

EFFECT OF A MAGNETIC PULSE ON THE ORIENTATION OF SILVEREYES, *ZOSTEROPS L. LATERALIS*, DURING SPRING MIGRATION

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Summary

The orientation behaviour of Australian silvereyes, *Zosterops l. lateralis*, was tested during their spring migration, when they head southward to their Tasmanian breeding grounds. With only the local geomagnetic field as a cue, the birds significantly preferred their normal southerly migratory direction. Treatment with a short, strong magnetic pulse designed to alter the magnetization of single-domain magnetite led to a significant deflection towards the east for the next 4 days. This was followed by a period of non-oriented behaviour. From day 10 onwards, the birds returned to their original southerly headings.

Together with previous findings, these data suggest that the navigational 'map' of these birds includes magnetic parameters and that a magnetite-based receptor provides them with information about their position. The transient nature of the effect is not easily explained on the basis of single-domain magnetite.

Key words: magnetite, pulse magnetization, bird migration, migratory orientation, magnetic compass, navigational 'map', *Zosterops l. lateralis*, silvereye.

Introduction

With the demonstration of magnetic orientation in an increasing number of animal species (for a summary, see R. Wiltschko and Wiltschko, 1995), the question of how animals perceive the earth's magnetic field has become increasingly important. One obvious possibility was the existence of a receptor containing ferromagnetic material. When small particles of the iron oxide magnetite (Fe₃O₄) were discovered in bees (Gould *et al.* 1978) and numerous other animals (for a summary, see Kirschvink *et al.* 1985; R. Wiltschko and Wiltschko, 1995), it seemed likely that these particles were involved in magnetoreception. Several models for magnetite-based magnetoreceptors have been discussed (e.g. Yorke, 1979, 1981; Kirschvink and Gould, 1981; Semm and Beason, 1990).

In birds, magnetite particles have been found in the head, in particular in the ethmoid region and in the beak (C. Walcott *et al.* 1979; B. Walcott and Walcott, 1982; Beason and Nichols, 1984; Holtkamp-Rötzler *et al.* 1997); remanence studies have indicated that they are mainly single domains (Beason and Nichols, 1984; Beason and Brennan, 1986; Edwards *et al.* 1992). To determine whether these particles indeed play a role in magnetoreception, birds were treated with a magnetic pulse designed to alter the magnetization of such single-domain magnetite. The first such tests were performed on Australian

silvereyes from Tasmania, *Zosterops l. lateralis*, while they headed northwards during their autumn migration. Adult birds responded to treatment with a magnetic pulse with a clockwise shift of their directional tendencies towards east (W. Wiltschko *et al.* 1994). Juvenile birds, in contrast, were unaffected by the same treatment and continued to orient in their migratory direction (Munro *et al.* 1997a,b). Here, we report similar tests during the Australian spring, when the birds are on their return migration, heading southwards.

Materials and methods

The test birds were again silvereyes from Tasmania, *Zosterops l. lateralis*. They migrate in flocks predominantly at dawn and dusk (Lane and Battam, 1971; Chan, 1995). Leaving their breeding grounds, they cross the Bass Strait and winter in Victoria, eastern New South Wales and southeastern Queensland. The birds for our experiments were mistnetted in Armidale, New South Wales (30°30'S, 151°40'E), two on 16 June 1995, the other eight on 10 September 1995. They were first kept outdoors in group cages; on 30 September, they were transferred to indoor cages where they remained, two in a cage, during the experimental period. The light regime in the room was synchronized to the local photoperiod.

Tests took place from 1 October to 22 November 1995, with the test design corresponding to that of previous studies using silvereyes (W. Wiltschko *et al.* 1994; Munro *et al.* 1997a,b). All tests were performed in a windowless room inside a wooden building, in the local geomagnetic field (56 000 nT, -62° inclination). The series began with a number of control tests to establish the normal directional preference of the test birds. After having produced eight or nine evaluable recordings (see below), each bird was subjected to the same brief, strong magnetic pulse that had been used in previous studies with migrants (W. Wiltschko *et al.* 1994; Beason *et al.* 1995; W. Wiltschko and Wiltschko, 1995; Munro *et al.* 1997a,b). The bird was placed into the coil with its head pointing straight forward to the end where the magnetic south pole of the pulse field was induced ('south-anterior' as defined by Beason *et al.* 1995, 1997). With an intensity of 0.5 T, the pulse would have been strong enough to remagnetize the magnetic material found in the head region of the bird, while the short duration of just 4–5 ms made it highly unlikely that magnetic particles would have been able to rotate into the direction of the magnetic field induced by the pulse and thus escape remagnetization (for a discussion, see Beason *et al.* 1995). Each bird was tested immediately after the treatment (day 1) and then, following a fixed schedule, on days 2, 4, 5, 8 and 10. One last test on day 11, 12 or 13 completed the series.

The test periods began approximately 30 min before sunset and lasted approximately 75 min. The birds were tested individually in funnel-shaped cages (Emlen and Emlen, 1966) lined with typewriter correction paper (Tipp-Ex, Germany), where they left scratches on the coating of the inclined walls when they jumped up (for details, see W. Wiltschko *et al.* 1994; Munro *et al.* 1997b). For data analysis, the paper was removed from the funnel, divided into 24 sectors, and the number of scratches in each sector was counted. Recordings with a total of fewer than 35 scratches were excluded from the analysis because of insufficient activity.

From the distribution of scratches, a heading for the test was calculated by vector addition. From the headings of each bird prior to the pulse, we calculated a mean vector for that bird, and the mean directions of all birds were compiled into a grand mean vector of the control data. The mean vectors of the individual birds and the grand mean vector were tested for directional preferences using the Rayleigh test. The data for the birds after the pulse were not pooled in a similar manner, because previous studies (W. Wiltschko *et al.* 1994) had shown that the behaviour changed with time. Consequently, we calculated mean vectors from all tests on the first day immediately following the pulse, from all tests on day 2, etc. These vectors were also tested for directional preferences using the Rayleigh test and, if significant, the confidence interval was used to determine whether the orientation behaviour on that particular day differed from the direction of the grand mean vector of the control data (see Batschelet, 1981).

Results

Before treatment with the magnetic pulse, all individuals showed southerly tendencies (see Fig. 1A), which

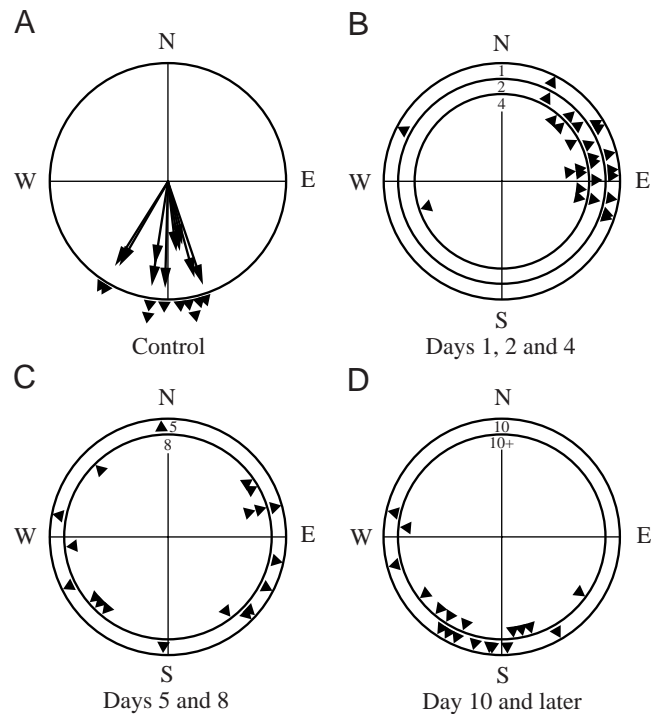


Fig. 1. Orientation behaviour of silvereyes before and after treatment with a short, strong magnetic pulse. (A) The control orientation before the pulse; the arrows represent the mean vectors of the ten birds based on eight or nine recordings each; the triangles at the periphery of the circle indicate the respective mean directions. (B–D) The triangles represent the headings of the ten birds on the days shown (day 1 is the day of treatment). For numerical values, see Table 1.

corresponded well with their natural migratory direction. The vector lengths ranged from 0.57 to 0.95 (median 0.86) and indicate a significant directional preference for all 10 birds (at least $P < 0.05$). The birds' behaviour after treatment with the pulse is summarized in Table 1. The pulse first led to a significant shift in direction to easterly or northeasterly headings (Fig. 1B) which, for each bird, lay clearly outside the confidence interval of the control vector (Table 1). This orientation persisted until day 4. On days 5 and 8, the birds preferred varying directions, resulting in shorter, non-significant vectors (Fig. 1C; Table 1). From day 10 onwards, however, the birds oriented significantly southwards again (Fig. 1D), which corresponds to their natural migratory direction (see Table 1).

Discussion

Two aspects of our findings are of particular importance for the discussion on magnetite-mediated orientation information: (1) as in previous tests during autumn migration, the pulse treatment in spring also caused a deflection towards east; (2) this effect was transient; it disappeared after approximately 8 days.

Table 1. Orientation of silvereyes before and after treatment with a brief, strong magnetic pulse

Day	<i>N</i>	α_m	r_m	ΔC	Significance
Control	10	182°	0.96***		
Day 1	10	73°	0.74**	-109°	**
Day 2	9	67°	0.93***	-115°	**
Day 4	9	73°	0.72**	-109°	**
Day 5	10	120°	0.40	-62°	
Day 8	10	148°	0.08	-34°	
Day 10	10	203°	0.81***	+21°	NS
Later	9	195°	0.75**	+13°	NS

Control: behaviour before treatment with the pulse; the vector is based on the mean of 8–9 tests per bird.

Day 1, day 2, etc., vectors calculated from the headings recorded on the respective day after treatment, with day 1 being the day of treatment.

N, number of birds producing an evaluable recording.

α_m , r_m , direction and length of mean vector, respectively, with asterisks at r_m indicating significance by the Rayleigh test.

ΔC , difference from control. Significance indicates whether the mean direction is significantly different from the mean of the controls (confidence interval); NS, not significant; ** $P < 0.01$; *** $P < 0.001$.

In the present study, we again observed a clear response to the magnetic pulse during the first few days after treatment. This corresponds to our previous findings on adult silvereyes (W. Wiltschko *et al.* 1994); juvenile birds, in contrast, had been unaffected by the pulse (Munro *et al.* 1997a). The exact age of our test birds is not known but, since they were tested during the spring migration, even first-year birds were at least 9 months old and thus mature. More important than age, however, might be their flying experience. The adult birds of the study published in 1994 had been mistnetted in their winter quarters; after being tested in other kinds of experiments (see W. Wiltschko *et al.* 1993, 1998) during the spring migration, they were held in captivity over the summer and tested for their response to the pulse treatment during the following autumn (W. Wiltschko *et al.* 1994). This means that they had flown around in Tasmania before migration, had completed the migration trip from Tasmania to Armidale and had roamed around in the Armidale area before they were caught. The test birds of our present study would have had the same kind of flying experience before they were captured. Both groups of birds were familiar with the distribution of navigational factors in their Tasmanian home region, on the migration route and in the Armidale area. Hence, they would be expected to have had a fully developed navigational ‘map’, a mental representation of the spatial distribution of these navigational factors (for details, see R. Wiltschko, 1997), which are assumed to include magnetic gradients (see R. Wiltschko and Wiltschko, 1995). The juveniles that had shown no response to magnetic pulsing (Munro *et al.* 1997a), in contrast, had been captured in Tasmania shortly after fledging and before they had had sufficient time to explore their home region. As a consequence, their experience was probably

too limited to have established a functional ‘map’. Having been transported to Armidale by aeroplane and having never been allowed to fly free in the Armidale region, they were totally unfamiliar with the local navigational factors. This difference in flying experience appears to be crucial for the control of migratory orientation: large-scale displacement experiments (Perdeck, 1958) showed that adult, experienced migrants (starlings *Sturnus vulgaris* and chaffinches *Fringilla coelebs*) use mechanisms of true navigation to head towards their familiar goal, whereas juvenile first-time migrants that have not yet had a chance to gather the information necessary for establishing a ‘map’ rely exclusively on innate information about their migratory course. Thus, the response of adult silvereyes in both migratory seasons (W. Wiltschko *et al.* 1994; present study), but the lack of response of young birds (Munro *et al.* 1997a,b), appears to depend on the amount of flying experience the test birds had before they were captured: the pulse seems to affect only birds that had sufficient experience to have developed a navigational ‘map’ (see also Löhrl, 1959; Sokolov *et al.* 1984).

This dependence of the pulse effect on flying experience suggests that the pulse affects the position-finding system associated with the ‘map’ rather than the magnetic compass. The magnetic pulse appears to interfere with a hypothetical magnetite-based receptor that allows birds to measure the local values of magnetic gradients, thus providing them with information on their position (for a detailed discussion, see Munro *et al.* 1997b). Our present findings support this hypothesis. In both seasons, despite the 180° difference in migratory direction, adult silvereyes responded to the pulse with oriented behaviour towards east. This is in agreement with an effect on the position-finding system, because the same pulse treatment should induce the same changes, leading to a similar response. An effect on the compass mechanism, in contrast, should have resulted in the same deflection relative to the migratory direction, e.g. both seasons clockwise (east in autumn and west in spring).

Two other findings also indicate that the ‘map’ system rather than the compass is affected by the pulse treatment. (1) Juvenile silvereyes continued in their seasonally appropriate direction after the pulse (Munro *et al.* 1997a). Altered input from the magnetite-based receptor would be as meaningless as unaltered input for juveniles without a ‘map’, which have to rely solely on innate information on their migratory direction. The fact that they oriented in their normal migratory direction shows that their magnetic compass was intact. (2) Adult bobolinks *Dolichonyx oryzivorus* also responded to magnetic pulsing with a deflection from their migratory direction; this deflection could be suppressed by blocking the ophthalmic nerve during testing. The ophthalmic nerve is the branch of the *nervus trigeminus* that innervates the region where magnetite was found in birds; blocking it would deprive the birds of input from the hypothetical magnetite-based receptor. The fact that under these conditions the birds continued in their normal migratory direction clearly shows that their magnetic compass was unaffected by the pulse (Beason and Semm, 1996).

This leaves the question of how the specific response of our test birds – oriented behaviour in a deflected direction – is to be interpreted. It might represent some kind of default response caused by a lack of input from the magnetite-based receptor. However, the above-mentioned data of Beason and Semm (1996) seem to suggest that birds fall back on their innate migratory direction if the input from that receptor is blocked. The other possibility is that the pulse altered the magnetic ‘map’ information and that the observed deflection is a response to false information on position. Recent studies with adult bobolinks and homing pigeons *Columba livia* clearly showed that the direction of the observed deflection depends on the direction in which the pulse was applied, i.e. the deflection induced by a pulse ‘south-anterior’ differed from that induced by a pulse ‘north-anterior’ or ‘south-left’ (see Beason *et al.* 1995, 1997). Together, these results suggest that the magnetic pulse modifies magnetic ‘map’ information, rather than rendering it totally indecipherable, and that the eastward deflection is caused by altered information about position, simulating some westward displacement.

The other important aspect of our findings is the transient nature of the pulse effect. Its disappearance had already been suggested in our previous study (W. Wiltschko *et al.* 1994), although only a few birds were tested after day 5. Our present study documents the disappearance of the initially observed deflection in all birds: after 10 days, their orientation was no longer affected. This phenomenon is difficult to explain. The pulse may have caused the remagnetization of an unknown portion of the magnetite particles which, in turn, resulted in the altered input. Remagnetization of single-domain magnetite, however, should be just as stable as the original magnetization. In view of this, the birds’ return to their original directional tendencies within a few days seems odd, and we can only speculate about possible reasons.

Homing pigeons treated with similar magnetic pulses also showed deflections compared with untreated controls when released at distant sites. These deflections were observed for approximately 3 days and they disappeared faster than the deflection in silvereyes: after 4 or 5 days during which the treated pigeons performed two homing flights, their orientation was no longer different from that of the controls (Beason *et al.* 1997). Here, one might argue that the pigeons on their way home realized that the altered magnetite-mediated information on position was misleading, at the same time experiencing the discrepancy between this information and that provided by other, non-magnetic ‘map’ factors. As a consequence, they might have recalibrated the magnetite-mediated information accordingly. Such a recalibration seems unlikely for the silvereyes in our present study, because they lacked experiences similar to those of the pigeons to prove that the magnetite-mediated information was incorrect. Recalibration against visual cues from their housing quarters also appears unlikely. It is unclear how such cues could dominate over factors integrated in the navigational ‘map’ and why recalibration processes should set in only after 4 days. However, when the birds continued to receive false

information on their position, they might have finally ignored it and fallen back on their innate migratory course.

Other possible interpretations of the transient nature of the effect involve the structure of the as yet unknown receptor and the possibility that the information provided by the receptor becomes correct again after a while. Are single-domain particles in the hypothetical receptor regularly replaced, with the new ones aligned in the same way as the old ones had been before treatment? Or does magnetite in the receptor exist in a form other than as single domains, for example, as superparamagnetic particles (see Kirschvink and Gould, 1981; Edwards *et al.* 1992)? In this case, the magnetization of the particles would outlast the pulse only briefly; however, the pulse might cause changes in the pattern and in the arrangement of these particles within their medium, thus leading to ‘false’ information, until some active process restores the receptor to its original state.

As long as our knowledge on magnetite-based receptors in general is so limited, we cannot decide between these possibilities. We can only hope that research will soon be successful in revealing the mechanisms of magnetoreception, the receptor structures and their connection to the central nervous system.

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