A Literature Review of Cell Repair, Electroreception, Electric Generation, Magnetic Orientation and Magnetic Sensing Mechanisms in Electric Rays and Other Marine Fishes

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INTRODUCTION

This report provides a literature review of electric and magnetic sensory systems in marine fish with emphasis on electric rays. Research on healing and tissue regeneration abilities in marine fishes has also been reviewed to determine if the literature reports that there is a correlation between electric properties and accelerated healing or regeneration.

All biological organisms require information from their environment in order to conduct the activities necessary to maintain life, such as feeding, reproducing, evading predators or any other myriad functions. A wide array of sensory systems has evolved to extract that critical information, including sensitivity to chemical compounds (taste and olfaction), light (vision), sound (hearing), gravity (senses of equilibrium) and physical contact (touch, lateral line systems).

In many species, the range of familiar senses is different from that in humans. Some insects and crustaceans are able to perceive light at ultraviolet wavelengths and to perceive the patterns of polarization in sunlight; pit vipers can find prey using infrared wavelengths; whales and elephants perceive frequencies of sound below the range accessible by humans; or dogs perceive higher frequencies of sound than do humans.

In addition, many animal species are sensitive to environmental stimuli that humans do not consciously perceive such as the presence of electrical and/or magnetic fields. Electric senses are more developed in many species of non-mammalian vertebrates, particularly fishes, than in humans or other mammals. All marine sharks, skates and rays (elasmobranchs) are sensitive to electric fields and use that sense to detect prey and, in a few species, for purposes of communication. In addition to electrically sensing prey, marine electric rays of the family Torpedinidae are highly specialized for the production of electric discharges that are used to capture prey and to repel attacks by predators.

The ability to sense and orient to magnetic fields is well known in a large variety of species ranging across the phyla from bacteria to marine mammals. Since movement through a magnetic field generates an electric field; magnetic sensitivity and electric field sensitivity are closely related. Electrically sensitive species may sense magnetic fields via their electroreceptors. However, many non-electric species are also sensitive to and orient by magnetic fields as well. Thus the basis of that sensitivity lies with other receptor mechanisms. One such mechanism is biogenic magnetite crystals that occur inside of cell membranes. Other structures, such as exogenous magnetite grains in the elasmobranch inner ear, may augment magnetic sense organs.

Recent studies indicate that neural tissue regeneration occurs in some bony fishes exhibiting electrical generating and sensing abilities throughout their lives. Teleost (bony skeleton) fish of many different species have a well-developed capability to repair damage to both central nervous system and peripheral neurons and to maintain active growth of neural tissue throughout adult life. This ability appears to be particularly developed in fishes that have specialized tissues for electric generation. In particular, the primary model for studies of neural cell death and regeneration has been the freshwater electric fish *Apteronotis leptorhynchus.*

Marine fishes, particularly the larger elasmobranchs are difficult to maintain in captivity for long term studies so the absence of literature documenting accelerated healing and regeneration has not been taken negatively, rather that studies on these marine organisms may provide new insights.

This literature review is intended to assemble reports of studies that include electric rays and other marine fishes that generate electric current, orient and sense electric and magnetic fields, or may show potential for rapid tissue regeneration or healing. The prime goal of this study is to establish if further studies using *Narcine brasiliensis* and other electric fishes may provide investigative insights into biomagnetic reception that may be applicable to spatial orientation, navigation and tissue healing in humans. The review with few exceptions is limited to marine fish. Although an extensive body of literature does exist for fresh water electric species, this literature remains beyond the scope of this review.

While the review covers the broad category of marine electric fishes, we provide extended background on one particular electric fish, the Lesser Electric Ray (*Narcine brasiliensis*), as orientation for members of a multidisciplinary team that is recommended to continue research in this topical area. *Narcine brasiliensis* has been of interest to neurobiological researchers as a model for research on the biochemistry of acetylcholine, the sole neurotransmitter used by electric organ tissue in this species. Larger electric ray species, *Torpedo californica, T. marmorata,* both *are* model organisms for neurophysiological studies. This extensive literature was not included in this review as it was outside the scope of work; however, we have included a list of citations on this literature as an appendix.

BACKGROUND

Marine Electric Fishes

All elasmobranchs (skates, rays, and sharks) have electroreceptors that detect electric fields in their immediate vicinity. Electric rays (marine elasmobranch fish of the family Torpedinidae, order Rajiformes) also generate electric discharges in addition to their electrosensitivity. Approximately 40 species of marine electric rays occur worldwide. The primitive coelecanth and lampreys are electroreceptive as are the deep-water rattails (Chimaeroidei).

Electric stargazers are marine teleost fishes of the family Uranoscopidae (9 genera, 25 species) who have electric organs on the head. The ecology and distribution of species of the genus *Asteroscopus* is reported by Schwartz (2000), De Jesus, Ellis et al. (1993), Modde (1980) and Cupka and Dias (1972). They are benthic predators that attack small fish from ambush while buried in sandy sediments (Burgess 1976). Little is known about the role of electric organs in these fishes, however, the neurophysiology of the electric organ was described by Leonard and Willis (1979) and Bennett and Pappas (1983). Pickens and McFarland (1964) had described the electric organ which is discharged in association with prey capture as being less than a volt and approximately 300 milliseconds in duration and not sufficient to stun prey.

Narcine brasiliensis, the Lesser Electric Ray, possesses large electric organs that deliver a discharge of approximately 80-100 volts that is used for protection and for feeding. It paralyzes and captures prey, which consists of eels, mud shrimp, and polychaete worms burrowing below the surface in sand.

Freshwater Electric Fishes

The freshwater teleost (bony) fishes known as knifefishes and elephant fishes (Gymnotiformes and Mormyridae respectively) occur in South America and Africa. These species generate and receive species-specific electric signals and use them to communicate species identity, gender, territorial boundaries and sexual receptivity. The freshwater knife and elephant fish species are also called "weakly electric fish" because their discharges are in the millivolt range as opposed to marine electric rays whose electric organ discharge (EOD) are in the tens of volts or freshwater electric eels that have EODs of hundreds of volts.

Catfish species of the family Ictaluridae are all electroreceptive as is the paddlefish, the only species known to use electroreceptors to feed on plankton (Wilkens, Russell et al. 1997).

Biology and Properties of the Lesser Electric Ray, *Narcine brasiliensis* – a Case Example

<u>*Ecology and Orientation*</u>

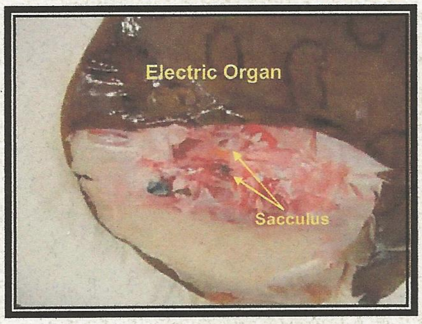
The lesser electric ray, *Narcine brasiliensis*, occurs in the Caribbean, Gulf of Mexico and the Atlantic Ocean from Brazil to North Carolina. *Narcine* is common but very restricted in its habitat requirements, most commonly being taken in trawls in the vicinity of barrier island passes and beaches where it lives in shallow, turbid estuarine environments. *Narcine brasiliensis* is known to occur in high concentrations in extremely localized areas of the sea floor and to travel in a highly oriented fashion from one such location to another over distances of approximately 80 kilometers. The sensory mechanism whereby *Narcine* orients as it travels through in turbid water at night is not known, but it is not visual. Magnetic orientation is a plausible possibility but has not been experimentally demonstrated.

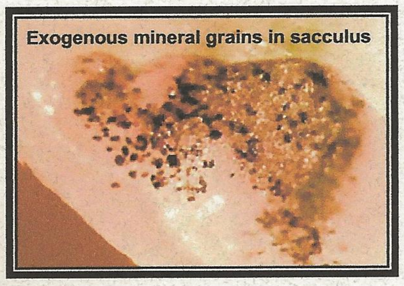
Predator Defense

In the northern Gulf of Mexico, trawling commonly produces great quantities of shrimp, fish and other marine life. Edible species are removed and other organisms are discarded overboard. The deluge of disoriented and stunned animals routinely attracts large numbers of predatory sharks and bottle-nosed dolphins, which follow the vessel and feed aggressively on discarded bycatch. *Narcine*, unlike all other species being thrown back, is actively avoided by both sharks and dolphins (Rudloe 2003). The electric rays are always unharmed and slowly swim back down to the bottom. On rare occasions, sharks have been observed to begin attacks on electric rays and break off the attack in mid strike. Hovering sea gulls refused to eat juvenile electric rays, even though they readily attacked similar-sized flat fish. Preliminary studies in an aquarium environment suggest that the rays sense the approach of a predator and actively discharge their electric organs to repel predators.

Exogenous Magnetite

Narcine brasiliensis, like several other species of elasmobranchs, is known to sift exogenous heavy mineral sand grains from the sea floor and concentrate them deep in the vestibular sacculus, a part of the inner ear that overlies the brain stem (Rudloe 2003). The grains are passed through the endolymphatic duct, which opens to the exterior environment on the dorsal surface between the eyes. Although the function of the magnetite, titanium, zircons and other heavy mineral grains is unknown, it is hypothesized that they may assist *Narcine* in orientation.





While much of the published literature on this species is concerned with neurobiology of the electric organs, this review also highlights the ray's unique ability to select and concentrate magnetic sand grains and other heavy minerals in its vestibular system as well as the electrical properties of the grains. Is *Narcine* using these exogenous magnetic sand grains as a primitive "device" to augment sensory abilities? Is this “device” facilitated in any way by the electric field generating capabilities of the organism? Is the exogenous magnetite providing a source for tissue uptake and the creation of nano-sized particles of endogenous magnetite?

References on the biochemical nature of the endolymphatic gel containing the grains have been reviewed, along with references on the anatomy of the elasmobranch vestibular system. Such information should provide a platform for modeling the ray's magnetic sensing mechanism to help design other avenues of research.

METHODS

The literature reviewed here was drawn from a number of sources including previous literature reviews and bibliographic assemblages by Kirschvink and others at the California Institute of Technology on magnetic properties and by Nelson and others at the Electrosensory Signal Processing Lab at the Beckman Institute at the University of Illinois, Urbana-Champaign on electric properties in fishes. Both of these research teams had prepared reports that were an important starting point for this study. Electronic searches were conducted in BIOSIS, PubMed, and across 274 university library catalogs accessible via EndNote[1]. Tables 1 and 2 summarize these results. Separate searches were conducted on the Internet to locate and / or identify other research; search engines included the following:

- All the Web
- Alta Vista
- Google
- Teoma
- Wise Nut

Category specific engines associated with COPERNIC (a meta crawler over many science and popular databases) and other electronic sources including RLG and HRAF. Search terms were modified to conform to search engine and database requirements.

In addition to citations drawn from computer searches, an additional 166 references were located for review by manual examination of the literature.

In addition to the literature reviewed herein, citations were generated for separate research fields that involve either the use of marine electric rays as models for neurophysiological research or the electrobiology of freshwater African and South American electric fish. The neurophysiological material predominately concerns the use of marine electric rays of the genera *Torpedo* and *Narcine* as

[1] http://www.endnote.com/support/enconnections.asp

Table 1. PubMed Database Search[2]		
Search #	**Search Term(s)**	**No. of Hits**
Search #1	"electric fish" and "marine"	96
Search #2	"elasmobranch" and "magnetic field"	9
	"elasmobranch" and "magnetic orientation"	12
	"elasmobranch" and "healing"	4
	"elasmobranch" and "regeneration"	22
	"elasmobranch" and "sacculus"	1
	"elasmobranch" and "acoustical lateralis"	0
	"elasmobranch" and "otolith"	0
Search #3	"teleost" and "magnetic field"	1
	"teleost" and "magnetic orientation"	0
	"teleost" and "healing"	9
	"teleost" and "regeneration"	87
	"teleost" and "sacculus"	7
	"teleost" and "acoustical lateralis"	0
	"teleost" and "otolith"	12
Search #4	"marine electric fish" and "magnetic field"	2
	"marine electric fish" and "magnetic orientation"	1
	"marine electric fish" and "healing"	0
	"marine electric fish" and "regeneration"	0
	"marine electric fish" and "sacculus"	0
	"marine electric fish" and "acoustical lateralis"	0
	"marine electric fish" and "otolith"	0
Search #5	"narcine"	33
Search #6	"torpedo" and "behavior"	84
	"torpedo" and "sensor*"	19
	"torpedo" and "magnet*"	20
	"torpedo" and "electric* field*"	24

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[2] http://www.ncbi.nlm.nih.gov/pubmed/ -- This is an HTTP-based connection file for the National Library of Medicine's PubMed database.

Table 2. Dialog® Query		
Search #	Search Term(s)	No. of Hits
Search #1	elasombranch? and (otolith? or saccul? or acoustical()lateralis or magnetic()orientation or regeneration or heal? or magnetic()field?)	107
Search #2	(narcine or torpedo) and (behavior? or sensor? or magnet? or electric?()field?)	1,143
Search #3	((narcine or torpedo) and (behavior? or sensor? or magnet? or electric?()field?)) and not (nicotinic or acetylcholine? or membrane? or neurotransmitter? or AChR or chloride? or fast() gate or chromatograph? or phospholipids? or vesicle? or neurotoxin?))	186

model organisms for the study of cell membrane physiology during the transmission of nerve impulses. While Narcine is the model organism in many of these studies the neurophysiology literature is not reported here since these papers are not concerned with cell repair, electric behavior, magnetic orientation, or magnetic sensing mechanisms and, consequently, were deemed to be outside the scope of work of this review. Similarly, the electrobiology of the freshwater electric fishes was also deemed to be outside the scope of the current work.

FINDINGS

Cell Repair and Healing

In humans, electric shocks from marine electric rays have been used therapeutically for head pain and gout since the time of the Roman Empire. Electric eels are used for pain relief in South America, as are electric catfish in China, as reviewed by Hughes (1999) reviewed this medical history. Anecdotal evidence from the late 20th century suggests that electric ray tissue is still being used in folk medicine.

For years it was believed that no new neurons could be grown in the adult mammalian brain, thus precluding the possibility of full recovery after damage to the central nervous system from injuries and strokes. However, adult brains in humans and other primates have recently been shown to have a limited ability to generate new neurons (Eriksson, Perfiliova et al. 1998; Gould, Tanapert et al. 1998). Zupanc and Clint (2003) demonstrates that, relative to mammals, teleost fish of many different freshwater species readily repair damage to both central nervous system and peripheral neurons and to maintain active growth of neural tissue throughout adult life. The freshwater weakly electric fish *Apteronotus leptorhynchus* has been the model for studies of neurogenesis, cell death and regeneration in adult teleost brains (Zupanc 1999; 2001; Zupanc and Clint 2001; 2003). Electroreceptor tissue is also quickly regenerated in the freshwater electric fish *Sternarchus albifrons*, making that species an additional model for studies of healing and regeneration of neural tissue (Waxman and Anderson 1982; 1985; Zakon 1991).

The central nervous system of teleost fish has therefore become a model of choice for the study of regeneration and healing of nerve tissues. The role of microglia and macrophage cells in this process is the object of particular investigation. The field is reviewed by Zupanc, Clint et al. (2003). According to Zupanc, rapid proliferation of central nervous system neurons appears to be associated with seasonal peaks in electric discharges by breeding males in *Apteronotus*. In other words, brain growth and regeneration is strongest in sexually excited males when they are frequently discharging their electric organs to attract females.

Scant attention has been given to numerous reports that wounds in sharks heal rapidly. Observations off Queensland noted by R. Aidan Martin (Personnal Communication 2004) several species of adolescent and mature females of Grey Reef Shark, *archarhinus amblyrhynchos*; Silvertip Shark, *C. albimarginatus*; Blackfin Reef Shark, C. *melanopterus*; and Whitetip Reef Shark, *Triaenodon obesus* often bore superficial but nasty-looking bite wounds that healed rapidly. Similar observations were noted by Klimley and Nelson (1981; 1984) in Scalloped Hammerhead Sharks *(Sphyrna lewini)* in the Sea of Cortez. Immersion in seawater, temperature and bacteria introduced into wounds were given as possible reasons for accelerated healing. Most of the reports on rapid healing in sharks have been associated with tagging studies where rapid healing of wounds was observed and noted over several weeks between capture of tagged individuals.

While there appears to be a correlation between neural regeneration and the presence of specialized tissue for generating and storing electric charges in freshwater fishes, the literature indicates that similar studies with marine fishes and particularly electric rays have not yet been conducted.

Electric Sensing and Reception

Marine invertebrates and fish produce bioelectric fields from ionic current flow across gill and gut epithelia (Paulin 1995). Marine elasmobranch fishes (sharks, skates, and rays) are sensitive to electric fields as weak as 5 nanovolts/cm (Kalmijn 1981) and use this sense to successfully detect and attack prey such as flounder buried in the sand (Murray 1962; Kalmijn 1966; 1974; 1978; 1982; 1984). Kalmijn's work, initially done in the laboratory, was extended to at-sea measurements (Kalmijn 1982) who documented the ability of dogfish sharks and blue sharks to detect electric fields and to attack electrical bait in the open ocean. Electroreception in prey detection in the stingray was described by Blonder and Alevizon (1988).

Male round stingrays, *Urolophis halleri,* detect buried females by electroreception (Tricas, Mitchael et al. 1995). The response characteristics of afferent electroreceptive neurons in the species are characterized by Tricas and New (1998). Male Atlantic stingrays, *Dasyatis sabina,* also locate buried females by electroreception. Their electrically mediated behavior and developmental changes in electrosensory neuron responses are described by Sisneros and Tricas (2000; 2002). The use of electroreception and electric discharge in intraspecific communication in the clear nosed skate, *Raja eglanteria,* is described both behaviorally and in terms of neural responses by Bratton and Ayers (1987), Bratton and Williamson (1993), New (1994) and Sisneros, Tricas et al. (1998). The literature on behavior and neuroethology of the elasmobranch electrosense is reviewed and summarized by Sisneros and Tricas (2002).

Among primitive fishes, the coelacanth has been reported to be electroreceptive (Northcutt 1980; Bemis and Herrington 1982) The deep-sea chimaerias or rattails are also electroreceptive (Fields and Lange 1980) as are lampreys (Bodznick and Northcutt 1981; Andrianov and Broun 1983; Bodznick and Preston 1983; Fritzsch, Crapon De Caprona et al. 1984). While no detailed behavioral studies concerning the use of the electrical sense have been published on these deep saltwater species, they are known to possess electroreceptors.

Electroreceptors

There are two basic types of electroreceptors: ampullary and tuberous. All electroreceptive fish species have ampullary receptors. They were first described by Stenonis (1664) and Lorenzini (1678) and were named the ampullae of Lorenzini. However, their function was not known for 300 years until Lissman determined that they were electroreceptors (Lissman 1958). These receptors are used in locating prey, conspecifics and in orientation. Ampullary organs have an epidermal ampulla that is connected to the exterior by a jelly filled canal. They respond slowly and give a long lasting discharge in response to low frequency stimuli. The sensitivity of the receptor is a function of the length of the canal (Tricas and New 1998).

The ampullae of Lorenzini are the electroreceptors in sharks and rays (Murray 1962; 1967; Akoev, Ilyinsky et al. 1976; Kalmijn 2000). The electroreceptive response of the ampullae of Lorenzini has been described for nine species of sharks and minimum voltage gradients reported for smooth dogfish, *Mustelus canis* (Kalmijn 1982; Pals, Valentijn et al. 1982), nurse shark *Ginglymostoma cirratum* (Johnson, Scronce et al. 1984) and reef blacktip shark *Carcharhinus melanopterus* (Haine, Ridd et al. 2001). Kajiura and Holland (2002) compared the electrosensory responses of juvenile scalloped hammerhead and sandbar sharks and concluded that the head morphology of hammerheads does not enhance their electroreceptivity relative to other sharks but does improve their turning radius while detecting and attacking prey.

The sensitivity of electroreceptors (Tsong 1994; Akoev, Avelev et al. 1995); depth related changes in electroreceptors (Raschi and Adams 1988); and electrosensory areas of the brain (Bodznick and Northcutt 1984) have been described. New (1994) discusses the use of electroreception in skate communication. Akoev, Avelev et al. (1992; 1995) describe the perception of low intensity and high frequency electromagnetic radiation in skates as well as the electroreceptors (Akoev and Ilinskii 1972; 1973). Bullock (1977), New (1997), Weaver, Vaughan et al. (1998), Montgomery and Bodznick (1999) and Kalmijn (2000) provide reviews of electroreception in elasmobranchs.

Tuberous receptors are found in the freshwater weakly electric fish. These fish have ampullary receptors but, in addition, they have tuberous receptors as well. Tuberous receptors are epidermal capsules with sensory epithelial tissue. They respond rapidly but briefly to high frequency stimuli. Tuberous receptors are the receptors for the complex species specific signaling and communication in the weakly electric fish.

Electric Sensing and Ocean Navigation

The pioneering physicist Faraday (1832) first proposed that electric fields are widespread in the ocean and are generated by physical processes such as the movement of ocean currents. Faraday also suggested that moving objects such as ships or organisms would induce an electric field by their movement relative to the earth's magnetic field. Larson (1968), Pals and Schoenhage (1979)and Pals Peters et al. (1982) described electric fields of various spatial and temporal scales and of various field strengths in shallow marine environments. Brown and Ilyinsky (1978) and Broun, Ilnskii et al. (1979) report that ampullary receptors respond to the electric fields generated by waves.

As elasmobranchs swim through the earth's magnetic field, an electric current is induced which the fish is able to sense, potentially allowing it to detect the magnetic field and use the information for orientation (Kalmijn 1971; 1974; Paulin 1995). Kalmijn (1982) has shown that rays orient in electrical fields as weak as fields that are induced by swimming in the geomagnetic field. Andrianov and Broun (1975) demonstrated that fish could detect magnetic fields via the electroreceptor system. The primary electroreceptors in elasmobranchs, the ampullae of Lorenzini, respond to changes in ambient magnetic fields (Brown, Ilyinsky et al. 1972; Andrianov, Brown et al. 1974; Kalmijn 1974; Akoev, Ilyinsky et al. 1976; Heiligenberg 1977; Brown and Ilyinsky 1978). Deedler (1952), Roth (1969), Kalmijn (1971)and Rommel and McCleave (1973) suggested that migrating eels and salmon in the ocean might detect and orient to such fields, using them to navigate across large distances. Paulin (1995) critiqued earlier theoretical models and provided a new theoretical framework explaining how the electrical sense might determine the compass direction in which the animal is swimming.

While elasmobranchs can detect magnetic fields through their electroreceptive ampullae of Lorenzini, Kirschvink, Walker et al. (2001), provide data that the electroreceptive system is not the basis of the magnetic orientation sense in short tailed stingrays. Therefore, while the electric sense is well known to be used in prey detection in marine elasmobranchs, and while it is a potential source of orientational information, the electric sense has not thus far been conclusively demonstrated to be a primary means of deriving navigational information over long distances. See discussion below related to Magnetic Orientation in Marine Species.

Electric Discharges In Marine Fishes

The marine electric rays of the family Torpedinidae, Order Rajiformes, are not only sensitive to ambient electric fields but generate strong electric discharges from the highly specialized tissues of the electric organs which are derived from muscle tissue. Lorenzini (1678) was the first to determine that muscle contraction is based on electric discharges and proposed that the electric organ of marine electric rays is derived from muscle tissue. Zakon and Unguez (1999) describe the repeated evolution of electric organs from muscle tissue in six lineages of fishes. The embryonic development of the electromotor system of electric rays is described by Fox, Kotting et al. (1985).

Belbenoit and Bauer (1972) and Belbenoit (1986) describe prey capture behavior and electric organ discharge (EOD) in *Torpedo marmorata*. Bray and Hixon (1978), and Lowe, Bray et al. (1994)describe the same behavior for *Torpedo californica*. Feeding and growth of newborn *Torpedo ocellata* is described by Michealson, Sternberg et al. (1979). The olfactory organ of *Narcine* is described by Waghray (1985)while O'Sullivan, McConnaughey et al. (1987)describe a parasitic snail that feeds only on the blood of *Torpedo californica*. The jelly of the ampullae of Lorenzini of electric rays is described by Ilyinski and Krasnikova (1974). Rudloe (1989a; 1989b)described the habitat and behavior of the lesser electric ray *Narcine brasiliensis* as well as their highly oriented movements in coastal waters, their avoidance by predators and techniques for maintenance of that species in captivity.

Magnetic Orientation in Marine Species

Viguier (1882) first proposed that animals could navigate by sensing the earth's magnetic field. Convincing experimental evidence of the use of the geomagnetic field for terrestrial animal orientation was first described in honeybees (Lindauer and Martin 1968; Walker and Bitterman 1989), homing pigeons (Keeton 1972; Gould 1982), and migratory birds (Wiltschko 1972; Wiltschko and Wiltschko 1995). None of these species possess any known electroreceptors. Therefore other magnetic sensory modalities must exist. The existence of magnetoreception has also been demonstrated in bacteria, planarians, mollusks, insects, elasmobranchs, salamanders, insects, mice, and moles (Schmidt-Koening and

Keeton 1978; Mather and Baker 1981; Walker and Bitterman 1989). The extensive behavioral literature on magnetic orientation by animals has been reviewed and summarized by Kirschvink (1983; 1997)and by Walker, Dennis, and Kirschvink (2002).

Several species of marine animals are known to travel direct routes of hundreds to thousands of kilometers in apparently featureless deepwater environments between specific locations with extraordinary accuracy. These animals can compensate for displacement by currents. Only the earth's magnetic field is on a scale sufficient to provide the necessary orientational clues for such oriented movement.

Electrosensitive elasmobranchs that orient to magnetic fields include migrating blue sharks that maintain straight courses for days over hundreds of kilometers (Carey and Scharold 1990)and hammerhead sharks that orient to magnetic anomalies on the sea floor (Klimley 1993). Broun, Andrianov et al. (1974), Brown, Illnskii et al. (1977), and Broun and Ilyinski (1978) report on magnetic field perception in Black Sea rays as do Knudtson and Stimers (1977). Orientation to magnetic fields has also been demonstrated in the marine short tailed stingray (Hodson 2000). Kalmijn (2000) reviews the ability of elasmobranchs to orient to the earth's magnetic field.

Nonelectric marine fishes, reptiles and mammals also orient to the earth's magnetic field. These species include tuna (Walker 1984; Walker, Kirschvink et al. 1984; Holland, Brills et al. 1990) and chinook and sockeye salmon (Quinn 1980; Taylor 1986; Taylor 1987; Mann, Sparks et al. 1988). In addition to fishes, the distribution of several species of whales and the locations of frequent whale strandings are associated with magnetic anomalies (Klinowska 1985; Kirschvink, Dizon et al. 1986; Walker, Kirschvink et al. 1992). Loggerhead sea turtle hatchlings also orient to the geomagnetic field (Lohmann and Lohmann 1996; Papi, Juschi et al. 1997; Irwin and Lohmann 2000; Papi, Luschi et al. 2000; Lohmann, Cain et al. 2001). The detection and use of the geomagnetic field for orientation in aquatic species is reviewed by Walker, Dennis et al. (2002) and by Walker, Diebel et al. (2003).

The ability of non-electric marine species to orient magnetically clearly indicates the existence of a non-electric magnetic sensory receptor.

Magnetic Receptor Organ

The behavioral data demonstrating the existence of a magnetic sense in non-electric species was questioned for years because no sensory receptor to directly detect magnetic fields had been demonstrated. However, in the past two decades, nanoscale magnetite crystals (Fe_3O_4) have been shown to be produced biologically in the tissues of many species, both terrestrial and aquatic, and ranging from bacteria to vertebrates taxonomically (Lowenstam 1962; Blakemore 1975).

Biogenic magnetite was proposed as the primary magnetic receptor by Kirschvink (1980)and by Kirschvink and Gould (1981). Walker (1984), and Walker, Kirschvink et al. (1984) described a candidate sense organ in the form of single domain magnetic crystals in a sinus of the dermethmoid bone of tunas. Evidence for the role of magnetite as the receptor for the magnetic sensory ability was also found by Walker, Quinn et al. (1988) in sockeye salmon. The receptor was further localized to magnetite in the superficial ophthalmic branch of the trigeminal nerve in vertebrates (Semm and Beason 1990; Walker, Diebel et al. 1997; Diebel, Proksch et al. 2000). This research was summarized by Kirschvink, Walker et al. (2001).

Magnetic Particles in the Inner Ear of Marine Fishes

Elasmobranchs including guitarfish and electric rays as well as deep-sea rattails are known to select exogenous grains of sediment and to sequester them in the sacculus of the inner ear that communicates directly with the exterior environment via the endolymphatic duct. Such grains include quartz (Stewart 1906)in the shark *Squatina;* black particles in the inner ear of *Squatina* and the electric ray *Torpedo ocellata* (Nisho 1926). Fange (1982)examined exogenous grains in the inner ear of two species of electric rays, *Torpedo nobiliana* and *T. marmorata*, and found the grains to be quartz, calcium carbonate and unidentified dark minerals embedded in a gelatinous material. O'Leary, Vailches-Troya et al. (1981) and Vilches-troya, Dunn et al. (1984) identified similar dark exogenous particles in the sacculus of the elasmobranch guitarfish as magnetite and described their distribution in a highly organized curved band relative to non magnetite grains. The organization of the exogenous magnetite grains into a band was found to be maintained by the gelatinous matrix. Vilches-troya, Dunn et al. proposed that these bands of exogenous magnetite could function as a magnetic receptor organ. In addition, the inner ear has also been proposed to be an electrosensory organ by Mark and Rattay (1991). Magnetite grains are also known to occur in similar bands in the lesser electric *ray Narcine brasiliensis* (Rudloe 2003).

Descriptions of otolith and sacculus anatomy in elasmobrach species have been made by Corwin, Lychakov, Boyadzhiera et al. (1985), Lychakov, Boyadzhiera-Mikhailova et al. (2000). Inner ear anatomy in marine teleost species has been reported by Popper (1978), Popper and Hoxter (1981), Platt and Popper (1984) and Ramcharitar, Higgs et al. (2001).

APPLICATIONS FOR ADDITIONAL STUDIES OF MARINE ELECTRIC FISH

Relatively large-sized, free-ranging marine species such as *Narcine brasiliensis* require large containment areas and specialized life support systems to maintain significant populations in captivity to allow investigation of the roles and interactions of specialized tissues, in orientation and predator avoidance or in electrical generation that may promote neural tissue regeneration. While the availability of test organisms and the difficulties associated with maintenance of healthy animals in captive situations would be challenging, specialized facilities are available for such work.

Further studies of the electrical and magnetic orientation abilities of *Narcine brasiliensis* are indicators that this organism may provide keys and insights into the role of electric current and tissue regeneration. The evidence for biogenic magnetite as the primary receptor of the geomagnetic sense is compelling. However, the highly organized bands of exogenous magnetite in the inner ear of elasmobranch, guitar fish, and electric rays remains unknown and could be an additional magnetic receptor system. This intriguing topic of research could have useful applications if better understood.

In addition, the function of highly organized bands of exogenous magnetite in the inner ear of elasmobranch guitarfish and electric rays remains unknown but is an intriguing topic of research that may have useful applications if better understood. Both guitarfish and electric rays are benthic species that move over scales of tens of kilometers. The lesser electric ray, *Narcine brasiliensis,* is known to consistently orient to extremely localized areas of the sea floor and to move between them over a distance of kilometers in a highly directed and well oriented path (Rudloe 1989b).

Marine species including small sharks, rays, and stargazers are all found in relative abundance in the northern Gulf of Mexico and adapt to captivity in large saltwater enclosures where additional studies of electrical properties and healing can be designed, controlled, and conducted.

Therefore, productive topics for further research include the following:

- Given the documented correlation between brain growth, electric discharges, and sexual behavior in *Apteronotis leptorhynchus*, what if any supporting or interactive role might specialized electric tissues have in accelerated healing and tissue regeneration?

- Given that rays and sharks exhibit unique electro sensing abilities and rapid healing has been reported is there a neurophysiological link?

- Given that *Narcine brasiliensis* has strong electro sensing and magnetic abilities, does this animal also exhibit rapid healing similar to other elasmobranchs?

- Given the proposal that organized bands of magnetite described in the literature represent a previously undescribed magneto receptor system, what is the function of exogenous magnetite in the inner ear of guitarfish and electric rays and are there biomimetic applications for the war fighter?

CONCLUSIONS / RECOMMENDATIONS

Lampl Herbert Consultants and Gulf Specimen Marine Laboratories conducted an extensive literature review of the electric and magnetic sensory systems in marine fish with emphasis on electric rays. Research on healing and tissue regeneration abilities in marine fishes was also reviewed to determine if the literature reports that there is a correlation between electric properties and accelerated healing or regeneration. This information creates a knowledge platform that may be applied to future studies on the electric ray.

The authors believe originally proposed that the results of a literature review could be used as a foundation for a workshop or “think tank” to create a working agenda and priorities for hypothesis-based research on electric fishes as they relate to areas of interest of DARPA and The Technical Basis. Think tank participants would include Lampl Herbert Consultants, Gulf Specimen Marine Laboratories, Technical Basis, and key individuals identified during the literature search and review.

Possible Applications

The authors believe additional studies related to *Narcine* brasiliensis and other electric fishes will contribute to the operational goals of the Department of Defense (DoD) and DARPA's strategic thrust, particularly in the Bio-Revolution area; see Table 1 below.

TABLE 1. CONTEXT OF THE PROPOSED RESEARCH

QDR Operational Goals for Transformation	DARPA's Strategic Thrust	Electric Fish Applicability to DARPA Interest
Protecting and sustaining U.S. Forces in distant anti-access or area-denial environments and defeating anti-access and area-denial threats	- Networked Manned and Unmanned Systems - Bio-Revolution	X
Denying enemies sanctuary by providing persistent surveillance, tracking, and rapid engagement with high-volume precision strike, through a combination of complementary air and ground capabilities, against critical mobile and fixed targets at various ranges and in all weather and terrains	- Detect, Identify, Track and Destroy Elusive Surface Targets - Characterization of Underground Structures - Bio-Revolution	X

Many ideas concerning specific applications of the properties of electric fish to military goals, several preliminary links to the war fighter readily come to mind:

- A separate literature review focused on the neural regeneration abilities of freshwater electric fishes would be useful in developing procedures for better treatment of spinal cord and head wounds and injuries with eventual broader applications to the treatment of stroke

- This line of investigation could be useful in developing an "augmentative device" for humans to exploit the biomagnetic reception possibly exhibited by *Narcine*. This application may be possible with a more complete understanding of the neurobiological role of endogenous and exogenous magnetite within the animal's own electric field. This line of inquiry has relevance and application to DARPA's ongoing research in spatial orientation in the human animal.

- *Narcine* is an electric ray that exhibits highly sensitive electrical current reception, generates, stores and discharges sizeable electric potential, and may well exhibit magnetic orientation; Is this ray also able to regenerate neural tissue?

- *Narcine's* disk design and soft skin may prove useful in designing physical and computer-driven models to enhance underwater stealth capabilities in manned and unmanned vehicles. Such models may enable engineers to design functional hardware inspired by knowledge of the ray's form and function.

- Significant literature exists on the biochemistry of electric organs and their value as neurotransmitters. An understanding of how the biological "batteries" used by electric fish function in nature could provide potential models for new underwater power sources.

- Unlike conventional AC electricity, which causes muscles to spastically contract, the EOD of Narcine forces a predator to release its grip – what is the source of this difference? The mechanism by which *Narcine* detects and repels sharks could be the basis of an early warning system to protect ships from hostile divers or stop an attack in progress.

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