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MAGNETITE AND MAGNETIC SENSITIVITY  
IN THE GREEN TURTLE, CHELONIA MYDAS

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## I. INTRODUCTION

### Green Turtle Migration

Migratory green sea turtles, Chelonia mydas, can accurately navigate in the open ocean over distances up to a few thousands of kilometers. Large-scale tagging projects have demonstrated that adult females of certain populations travel back and forth between feeding and breeding sites every two to four years, returning to the same nesting beach repeatedly (Carr and Carr 1970; Pritchard 1973; Balazs 1976). Indirect evidence suggests that the turtles are returning to their natal beaches (Carr 1967), and that the hatchlings born at these beaches then pilot themselves back to the adult feeding pastures; across enormous stretches of open ocean and without obvious landmarks to guide them.

The length of the journey from nesting site to feeding pasture varies among populations. Possibly the best-researched population, and one of the most far-ranging, is the Ascension Island turtle colony. This tiny island, only ten km in length, lies in the mid-Atlantic east of Brazil. Turtles nesting there must cross 2,000 km of open ocean from their feeding pastures along the coast of South America. Other populations that undertake long-distance migrations include those that nest on remote beaches in Costa Rica, the Gulf of Aden, South Africa, islands off Australia, and in the Northwestern Hawaiian Islands.

The migrations of the Hawaiian turtles are bi-directional and are therefore of particular interest. Hawaiian Chelonia are present throughout the Hawaiian Archipelago ( $19^{\circ}$ - $29^{\circ}$ N;  $155^{\circ}$ - $179^{\circ}$ W), but present-day breeding sites are confined to the low coral islands in the northwest. The only colonial breeding site now active is at French Frigate Shoals ( $24^{\circ}$ N  $160^{\circ}$ W), though islands to the northwest of French Frigate Shoals may occasionally host a few nesting females (Balazs 1976). Tagging studies conducted since 1973 by Balazs have demonstrated that reproductive migrations to French Frigate occur from both the low Northwestern Hawaiian Islands and the high, inhabited islands to the southeast. Carr and Coleman (1974) offered a sea-floor spreading theory to explain open sea migratory adaptations in Chelonia nesting at Ascension Island. Since Hawaiian turtles journey to feeding grounds in both the geologically older low islands in the northwest and in the younger, high, southeastern islands, this theory alone does not provide a complete explanation for the Hawaiian colony's migrations. At present there is no way of determining whether turtles hatching at French Frigate Shoals follow genetically-determined migration routes toward the islands where their parents have their feeding pastures. The adult populations north and south of French Frigate do not appear to be morphologically distinct from one another (Balazs 1976). In order for geographic distribution to be genetically determined by both parents, selective mating would have to occur at the breeding site, an unlikely event in view of the polygamous behavior observed by researchers. Hatchlings could, of course, inherit a geographic fix from the mother only.



Surface drift patterns compiled from average current measurements in the vicinity of the Hawaiian Archipelago indicate that some hatchlings may be carried from French Frigate Shoals close to the islands to the northwest merely by passive drifting (Balazs 1976). This likelihood is increased if turtles leave the hatching beaches in mid-summer, when the prevailing currents are of a more northerly set than during other seasons. The trip from the breeding ground to the high islands, however, would be against the average currents, and the hatchlings probably could not regularly accomplish it just by drifting. Hatchlings that travel toward the high islands therefore need some sort of navigational system, presumably based on sensory cues, to guide them, and as adults they must also use cues to find their way back to the breeding area.

The problems of open-ocean direction finding, as well as of animal orientation and navigation in general, have been studied extensively over the past two decades (Storm 1967; Galler, Schmidt-Koenig, Jacobs and Belleville 1972; Schmidt-Koenig and Keeton 1977; Gauthraux 1980). In particular, Carr and his students and associates have examined the problem of migration in Chelonia mydas (Carr 1965, 1967, 1972, 1975; Koch, Carr and Ehrenfeld 1969; Manton, Karr and Ehrenfeld 1972a,b; Carr and Coleman 1974). Hirth (1971) has suggested that green turtles employ several senses and a multiplicity of cues for navigation, possibly including a sun compass, celestial navigation, olfactory cues, perception of Coriolis force, inertial guidance, sonar sense, current

and wave pattern detection, polarized light detection, and a magnetic field sense. To date, few of these mechanisms have been examined experimentally. Ehrenfeld and Koch (1967) found that green turtles are extremely myopic when their eyes are out of water, thereby ruling out star navigation as a plausible mechanism. Manton et al. (1972a,b), using operant conditioning techniques, demonstrated acute olfactory sensitivity in juvenile green turtles, and suggested that turtles use their sense of smell to follow chemical gradients toward island nesting sites. Koch et al. (1969) discuss the many problems associated with using chemoreception for navigation, including the question of how an animal would detect concentration differences over time, and the problem of dilution over great distances. Balazs (1976) notes that, in Hawaii, direct use of chemical cues originating from the breeding site would not be available to those animals moving toward the site from the southeast, as they would be traveling in the direction of the prevailing currents.

Baldwin (1972) looked at the possibility of a geomagnetic sense by comparing the headings of adult turtles with a brass bar attached to the plastron versus those with a small bar magnet attached. His preliminary findings suggest that in deep water, where the bottom is not visible, sensing the magnetic field may be important in turtle orientation.

## Magnetic Sensing and Magnetite in Animals

Researchers have found evidence of sensitivity to magnetic cues in an increasing variety of organisms. Among the vertebrates, the list includes homing pigeons and migratory birds (Keeton 1974; Emlen 1975; Ossenkopp and Barbeito 1978), elasmobranch and teleost fishes (Kalmijn 1977; Tesch 1980; Walker, Dizon, and Kirschvink, unpublished manuscript), salamanders (Phillips 1977), woodmice (Mather and Baker 1981) and possibly humans (Baker 1981). The sensory apparatus that detects magnetic fields has not been definitely established. Yorke (1979, 1981), and Gould and Kirschvink (Gould 1980; Kirschvink and Gould 1981) have proposed that the magnetic mineral magnetite ( $\text{Fe}_3\text{O}_4$ ) could serve as the active element in a geomagnetic sensing system. Such a system could assist in local orientation as well as in long-distance migrations. Biogenic magnetite in magnetically-sensitive organisms was first found in mud bacteria (Blakemore 1975), honey bees (Gould, Kirschvink and Deffeyes 1978), and homing pigeons (Walcott, Gould and Kirschvink 1979).

The use of magnetite for magnetic orientation is most simply and clearly demonstrated by the bacteria. Magnetite-containing mud bacteria align with the earth's magnetic field, much like minute compass needles. When placed in a jar next to a bar magnet, they will swim "northward" (toward the south pole of the magnet), if they have been collected in the Northern Hemisphere. Blakemore hypothesized that the role of this response was to direct the bacteria down into the mud,

by following the geomagnetic inclination. Kirschvink (1980a) demonstrated that in the Southern Hemisphere bacteria seek south rather than north, which would also direct them downward.

Magnetite has recently been found in several pelagic species, including the Pacific dolphin (Zoeger, Dunn and Fuller 1981), blue marlin (Walker, Perry, Kirschvink and Dizon, manuscript in preparation) and yellowfin tuna (Walker, Dizon and Kirschvink). The last-cited study included behavioral experiments which demonstrated that tuna can sense changes in magnetic field strength. Magnetic material, possibly magnetite, was also found in hatchlings of the migratory loggerhead turtle (Kirschvink 1980b).

A magnetic field sensing capability could be important for green turtle migrations. This study provides evidence for a magnetic sense obtained from examining turtle specimens for the presence of magnetite and from behavioral experiments with juvenile turtles to test magnetic field discrimination.

## II. ISOLATION AND IDENTIFICATION OF MAGNETITE

### Materials and Methods

In the fall of 1980, more than 200 green turtle hatchlings were collected at French Frigate Shoals, Northwestern Hawaiian Islands. Those that died in captivity, and two adult specimens that had died in the wild, were used in magnetite isolation work.

Specimens of hatchling, juvenile, and adult green turtles were examined for magnetic remanence using the SQUID (superconducting quantum interference device) magnetometers at the Hawaii Institute of Geophysics and at the California Institute of Technology. To reduce the risk of contamination the magnetometer enclosure was thoroughly cleaned, and only non-magnetic instruments (chopsticks, glass knives) were used in all handling and dissection. Whole hatchlings and samples of tissue from all age classes were rinsed with glass-distilled water, and in some cases ultrasonicated, to insure that particles possibly adhering to tissue surfaces were removed. The samples were then frozen in liquid nitrogen (to reduce thermal noise) and saturated with a 3000 gauss cobalt/samarium magnet. Saturation isothermal remanent magnetism (sIRM) was measured in the SQUID. Background signal measurements were taken periodically for comparison with tissue signals, and to insure that the magnetometer chamber remained magnetically clean. Coercivities for dura mater and muscle tissues, which had remanence at

least an order of magnitude greater than background, were determined from alternating-field (AF) demagnetization.

For further analysis, magnetic material was extracted from the dura mater of six juveniles and one adult, and from facial muscle of the adult. The samples were ground with a teflon pestle, fats extracted with ether, and the remaining tissue repeatedly digested with filtered 5% sodium hypochlorite solution (household bleach) and centrifuged. These procedures were also carried out on muscle tissue from a skipjack tuna (Katsuwonus pelamis), previously found to be non-magnetic, to serve as a control. After repeated bleaching and centrifugation a residue containing minute black magnetic particles remained in the bottom of all turtle sample centrifuge tubes. No particles were found in the control tubes. The particles were washed in glass-distilled water, and pipetted either onto plugs for scanning electron microscopy (dura mater and muscle), or onto slides for X-ray diffraction and electron microprobe analysis (dura only). For SEM, particles were dried onto glass cover slips attached to the plugs with silver paste. The samples were then coated with a thin layer of gold and paladium. X-ray diffraction patterns were made from aggregated grains glued on slides with Duco cement and exposed for 80 hours to molybdenum K-alpha radiation. For electron microprobe analysis, aggregated particles were mounted in epoxy resin, polished, and coated with carbon. Magnetic remanence measurements on one adult turtle were carried out at the California Institute of Technology; all other analyses were done at Hawaii Institute of Geophysics.

## Results

Magnetic remanence was found in the head region of all turtles examined (Table 1). The greatest concentration of magnetic material occurred in the anterior portion of the dura mater, although it was also present diffusely throughout the facial muscle. SIRM in the adult duras was  $9 \times 10^{-6}$  electro-magnetic units (emu), about 50X background. Dura tissue was therefore the primary material examined in further tests, although facial muscle was also digested and its magnetic particles photographed under the SEM. Since no magnetic material was recovered from the tuna sample after digestion, it was concluded that the magnetic material isolated from turtle tissues originated within those tissues and was not inadvertently introduced during the extraction or measuring procedures.

Remanence was also found in whole hatchlings. When these were further dissected, the highest readings were obtained from the stomach; they probably came from magnetic particles present in sand and dirt ingested by the turtles. Remanence associated with surface tissues, such as carapace scutes, could be the result of external contamination and was therefore not measured separately or examined in subsequent tests.

The sIRM measured in the turtle is within the range of that found in other vertebrate species as recorded in the literature (Table 2). Adult turtles contained more magnetic material than juveniles, a

TABLE 1. -- Saturation isothermal remanent magnetism (sIRM) in three age classes of green turtles.

<u>Samples</u>	<u>emu</u>	
Whole hatchlings	$3.8 \times 10^{-6}$	
	$8.7 \times 10^{-6}$	
	$1.3 \times 10^{-5}$	
	$2.3 \times 10^{-5}$	
Hatchling heads	$1.4 \times 10^{-6}$	
	$1.6 \times 10^{-6}$	
Hatchling necks	$7.0 \times 10^{-8}$	
	$8.3 \times 10^{-8}$	
Juvenile heads	$1.1 \times 10^{-6}$	
	$3.0 \times 10^{-6}$	
	$9.5 \times 10^{-6}$	
Juvenile flippers		
	front left	$3.7 \times 10^{-7}$
	front right	$2.8 \times 10^{-7}$
	rear left	$9.7 \times 10^{-7}$
	rear right	$6.3 \times 10^{-7}$
Adult brain	$3.2 \times 10^{-7}$	
	$6.0 \times 10^{-7}$	
Adult eyeball	$6.3 \times 10^{-7}$	
Adult facial muscle blocks		
	1x1x1 cm	$4.4 \times 10^{-7}$
	1x1x2 cm	$5.5 \times 10^{-7}$
	1x2x3 cm	$4.4 \times 10^{-6}$
	1x3x3 cm	$6.1 \times 10^{-6}$
Adult dura mater		
	posterior	$1.0 \times 10^{-6}$
		$1.5 \times 10^{-6}$
	anterior	$9.0 \times 10^{-6}$
		$9.2 \times 10^{-6}$
Empty sample holder	$4.2 \times 10^{-8} - 2.3 \times 10^{-7}$	

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TABLE 2. -- Summary of induced magnetic remanence in the heads of various vertebrates. For comparison, sIRM in the heads of adult green turtles measured  $0.4 - 9 \times 10^{-6}$  emu.

<u>Source</u>	<u>Animal</u>	<u>emu x 10<sup>-6</sup></u>
Presti & Pettigrew 1980	homing pigeon ( <u>Columba livia</u> )	1 - 15
	white-crowned sparrow ( <u>Zonotrichia leucophrys</u> )	1 - 8
	tree swallow ( <u>Irotoprocne bicolor</u> )	5
	western grebe ( <u>Aechmophorus occidentalis</u> )	9
	pintail duck ( <u>Anas acuta</u> )	6
Walker et al.	yellowfin tuna ( <u>Thunnus albacares</u> )	3
Mather & Baker 1981	woodmouse ( <u>Apodemus sylvaticus</u> )	1 - 6
Zoeger et al. 1981	Pacific dolphin ( <u>Delphinus delphis</u> )	20 (NRM)

Note: Natural magnetic remanence (NRM) is the net magnetic moment due to a preferential direction of alignment among the many individual magnets within a sample. Induced remanence (sIRM) is a measure of the total amount of magnetic material in a sample.

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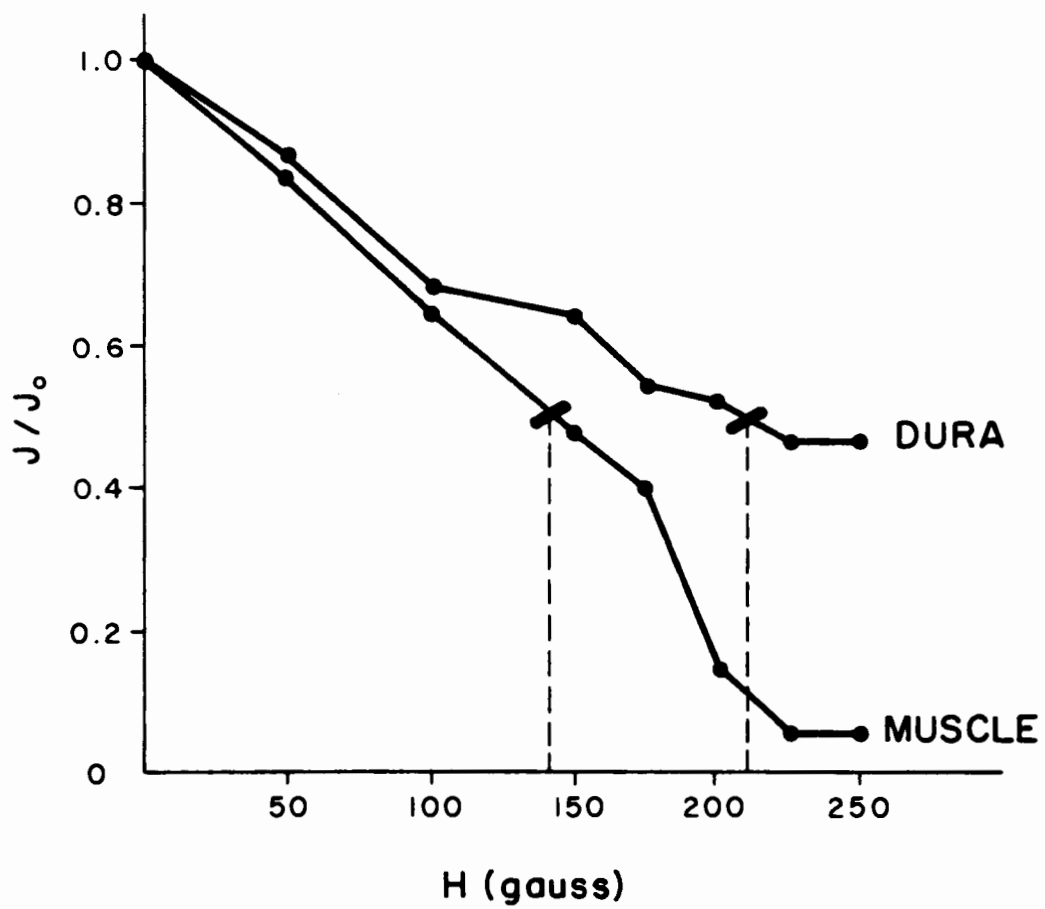
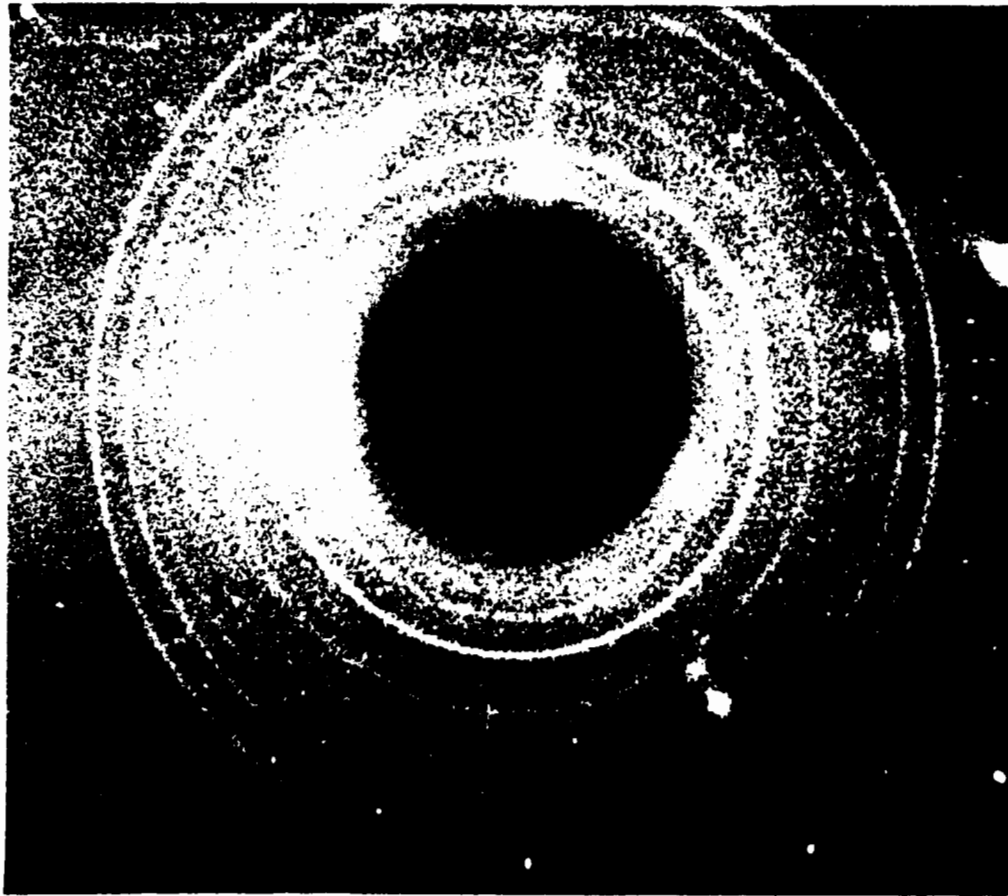


FIGURE 1. -- Alternating field demagnetization of dura mater and muscle tissue magnetic remanence. Abbreviations:  $J_0$ , initial magnetic moment;  $J$ , magnetic moment after demagnetization; and  $H$ , magnetic field (alternating). Bars mark median destructive field strength.

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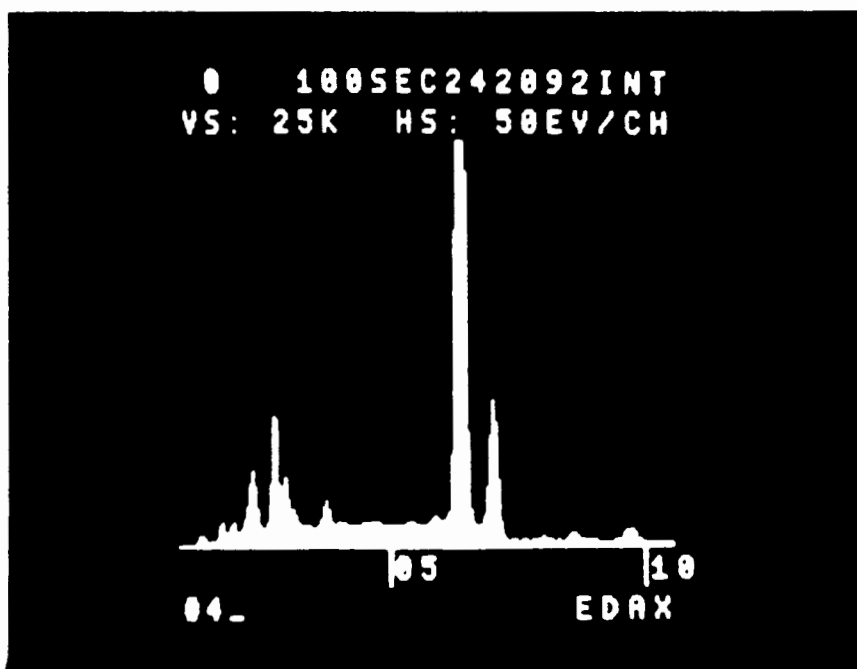
FIGURE 2. -- X-ray diffraction pattern from green turtle dura mater sample.

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phenomenon also observed in honey bees (Gould et al. 1978), yellowfin tuna (M. Walker, personal communication), and woodmice (J. Mather, personal communication.). Remanence in the dura was found from AF demagnetization to be magnetically hard, or stable, while that in the facial muscle was somewhat softer (Figure 1). The median unblocking field for net magnetic alignment in the dura was approximately 225 gauss, which indicates that single-domain magnetite crystals are present in the dura samples (Kirschvink and Lowenstam 1979). The gradual slopes of both curves indicate that some multi-domain crystals are also present.

The X-ray diffraction pattern produced by aggregated grains is shown in Figure 2. The pattern obtained is that expected for magnetite. The lattice spacing parameter estimate calculated from this pattern was  $8.375 \pm 0.04 \text{ \AA}$ , which compares well to the reference lattice parameter for magnetite of  $8.396 \text{ \AA}$ . Relative intensities of rings in the pattern, specific for each crystal type, also closely match the reference intensities (Joint Committee on Powder Diffraction Studies 1974).

Electron microprobe analysis revealed that the extracted particles were very rich in iron and contained no measurable titanium or chromium, which generally occur in magnetite isolated from rock. Unlike rock magnetite, small amounts of manganese and calcium oxides were persistently associated with the crystals (Table 3). Analysis by EDAX probe corroborated the microprobe data and showed that the crystals contained no measurable nickel (Figure 3).



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FIGURE 3. — EDAX spectrum for magnetite sample from green turtle dura mater. The two large peaks in the center of the spectrum represent the wavelengths of X-rays emitted by iron. Peaks to the left of the iron peaks correspond to the following elements, as viewed from left to right:

1. Sodium
2. Aluminum
3. Silica (from glass cover slip)
4. Gold (from gold/paladium coating)
5. Chlorine (from bleach digestion)
6. Paladium (from gold/paladium coating)
7. Calcium
8. Manganese

Scanning electron microscopy revealed two types of crystal structures in dura samples: colloids (Figure 4), and spheres (Figures 5-9). A third crystal type was observed in one facial muscle sample (Figure 11). Treatment of tissue samples with bleach apparently did not remove organic material completely, and all crystals were embedded in organic debris.

TABLE 3. -- Electron microprobe analysis of magnetite particles isolated from green turtles.

<u>Oxide</u>	<u>Weight % of sample</u>	
	Magnetite standard (NMNH 11487)	Turtle
FeO	90.9	85.5 $\pm$ 1.7
TiO <sub>2</sub>	0.2	0.0 $\pm$ 0.0
Cr <sub>2</sub> O <sub>3</sub>	0.2	0.0 $\pm$ 0.0
MnO	0.0	0.3 $\pm$ 0.0
CaO	-	0.3 $\pm$ 0.1
Total	91.3	86.1

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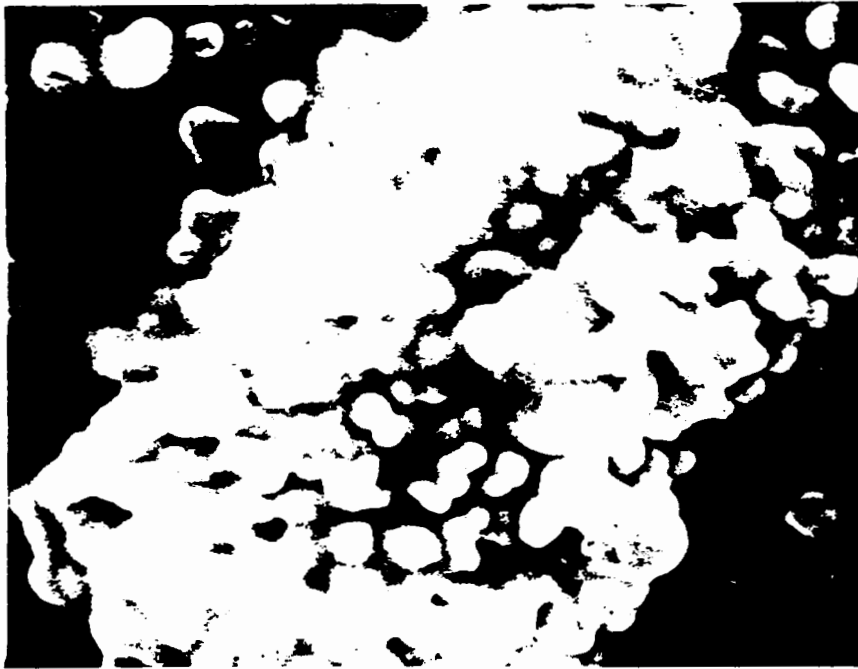
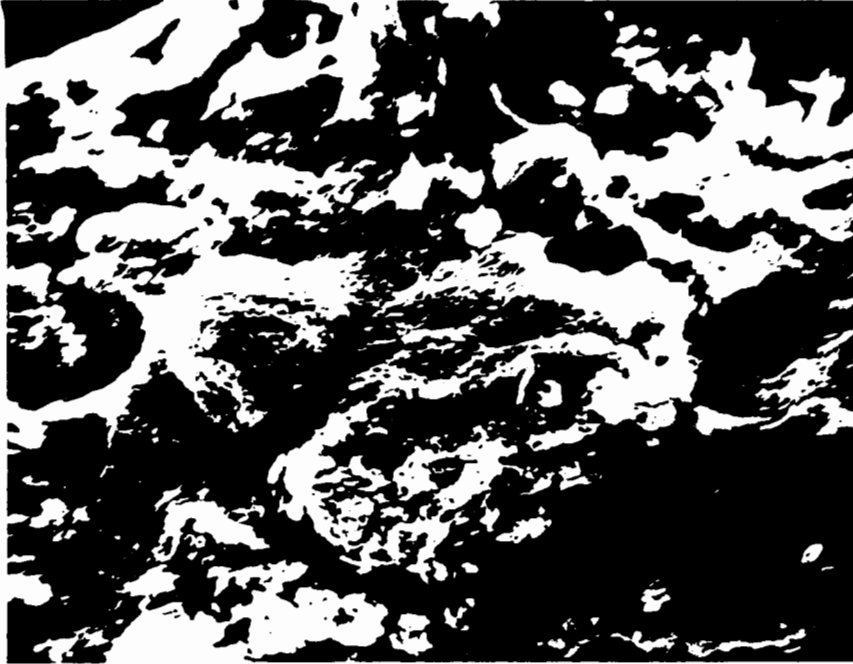
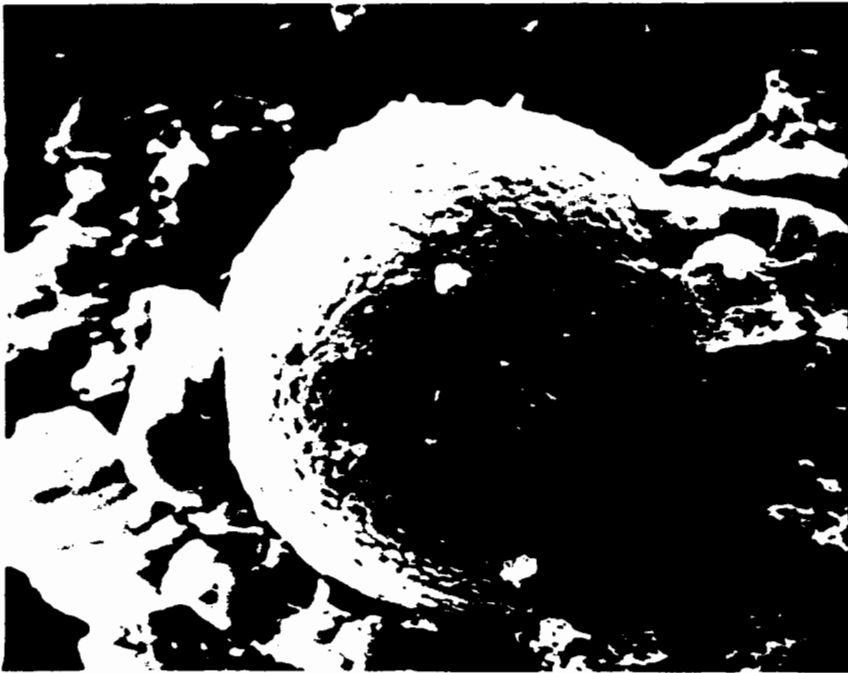


FIGURE 4. -- Scanning electron micrograph of colloidal crystal structure from green turtle dura mater sample. (14,750x)

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1500x



2950x

FIGURES 5. and 6. -- Scanning electron micrographs of juvenile green turtle dura mater samples. Figure 5 shows two iron-rich spheres; the left sphere is covered by an organic coat. Figure 6 is a closeup of the sphere on the right in Figure 5.





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FIGURE 7. -- Scanning electron micrograph of juvenile green turtle dura sample. This sphere is attached to the same tissue fragment as those depicted in Figures 5 and 6. (750x)

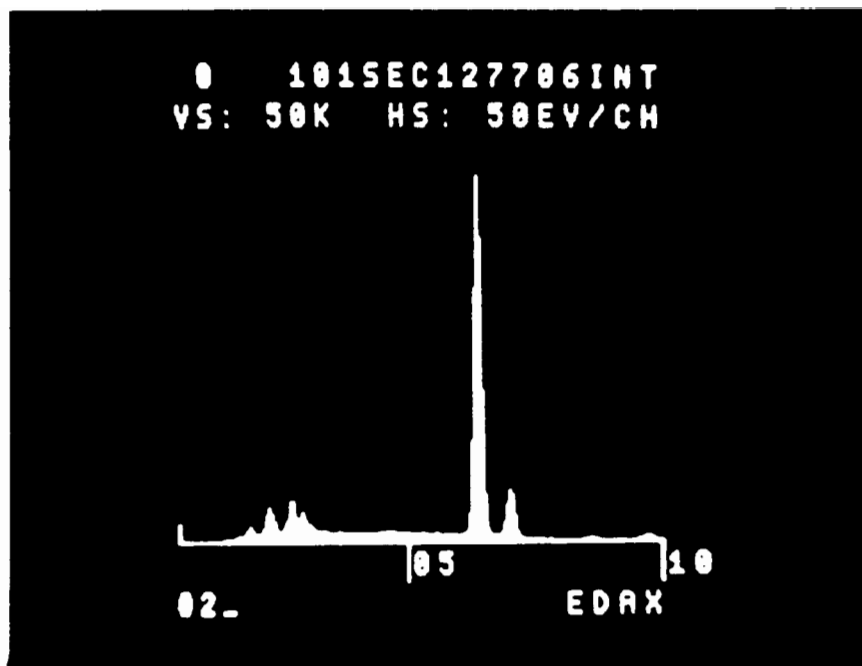


1500x



17,500x

FIGURES 8. and 9. -- Scanning electron micrographs of adult green turtle dura mater samples. These spheres were located on separate samples from the same turtle. Note the similar surface structure of the spheres in Figures 6 and 9.



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FIGURE 10. -- EDAX spectrum from sphere depicted in Figure 7. Peaks from left to right correspond to the following elements:

- 1. Silica
- 2. Gold
- 3. Chlorine
- 4. Palladium
- 5. and 6. Iron

## Discussion

The colloidal crystal structure observed in the dura may comprise a cluster of single-domain magnetite crystals. Though the apparent size of each nodule in the clump is larger than that which would produce single-domain behavior in magnetite, each crystal may be surrounded by an organic coat. Resolution was not high enough to determine if such is the case.

The spheres of magnetite (Figures 5-9) have not previously been observed in organisms, although cosmic spherules containing magnetite are common (Parkin, Sullivan and Andrews 1977). It is therefore possible that the spheroid configurations are not of biological origin, but are contaminating cosmic spherules. Three pieces of evidence, however, suggest that what was observed in the turtle samples was the result of biological precipitation rather than cosmic contamination:

1. Five balls on three samples from the duras of two animals were observed. One animal was a wild adult, the other a captive juvenile. Contamination of samples from each animal could have occurred during handling, extraction, or measurement procedures. This seems unlikely, as dissection, tissue digestion, and observation under SEM of the samples were separated from one another in both space and time. The juvenile sample preparation was carried out in November, 1981, at Hawaii Institute of Geophysics; the adult was dissected at California Institute of Technology the following December and samples from it examined in March, 1982. Cosmic spherules are not a common laboratory

contaminant, and it is doubtful that they would appear in both sample groups.

2. In addition to iron, cosmic spherules usually contain high proportions of magnesium and nickel, neither of which was present in the sample (Figure 10).

3. The spheres were not found in control samples or in tissues other than dura.

The spheres may be single crystals, in which case they would be too large to be magnetic single-domains, or they may be packets of closely-bound smaller crystals. Since the AF demagnetization measurements of magnetic material in the dura showed primarily single-domain behavior, the second hypothesis seems more plausible.

The crystal observed in a facial muscle sample (Figure 11) is probably ferrihydrite ( $Fe_2O_3$ ), which is the core molecule for the iron-storage protein ferritin, and which has been shown to be the precursor for magnetite synthesis in chiton teeth (Lowenstam 1967). Ferrihydrite is not magnetic, but if it were closely associated with magnetite in a sample it would also be isolated during the extraction procedures.

In a wide variety of vertebrates, high concentrations of magnetic material have been found in tissue associated with the dura mater or the front of the skull. These include the yellowfin and kawakawa tunas & Pacific blue marlin (Walker, Perry, Kirschvink and Dizon, manuscript

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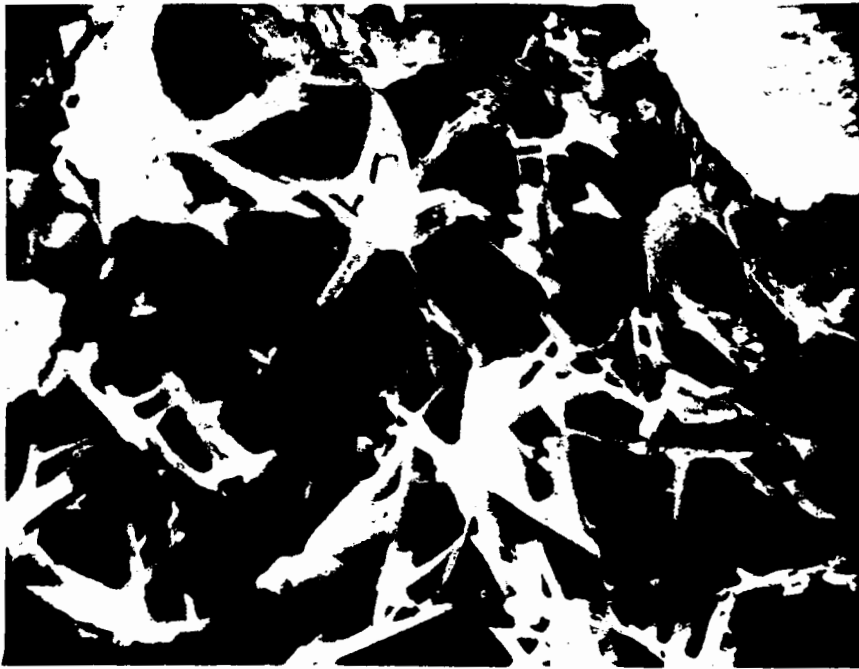


FIGURE 11. -- Scanning electron micrograph of crystal from adult facial muscle. (6800x)

in preparation), homing pigeons (Walcott et al. 1979), migratory birds (Presti and Pettigrew 1980), Pacific dolphin (Zoeger et al. 1981), woodmouse (Mather and Baker 1981) and man (R. Baker, personal communication). The high concentration of magnetite in the anterior portion of the dura mater in the green turtle is of particular interest in light of these findings. Presti and Pettigrew (1980) examined some 40 species of birds and found appreciable remanence associated only with migratory birds (for examples see Table 2). Kirschvink (1980b) was also unable to find magnetic material in non-migratory snapping turtles, although it is present in the two cheloniids thus far examined.

The size that a magnetite crystal must be in order to function efficiently in magnetic field detection is rather restricted (Yorke 1979, 1981; Kirschvink and Gould 1981). The crystal must be large enough to become stably magnetic (thermal agitation will randomize the alignment of a magnetic moment in a too-small crystal), but not so large that several magnetic domains, which would have a tendency to cancel net alignment in an external field, are formed. A unit magnet of this type is called a single-domain magnet. For magnetite, the size of a single-domain crystal is on the order of 0.1  $\mu\text{m}$ . One single-domain crystal has a magnetic moment of about  $3.1 \times 10^{-14}$  emu. Thus there are about  $10^9$  crystals of magnetite in the dura mater alone of an adult green turtle (if most of the crystals are single-domains). This quantity is enough to resolve background magnetic field intensity differences of less than one gamma ( $10^{-5}$  gauss), or magnetic field

direction to within a few seconds of arc (Kirschvink, manuscript in review). The earth's magnetic field intensity increases in strength away from the equator at an average rate of 5 gamma/km, so that a magnetic sense with this degree of resolution could be extremely useful to a migrating animal.

Magnetic clues other than the earth's overall field intensity or polarity are also available to marine animals. The ocean floor exhibits a magnetic striping pattern due to continuous sea floor spreading during epochs of normal and reversed magnetic field direction. In addition, volcanic islands and seamounts are sites of magnetic anomalies due to the high iron content of the basaltic lavas that formed them. An animal that could integrate magnetic information from one or more of these sources could make a magnetic "map" of an area. Such a map, coupled with a magnetic or sun compass sense (or with other cues, such as olfactory ones), would provide sufficient information to locate even a very small island in an otherwise featureless ocean.

Kirschvink and Gould (1980) have noted that there are probably one or more non-sensory metabolic functions for magnetite from which magnetoreceptors could have evolved. This hypothesis is supported by the fact that synthesis of magnetite occurs among extremely diverse phylogenetic branches, from bacteria to vertebrates. Lowenstam (1981) believes that magnetite may prove to be the fourth-most-extensively formed biogenic mineral. The presence of magnetite in an organism does



not, therefore, imply a priori a magnetic-field sensory function. As discussed above, however, the size (and also shape) of magnetite crystals is important if they are to function as transducers to the nervous system. In magnetically-sensitive organisms for which crystal size and shape have been measured (several species of magnetotactic bacteria, honey bees, homing pigeons), the crystals have been found to be fairly uniform and to fall within or just below the size-shape range for the single-domain field. Such uniformity suggests that natural selection has acted to produce crystals of a size best suited to their particular sensory function. Magnetite crystals in different species of chitons, however, range in size and shape so that they fall into sub-single-domain, single-domain, and multi-domain fields (Kirschvink and Lowenstam 1979). Chitons apparently use magnetite to harden their teeth, not in a sensory function, so that presumably their crystals are not selected for single-domain behavior. Green turtles, on the other hand, synthesize primarily single-domain crystals, at least in the dura mater. This is as one would expect if, like the birds and the bees, the turtle is using magnetite in a magnetoreceptor.

### III. BEHAVIORAL STUDY OF MAGNETIC SENSORY CAPABILITY

#### Materials and Methods

Sixty turtles collected at French Frigate Shoals in September, 1980, were used in the behavioral studies. The experiments were performed at the National Marine Fisheries Service Kewalo Research Facility during the period June-December 1981; the turtles were nine months old at the start of the study.

Using classical conditioning techniques, I attempted to train 50 turtles to respond to an altered magnetic field. Before training began the captive turtles had been fed fish and trout chow pellets by hand from a position just outside their tank. Whenever any person approached the tank the turtles would congregate close to the side in anticipation of food delivery. The conditioning experiment was designed to take advantage of this consistent behavior before feeding. The working hypothesis was that the turtles could learn to assemble at a plainly marked feeding station when, in lieu of a person appearing, magnetic field intensity in the tank was increased just before food delivery.

The experiment was conducted in a circular, non-metallic pool, 6 meters in diameter. A Helmholtz coil made up of 100 turns of 18 AWG magnet wire encircled the pool. A one ampere current through the coil

added a vertical field component of 0.30-0.50 gauss to the normal Hawaiian magnetic field of about 0.35 gauss. Twine strung across the top of the tank marked it off into quadrants. A PVC feeding tube was suspended from a three-meter-high observation blind, and the tube's delivery end was secured to the inside edge of the tank in one quadrant: the A-quadrant. Approximately 50 grams of trout chow pellets at a time were delivered down the tube. Before the introduction of food, the turtles were generally found floating or slowly swimming at the surface, or occasionally resting on the bottom. After food delivery the turtles would swim rapidly over to the pellets.

A trial began with a count of the turtles in A-quadrant. Thereafter, turtles in this quadrant were counted every 30 seconds. One minute into the trial (immediately following the third count) the normal geomagnetic field was altered by supplying one ampere of current to the coil encircling the tank. One minute later food was delivered down the tube, and the field was turned off 30 seconds after food delivery. Two more counts were made before the trial ended. The next trial began after a variable interval of 5-10 minutes. This interval ensured that chow previously delivered had been eaten and that the turtles were re-distributed throughout the tank. After two weeks the inter-count periods were reduced to 20 seconds, thus shortening the interval between magnetic field activation and food delivery. Counts before and after alteration of the magnetic field were examined for evidence of response to the stimulus.

Individual turtles were also tested for magnetic sensitivity, using two operant conditioning experimental designs. The first experiment was conducted in a 1.5 meter circular tank that was encircled with a coil of 100 turns of 18 AWG magnet wire. The tank was enclosed with black plastic sheeting to reduce outside distractions to the experimental turtle. Soft overhead lighting illuminated the tank enclosure. A turtle (Turtle C) was trained to press a paddle for a reward (reinforcement) of a small piece of smelt. After initial training the reward was offered on a variable ratio schedule--Turtle C would press repeatedly for food delivered on average at every third press. A small white light attached above the paddle acted as a secondary reinforcer. The light was turned on just before food delivery and stayed on for five seconds. When the paddle pressing behavior was consistent Turtle C was then rewarded only if a blue, 25-watt bulb also attached above the paddle was turned on. During training the blue light was on for half of the trials in a given day's session. Turtle C learned quite rapidly, and only occasionally pressed the paddle when the blue light was out. The next step in the experiment was to transfer control of the paddle press response from the blue light to an altered magnetic field. The light was progressively dimmed with an electronic dimmer. When it was at 40% of its initial setting the Helmholtz coil was activated during the light-on trials, adding a vertical magnetic field component (0.30-0.50 gauss) to the normal field in the tank. For subsequent trials the blue light was gradually dimmed until it was at 20% of its original value. Thereafter, half of the rewarded trials in each day's session were

carried out with the light on at 20% setting and the additional field activated (referred to as S+ and light trials). The other half had only the magnetic field activated (S+). Both types of S+ trials were presented with S- (no reward) trials in a balanced random order, with no more than three S+ or S- trials in a row and with an equal number of trials under each condition in a session. Each day's session consisted of forty one-minute trials.

Counts of paddle presses, S+/S- choice, and switching of lights and power to the coil were controlled with an Apple II desktop computer.

The second operant conditioning experiment also required a paddle press response, but reward was offered on a continuous reinforcement schedule after each trial. A turtle (Turtle A) was placed in the 6 meter pool previously used in the classical conditioning experiment. Turtle A was trained to press a paddle repeatedly during a 30-second trial period for a reward of a small piece of smelt. At the start of each trial the paddle was manually introduced into the tank. A frame covered with black cloth was attached to the tank side to obscure the turtle's view of the experimenter. A microswitch attached to the back of the paddle and connected to an automatic counter recorded the number of presses per trial.

Each trial began after a random interval of 20-60 seconds (mean 30 seconds) with simultaneous presentation of the paddle and the altered

(S+) or normal (S-) magnetic field. During S- trials paddle presses during the 30-second period earned nothing and, as punishment, the paddle was left in another 10 seconds. Presses during the punishment period resulted in subsequent 10-second delays in paddle removal, up to 30 seconds total. The punishment period was increased to 20 seconds after two weeks of trials with Turtle A, and was kept at 20 seconds (up to 60 seconds total) for all subsequent trials. For S+ trials, the first press after the 30-second period resulted in reward presentation and paddle removal (procedure modified from Walker, Dizon and Kirschvink). S+ and S- trials were presented in random order, with no more than three trials of one type in a row and an equal number of S+ and S- trials in a session. A day's session consisted of 40 trials.

Data recording and magnetic field switches were performed manually. A stopwatch was used to measure trial and punishment durations.

The experiment was repeated with a second turtle (Turtle B). After initial training, discrimination trials were run for seven consecutive days (280 trials). All parameters were kept as they had been for Turtle A, except that the punishment period was 20 seconds (up to 60 seconds) throughout all trials.

## Results

### 1. Classical Conditioning

Although many of the turtles moved into the A-quadrant after food delivery, as expected, they were not observed to move toward the quadrant, or directly to the feeding tube, until the chow dropped into the water. No changes in behavior were noted between pre- and post-magnetic-field-on conditions, or before and after shortening of the interval between stimulus and reinforcement. The turtles did not congregate near the feeding tube when the magnetic field was activated, counts in A-quadrant under altered field conditions did not increase (Table 4), nor was any behavior such as orientation toward the tube or increased swimming speed observed. Thus, even if the turtles were sensing the magnetic field, they were apparently not using it as a cue for subsequent food delivery.

### 2. Operant Conditioning with Variable Reinforcement Ratio

When the blue light above the tank was dimmed to below 20% of its original setting, Turtle C had difficulty perceiving it and response rate during S+ dropped, though the rate was still higher during S+ than during S-. With no light and only the field on, the rate of response during S+ was slightly greater than for S-, but total responses dropped so low (less than one hit per trial), that a new condition was imposed in order to keep the rate high enough to evaluate statistically (Table 5). Under the new regime, the light was on at 20% value during blocks of trials within a session, and off during an equal number of trials.

TABLE 4. -- Mean number of turtles in A-quadrant during three conditions: before activation of magnetic field stimulus, after activation, and after food delivery. Each number represents the average of three counts per trial, five trials per day (15 counts total).

<u>Before field activation</u>	<u>After field activation</u>	<u>After food delivery</u>
13.9	16.3	14.8
10.0	11.2	14.0
12.6	11.6	10.8
11.5	12.7	20.3
14.0	14.4	19.4
13.8	13.9	16.9
12.2	12.1	16.4
11.6	13.1	13.5
11.1	11.9	14.8
10.4	8.6	14.9
18.1	15.5	22.3
10.7	10.5	18.8
13.3	12.9	21.1
10.1	11.5	18.8
12.3	9.0	10.7
14.0	12.6	14.0
8.8	9.8	9.6
11.6	9.8	11.8
9.6	13.2	11.2
10.3	14.0	13.7
10.5	14.3	18.8
10.8	12.0	14.4
8.5	9.5	10.5
11.5	13.5	12.5
11.7	12.9	15.3
12.3	12.9	14.1
7.7	7.3	8.0
15.4	12.1	16.2
12.0	14.1	12.6
10.5	11.5	10.0
13.6	11.6	13.6
10.0	10.0	12.0
13.2	13.2	14.4

The difference in the number of animals in A-quadrant between the pre- and post-magnetic field activation was not significant (evaluated by paired-comparisons t-test;  $t_{\text{obs}} = 0.287$ ,  $df = 32$ ).



3

The magnetic field was turned on for all S+ trials. For example, a day's session might consist of four blocks of ten trials per block. Blocks 1 and 3 would each consist of five S- trials and five field-only (S+) trials. Blocks 2 and 4 would each consist of five S- trials and five field-and-blue-light-on (S+ and light) trials. The number of trials within a block and the order of (S+) and (S+ and light) presentations was quasi-random to insure that the turtle was not responding to temporal cues. After one week (280 trials) the average percent of correct hits during (S+ and light) trials was 79%; during (S+) only, correct response rate was 54% (Figure 12). The daily response rate for field-only S+ was evaluated against that for S- using the paired-comparisons t-test (Sokal and Rohlf 1969). The rate of response was not significantly different ( $t\text{-obs} = 1.70$ ,  $d.f. = 6$ ). With only the altered magnetic field as a cue, Turtle C did not discriminate between S+ and S- conditions.

### 3. Operant Conditioning with Continuous Reinforcement

After the first three days of discrimination testing, the rate of Turtle A's response during S+ trials was slightly greater than that during S- trials (average of 2.6 hits during S+, 2.3 during S-), for the next eight days, a total of 320 trials. The rate of S+ paddle presses was significantly greater at the 0.001 level when evaluated by the paired-comparisons t-test ( $t\text{-obs} = 5.52$ ,  $d.f. = 7$ ). On the 9th and 10th days (sessions 12 and 13), however, response rate under the two conditions was equal. At this point the punishment time after a press during the S- period was increased to 20 seconds, in an attempt

TABLE 5. -- Mean number of paddle presses per trial by Turtle C under conditions of decreasing light intensity (numbers are the averages of 20 trials in one day's session).

<u>% initial light setting</u>	<u>Mean number of hits per S+ trial</u>	<u>Mean number of hits per S- trial</u>
100	6.0	0.4
80	8.0	0.4
60	10.4	0.8
-- Altered magnetic field was on for all subsequent S+ trials --		
40	13.6	2.2
40	15.8	3.2
30	9.0	10.8
25	--- computer malfunction, paddle presses not recorded ---	
20	3.4	2.0
20	6.6	2.8
15	6.6	3.4
10	4.0	3.0
0	0.9	0.7

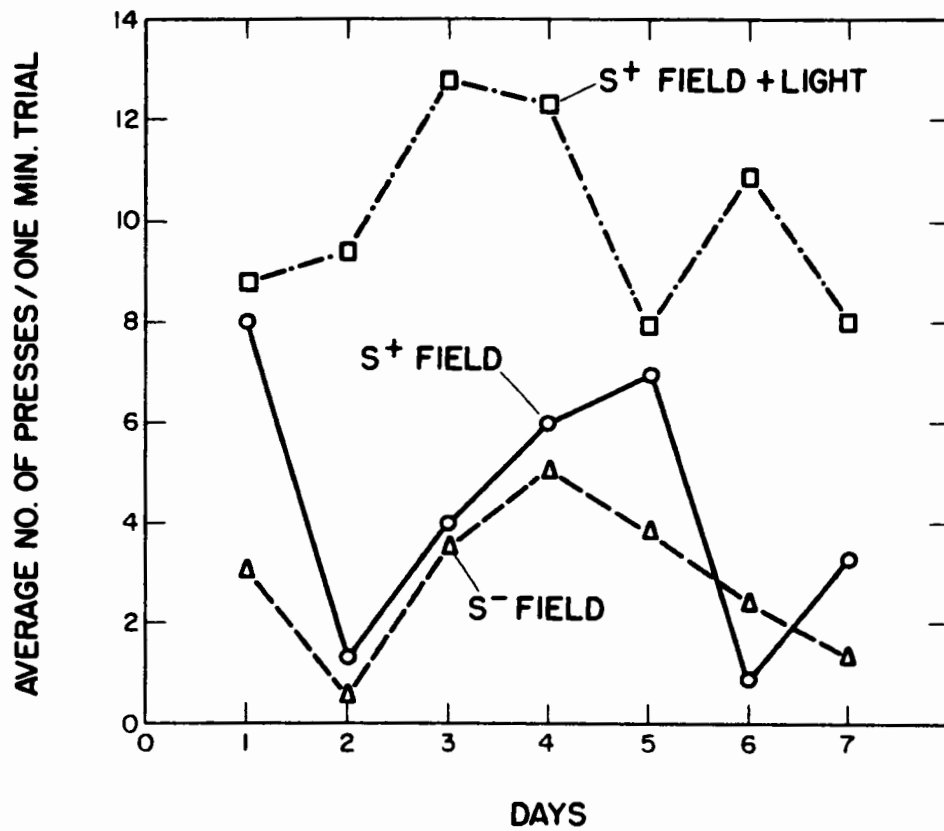


FIGURE 12. -- Daily averaged rate of paddle presses by Turtle C under three conditions.

to decrease response rate during S- trials. Response rate did drop, but for both S+ and S- trials (average of 2.2 hits during S+, 1.6 during S-), and the overall separation of rates achieved was slight. Response rate during S+ was significantly greater at the 0.005 level ( $t\text{-obs} = 6.4$ ,  $d.f. = 4$ ) over the next 200 trials (sessions 14-18), after which the turtle again stopped discriminating and the experiment was halted (Figure 13 and Table 6).

Though there were no changes in the experimental setup, Turtle B did not evince discrimination between S+ and S- conditions (Figure 14).

TABLE 6. -- Mean number of paddle presses per trial by Turtle A  
 (numbers are the averages of 20 trials in one day's session).

<u>Session</u>	<u>Mean number of hits per S+ trial</u>	<u>Mean number of hits per S- trial</u>
1	4.2	4.0
2	3.9	3.0
3	3.1	3.8
4	1.6	1.4
5	1.8	1.6
6	2.4	2.0
7	2.4	2.0
8	3.3	2.5
9	2.6	2.2
10	3.0	2.8
11	4.0	3.5
12	2.9	3.0
13	2.7	2.7
14	2.4	1.6
15	2.2	2.0
16	2.1	1.6
17	2.2	1.6
18	1.9	1.4
19	2.1	2.1

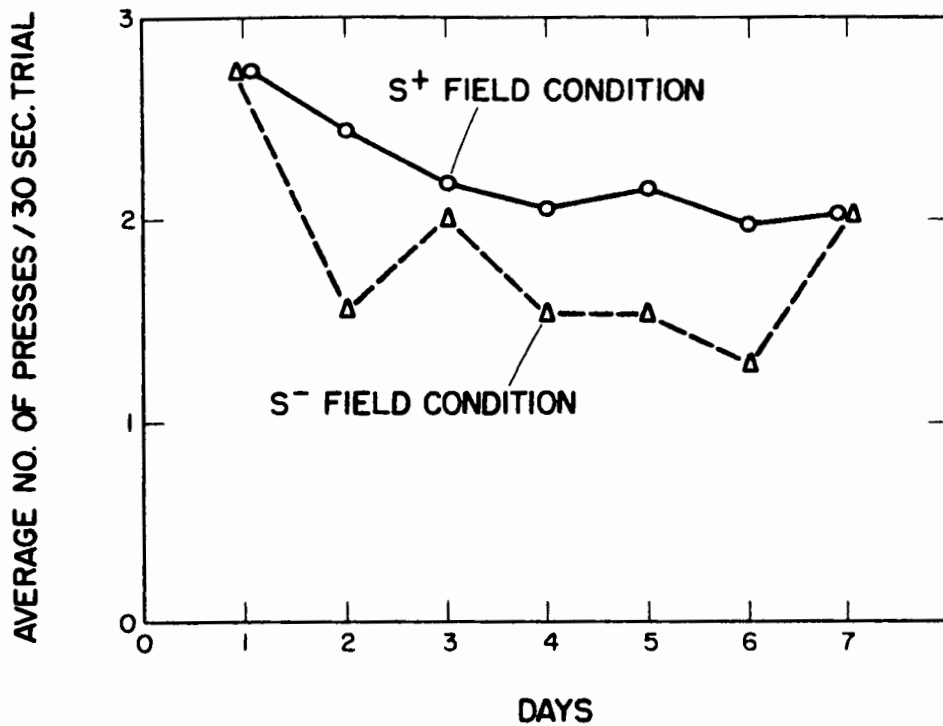


FIGURE 13. -- Daily averaged rate of paddle presses by Turtle A after initiation of 20 second punishment period.

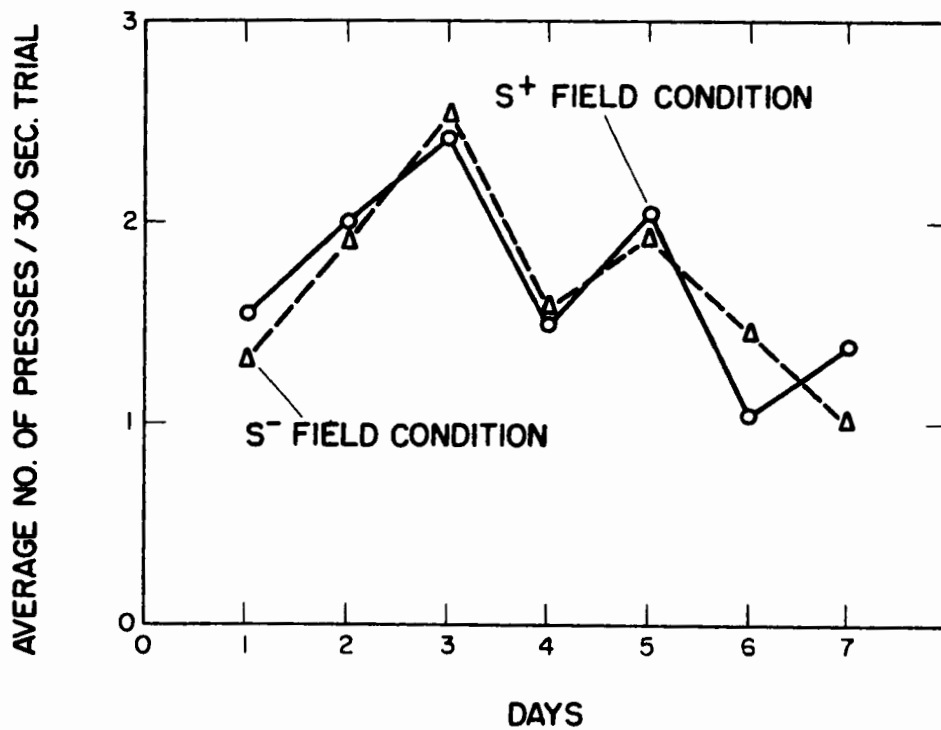


FIGURE 14. -- Daily averaged rate of paddle presses by Turtle B after initial shaping.

Discussion

Discrimination training with selective reinforcement would seem to be a valid and powerful method to employ for the behavioral analysis of magnetic sensory function. For some sorts of stimuli, however, requesting a behavioral response such as paddle pressing or stationing for a food reward can sometimes give negative results even when the stimulus is perceived by the experimental animal. Three of the four experiments performed in this study elicited no positive response. The failure of these experiments may arise from the turtles' inability to detect magnetic field changes, or it may result from a more generalized inability to signal discrimination between the two magnetic field conditions under the given experimental conditions.

According to the classic equipotentiality premise (Pavlov 1927), any stimulus can be conditioned to any response with equal success. Behavioral research conducted over the past twenty years indicates that the premise simply may not be true. Garcia and Koelling (1966) demonstrated that rats could not pair radiation sickness with an audiovisual stimulus, though they could with a taste stimulus. Similarly, Herman (1980) found that dolphins could not match visual comparison stimuli to a visual form/brightness sample unless auditory cueing was used in conjunction with the visual stimulus. Apparently, as a result of an organism's phylogenetic history, there are biological constraints which limit or inhibit certain types of response (Hinde and

Stevenson 1973). The responses sought in the turtle experiments may not be the relevant ones that are "biologically prepared" to occur in the presence of magnetic cues. Related to this problem is the role of the physiological state of an animal. For example, Bookman (1977) found motor activity in pigeons to be an important component of the magnetic field sense--birds stationary on perches did not respond to altered fields, while those in flight tunnels did. Turtles in all my experiments were allowed free movement, but may not have spent enough travel time in a consistent direction to integrate the magnetic information. Measurements of motor activity were not made, so for example it is not known whether Turtle A swam more, more rapidly, or in a more consistent direction than Turtle B, which may have influenced their responses.

Another factor which may come into play is the age, or size, of an organism. Keeton and Gobert (1970) demonstrated that young, inexperienced pigeons responded differently from older birds under altered magnetic orientation conditions, indicating that developmental processes may be involved in stimulus response. Young turtles possess less magnetite than older animals, and, if magnetite is responsible for magnetic field sensitivity, this lower concentration could affect discrimination ability. The increase in magnetite concentration with age could be important for migrational activities. Wild green turtles spend approximately the first year of their lives in the open ocean (Witham 1976), perhaps passively drifting until they reach a given age, or size, when they begin active navigation in order to locate coastal



feeding pastures. Turtle A was the largest of the three turtles tested by operant conditioning techniques, and perhaps the only one physiologically ready to respond to magnetic cues.

Specific conditions of each experiment might also influence the turtles' behavior and affect the final results. The failure of the classical conditioning experiment may have been caused by the turtles' inability to pair a diffuse stimulus, the magnetic field switch, with a punctate response, stationing at a particular area of the tank. In the operant conditioning experiments, punishment for paddle presses during S- conditions was either absent or perhaps not severe enough to discourage the behavior.

Too few animals were tested in the operant conditioning experiments to draw firm conclusions about either the applicability of the techniques employed or the ability of the turtles to discriminate between normal and altered magnetic field conditions. The positive response of Turtle A, however, encourages further testing of the hypothesis that the green turtle can perceive magnetic field changes.

IV. SUMMARY AND CONCLUSION

1. Magnetic material was found in the heads of green turtles of all age classes, with the highest concentration in the dura mater membrane.

2. AF demagnetization of tissue samples showed that the material was magnetically hard, or stable.

3. The magnetic material was extracted from dura mater and facial muscle by tissue digestion, centrifugation, and magnetic isolation.

4. Analysis of dura mater material via X-ray diffraction and electron microprobe demonstrated that the material was very pure magnetite, with negligible amounts of non-ferrous elements present.

5. Scanning electron microscopy of dura mater material revealed two crystal types; a colloidal crystal and several spheres. The crystals may be composed of smaller magnetite subunits. A third crystal type was observed in a facial muscle sample. This crystal was not positively identified, but is probably ferrihydrite.

6. Behavioral studies using classical and operant conditioning techniques were conducted to determine if juvenile turtles could discriminate between normal and altered magnetic fields. One animal showed discrimination between the two field conditions, while positive results were not obtained with the other turtles tested. Negative results could indicate that the turtles do not sense field changes, or may result from methodological difficulties.

The question of whether magnetite is the sensory transducer to the nervous system of magnetic field information has yet to be answered. Evidence that the green turtle, like many other vertebrates, synthesizes magnetically-stable magnetite and concentrates the mineral in the anterior of the head, lends credence to the hypothesis that the magnetite is a component in some sensory system, possibly that of magnetic field detection.

A geomagnetic sensing mechanism would be of significant evolutionary advantage to an open-ocean migrant. Baldwin's observations (discussed in the Introduction) and my results with Turtle A support the hypothesis of such a mechanism in the green turtle. Further research must examine the association of magnetite with the turtle nervous system, and must utilize more appropriate behavioral testing regimes in order to clarify the role of magnetite and magnetic orientation in the migrations of the green turtle.

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