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MAGNETIC ORIENTATION IN BIRDS

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Summary

The magnetic field of the earth is an omnipresent, reliable source of orientational information. A magnetic compass has been demonstrated in 18 species of migrating birds. In all species studied with regard to its functional properties, it was found to be an 'inclination compass', i.e. the birds derive directional information from the inclination of the field lines, and thus distinguish between 'poleward' and 'equatorward' rather than 'north' and 'south'. Such a mechanism means that birds from the northern and southern hemisphere may rely on the same migratory programme. Long-distance migrants, however, face the problem that their magnetic compass gives bimodal information at the magnetic equator. Transfers of information between the magnetic field and celestial sources of directional information have been demonstrated; the two systems interact in a complex way.

The data on the use of magnetic parameters for position finding are less clear. The experiments involve releases of homing pigeons; correlations of their orientation with natural variations in the magnetic field and the effects of magnetic manipulation reveal an enormous variability. The role of magnetic parameters in the multifactorial navigational system is poorly understood.

Key words: geomagnetic field, compass orientation, 'inclination compass', homing, navigational 'map'.

The magnetic field of the earth

The geomagnetic field is a dipole field whose poles lie in the vicinity of the geographic (rotational) poles. The field lines leave the ground at the antarctic pole, then curve around the earth and re-enter its surface at the arctic pole, i.e. the magnetic vector points upwards in the southern and downwards in the northern hemisphere, being parallel to the earth's surface at the magnetic equator (Fig. 1). The angle between the magnetic vector and the horizon is called inclination or dip; lines of equal inclination run roughly parallel to the lines of equal latitude. Magnetic north and geographic north mostly differ by a certain number of degrees. This deviation, declination or variation, may be considerable near the magnetic poles, but it soon becomes negligible at lower latitudes. In most parts of the world, the field lines run roughly south–north. The total intensity of the field decreases gradually – roughly symmetrically in both hemispheres – from maximum values of about 60 000 nT at the poles to about 30 000 nT near the magnetic equator.

A number of spatial and temporal irregularities are superimposed on the general pattern described above. Extended deviations from the ideal values show continent-wide patterns; different degrees of magnetization of rock units cause local magnetic anomalies, which, however, rarely exceed 1000 nT. Temporal variations of the geomagnetic field occur on a daily, on a secular and on a geological time scale. The latter two types of changes are so slow that they have to be taken into account only in evolutionary considerations. The regular daily variations, in contrast, mostly in the range 30–100 nT, and irregular fluctuations associated with magnetic storms (characterized indicated by K-values, a geomagnetic index, see Lincoln, 1967) are important for all considerations of a navigational 'map' (see below). A detailed description of the geomagnetic field and its variations in time and space was given by Skiles (1985).

Because of its structure, described above, the geomagnetic field represents a very reliable, omnipresent source of information. The magnetic vector provides directional information, and the spatial distribution of factors such as total intensity and inclination may provide information about position. Indeed, the use of magnetic information in bird orientation was discussed in the last century, when von Middendorff (1859) proposed what we, in modern terms, would call a 'magnetic compass', and Viguier (1882) suggested that displaced pigeons use total magnetic intensity and inclination to determine their home direction.

The magnetic compass of birds

Demonstrating magnetic compass orientation

The magnetic compass was first described for European robins (*Erithacus rubecula*), a passerine species that migrates at night. Captive individuals of migrants become restless in their cages at the times of the year when their free-living conspecifics migrate, and they prefer to stay at the side of their cage pointing towards their migratory direction. This behaviour was used to analyze the birds' orientation in the laboratory, where magnetic conditions can easily be changed in a controlled way. When the magnetic north was rotated by coil systems, while the field's total intensity and inclination

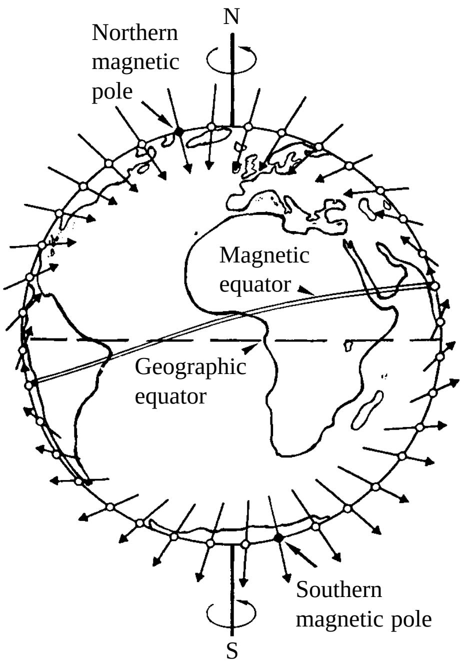


Fig. 1. Schematic view of the earth and the geomagnetic field.

were almost unchanged and all other potential directional cues remained the same, the birds altered their directional preferences according to the change in magnetic north (Fig. 2). This behaviour indicates that they used the magnetic field for direction finding (W. Wiltschko, 1968).

Functional characteristics

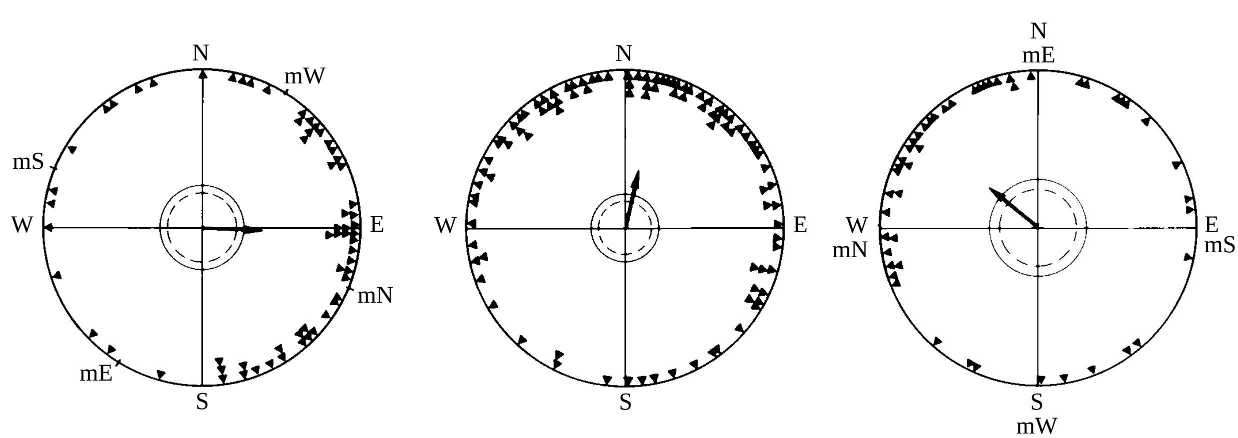
Analyses of the birds' magnetic compass showed some remarkable differences in comparison with the technical magnetic compass used by humans. For example, it was found to be narrowly tuned to the total intensity of the ambient magnetic field (W. Wiltschko, 1978). When living at an intensity of 46 000 nT, robins were not oriented in fields of 34 000 nT and below or, even more surprisingly, of 60 000 nT and above. However, birds housed for at least 3 days in such fields regained their ability to orient. Apparently, the potential window of the magnetic compass is much wider than the actual functional range (W. Wiltschko, 1978).

Another noteworthy feature of the birds' magnetic compass is that it works as an 'inclination compass', i.e. it is based on the axial course of the field lines and their inclination in space, ignoring polarity. Inverting the vertical component had the same effect as reversing the horizontal component; a reversal of both components, which means an inversion of polarity while maintaining the course of the field lines, did not alter the birds' behavior (W. Wiltschko and Wiltschko, 1972). The magnetic compass of birds is an inclination compass: instead of indicating 'north' and 'south', it distinguishes between 'poleward', where the field lines point to the ground, and 'equatorward', where they point upwards (Fig. 3). In a horizontal field, magnetic compass information is bimodal.

Orientation with the help of the magnetic compass

The magnetic compass in migratory orientation

A number of other migrant species have been tested in altered magnetic fields and were found to use a magnetic compass. The list (see Table 1) includes short-distance and long-distance migrants, and birds of the northern as well as birds of the southern hemisphere, such as the yellow-faced honeyeater and the Australian silvereye. The majority of species are nocturnal migrants; however, silvereyes migrate during the twilight hours and the honeyeaters are day migrants, with their peak migration in mid-morning (Munro and Wiltschko, 1993). The family Meliphagidae is endemic to the Australian faunal region and not closely related to any other



43 000 nT, mN=120 °, 42 ° inclination

46 000 nT, mN=360 °, 66 ° inclination, local geomagnetic field

54 000 nT, mN=270 °, 37 ° inclination

Fig. 2. Orientation of European robins: when magnetic north (mN) is deflected, the birds alter their preferred direction accordingly. The symbols at the periphery of the circle indicate the bearings of single test nights, the arrows represent the mean vectors with the length proportional to the radius of the circle=1. The two inner circles mark the 5 % (dashed) and the 1 % significance border (data from W. Wiltschko, 1968).

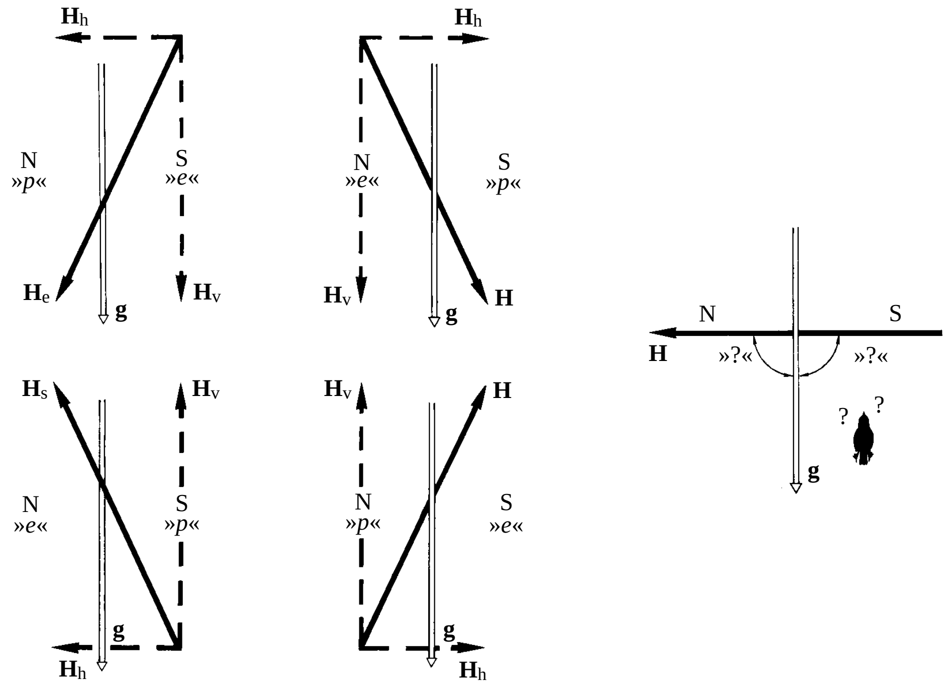


Fig. 3. Vertical cross section through the magnetic field illustrating the 'inclination compass'. **H**e, vector of the local geomagnetic field. **H**, vector of an experimental magnetic field; **H**s, vector of an experimental field corresponding to that of the southern hemisphere; **H**h, **H**v, horizontal and vertical components; **g**, gravity vector; N, S, north and south. »*p*«, »*e*«, poleward, equatorward, the readings of the birds' magnetic compass. In a horizontal field, the directional information becomes bimodal.

species studied so far. Together, these findings suggest that the magnetic inclination compass is a rather widespread mechanism among birds, regardless of their systematic relationship, their geographic distribution and their migratory habits.

This insight has interesting implications for bird migration. Experiments with young migrants that were handraised and tested without ever seeing celestial cues (e.g. W. Wiltschko and Gwinner, 1974; Beck and Wiltschko, 1982) indicate that the migratory direction is genetically encoded as a compass course relative to the geomagnetic field. In both hemispheres, birds start out in autumn heading 'equatorward', which means 'south' for the northern and 'north' for the southern birds. Because of the differences in inclination (see Fig. 1), migrants may have a common migratory programme (Fig. 4; W. Wiltschko *et al.* 1993).

Three species shown to use an inclination compass (see Table 1), namely garden warblers, pied flycatchers and bobolinks, are transequatorial migrants. They face two problems: (1) their inclination compass becomes ambiguous in the horizontal field of the magnetic equator, and (2) beyond the magnetic equator, they must reverse their migratory direction with respect to the inclination compass in order to continue in the same (geographic) direction. Birds that regularly cross the magnetic equator have developed means to overcome this situation. Experiments with garden warblers indicate how they

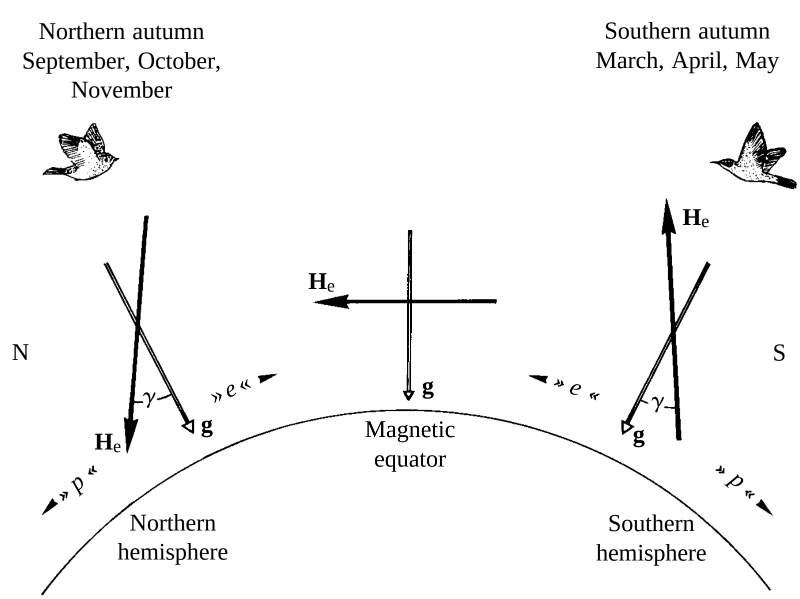


Fig. 4. Because of the different inclination, migratory birds from the northern and the southern hemisphere may use the same migratory programme, which tells them: 'when the days get shorter, start out heading equatorward' (after W. Wiltschko *et al.* 1993). Abbreviations are explained in Fig. 3; γ, smaller angle between gravity and the magnetic field lines.

Table 1. *Migratory birds that have been shown to use a magnetic compass*

Bird species	Reference
European robin, *Erithacus rubecula* (Muscicapidae)*	W. Wiltschko and Merkel (1966) W. Wiltschko and Wiltschko (1972)*
Pied flycatcher, *Ficedula hypoleuca* (Muscicapidae)*	Beck and Wiltschko (1981)*
Wheatear, *Oenanthe oenanthe* (Muscicapidae)	Sandberg *et al.* (1991)
Common whitethroat, *Sylvia communis* (Sylviidae)	W. Wiltschko and Merkel (1971)
Garden warbler, *Sylvia borin* (Sylviidae)*	W. Wiltschko (1974)*
Subalpine warbler, *Sylvia cantillans* (Sylviidae)	W. Wiltschko and Wiltschko (1975*a*)
Blackcap, *Sylvia atricapilla* (Sylviidae)*	Viehmann (1979)*
Goldcrested kinglet, *Regulus regulus* (Sylviidae)*	Weindler (1994)*
Dunnock, *Prunella modularis* (Prunellidae)	Bingman and Wiltschko (1988)
Silvereye, *Zosterops lateralis* (Zosteropidae)*	W. Wiltschko *et al.* (1993)*
Yellow-faced honeyeater, *Lichenostomus chrysops* (Meliphagidae)*	Munro and Wiltschko (1993)*
Red-eyed vireo, *Vireo olivaceus* (Vireonidae)	R. Sandberg and F. R. Moore (in preparation)
Scarlet grossbeak, *Carpodactus erythrinus* (Fringillidae)	Shumakov and Vinigradova (1992)
Chaffinch, *Fringilla coelebs* (Fringillidae)	R. Sandberg (personal communication)
Indigo bunting, *Passerina cyanea* (Emberizidae)	Emlen *et al.* (1976)
Savannah sparrow, *Passerculus sandwichensis* (Emberizidae)	Bingman (1981); Able and Able (1993)
Snow bunting, *Plectrophenax nivalis* (Emberizidae)	R. Sandberg and J. Pettersson (in preparation)
Bobolink, *Dolichonyx oryzivorus* (Icteridae)*	Beason and Nichols (1984); Beason (1989)*

*Species that have been shown to use an inclination compass and the respective reference.

master the problem of changing their migratory direction from ‘equatorward’ to ‘poleward’. During autumn migration, birds that had been kept in a horizontal magnetic field for 2 days reversed their directional tendencies, now heading northward (i.e. poleward), whereas untreated controls continued southward (i.e. equatorward) until migration ended (W. Wiltschko and Wiltschko, 1992). Apparently, the horizontal field of the magnetic equator itself serves as a trigger and causes the birds to begin flying ‘poleward’.

This leaves the problem of the specific situation at the magnetic equator. In laboratory tests, garden warblers were disoriented when a horizontal magnetic field was the only available cue (W. Wiltschko, 1974). In nature, however, additional factors may help the birds to master the situation (see Beason, 1992).

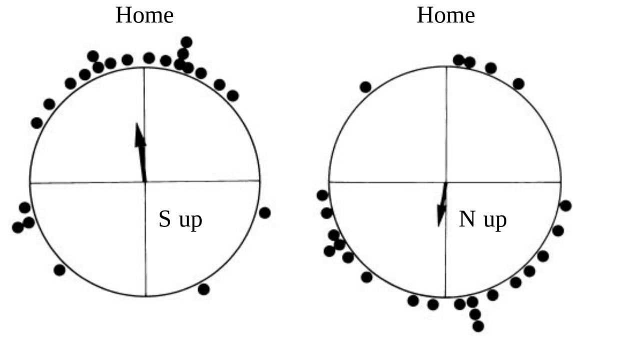


Fig. 5. Under overcast, small magnetic coils around the head may affect the orientation of homing pigeons; vanishing bearings of pigeons with a resulting field pointing downwards (south up, S up) and pointing upwards (north up, N up). Symbols at the periphery indicate the vanishing bearings of individual birds; the arrows represent the mean vectors with respect to the home direction (upward), drawn proportional to the radius of the circle (data from Walcott and Green, 1974).

Magnetic compass orientation in homing behavior

Carrier pigeons, *Columba livia* (Columbiformes), are the only non-migrants whose magnetic orientation has been studied. Pigeons use the magnetic compass in homing, where the appropriate course is determined by a navigational process. Pigeons have to be released in order to record their directional behaviour, which makes manipulations of the ambient magnetic conditions rather difficult. Keeton (1971) and later Ioalè (1984) reported that magnets caused disorientation in pigeons when the birds were released under total overcast.

A report by Moore (1988), claiming that Keeton could not repeat his own findings, is based on an unfortunate misinterpretation of Keeton’s later results: a critical comparison of these data with those presented by Keeton (1971) reveals that the behaviour of the pigeons carrying magnets is similar, whereas, for reasons unknown, the orientation of the controls is much more scattered than in Keeton’s original study. This disorientation of the control pigeons deprived Keeton of a baseline for further studies; his later data (published by Moore, 1988) are inconclusive (see R. Wiltschko and Wiltschko, 1995, for details).

The findings by Keeton (1971) provided the first indications for magnetic compass orientation in homing. More direct evidence was reported by Walcott and Green (1974) and Visalberghi and Alleva (1979), who equipped their birds with pairs of small, battery-operated coils that changed the field around the head. While these coils had little effect under sun, their effect under overcast depended on the direction of current. When magnetic north of the induced field pointed upwards, so that the resultant field roughly corresponded to an inversion of

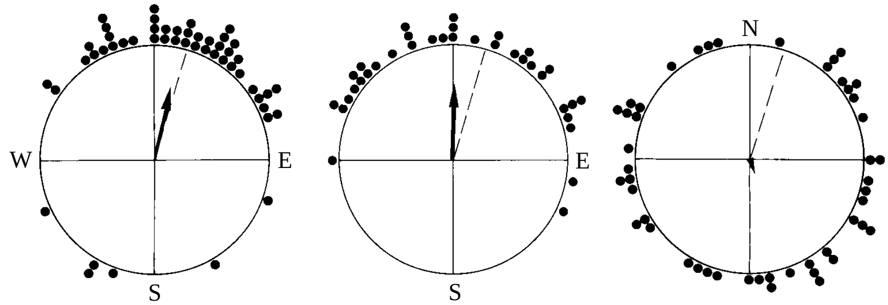


Fig. 6. Young, inexperienced pigeons are disoriented when transported in a distorted magnetic field, while staying in the distorted field alone did not affect their orientation. The home direction is indicated by a dashed line; other symbols as in Fig. 5 (data from R. Wiltschko and Wiltschko, 1978).

the vertical component, the test birds showed a tendency to fly away from home (Fig. 5). These findings suggest that the magnetic compass of pigeons, too, is an inclination compass.

In homing, the magnetic compass is not only involved in locating the course determined by navigational processes. It may also be part of these navigational processes themselves, namely, when they are based on information obtained during the outward journey. Young, inexperienced pigeons were disoriented when transported to the release site in a distorted magnetic field, whereas a second group that had experienced the same distorted magnetic field for an equal length of time while waiting at the release site were homeward-oriented (Fig. 6). This clearly shows that it was not the distorted field *per se* but being transported in the distorted field that was crucial (R. Wiltschko and Wiltschko, 1978). These findings are usually explained by the assumption that pigeons use the magnetic field as a reference system for storing information about the course of the outward journey and the home course, and that the distortion of the magnetic field during displacement prevented the experimental birds from storing such information.

This navigational strategy is only used by very young, inexperienced birds, however. Older and more experienced pigeons seem to be hardly affected by magnetic treatments during displacement (Kiepenheuer, 1978; Wallraff, 1980; Wallraff *et al.* 1980), suggesting a change in navigational strategy (see R. Wiltschko and Wiltschko, 1985).

The interaction of magnetic compass information with other directional cues

Apart from the magnetic compass, birds have two celestial compass mechanisms which supply them with essentially the same type of directional information: the sun compass during daytime and the star compass at night. Since the sun and the stars change their positions with time and with geographic latitude, seeing them *per se* does not provide any directional information. Birds acquire the ability to interpret celestial cues by learning processes during the first months of life (see Emlen, 1972; R. Wiltschko, 1983). Numerous studies that revealed manifold interactions between the various systems will be briefly summarized below.

The magnetic compass is involved in the learning processes that lead to the establishment of the sun compass. Young, inexperienced pigeons use the magnetic compass before they can use the sun compass (R. Wiltschko and Wiltschko, 1981), and there are indications that the magnetic compass serves as a directional reference system to establish the sun compass (W. Wiltschko *et al.* 1983). Later, however, the sun compass becomes the preferred system. This development is demonstrated by the effects of manipulating the birds' internal clock, which alters the readings of the sun compass without affecting the magnetic compass: these birds show characteristic deflections from the mean headings of untreated controls (e.g. Schmidt-Koenig, 1961). However, a recent analysis of clock-shift experiments suggests that the magnetic compass is possibly still involved to some extent (R. Wiltschko *et al.* 1994). Also, the magnetic compass may play an important role when clock-shifted pigeons return home. Despite their deflected departure directions, the majority of these birds return on the day of release, i.e. before the sun compass is readjusted. It seems most likely that in these cases the sun compass is abandoned in favour of the magnetic compass.

The interaction of the magnetic compass and the star compass in the orientation of nocturnal migrants is more complex. The star compass develops with celestial rotation as a directional reference, independently from the magnetic field (Emlen, 1970; W. Wiltschko *et al.* 1987). During the premigratory phase, celestial rotation proved dominant over magnetic information in cases of conflict; it altered the migratory course with respect to the magnetic field (e.g. Bingman, 1983; Able and Able, 1990, 1993, 1995; Prinz and Wiltschko, 1992). However, when celestial cues and the magnetic field gave conflicting information during migration, the magnetic compass turned out to be the dominant system that changed the directional significance of the stars (e.g. W. Wiltschko and Wiltschko, 1975*a,b*; Bingman, 1987; Beason, 1989) and of the pattern of polarized light at sunset (Bingman and Wiltschko, 1988).

The interactions between the various systems have been reviewed extensively by W. Wiltschko and Wiltschko (1988, 1991), Able (1991, 1993) and R. Wiltschko and Wiltschko (1995).

The accuracy of magnetic compass orientation

For a long time, the magnetic compass had the reputation of

Table 2. *Accuracy of magnetic compass orientation*

Species	*N*	Median *r*	(qu 1; qu 3)	±α (degrees)	Reference
Silvereye	17	0.74	(0.57; 0.85)	±41	W. Wiltschko *et al.* (1993)
Pied flycatcher	18	0.63	(0.52; 0.92)	±49	Weindler *et al.* (1995)
European robin	12	0.77	(0.46; 0.93)	±39	W. Wiltschko and Wiltschko (1995)

Data were recorded in the geomagnetic field in the absence of visual cues; the number of tests per individual bird ranged from 4 to 9; the median was 5 in all three species.

N, number of test birds; med. r, median vector length; qu 1, qu 3, quartiles 1 and 3; ±α, angular deviation indicated by the median vector lengths.

being inferior to the celestial compass mechanisms with regard to accuracy, because the orientation of birds looked much more clear-cut when visual cues were available. This view, however, was based on a misinterpretation of cage data. The activity within a test cage is indeed more concentrated in the presence of visual cues; yet the accuracy with which birds select their migratory direction, represented by the distribution of the headings of each test, is similar with and without celestial cues (R. Wiltschko and Wiltschko, 1978).

In most test series with migrants, vector lengths are in the range of about 0.5, which does not seem to suggest a very high accuracy. However, the vectors are often based on the pooled data of several individuals, and inter-individual differences may have contributed to the general variance. Data on the performance of individual birds are scarce; examples for three species are given in Table 2. The medians suggest an average accuracy in the range of about ±40˚. Since a considerable part of the variance might be caused by an imperfect reflection of the behaviour by the rather artificial test situation in a cage, the actual accuracy of individual birds must be assumed to be even higher.

The behaviour of free-flying birds indeed suggests a rather high accuracy. Pigeons released under overcast skies, i.e. in a situation in which they have to rely on the magnetic compass (see below), may produce vectors above 0.9, which means that in this case inter-individual variances and individual inaccuracy in the navigation process and compass orientation add up to an angular deviation of less than 25˚. If pigeons are accustomed to flying under overcast skies, their orientation under sunny and under overcast skies does not differ (Keeton, 1969, 1974; R. Wiltschko, 1992), which indicates that the accuracy of the magnetic compass is equal to that of the sun compass.

Magnetic 'map' factors in avian navigation

Another use of magnetic information has been discussed, namely, that magnetic parameters may constitute coordinates of the navigational 'map', i.e. of the mechanisms used by displaced birds to determine the home direction from local information (for a detailed description, see Wallraff, 1974; W. Wiltschko and Wiltschko, 1982, 1987). Unfortunately, our ideas about the nature of this 'map' are still very vague, so that it is impossible to supply birds with meaningful 'false' information in this respect. The findings suggesting that displaced pigeons use magnetic cues when determining their home direction are mainly correlations with natural changes of magnetic parameters, observed break-downs of orientation when the magnetic field is disturbed, and the effects and after-effects of magnetic treatments.

Experimental evidence suggesting magnetic 'map' factors

The data mentioned below were recorded under sun, i.e. when the sun compass was available; hence, they are considered to represent effects associated with the navigational 'map'. They may be grouped into three categories: (i) effects of local anomalies, (ii) effects of temporal variations, and (iii) effects and after-effects of magnetic treatments.

Anomalies

If pigeons used magnetic map factors, their orientation should be affected at sites where local magnetic values deviate markedly from the general course of the magnetic field in the region. This prediction is supported by observation: at weak anomalies, considerable deviations from the home course were observed (e.g. Wagner, 1976; Frei, 1982); at strong anomalies with a steep magnetic gradient, the pigeons showed a dramatic increase in scatter and even became disoriented. Walcott (1978) and Kiepenheuer (1982) found a negative correlation between the rate of change in magnetic intensity at the respective sites and the vector lengths (Fig. 7). This relationship seems to suggests that the magnetic parameters at strong anomalies deviate so much from normal that they become 'non-readable' to the birds. However, not all pigeons are equally affected. A recent study by Walcott (1992) indicated that the conditions at the home loft are crucial for the pigeons' response at magnetic anomalies.

Temporal variations

Since pigeons using magnetic 'map' information would have to consider magnetic variations, their response to temporal fluctuations of the geomagnetic field became of interest. At some sites, the mean bearings of pigeons repeatedly released from these sites were correlated with the magnetic fluctuations during the 12 h interval before release, as characterized by the K-index (e.g. Keeton *et al.* 1974;

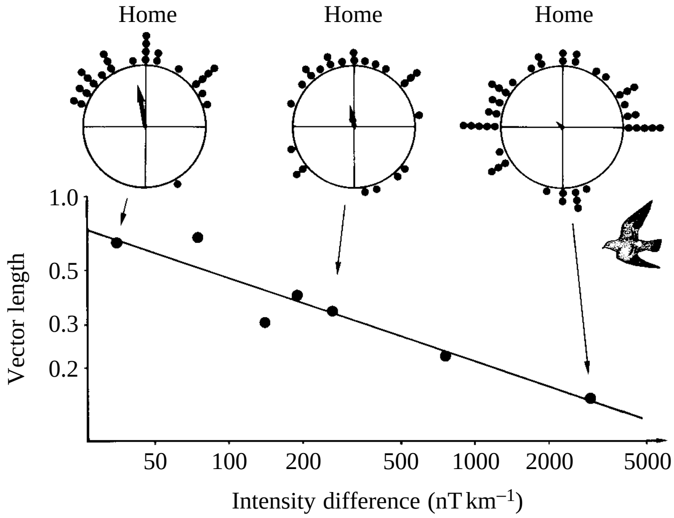


Fig. 7. Orientation behaviour in an area of a strong anomaly. The vector lengths (ordinate, logarithmic scale) are correlated with the maximum difference in intensity (abscissa, logarithmic scale) within 1 km in the homeward direction (coefficient of correlation r=0.96, P<0.05). Three releases are given as examples (home, upwards; symbols as in Fig. 5) (data from Walcott, 1978).

Kowalski *et al.* 1988; see also Schmidt-Koenig and Ganzhorn, 1991). These correlations disappeared when the birds were released with magnets attached to their backs (Larkin and Keeton, 1976). The regular daily variations of the geomagnetic field also seemed to affect pigeon homing: in some cases, mean bearings recorded at 06:00 h differed from those of the same birds released at noon by up to 30 °. These differences were, again, cancelled by magnets (W. Wiltschko *et al.* 1986). However, this effect was observed only in some years, but not in others (Fig. 8; Becker *et al.* 1991), and not all birds were equally affected. Another odd aspect of effects associated with temporal variations in the magnetic field is that their manifestation is not always as predicted by the traditional 'map' concept. A plausible interpretation for this phenomenon has not yet been put forward (for a more detailed discussion, see R. Wiltschko and Wiltschko, 1995).

Magnetic treatments

The effects of various treatments before and during release have also been discussed in view of magnetic 'map' components. Bearings of pigeons released with small magnets on their back or coils around their head (see Fig. 5) under sun deviated slightly from those of untreated controls, deviations ranging up to about 30 ° (e.g. Keeton, 1971; Walcott, 1977; Visalberghi and Alleva, 1979; Lednor and Walcott, 1983). Treatments with oscillating fields prior to the release caused marked deviations in vanishing bearings from those of the controls, an increase in scatter, or both (e.g. Papi *et al.* 1983; Papi and Ioalè, 1988). The strength of the effect depended on impulse shape and the frequency of the applied fields (Fig. 9; Ioalè and Guidarini, 1985; Ioalè and Teyssèdre, 1989). After-effects observed after treating pigeons with extremely strong fields or short, strong pulses also varied greatly; they ranged from a deflection of more than 90 ° to no deflection at all.

Open questions about the use of magnetic 'map' factors

All theoretical considerations on position finding start from the idea of a grid of gradients that forms the coordinates of the 'map'; birds are assumed to compare their local values with the ones remembered from home. Parameters showing gradients, such as total intensity and inclination, could theoretically serve as 'map' factors. However, the birds would be required to detect minute difference in the range of 10 nT against a background of 30 000–50 000 nT. Additional problems arise because the two parameters, although showing world-wide gradients, may be rather irregular on a more local scale, with anomalies exceeding the differences to be measured. The daily variations in both parameters are of similar size, not to mention magnetic storms which may cause differences far exceeding these small ones. How birds might cope with the problem of distinguishing changes caused by spatial variations from those caused by temporal variations, at the same time taking local irregularities into account, is still unclear.

Taken together, the findings suggesting a role of magnetic factors in the birds' navigational 'map' do not form a consistent picture. In part, they even seem to contradict each

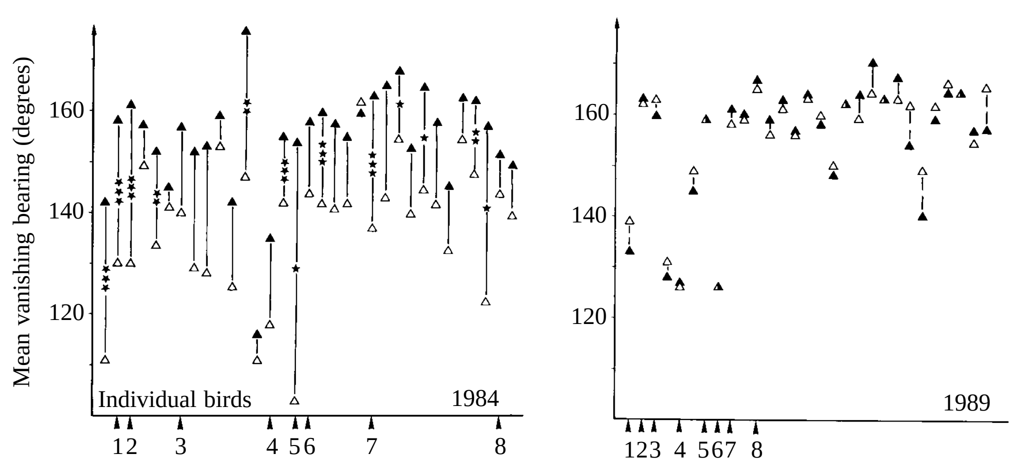


Fig. 8. Mean vanishing bearings of individual pigeons repeatedly released at a site 30 km north of the loft (home direction 185 °). Each triangle is based on more than 12 bearings. Stars mark significant difference between orientation at 06:00 h (open triangles) and orientation at 12:00 h (filled triangles): ⋆P<0.05; ⋆⋆P<0.01 and ⋆⋆⋆P<0.001. The numbers 1–8 mark the data of the same individual pigeons (from Becker *et al.* 1991).

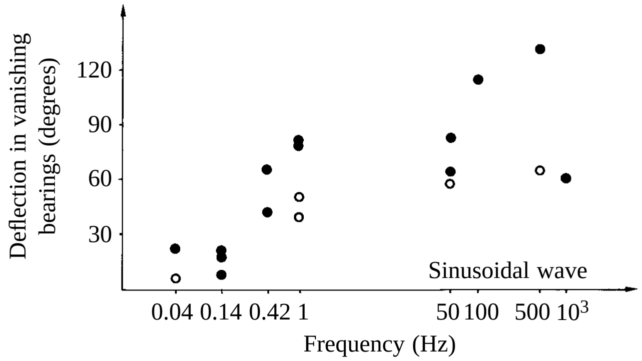


Fig. 9. Correlation between the frequency of a sinusoidal alternating magnetic field and the deflection induced in the vanishing bearings. Open symbols, release site in the north; filled symbols, release site in the south of the loft (from Ioalè and Teyssèdre, 1989).

other. For example, it appears paradoxical that strong anomalies should cause disorientation, whereas magnets, which represent a much greater distortion of the magnetic field than most anomalies, cause only slight deviations. The deflections induced by temporal variations of the magnetic field are also unexplained, and a number of other open questions also await answers (see R. Wiltschko and Wiltschko, 1995).

The general role of magnetic cues in the pigeons' navigational 'map' is not entirely clear. One characteristic of magnetic 'map' effects is the immense variability observed at all levels. Not all pigeons were disoriented at strong anomalies, K-correlations could not be observed at all sites, and differences between morning and noon bearings could not be observed in all years. The same variability appears to apply for the results of the various kinds of magnetic treatment (e.g. Benvenuti and Ioalè, 1988; Ranvaud *et al.* 1991). This does not mean, however, that the effects are small and disappear in the general noise. On the contrary, when they occur, they are highly significant and quite spectacular; yet they do not occur everywhere or every time. Moreover, even when magnetic 'map' effects are observed, not all pigeons within a group are equally affected; the variability at the individual level is enormous (for examples, see Larkin and Keeton, 1976; W. Wiltschko *et al.* 1986; Kowalski *et al.* 1988). Homing performance, in contrast, is hardly affected by magnetic manipulations, which suggests that magnetic cues are not essential. Taken together, these findings can only be explained by assuming that a multitude of factors is involved in the navigational process. Apparently, birds have alternatives and can choose between several options; circumstances yet unknown determine which cues are preferentially used in a given situation.

Conclusions

The findings summarized in this paper clearly show that the geomagnetic field provides important orientational information. The use of a magnetic compass is widespread among birds. Its way of functioning as an inclination compass, its biological relevance as a directional reference system in migration and homing, and its interactions with other types of directional information are fairly well understood. An involvement of magnetic information in the navigational 'map', in contrast, is still largely unclear. Several authors (e.g. Wallraff, 1983; Gould, 1985; Walcott, 1991), reviewing the available evidence, have hesitated to accept an important role of magnetic cues because of the unexplained variability and seeming discrepancies between findings. Taken together, the positive evidence cannot be dismissed, but a convincing hypothesis explaining all the known details of magnetic phenomena in a consistent way has not yet been put forward. We are still far from understanding how magnetic 'map' factors might work.

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