

MAGNETIC SENSITIVITY AND ITS POSSIBLE PHYSICAL BASIS
IN THE YELLOWFIN TUNA, *THUNNUS ALBACARES*

Michael M. Walker

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center, Honolulu Laboratory
Honolulu, Hawaii 96812 USA and
Department of Zoology
University of Hawaii
Honolulu, Hawaii 96822 USA

ABSTRACT

Many animals are known to orient to magnetic fields. However, two central problems in the study of magnetic sensitivity have been the almost complete failure of magnetic field conditioning experiments and the lack of evidence for a feasible transduction mechanism. In the studies reported here yellowfin tuna learned to discriminate between two Earth-strength magnetic fields in a discrete-trials/fixed-interval conditioning procedure. Magnetometry experiments, diffraction spectra and electron microscope analyses demonstrated single-domain crystals of the ferromagnetic mineral magnetite in the head of this species. The crystals are concentrated in tissue contained within a sinus formed by the ethmoid bones of the skull. Theoretical analyses show that the crystals would be suitable for use in magnetoreception if linked to the nervous system. The physical properties of the crystals would determine the operation of magnetoreceptor organelles and constrain the capacities of the magnetic sense. Tests of these constraints in appropriately designed conditioning experiments will provide powerful tests of the ferromagnetic magnetoreception hypothesis.

INTRODUCTION

For pelagic fishes migration represents a substantial investment of energy (Sharp and Dotson 1977). These energetic costs imply

intense selection on the sensory mechanisms that guide migration. With the exception of the upstream migration of salmon (Hasler et al. 1978) the known capacities of the sensory systems of fishes are not sufficient to explain their navigational achievements (Tesch 1980). We must therefore either reexamine the capacities of the known sensory systems or attempt to find new systems that could provide fish with the necessary sensory abilities (Kreithen 1978). This paper takes the second of these approaches, investigating the responses of yellowfin tuna to magnetic fields and a possible transduction mechanism for the magnetic sense of this and other migratory fishes.

Many animals from different taxa are known to respond to one or more features of the geomagnetic field (Keeton 1971, 1972; Wiltschko 1972; Walcott and Green 1974; Lindauer and Martin 1972; Martin and Lindauer 1977; Quinn 1980; Wiltschko et al. 1981). These responses fall into two general categories--responses to magnetic field direction and to magnetic field intensity. Although the experimental results are repeatable, they are primarily based on unconditioned responses and tell us little about the sensory mechanism and its capacities.

The central problems in the study of magnetic sensitivity in animals have been the almost universal failure of magnetic field conditioning experiments and the lack of evidence for any of the hypothesized magnetic field transduction mechanisms. Conditioning experiments have either failed or been unrepeatable (Reille 1968; Kreithen and Keeton 1974; Beaugrand 1976; Bookman 1977, 1978). Where conditioning was obtained (Kalmijn 1978) subsequent psychophysical analyses of the capacities of the sense were either not done or not reported. Numerous magnetic field transduction mechanisms have been suggested (e.g., Kalmijn 1974; Leask 1977; Jungerman and Rosenblum 1980), but many are unacceptable because they do not explain the general responses to magnetic fields by animals or because magneto-reception is known to occur when the special conditions required by the hypotheses are not met (e.g., Phillips and Adler 1978; Quinn et al. 1981).

The hypothesis that the basis of the magnetic sense is single-domain crystals of magnetite produced by animals has attracted much attention in recent years (Gould et al. 1978; Walcott et al. 1979; J.L. Kirschvink, M.M. Walker, A.E. Dizon, and K.A. Peterson unpublished). This hypothesis is appealing because it can explain the general responses of animals to magnetic fields (Yorke 1979, 1981; Kirschvink and Gould 1981) and lends itself to behavioral testing (Kalmijn 1981; Kirschvink 1981). It also provides us with the basis for a search for receptors which could mediate the behavioral responses.

In this paper I report the use of an orthodox behavioral

conditioning paradigm (Woodard and Bitterman 1974) to train yellowfin tuna to discriminate between two different earth-strength magnetic fields. I also demonstrate the presence of single-domain magnetite crystals in the skull of this species. Based on the theoretical analysis of J.L. Kirschvink and M.M. Walker (unpublished) I then propose behavioral experiments to test for constraints on magnetoreceptor operation resulting from the physical properties of the magnetite crystals. Pending demonstration of a functional link between the crystals and the nervous system these experiments will provide the best test of the ferromagnetic magnetoreception hypothesis.

CONDITIONING EXPERIMENTS

Different magnetic field stimuli can be delivered only successively and not simultaneously. Therefore, in magnetic field conditioning experiments the subject cannot make a simultaneous comparison of stimuli. This limits the choice of conditioning procedures to those which are effective using singly presented discriminative stimuli. The approach I chose was to define a single response, to reward that response under one set of magnetic field conditions and not under another, and to compare the readiness with which the response was expressed under the two conditions (Bitterman 1966). The measure of behavior compared between the stimulus conditions was the rate of performance of a conditioned response. The primary advantage of rate as a measure of discrimination is its sensitivity; it can vary widely and rapidly in response to changes in experimental conditions and can accommodate short-term variability in behavior (Kling 1971). This approach seemed likely to test efficiently the ability of yellowfin tuna to discriminate between different magnetic fields.

These experiments were conducted at the Kewalo Research Facility of the National Marine Fisheries Service, Honolulu Laboratory. The fish used were juvenile yellowfin tuna (40-50 cm fork length) tested individually in one of two cylindrical test tanks (6 m diameter, 0.75 m depth). The experimental tanks contained no metal and each had 100 turns of number 18 AWG copper wire wrapped around its perimeter. A 1-ampere direct current passing through these wires added a vertical magnetic field to the background field. This field was nonuniform, adding from 10 microTesla (μT) in the center to 50 μT at the edge of each tank. The response apparatus was a 60- x 30-cm pipe frame lowered into the tank during trial periods and retracted during intertrial periods. The frame, the magnetic field and a semi-automatic feeder mounted at the side of the tank (Jemison et al. 1982) were operated by mechanical and electrical linkages from the experimental control room. The control room was physically isolated from the experimental tank and was darkened during experiments. The fish were observed through small viewing ports and their responses recorded manually.

The differences between the two magnetic fields used in the discrimination experiments were as follows. The local Hawaiian field was uniform throughout the tanks. That is, inclination, declination and total field intensity were the same at any point in the area occupied by the fish. The altered field introduced significant radially oriented gradients of both intensity and inclination within the tanks. These experiments therefore provided the fish with two very different magnetic fields as discriminative stimuli. The fish could conceivably monitor differences in magnetic field inclination, intensity or the gradients in these two parameters to make the discrimination.

After being allowed to acclimate to the experimental tanks fish were trained to swim through the pipe frame for a food reward (a piece of cut smelt, *Osmeridae*) delivered from the feeder. In discrimination testing a trial began with simultaneous presentation of the pipe frame and either the positively (S+) or negatively (S-) reinforced stimulus. All responses by the fish within a 30-second trial period were counted. In S+ trials the fish was rewarded with a piece of food following the first response after 30 seconds. In S- trials a 10-second penalty timer started at the end of the trial period. The timer was reset by each subsequent response by the fish until either the penalty time elapsed or a total of 30 seconds of penalty had accumulated. Response to S- was thus penalized by extending the trial without any possibility of the fish obtaining food. After reinforcement had been given the pipe frame was retracted for a variable intertrial interval (mean 90 seconds) after which another trial sequence began.

The fish were given 30 trial training sessions once daily. In any trial session the S+ and S- were presented 15 times, with no more than three S+ or S- trials in succession. Testing was balanced by training two fish with the normal Hawaiian field and two with the altered field as S+. Statistical treatment of the data was by analysis of variance.

Discrimination between the two magnetic field conditions occurred after two 30 trial sessions (Fig. 1). During the first two sessions there was no separation of response rates but from the third day all four fish maintained different rates of responding during S+ and S- trials. An analysis of variance comparing S+ and S- response rates before and after 60 trials for all four fish yielded an $F(1,3)$ stimuli 7.61, $P = 0.07$, and an $F(1,3)$ stimuli by blocks = 102.55, $P = 0.002$. All other comparisons within the analysis did not approach significance.

Control trials were performed with one fish by interrupting the current to the coil; normal procedures were then followed. The

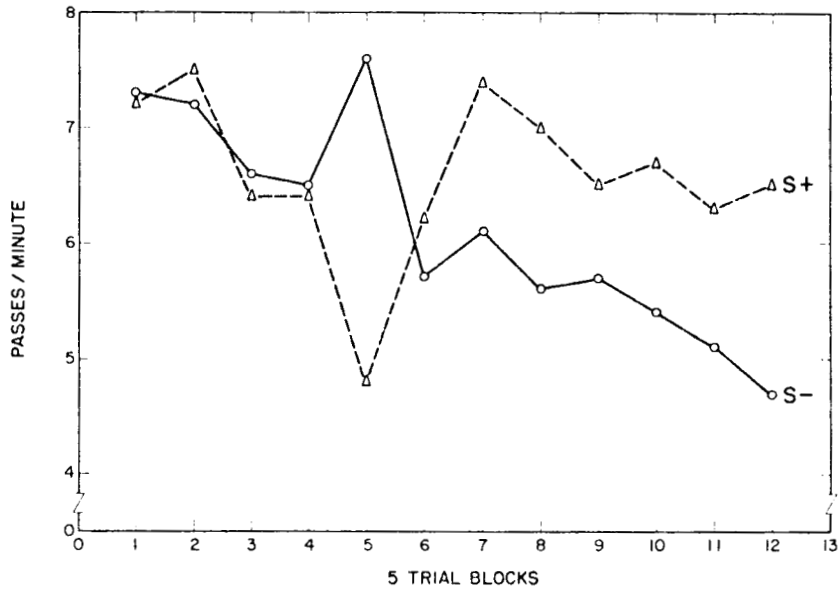


Figure 1. Magnetic field discrimination learning in yellowfin tuna. Each point is the average of five S+ or S- trials for the four fish tested. (Walker et al. 1982; (C) 1982 IEEE.)

response rates during S+ and S- trials fluctuated randomly during this period (Fig. 2). When the power supply was reconnected to the coil the fish was again able to make the discrimination, although

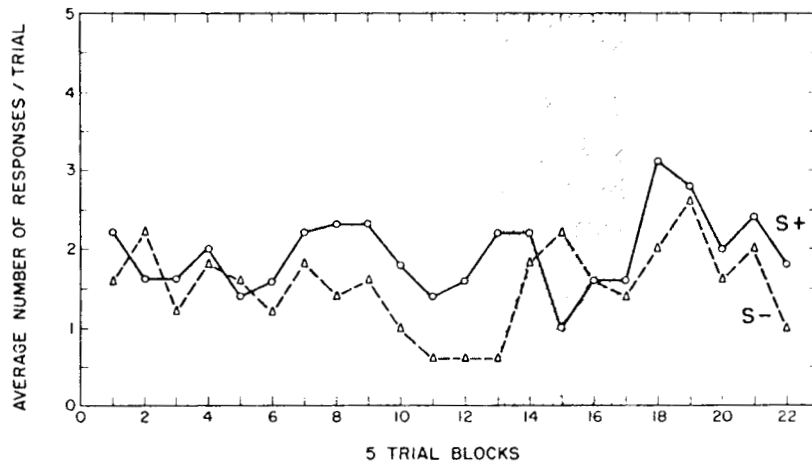


Figure 2. Magnetic field discrimination learning in yellowfin tuna. Control tests shaded. (Walker et al. 1982; (C) 1982 IEEE.)

less strongly than before the control trials were conducted. Evidently the magnetic fields used in the experiment were necessary for anticipation of positive and negative reinforcement by the fish.

These experiments demonstrate the ability of yellowfin tuna to discriminate between different earth-strength magnetic fields. Although the discrimination is consistent in all individuals it is consistently weak. This results from limitations imposed by the fish themselves. Tunas swim continuously and can only be conditioned to produce responses involving movement of their whole body (Iversen 1967; Nakamura 1968). The fish therefore did not attain high rates of performance of the response used to compensate for this limitation. Consequently the scope for change in response rate was low and the variation in responding was high compared to the mean response rate. The upper limit of 30 seconds of penalty time was established because some fish jumped out of the experimental tanks during development of the procedure. This made the "cost" of response to S- low so that the penalty time could only be expected to suppress S- responding weakly. That the fish were able to discriminate between the two fields at all, given these limitations on the procedure, suggests that their magnetic sense is well developed and underlines the sensitivity of response rate as a measure of discrimination.

The conditioning technique used here should be applicable to a range of studies on magnetic sensitivity. Other tunas (skipjack tuna, *Katsuwonus pelamis*, and kawakawa, *Euthynnus affinis*) have shown evidence of magnetic sensitivity in preliminary conditioning experiments (Walker unpublished data). These studies should be continued and extended to other species. The technique can also be used to test whether fishes possess a magnetic compass responding to magnetic field inclination or polarity. This can be achieved by testing for the ability of fish to discriminate between fields in which horizontal or vertical components of the field are reversed. A polarity sensitive compass should discriminate between fields with horizontal, but not vertical, components reversed. An axial or inclination sensitive compass should permit the fish to discriminate between fields with vertical, but not horizontal, components reversed (Wiltschko 1972).

The experiments carried out so far reveal nothing about the mechanism by which the tunas detect magnetic fields. I saw no evidence that the induced electrical fields associated with the presence or absence of water currents in the experimental tanks or the rate at which the magnetic field was changed affected discrimination by the fish. Similarly, Quinn et al. (1981) concluded that sockeye salmon fry and smolts must be able to detect magnetic fields in the absence of water flow in both fresh and salt water. From this behavioral evidence it seems unlikely that these teleost fishes detect magnetic fields by electrical induction in spite of the known

electric field sensitivity of Atlantic salmon, *Salmo salar* (Rommel and McCleave 1973). It therefore seems important to identify and test other hypotheses for magnetic field transduction mechanisms in teleost fishes.

PHYSICAL BASIS FOR MAGNETIC FIELD TRANSDUCTION

Magnetometry Experiments

Magnetic material has been detected in a variety of domain states in tissues of a number of different animals (Gould et al. 1978; Walcott et al. 1979; Presti and Pettigrew 1980; Mather and Baker 1981; Zoeger et al. 1981; Jones and MacFadden 1982). In the yellowfin tuna I sought to distinguish magnetic material that might be used in magnetoreception from other deposits by identifying particles in a suitable domain state that could be consistently found in the same place in different individuals. All the tissues that could be identified and extracted from the body of the yellowfin tuna using glass microtome knives were tested for saturation isothermal remanent magnetization (sIRM) in a superconducting magnetometer. A feature of these studies is the small amounts of material involved and the ease with which contamination can influence the results. Procedures for avoiding entry of contaminants and tests for their presence in sample tissues have been developed and described in detail elsewhere (Kirschvink 1983).

There is a battery of paleomagnetic techniques available for the study of magnetic minerals. These techniques require some special adaptations for use in the study of biomagnetism. The magnetic fields associated with crystals of magnetic minerals in animals are very small and could not be detected in the presence of a background field. In a null field environment and at room temperature the crystal moments would be randomly oriented and not detectable. To detect the crystals it is necessary to freeze the sample tissue and prevent the orientation of the crystals from changing under the influence of thermal agitation (Kirschvink 1983). It is then possible to realign the moments of the crystals with a strong inducing magnetic field pulse (>0.3 T). The crystal moments then sum to produce the sIRM (also known as the moment of the sample) and become detectable in a superconducting magnetometer, if they are sufficiently concentrated in a tissue (1 100 nm crystal per 30,000 cells in a 9 mm^3 sample (Kirschvink 1983)).

A superconducting magnetometer detects weak magnetic fields in the samples and also magnetic field noise within the magnetometer itself. These measurements are combined to produce a signal to noise ratio for a tissue sample. Intensity of magnetization indicates the concentration of magnetic material within a sample and is estimated by dividing its moment by its volume (Kirschvink 1983). In this

study to be considered magnetic a tissue had to show high values for both these measures compared to other tissues taken from the same fish.

Magnetic crystals tend to have their moments aligned in an "easy" direction, usually the long axis of the crystals (Kirschvink and Gould 1981). The microscopic coercivity of the crystals is the magnetic field required to cause their moments to reverse direction. This coercivity is dependent on the size, shape and domain state of the crystals. Progressive alternating field (AF) demagnetization of a magnetic sample subjects the aligned crystal moments to decaying sinusoidal magnetic fields oriented in one axis. The orientation of the moments of magnetic crystals with coercivities less than the maximum alternating field applied will be randomized by this procedure. The contribution of the randomized crystal moments to the IRM will thus be removed and can be detected in the magnetometer as a reduction in the moment of a sample. The size of the randomizing field required to decrease the IRM to half its saturation value gives an estimate of the median coercivity of the crystals present in a sample. From this we can determine the likely source of the sIRM and the size, shape and domain state of the magnetic crystals.

The magnetometry experiments demonstrated that magnetic material is concentrated only in the head of the yellowfin tuna. Eighteen samples of tissues and organs extracted from a representative fish were not magnetic. A few samples showed either high signal to noise

Table 1. Values of saturation isothermal remanent magnetization in various tissues of a representative yellowfin tuna. Signal-to-noise values are the ratio of the measured value of the tissue to the mean of the noise level before and after the sample was measured. (Walker et al. 1982; (C) 1982 IEEE.)

Tissue	Signal-to-noise ratio	Magnetic intensity (picoTesla)
Left pectoral fin	1.5	45.3
Peduncle tendon	2.5	35.8
Gill	4.6	20.3
Eye	10.1	4.1
Whole parathyroid	15.4	39.4
Left rear parathyroid	11.0	47.4
Right rear parathyroid	18.5	255.3

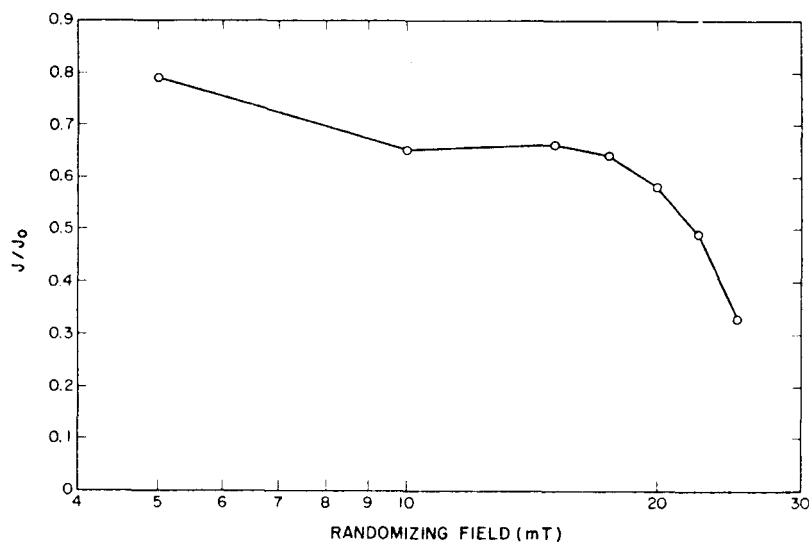


Figure 3. Progressive alternating field demagnetization of the ethmoids of three yellowfin tuna.

ratios or intensities of magnetization (Table 1). These I judged to be nonmagnetic and excluded from consideration. Only samples from the ethmoid bones of the fish's skull exhibited high values for both measures of magnetization (Table 1) in that and all other individuals tested. Progressive AF demagnetization of the ethmoid bones of three yellowfin tuna gave an estimate of median coercivity for the magnetic particles of 22.5 mT (Fig. 3). This is consistent with the presence of a dispersion of single-domain magnetite crystals with particle lengths and diameters of approximately 50 and 40 nm (McElhinny 1973). The narrow range of particle sizes is unlike the pattern observed for geologic and synthetic magnetite crystals, which commonly exhibit log-normal distributions (J.L. Kirschvink personal communication).

Identification of the Magnetic Material

Although the magnetometry experiments indicate that the ethmoids of the yellowfin tuna contain ferromagnetic particles they do not uniquely identify the mineral involved. Extraction of the crystals themselves is necessary to do this and to confirm the estimates of their size and shape. Using glass knives I removed the tissue from within the ethmoids of five yellowfin tuna, ground the tissue in a glass tissue grinder, extracted released fats with ether and digested the remaining cellular material in several changes of millipore-filtered 5% hypochlorite solution (commercial bleach). After centrifuging and washing the digested material small black aggregates of crystals could be attracted to a magnet held to the side of the

test tube. These aggregates could then be pipetted onto slides for analyses of diffraction spectra. A brief digestion in buffered EDTA was necessary to obtain aggregates that could be dispersed completely by an alternating magnetic field after they were pipetted onto carbon-coated copper mesh grids. This made it possible to examine individual crystals in the transmission electron microscope (TEM).

X-ray diffraction of the magnetic aggregates extracted from the ethmoid tissue of the yellowfin tuna uniquely identified the crystals as magnetite. An electron microprobe analysis showed that the crystals contained no measurable titanium, manganese, nor chromium, indicating that the crystals were probably not of geologic origin. The crystals averaged 45 x 38 nm and appeared to be hexagonal in cross section. They are thus single-domains and conform to the sizes estimated from their coercivities. The nonoctahedral crystal habit adopted by these crystals in the yellowfin tuna distinguishes them from all geologic and synthetic magnetites. Thus we have evidence from a number of sources that the magnetite crystals found in the ethmoid tissue of the yellowfin tuna must have been produced by the fish themselves. The fish do this with close control over the size, shape and composition of the crystals. They therefore control the physical properties of the crystals and so control their operation in the hypothetical magnetoreceptors considered next.

THE FERROMAGNETIC MAGNETORECEPTION HYPOTHESIS

The basis for magnetite-based magnetoreception is the torque exerted on single-domain magnetite crystals by the geomagnetic field. This torque is described by the relation $\tau = \mu \times B$ where τ is the torque, μ is the moment of a magnetite crystal and B is the intensity of the external magnetic field. The torque will cause the crystals to align with the external field. At physiological temperatures in a live fish the crystals will be subject to thermal agitation, which will cause their vector direction to wander randomly about the applied field direction. The mean alignment of the crystals will be in the direction of the external field so that a compass receptor system needs only to monitor the orientation of up to 1,000 crystals or groups of crystals to detect magnetic field direction accurately (Yorke 1979). The variance of the orientation of the crystals about the external field will depend on its intensity (Kirschvink and Gould 1981; Yorke 1981). Monitoring the variance will thus provide the physical basis for a response to magnetic field intensity (Gould 1980, 1982; Moore 1980; Walcott 1980).

The above analysis yields three testable behavioral predictions (J.L. Kirschvink and M.M.Walker unpublished). The first is that the magnetic sense organ should be made up of separate, independent compass and intensity receptors with different magnetic moments. The second is that the accuracy of the compass response should be

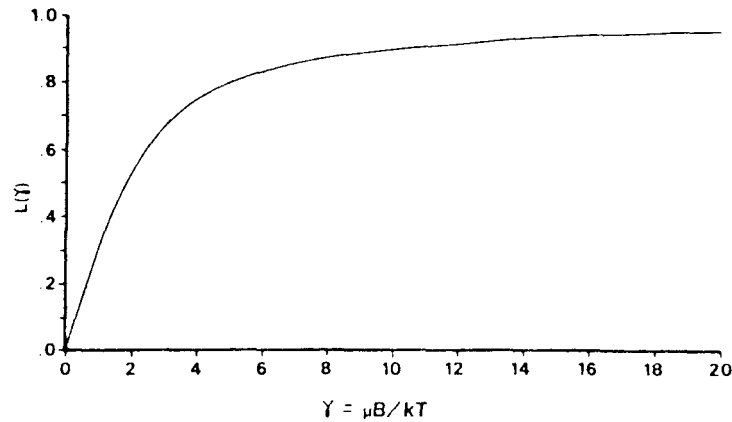


Figure 4. The Langevin function plotted against γ , the ratio of magnetic to thermal energies for single domain magnetite crystals. The accuracy of alignment of the crystals ($L(\gamma)$) increases rapidly up to γ values of about six and increases asymptotically thereafter. The accuracy of behavioral responses to magnetic field direction mediated by magnetite-based magnetoreceptors should at first increase rapidly with external field intensity. Beyond a certain point further increase in external field intensity should not lead to greater compass accuracy. (Modified from Kirschvink 1981.)

quantitatively defined by the Langevin function (Fig. 4; Kirschvink 1981), i.e., the accuracy of the compass response should increase asymptotically with external field strength. The third prediction is that the threshold sensitivity to changes in magnetic field intensity will be defined by the first derivative of the equation for the root mean square deviation of the crystals' alignment in the intensity receptor organelle. Plotted against external field strength the threshold sensitivity should increase to a maximum at about 50 μT (= 0.5 Gauss) and decline monotonically thereafter (Fig. 5; J.L. Kirschvink and M.M. Walker unpublished).

These predictions are testable with currently available behavioral conditioning procedures. The first prediction is testable using the conditioning paradigm reported here. A factorial design is suggested in which experiments test for separate responses to magnetic field direction and intensity. The tests require fish to discriminate between magnetic fields with different vector directions but the same total intensity and between fields with the same direction but different intensities. The second and third predictions are testable with suitable modifications of the conditioning procedure used for testing sun-compass orientation in

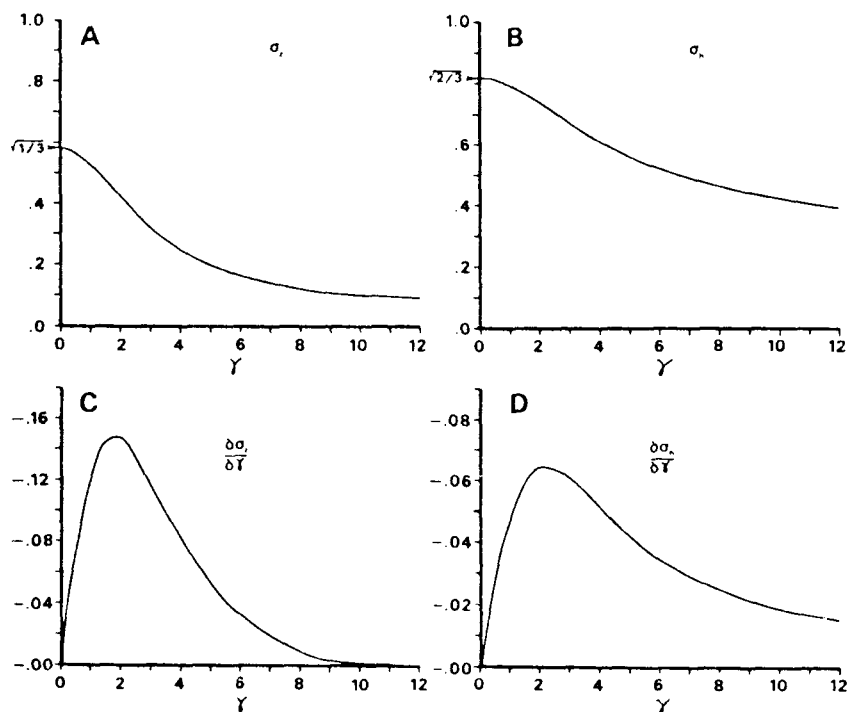


Figure 5. A,B. Plots of the variance of the Langevin function parallel and perpendicular to external field direction against γ , the ratio of magnetic to thermal energies of single domain magnetite crystals. C,D. Plots of the first derivative of the Langevin variance parallel and perpendicular to external field direction. The Langevin variance declines with increasing γ , and, for magnetite-based magnetoreceptors, will be dependent on external field intensity. It follows that receptors monitoring some component of this variance will be most sensitive to changes in intensity when the change in variance with intensity is a maximum. C,D show that the maximum rates of change of variance with intensity occur at about $\gamma = 2$. Behaviorally measured thresholds to magnetic field intensity changes should follow the form of these plots. Threshold sensitivity should increase rapidly with external field intensity to a maximum and decline thereafter. (J.L. Kirschvink and M.M. Walker, unpublished data.)

white bass by Hasler et al. (1958). The accuracy of a directional response should increase asymptotically with magnetic field strength and should conform to the Langevin function (Fig. 4) (Kalmijn 1981; Kirschvink 1981). The same conditioning approach can be adapted to

test for the smallest changes in magnetic field intensity that the fish can detect. Fish should be required to produce or withhold a single response with accuracies approaching 90-100%. Threshold sensitivity is then measured by decreasing the difference between positively and negatively reinforced stimuli using appropriate procedures (Engen 1971). This threshold sensitivity to magnetic field intensity changes should change with field strength in the manner shown in Fig. 5 (J.L. Kirschvink and M.M. Walker unpublished).

CONCLUDING REMARKS

This and other recent studies have demonstrated repeatable behavioral responses to magnetic fields by migratory fishes (Quinn 1980; Quinn et al. 1981; Quinn and Brannon 1982). Theoretical analyses based on the physical properties of single-domain magnetite discovered in yellowfin tuna and other animals easily explain the separate magnetic compass and intensity responses of vertebrates and invertebrates (Yorke 1979, 1981; Kirschvink 1981; Kirschvink and Gould 1981). J.L. Kirschvink and M.M. Walker (unpublished) extend these analyses and make testable predictions on the nature and organization of ferromagnetic magnetoreceptor organelles and the constraints they place on the capacities of the magnetic sense.

Gross dissection of the anterior region of the skull of yellowfin tuna reveals the supraorbital nerve. This trunk carries the anterior acousticolateralis nerve and ramifies in the region of the ethmoid bones. The hair cells associated with the acousticolateralis nerve system could provide ideal mechanoreceptors for use in magnetoreception with the magnetite crystals. Preliminary histological studies suggest the presence of nerves in a thin band of tissue in the midline immediately beneath the dermethmoid bone (Walker unpublished data). Thus for the first time there is found together in a species a repeatable behavioral response to magnetic fields and the necessary physical and neural components of a ferromagnetic sense organ. Proving the links between these components of a magnetic sense should be an important goal for future research.

It now seems opportune to speculate on the possible utility of the magnetic sense of pelagic fishes for navigation. Acoustic tracking experiments have shown that swordfish *Xiphias gladius* can maintain a compass heading for periods of up to several days (Carey and Robison 1981). Skipjack tuna make diurnal horizontal movements without retracing their path onto and off shallow banks where they feed during daylight hours (Yuen 1970). These movements suggest that these fishes are able to determine their position and set a compass course toward a goal. The knowledge that pelagic fishes respond to magnetic fields suggests the possibility that they use the geomagnetic field to guide their migrations. Field experiments to

test this hypothesis should not only show whether fish do use the geomagnetic field in navigation but may also indicate how the fish use the sense. This should contribute greatly to our understanding of the mechanisms of migration in fishes.

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