Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*

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Summary. 1. Yellowfin tuna, *Thunnus albacares*, were trained individually to discriminate between two Earth-strength magnetic fields by differential reinforcement of a swimming response.

2. Seven subjects, of which two were trained with a double blind procedure designed to control for the possibility of cues from the experimenter, learned to discriminate between ambient and altered fields (Figs. 1–3).

3. Two additional fish trained with the same double blind procedure failed to discriminate between two magnetic fields in which the gradients of intensity were equal and opposite (Fig. 4).

4. The results suggest that the responses to magnetic fields by yellowfin tuna are neurally mediated and that magnetic field detection by this species can be analyzed by the same means as other sensory modalities.

Introduction

Classical and instrumental conditioning techniques often have failed to demonstrate responses by animals to magnetic fields (Ossenkopp and Barbeito 1978). For example, Reille (1968) reported successful heart rate conditioning to magnetic field stimuli in homing pigeons. However, Kreithen and Keeton (1974) and Beaugrand (1976) were unable to repeat this result. Homing pigeons showed statistically significant responses to magnetic fields when they fluttered in a flight tunnel before entering one or the other of two goal boxes in a choice condition-

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Abbreviation: ITI intertrial interval

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ing procedure (Bookman 1977). However, an attempt to replicate this experiment failed (C. Walcott, Cornell University, Ithaca, New York, personal communication, 1982) and starlings failed to discriminate between two magnetic fields under similar conditions (Griffin 1982). In contrast, Phillips (1977) and Kalmijn (1978) were able to demonstrate conditioned responses to magnetic fields using salamanders and rays in choice procedures. Thus, despite conflicting results, there is evidence that animals can be trained to discriminate magnetic field stimuli. However, a wide range of techniques for demonstration and analysis of magnetic field detection by animals has been neither developed nor applied. Here I report training yellowfin tuna, *Thunnus albacares*, to distinguish between two different Earth-strength magnetic fields by requiring the fish to produce a single response and then manipulating the consequences of that response. Results obtained using this unitary discriminative training procedure permit inferences concerning the mechanism of magnetic field detection by these fish.

I tested juvenile yellowfin tuna for unconditioned responses to novel magnetic field stimuli and obtained results suggesting that this species might respond to magnetic fields in conditioning experiments. Fish were trained individually to swim through a narrow tunnel (60 × 30 cm) between two experimental tanks and reinforced according to a randomized schedule that provided the fish with a food reward on average once every five responses. The fish swam through the tunnel at a steady rate during training sessions held once daily. Swimming through a magnetic field anomaly induced momentarily within the tunnel caused the fish to delay returning through the tunnel even though the anomaly was removed before the fish could have responded again. The delay in response

caused by subsequent presentations of the anomaly decreased rapidly for all but one fish tested, suggesting that at first the fish were disturbed by the stimulus but that they later paid no attention to it.

The nature of magnetic fields, which are pervasive stimuli that can only be presented one at a time, influenced my choice of conditioning procedure. Discrimination training experiments in which subjects are presented with a choice of responses contingent upon such singly presented stimuli are very difficult discrimination problems and will frequently fail even with well understood, salient stimuli (Mackintosh 1974; Bitterman 1979). Consequently, I elected not to use a choice procedure for discrimination testing. Instead, I used a unitary discrimination training technique, known as a discrete-trials/fixed-interval training procedure (Woodard and Bitterman 1974), in which subjects could produce a single response repeatedly during trials of fixed duration but not during an interval which separated the trials. Rate of production of the response during trials provided a sensitive measure of discrimination of the stimuli by the fish.

The magnetic fields used in these experiments provided changes in angle of inclination, magnetic field intensity, and the gradients in inclination and intensity of the magnetic field. The fish could conceivably monitor any or all of the varying features to make the discrimination. The unitary procedure and the discriminative stimuli used in these experiments therefore provided as general a pair of stimuli as possible for the fish to distinguish in as simple a testing procedure as I could devise.

Materials and methods

Experimental facilities, apparatus, and animals. These experiments were conducted at the Kewalo Research Facility of the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service. Experimental tanks used were constructed of fiberglass or plywood and were 6 m in diameter by 0.75–1.0 m in depth. The absence of metal prevented distortion of the magnetic fields in the tanks arising from the tank construction. A direct current passed through 100 turns of No. 18 AWG magnet wire wrapped around the wall of each tank induced vertical magnetic fields in the tanks. The artificial fields were non-uniform, adding from 10 microTesla (μT; 10 $\mu T = 0.1$ Gauss) in the center to 50 μT at the edge of the tanks to the uniform Hawaiian field (inclination 38°; declination 11°30′ E; total intensity measured in the tanks with a Develco[1] 3-axis fluxgate magnetometer = approximately 30 μT).

Experiments were run from control rooms that were physically isolated from the tanks. Mechanical and electrical linkages in the control rooms operated the response apparatus and feed-

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

ers, and direct current power suppliers generated the altered magnetic fields used in the experiments. The fish were observed through small viewing ports and their responses recorded manually.

Fish used in the experiments were juvenile yellowfin tuna (40–50 cm fork length) held in outdoor holding tanks at the Kewalo Research Facility. For testing, fish were moved individually to one of the experimental tanks and allowed to adapt to the new situation for 2 days. During this time they were fed from a feeder which dropped food into the water approximately 1 m from the edge of the experimental tank (Jemison et al. 1982).

Discriminative training procedure. After the adaptation period, the experiments were conducted in two stages. The fish were first pre-trained to produce a conditioned response at a steady rate in anticipation of a food reward. In the second, discrimination training stage, this response was reinforced with food or not reinforced depending on the magnetic field present in the tank. Discrimination was detected by comparing the rates at which the response was produced in the presence of the two stimuli. Training sessions lasted 1–2 h, were held once daily between 0800 and 1600, and took place at approximately the same time each day for each fish. The 60- × 30-cm pipe frame was lowered into the water and the fish enticed through it using a bait hanging in front of the opening. The bait was removed as the fish struck at it and became committed to swimming through the frame. A piece of food (cut smelt) was then delivered to the fish to reinforce the response. By the end of the first session, the fish usually began to swim through the frame spontaneously and all fish responded freely after the second training session.

Each subsequent session consisted of 15 30-s trial periods during each of which the pipe frame was lowered into the tank and the fish allowed to respond freely. The first response after 30 s brought food from the feeder and the frame was retracted for a variable inter-trial interval (ITI), which averaged 3 min in this pre-training period.

To ensure that the fish only gained experience from receiving food in association with the correct stimulus, the magnetic field that was later to become the reinforced stimulus (designated S+) was presented simultaneously with the pipe frame during pre-training. That is, if the altered field was to become S+ during discrimination training, the field was switched on at the same time as the pipe frame was lowered into the tank and switched off at the end of the trial when the frame was removed. If the altered field was later to become the non-reinforced stimulus (designated S−), the fish gained no experience with that field at any stage during the pre-training period.

After 2 days of pre-training, discrimination training began. In this training, each trial began with simultaneous presentation of the pipe frame and either the reinforced or non-reinforced stimulus. All responses by the fish in the 30-s trial were counted. On S+ trials the fish was given a piece of food at the first response after 30 s and the trials were terminated. On S− trials a 10-s penalty timer started at the end of the 30-s period. If the fish responded before the 10 s had elapsed, the timer was reset. The timer was reset by each subsequent response until either the fish failed to respond for 10 s or until a total of 30 s of penalty time had elapsed. Response to S− was thus penalized by extending the trial without any possibility of the fish obtaining food for producing the response (Woodard and Bitterman 1974). After the trials were terminated, the pipe frame was retracted for a variable ITI (mean 90 s) after which another trial sequence began. The upper limit of 30 s of accumulated penalty time per trial was initially established because the fish often jumped out of the experimental tanks when the

penalty time was longer during pilot experiments used to develop the procedure. In subsequent experiments (see below), the maximum penalty time allowed was increased without causing the fish to jump out of the experimental tanks. An important feature of the discrete-trials/fixed-interval training method is that the rate of response to the stimuli is measured during a trial period in which the fish receives no reinforcement for responding. Therefore, the possibility that the reinforcement itself might provide a cue is excluded.

The fish were trained in 30-trial sessions held once daily. In each session, S+ or S— were presented equally often in a quasi-random order with no more than three S+ or S— trials in succession. Reduction of the mean ITI from 3 min to 90 s resulted in the fish receiving about the same number of reinforcements per unit time as in the pre-training. To ensure that any difference in response to the two magnetic field stimuli was not due to some differential effect of the fields on the general behaviour of the fish (as, for example, disorientation caused by the altered field), testing was balanced by training some fish with the normal Hawaiian field as S+ and others with the altered field as S+.

In subsequent experiments, designed to exclude possible observer-related cues, fish were tested using double blind procedures. The penalty timer was set at 15 s and the total allowable penalty time was up to 90 s. In the double blind procedure, two people working in different rooms controlled different components of the experiment. Communication was by signal light and a simple code. The first person (the field controller) timed the trials and presented the discriminative stimuli. The second person (the apparatus controller) was directed by the first to raise and lower the pipe frame and, at the end of each trial, whether or not to deliver food. The apparatus controller recorded the responses made by the fish during the trials and signaled the field controller when each command had been executed. The apparatus controller was given no knowledge of the magnetic field conditions or which was S+ or S—', whereas the field controller had no knowledge of events under the control of the apparatus controller.

A second manipulation of the experimental procedure involved use of a different pair of discriminative stimuli in the same double blind procedure. In the original procedure, the normal Hawaiian magnetic field was used as one of the discriminative stimuli. This field was present at all times outside the experimental training sessions and so may have adversely influenced the performance of the fish during discrimination training in which it was S+. An attempt was therefore made to use as discriminative stimuli two magnetic fields that could only be detected during the experiments. A second altered field was generated by reversing the direction of the current through the coil around one of the experimental tanks. The fields added to the background field were of equal intensity but were opposite in their inclination and in their gradients of intensity and inclination. As a result, total intensity and inclination at any point in the tank differed between the two experimental fields. The gradients of intensity in the tank were the same, although of opposite sign.

Results

Mean response rate data for sequential blocks of five pre-training, S+, and S— trials were used in graphical presentation and statistical analysis of results of the experiments. In the pre-training period the fish established variable baseline response rates. At first the fish responded at low rates but
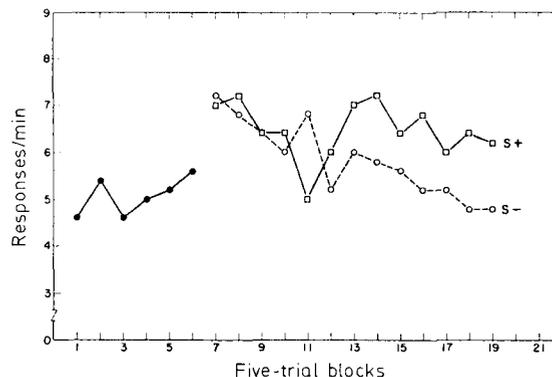

Fig. 1. Response acquisition and discrimination learning in five yellowfin tuna. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S— (open circles) (blocks 7–19) trials for all fish tested

over the course of two training sessions their response rates increased considerably (Figs. 1–4). Rates produced by individual fish usually appeared to stabilize after two pre-training sessions, although this is not reflected in the pooled data. Differences among the rates produced by individual fish seemed to be due primarily to the different sizes of the fish relative to the opening in the pipe frame and the different approaches to the frame employed by each fish. The smallest fish were usually more active and able to turn more rapidly near the pipe frame than the larger fish used. Fish that swam in circles and approached the frame predominantly from one direction established lower rates of response than fish that approached it freely from both sides in figure-eight patterns centered on the frame.

For five fish used in the first series of experiments, discrimination between the two magnetic fields became evident after two training sessions. On the first 2 days (blocks 7–12 in Figs. 1 and 2), response rates to the two stimuli fluctuated about each other. By the third day, all fish produced higher rates of response to the reinforced than to the non-reinforced stimulus and continued to do so for the remainder of the experiments. Comparison of response rates between paired five-trial blocks demonstrated significant differences in response to S+ and S— by all except one of the fish (Wilcoxon rank sum, $P<0.01$ for fish 1 and 3, $P<0.05$ for fish 2 and 5 in Fig. 2). However, the positive ranks for this fish (Fish 4 in Fig. 2) were all contained in the last 8 five-trial blocks, suggesting that the response of the fish to S+ and S— changed during the course of the experiment.

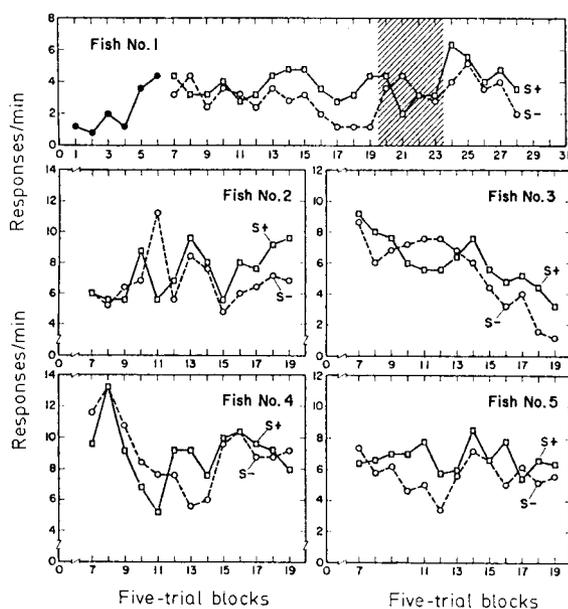All fish completed at least 13 five-trial blocks

Fig. 2. Individual results of dicsrimination training for the same five fish shown in Fig. 1. Each point is the mean of five pre-training (closed circles, blocks 1–6, shown for Fish 1 only), or S+ (open squares), and S− (open circles) trials. Shaded area indicates control trials (in which the connection between the coil and the power supply was broken) for Fish 1

Table 1. Magnetic field discrimination learning. Results of analysis of variance comparing S+ and S− response rates for five yellowfin tuna. *b* blocks; *s* stimuli; *j* subjects; *t* trials

Source	d.f.	Mean square	F	Proba-bility
Total	649			
Blocks	4			
s	1	13.8846	8.4543	0.0438
js	4	1.6423		
b	12	3.3087	0.6881	0.7544
jb	48	4.8084		
sb	12	3.4046	2.8776	0.0046
jsb	48	1.1831		
t	4	1.3054	1.1538	0.3675
jt	16	1.1313		
st	4	2.6731	2.2011	0.1151
jst	16	1.2144		
bt	48	1.3379	0.9855	0.5072
jbt	192	1.3576		
sbt	48	1.4722	0.9595	0.5534
jsbt	192	1.5344		

of discrimination training (blocks 7–19 in Fig. 1). An analysis of variance (ANOVA) demonstrated a significant difference in overall mean response rates to S+ and S− during discrimination training $F_{(1,4)\text{ stimuli}} = 8.4543$, $P = 0.0438$; Table 1). Analysis of interactions within the ANOVA demonstrated only one significant source of variance, the stimuli by blocks or learning effect interaction $F_{(12,48)}$ stimuli by blocks $= 2.8776$, $P = 0.0046$). This result indicates that response rates to the two stimuli changed differentially with time as the fish learned to discriminate between the stimuli during the experiments.

To test whether the fish were responding to possible equipment or observer-related cues, control trials were conducted with one fish. One of the wires connecting the power supply to the coil around the tank was disconnected and all procedures followed as before. The response rates during reinforced and non-reinforced trials fluctuated about each other during this period (Fish 1 in Fig. 2). When the circuit between the power supply and the coil was reestablished, the fish again produced higher response rates to the reinforced than to the non-reinforced stimulus (Fig. 2). However, the differences between response rates was less
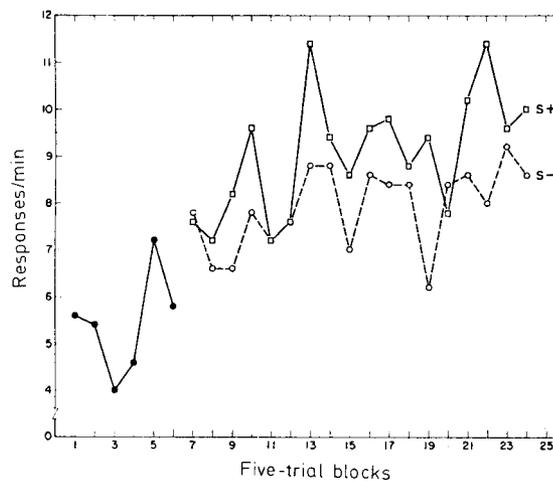

Fig. 3. Response acquisition and magnetic field discrimination learning in two yellowfin tuna tested in double blind experiments. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S− (open circles) (blocks 7–24) trials

than immediately before the control trials were conducted.

The two fish tested had little difficulty in learning the discrimination in spite of the extensive precautions taken to remove observer-related cues in the first set of double blind experiments. In addition, discrimination became evident considerably earlier, by the end of the first 30-trial session, than in the previous experiments (Fig. 3). This improvement in response is attributed to the greater pen-
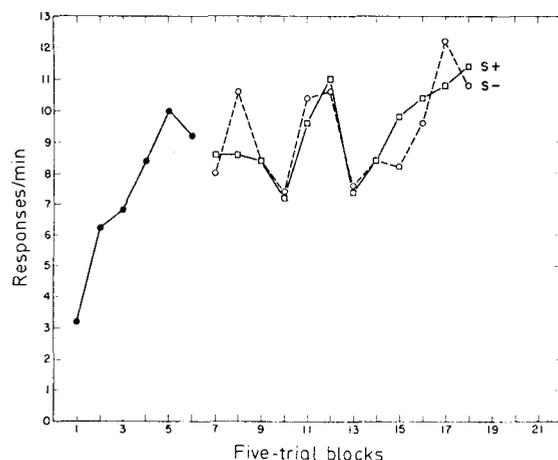
Fig. 4. Response acquisition and discrimination performance in two yellowfin tuna tested using the same double blind procedures as in Fig. 3. Magnetic fields used in these experiments were generated by currents of equal magnitude but reversed polarity. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S— (open circles) (blocks 7–18) trials

alty the fish incurred for continued response to S— in these experiments.

In the second set of double blind experiments, an attempt was made to improve discrimination by providing stimuli that were not present in the tank at any time other than during the training. As noted above, the two fields used in these experiments were produced by currents of equal magnitude but reversed polarity passing through the coil. At no stage of training did either of the two fish tested show evidence of discrimination (Fig. 4). It seems unlikely that two fish would fail to respond in this procedure when seven had previously done so in experiments that were either identical or differed only in the amount of penalty time allowed. It therefore appears that the fish could not distinguish between the two fields used in these experiments whereas they could distinguish between the fields used in all the previous experiments.

Discussion

The discrimination training reported here demonstrated reproducible conditioned responses to Earth-strength magnetic field stimuli in experiments employing a new procedure and a new species. The discrete-trials/fixed-interval training procedure had several advantages for demonstrating magnetic field discrimination in the yellowfin tuna. Requiring multiple responses sharpens discrimination (Bitterman 1979), and rate of response is an

effective measure of discrimination because it accommodates variability in behaviour but can vary widely and rapidly in response to changes in experimental conditions (Kling 1971). In addition, discrimination between singly presented stimuli is generally more easily demonstrated with unitary than with choice procedures (Bitterman 1979; Mackintosh 1974).

Variation in control of the conditioned behaviour by the discriminative stimuli was evident in the control experiment. Only the background Hawaiian magnetic field was present in the tank during the control trials, and this field was associated with both reinforcement and non-reinforcement. When the two discriminative stimuli were again presented the difference between response rates was smaller than before the control trials were conducted (Fig. 2), suggesting that experience gained during the control trials modified subsequent responding by the fish.

Despite its success the unitary procedure as used in these experiments does have clear limitations. The use of a 'whole body' response caused the rates of response produced by the fish to be low compared with rates obtained using conditioned responses such as hitting a target (Woodard and Bitterman 1974). Consequently, the scope for change in response rate was low and the variability in responding high compared with the performance ceiling. The ability of tunas to maintain high swimming speeds was probably an important factor in overcoming this difficulty. The wide scope for changes in the swimming activity of the fish increased the sensitivity of the conditioning technique by allowing a wider scope for change in response rates during the experiments than might have been obtained with other, less active fishes.

Although they have proven useful in using the discrete-trials/fixed-interval procedure to demonstrate conditioned responses to magnetic fields, yellowfin and other tunas are probably not ideal subjects for magnetic field conditioning studies. The size of the fish and the tanks required to house them make it difficult to obtain good control of the experimental environment and stimulus. A further difficulty in working with tunas is that the fish are under stress in captivity and are difficult to maintain alone in experimental tanks. More specific experiments, for example those that require handling of the fish for impairment of sensory function, would be impossible with tunas because of their fragility (Queenth and Brill 1983). For these reasons, other species may be found to be more suitable for magnetic field conditioning studies as the techniques are developed further.

It is not known which features of the magnetic fields the fish used to make the discrimination. The first two groups of experiments used magnetic fields varying in their angles of inclination, total intensity, and the gradients in these two features in the experimental environment. The fields used in the third group of experiments differed in total intensity and inclination at any point in the experimental tank. However, the gradients in intensity in the tank were equal (high near the edge and low near the center of the tank) although opposite in sign (increasing and decreasing to 0 from the edge to the center of the tank). Two fish were completely unable to discriminate between these two magnetic fields (Fig. 4) when seven others tested under the same conditions but with different fields showed good discrimination (Figs. 1–3). Although other interpretations are possible, the very large differences in intensity gradients between the normal and altered fields probably made discrimination easier for fish presented with these fields as discriminative stimuli.

The experiments permit the inference that magnetoreception by yellowfin tuna is neurally mediated. Training different fish with either the altered or the normal field as S+ and the highly significant learning effect interaction in the analysis of variance exlude the explanation that the differences in response to S+ and S− merely resulted from some differential physiological effect of the fields on the behaviour of the fish. In addition, the rapidity with which the fish were able to make the discriminatory decision in each trial suggests that magnetoreception occurs through neural rather than non-neural processes.

A second inference that can be made from these experiments concerns the magnetic field transduction mechanism. The suggestion that movement is required for use of magnetic field stimuli (Kreithen and Keeton 1974; Bookman 1977) is compatible with the hypothesis of magnetoreception by electrical induction (Kalmijn 1974; Jungerman and Rosenblum 1980). However, yellowfin tuna do not possess the large ampullary canals necessary for ampullary electroreception in salt water. In addition, 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. Magnetoreception might occur by induction in the labyrinth organ of the inner ear of the yellowfin tuna, although the fish cannot make the rotatory movements of the head that Jungerman and Rosenblum (1980) consider necessary for this mechanism. Al-

though magnetoreception based on electrical induction mechanisms cannot be excluded, these observations suggest it is unlikely that yellowfin tuna detect magnetic fields by electrical induction.

My results are also compatible with the magnetite-based magnetoreception hypothesis suggested to explain responses to magnetic fields in honeybees and homing pigeons (Yorke 1979, 1981; Kirschvink and Gould 1981). With my colleagues, I have reported elsewhere that the yellowfin tuna produce single-domain crystals of magnetite in tissue found within the dermethmoid bone of the skull (Walker et al. 1984). These particles could provide an ideal physical basis for the behavioural responses to magnetic fields by yellowfin tuna reported in this paper. However, specific tests will be necessary to determine whether magnetoreception by yellowfin tuna has a ferromagnetic transduction mechanism.

In summary, these behavioural studies demonstrated reproducible responses to magnetic fields in yellowfin tuna. The success of the experiments is attributed to use of a species that is very likely to benefit from possession of a magnetic sense (Tesch 1980) using very different magnetic field stimuli in an appropriate testing procedure. The results suggest that magnetic field detection is neurally mediated and can be analyzed by the same means as other sensory modalities. Future work must seek to repeat these results, develop tests for responses to individual components of the geomagnetic field, and begin analyzing the magnetic field transduction mechanism.

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