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Chains of single-domain magnetite particles in chinook salmon, *Oncorhynchus tshawytscha*

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Summary. Although the presence of magnetite in their tissues is correlated with the ability of different species to detect magnetic fields, proof that the magnetite is involved in magnetoreception has not yet been provided. Using the approach employed to localize and isolate magnetic particles in the yellowfin tuna, we found that single-domain magnetite occurs in chains of particles in tissue contained within the dermethmoid cartilage of adult chinook salmon, *Oncorhynchus tshawytscha*. The particles are present in sufficient numbers to provide the adult fish with a very sensitive magnetoreceptor system. Magnetite in the chinook can be correlated with responses to magnetic fields in a congeneric species, the sockeye salmon. Based on the presence of the chains of particles, we propose behavioral experiments that exploit the responses of sockeye salmon fry to magnetic fields to test explicit predictions of the ferromagnetic magnetoreception hypothesis.

Introduction

Discoveries of fine-grained magnetite in the bodies of honeybees and homing pigeons (Gould et al. 1978; Walcott et al. 1979) stimulated theoretical analyses of the suitability of the particles for use in magnetoreception (e.g. Yorke 1979, 1981; Kirschvink 1979; Kirschvink and Gould 1981) and attempts to demonstrate magnetite and magnetosensory abilities in other species. For example, recent studies found conditioned responses to magnetic field stimuli and approximately 100 million interacting particles of pure single-domain magnetite, possibly associated with nervous tissue, in tissue contained within the dermethmoid bone of the skull of the yellowfin tuna, *Thunnus albacares* (Walker 1984; Walker et al. 1984). Magnetic material, at least some of which is fine-grained magnetite, has been found in tissue from the premaxilloethmovomerine block of bones in the skull of the European eel, *Anguilla anguilla* (Hanson et al. 1984a, b), which also responds to magnetic fields (Branover et al. 1971; Tesch 1974). These results from phylogenetically distant species imply that magnetite and magnetosensory abilities are widespread among teleost fishes.

Proof that magnetite mediates magnetoreception, however, will depend on behavioral tests of predictions of the magnetite-based magnetoreception hypothesis. Such tests require identification of species that make appropriate responses to magnetic fields in experimental situations and that also possess magnetite suitable for use in magnetoreception. One possibility is juvenile sockeye salmon, *Oncorhynchus nerka*, which exhibit spontaneous directional preferences in orientation arenas that generally correspond to the axis of the nursery lake to which newly emerged fry migrate (Brannon 1972). In a series of investigations into the behavior of sockeye salmon, Quinn and his colleagues (Quinn 1980; Quinn et al. 1981; Quinn and Brannon 1982) have shown that the directional preferences in orientation arenas of lake-migrating sockeye salmon fry and smolts can be controlled by magnetic fields. Quinn et al. (1981) were able to predict from their behavioral observations that the magnetoreceptor of the salmon must be capable of operating in the dark, in the absence of water flow in both fresh and sea water, and be adaptable to geomagnetic field changes occurring over geologic time. These predictions are compatible with

the hypothesis that the magnetoreceptor of the salmon is based on magnetite. Demonstration of magnetite in salmon, therefore, should open the way for adaptation of currently available procedures for behavioral tests of predictions of the ferromagnetic magnetoreception hypothesis.

Here we report that single-domain magnetite occurs in tissue from the same area of the skull of adult chinook salmon, *Oncorhynchus tshawytscha*, as it has been found in the yellowfin tuna and the European eel. We also have isolated chains of the particles from the tissue where previously we could not, although the particles had been inferred to lie in small clumps or chains from their magnetic properties (Walker et al. 1984). Sufficient numbers of the particles are present to form a very sensitive magnetoreceptor organ. We conclude by proposing behavioral tests of the magnetite-based magnetoreception hypothesis that exploit the responses of sockeye salmon fry to magnetic field polarity in the orientation arenas used by Quinn et al. (1981).

The magnetite-based magnetoreception hypothesis predicts, *inter alia*, that for magnetic particles to be used in magnetoreception they, or groups of them, must (1) be magnetized uniformly and be large enough to align with the geomagnetic field against the randomizing effects of thermal buffeting (Kirschvink 1983; Kirschvink and Walker, in press), and (2) be biochemical precipitates to provide the uniform magnetophysical properties necessary for magnetoreception. Magnetic material that could be used for detecting both magnetic field direction and intensity (see Discussion) therefore should have a high remanent magnetic moment concentrated in a small volume of sample, a consistent anatomical position, and similar bulk magnetic properties within and among species (Walker et al. 1984). Magnetic material has been located most consistently in the heads of vertebrates (Walcott et al. 1979; Mather and Baker 1981; Zoeger et al. 1981; Baker et al. 1983; Beason and Nicholls 1984; Perry et al., in press), and in the front of the skull in particular in fishes. From these results we predict that magnetite should be located in the front of the skull of the salmon.

Materials and methods

Heads from four adult, net-caught chinook salmon were dissected using glass knives and non-metallic tools in a magnetically-shielded, dust and magnetic particle-free clean laboratory at the California Institute of Technology. The techniques for conducting non-magnetic dissections and avoiding contamination of samples have been described extensively, elsewhere (Kirschvink 1983; Walker et al. in press). Tissue samples were removed from each head, washed in glass distilled water, and rapidly frozen in liquid nitrogen. Each sample was exposed to a 4 ms duration, unidirectional magnetic pulse with a peak magnetic field of 0.7 Tesla (7,000 Gauss) generated by an impulse magnetizer (Furth and Waniek 1956; Kirschvink 1983) and immediately assayed for Isothermal Remanent Magnetization (IRM, a measure of the total volume of ferromagnetic material present) in the zero field environment of a superconducting magnetometer of the type described by Goree and Fuller (1976). The procedure was repeated for each sample, after which the mass of each sample was measured to the nearest 0.1 g. Tissues sampled in all fish included muscle, eye, brain, cartilage from the skull, and fatty tissue from within the anterior portion of the skull (the dermethmoid region). Other samples not taken in all fish included the olfactory rosette, the olfactory nerve, and gills.

The background signal in the magnetometer fluctuated at or below 5 pA^2 (5×10^{-9} emu), while the empty sample holder was kept below the 50 pA^2 level by regular washing and ultrasonic cleaning. A tissue sample was judged to be magnetic when the signal from the magnetometer, the magnetometer's signal to noise ratio at the time of measurement, and the calculated intensity of magnetization (moment/volume) were high compared with those obtained from other tissues taken from the same fish. Samples that were magnetic in all fish then were subjected to progressive alternating field (Af) demagnetization and IRM acquisition experiments similar to those done to geological samples by Cisowski (1981) and to yellowfin tuna by Walker et al. (1984). In these experiments, samples were frozen to and suspended from a thin, non-magnetic cotton thread as described by Kirschvink (1983). The advantage of this technique is that the measurement sensitivity is limited only by the noise of the vertical field sensor ($\simeq 5$ pA^2) rather than the sample holder. While frozen, the samples were Af demagnetized completely by placing them in a strong, 400 Hz vertically oscillating magnetic field produced by an air core solenoid which was itself in a zero-field environment. As the alternating field decays linearly from an initial amplitude of 0.1 Tesla to zero over about 15 s, it leaves equal numbers of the still fully magnetized particles with their magnetic moments oriented in opposite directions, leaving the sample with no net magnetic moment. The frozen samples then were exposed to a series of progressively stronger magnetic impulses, and their moments remeasured after each step. After the samples reached saturation (that is, they gained no further remanence with increasing pulse strength), they were sequentially demagnetized and remeasured in a similar fashion using progressively stronger peak oscillating fields.

We extracted the magnetic material for other experiments by grinding the magnetic tissues from several fish in a glass tissue grinder, separating the released fats by dissolving them in ether, and digesting the remaining tissue in nitrocellulose (0.42 μm pore size)-filtered 5% sodium hypochlorite solution (commercial bleach). Aggregates of magnetic particles released by this procedure were treated briefly with EGTA solution (rather than with EDTA as done previously; Walker et al. 1984). After washing, centrifugation, and magnetic separation, the fine powder obtained was identified by X-ray diffraction. Particles then were dispersed magnetically in an alternating magnetic field and mounted on carbon-coated copper mesh grids for transmission electron microscope (TEM) analysis.

Results

We found inducible remanent magnetization in several of the tissue samples examined (Table 1).

Table 1. Magnetic survey of selected tissues in four chinook salmon. For each tissue type examined, the mass is reported in g, the moment in units of 10^{-12} A^2 (10^{-9} emu), the intensity in pT, and the S/N quantity gives the signal to noise ratio of the sample holder and instrument at the time of measurement. A 0.6 g sample of the olfactory rosette from fish no. 1 also had low values (moment, intensity, and S/N) of 4.0, 6.6, and 0.8 respectively

	Muscle				Eye				Brain				Dermethmoid			
	Mass (g)	Moment 10^{-12} A^2	Int. pT	S/N	Mass (g)	Moment 10^{-12} A^2	Int. pT	S/N	Mass (g)	Moment 10^{-12} A^2	Int. pT	S/N	Mass (g)	Moment 10^{-12} A^2	Int. pT	S/N
Fish #1	1.3	50	3.9	0.7	9.0	163	1.8	3.3	1.4	52	3.7	1.1	0.5	895	178.0	11.9
Fish #2	1.8	140	7.8	2.8	6.3	3,300	52.4	97	1.3	51	3.9	0.8	1.0	517	51.7	14.6
Fish #3	2.1	730	34.7	40.7	6.9	270	3.9	20.9	1.9	25	1.4	2.5	0.3	320	106.7	24.8
Fish #4	2.0	140	7.0	10.9	5.0	551	11.0	42.7	1.3	776	59.7	60.2	1.2	300	25.0	10.1

Measures of magnetization were sufficiently low for most muscle and brain samples to permit the conclusion that these tissues were non-magnetic in these fish and could serve as control samples. Although the eye was sufficiently magnetic in at least two fish to invite more detailed study, two features of the data suggested it was unlikely to be the site of magnetoreception. First, the magnetic moment acquired by the eye was more variable from individual to individual than were the muscle and brain samples and, because the eye is in contact with the environment, the possibility that magnetic contaminants contributed to the moments acquired by the eyes examined can not be excluded. Second, the eye was the most massive sample measured in all fish. Eyes for three of the animals examined had intensities of magnetization, a measure of the concentration of magnetic particles in a sample, in the same range as the muscle and brain samples from the same fish. In contrast, moments acquired by the dermethmoid tissues were far less variable among fish and the intensities of magnetization were consistently higher for these samples than for muscle and brain samples from the same individuals. These results are consistent with the prediction that magnetic particles involved in magnetoreception should be concentrated in a small volume of tissue in a consistent anatomical position and led us to focus more detailed studies on the dermethmoid tissue.

Upon warming to room temperature, the dermethmoid tissues lost much of their remanent magnetization, indicating that the magnetic particles were at least partly free to rotate under the influence of thermal agitation in the low field environment of the magnetometer enclosure. When the dermethmoid tissue samples were subjected to the progressive IRM acquisition and Af demagnetization procedure described above, they acquired virtually all their remanence in fields less than 200 mTesla (mT), and lost it again in alternating

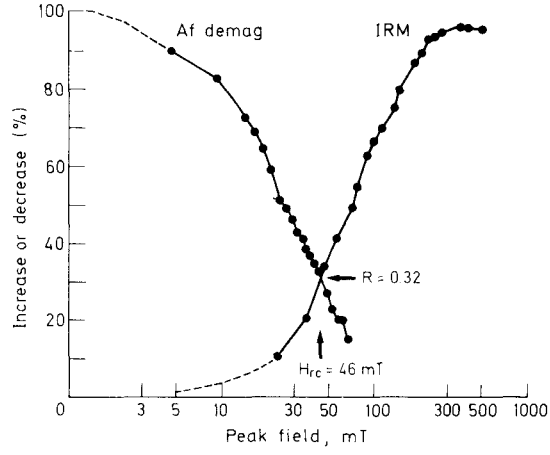

Fig. 1. Progressive acquisition and Af demagnetization of IRM for dermethmoid tissues from four chinook salmon. The intersection point of the two curves yields an estimate of the remanent coercive field (H_{rc}) of 46 mT, as well as the R value of interaction described in the text. These data are consistent with an assemblage of moderately interacting single-domain magnetite crystals

fields of less than 100 mT (Fig. 1). Acquisition and loss of remanence over this range of fields is consistent with the presence in the dermethmoid tissue of large numbers of single-domain crystals of magnetite. The flattening of the IRM acquisition curve at fields above 200 mT rules out most of the common ferromagnetic contaminants such as hematite (α Fe_2O_3) or metallic iron alloys, which continue to acquire remanence in much higher fields, and also multi-domain magnetite particles, which acquire and lose remanence at much lower fields than observed here (Zoeger et al. 1981; Kirschvink 1983; Walker et al. in press).

As shown by Cisowski (1981) and Walker et al. (1984) for the magnetite particles in chiton teeth and the dermethmoid tissue of the yellowfin tuna respectively, the intersection of the Af demagneti-

zation and IRM acquisition curves falls below the 50% magnetization point. For samples with completely non-interacting single-domain particles these curves should be symmetrical about the 50% magnetization point because particle moments will be aligned or randomized equally easily by unidirectional or alternating fields of equal intensities. The interactions between the fields produced by the particles themselves increase and decrease the fields necessary to align and randomize the particle moments respectively (Dunlop and West 1969), causing the IRM acquisition and Af demagnetization curves to shift apart and their intersection to fall below the 50% magnetization point. These data therefore imply that the magnetic particles in the dermethmoid tissue of the salmon are close enough to some of their neighbors to interact with each other (e.g. within one grain diameter).

Limited constraints on the average size and shape of the particles are provided by the abscissa of the intersection point of the IRM acquisition and Af demagnetization curves. This value approximates the remanent coercive field (H_{rc}) for the particles (Cisowski 1981) and is about 46 mT for the salmon. From Fig. 2, which combines the single-domain stability field boundaries of Butler and Banerjee (1975) with the contours of equal coercivity given by McElhinny (1973), a tentative length range of 40–100 nm can be established for the particles. Depending on the distribution of particle sizes, somewhere between 1 and 100 million such crystals would be necessary to produce the magnetic remanence observed in the salmon dermethmoid tissue. These numbers compare favorably with those reported for honeybees (Gould et al. 1978), homing pigeons (Walcott et al. 1979) and yellowfin tuna (Walker et al. 1984) and, if organized into interacting groups of several particles, would be more than enough to provide the salmon with a magneto-sensory system capable of responding to both magnetic field direction and intensity (Yorke 1979, 1981; Kirschvink 1979, 1981; Kirschvink and Gould 1981).

An X-ray diffraction pattern uniquely identified magnetic particles extracted from the dermethmoid tissue as crystalline magnetite. When viewed in TEM the particles were not completely dispersed but were arranged in linear chains of particles having similar dimensions to those found in the yellowfin tuna (Fig. 3). The particles appear to be bound in some form of organic matrix, which yields an occasional electron-transparent gap between adjacent crystals. The matrix apparently prevents the particles from contacting each other as a result of magnetic attractions but preserves

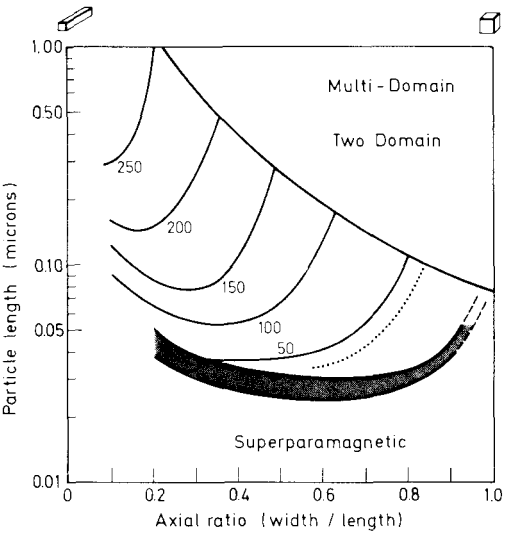

Fig. 2. Approximate contours of equal microscopic coercive force in mT (from McElhinny 1973) superimposed on the size and shape boundaries for single-domain magnetite of Butler and Banerjee (1975). Magnetite particles which spontaneously display single-domain behavior are those which have lengths and widths which plot in the central area of the diagram, between the areas labelled superparamagnetic and multi-domain. Kirschvink (1983) provides a further description of this figure. Single-domain crystals with remanent coercive fields of 46 mT, as measured here for the salmon (Fig. 1), should lie approximately in the region indicated by the dotted line. These inferred crystal sizes and shapes agree well with biogenic magnetite crystals reported from bacteria by Blakemore (1975) and Towe and Moench (1980) and from yellowfin tuna by Walker et al. (1984)

Fig. 3. Chains of magnetite particles isolated from the chinook salmon dermethmoid tissue. Scale bar 100 nm

their linear arrangement. However, folding of the chains, possibly occurring after extraction, is evident.

Discussion

The experiments reported here clearly show that adult chinook salmon possess large numbers of single-domain magnetite particles suitable for use in magnetoreception. Their narrow coercivity distribution, which indicates a restricted size range, and their presence in linear chains imply that the magnetite particles detected in the dermethmoid tissue of the salmon are produced as biochemical precipitates. As in the yellowfin tuna (Walker et al. 1984), the magnetite particles are too small to be used individually in magnetoreception as their magnetic to thermal energy ratio in the earth's magnetic field is only about 0.5. The inter-particle interaction effects detected in both the tuna and the salmon indicate that the particles are organized into arrays that could attain easily the size required for magnetoreception. Because the magnetite particles extracted from the salmon were dispersed before mounting using the same alternating magnetic field that produced isolated particles in samples taken from the yellowfin tuna, it is unlikely that the chains of particles observed in TEM in this study arose as an artifact. The hypothesis that magnetite particles in the dermethmoid tissues of the salmon and the tuna are organized in chains like those in the magnetosomes of bacteria (Balkwill et al. 1980) therefore seems reasonable. Mechanoreceptors such as hair cells could have the dimensions and sensitivity (e.g. Hudspeth 1983) to monitor the movements of the particle groups accurately.

Final demonstrations that the magnetite particles are organized as we infer can only be achieved by their identification in situ. It will be difficult to locate any such structures with normal transmission electron microscopy, however, as our magnetometry study constrains their volume fraction to be less than 5 parts per billion in the dermethmoid tissue. Each particle chain is likely to be no more than a few micrometers in length and a few hundredths of a micrometer wide. There is only a small probability of locating such a structure in a normal 0.1 micrometer thick TEM section.

It is interesting to note that many studies of other vertebrates have converged on regions of the skull close to the ethmoid bones as the likely site of a vertebrate magnetoreceptor organ (Walcott et al. 1979; Mather and Baker 1981; Zoeger et al. 1981; Baker et al. 1983; Beason and Nicholls 1984; Hanson et al. 1984a, b; Perry et al., in press). As in many of these other studies (e.g. Quinn et al. 1981; Presti and Pettigrew 1980; Baker et al. 1983), we also detected magnetic material that was not always in the same place in all individuals sampled. Some of this material, particularly that associated with tissues such as the gills and gut of the salmon, was clearly contamination that could be removed by thorough cleaning, but other magnetic samples could well have contained true biochemical precipitates. If so, the functions of these deposits remain unknown. A magnetoreceptive role seems unlikely, however, since they usually are not reproducible in all individuals (Walker et al. 1984, this study), often are detected from their natural remanent magnetization (e.g. Zoeger et al. 1981), or are magnetically unsuited to magnetoreception (Presti and Pettigrew 1980; Zoeger et al. 1981; Vilches-Troya et al. 1984).

Our results using adult chinook salmon are at variance with those of Quinn et al. (1981) who failed to find magnetic material anywhere except contaminants within the gastrointestinal tract of sockeye salmon fry. The most likely explanation for this discrepancy is that Quinn et al. (1981) carried out their studies on samples at room temperature (T.P. Quinn, personal communication). We have found in both the chinook salmon and the yellowfin tuna (Walker et al. 1984) that the dermethmoid tissue loses remanence on warming from liquid nitrogen to room temperature. Such loss of remanence is understandable based on the assumption that the magnetite particles must be at least partly free to rotate if they are to be used in magnetoreception (Yorke 1979, 1981; Kirschvink and Gould 1981). Thus magnetite suitable for use in magnetoreception can be detected consistently only by using frozen samples. The presence of IRM or natural remanent magnetization in samples at room temperature suggests the presence of magnetic material serving other functions or arising from external sources.

A second possible explanation is that magnetic material is present in salmon fry in quantities sufficient to mediate the observed responses of fry to magnetic field direction but too small to be detected by currently available superconducting magnetometers. Animals respond either to magnetic field direction (the compass response; Wiltschko 1972; Lindauer and Martin 1972; Walcott and Green 1974) or to some feature related to intensity (the inferred map response; Walcott 1980; Gould 1982). Yorke (1979) and Kirschvink and Gould (1981) found that only a few hundred single-domain crystals would be necessary to determine ac-

curately the direction of the geomagnetic field; the small IRM produced by this number could not be detected with present superconducting magnetometers. In contrast, detection of magnetic field intensity during movements requiring the ability to determine both position and direction, as seems to occur in homing pigeons (Walcott 1980; Gould 1982), requires millions of magnetite-based magnetoreceptors. It is possible that magnetite is present in sockeye salmon fry in quantities sufficient to provide them with the ability to determine magnetic field direction but not sufficient to be detected by a superconducting magnetometer. The movements of adult salmon from the ocean to the outlet of their natal stream could require sensitivity to magnetic field intensity, and so require millions of magnetite particles. We suggest the hypothesis that magnetite is produced continuously throughout the life of the organism and so could be detected more easily in adult than in juvenile fish. A controlled magnetometric study of an ontogenetic series to distinguish among these alternative explanations of the different results for sockeye and chinook salmon is presently in progress.

Thus the presence of magnetite can be correlated with magnetic sensitivity in representatives of three orders of fishes: the European eel and yellowfin tuna, which are known to respond to magnetic fields, and a congener of a third magnetically sensitive fish, the sockeye salmon. The critical tests of the magnetite-based magnetoreception hypothesis, however, will be of behavioral constraints on magnetoreception caused by the properties of the magnetite particles themselves. The behavioral assay developed by Quinn et al. (1981) could be used to test the prediction that accuracy of compass orientation should be poor in very weak fields ($< 10\ \mu T$ or 0.1 Gauss), should increase rapidly in fields up to earth-strength, and asymptotically in fields up to a few times earth-strength. This result holds for magnetotactic algae and bacteria (Kalmijn 1981; Lins de Barros et al. 1981) and also for honeybees (Kirschvink 1981). The response of sockeye salmon fry to magnetic field polarity also can be used in a powerful test of ferromagnetic effects on their magnetic orientation. A short magnetic impulse strong enough to reverse the moments of any magnetite particles present will cause the fry to exhibit reversed magnetic field directional preferences in orientation arenas only if the magnetite particles form the basis for their magnetoreceptor system. Thus the opportunity exists to link magnetite suitable for magnetoreception to the behavior of animals that are known to respond to magnetic fields.

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References

Baker RR, Mather JG, Kennaugh JH (1983) Magnetic bones in human sinuses. Nature 301:78–80

Balkwill DL, Maratea D, Blakemore RP (1980) Ultrastructure of a magnetotactic spirillum. J Bacteriol 141:1399–1408

Beason RC, Nicholls JC (1984) Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. Nature 309:151–153

Brannon EL (1972) Mechanisms controlling migration of sockeye salmon fry. Int Pac Sal Fish Comm Bull 21:1–86

Branover GG, Vasil'yev AS, Gleyzer SI, Tsinober AB (1971) A study of the behavior of the eel in natural and artificial magnetic fields and an analysis of its reception mechanism. J Ichthyol 11:608–614

Butler RF, Banerjee SK (1975) Theoretical single-domain size in magnetite and titanomagnetite. J Geophys Res 80:4049–4058

Cisowski S (1981) Interacting vs non-interacting single-domain behavior in natural and synthetic samples. Phys Earth Planet Interiors 26:56–62

Dunlop DJ, West GF (1969) An experimental evaluation of single-domain theories. Rev Geophys 7:709–757

Furth HP, Waniek RW (1956) Production and use of high transient magnetic fields. Rev Sci Instr 27:195–203

Goree WS, Fuller M (1976) Magnetometers using RF-driven SQUIDS and their applications in rock magnetism and paleomagnetism. Rev Geophys Space Phys 14:591–608

Gould JL (1982) The map sense of pigeons. Nature 296:205–211

Gould JL, Kirschvink JL, Deffeyes KS (1978) Bees have magnetic remanence. Science 201:1026–1028

Hanson M, Karlsson L, Westerberg H (1984a) Magnetic material in European eel, (*Anguilla anguilla* L.). Comp Biochem Physiol 77A:221–224

Hanson M, Wirmark G, Oblad M, Strid L (1984b) Iron-rich particles in European eel (*Anguilla anguilla* L.). Comp Biochem Physiol 79A:311–316

Hudspeth AJ (1983) Mechanoelectrical transduction by hair-cells in the acousticolateralis sensory system. Annu Rev Neurosci 6:187–216

Kalmijn AJ (1981) Biophysics of geomagnetic field detection. IEEE Trans Mag 17:1113–1124

Kirschvink JL (1979) PhD Thesis. Princeton University. Xerox Univ Microfilms Internat, NY

Kirschvink JL (1981) The horizontal magnetic dance of the honeybee is compatible with a single-domain ferromagnetic magnetoreceptor. Biosystems 14:193–203

Kirschvink JL (1983) Biogenic ferrimagnetism: A new biomagnetism. In: Williamson SJ, Romani G-L, Kaufman L, Modena I (eds) Biomagnetism: An interdisciplinary approach. NATO Adv Study Inst Ser, Plenum Publ Corp, New York, pp 501–531

Kirschvink JL, Gould JL (1981) Biogenic magnetite as a basis for magnetic field detection in animals. Biosystems 13:181–201

Kirschvink JL, Walker MM (in press) Particle-size considerations for magnetite-based magnetoreceptors. In: Kirschvink

JL, Jones DS, MacFadden BJ (eds) Magnetite biomineralization and magnetoreception in living organisms: A new biomagnetism. Plenum Publ Corp, New York

Lindauer M, Martin H (1972) Magnetic effect on dancing bees. In: Galler SR, Schmidt-Koenig K, Jacobs GJ, Belleville RE (eds) Animal orientation and navigation. Nat Aeronaut Space Adminstr, Special Publ 262, Washington DC USA

Lins De Barros HGP, Esquivel DMS, Danon J, De Oliveira LPH (1981) Magnetotactic algae. Acad Brasileria Notas de Fisica CBPF-NF-48

Mather JG, Baker RR (1981) Magnetic sense of direction in woodmice for route-based navigation. Nature 291:152–155

McElhinny MW (1973) Paleomagnetism and plate tectonics. Cambridge Univ Press, London New York

Perry A, Bauer GB, Dizon AE (in press) Magnetoreception and biomineralization of magnetite in amphibians and reptiles. In: Kirschvink JL, Jones DS, MacFadden BJ (eds) Magnetite biomineralization and magnetoreception in living organisms: A new biomagnetism. Plenum Publ Corp, New York

Presti D, Pettigrew JD (1980) Ferromagnetic coupling to muscle receptors as a basis for geomagnetic field sensitivity in animals. Nature 285:99–101

Quinn TP (1980) Evidence for celestial and magnetic compass orientation in lake-migrating sockeye salmon fry. J Comp Physiol 137:243–248

Quinn TP, Brannon EL (1982) The use of celestial and magnetic cues by orienting sockeye salmon smolts. J Comp Physiol 147:547–552

Quinn TP, Merrill RT, Brannon EL (1981) Magnetic field detection in sockeye salmon. J Exp Zool 217:137–142

Towe KM, Moench TT (1981) Electron-optical characterization of bacterial magnetite. Earth Planet Sci Letters 52:213–220

Vilches-Troya J, Dunn RF, O'Leary DP (1984) Relationship of the vestibular hair cells to magnetic particles in the otolith of the guitarfish sacculus. J Comp Neurol 226:489–494

Walcott C (1980) Magnetic orientation in homing pigeons. IEEE Trans Magn 16:1008–1013

Walcott C, Green RP (1974) Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. Science 184:180–182

Walcott C, Gould JL, Kirschvink JL (1979) Pigeons have magnets. Science 205:1027–1029

Walker MM (1984) Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. J Comp Physiol A 155:673–679

Walker MM, Kirschvink JL, Chang RS-B, Dizon AE (1984) A candidate magnetoreceptor organ in the yellowfin tuna, *Thunnus albacares*. Science 224:751–753

Walker MM, Perry A, Dizon AE, Kirschvink JL (in press) Detection, extraction, and characterization of biogenic magnetite. In: Kirschvink JL, Jones DS, MacFadden BJ (eds) Magnetite biomineralization and magnetoreception in living organisms: A new biomagnetism. Plenum Publ Corp, New York

Yorke ED (1979) A possible magnetic transducer in birds. J Theor Biol 77:101–105

Yorke ED (1981) Sensitivity of pigeons to small magnetic field variations. J Theor Biol 89:533–537

Zoeger J, Dunn J, Fuller M (1981) Magnetic material in the head of a common Pacific dolphin. Science 213:892–894