

In: Avian Migration, P. Berthold, E. Gwinner & E. Sonnenschein (Eds.), Springer-Verlag, Heidelberg New York (in press).

Magnetic navigation by an avian migrant?

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Key words: magnetic navigation, magnetoreception, avian migration

Abstract

The question of whether birds navigate using "map" information derived from spatial gradients in the Earth's magnetic field has been debated for half a century (Yeagley 1947). Although there is evidence that vertebrates possess the sensory abilities necessary to perceive the geographic variation in one or more magnetic parameters (i.e., inclination, intensity), there previously has been no direct test of the use of information about geographic position derived from the magnetic field by experienced avian migrants that navigate using map information. Here we report evidence that is consistent with magnetic information being involved in the map used by experienced adult Tasmanian silvereyes (*Zosterops l. lateralis*) during migration to their over-wintering grounds.

Introduction

Spatial variation in the geomagnetic field provides a potential source of information about geographic position ('map' information) that has been suggested to play a role in animal navigation (Yeagley 1947; Gould 1980; Moore 1980; Walcott 1980). To use a magnetic map, an animal would have to learn the alignment, and perhaps the steepness, of the gradient of at least one magnetic parameter within its normal range of movement. It would then have to extrapolate this gradient or gradients beyond its area of familiarity. A comparison of the value of a magnetic field parameter at an unfamiliar site with the 'home value' of that parameter would provide information about the animal's position along the gradient (Phillips 1996; Wallraff 1991). Non-parallel gradients of two different parameters (either or both of which could be magnetic) could then provide the basis for bicoordinate position-fixing (true navigation; Griffin 1952). Spatial gradients in

the geomagnetic field are, however, extremely weak. The average rate of change in magnetic total intensity is only 3-5 nT/km, ranging from values of approximately 25,000 nT near the magnetic equator to 65,000 nT at the magnetic poles. The average rate of change in magnetic inclination is only about 0.01°/km, ranging from 0° at the magnetic equator to 90° at the magnetic poles. The accuracy of map information derived from the geomagnetic field depends in part upon the sensitivity of the underlying magnetoreception mechanism. For example, a map with a resolution of 100 km would require total intensity measurements accurate to approximately 1% (500 nT), whereas a resolution of 1 km would require measurements accurate to approximately 0.01% (5 nT). The use of a magnetic map, therefore, may require an extremely high level of sensitivity to variation in the intensity and/or inclination of a static magnetic field and, thus, may help to establish the lower limits of such sensitivity in a biological system (Kirschvink and Gould 1981; Semm and Beason 1990; Walcott 1991). The possibility of a magnetic map or geographic position sense, therefore, raises fundamental questions not only about bicoordinate navigation, but also about the biophysical mechanism(s) that mediate sensitivity to the geomagnetic field and about the limits of sensory perception.

Perdeck (1958) showed that experienced adult migratory birds possess a "map" and rely on true navigation (Kramer 1953) to reach their summer or winter ranges. In contrast, young birds migrating for the first time rely on an innate migration program that specifies the general compass direction and duration of migration, but not the goal or end point (Berthold 1988).

Several studies have provided evidence consistent with the involvement of the geomagnetic field in the map or geographic position sense of vertebrates, including migratory birds. Recent experiments with silvereyes from the same population used in

the present study suggest that a magnetite-based receptor system may be involved in deriving at least one coordinate of a magnetic map. In these experiments a brief, high intensity magnetic pulse that was strong enough to re-magnetize single-domain magnetite particles caused the migratory orientation of experienced adults to shift by roughly 90° to the east during both the Spring and Fall migrations (Wiltschko et al. 1994, 1998). In contrast, migratory orientation was unaffected in young silvereyes captured before their first migration (Munro et al. 1997a). The absence of an effect on young silvereyes, even though young and old birds appear to have the same magnetic compass mechanism (Munro et al. 1997b), suggests that pulse remagnetization may have affected a specialized magnetoreception mechanism used only by experienced migrants. Such a mechanism could involve single-domain particles of magnetite (Kirschvink and Gould 1981) that play a role in the map used by experienced adult migrants. Moreover, the roughly 90° eastward shift in orientation of adult silvereyes exposed to the magnetic pulse (with no change in the strength of orientation) suggests that the effect of this treatment might have been perceived by the birds as a displacement to the west perpendicular to the normal migratory route.

Several other lines of evidence have suggested that the geomagnetic field may be involved in a vertebrate map sense. Navigation by American alligators, *Alligator mississippiensis* (Rodda 1984), and homing pigeons, *Columba livia* (Keeton et al. 1974; Larkin and Keeton 1976; Kowalski et al. 1988; but see Dornfeldt 1991), is reported to be sensitive to natural temporal variation in the geomagnetic field. Such variations (typically less than 0.1% of the background field) are too weak to affect a magnetic compass (Wiltschko 1972), but could produce large errors in estimates of geographic position derived from subtle geomagnetic gradients (Lednor 1982). Consistent with this interpretation, in Rodda's (1984) study, older alligators that appeared to be using map

information for homing were affected by temporal variation in the magnetic field while younger individuals relying on route-based cues (i.e., path integration) were not. Two other studies have shown that young inexperienced individuals are sensitive to geographic variation in the magnetic field, but do not appear to be using map information derived from the magnetic field. Newly hatched loggerhead sea turtles (*Caretta caretta*) are reported to shift their direction of orientation in response to values of magnetic inclination (Lohmann and Lohmann 1994) and total intensity (Lohmann and Lohmann 1996) that they would normally encounter along their migratory path. These responses do not appear to be associated with true navigation (i.e. orientation to a specific goal), but may help to keep young sea turtles from straying beyond their species' range into regions where conditions are unsuitable for survival (Lohmann and Lohmann 1994). Similarly, young migratory pied flycatchers (*Ficedula hypoleuca* Pallas) from populations in western Europe exhibited a discrete anticlockwise change in compass heading when exposed to values of the magnetic field normally encountered in southern Europe, where the normal migratory route shifts from southwest to south. The altered magnetic fields triggered the shift in orientation only when applied at the appropriate time during the migratory period (Beck and Wiltschko 1988).

Recent studies of homing orientation by an amphibian, the Eastern red-spotted newt *Notophthalmus viridescens* (Fischer et al. 2001; Phillips et al., in prep.), have provided direct experimental evidence that magnetic inclination or one of its components (vertical or horizontal intensity) is used to derive one coordinate of a bicoordinate navigational map. Adult male newts exposed to values of magnetic inclination normally encountered on the opposite side of their home ponds from the testing site reversed their direction of homing orientation relative to controls, while newts exposed to values close to the home value failed to exhibit a consistent direction of homing orientation. Similar

changes in magnetic inclination had no effect on the shoreward magnetic compass orientation of newts, which does not require map information, suggesting that the effects on homing orientation were specific to the map (Fischer et al. 2001).

The present study was an initial investigation of the magnetic field's involvement in the navigational map of an experienced adult migratory bird. Tasmanian silvereyes tested near the mid point of their Fall Migration along the southeast coast of Australia, were exposed to magnetic field values that would normally be encountered near the beginning and end of their Fall migration. If the magnetic field was being used to derive map information, we predicted that silvereyes exposed to values normally encountered near the beginning of the Fall migration would continue to exhibit seasonally appropriate migratory orientation, while those exposed to values normally encountered near the end of the Fall migration would exhibit a change in the direction of orientation or be disoriented.

Methods

Experimental subjects were adult silvereyes (*Zosterops l. lateralis*) that had completed at least one round-trip migration, and therefore had sufficient experience to develop a navigational map. The birds were captured on their breeding grounds in Hobart, Tasmania (42.54° S, 147.8° E) in February 1994, and transported to Armidale, NSW, Australia (30.5° S, 151.7° E), a location approximately halfway along their migratory route. Birds were kept indoors in cages in the ambient magnetic field of Armidale (55,000 nT, -62° inclination; Fig 1B), under a photoperiod initially corresponding to the natural day/night cycle of Hobart. The light regime was subsequently adjusted to simulate the photoperiods silvereyes experience during

migration. Testing began in April 1994, when birds exhibited migratory restlessness.

At the onset of migratory activity, the silvereyes were tested in the ambient magnetic field, at values of 55,000 (total intensity) and -62° (inclination). The methods used in testing have been described previously (Wiltschko et al. 1993; Wiltschko et al. 1994; Munro et al. 1997a). Orientation responses were recorded under diffuse lighting in Emlen orientation funnels (Emlen and Emlen 1966). Typewriter correction paper (Tipp-Ex, Germany), which retained the scratch marks corresponding to the bird's direction of hopping, lined the funnels. The paper was divided into 24 sectors, and scratch marks within each sector were counted. Mean nightly bearings were calculated from the scratch marks. Individual birds were tested repeatedly under the control conditions and one of the two treatment conditions.

The birds were subsequently separated into two treatment groups (Fig 1). Each group was housed and tested in separate four element cube surface coils (Merritt et al. 1983). Each housing coil was 1.29 m, with a current of 167 mA, with the birds' cages occupying the central portion ($\leq 0.2\%$ variation from uniform field; Kirschvink 1992). Although the cages were constructed of largely non-magnetic materials, subsequent measurements revealed that the cage floors were slightly magnetic. As a consequence, there was some distortion of the magnetic fields in the holding cages that was not present in the testing funnels. The testing coil was 2.08 m, with a current of 269 mA. The testing funnels were located within the centermost portion ($\leq 0.02\%$ variation from uniform field; Kirschvink 1992). In one treatment, the birds were exposed in both housing and testing to a vertical intensity increased by 12% (simulated southern displacement, "SimS"; Fig 1A), resulting in values of total intensity and inclination they would normally experience near the beginning of their fall migration. In the second

treatment, birds were exposed in both housing and testing to a vertical intensity decreased by 12% (~6000 nT, simulated northern displacement, "SimN"; Fig 1C), resulting in values of total intensity and inclination the birds would normally encounter within (inclination values) or beyond (intensity values) their winter range. Both groups were exposed to altered magnetic fields for at least six days prior to being tested in that same field. The same magnitude of change in vertical intensity was used in the SimS and SimN conditions so that any difference in the response of silvereyes exposed to these two experimental conditions could be attributed to a difference in the sign, rather than the magnitude, of the change in the magnetic field. The specific combinations of inclination and intensity values used in simulated displacement treatments do not necessarily correspond to particular locations that silvereyes would normally encounter along the migratory route.

Birds in the two experimental treatments were tested on alternate nights. Six birds were exposed to the SimS condition and tested on a total of five nights each. Five birds were exposed to the SimN condition and tested on a total of six nights.

Results

As in previous tests of adult silvereyes in the ambient geomagnetic field of Armidale (Wiltschko et al. 1993, 1994), the distribution of nightly bearings and mean vector bearings of controls was significantly oriented to the north-northeast (NNE; Fig 2B). Birds exposed to the SimS condition exhibited NNE orientation (Fig 2A) that was indistinguishable from that of the same birds under the control condition (data included in Fig 2B). In contrast, birds exposed to the SimN condition ceased to show significant direction of orientation (Fig 2C), and the distribution of mean vector bearings was

significantly different from their responses in the control condition (data included in Fig 2B) and from the responses of the SimS silvereyes (Fig 2A) ($p < 0.01$, two-sample Hotelling's test). There was no difference in the activity level of SimN and SimS birds ($p > 0.10$, Wilcoxon-Mann-Whitney test; Batschelet 1981).

Discussion

Silvereyes in the SimN condition failed to exhibit a consistent direction of orientation, while the orientation of silvereyes in the SimS condition was unaffected. The disorientation of the SimN birds did not result from an inability to orient with respect to the magnetic field, since these individuals had exhibited significant magnetic orientation when tested previously in the ambient magnetic field of Armidale (data included in Fig 2b). Nor was it due to an end-of-season decrease in migratory motivation since the SimN and SimS birds were tested on alternate nights and the SimS birds maintained seasonally-appropriate migratory orientation. It is unlikely that the SimN magnetic field values interfered with the silvereyes' ability to use their magnetic compass for the following reasons. *i*) SimS silvereyes, exposed to the same magnitude of change as the SimN birds but in the opposite direction, exhibited seasonally-appropriate magnetic compass orientation. *ii*) Changes in intensity and inclination greater than those used in our experiments have been shown to not affect the magnetic compass of another migratory bird (Wiltschko 1972). *iii*) An acclimation period of as little as three days has been found to enable young migratory birds relying on an innate compass program (Berthold 1988) to exhibit seasonally-appropriate magnetic compass orientation in fields differing from the ambient field in intensity by as much as 65-75% (Wiltschko 1972). The response of the silvereyes in the SimN condition, therefore, is consistent with an effect on the map and, more specifically, with the possibility that silvereyes are deriving map information

from the geomagnetic field.

Several possible explanations for the absence of orientation by silvereyes in the SimN condition are compatible with the use of magnetic map information. One possibility is that specific values of the magnetic field serve as a “sign post” that labels the northern extent of the winter range. Such a response would be analogous to the discrete changes in directional headings exhibited by young pied flycatchers and loggerhead sea turtles when they are exposed to magnetic field values normally encountered at critical points along their migratory route (Beck and Wiltschko 1988, Lohmann and Lohmann 1994, 1996). According to the sign post hypothesis, during the autumn migration, Tasmanian silvereyes might maintain a fixed compass direction (i.e. fly to the NNE) until they encountered the magnetic values associated with the winter range. This hypothesis predicts that silvereyes, in contrast to the European starlings (*Sturnus vulgaris*) studied by Perdeck (1958), should not be able to compensate for a displacement perpendicular to the normal migratory route by a corresponding shift in migratory orientation. However, previous experiments have shown that exposure to a strong magnetic pulse caused experienced adult silvereyes to exhibit 90° eastward shifts in the direction of migratory orientation during both the Spring and Fall migrations (Wiltschko et al. 1994; Wiltschko et al. 1998). These findings indicate, at the very least, that experienced adults, in contrast to young silvereyes which are unaffected by this treatment (Munro et al. 1997a), are not predisposed to maintain a fixed compass direction as predicted by the “sign post” hypothesis, and are consistent with the possibility that experienced adults are able to derive one or both coordinates of a bicoordinate map from the geomagnetic field.

Bicoordinate navigation, however, involves a graded response to a *continuous*

range of magnetic field values and consists of altering the direction of orientation to compensate for changes in map-derived estimates of geographic position relative to a particular destination. If silvereyes derive one or both coordinates of a bicoordinate map from the geomagnetic field, why then should they have failed to exhibit a consistent direction of orientation in the SimN condition? The answer to this depends, in part, on which component or components of the magnetic field the silvereyes were responding to in these experiments. If silvereyes use magnetic inclination to derive map information, the SimN value of magnetic inclination would have indicated a geographic position within the estimated winter range at approximately the end of the fall migration route. The absence of consistent orientation without a decrease in migratory activity, therefore, could have been the result of individual birds attempting to disperse to different sites within the winter range. If, however, silvereyes use total (or vertical) intensity to derive map information, they would not have encountered the value in SimN during previous migrations, because this value normally is found to the north of the winter range. This might explain the absence of consistent orientation if silvereyes are unable to derive map information using magnetic field values outside of the range that they had previously experienced. Finally, if silvereyes use both inclination and intensity to derive map information (despite the fact that the gradients of these parameters are more-or-less parallel in southeastern Australia and would provide redundant map information), they may have been confused because the values of these magnetic field parameters in SimN correspond to different geographic locations (K. Lohmann, pers. commun.). Contrary to this hypothesis, the values of these magnetic field components in SimS also corresponded to different geographic positions (Fig 2), and yet the orientation of silvereyes in the SimS condition was indistinguishable from their response in the control condition ($p > 0.10$, two-sample Hotelling's test).

In summary, the present findings point to the involvement of the geomagnetic field in the navigational map of adult silvereyes. Consistent with this interpretation, in a more recent study in which silvereyes were exposed to somewhat larger changes in the magnetic field, the SimN condition was found to effect the orientation of adult silvereyes, but not that of young birds captured prior to their first migration (Deutschlander et al., in prep.). The nature of the magnetic field's involvement in the map, however, remains unclear. Distinguishing between the alternatives outlined above will require studies of migratory orientation using experimental approaches in which individual parameters of the magnetic field (intensity, inclination) are varied independently and over a larger range of values (Phillips 1996).

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Figure 1. Magnetic field conditions used in testing. **A)** Simulated southern displacement (SimS) condition produced by increasing the vertical component of the magnetic field by 12%, resulting in an increased total intensity, and a steeper inclination. The changes in all three components of the magnetic field resulted in values that would normally be encountered to the south of Armidale. **B)** Control condition was the ambient magnetic field of Armidale. **C)** Simulated northern displacement (SimN) condition produced by decreasing the vertical component by 12%, resulting in a decreased total intensity, and a shallower inclination. These changes resulted in values that would normally be encountered to the north of Armidale. Schematic diagrams show how the experimental fields were produced. Thick black arrows indicate fields to which birds were exposed. Thin black arrows show vertical and horizontal components, with short arrows labeled +12% or -12% in **A** and **C** indicating changes in the vertical component in the SimS and SimN conditions (not to scale). Dashed arrows in **A** and **C** show ambient field for comparison.

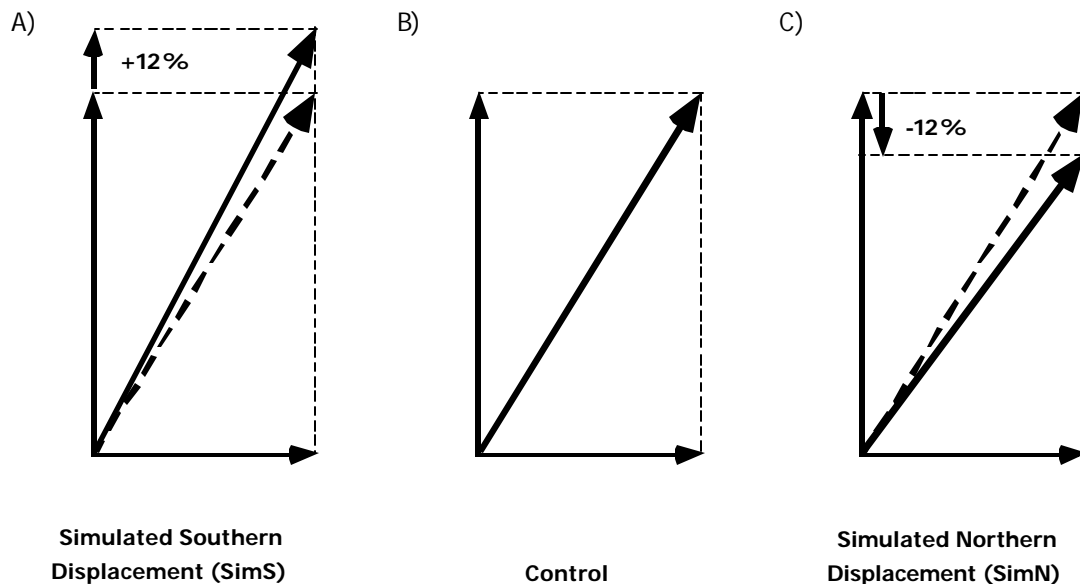
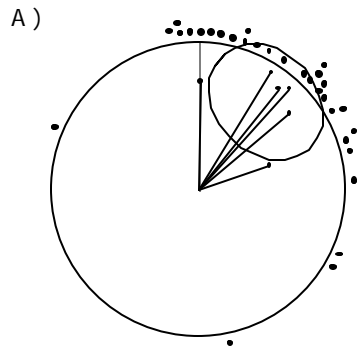
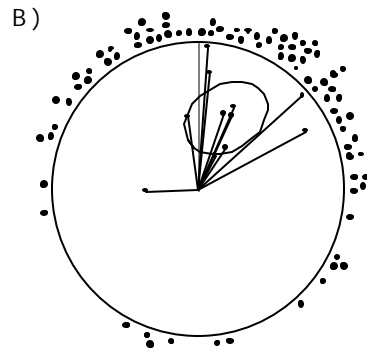


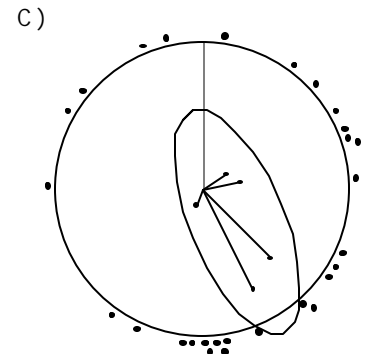
Figure 2. Effects of changes in magnetic intensity and inclination on the migratory orientation of adult Tasmanian silvereyes. **A)** SimS birds tested in a magnetic field with values of approximately 60,200 nT (total intensity) and -65° (inclination) oriented to the NNE (38° , $r = 0.75$, $p < 0.01$, one-sample Hotelling's test); and did not differ significantly from the responses of these birds in the control condition ($p > 0.10$, two-sample Hotelling's test; control data, data included in **B**). **B)** Controls tested in the ambient magnetic field with values of approximately 55,000 nT (total intensity) and -62° (inclination) exhibited seasonally appropriate orientation to the NNE (22° , $r = 0.52$, $p < 0.001$, one-sample Hotelling's test). **C)** Responses of SimN birds tested in a magnetic field with values of approximately 49,950 nT (total intensity) and -58.5° (inclination) were randomly distributed ($p > 0.10$; one-sample Hotelling's test) and differed significantly from their responses in the control condition ($p < 0.01$, two-sample Hotelling's test; data included in **B**). Responses of silvereyes in SimN and SimS (**A** vs **C**) also differed significantly ($p < 0.01$, Hotelling's two-sample test). Data points outside circles indicate nightly mean vector bearings of individual birds relative to magnetic north. Vectors originating at centers of circles represent second order mean vector bearings for each of the birds, calculated by vector addition from each bird's nightly mean vector bearings (Batschelet 1981). Radii of circles correspond to a mean vector length of 1. Ellipses indicate 95% confidence intervals for second order mean vectors.



**Simulated Southern
Displacement (SimS)**



Control



**Simulated Northern
Displacement (SimN)**