BEHAVIOURAL EVIDENCE FOR THE USE OF MAGNETIC MATERIAL IN MAGNETORECEPTION BY A MIGRATORY BIRD

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Summary

The biophysical mechanism of vertebrate magnetic sensory perception has not been completely resolved. We here provide evidence for the use of a magnetic material (probably magnetite) by a vertebrate to detect the earth's magnetic field. The role of magnetite in bobolink (*Dolichonyx oryzivorus*) orientation was assessed by magnetizing the birds with a magnetic pulse in one of three orientations. Bobolinks magnetized with different polarities were significantly oriented in directions different from one another and from their controls. Treatment with a second pulse having the opposite polarity to the first resulted in random orientation for each group. These results indicate an effect specific to a particle-based magnetoreceptor. The use of magnetite particles for magnetoreception is not in conflict with other reports on the use of photopigments for this purpose. The two mechanisms could be used in a complementary manner for detecting the same or different aspects of the magnetic field.

Key words: magnetoreception, magnetite, magnetoreceptor, orientation, bobolink, *Dolichonyx oryzivorus*.

Introduction

Although many studies have shown that alterations in the ambient magnetic field elicit physiological, cellular and behavioural responses in animals, the biophysical mechanism of magnetic sensory perception is not understood. Of the various transduction mechanisms that have been proposed, the use of biological radicals (photopigments) (Leask, 1977) and magnetic particles (magnetite) (Kirschvink and Gould, 1981) have received the most attention (Beason and Semm, 1994). Magnetic compass orientation in some birds may involve photopigments and has been shown to be sensitive to the wavelength of light, indicating that the compass probably has its basis in the visual system (Wiltschko and Wiltschko, 1988; Wiltschko *et al.* 1993). Additional support for the role of the avian visual system as a magnetic compass is that neurones in the visual system of the pigeon have been reported to respond to changes in the direction (but not the intensity) of the magnetic field (Semm and Demaine, 1986). True navigation also requires that an animal knows its location with respect to its goal and may involve a mechanism analogous to a map. Unlike the receptors associated with a magnetic compass, magnetoreceptors used for a magnetic map must detect minute variations (less than 1 % of the total) in the earth's magnetic field (Wiltschko and Wiltschko, 1988). Because of their sensitivity to such small changes in the magnetic field, the receptors associated with the trigeminal nerve are thought to serve some function in this role (Semm and Beason, 1990). Of the various transducer materials that have been proposed, magnetite is the only one that can theoretically (Yorke, 1981) account for the sensitivities that are observed in the trigeminal nerve and are required for a magnetic map.

The objective of these experiments was to determine whether magnetic field transduction is based on a magnetizable material. Bobolinks (*Dolichonyx oryzivorus*) have been shown to contain ethmoidal magnetite in sufficient quantities to serve as a magnetic map receptor (Yorke, 1981; Beason and Brennan, 1986; Beason, 1989a; Wheeler, 1991). Unlike nonmagnetic and paramagnetic compounds, ferromagnetic compounds such as magnetite possess permanent magnetic moments and can retain changes in the alignment of their magnetic moments produced by strong external fields. The use of a ferromagnetic material to detect the magnetic field can be established by using a strong external field to alter the magnetic dipole of the particles. Homing pigeons (*Columbia livia*) treated with strong magnetizing or demagnetizing fields produced by electromagnets show little effect on their homing orientation (Kiepenheuer *et al.* 1986; Walcott *et al.* 1988), as do bobolinks similarly treated and tested in a planetarium (R. C. Beason, unpublished observations).

Although subjecting pigeons and bobolinks to strong electromagnets has little effect on their navigational abilities, the effects of the treatments may have been minimized by the manner in which the magnetic fields were applied. Single-

domain magnetite particles (reported in both species; Walcott *et al.* 1979; Beason, 1989*a*) are small (maximum size about 1 μm; McElhinny, 1973) and will rotate to align with the field of the electromagnet if they are not rigidly held in place. As a result of treatment with an electromagnet, any freely moving particles would be rotated temporarily by the external field and could return to their original positions after the external field was removed. This problem can be overcome by magnetizing the bird with a brief rapid pulse, strong enough to overcome the coercivity of magnetite (Kirschvink, 1983). Frankel *et al.* (1981) effectively used such a technique to reverse the polarity of north-seeking and south-seeking magnetotactic bacteria. Coercivity is the magnetic force that is needed to overcome the internal magnetization of a material. The theoretical maximum coercivity of single-domain magnetite is 0.3 T for long, needle-shaped particles and about 0.1–0.2 T for more elliptically shaped particles, such as those found in most biological samples (McElhenny, 1973).

Materials and methods

For these experiments, 67 adult bobolinks (Aves: Icteridae) *Dolichonyx oryzivorus* (L.) were captured using mist nets during the summer prior to testing. All birds were housed indoors without a view of the natural sky throughout the experiment. The experimental treatment was to apply a brief (approximately 5 ms) magnetic pulse of approximately 0.5 T to the head (strong enough to overcome the maximum coercivity of single-domain magnetite, 0.3 T, and too brief to allow particles capable of movement to rotate). The pulse was produced by an E–W oriented solenoid connected to a bank of nine 1100 μF electrolytic capacitors charged to 250 V d.c. and discharged through a silicon-controlled rectifier. A diode across the coil produced unidirectional current flow within the solenoid and a unidirectional magnetic field. When the bobolinks exhibited migratory readiness, they were tested under the natural magnetic field within a planetarium using the 'inked footprint' technique (Emlen and Emlen, 1966). The planetarium was used for testing because it is in a single-floor wing of the building with little disturbance from human activity or magnetic fields produced by electrical wiring. The birds were transported from the basement animal room in a wooden case at 19:30 h each evening and placed into the test cage in the planetarium. They were removed at 07:30 h the following morning, when they were returned to the animal room using the same wooden case. The test cages were covered by translucent tops to prevent the use of external visual cues. Each bird was tested on 5–7 consecutive nights as a control before treatment. Treatment consisted of each bird being magnetized in one of three orientations (north-anterior, south-anterior or north-up) at about 16:00 h on the first day of the experimental period and tested on 5–7 consecutive nights to determine the effect of the first treatment on its orientation. The north-anterior birds were magnetized such that, if the bill were made of iron, the tip would attract the south end of a compass. South-anterior birds were magnetized with the opposite

polarity, and north-up birds were magnetized with the external magnetic field passing vertically through their heads. After 5–7 nights of testing, a second magnetizing pulse was applied with the opposite polarity to the first and the birds were retested for an additional 5–7 nights.

Each bird's modal nightly direction of activity was measured to the nearest 10°. The modal direction, the direction with the greatest amount of activity, was used as a measure of central tendency because it is easier to evaluate (Bingman, 1983) and is not significantly different from the mean direction, based on semi-quantitatively measuring activity in 24 sectors (Cherry and Able, 1986). Because the objective of the experiment was to determine the influence of the treatment with a magnetic pulse on the orientation of individual birds, each bird served as its own control. The control or reference direction for each bird was computed as the mean of its nightly modal directions during the control segment of the experiment. The nightly modes for each bird were computed as deviations from that bird's control mean to reduce the effects of seasonality and interindividual variation in preferred headings (Beason, 1989*b*). The effect of the treatments was assessed in an analysis of the second-order means pooled by two criteria: by bird and by night. Means were calculated for each bird or night for each condition (control, first treatment, second treatment) and the means were pooled for each treatment. The significance of orientation for each pooled data set was tested with the Rayleigh test and means were compared with the control direction using confidence intervals and with each other using Watson's U^2-test (Zar, 1984). The presence of axial bimodality was tested by doubling each nightly angle and testing the significance of the pooled data with the Rayleigh test. If the data were more significantly grouped (i.e. the resultant vector was longer) by doubling the angles than without doubling the angles, the pooled sample was considered to be bimodal rather than unimodal. A pooled second-order mean based on geographical direction was not calculated because the experiments were conducted during three migratory periods: spring, early autumn and late autumn. Consequently, such a composite vector would not provide any useful information about the preferred directions of the birds.

Results

The second- and third-order mean direction for all the birds during the control period is 0° by definition, because the individual mean control direction is the reference for all deviation measurements. The mean of the individual vector lengths (**r**) of all 67 birds during the control period was 0.569, and the mean vector length (**r**) of all 308 bird-nights during the control period was 0.531. Birds that were magnetized north-anterior had a significantly different ($U^2=0.2903$, $P<0.01$) mean heading ($\alpha=255°$, **r**=0.39, $N=21$, $P<0.05$) from that of birds magnetized south-anterior ($\alpha=51°$, **r**=0.40, $N=19$, $P<0.05$), and each group differed significantly ($P<0.05$) from its control (Fig. 1, Table 1). Birds magnetized north-up had a group mean that was axially bimodal ($\alpha=145–325°$, **r**=0.41,

Table 1. *Orientation of control and magnetized bobolinks analyzed for unimodal and bimodal headings*

		Heading					
		Unimodal			Bimodal		
Experiment	Treatment	α (degrees)	r	N	α (degrees)	r	N
N-S	Control	0		21			
	N-A	255	0.390*	21	106–286	0.219	21
	S-A	223	0.179	21	23–203	0.300	21
S-N	Control	0		19			
	S-A	51	0.400*	19	0–180	0.193	19
	N-A	30	0.107	19	161–322	0.335	19
U-D	Control	0		19			
	N-up	336	0.362	19	145–325	0.413*	19
	S-up	312	0.302	19	127–307	0.138	19

N-S birds were first magnetized north-anterior (N-A) followed by south-anterior (S-A). S-N birds were first magnetized south-anterior followed by north-anterior. U-D birds were first magnetized north-up (N-up) followed by south-up (S-up).
α, mean direction; r, vector lengths; N, sample size.
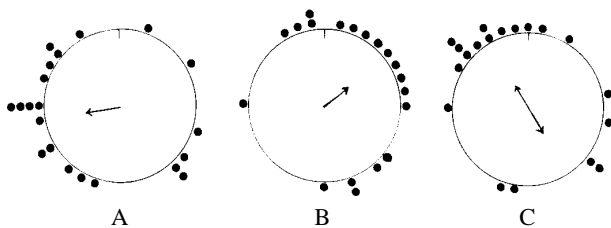Significance of concentration about the mean: *$P<0.05$.

Fig. 1. Orientation of magnetized bobolinks following their initial treatment. Each point represents the mean direction for one bird following treatment relative to its mean direction during the control period (see text for details). (A) Responses of birds magnetized north-anterior. (B) Responses of birds magnetized south-anterior. (C) Responses of birds magnetized north-up. The direction and length of the mean vectors are represented by the line inside the circle.

$N=19$, $P<0.05$) and differed significantly ($P<0.05$) from the 180–360° axis. Analysis of the second-order means for each treatment pooled by night (instead of by bird) revealed a similar pattern. The mean heading of birds magnetized north-anterior ($\alpha=283$°, r=0.831, $N=6$, $P<0.05$) differed from that of birds magnetized south-anterior ($\alpha=49$°, r=0.888, $N=5$, $P<0.01$), and both groups differed from their controls (Table 2). North-up treated birds were significantly oriented towards 320° (r=0.797, $N=7$, $P<0.01$) rather than being bimodal.

Magnetizing the birds in each of the three groups for a second time, with the polarity opposite to their original treatment, resulted in random orientation for individual groups (Table 1). When the data from the second magnetization of two groups (north-anterior and south-anterior) are combined, the pooled mean is significant ($\alpha=23–203$°, r=0.324, $N=40$, $P<0.05$), but axially bimodal (Fig. 2). Bimodality was a result of different birds selecting different (opposite) mean headings.

Table 2. *Mean vectors analyzed by night for control and magnetized bobolinks*

Experiment	Treatment	α (degrees)	r	N
N-S	Control	2		7
	N-A	283	0.831*	6
	S-A	231	0.561	6
S-N	Control	0		6
	S-A	49	0.888**	5
	N-A	60	0.361	5
U-D	Control	5		7
	N-up	320	0.797**	7
	S-up	302	0.912***	7

Abbreviations are as in Table 1.
Significance of concentration about the mean: *$P<0.05$; **$P<0.01$; ***$P<0.001$.

A single mean was calculated for each bird. Likewise, nightly pooled means for the second treatment were not significantly oriented, nor was the pooled nightly second-order mean of the north-anterior and south-anterior groups combined (Tables 1, 2).

Discussion

These results indicate that treatment with a brief magnetic pulse influenced the direction that the birds selected in the absence of visual cues. Because magnetization with different polarities (north-anterior *versus* south-anterior *versus* north-up) produced orientation in a different mean direction for each group, it appears that the birds were using the magnetic information that was transduced by a ferromagnetic material
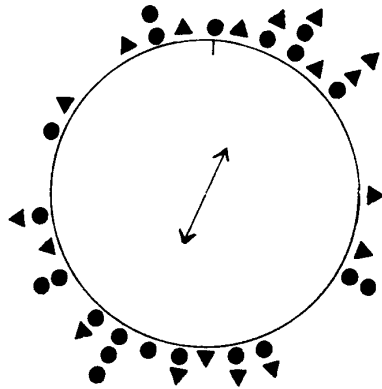
Fig. 2. Pooled results showing the orientation of doubly magnetized bobolinks following the second treatment. Circles represent birds that were magnetized first north-anterior, then 5–7 days later south-anterior. Triangles represent birds that were magnetized south-anterior then north-anterior.
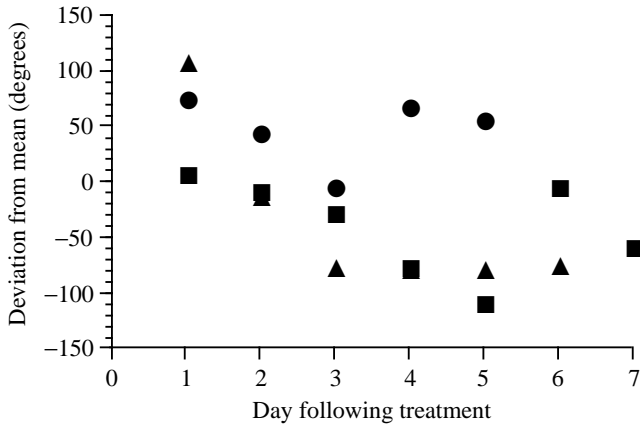

Fig. 3. Pooled nightly mean directions of bobolinks following their first magnetic treatment relative to their control direction. Squares, north-up; circles, south-anterior; triangles, north-anterior.

Table 3. *Pooled nightly mean vectors of bobolinks following their first magnetization*

Treatment	Night	α (degrees)	**r**	N
N-A	1	109	0.176	18
	2	348	0.199	18
	3	284	0.546*	10
	4	282	0.527**	16
	5	283	0.831***	19
	6	287	0.690**	10
S-A	1	75	0.363	14
	2	45	0.335	8
	3	357	0.492	10
	4	69	0.369	11
	5	57	0.208	13
N-U	1	8	0.397	17
	2	354	0.304	18
	3	334	0.213	17
	4	285	0.550**	17
	5	252	0.188	18
	6	336	0.413	14
	7	303	0.160	17

Abbreviations are as in Table 1.
Significance of concentration about the mean: *$P<0.05$; **$P<0.01$; ***$P<0.001$.

instead of ignoring it. The first night's responses indicate the birds may have been confused by the treatment (Fig. 3), but they adapted to the change. This response is most evident in the north-anterior group (Table 3). These differences indicate that the effect of the initial treatment did not disrupt the receptor in such a way as to prevent the birds from obtaining usable (but inaccurate) magnetic information. The lack of meaningful magnetic information would produce random orientation in the absence of other cues.

The directional differences between treatments also indicate that the effect is specific to the receptor and is not a generalized effect on the whole animal. A generalized effect should result in responses to changes in the intensity of the applied field, not from changes in its orientation. Furthermore, it is unclear how, or why, a generalized effect could have an effect on the direction selected by the bobolink. Generalized effects would be more likely to influence motivation and levels of activity.

Because the pulse applied was so brief, it is unlikely to have had a long-lasting, generalized effect on the bird; however, there are no data to test this idea. In a related experiment, treatment of homing pigeons (*Columbia livia*) with a second magnetizing pulse identical to the first had no effect on their homing ability whereas the first treatment did (Wiltschko and Beason, 1991). Papi *et al.* (1992) reported a generalized effect of magnetic fields on opiate receptors in the homing pigeon. Their manipulations exposed pigeons to earth-strength oscillations of the magnetic field for 3 h and the birds were tested immediately for physiological effects. Our treatment differed in that exposure to the magnetic field was brief (milliseconds) and applied from several hours to several days prior to testing. It is unlikely that the changes in orientation we observed are the result of an effect on photopigments or any other organic molecule, because such molecules are not ferromagnetic. Rhodopsin, haemoglobin and some other biological molecules are paramagnetic (Hong, 1980) and, consequently, they lose the imparted magnetic moment when the external magnetizing field is removed.

A logical conclusion from these experiments is that the bobolinks are using a magnetizable material for transducing the magnetic field. Because initial exposure to the north-anterior and south-anterior treatments resulted in nearly opposite headings (Fig. 1), it is tempting to speculate that it is the magnetic compass that was affected, but such conclusions may be premature for several reasons.

The magnetic remanence of bobolink heads appears to be

carried by single-domain (SD) grains of biogenic magnetite (Beason and Nichols, 1984; Beason and Brennan, 1986; Wheeler, 1991). Coercivity (the strength of an external field needed to reorient the magnetic moment) of SD grains depends on the anisotropy (directional dependence) of the particle's magnetic energy. Three factors contribute to the total anisotropy of SD magnetite: stress, magnetocrystalline structure and shape (Evans and McElhinny, 1969). For magnetite in biological tissues, stress and magnetocrystalline anisotropy are weak (Evans and McElhinny, 1969) and can account for only a small amount of the total anisotropy observed in bobolink samples (0.2 T; Beason and Brennan, 1986). The remaining coercivity of biogenic magnetite must therefore be the result of shape anisotropy. Shape anisotropy of a prolate ellipsoid of SD magnetite (a shape similar to that found in the bobolink) forces the magnetic energy to lie parallel or antiparallel to the 'easy direction' of magnetization, i.e. along the long axis of the particle. If a strong external field is applied away from this axis, the orientation of the particle's magnetic field will return to the long axis when the external field is removed. Thus, the orientation of the particle's magnetic field is always near $0°$ or $180°$ relative to the long axis of the particle. Any other orientation is unstable and reverts to the long axis. It is possible that this anisotropy may account for the opposite directions selected by birds after their initial magnetization, but not enough data are available to evaluate such an idea.

For our experiments, the earth's magnetic field was used for biasing prior to magnetization. The solenoid was oriented E–W, so that the pulse was applied nearly perpendicular to any biasing of the particles by the earth's magnetic field that may have occurred. If the particles were completely free to move, the applied field would have been almost perpendicular to the 'easy direction' of magnetization for the particle. When the external field was removed, the resulting magnetization of the particle would assume only one of two directions: the same as its original direction or the opposite direction. If, and only if, all of the particles were free to rotate in all directions and were always aligned parallel to one another, then applying a strong external field (i.e. not exactly perpendicular to the 'easy axis') would result in all the particles having the same magnetic orientation: parallel or antiparallel to their original orientation. The results of experiments using electromagnets indicate that the magnetic material of bobolinks probably has some freedom of movement or rotation (R. C. Beason, unpublished observations), but there is no evidence that the particles can move freely in all directions. Magnetic remanence data (Beason and Brennan, 1986) indicate that the particles lie in close proximity to one another and could be arranged in chains similar to the configurations of the magnetotactic bacteria (Blakemore, 1982). This arrangement would cause the polarity of the individual particles to be serial within the chain (i.e. N to S along the chain). If magnetite is involved in avian magnetoreception, then each receptor cell might have a chain of these particles. However, there is no reason to expect that

the chain of magnetite in one receptor is oriented parallel to the chains in other receptors.

How a bird responds (i.e. the direction in which it orients) to the various magnetizing treatments depends not only on how the material of individual receptors is affected but also on how the animal interprets the information from the reconfigured receptors. There are probably many differently oriented individual magnetic receptors involved in magnetoreception. The evidence from the magnetic remanence analysis indicates that the net natural magnetization of bobolink heads is only about 1 % of the total potential magnetization (Beason and Brennan, 1986). This would indicate a nearly random orientation of the magnetic receptors relative to one another. Data from electrophysiological recordings of the avian trigeminal nerve (with which the magnetite is thought to be associated) indicate that individual neurones respond differently to the same magnetic stimulus (Beason and Semm, 1987; Semm and Beason, 1990). Further interpretation of whether our results indicate that a magnetic compass mechanism was influenced by the magnetization is difficult because we do not know how the avian brain processes the information from the receptors.

Furthermore, we cannot exclude a 'map' effect because the test birds were captured as adults that had made at least one migratory round trip previously and could be attempting to compensate (Perdeck, 1958) for the apparent 'displacement' caused by the treatment. Similar results could be predicted for birds compensating for longitudinal displacement such as that caused by natural wind drift (Richardson, 1991) or by nefarious experimenters transporting the birds to a new location to test their homing abilities.

The similarity of the results obtained by pooling the data by night with pooling by bird within each experimental treatment supports our conclusion that the magnetizing treatment affected a magnetic receptor. Although the Australian silvereye (*Zosterops lateralis*) appears to compensate for the magnetization after a few days (Wiltschko *et al.* 1994), there was no indication that the bobolinks were doing so in our experiments (Fig. 3). If anything, there was an increase in deviation away from the control means with time, rather than the decrease that would be expected if the birds were compensating.

The presence of a magnetite-based magnetoreceptor does not preclude the existence of the wavelength-sensitive (probably photopigment-based) magnetoreceptors that have been reported in the Australian silvereye, another migratory bird (Wiltschko *et al.* 1993). In fact, the two magnetoreceptor systems may be complementary and function in the same or different contexts (Phillips, 1986; Semm and Beason, 1990). Electrophysiological recordings from the bobolink nervous system indicate that both the visual system (perhaps using a photoreceptor) and the trigeminal nerve system (perhaps using magnetite) respond to changes in the ambient magnetic field (Beason and Semm, 1987).

The results of this study are consistent with the hypothesis that magnetite, or some other magnetizable material, is

involved in magnetic field transduction by the bobolink. However, nothing is known about how magnetite might transduce magnetic information or how the central nervous system processes the information from the magnetoreceptors. The exact location, structure and functioning of the receptor(s) associated with the magnetic particles are unknown, although the ethmoidal magnetite deposits are the most likely location. Understanding the role and functioning of the magnetite-based receptor in navigation must await further research.

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