Bird navigation: what type of information does the magnetite-based receptor provide?

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Previous experiments have shown that a short, strong magnetic pulse caused migratory birds to change their headings from their normal migratory direction to an easterly direction in both spring and autumn. In order to analyse the nature of this pulse effect, we subjected migratory Australian silvereyes, *Zosterops lateralis*, to a magnetic pulse and tested their subsequent response under different magnetic conditions. In the local geomagnetic field, the birds preferred easterly headings as before, and when the horizontal component of the magnetic field was shifted 90° anticlockwise, they altered their headings accordingly northwards. In a field with the vertical component inverted, the birds reversed their headings to westwards, indicating that their directional orientation was controlled by the normal inclination compass. These findings show that although the pulse strongly affects the magnetite particles, it leaves the functional mechanism of the magnetic compass intact. Thus, magnetite-based receptors seem to mediate magnetic ‘map’-information used to determine position, and when affected by a pulse, they provide birds with false positional information that causes them to change their course.

Keywords: magnetoreception; magnetite; pulse magnetization; migratory orientation; inclination compass; *Zosterops lateralis*

1. INTRODUCTION

The two hypotheses favoured in the current discussion on magnetoreception assume primary processes based on different physical mechanisms. The *magnetite hypothesis* proposes that magnetic input is mediated by particles of magnetite (Yorke 1979; Kirschvink & Gould 1981; and others), whereas the *radical pair model* suggests that magnetic input is mediated by magnetically sensitive chemical processes involving specialized photo pigments (Schulten & Windemuth 1986, later detailed in Ritz *et al.* 2000). These two hypotheses were first considered as alternatives that largely exclude each other, and experiments that would help to decide between them were needed. Hence, we began to test the two hypotheses in behavioural experiments with migrating birds, using their orientation in migratory direction as an indicator of whether magnetoreception worked properly. Subsequent tests with passerine migrants yielded evidence that supports both the hypotheses. As predicted by the magnetite hypothesis, migratory orientation was affected by a short, strong magnetic pulse designed to alter the magnetization of magnetite particles, with birds that had been heading in their northerly or southerly migratory direction now deflected towards east (Wiltschko *et al.* 1994, 1998). At the same time, as predicted by the radical pair model, migratory orientation required light and proved wavelength-dependent, being ineffective under long-wavelength light of 590 nm and beyond (e.g.

Wiltschko *et al.* 1993a; for summary see Wiltschko & Wiltschko 2002). Recent experiments in high-frequency fields directly indicated an underlying radical pair mechanism (Ritz *et al.* 2004; Thalau *et al.* 2005; Wiltschko *et al.* 2005). Together, these findings suggested that migratory birds used receptors based on magnetite as well as on radical pair mechanisms.

Details of these results allowed an interpretation of these findings: the pulse effect was restricted to old, experienced birds, thus indicating that a learned system was involved, whereas the disorientation under long-wavelength light was observed in old, experienced and young, inexperienced migrants alike, thus suggesting an effect on an innate system (Munro *et al.* 1997). Hence, we tentatively concluded that the magnetite-based mechanism provided birds with magnetic information that was interpreted with the help of the experience-based navigational ‘map’ to indicate position, while radical pair processes provided directional information for the innate magnetic compass (Munro *et al.* 1997; see Wiltschko & Wiltschko 2005; Wiltschko & Wiltschko 2006 for review). This was in agreement with electrophysiological studies, where units in the trigeminal system (ophthalmic nerve, trigeminal ganglion) that innervate the region, where magnetite is located in birds (e.g. Beason & Brennon 1986; Hanzlik *et al.* 2000; Williams & Wild 2001; Fleissner *et al.* 2003), were found to respond to changes in magnetic intensity (Semm & Beason 1990), a parameter that shows gradients and thus could be used to determine position. On the other hand, units in parts of the visual system (nBOR, *tectum opticum*) responded to changes in magnetic direction

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(Semm *et al.* 1984; Semm & Demaine 1986). Thus, two independent receptor systems seemed to provide birds with two different types of magnetic information.

A recent observation, however, raised a novel caveat. Migratory birds tested under monochromatic blue to green light of low intensity are oriented in their seasonally appropriate migratory direction, and this orientation is controlled by their normal inclination compass and is based on radical pair mechanisms (Wiltschko *et al.* 2003, 2005). However, when the intensity of the same monochromatic lights was increased, the birds ceased to show migratory orientation. Instead, they headed into 'fixed' directions that did not show the seasonal change between spring and autumn (Wiltschko *et al.* 2000). A detailed analysis showed that this behaviour was not controlled by the inclination compass—it was polar rather than axial and that it did not involve radical pair processes (Wiltschko *et al.* 2003, 2005). Thus, the fixed directions observed under certain light regimes do not represent normal compass orientation, but are responses of fundamentally different nature.

The responses of the Australian silvereyes, *Zosterops lateralis*, to pulse treatment had been a deflection to the east in spring as well as in autumn (Wiltschko *et al.* 1994, 1998). This obvious similarity to the fixed directions raised the question about the nature of the pulse effect: were the responses to the pulse related to the fixed directions? To answer this question, we again subjected silvereyes to a magnetic pulse and analysed their subsequent orientation in a magnetic field with reversed inclination in order to see whether or not their responses were still controlled by their normal inclination compass (see Wiltschko *et al.* 1993b). If this is true, it indicates that the pulse does not affect the compass, but is likely to involve the mechanisms providing the magnetic map information.

2. MATERIAL AND METHODS

The experiments took place in Armidale, NSW, Australia (30°30' S, 151°40' E), during southern spring from 22 September to 21 October 2003.

(a) Test birds

As in the previous studies, the test birds were Australian silvereyes of the migratory Tasmanian population, *Zosterops l. lateralis*. Most birds of this subspecies spend their winter on the Australian continent, moving north as far as northern New South Wales and southern Queensland. They migrate in flocks predominantly during the twilight hours at dawn and dusk (Lane & Battam 1971).

The test birds were captured on their wintering ground at the campus of the University of New England in Armidale between 8 and 9 September 2003. Since in previous studies (Wiltschko *et al.* 1994, 1998), we had observed occasional headings in the opposite direction after pulse treatment, we used 24 birds to have a larger sample size for statistical analysis. The birds were housed indoors in groups of four in large cages, with the light regime synchronized with the local photoperiod. When the tests were completed, the test birds were released at the place of capture.

(b) Pulse treatment and data collection

The test protocol replicates that of the previous studies (Wiltschko *et al.* 1994, 1998; Munro *et al.* 1997). Testing began with a series of six control tests in the local

geomagnetic field ($mN=360^\circ$, 56 000 nT, -62° inclination) to determine the directional preference of each individual in order to assure that the birds showed appropriate migratory orientation. Then the birds were subjected to a pulse with an intensity of 0.5 T and a duration of about 4–5 ms, which was administered in the same way as earlier. A solenoid was aligned in east–west direction; the birds were placed into the solenoid facing east with the 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). Three critical tests followed, one immediately after the pulsing, the others on the two following evenings. During this phase, all the birds were tested in three magnetic conditions: (i) local geomagnetic field, (ii) in a magnetic field with the horizontal component shifted by 90° anticlockwise ($mN=270^\circ$, 56 000 nT, -62° inclination) and (iii) a magnetic field with the vertical component inverted ($mN=360^\circ$, 56 000 nT, $+62^\circ$ inclination). Eight birds started in the geomagnetic field, eight in the field with horizontal component shifted and eight in the field with the vertical component inverted; they were tested in the other two conditions, respectively on days 2 and 3. On day 10 after pulsing, all the birds were again tested in the local geomagnetic field.

The daily testing period began about 30 min before sunset and lasted approximately 75 min. The birds were tested individually in funnel-shaped cages (Emlen & Emlen 1966) lined with coated paper (typewriter correction paper, BIC Germany, formerly Tipp-Ex; for details about the test cage and test performance, see Wiltschko *et al.* 1994). During testing, the cage was lit by 'white' light of about 39 mW m^{-2} produced by an incandescent light bulb, which passed through a diffuser before reaching the bird in the cage.

(c) Data analysis

For evaluation, the coated paper was removed from the test cage, divided into 24 sectors, and the number of scratches in each sector was counted. One recording with fewer than 35 scratches was excluded because of insufficient migratory activity.

From the distribution of activity, we calculated the heading of each recording. Based on the headings of the 24 birds, a mean vector of each day and, after pulsing, of each condition was calculated by vector addition, with the direction α_m and the length r_m (see Batschelet 1981). To characterize the behaviour during the control phase, we also determined the individual birds' mean vectors from the six control headings per bird, comprised of the mean headings in a grand mean vector for the control period before pulsing. After pulsing, we determined mean vectors from the headings recorded in the three magnetic conditions.

The mean vectors were tested with the Rayleigh test for directional preference. The behaviour of the birds after pulse treatment was compared with their behaviour during the control phase before treatment, using day 6 as reference. In addition, behaviour in the three magnetic conditions was also compared to assess the changes caused by altering the ambient magnetic field. For this comparison, we used the Mardia Watson Wheeler test indicating differences in distribution (see Batschelet 1981).

Table 1. Orientation behaviour of the test birds on the various days of testing (mN=270°, magnetic north shifted by 90°–270° west, vert. comp. inv., vertical component of the magnetic field inverted; median activity, median number of scratches left by the birds during individual recordings on the respective testing-day or in the respective condition, respectively; median concentr., median concentration of activity in the cage, with concentration corresponding to the length of the vector calculated from the distribution of activity within the 24 sectors. (The mean vector, with the direction α_m and the length r_m , was calculated from the headings of the n birds on the respective testing-day or in the respective condition. Δ control indicates the difference between the mean direction after the pulse and day 6 before the pulse; Δ geomagnetic field gives the difference between the respective data and those obtained in the geomagnetic field. Asterisks at the vector length r_m indicate a significant directional preference (Rayleigh test); asterisks at the differences indicate significance of these differences (Mardia Watson Wheeler test). Significance levels: ***, $p < 0.001$; n.s., not significant.)).

conditions	n	median activity	median concentr.	mean vector		Δ control (day 6)	Δ geomagnetic field
				α_m	r_m		
<i>control before pulsing</i>							
day 1	24	582	0.22	176°	0.63***		
day 2	24	425	0.27	210°	0.59***		
day 3	24	352	0.33	182°	0.72***		
day 4	24	265	0.34	183°	0.76***		
day 5	24	266	0.31	178°	0.74***		
day 6	24	279	0.30	185°	0.73***		
control (day1–6)	24	347	0.28	186°	0.89***		
<i>first 3 days after pulsing</i>							
geomagnetic field	24	232	0.35	79°	0.54***	−106°***	
mN = 270°	24	161	0.34	1°	0.57***	+176°***	−78°***
vertic. comp. inv.	24	191	0.40	272°	0.70***	+87°***	−167°***
<i>day 10 after pulsing</i>							
day 10	23	276	0.31	178°	0.67***	−8° n.s.	

3. RESULTS

The mean vectors of the various days are given in table 1. Before pulse treatment, the silvereyes showed very good orientation in their seasonally appropriate southerly migratory direction, with each day being significantly oriented. Summarizing the six data points of each bird, we obtain mean vectors with directions ranging from 153° to 217° (with one stray heading at 355°) and vector lengths ranging from 0.50 to 0.98 (see figure 1). The generally long individual vectors with a median of 0.81 indicate a good agreement of the individuals' directional choices, while the grand mean vector of 0.89 (see table 1) reflects excellent agreement among the birds.

As before, the pulse caused a significant change in the birds' headings on the day of pulsing and in the following 2 days (figure 2). In the geomagnetic field, the birds headed eastward as before, and when magnetic north was shifted 90° anticlockwise to 270° west, they altered their headings accordingly, now heading northward. The behaviour in the field with the vertical component inverted is diagnostic for the inclination compass. Here, the silvereyes reversed their headings to westward, indicating their use of this mechanism. The orientation in the local geomagnetic field is significantly different from that in the other two conditions (see table 1), which are also significantly different from each other ($p < 0.001$, Mardia Watson Wheeler test).

On day 10 after pulsing, the birds preferred their normal southerly migratory direction again, with their behaviour no longer different from that during the control phase before pulsing (table 1).

4. DISCUSSION

As in previous studies (Wiltschko *et al.* 1994, 1998), our test birds responded by changing to easterly headings.

Figure 1. Orientation of silvereyes in the geomagnetic field before pulse treatment. The arrows represent the mean vectors of the 24 individual test birds based on six recordings each; the triangles outside the circle mark the respective mean headings.

Their behaviour when the vertical component had been reversed reveals that their headings after the pulse were still controlled by the inclination compass. This is a crucial difference to the 'fixed direction' observed under certain light regimes, which were found to be polar responses (e.g. Wiltschko *et al.* 2003, 2005). It clearly shows that the birds' behaviour after the pulse represents normal compass orientation, even if the birds did not choose their southerly migratory direction. The magnetic compass of our test birds was working in the normal way; they just preferred easterly instead of a southerly compass course.

In previous studies, an effect of the pulse was not observed in young, inexperienced migrants (Munro *et al.* 1997) and it was suppressed in birds, whose ophthalmic nerve had been anaesthetized (Beason & Semm 1996). In both the cases, the birds continued in their normal

Figure 2. Orientation of silveryeyes immediately after the pulse and on the following two evenings. The *triangles* at the periphery indicate the individual headings of the 24 birds and the *arrows* represent the mean vectors under the different magnetic conditions. The two inner circles give the 5% (dashed) and the 1% significance border of the Rayleigh test (Batschelet 1981).

migratory direction, suggesting that the pulse did not affect the magnetic compass. In the present study, the birds' normal use of their inclination compass after pulsing demonstrates that the compass remained intact although a pulse effect was observed. Together, these findings strongly argue that the magnetic compass of birds does not involve magnetite, but is based on an entirely different physical principle, which has recently been identified as a radical pair mechanism (Ritz *et al.* 2004; Thalau *et al.* 2005; Wiltschko *et al.* 2005).

These considerations lead to the conclusion that the pulse affected another part of the navigational system, namely the one that determines which compass course the birds will fly. This is in agreement with previous electrophysiological (e.g. Semm & Beason 1990) and behavioural findings (Munro *et al.* 1997) suggesting that the magnetite-based receptors provide birds with information on magnetic intensity, which can be used as a component of the navigational map for determining position and deriving the compass course to the goal. The findings by Beason *et al.* (1995, 1997) have shown that the same magnetic pulse applied in different orientations resulted in different deflections from untreated control birds, indicating that the observed headings still depend on the output of the magnetite-based receptors. This indicates that the pulse does not silence these receptors altogether, but instead causes them to provide birds with false information, resulting in a change of the courses to be pursued.

Magnetic intensity shows gradients between the poles and the magnetic equator, indicating something like 'magnetic latitude'. Following the traditional concept of the map, one would intuitively expect that magnetic map components mainly indicate north–south displacements. Hence, the observation that pulsing evokes easterly headings seems odd, but it is a consistent, reproducible response to the pulse and the way it was applied here and in the previous studies (Wiltschko *et al.* 1994, 1998). The structure of the magnetite-based receptors in birds is not entirely clear. Single domains (Beason & Brennon 1986) as well as superparamagnetic particles have been reported (Hanzlik *et al.* 2000; Fleissner *et al.* 2003), and although several hypotheses of how magnetite-based receptors may convey magnetic input have been suggested (e.g. Yorke 1979; Kirschvink & Gould 1981; Davila *et al.* 2003), a

Figure 3. Model illustrating the use of magnetic information obtained by different types of receptors in different parts of the navigational system.

consistent model has not yet been generally agreed upon. In any case, a 0.5 nT pulse, as applied in the present study, must be expected to markedly change its output. In the present stage, however, it seems premature to speculate on the specific nature of the altered signal and how it might be processed.

In his 'map-and-compass' model, Kramer (1953, 1959) characterized avian navigation as consisting of two different steps. In the first step, the birds determine their position with respect to the goal and derive the goal direction as a compass course. In the second step, they locate this course with the help of a compass and convert it into an actual heading to be pursued (see Wiltschko & Wiltschko 2003). Kramer originally designed this model to describe the navigation of displaced homing pigeons, but it can also be applied to the navigation of migratory birds. The use of magnetic map components is indicated in homing pigeons as well as in migrants (e.g. Walcott 1978; Beason *et al.* 1997; Fischer *et al.* 2003). Our test birds had been caught in their wintering area; they had already completed their first migration and, during the tests, were heading home towards their familiar Tasmanian breeding ground. They had developed a navigational map and were able to use mechanisms of true navigation (see Perdeck 1958, 1983). By showing that the effect of the pulse is restricted to receptors providing information for

the map mechanisms, our findings support the existence of two largely independent mechanisms in the navigational system. Both mechanisms—the map and the compass—can utilize information from the geomagnetic field, but they use different magnetic parameters and make use of different physical principles to obtain the respective information (see figure 3). The magnetite-based system, which is affected by the pulse, records magnetic intensity for use in the map, and radical pair processes, untouched by the pulse, provide directional information for the inclination compass.

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