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A magnetic pulse leads to a temporary deflection in the orientation of migratory birds

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Abstract. Migratory Australian Silvereyes were treated with a strong magnetic pulse designed to alter the magnetization of the small magnetite particles that are found in birds' heads. Prior to the treatment, the birds preferred the northeasterly migratory direction. The pulse initially resulted in a 90° clockwise shift of orientation; however, within about a week, the birds seemed to return to their original headings. These findings, which seem to suggest an involvement of magnetite in migratory orientation, are in contrast with previous findings which indicated that it is a light-dependent process. They are discussed in view of the current concepts on magnetoreception and on the role of magnetic information in avian orientation.
Key words. Bird migration; orientation; magnetic field; magnetite; magnetoreception; Silvereye; *Zosterops l. lateralis*.

Magnetic orientation responses have been reported in various kinds of animals[1-3], which suggests that the use of magnetic information is fairly widespread in the animal kingdom. The transduction mechanisms and the neurophysiological basis of magnetoreception, however, are still largely unknown. In terrestrial vertebrates, the discussion focuses mainly on two mechanisms, namely 1) biochemical bi-radical reactions of excited macromolecules in connection with light-dependent processes[4,5] and 2) small particles of magnetite[1,6]. Behavioural[7] and electrophysiological data[8] on pigeons, as well as the results of orientation studies with newts[9] and migratory birds[10] are in agreement with the hypothesis that light-dependent processes are involved. Experiments designed to alter the migration of magnetite particles found in the head region of pigeons[6] have yielded inconsistent results so far, as the treatment sometimes led to considerable effects[11,12], and sometimes to no effect at all[13].

All experiments testing for a possible role of magnetite so far have been performed with homing pigeons. Here we describe the first observations of the effect of a strong magnetic pulse on migratory orientation.

Material and methods

The Australian Silvereye (*Zosterops l. lateralis*, Zosteropidae) shows regular seasonal movements between Tasmania and the Australian mainland. The test birds had been mist-netted during the winter of 1991 in Armidale, New South Wales. Laboratory tests in the spring of 1991 had revealed that they use a magnetic inclination compass to locate their migratory direction[14].

The orientation tests described here—all conducted indoors in the local geomagnetic field—were performed with eleven individuals from the same group in the Australian autumn between 10 March and 14 April, 1992. The birds were tested one at a time for a period of approximately 1 h. Their orientation was recorded in funnel cages lined with typewriter correction paper (TippEx, Germany) on which the birds left scratch marks while moving around[14,15]. From the distribution of these marks, the heading of each recording was calculated. Recordings with fewer than 35 scratches were excluded from the analysis because of insufficient activity. From the headings, mean vectors were calculated by vector addition. From the data recorded before treatment, a mean vector was calculated for each individual bird, and these vectors were tested with the Hotelling Test[16] for a common directional tendency (see table). A mean vector based on the mean headings only was also calculated; this and the vectors based on the headings of the various days after treatment were tested for directional preference with the Rayleigh Test[16]. Two distributions were compared with the Watson Williams Test[16].

The series began with a number of control tests in order to establish the normal directional preference of the test birds (see fig., upper left diagram; these tests are part of the series under 'white' light[10]). The experimental treatment consisted of a magnetic pulse of approx. 0.5 T and approx. 4 ms duration. It was produced by a solenoid with 7700 μF capacitors charged to 250 V DC, which were discharged through a silicon controlled rectifier. A diode across the coil reduced any current flowing backwards to a negligible minimum. The physical north pole of the induced field was directed towards the end of coil where the heads of the test birds were placed. The treatment was applied in the evening immediately be-

Orientation of silvereyes before and on consecutive days after treatment with a strong magnetic pulse, given with respect to the control directions of the individual birds.

Day	N	n	α_m	r_m
before treatment	11	57	24°	0.68***
day of treatment	11	11	+91°	0.73**
day 2:	10	10	+79°	$0.54^{n.s.}$
day 3:	9	9	+53°	$0.50^{n.s.}$
day 4:	10	10	+77°	$0.49^{n.s.}$
day 5:	6	6	+35°	$0.35^{n.s.}$
days 8 and 9	7	9	−21°	$0.31^{n.s.}$
day 10 to 12:	6	11	−53°	$0.46^{n.s.}$
day 13 and later:	3	13	−10°	0.69***

N, Number of birds tested; n, number of tests.
Before treatment: α_m represents direction with respect to magnetic north; r_m, mean vector length based on the 11 individual vectors; asterisk at r_m indicates significance by the Hotelling test[16].
Day of treatment and later: α_m, r_m, direction and vector lengths of mean vector calculated from the headings with respect to the individual bird's mean under control conditions; asterisks at r_m indicate a significant directional preference by the Rayleigh test[16].
Significance levels: n.s., not significant; ** = $p < 0.01$, *** = $p < 0.001$.

fore a test began. The birds were again tested on subsequent evenings. After 5 days, the birds were allowed to rest for two days; then the tests continued. Various individuals were treated at different dates in the course of the season; hence the number of tests after treatment varies considerably.

Results

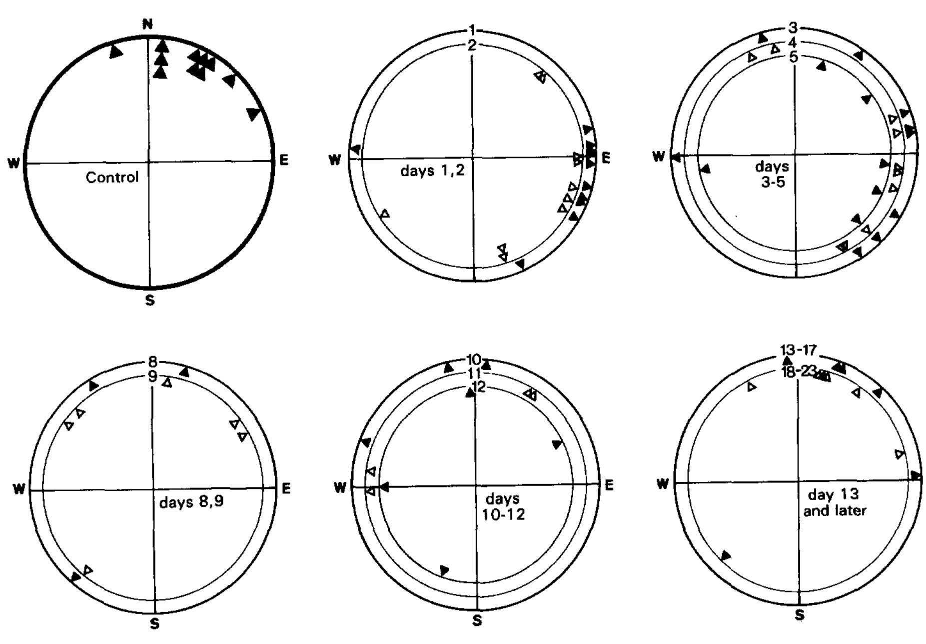
The figure presents the means of the control data and the headings recorded on various days after the treatment with respect to local magnetic north. The day of treatment is counted as 'day 1'. The table summarizes the headings with respect to the individual means of the birds.

Prior to the treatment, the mean headings of the 11 test birds, based on 4 to 6 headings per bird (see table), showed a significant tendency towards 24°, with a vector length of 0.93 ($p < 0.001$, Rayleigh Test). That is, the birds clearly preferred a north-northeasterly direction which corresponds well with their autumn migratory direction.

The initial response to the magnetic pulse was rather uniform, being a significant clockwise shift of approx. 90° ($p < 0.01$, Watson Williams Test). During the next 4 days, the scatter generally increased. After that the birds seemed to return gradually to their original directional preference; from day 8 onward, there were no more southeasterly headings.

Discussion

The magnetic pulse produced a clear effect, at least immediately after its application. As the treatment was designed to change the magnetization of small particles, the effect seems to support an involvement of magnetite in the processes controlling migratory orientation. However, in view of the present discussion about mag-



Orientation behaviour of migratory silvereyes tested under control conditions prior to the treatment and on successive days after treatment, represented as magnetic bearings (magnetic north = geographic 11°). The data for each bird are given as a triangle at the periphery of a circle. The control data represent the mean of 4 to 6 headings per bird; the other data represent the headings of single recordings in successive tests after treatment, with the day of treatment counting as day 1. They are placed at different circles, with solid and open symbols alternating for easier identification.

netoreception and the role of magnetic information in avian orientation our findings raise a number of questions, as they are not easily reconciled with some of the current views.

In orientation, the magnetic field may be employed in two different functions, involving very different types of information. The vector of the magnetic field may serve as the basis for a compass providing *directions*. The spatial distribution of total intensity, inclination etc., in contrast, may provide information on *position*; hence magnetic parameters are discussed as components of the navigational 'map' which allows birds to determine the course to their destination (see ref. 17 for a detailed discussion).

Two neuronal complexes responding to changes in the ambient magnetic field have been identified electrophysiologically in birds so far. Neurons in the visual system projecting into the tectum opticum respond to directional changes at constant intensities; this response is only observed in the presence of light[8,18]. Neurons of the ophthalmic nerve, a branch of the nervus trigeminus innervating the region above the beak where magnetite has been regularly found, respond to small changes in total intensity regardless of the direction of the magnetic field[19]. It is therefore thought that the visual system processes magnetic compass information[8], whereas the trigeminal system is usually assumed to be associated with the navigational 'map'[19].

So far, behavioural studies seemed to agree with this view: Light-dependent responses were observed in behavioural patterns assumed to express compass orientation, like the Y-axis orientation of newts towards the shore[9], the obtaining of information on the direction of the outward journey in pigeons[7], and the migratory orientation of silvereyes[10]. In contrast, after-effects of magnetic treatments designed to change the magnetization of magnetite particles have been reported mainly in pigeon homing. Since these effects were observed in sunny weather, when the pigeons use their sun compass, they are usually assumed to involve the 'map'. The effects varied considerably, however; while magnetizing and demagnetizing hardly affect the orientation of pigeons[13], treating pigeons for approximately 1 min with an ultra-strong field of 10 T (=approx. 20,000,000 times the geomagnetic field) resulted in an approximately 90° clockwise deflection[11]. Treatments using the same type of pulse as in the present study caused directional changes in the range of about 30°[12]. Taken together, these findings seemed to support the concept of both, 'compass/light-dependent responses/visual system' on the one hand and 'map/magnetite/trigeminal system' on the other hand.

Our present results appear to break this pattern – a treatment designed to affect magnetite particles apparently altered a behaviour which is normally seen as compass orientation[20]. However, on the basis of our results, we cannot yet decide whether a magnetic 'map'-component or the compass was affected. Since the test birds had been captured as adult birds that had migrated in the wild before, they may have been familiar with the navigational factors of their destination; the observed deflection might reflect a temporary attempt to compensate for an apparent 'displacement' simulated by the treatment (see ref. 21).

A compass mechanism involving magnetite appears to be an alternative possibility. Yet the magnetic compass of silvereyes has been shown to be an inclination compass[14], it is unclear how such a mechanism, which ignores polarity, could be affected by a reversal of the magnetization of magnetite particles.

On the other hand, the functional background of the effect is not entirely clear, and non-magnetite effects can also not be ruled out. In our case, negative results would have argued against a role of magnetite in the migratory orientation of the test birds; the positive result, however, allows several interpretations, since we do not know what side-effects the treatment might have had. The nature of the response—an initial 90° deflection which gradually disappeared in the course of a week—is difficult to explain on the basis of magnetite. Normally, particles can be magnetized only along their long axis; hence any change in magnetization must be expected to be a reversal. Any new magnetization should be as stable as the original one. The birds had no access to celestial cues which might have made them realize that their magnetic compass was disturbed. Under very rare circumstances, particles of a specific size and shape might acquire a non-stable magnetization perpendicular to the original one which would return to the stable position in the course of time. Yet as long as nothing is known about magnetite particles in silvereyes, such an explanation seems rather far-fetched.

A non-specific interference appears unlikely in view of the rather homogeneous initial response. An effect on non-magnetite receptor mechanisms cannot be excluded, although it would seem that other proposed transducer mechanisms, such as photopigments, are affected only while the external field is present. In pigeons, however, transient after-effects of treatment with an alternating field, much too weak to effect the magnetization of magnetite, have been described[22,23]. The existence of after-effects per se thus does not seem to be limited to magnetite.

The most puzzling aspect of our findings, however, is the fact that in a second experimental series performed simultaneously, birds from the same group of silvereyes were disoriented under red light[10], which suggests light-dependent receptors. Hence we are faced with the surprising result that two treatments that were designed to interfere with very different types of receptors both affected the orientation of our test birds. The observed effects differ greatly: disorientation under red light, and a transient deflection after a magnetic pulse. The functional background of both these effects is still open, as neither the biological mode of action of magnetite nor the nature of light-dependent perception mechanisms is known in detail. Our two treatments might work at different levels, for instance one in the 'map' and the other in the compass, or they might affect complementary components of the same complex mechanism, e.g. a light-dependent process might include a magnetite component.

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