

Avian magnetic compass: Its functional properties and physical basis

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Abstract The avian magnetic compass was analyzed in bird species of three different orders – Passeriforms, Columbiforms and Galliforms – and in three different behavioral contexts, namely migratory orientation, homing and directional conditioning. The respective findings indicate similar functional properties: it is an inclination compass that works only within a functional window around the ambient magnetic field intensity; it tends to be lateralized in favor of the right eye, and it is wavelength-dependent, requiring light from the short-wavelength range of the spectrum. The underlying physical mechanisms have been identified as radical pair processes, spin-chemical reactions in specialized photopigments. The iron-based receptors in the upper beak do not seem to be involved. The existence of the same type of magnetic compass in only very distantly related bird species suggests that it may have been present already in the common ancestors of all modern birds, where it evolved as an all-purpose compass mechanism for orientation within the home range [*Current Zoology* 56 (3): 265–276, 2010].

Key words Magnetic compass, Migration, Homing, Directional training, Inclination compass, Radical pair processes

The geomagnetic field originates in the earth itself. The field lines leave the earth at the magnetic pole near the geographic south pole, curve around the earth and re-enter at the magnetic pole near the north pole. The inclination or dip, defined as the angle between the field lines and the horizontal plane, is 90° at the magnetic poles and 0° at the magnetic equator; at the latter, the field lines run parallel to the earth's surface. At the northern hemisphere, field lines point downward with a positive inclination, at the southern hemisphere they point upward. The intensity of the geomagnetic field also varies: it has its maximum, about $60 \mu\text{T}$, near the magnetic poles and decreases towards the magnetic equator to about $30 \mu\text{T}$, with a local minimum in eastern South America (Skiles, 1985).

For animals capable of sensing the geomagnetic field, it provides an omnipresent source of directional information. Its use as a compass is widespread and includes species of all major phyla (R. Wiltschko and Wiltschko, 1995). Birds were the first group where a magnetic compass was demonstrated more than 40 years ago (W. Wiltschko, 1968), and they are still the group where the magnetic compass has been analyzed in most detail, mainly by behavioral methods. In the present paper, we compare the magnetic compass of birds of three orders - passeriforms, columbiforms and galliforms. The respec-

tive studies involve three different behaviors, namely migration, homing and small-scale orientation based on directional training.

1 Magnetic Compass of Passerine Migrants

Demonstrating magnetic compass orientation requires a behavior that is reliably oriented in a specific direction. This is not an easy precondition, because for most tasks in animals' life, directions are of little importance. Migratory orientation, however, ideally satisfies this condition, because migration is an innate behavior that, during the respective seasons, causes in birds a strong spontaneous urge to orient in their migratory direction. In the northern hemisphere, migratory birds head southward in autumn and northward in spring. In the southern hemisphere, their movements are a mirror image.

These directional tendencies can be recorded in suitable orientation cages, like e.g. the funnel-shaped cage originally designed by Emlen and Emlen (1966). The limited space of such a cage allows easy manipulations of the ambient magnetic conditions, e.g. with Helmholtz coils (see R. Wiltschko and Wiltschko, 1995 for technical details). Birds are then tested in the local geomagnetic field and an experimental field with the horizontal

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component shifted, while inclination and intensity remain the same. A comparison of their behavior in these two fields is indicative: if the birds use a magnetic compass, they should follow the shift in magnetic North and alter their headings. This way, a magnetic compass was first demonstrated in European robins *Erithacus rubecula* (Fig. 1, left and center diagram): when the horizontal component of the magnetic field was turned to 120° ESE, the birds changed their directional preferences accordingly (W. Wiltschko, 1968; W. Wiltschko and Wiltschko, 1972, 1999).

Meanwhile, a magnetic compass has been demonstrated in a number of other passerine migrants from different continents – Europe, North America, Australia – with different migratory habits. The species include day migrants, night migrants and twilight migrants, with migration distances varying from short to long (Table 1). Magnetic compass orientation was also demonstrated in one non-passerine migrant, the sanderling *Calidris alba* (Charadriiformes: Scolopacidae) by Gudmundsson and Sandberg (2000). This suggests a very important role of the magnetic field in directing migratory orientation.

1.1 Functional properties of the magnetic compass of passerines

With the same method—using orientation in migratory direction as an indicator—the functional properties of the magnetic compass were analyzed. Many of these experiments used European robins, the species whose magnetic compass is known in most detail. Tests in an experimental field with the vertical component inverted revealed an unexpected characteris-

tic: in this situation, robins reversed their headings, in spring preferring magnetic South instead of magnetic North (Fig. 1, right diagram). When both components had been reversed, however, they preferred the same direction as in the local geomagnetic field (W. Wiltschko and Wiltschko, 1972). These observations indicate that the functional principle of the robins' magnetic compass is fundamentally different from that of our technical compass: while the technical compass responds to the polarity of the magnetic field, the robins' compass is an 'inclination compass' that ignores polarity and instead relies on the axial course of the field lines (see Fig. 2), using their inclination to distinguish between the two ends. The same type of mechanisms exist in the other passerine migrants tested for it (marked in Table 1). It means that birds do not detect magnetic North and South (a distinction based on polarity), but 'poleward', where the field lines point to the ground, and 'equatorward', where they point upward (Fig. 2).

When robins were tested in experimental fields with different intensities, it became evident that their magnetic compass is narrowly tuned to the ambient magnetic field. At the test site in Frankfurt am Main, Germany (50°08'N, 8°40'E), the local geomagnetic field has an intensity of about 46 μ T. Robins caught and kept at this intensity were disoriented when the total intensity was decreased or increased by about 30%, indicating a narrow functional window (W. Wiltschko, 1978). Especially the disorientation in higher fields was surprising, because it clearly showed that the loss of orientation does not only involve the intensity getting below

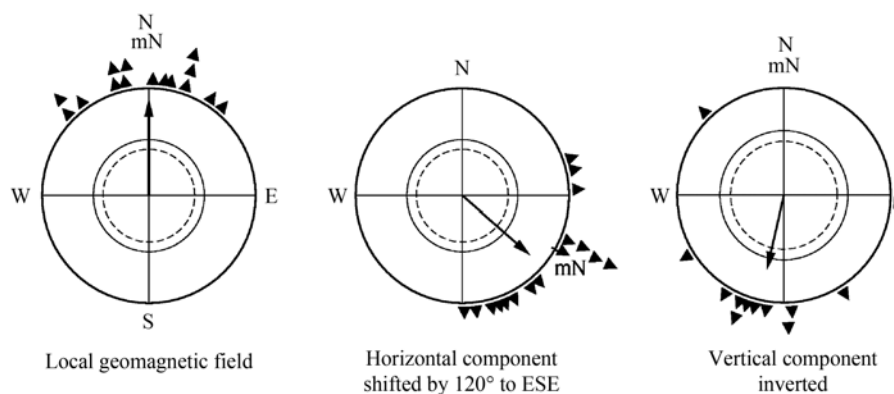


Fig. 1 Demonstrating a magnetic inclination compass in European robins

Tested in spring in the local geomagnetic field, the robins head into the northerly migratory direction; when magnetic North (mN) is shifted, the birds alter their headings accordingly, and when the vertical component is inverted, they reverse their headings (data from W. Wiltschko and Wiltschko 1999; W. Wiltschko et al. 2001). The symbols at the periphery of the circle mark the mean headings of the test birds; the arrow represents the mean vector drawn proportional to the radius of the circle = 1. The two inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test.

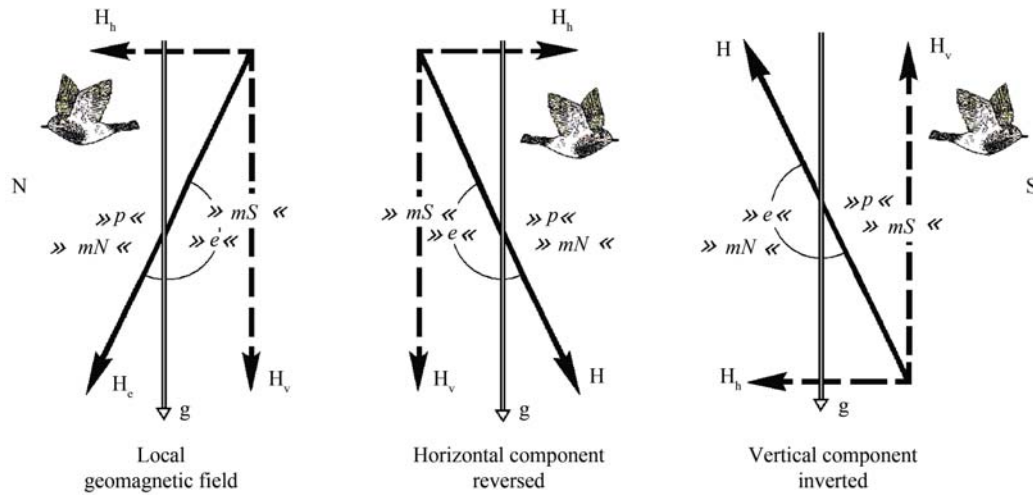


Fig. 2 Schematic section through the geomagnetic field from the west to illustrate the functional mode of the inclination compass N, S, North and South; H_e , vector of the local geomagnetic field; H , vector of the experimental field, H_h , H_v , horizontal and vertical components of the magnetic fields, g , gravity vector. The arrow heads represent the polarity of the fields, with »mN«, »mS«, indicating magnetic North and magnetic South, the readings of a polarity compass. The axial direction of the vector and its inclination, i.e. its relation to gravity, is crucial for the inclination compass, with »p«, »e« indicating 'poleward' and 'equatorward', the readings of the inclination compass.

Table 1 Passerine migrants that have been demonstrated to use a magnetic compass

Species (family)	Distribution	Distance	Times of day
<i>Hirundo rustica</i> (Hirundinidae)	Holarctic	long	day
<i>Prunella modularis</i> (Prunellidae)	Europe	medium-short	night
<i>Sylvia borin</i> (Sylviidae) * ^o	Europe	long	night
<i>Sylvia communis</i> (Sylviidae)	Eurasia	long	night
<i>Sylvia atricapilla</i> (Sylviidae) *	Europe	medium-long	night
<i>Sylvia cantillans</i> (Sylviidae)	Mediterranean	medium	night
<i>Regulus regulus</i> (Sylviidae)	Europe	short	day and night
<i>Ficedula hypoleuca</i> (Muscicapidae) *	Europe	long	night
<i>Erithacus rubecula</i> (Turdidae) * ^{†,o}	Europe	medium	night
<i>Oenanthe oenanthe</i> (Turdidae)	Eurasia	long	night
<i>Carpodacus erythrinus</i> (Fringillidae)	Eurasia	long	night
<i>Fringilla coelebs</i> (Fringillidae)	Europe	short	day
<i>Plectrophenax nivalis</i> (Emberizidae)	Arctic	short	day and night
<i>Passerina cyanea</i> (Emberizidae)	North America	long	night
<i>Vireo olivaceus</i> (Vireonidae)	North America	long	night
<i>Dolichonyx oryzivorus</i> (Icteridae) *	North America	long	night
<i>Zosterops lateralis</i> (Zosteropidae) * ^{†,o}	Australia	medium	twilight
<i>Lichenostomus chrysops</i> (Meliphagidae) *	Australia	medium-long	day

* marks species where an *inclination compass* has been demonstrated. † marks species where *lateralization* of the magnetic compass has been demonstrated. ° marks species where *light-dependency* of the magnetic compass has been demonstrated.

threshold. Further tests showed that the functional window of the magnetic compass is not fixed, but flexible. It can be adjusted to intensities outside the normal functional range. Robins regained their ability to orient when they were exposed lower or higher intensities, with an exposure of about 1 h at 92 μ T sufficient to en-

able them to orient at this intensity (W. Wiltshcko et al., 2006). At the same time, the birds did not loose their ability to orient in the local geomagnetic field. Interestingly, robins adjusted to 150 μ T could orient at this intensity and at the local intensity of 46 μ T, but were dis-oriented at the intermediate intensity of 81 μ T (W.

Wiltschko, 1978). This suggests that the adaptation to new intensities is neither a shift nor a simple enlargement of the functional range; rather, experiencing an intensity outside the normal functional range seems to establish a new functional window around the respective intensity.

Experiments testing robins with one eye covered indicated the eye as site of magnetoreception, revealing a strong lateralization of the magnetic compass in favor of the right eye (Fig. 3). Monocular birds that had to rely solely on their right eye were just as well oriented in their migratory direction as with both eyes open, whereas they were disoriented when they had to rely solely on their left eye (W. Wiltschko et al., 2002). The same was found in Australian Silvereyes, *Zosterops l. lateralis* (W. Wiltschko et al., 2003). These findings indicate an extreme asymmetry in sensing the direction of the magnetic field in these species. Since in birds the fibers of the optic nerve cross over completely and interhemispheric commissures are comparatively small (Vallortigara, 2000), this means that magnetic input for compass orientation in these species is processed predominantly in the left hemisphere of the brain. Yet lateralization does not seem to be equally strong in all passerines. Recent experiments with garden warblers *Sylvia borin* showed that this species could use its magnetic compass also when it had to rely on input from the left eye alone (Hein et al., 2010).

Another interesting characteristic of the magnetic compass of passerine birds is its light-dependency (Fig. 4). Normal compass orientation requires light from the short-wavelength part of the spectrum. Robins and silvereyes were well oriented in their migratory direction under 373 nm UV, 424 nm blue, 502 nm turquoise and 565 nm green light. Under 590 nm yellow and beyond, they were disoriented, indicating that their magnetoreception system does no longer work properly un-

der longer wavelength (W. Wiltschko et al., 1993; W. Wiltschko and Wiltschko, 1995, 1999; R. Wiltschko et al., 2007a). A similar wavelength-dependency was found in Garden Warblers (Rappl et al., 2000). These findings are important in view of considerations on the reception mechanisms (see below), as they represent a first indication that light may be involved in the physical processes mediating magnetic compass information.

1.2 Physical principles underlying the magnetic compass

The nature of the physical mechanisms underlying magnetoreception in birds and other animals has long been an open question. A number of hypotheses have been forwarded to explain magnetosensitivity, with the discussion presently focusing on two types of models:

(1) The *Magnetite-Hypothesis* proposes magnetoreception based on a specific type of an iron oxide with magnetic properties depending on particle size: larger crystals form multi-domains with a low net moment; small particles in the range of 1 μm form single domains with a stable magnetic moment, and even smaller particles of 50 nm and below are superparamagnetic, i.e. their magnetic moment fluctuates, but can be aligned by an external magnetic field (see Kirschvink and Gould, 1981 for details). Several hypotheses on how such particles could mediate magnetic information have been forwarded, some based on single domains, others on superparamagnetic crystals and even others on a combination of both (e.g. Yorke, 1979; Kirschvink and Gould, 1981; Shcherbakov and Winklhofer, 1999; Davila et al. 2003; Fleissner et al., 2007; Walker, 2008). Iron-rich particles, identified crystallographically as superparamagnetic magnetite (Hanzlik et al., 2000), were found in six clusters in the upper beak and were described as putative magnetoreceptors (Fleissner et al., 2003, 2007).

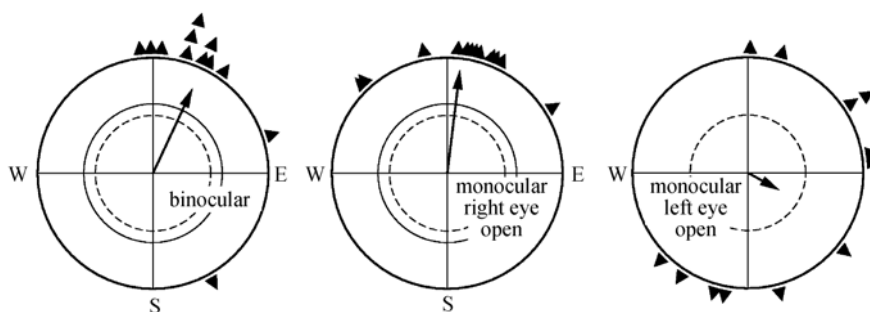


Fig. 3 Orientation of robins tested with both eyes (binocular) and with only the right and only the left eye open; in the latter situation, they were disoriented (data from W. Wiltschko et al., 2002)

Symbols as in Fig. 1.

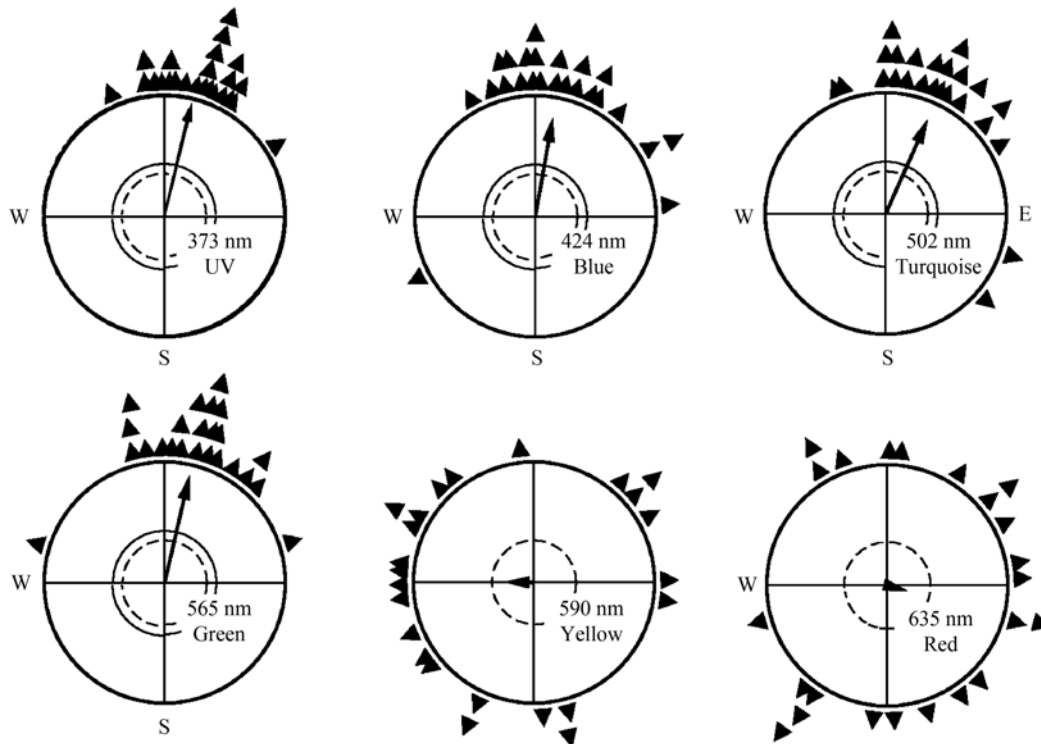


Fig. 4 Wavelength-dependency of the magnetic compass

Robins tested under monochromatic lights of different wavelengths were oriented in their migratory direction under short-wavelength light up to 565 nm green; from 590 nm yellow onward, they were disoriented.

(2) The 'radical pair' model (Schulten, 1982; Ritz et al., 2000) assumes a crucial role of specialized photopigments in the retina. Absorption of a photon leads to a light-induced electron transfer reaction and creates a spin-correlated radical pair. The magnetic field alters the dynamics of the transition between spin states and thereby modify the yields of the singlet and triplet products, with the magnitude of the response depending on the orientation of the radical pair with respect to the direction of the external magnetic field. Hence, with a sufficient number of radical pairs aligned within a receptor cell, the responses of this cell will also depend on the direction of the field. By comparing the responses of receptors aligned in different spatial orientations, birds could thus obtain information on the direction of the external field. The spherically shaped retina of birds, where photoreceptors point in different directions and contain spatially organized photopigments, has been suggested as a likely site of magnetoreception (Ritz et al., 2000). The characteristics of the robins' magnetic compass described above – functional mode as an inclination compass, eye as site of magnetic reception and its wavelength-dependency – are in good agreement with this model.

To distinguish between the models, it was important to identify the physical mechanism underlying the robins' magnetic compass. Radical pair processes can be affected by weak radio-frequency magnetic fields in the MHz range that do not affect magnetite particles, whereas the local anesthesia of the upper beak should temporarily disable the putative receptor located there without affecting light-dependent processes in the eyes.

The respective tests indicated that the magnetic compass of robins is based on radical pair processes: oscillating fields of 1.3 MHz or 7.0 MHz caused disorientation (Ritz et al., 2004; Thalau et al., 2005), indicating that the crucial reception processes were disrupted (Fig. 5, center diagram), with the response to the 1.3 MHz field being remarkably sensitive (Ritz et al., 2009). Local anesthesia of the upper beak, in contrast, did not interfere with migratory orientation: robins and silver-eyes continued to prefer their normal migratory direction (Fig. 5, right diagram), indicating that the iron-based receptors in the upper beak are not involved in magnetic compass orientation (R. Wiltshko et al., 2007b, 2008; Stapput et al., 2008; see also Beason and Semm, 1996; Zapka et al., 2009).

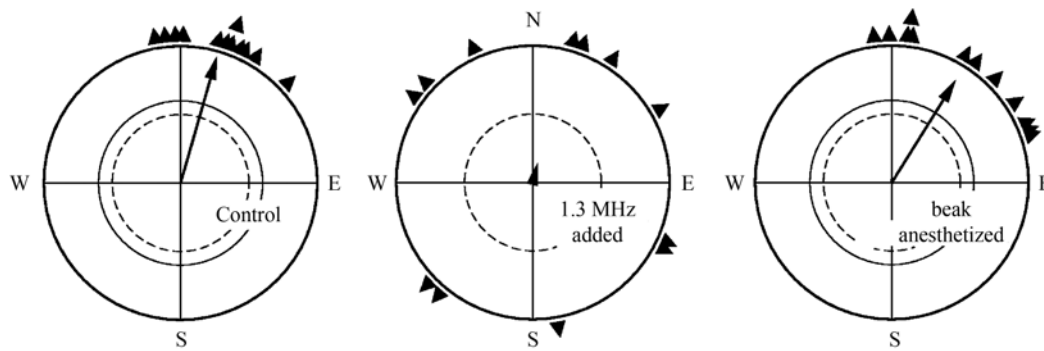


Fig. 5 Identifying the physical mechanism on which the magnetic compass is based

In control tests in the geomagnetic field, robins were oriented in the northerly migratory direction. Adding an oscillating field disrupted their orientation, indicating an underlying radical pair mechanism. Local anesthesia of the upper beak, in contrast, did not interfere with orientation, indicating that the iron-based receptors located there are not involved. Symbols as in Fig. 1 (data from Thalau et al. 2005; R. Wiltschko et al., 2007b).

2 Magnetic Compass of Homing Pigeons *Columba livia f. domestica*

In pigeons, orientation is usually studied in connection with homing behavior. Homing differs from migratory orientation as here the compass course is not innately fixed, but varies according to the pigeons' position with respect to home. When released at a distant site, pigeons first determine their home direction as a compass course and then use a compass – their sun compass or magnetic compass – to locate this course (Kramer, 1957; R. Wiltschko and Wiltschko, 2003, for details). That is, the magnetic compass is an integrated component of the navigational system. The common method to study pigeon navigation and its component involves displacing pigeons and recording the directions in which they depart from the release site.

The fact that pigeons have to be set free to fly renders the demonstration and the analysis of the magnetic compass considerably more difficult, which is further complicated by fact that the sun compass provides an alternative mechanism indicating directions. First evidence for magnetic compass orientation came from experiments with pigeons that had a small magnet fixed on their back between the wings. This magnet was sufficiently strong to temporarily disrupt their magnetic compass, and when released under solid overcast so that the sun compass was not available, these birds were disoriented (Keeton, 1971).

2.1 Characteristics of the magnetic compass of pigeons

Further experiments produced more direct evidence for magnetic compass use. A small set of mini-coils was placed around the pigeon's head, and, when connected

with a battery on the pigeon's back, these coils could locally alter the magnetic field at the pigeon's head. Birds equipped with such coils, released under overcast departed more or less homeward oriented when the induced magnetic field was directed downward, but reversed their headings when the induced magnetic field was directed upward (Fig. 6; Walcott and Green, 1974; Visalberghi and Alleva, 1979). This suggests that the magnetic compass of pigeons also works as an inclination compass.

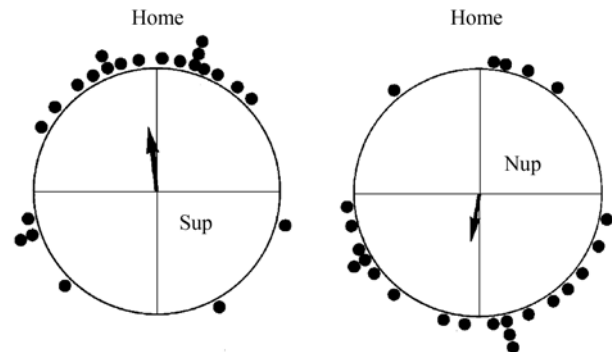


Fig. 6 The orientation of pigeons released with a small set of battery-operated coils around their head depended on the direction of the induced magnetic field

With South pointing upward (Sup), they headed roughly in home direction, with North pointing upward (Nup), they headed in the reverse direction, indicating that their magnetic compass works as an inclination compass (data from Walcott and Green, 1974). The symbols at the periphery of the circle mark the departure bearings of individual pigeons, the arrows represent the mean vectors.

Further analysis of the magnetic compass of pigeons reveals parallels to the magnetic compass of migrating passerines. The behavior of pigeons released with one eye covered deviated from binocular control birds to the side of the open eye. This effect was asymmetric: cov-

ering the right eye caused a much larger deviation than covering the left one, with the observed effects being most dramatic under overcast skies (Ulrich et al., 1999; Prior et al., 2004). The interpretation of these findings is not easy because, aside from possibly indicating a lateralization of the magnetic compass in favor of the right eye, they might reflect an interference with the mechanisms of flight control. A recent study using directional training (see below) showed that the lateralization of the magnetic compass in pigeons is much less pronounced than in robins or silvereyes: pigeons can perceive magnetic compass information with both eyes, but while right-eyed birds oriented as well as binocular ones, birds forced to rely on their left eye alone confused opposite directions (Wilzeck et al., 2010a).

2.2 Indications of the underlying principles

A wavelength dependency of the magnetic compass is also indicated in pigeons. The respective experiments were based on a slightly different test design, namely manipulations during displacement to the release site. Very young, inexperienced pigeons rely on route-based information obtained during the outward journey (R. Wiltshko and Wiltshko, 1985, 2003): they record the direction of the displacement; reversing this direction yields the home course. This strategy cannot only be used during active flight, but also during passively displacement. The magnetic compass was shown to provide the crucial directional reference: young pigeons that could use it during displacement departed home-ward oriented, whereas birds transported in a distorted magnetic field were disoriented (R. Wiltshko and Wiltshko, 1978, 1985). In view of a possible wavelength dependency of their magnetic compass, young pigeons were transported to the release site under

monochromatic light of different wavelengths. When released, the birds transported under 565 nm green light oriented just as well as the controls transported under natural sky light; the birds transported under 630 or 660 nm red light, in contrast, were disoriented (Fig. 7), presumably because red light disrupted their magnetic compass and thus prevented them from recording the direction of the outward journey (R. Wiltshko and Wiltshko, 1998). Experiments with young pigeons transported under monochromatic light of other wavelengths are still missing, but the effect of green and red light suggests a wavelength dependency similar to that found in passerine migrants.

The physical principles upon which the pigeons' magnetic compass is based have not yet been analyzed. The functional mode as an inclination compass and the indicated wavelength dependency, however, suggests a light-dependent mechanism, which implies underlying radical pair processes.

3 Magnetic compass of domestic chickens *Gallus gallus* in a directional training task

Domestic chickens do not show a spontaneous behavior that is directionally oriented. The only way to demonstrate magnetic compass orientation in this species was to induce a reliable directional tendency by conditioning. This seemed problematic at first: training birds to magnetic directions had been attempted before and led to a long list of mostly negative results (e.g. Kreithen and Keeton, 1974; Beaugrand, 1976; Katz, 1978; Griffin, 1982; Alsop, 1987). In most of these experiments, however, the training paradigm involved

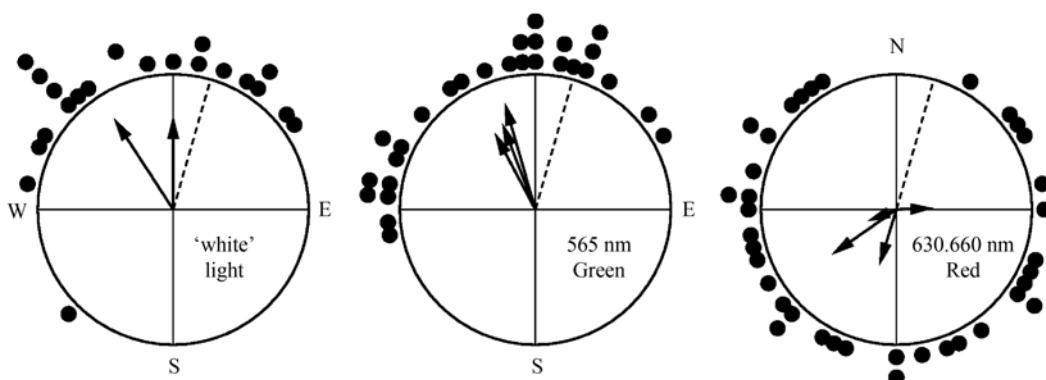


Fig. 7 Orientation of young, inexperienced homing pigeons released at a site 42 km south of the loft after being displaced under 'white', monochromatic green and red light as indicated

The home direction, 16°, is marked by a dashed line (data from R. Wiltshko and Wiltshko, 1998). Symbols as in Fig. 6; the arrows represent the mean vectors of the individual releases.

situations and tasks where birds do not normally use their magnetic compass – e.g. the direction of the magnetic field indicated which of two keys was the correct one – and/or used completely unnatural stimuli like abrupt changes in direction (see W. Wiltschko and Wiltschko, 2007 for discussion).

Recent conditioning experiments used a more adequate test design, with the test situation avoiding all unnatural stimuli and involving a spatial task, the natural context where the magnetic compass is used. This proved successful (Freire et al., 2005): young chicks were imprinted on a red table tennis ball that they believed to be their mother and which induced a strong urge to be near that ball and to search for it when it was concealed. The chicks were then released in the center of a square, featureless arena and trained to search for their 'mother' behind one of four equal-looking screens in the four corners. The direction of the magnetic field as the only cue. Magnetic North was always kept constant while a chick stayed in the arena and only altered between trainings or tests. The chicks learned this task, but their choices were axial rather than unimodal, that is, they preferred the correct screen and the opposite screen, with about 77% of the choices on the correct axis. For the critical tests, the magnetic field around the arena was turned by 90°, and the chicks changed their direction of search accordingly. They now preferred the other axis, thus indicating that they used their magnetic compass to locate the correct screen (Freire et al., 2005).

With a similar test design, keeping the magnetic field constant during the test, taking the bird out and reintroducing it anew into the test apparatus after the magnetic field had been changed, conditioning was also success-

ful with food rewards. A magnetic compass could be demonstrated this way in a non-migratory passerine species, zebra finch *Taeniopygia guttata* (Estrididae). Here, too, the birds were released in the center of a test apparatus and had to move behind one of four screens, a spatial task with the magnetic field as only cue (Voss et al., 2007). Recently, also homing pigeons could be trained to prefer specific direction in a small Skinner box-like apparatus where they had to peck one of four keys in the cardinal compass directions (Wilzeck et al., 2010b). This provides a much better chance to study the pigeons' compass under different magnetic conditions than the traditional pigeon releases.

3.1 Characteristics of the magnetic compass of chickens

The method used to demonstrate the chickens' magnetic compass was also employed to analyze its functional characteristics. Since the chicks' directional choices had been axial rather than unimodal – chickens preferred the correct screen and the opposite one (Freire et al., 2005) – it was not possible to test them for an inclination compass. However, the other types of tests that had been conducted with migratory birds could also be performed with chickens.

Testing in magnetic fields with different intensities revealed that the chickens' magnetic compass also operates within a narrow functional window: decreasing or increasing the local intensity by 50% led to random choices (Fig. 8). The functional range was found to be slightly asymmetric, for the chicks were still oriented in a magnetic field with the intensity decreased by 25%, while they were already disoriented in a field with 25% higher intensity (W. Wiltschko et al., 2007).

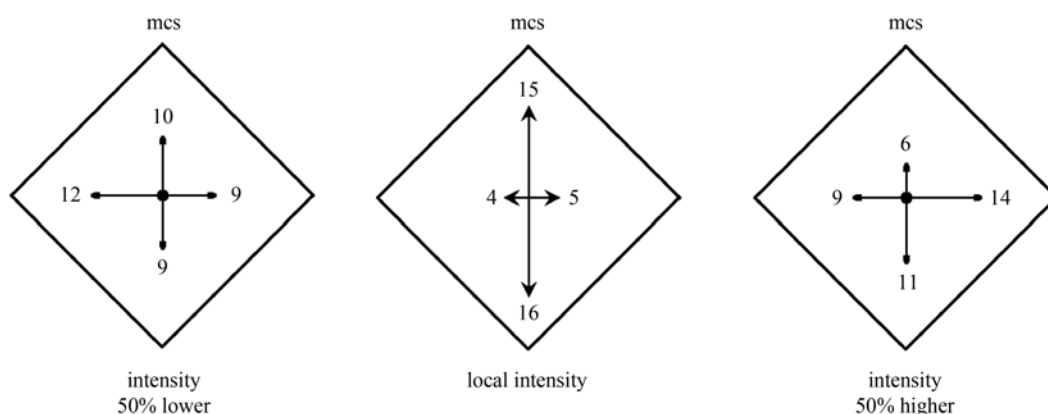


Fig. 8 Directional choices of young chickens in magnetic fields with different intensity, demonstrating the functional window

The chicks were trained to look for a red ball behind a screen in a specific magnetic direction. mcs, magnetically correct screen. Eight chicks were tested five times; the arrows indicate the sum of their choices, given numerically at the ends, with pointed arrows if the distribution is different from random (data from W. Wiltschko et al., 2007).

In monocular tests with their right eye open, the chicks, too, followed a shift in magnetic North, with their performance not different from that with both eyes open. When tested with only their left eye open, however, they failed to respond to the shift in magnetic north (Rogers et al., 2008). This suggests that their magnetic compass, like that of European Robins and Australian Silvereyes, is also lateralized in favor of the right eye and the left hemisphere of the brain.

Tests in view of a wavelength dependency under 'white' and monochromatic blue and red light suffered from a low number of chicks that could be tested. The results, with 73 % correct choices under 465 nm blue and only 50 % correct choices, the value expected for random choices, under 645 nm red, indicate a similar wavelength dependency as observed in robins (W. Wiltshko et al., 2007).

3.2 Physical principles underlying the magnetic compass of chickens

To identify the physical principles underlying the magnetic compass of chickens, we used the same techniques we had used with European Robins before: chicks were subjected to oscillating magnetic fields in the MHz range to test for a radical pair mechanism, and they were tested with their upper beak locally anesthetized in view of an involvement of the iron-rich receptors located there.

The results corresponded to those with robins: oscillating fields disrupted the chicks' orientation, leading to random choices (Fig. 9), whereas temporarily disabling the receptors in the upper beak had no effect. These findings suggest that the magnetic compass of chickens

is also based on radical pair processes (W. Wiltshko et al., 2007), which, in turn, implies that it is an inclination compass, because a radical pair mechanism is not sensitive to the polarity of the magnetic field.

Directionally trained Zebra Finches were also subjected to oscillating fields in the MHz range. The resulting disorientation indicates that their magnetic compass is also based on radical pair processes (Keary et al., 2009).

4 Discussion

Table 2 summarizes the results from the European Robins, Australian silvereyes, homing pigeons and domestic chickens. Although three different kinds of behavior were used, the magnetic compass mechanisms of these species show largely the same characteristics and seem to be based on the same physical processes. Even if the compass of pigeons has not yet been analyzed in detail, the indicated similarity to that of robins and chickens suggests an identical mechanism, namely light-induced electron transfer reactions involving radical pairs in specialized photopigments.

The species whose magnetic compass has been analyzed so far are not at all closely related. Chickens belong to an ancient line of birds, the Galloanseres, that separated from the remaining modern birds, the Neoaves, more than 90 million years ago in the beginning of the Late Cretaceous (Fig. 10; Ericson et al., 2006). Within the Neoaves, pigeons and passerines also have a long diverging evolutionary history as they are only distantly related, belonging to different avian lines that separated already more than 70 million years ago in

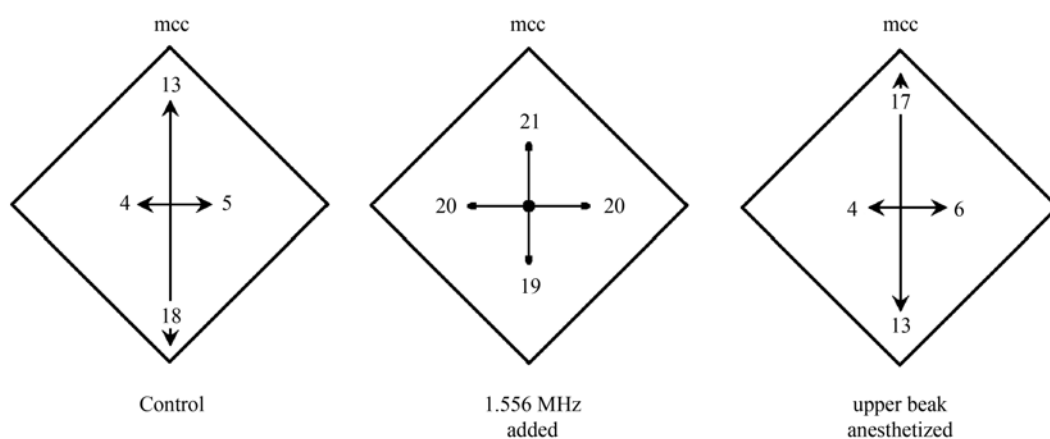


Fig. 9 Directional choices of young chickens under different conditions

In a control field with an intensity and inclination like the local geomagnetic field, the chicks oriented in the magnetically correct and the opposite direction. With an oscillating field added, they were disoriented, whereas they were normally oriented when their upper beak was anesthetized. These findings indicate that the chickens' magnetic compass, too, is based on radical pair processes, with the iron-based receptors in the upper beak not involved (data from W. Wiltshko et al., 2007). Symbols as in Fig. 8.

Table 2 Characteristics of the magnetic compass in different bird species

Bird species	European robin	Austral. silveryeye	Homing pigeon	Domestic chicken
<i>Behavior tested</i>	migration	migration	homing	conditioning
<i>Characteristics:</i>				
(1) inclination compass	yes	yes	yes?	yes?
(2) functional window	yes	??	??	yes
(3) lateralization to the right eye	yes	yes	little	yes
(4) wavelength-dependency	yes	yes	yes	yes
<i>Physical principles:</i>				
(5) radical pair mechanism	yes	??	??	yes
(6) iron-based receptors in beak	no	no	??	no

yes? indicates indirect evidence; ?? indicates that this was not tested

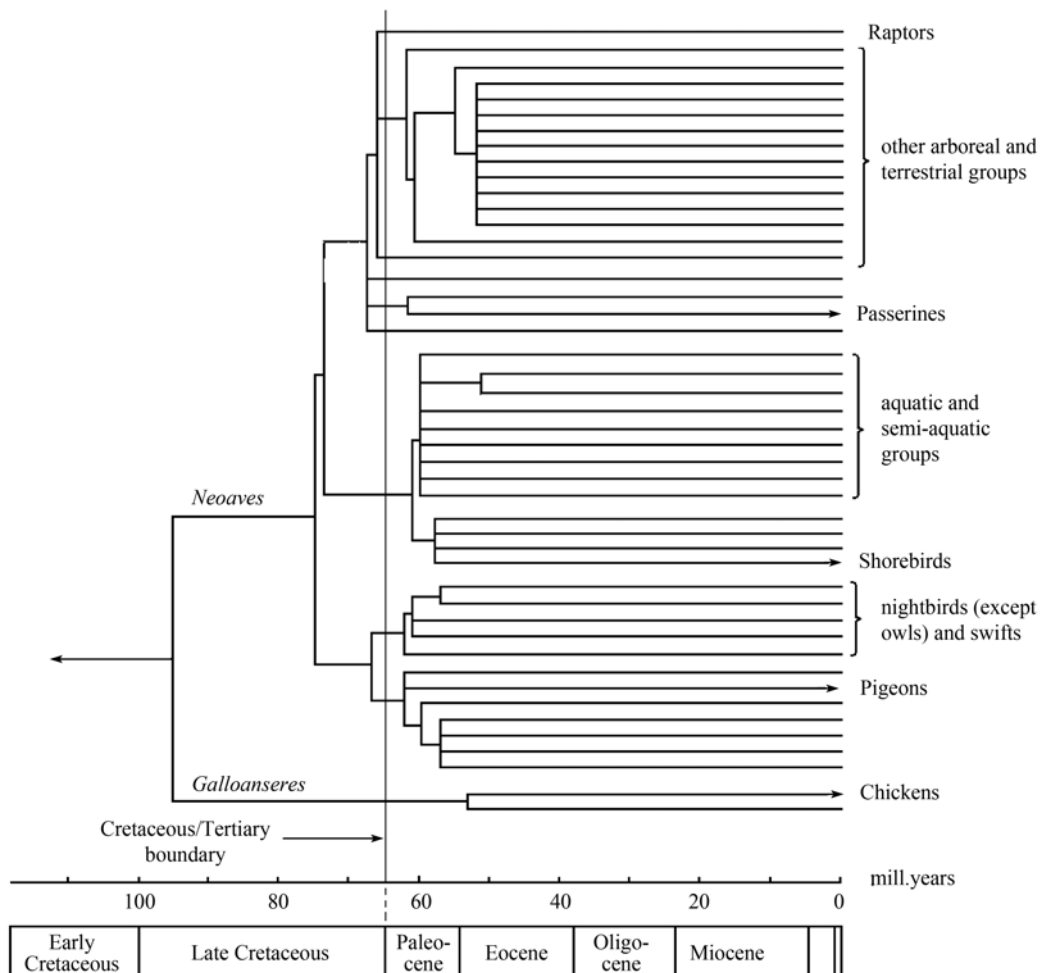


Fig. 10 Phylogenetic tree of modern birds, showing the branching of the different lines in the late Cretaceous (from Ericson et al., 2006, simplified)

Lines to groups that include species that have been shown to have a magnetic compass are marked with a small arrow head.

the Late Cretaceous (Ericson et al., 2006). Finding the same type of magnetic compass in species of all three groups suggests that this compass mechanism may have already been present in their common ancestor. The light-dependent inclination compass based on radical pair processes thus appears to be a rather ancient mechanism that is common to all modern-day birds – a basic orientation tool of great importance for these highly mobile, flying animals. Whether it may have already been present in the reptilian ancestors of birds is not known, since the mechanisms underlying the magnetic compass of reptiles have not yet been analyzed.

Finding the same type of magnetic compass being used in three very different behaviors illustrates the general applicability of this mechanisms in all kinds of tasks where directional information is required: it is used during migration to locate an innate compass course, it is used during homing to locate the home direction determined by navigational processes, and it can be used to locate learned or otherwise acquired directions. The great age of the magnetic compass and the observation that also non-migratory species like homing pigeons, zebra finches and chickens have the same mechanism indicates the ecological background of its development: it is by no means a special development of migratory birds associated with their extended flights in the course of migration; rather, we must assume that the magnetic compass was originally evolved as an all-purpose mechanism for orientation within the home range long before migration began. It is helpful in small-scale tasks as it is in large-scale tasks – the young chickens and the zebra finches tested used it within a space of less than 1 m. It was developed in order to organize space and to facilitate orientation of the everyday movements of birds, allowing fast and efficient flights between roosts, nest site, feeding places, water holes etc. - a function which it still serves today in non-migrants and also in migrants when they are staying in the breeding or wintering area. When migration evolved and some birds began with seasonal movements, they could fall back on an already existing mechanism; it only had to be combined with innate information on a specific course to cover extended distances. The existence of the magnetic compass in domestic chickens after thousands of years of domestication documents its generally important role in the birds' everyday life. However, today, chickens are often no longer kept under natural or semi-natural conditions. Not all strains of chicken still have a functioning magnetic compass; some seem to have lost it in the course of being bred

and modified for human purposes (Freire et al., 2008).

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