomagnetic field lines intersect the Earth's surface at a specific angle of inclination. Because inclination angle varies with latitude, an animal able to distinguish between different field inclinations might be able to approximate its latitude (Skiles, 1985; Lohmann *et al.*, 1999). Experiments have revealed that hatchling loggerheads can indeed distinguish between different inclination angles (Loh-

mann and Lohmann, 1994). They can also distinguish between different field intensities corresponding to those that they encounter in different locations along their migratory route (Lohmann and Lohmann, 1996). Thus, hatchling loggerheads evidently emerge from their nests already capable of detecting two different magnetic field elements that vary across the Earth's surface and might provide positional information useful in guiding a long-distance migration.

To investigate further whether loggerheads can exploit positional information inherent in the Earth's magnetic field, hatchlings were subjected to fields replicating those found in three widely separated locations along the perimeter of the North Atlantic Gyre (Fig. 1a; Lohmann *et al.*, 2001). Turtles tested in a magnetic field replicating one that exists offshore near northern Florida swam east-southeast (Fig. 1b). Those exposed to a field like one found near the northeastern edge of the gyre swam approximately south (Fig. 1c). Turtles exposed to a field replicating one found near the southernmost part of the gyre swam west-northwest (Fig. 1d). Thus, the results demonstrate 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 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 (Carr, 1986, 1987; Hays and Marsh, 1997). 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 remain in favorable currents that facilitate movement back toward the North American coast, where most Florida loggerheads spend their late juvenile years (Musick and Limpus, 1997).

Thus, 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 results imply that young loggerheads in effect exploit such fields as navigational markers.

Magnetic navigation of spiny lobsters

The finding that young sea turtles use regional magnetic fields as navigational markers demonstrates that animals can exploit positional information in the Earth's field during long-distance migrations. Recent

results, however, suggest that magnetic field information can also be used in position-finding by marine animals that move over much smaller distances.

The Caribbean spiny lobster, *Panulirus argus*, lives on hard bottoms and coral reefs throughout the waters of the Caribbean and the southeastern United States. *P. argus* is a nocturnal forager and spends the day protected within crevices and holes (Herrnkind, 1980). During nightly foraging trips, lobsters often travel significant distances from the den, and at the end of the trip return either to the same den or another one nearby (Herrnkind and McLean, 1971; Herrnkind, 1980). Tag and recapture studies have shown that lobsters are capable of homing after being displaced several kilometers from a capture site (Creaser and Travis, 1950).

Spiny lobsters have a magnetic compass sense (Lohmann *et al.*, 1995a), but the apparent ability of these animals to return to specific areas after experimental displacements suggests that they also have an ability to determine their position relative to a geographic target area. Animals are said to be capable of "true navigation" if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey (Phillips *et al.*, 1995; Phillips, 1996). Until recently, those few animals shown to possess true navigation were all vertebrates (Phillips *et al.*, 1995; Phillips, 1996). In contrast, those few invertebrates that had been carefully studied had been found to return to specific sites by using path integration, landmark recognition, compass orientation, and other mechanisms that cannot compensate for displacement into unfamiliar territory (Wehner, 1996; Wehner *et al.*, 1996; Wehner, 1998; Collett and Collett, 2000; Collett *et al.*, 2002; Graham and Collett, 2002).

Recent experiments, however, have clouded the tidy dichotomy that was once thought to exist between vertebrate and invertebrate navigational abilities. Spiny lobsters were found to orient reliably toward capture sites when displaced to unfamiliar sites over distances of 12–37 km, even when deprived of all known orientation cues *en route* (Fig. 2a; Boles and Lohmann, 2003). Thus, lobsters are the first invertebrates known to fulfill the criteria of true navigation.

Little is known about the sensory cues and mechanisms that underlie true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field that exists north of the capture site oriented southward, whereas those tested in a field like one that exists south of the capture site oriented northward (Fig. 2b; Boles and Lohmann, 2003). These results provide strong evidence that spiny lobsters possess a magnetic positioning system that is capable of helping them navigate to specific geographic areas. Thus, true navigation in lobsters, and perhaps in other animals, may be based at

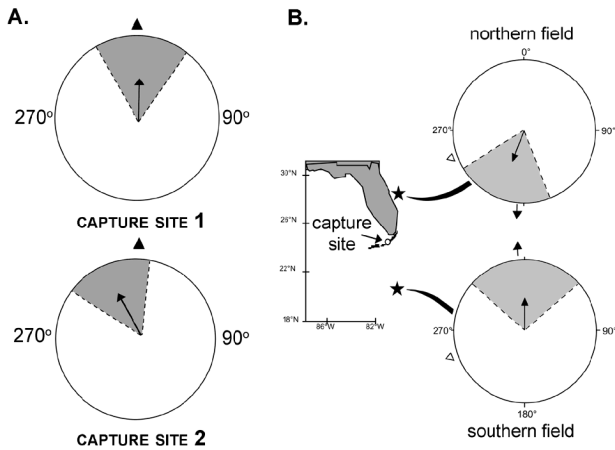


FIG. 2. **A.** The orientation of displaced spiny lobsters. Lobsters were captured from one of two sites (capture sites 1 and 2, indicated by CS1 and CS2) and their orientation behavior tested at one of two test sites (TS1 and TS2). Lobsters captured at CS1 were tested at TS1 only. Animals from CS1 were tested at TS1 and TS2. In each orientation diagram, each dot represents the mean heading of one lobster, the arrow represents the mean heading of the group and the dashed lines represent the 95% confidence interval for the mean angle. Dark arrows outside each circle indicate the heading from the test site to the capture site. In all cases, the lobsters oriented in a direction that coincided approximately with the bearing to the capture site. **B.** The orientation of lobsters tested in magnetic fields replicating the fields that exist at two distant locations (marked by stars on the map). Lobsters were captured at CS2 on Figure 2A, a location indicated by the tip of the arrow in Figure 2B, and then transported to TS 1 on Figure 2A (the small open circle on Fig. 2B). Lobsters tested in a field characteristic of a location north of the test site oriented approximately southward, whereas those exposed to a field that exists south of the test site oriented northward. The dark arrows on the outside of each orientation diagram indicate the direction in which lobsters would be expected to orient if homing from each fictive location. The open triangle outside each orientation diagram indicates the actual direction to the capture site from the test site. In each case, lobsters responded as if they had been displaced to the locations marked by the stars rather than by orienting in the direction that was actually towards the capture site. From Boles and Lohmann (2003).

least partly on a magnetic map sense. Indeed recent experiments with sea turtles have suggested that, as these animals mature, they become capable of true navigation (Avens *et al.*, 2003; Avens and Lohmann, 2004) and acquire a magnetic map similar to the one used by lobsters (Lohmann *et al.*, 2004).

NEURAL MECHANISMS OF MAGNETIC ORIENTATION IN *TRITONIA DIOMEDEA*

Despite our growing understanding of how animals use the Earth's magnetic field, little is known about the neural mechanisms that underlie magnetic orientation behavior (Deutschlander *et al.*, 1999; Lohmann and Johnsen, 2000). One factor that has complicated such analyses is that most magnetic orientation research has focused on vertebrate animals (Phillips, 1986; Beason and Semm, 1987; Lohmann, 1991; Wiltschko and Wiltschko, 1991, 1995a; Able and Able, 1995). Although several vertebrates have proven to be excellent subjects for behavioral experiments, the complexity of the vertebrate nervous system makes

cellular-level investigations of neural circuitry challenging.

One animal model system that appears particularly promising for studies of the neural circuitry underlying magnetic orientation behavior is *Tritonia diomedea*, a nudibranch mollusc. Behavioral experiments have demonstrated that this animal orients to the Earth's magnetic field (Lohmann and Willows, 1987) in the lab, and field displacement experiments suggest that they use magnetic orientation to guide themselves between shallow and deeper areas (Willows, 1999). In addition, the central nervous system is relatively simple, consisting of approximately 7,000 neurons in six fused ganglia (Boyle *et al.*, 1983). Many of these neurons can be identified individually on the basis of color, size, and location within the central ganglia (Fig. 3a). Moreover, the nervous system is readily accessible for electrophysiological recordings both in semi-intact and isolated brain preparations (Willows *et al.*, 1973).

Intracellular electrophysiological recordings have demonstrated that three bilaterally symmetric pairs of identifiable neurons respond with altered electrical activity to changes in earth-strength magnetic fields (Lohmann *et al.*, 1991; Wang *et al.*, 2003, 2004). Two of these pairs, known as the Pd5 and Pd6 neurons, are excited by changes in direction of the ambient magnetic field (Lohmann *et al.*, 1997; Popescu and Willows, 1999; Wang *et al.*, 2003). The third pair, known as the Pd7 neurons, is inhibited by the same magnetic stimuli that excite Pd5 and Pd6 (Wang *et al.*, 2004). All six of the magnetically responsive cells (LPd5, RPd5, LPd6, RPd6, LPd7, and RPd7) presumably function in the neural circuitry underlying magnetic orientation behavior.

The function of the Pd5 and Pd6 neurons

Recent anatomical, electrophysiological, and immunochemical analyses have provided insight into the roles that some of these neurons are likely to play (Popescu and Willows, 1999; Wang *et al.*, 2003; Cain *et al.*, in review). Both Pd5 and Pd6 have neurites that branch extensively within the pedal ganglia, as well as peripheral branches (axons) of the primary neurite that enter ipsilateral pedal nerves (Lohmann *et al.*, 1991; Wang *et al.*, 2003). These peripheral axons appear to innervate parts of the ipsilateral foot epithelium (Fig. 3b; Wang *et al.*, 2003; Cain *et al.*, in review). Action potentials carried by these axons propagate from the CNS to the peripheral tissues (Wang *et al.*, 2003; Cain *et al.*, in review).

Pd5 and Pd6 are large cells (often >400 μm) and appear white under epi-illumination. Both of these features are characteristic of neurons that produce peptide neurotransmitters (Snow, 1982). A previously unknown group of three neuropeptides (TPeps) has been isolated from the cell bodies of Pd5 and Pd6 using HPLC (Fig. 4a; Lloyd *et al.*, 1996). These peptides localize to the foot tissues innervated by the nerves containing axons of Pd5 and/or Pd6 (Fig. 4b; Willows *et al.*, 1997). Moreover, these peptides are found in

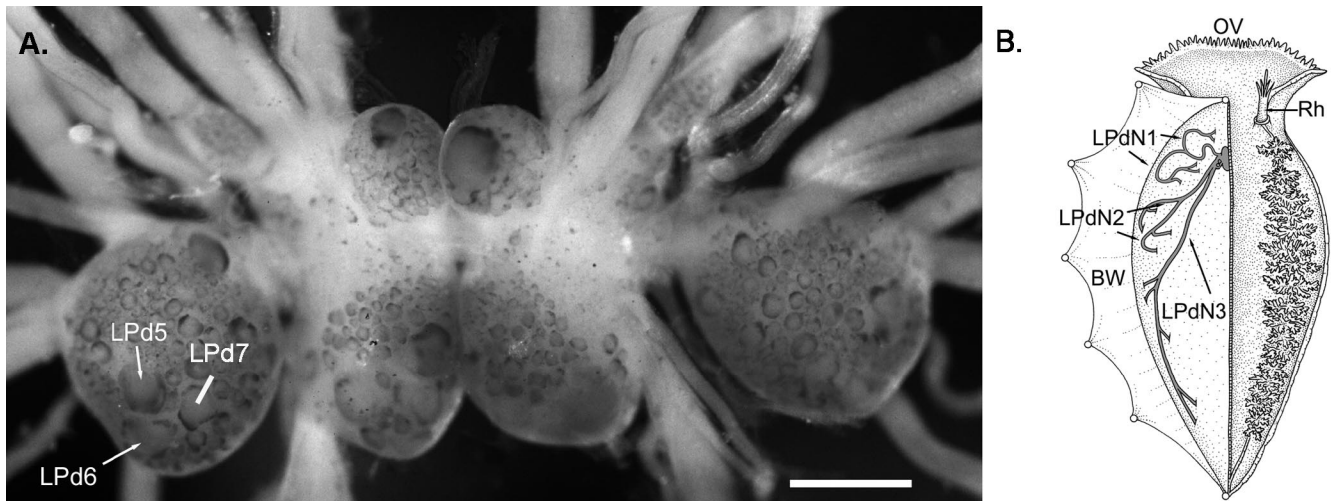


FIG. 3. **A.** The dorsal surface of the fused central ganglia of *T. diomedea*. Many large, individually identifiable neurons are visible on the surface of the brain. Three of these cells, LPd5, LPd6, and LPd7, are labeled. Scale bar = 1 mm. **B.** Schematic representation of the innervation patterns of the left pedal nerves 1, 2, and 3. LPdN1 and LPdN2 contain axons from LPd6. LPdN2 and LPdN3 contain axons from LPd5. All three nerves innervate the lateral body wall (BW) and the ciliated pedal epithelium. OV = oral veil, Rh = rhinophore.

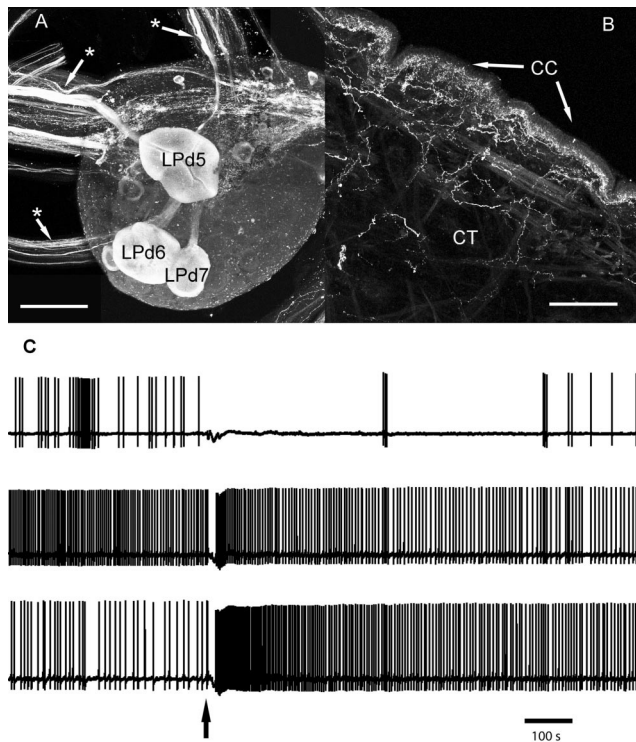


FIG. 4. **A.** TPeP labeling of the CNS. The left pedal ganglion contains TPeP-immunoreactive cell bodies and neurites. Immunoreactive axons are visible in the pedal nerves (*). Scale bar = 500 μ m. **B.** TPeP labeling of the foot. The ciliated foot epithelium (the tissue was sectioned transverse to the ciliated surface) contains TPeP-immunoreactive processes throughout the connective tissue (CT) with dense labeling near the proximal surface of the ciliated cells (CC). Scale bar = 60 μ m. **C.** Simultaneous recordings of the LPd5, LPd6, and LPd7 before, during, and after a swim bout. The black arrow indicates when the swim stimulus was applied to the animal.

dense-cored synaptic vesicles within neurites throughout the foot epithelium (Cain *et al.*, in review).

These findings indicate that the Pd5 and Pd6 are peptidergic, efferent neurons that are likely to function in generating or modulating the motor output of the magnetic orientation circuitry. Although the precise role of these cells has not been determined, three major types of effector cells in the periphery of *Tritonia* might plausibly be affected by TPePs released from the Pd5 and Pd6 cells: muscles, cilia, and mucus glands.

The muscles of the foot generate dorsal and ventral flexions during the escape swim and also help turn the animal during mucociliary crawling (Willows *et al.*, 1973). At the onset of swimming, both the Pd5 and the Pd6 neurons burst briefly, but then remain inactive for the duration of the swim (Fig. 4c). This pattern of activity implies that these cells are not directly involved in producing the dorsal and ventral flexions that comprise swimming. Similarly, neither intracellular stimulation of Pd5 or Pd6 nor direct application of TPePs to isolated foot patches results in discernable muscle contraction (Willows *et al.*, 1973; S.D.C., unpublished). Thus, at present, no evidence exists to suggest that the Pd5 or Pd6 neurons control muscle contraction.

The Pd5 and Pd6 cells do, however, appear to control or modulate the activity of ciliated cells (Popescu and Willows, 1999; Wang *et al.*, 2003; Cain *et al.*, in review). A dense field of cilia covers the pedal epithelium and propels the animal forward during mucociliary crawling, the primary mode of locomotion in this animal (Audesirk, 1978a, b). Application of TPePs to isolated foot patches or to isolated ciliated cells results in increased ciliary activity (Willows *et al.*, 1997). In addition, increases in electrical activity in the Pd5 cells are correlated with increases in muco-ciliary transport

across the foot (Popescu and Willows, 1999). These findings suggest that the role of the Pd5 and Pd6 neurons is cilio-motor in nature.

The precise mechanism by which TPeps increase ciliary beating and ciliary transport rate is not known. Both processes are tightly coupled to mucus secretion, as mucus provides the viscous environment in which the cilia beat (Denny, 1981). Thus, whereas one possibility is that TPeps act directly on cilia to increase their beat frequency, another is that Pd5 and Pd6 influence crawling by altering the amount or types of mucus being secreted. The two possibilities are not mutually exclusive, and clear evidence for either has not yet been obtained.

The function of the Pd7 neurons

Despite some morphological similarities between the Pd7 neurons and the Pd5/Pd6 (*i.e.*, large size, whitish cell body, location in the pedal ganglia), the function of the Pd7 cells may differ from that of the other two pairs of magnetically responsive neurons (Figs. 3a and 4a; Wang *et al.*, 2004). Unlike the Pd5 and Pd6 neurons, the Pd7 cells are inhibited by rotations of the ambient magnetic field. The neurites of Pd7 extend to the cerebral ganglia and one large axon projects from the brain to the anterior tissues through cerebral nerve 3. Action potentials in the Pd7 neuron propagate from the central ganglia toward the periphery (Wang *et al.*, 2004). The target cells to which the Pd7 project have not yet been determined, but the nerves that contain Pd7 axons innervate areas near the mouth, oral veil, and rhinophores (Willows *et al.*, 1973).

Although the function of the Pd7 neurons is not known, one possibility is that these cells control or modulate some subtle aspect of turning or locomotion that occurs during magnetic orientation behavior. For example, the cells might play a role in controlling movements of the oral veil, rhinophores, or other anterior structures as the animal alters or maintains its heading.

An alternative possibility is that the Pd7 neurons function in suppressing behavior that might otherwise impede orientation or locomotion. It is noteworthy that, during the period immediately after an escape swim when *Tritonia* normally crawls vigorously (Audesirk and Audesirk, 1980), spiking in the Pd7 neurons is greatly reduced relative to pre-swim levels (Fig. 4c). In contrast, spiking in the Pd5 and Pd6 increases after an escape swim (Fig. 4c). An interesting speculation is that the Pd7 neurons might modulate cilia that line the esophagus and are involved in feeding, and that feeding is suppressed during magnetic orientation and after swimming. At present, however, no evidence exists to support or refute this scenario, and additional research will be needed to determine the function of the Pd7 cells.

In summary, a reasonable working hypothesis is that the Pd5 and Pd6 neurons are involved in controlling or modulating the motor output of the magnetic orientation circuitry. These neurons appear likely to in-

fluence the ciliary beat rate of the foot epithelium and may therefore play a role in helping the animal align itself with a particular magnetic direction, crawl along a particular heading, or both. The function of the Pd7 neurons is less clear, but a possible role in suppressing behavior incompatible with orientation or locomotion is presently suspected.

As the search for neurons involved in the magnetic orientation circuitry expands, some logical targets for future investigation are neurons presynaptic to the Pd5, Pd6, and Pd7. Among these are neurons that have previously been identified as part of the *Tritonia* swim central pattern generator (DSIs, VSIs, C2), which also appear to mediate post-swim crawling by influencing Pd5 and Pd6 (Popescu and Frost, 2002). Therefore, this set of neurons might represent a multifunctional swim/crawl network as proposed by Popescu and Frost (2002). The relative simplicity of the *Tritonia* nervous system provides reason to hope that careful, sustained investigation will eventually lead to a thorough understanding of the neural circuitry underlying magnetic orientation behavior in this neuroethological model animal.

NEUROETHOLOGY OF MAGNETIC ORIENTATION BEHAVIOR

Aside from the neurobiological work done in *Tritonia* relatively few studies have attempted to investigate the neural mechanisms that underlie magnetic orientation behavior. Some initial progress has been reported with electrophysiological approaches in birds (Semm and Demaine, 1986; Beason and Semm, 1987; Semm and Beason, 1990; Semm and Schneider, 1991), mole rats (Marthold *et al.*, 1997; Nemeč *et al.*, 2001), and fish (Walker *et al.*, 1997). Nevertheless, much of what is known or assumed about the neural basis of magnetic orientation behavior has been inferred from behavioral experiments. The reliance on behavioral studies is understandable, given that primary magnetoreceptors have not yet been identified with certainty in any animal. Yet behavioral experiments can ultimately provide only limited insight into the myriad complex and often non-intuitive ways in which nervous systems detect sensory information, process it, and integrate it with other neural input to generate motor responses.

In parallel with behavioral experiments, several theoretical models of magnetoreception have been proposed to explain how animals might detect magnetic fields (Kalmijn, 1978; Kirschvink and Gould, 1981; Schulten and Windemuth, 1986; Ritz *et al.*, 2000, 2002). These models have been invaluable in guiding investigations of possible transduction mechanisms. At the same time, receptor mechanisms (whatever they may be) represent only one small part of the neural processes that comprise magnetoreception. Surprisingly, none of the models proposed so far have considered the crucial role that higher-order processing typically plays in circuits involving sensory information. In all other sensory systems, signal processing results in sig-

nificant alterations in the neural information that is passed along at each step of a circuit (Kandel *et al.*, 1997). As a result, the neural activity that actually reaches neurons responsible for initiating or modulating behavior often bears little resemblance to the activity of receptor cells. Moreover, higher-order processing often acts as a filter that discards aspects of the sensory world that are not directly relevant to the task which must be performed.

Whereas higher-order mechanisms in vision and hearing have been studied extensively (Kandel *et al.*, 1997), such mechanisms have received little attention in the context of magnetoreception. Nevertheless, the clear lesson to be drawn from other sensory systems is that filtering and feature extraction are often at least as important as receptor responses in shaping the motor outputs that comprise behavior. Thus, identifying areas of the brain that process magnetic field information, determining the role of centers known to be "responsive" to field stimuli, and studying how motor responses are generated are all as important as identifying receptor cells. Only by expanding studies to include higher order processing can the neural mechanisms that underlie magnetoreception and magnetic orientation behavior be fully understood.

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