Magnetic inclination compass: a basis for the migratory orientation of birds in the Northern and Southern Hemisphere

W. Wiltschko[a], U. Munro[b], H. Ford[b] and R. Wiltschko[a]

[a]Department of Zoology, University of Frankfurt, Siesmayerstrasse 70, D-6000 Frankfurt a.M. (Federal Republic of Germany), and [b]Department of Zoology, University of New England, Armidale, New South Wales 2351 (Australia)
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Abstract. We conducted orientation experiments with Silvereyes, *Zosterops lateralis*, Australian passerine migrants, to see whether birds living in the Southern Hemisphere in a magnetic field with an upward inclination orient in the same way as birds in the Northern Hemisphere that experience a downward inclination of the magnetic field. Tested indoors in the local geomagnetic field, the birds preferred southerly directions corresponding to their migratory direction in spring. In a magnetic field with a reversed vertical component, they reversed their directional tendencies. This shows that the magnetic compass of Silvereyes also functions as an inclination compass based on the inclination of the field lines instead of the polarity.
Key words. Bird migration; southern hemisphere migrants; migratory orientation, geomagnetic field; magnetic compass; inclination compass; *Zosterops.*

When the magnetic compass of migratory birds was analysed twenty years ago, it was found to be fundamentally different from man's technical compass: the reversal of the horizontal component as well as the reversal of the vertical component of the geomagnetic field caused the birds to reverse their directional tendencies[1]. This clearly showed that the birds did not use the polarity of the magnetic field; instead they used the axial course of the field lines and their inclination in space. Thus birds do not distinguish between magnetic north and south, but between poleward, i.e., the side where the axis of field lines is inclined into the ground, and equatorward, the side where it points upward.

The bird used in these early experiments was the European Robin, *Erithacus rubecula*, a small passerine breeding in northern and central Europe and wintering in the Mediterranean countries. Such an inclination compass has since been described for a number of other nocturnal migrants (for summary[2]). All of these species, however, breed in the Northern Hemisphere where the geometric field has a positive inclination, i.e., the polarity points north and downward. In the Southern Hemisphere, the geomagnetic field is pointing north and upward. This raises an interesting question about magnetic orientation in birds that live in such an environment. Theoretically, their magnetic compass could also function as an inclination compass, but evidence is lacking. An analysis of the orientation mechanisms of Southern Hemisphere migrants began only recently in Australia[3-5]. Here we report the first result of magnetic field experiments with Silvereyes, *Zosterops lateralis* (Zosteropidae).

Material and methods

Silvereyes are small passerines breeding in the southern and eastern parts of Australia including Tasmania. Birds from the Tasmanian population *Zosterops l. lateralis* migrate northward in the southern autumn. They cross Bass Strait and move along the Great Dividing Range and the Australian east coast to reach their wintering grounds in northern New South Wales and southern Queensland.

The test birds were mist-netted near Armidale, NSW, (30°30'S 151°40'E) between 17 July and 13 August 1991. They were from the Tasmanian population, as indicated by their slightly larger size, rufous flanks and whitish-grey throats[6]. The birds were kept indoors where they lived in large group cages (5 individuals/cage). The photoperiod inside simulated the natural day and night cycle of Armidale.

The orientation tests took place in the southern spring, between 25 October and 25 November 1991. The birds were tested under two magnetic conditions:

1) in the local geometric field: 56,000 nT, mN = 360°, −62° inclination, and

2) in a test field with a reversed vertical component: 56,000 nT, mN = 360°, +62° inclination.

(Unless stated otherwise, directions are given with respect to magnetic north; magnetic north = geographic 11°.)

The birds were tested one at a time for a period of approximately 1 h. Their orientation was recorded in funnel-shaped cages[7] lined with typewriter correction paper (TippEx, Germany) on which the birds left scratch marks while moving around[8]. The distribution of these marks was used to calculate a heading for this registration period. Hereby recordings with fewer than 35 scratches were excluded from the analysis due to insufficient activity. From these headings, a mean vector for each bird was calculated by vector addition, and tested for directional preference with the Rayleigh Test[9]. 23 birds were tested altogether, but many of them failed to show consistent activity levels during the testing period. The present analysis focuses on those 10 birds that contributed at least 3 data points to both test conditions. The center of distribution of their mean vectors was calculated and tested for a common directional tendency using the Hotelling test[9]. The data obtained in both magnetic fields were compared by using non-parametric tests of circular statistic[9] (see below).

Results

The distribution of headings produced by the 10 birds, together with the birds' mean directions, are shown in figure 1. The table lists the vectors of the individual birds. In the local geomagnetic field, the birds tended to prefer southerly directions with a mean of 190° (= geographic 201°), which corresponds well with the direction that would have led them towards their breeding grounds in Tasmania. When the vertical component of the magnetic field was reversed so that it corresponded to the type of field found in the Northern Hemisphere, the birds reversed their tendencies and preferred northern directions with a mean of 18°. The difference of −172° is highly significant ($p < 0.001$, Mardia's two-sample test for bivariate samples, see table).

An analysis of the headings of the less active birds revealed a similar tendency: local geomagnetic field: $n = 23$, $\alpha_m = 175°$, $r_m = 0.51$ ($p < 0.01$, Rayleigh test); field with a reversed vertical component: $n = 24$, $\alpha_m = 28°$, $r_m = 0.71$ ($p < 0.001$). Both samples are significantly different from each other ($p < 0.001$, Mardia Watson Wheeler test); at the same time, they do not differ from the corresponding sample of the 10 highly active birds ($p > 0.05$).

Discussion

These findings clearly show that Silvereyes have a magnetic compass which functions as an inclination compass. This means that they use the inclination of the field lines instead of their polarity. Our birds reacted both to the natural and the manipulated magnetic field just as European Robins would have reacted in the northern spring: they migrated poleward, thereby preferring the direction of the magnetic axis where the course of the field lines formed the smaller angle with gravity (see fig. 2). To them, living in the Southern Hemisphere, however, poleward meant south instead of north.

These findings, together with similar results recently obtained with the Yellow-faced Honeyeater, *Lichenostomus chrysops* (Meliphagidae), another Australian migrant[4], show that the inclination compass is a widespread orientation mechanism in birds which is not restricted to species breeding in the Northern Hemisphere. This, and corresponding findings on homing pigeons[10,11], suggests that the inclination compass might be a common mechanism for magnetic orientation in birds. How widespread such a type of mechanism is among other animals, however, is still largely unknown. Magnetic compass orientation has been described for a number of invertebrate species belonging to the phyla Mollusca and Arthropoda, and for all major vertebrate groups (see Wiltschko and Wiltschko[12] for summary). However, the functional properties have been analysed

Table. Orientation behavior of Silvereyes tested indoors

Bird	Local geomagnetic field			Vertical component reversed			Difference	Significance
	n_b	α_b	r_b	n_b	α_b	r_b	$\Delta\alpha$	
80209	8	190°	0.41	4	38°	0.76	−152°	n.s.
80211	11	197°	0.72*	6	14°	0.38	+177°	*
82616	3	219°	0.85	3	354°	0.57	+135°	-
83612	6	211°	0.51	6	31°	0.71*	180°	*
83618	7	170°	0.76*	9	345°	0.62*	+175°	***
83629	7	191°	0.36	5	23°	0.79*	−168°	**
83642	6	208°	0.70*	7	13°	0.54	+165°	n.s.
83643	3	210°	0.55	3	352°	0.93	+142°	-
83658	3	101°	0.61	4	26°	0.88*	−75°	-
83666	7	169°	0.65*	4	91°	0.48	−78°	n.s.
10 birds:		190°	0.52***		18°	0.60***	−172°	***

n_b, α_b, r_b: number of data points, mean direction and vector lengths of each individual bird, asterisks at r_b indicate significance by the Rayleigh test. The last two columns give the angular difference, $\Delta\alpha$, between the mean directions recorded in the two magnetic conditions (+ clockwise, − counterclockwise) and indicate whether the data differ in distributions (Mardia Watson Wheeler test): asterisks indicate significance, n.s. = not significant, − = samples too small. The bottom line represents a second order statistic, indicating the center of distribution of the 10 vectors; asterisks at the vector lengths indicate significance by the Hotelling test, and the symbol in the last column indicates significance of the difference by Mardia's two sample test. Significance levels: *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

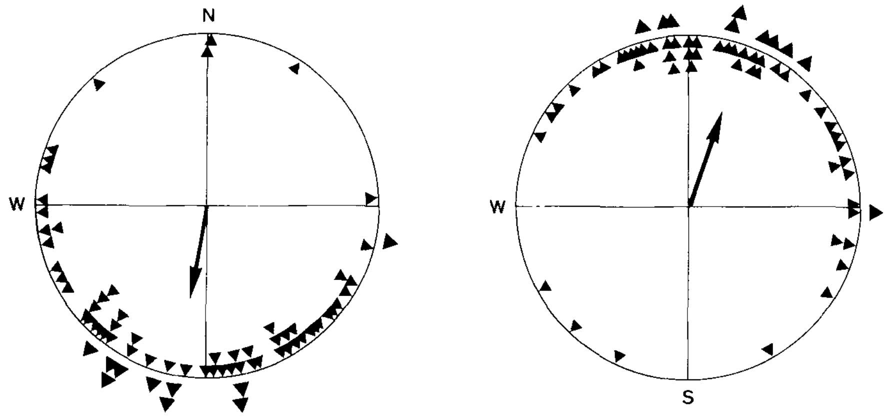

Figure 1. All headings (symbols inside at the periphery of the circle) and mean directions (symbols outside the circle) of 10 birds that contributed at least 3 data points to both experimental conditions (see table). The vectors represent the first order means of the headings: geomagnetic field: $n = 61$, $\alpha_m = 190°$, $r_m = 0.55$ ($p < 0.001$, Rayleigh test); magnetic field with reversed vertical component: $n = 51$, $\alpha_m = 17°$, $r_m = 0.58$ ($p < 0.001$, Rayleigh test); difference: $-173°$ ($p < 0.001$, Mardia Watson Wheeler test).

only in very few species. Sockeye salmon *Oncorhynchus nerca* (Salmonidae)[13], mole rats *Cryptomys hottentotus* (Bathyergidae)[14] and the only invertebrate tested, the flour beetle *Tenebrio molitor* (Tenebrionidae)[15], did not react to an inversion of the vertical component, which indicates that their magnetic compass is based on the polarity rather than the inclination. In the red-spotted newt *Notophthalmus viridescens* (Salamandridae), two types of magnetic compass have been described: an inclination compass for directional orientation towards the shore, and a polarity compass for homing[16].

For migratory birds, this particular type of magnetic compass has an interesting consequence. Migrants possess an innate migration program which includes information on the course of their migration route[17]. Here, the magnetic field provides a directional reference[2]. For Northern Hemisphere migrants, the migratory directions usually contain southerly components in the autumn and northerly components in the spring, while in Southern Hemisphere migrants, these components are reversed. A magnetic compass based on the inclination, which recognizes poleward and equatorward, means that these components of the migratory direction are given in common terms for birds living in very different parts of the world: The migratory program causes all birds to start out moving equatorward when day lengths are decreasing in autumn, and they all complete their migratory journey by flying poleward in spring. In summary, because there are differences in the magnetic inclination, the migration program of birds from the (magnetic) Northern and Southern Hemisphere is similar in this respect (fig. 2). Transequatorial migrants,

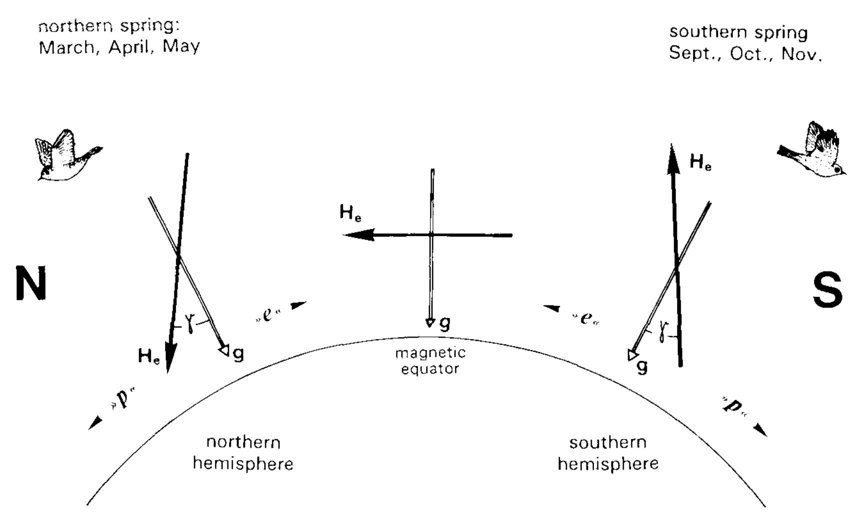

Figure 2. Section through the earth illustrating the inclination of the magnetic field and the spring migratory direction of northern and southern hemisphere birds. N, S = geographic north and south; H_e = vector of the geomagnetic field, g = vector of gravity, γ = smaller angle between the field lines and gravity. »p«, »e« = poleward, equatorward = readings of the magnetic inclination compass of birds.

however, have to reverse their magnetic response when they cross the magnetic equator[18].

This common migration program might have helped many Palearctic species which are now living in the Southern Hemisphere. When forced to move because of deteriorating conditions in the southern autumn, these birds could have followed their traditional tendencies and flown equatorward, which would have brought them north into areas closer to the equator. This would apply to birds that were introduced by European settlers as well as to Holarctic migrants that began to establish breeding populations in their traditional wintering areas. European starlings, *Sturnus vulgaris*, in Australia and New Zealand, might be an example for the former case, while White Storks, *Ciconia ciconia*, and European Bee-eaters, *Merops apiaster*, in South Africa provide examples for the latter case. Members of these two species have been reported to head northward in the southern autumn[19-21]. In a certain sense, these considerations might also apply to our own experimental bird, the Silvereye. The center of distribution of the family Zosteropidae is in Asia, and several of the Asian species migrate considerable distances[6]. Possibly the ancestors of *Zosterops l. lateralis* arrived in Australia already with a similar migratory program.

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