

The magnetic compass of domestic chickens, *Gallus gallus*

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Summary

By directional training, young domestic chickens have been shown to use a magnetic compass; the same method has now been used to analyse the functional characteristics and the physical principles underlying the chickens' magnetic compass. Tests in magnetic fields with different intensities revealed a functional window around the intensity of the local geomagnetic field, with this window extending further towards lower than higher intensities. Testing chickens under monochromatic 465 nm blue and 645 nm red light suggested a wavelength dependence, with orientation possible under blue but not under red light. Exposing chickens to an oscillating field of 1.566 MHz led to disorientation, identifying an underlying radical pair mechanism. Local anesthesia of the upper beak, where

iron-rich structures have been described as potential magnetoreceptors, did not affect the performance, suggesting that these receptors are not involved in compass orientation. These findings show obvious parallels to the magnetic compass described for European robins, indicating that chickens and small passerines use the same type of magnetic compass mechanism. This suggests that the avian magnetic compass may have evolved in the common ancestor of all present-day birds to facilitate orientation within the home range.

Key words: directional training, magnetic compass, functional window, radical pair mechanism, *Gallus gallus*, domestic chicken.

Introduction

The avian magnetic compass was first demonstrated 40 years ago in a night-migrating passerine, the European robin, *Erithacus rubecula* (Turdidae). During the migratory season, these birds also prefer their natural migratory direction when they are in captivity, and when the North direction of the ambient magnetic field was shifted, they changed the direction of their headings accordingly. This indicated that they located their migratory direction with the help of the magnetic field (Wiltschko, W. and Merkel, 1966).

Migratory behaviour of robins has also been used to analyse the functional properties of this compass mechanism, and two surprising characteristics have become evident. Firstly, the robins' magnetic compass is an 'inclination compass', not based on the polarity of the magnetic field but rather on the course of the field lines and their inclination in space (Wiltschko, W. and Wiltschko, 1972). Secondly, the compass is closely attuned to the intensity (field strength) of the local geomagnetic field, with a functional window that can be adjusted to intensities outside the normal functional range (Wiltschko, W., 1968; Wiltschko, W., 1978; Wiltschko, W. et al., 2006a).

Recent experiments have focused on the physical mechanisms underlying the reception of magnetic compass information. The Radical Pair model (Ritz et al., 2000) proposes that the avian magnetic compass is based on radical pair processes in specialized photopigments, with the first step leading to magnetoreception being the absorption of a photon. This model allows two testable predictions, namely (1) magnetoreception should be light dependent and (2) oscillating fields in the MHz range that interfere with radical pair processes should disrupt magnetoreception (Ritz et al., 2000). Both predictions have been tested with European robins and were found to be true. The avian magnetic compass requires light from the short-wavelength part of the spectrum. Under 590 nm yellow light and beyond, robins were disoriented (Wiltschko, W. and Wiltschko, 1995; Wiltschko, W. and Wiltschko, 1999; Muheim et al., 2002). Using oscillating fields as a diagnostic tool, a radical pair mechanism was identified as the primary process mediating magnetic compass information (Ritz et al., 2004; Thalau et al., 2005; Wiltschko, R. et al., 2005). Magnetite, found in birds in the ethmoid region and the upper beak (e.g. Beason and Brennon,

1986; Hanzlick et al., 2000; Fleissner et al., 2003; Fleissner et al., 2007), on the other hand, does not seem to be involved in the processes providing passerine birds with compass information (e.g. Beason and Semm, 1997; Munro et al., 1997; Wiltschko, W. et al., 2006b; Wiltschko, R. et al., 2007).

Meanwhile, a magnetic compass has been demonstrated in more than 20 species of birds [see Wiltschko, R. and Wiltschko (Wiltschko, R. and Wiltschko, 1995) for a summary (Bäckman et al., 1997; Gudmundsson and Sandberg, 2000)]. The vast majority are passerine migrants. The reason for this bias towards migrating species appears to be based on the fact that, during the migration season, orientation in the migratory direction is a very reliable behaviour that provides an excellent tool for analysing the underlying compass mechanism.

Until recently, the carrier pigeon, *Columba livia*, was the only non-migratory avian species for which a magnetic compass had been demonstrated; here, homing after displacement produced reliable directional tendencies for analysis (Keeton, 1971). Conditioning experiments using magnetic stimuli, on the other hand, have been largely unsuccessful, with the negative results by far outnumbering the few positive ones (for a review, see Wiltschko, R. and Wiltschko, 1995). The only successful operant studies involved detection of changes in magnetic intensity and the presence or absence of a magnetic anomaly rather than magnetic directions (Bookman, 1977; Mora et al., 2004; Thalau et al., 2007). Directional training has for a long time failed to elicit stable directional tendencies in birds (e.g. Katz, 1978; Griffin, 1982; Alsop, 1987), as birds do not easily respond to changes in the direction of the magnetic field around them.

Recently, however, a magnetic compass has been demonstrated in domestic chicken, *Gallus gallus*, using training to locate a model social companion (Freire et al., 2005); the young chickens were imprinted on a red ball, which was then hidden behind one of four screens in each corner of a test apparatus. The chicks were trained to locate the ball and to solve this spatial task by remembering that it was always behind, for example, the screen in the North. When the chicks were tested with North of the ambient magnetic field shifted by 90° to the East, they shifted their search accordingly. This study was the first to demonstrate magnetic compass orientation in an avian species by conditioning.

In the present study, we follow up this initial work and, using the same method as Freire et al. (Freire et al., 2005), analyse the functional properties of the chickens' magnetic compass and the nature of the physical processes underlying this mechanism.

Materials and methods

The experiments were performed in Armidale, NSW, Australia during three testing periods. The series analyzing the biological window of the chickens' magnetic compass

were begun in August 2005 and were completed in March 2006, when the chickens were also tested for an effect of the local anesthetic applied to their upper beak and for their response to monochromatic lights, partly using the same chicks. The test series subjecting the chickens to high-frequency fields was conducted in November 2005. Technical constraints and time limitations resulted in differing numbers of chickens and differing numbers of tests per chick in the various series.

All training and testing took place in a wooden building, where the local geomagnetic field of 55.9 μ T, -62° inclination was undisturbed.

Test animals, imprinting and housing

We used brown-layer chicks from Nulkaba Hatchery, Cessnock, NSW, Australia. The chicks were reared in isolation in cardboard pens (35×40×40 cm high) from about 2 h after hatching. A red table-tennis ball (4 cm diameter) was suspended on a string in the centre of the pen to provide the imprinting stimulus. The chick adopted it as its 'mother'; it was at ease in the presence of the ball and would search for it when it was removed.

To encourage pecking and eating, the floor of the pen was lined with white paper and sprinkled with chick starter crumbs that were periodically tapped with a small round rod. Water was available *ad libitum*. On day 3, wood shavings and an externally placed drinker were added to the pen. When the chicks were about 4–5 days old, they were moved to a wooden building where training and testing took place (for details, see Freire et al., 2005).

Test arena, training and critical tests

The test protocol was identical to that used in previous experiments demonstrating the chicken's ability to use the magnetic field for orientation (Freire et al., 2005).

Test arena

The test arena consisted of a square white pen (80 cm×80 cm, 70 cm high) with wood shavings on the floor. At each corner, corresponding to magnetic North (mN), South (S), East (E) and West (W), were white screens (15 cm wide, 25 cm high) positioned perpendicularly to the diagonal, 15 cm from the side walls of the arena. Diffuse 'white' lighting was provided from above by four incandescent light bulbs placed above the screens. This light reached the birds after passing through a diffuser that formed the ceiling of the arena [see fig. 1 in Freire et al. (Freire et al., 2005)]. An overhead camera (Kobi DSP), placed above the centre of the arena with the lens positioned through a 5 cm-diameter hole in the ceiling, was used to observe the chick's behaviour on a monitor.

Care was taken to make the arena as uniform as possible. In order to minimize the impact of other cues that chicks could use for relocating the ball, the arena was rotated by 90°, 180° or 270° after each trial and test (see below), determined by a pseudorandom sequence. Additionally, the direction that

the chick was facing when placed in the start cage and the side of the arena from which it was handled was also determined by a pseudorandom sequence.

Training phase

Chicks were trained to locate the red ball behind one of four screens, with an equal number of chicks trained to North, South, East and West, the series with the local anesthetic being an exception. A chick was placed in the centre of the arena in a transparent plastic start cage (20×15 cm or 20×20 cm, 25 cm high) for 20 s next to the red ball that had served as the imprinting stimulus. The ball was then slowly moved behind one screen; the chick was released and allowed to search for it. This procedure was termed a 'visual displacement trial'. When the chick had moved behind the correct screen and approached to within 5 cm of the ball, it was left there for 1 min to stay with the ball (its social reward), then it was picked up and returned to its home pen. Failure to approach the screen within 3 min led to termination of that trial.

After successful completion of three visual displacement trials, the chick was placed in the start cage with the ball already behind the screen; it was then released and allowed to search for the ball. This was termed a 'relocation trial'. When the chick had moved behind the correct screen and approached to within 5 cm of the ball, it was allowed to stay there for 1 min and then returned to its home pen. If a chick failed to move behind the screen within 3 min of release, it was reintroduced into the start cage and received a visual displacement trial before being returned to its home pen. In order to take the axially of the responses (see Freire et al., 2005) into account, a second identical ball was placed behind the screen directly opposite the screen concealing the first ball but only after a chick had chosen this screen twice in subsequent relocation trials. The reason for adopting this procedure was to provide a reward in order to prevent extinction of the response.

Each chick continued to receive relocation trials until it reached 'criterion', which was defined as moving behind the screen and approaching to within 5 cm of the ball in less than 20 s of release on three consecutive relocation trials. Trials in which a chick moved behind other screens not concealing a ball prior to locating the ball were scored as incorrect.

All training, i.e. visual displacement trials and relocation trials, took place under 'white' light in the local geomagnetic field.

Testing

The critical tests were performed when the chickens were between 12 and 22 days old. The procedure was similar to that used in the relocation trials, except for two aspects: (1) these tests were unrewarded, i.e. there was no ball behind the correct or the opposite screen, and (2) magnetic North was shifted to the East (see below). That is, the chicks never got to see the red ball in a field with magnetic North shifted.

These tests were interspersed with relocation trials in the

local geomagnetic field with the red ball present in order not to discourage the chicks. After a test, the chick with the ball was returned to the home pen for a few minutes before being placed into the start cage and presented with a relocation trial. When a chick moved behind the screen and approached the ball in less than 20 s of release without prior walking behind other screens, it was allowed to remain in the arena for a further minute with the ball as a reward. After this, it was returned to the home pen before it was presented with the next test. If the chick failed to approach the ball within 3 min of release in the relocation trial, it received another visual displacement trial and then returned to the home pen. After the next successful relocation trial, it was again presented with a critical test.

Each chick received an equal number of tests in each of the test conditions to which it was assigned (see below). The order of presentation of these test conditions was randomized in the series testing for the biological window and for the effect of the high-frequency fields. The series under monochromatic light and those with local anesthesia of the upper beak took place at the end of an individual chick's testing period and involved some chicks that had already been tested in one of the series determining the biological window; in these cases, the respective control tests also served as control tests for these series. The blue and red lights were presented in pseudorandom order; the tests using the local anesthetic were performed one after the other (see below).

Experimental conditions

The experimental conditions involved experimentally altered magnetic fields that were presented to the chicks only during testing. The various test fields were produced by pairs of Helmholtz coils (2 m diameter, 1 m clearance) with 30 windings of copper wire on each side. When testing for the functional window and for the effect of the local anesthetic, we used three pairs of coils with their axes aligned horizontally in the North–South direction, horizontally in the East–West direction and vertically. These coils could be operated independently to modify each component of the magnetic field separately. For the tests for the effect of high-frequency fields and the effect of the wavelength of light, we used one pair of coils with its horizontal axis aligned 135–315°, which allowed us to turn magnetic North by 90° clockwise to the East without altering inclination and intensity.

All critical tests took place in experimental magnetic fields with North turned by 90° to the East with the inclination unchanged (mN=E, –62° inclination), to ensure that the chicks were relying on the ambient magnetic field for locating the imprinting stimulus. This field with the intensity equivalent to that of the local geomagnetic field (55.9 μT) served as the control condition and provided the reference for assessing the performance in the other test conditions. The other conditions varied according to the experimental series.

Testing for a functional window

For analyzing the functional window, the chicks were additionally tested in magnetic fields with different intensities but with the same direction and inclination as the control field. In the first part of the series, these fields were 50% weaker and stronger than the local geomagnetic field, with total intensities of 27.9 μT and 83.8 μT , respectively. In the second part of the series, the intensity differences were 25%, with the respective intensities being 41.9 μT and 69.9 μT .

Monochromatic lights

To test for wavelength dependence of the chickens' magnetic compass, the chicks were tested in the same magnetic field as in the control condition under monochromatic blue and red light, with the tests under 'white' light serving as controls. The test lights were produced by four sets of bright light-emitting diodes (LEDs) mounted above the screens so that the light passed through a diffuser that formed the ceiling of the test arena. The blue diodes had a peak wavelength of 465 nm and a bandwidth of 50% intensity between 454 and 476 nm; the red diodes had a peak wavelength of 645 nm and a bandwidth of 625–666 nm. The monochromatic lights were of about equal quantal flux, with the intensity of blue light in the arena being 0.60 W m^{-2} and that of red light being 0.45 W m^{-2} .

Effect of high-frequency fields

In this test series, the chicks were subjected to a high-frequency field of 1.566 MHz. This oscillating field was produced by a coil antenna consisting of a single winding of coaxial cable with 2 cm of the screening removed. The antenna was mounted on a horizontal wooden frame surrounding the test apparatus and was fed by oscillating currents from a high-frequency generator (for details, see Ritz et al., 2004). This way, the high-frequency field was presented vertically, forming a 28° angle to the static magnetic vector. The high-frequency field was presented at two intensities: 480 nT, which is a little less than 1% of that of the geomagnetic field, and 48 nT, one tenth of the preceding one.

Effect of local anesthesia of the upper beak

Chicks were tested in the control field with the skin of their upper beak anesthetized with the local anesthetic xylocaine® (active substance: lignocaine hydrochloride 2%; produced by AstraZeneca, North Ryde, NSW, Australia). It was applied externally by gently rubbing a cotton bud soaked with the anesthetic along the edges of the upper beak. After waiting for about 10 min for the effect to set in, testing began. In this test series, the procedure was adjusted to the lasting effect of the anesthetic: the control tests were done first, followed by the tests with the anesthetic applied. The latter were conducted in sequence without relocation tests, and the anesthetic was reapplied after the third test.

Data analysis and statistics

In each test series, eight or 12 chicks were tested five or 10 times in each test condition. As before (Freire et al., 2005), the chickens' choices were axial, focusing on the correct screen and the screen directly opposite. The null hypothesis thus predicts about 50% choices on the correct axis and 50% on the axis perpendicular to it. We determined the percentage of choices on the correct axis for each bird and calculated the mean \pm standard deviation for each series. The sign test was used to test whether or not there were more choices on the correct axis than chance level, with significance indicating that the chicks were oriented along this axis in the respective test condition.

The proportion of correct choices was then arcsine transformed [$p' = \arcsin(\sqrt{p}) \times 57.298$], as described by Zar (Zar, 1999), and analyzed in a repeated-measures analysis of variance (ANOVA). The *F*-test was used to look for differences between the various test conditions.

Results

Altogether, 36 chickens were involved in the analysis of the magnetic compass. They showed considerable variation in the ease with which they learned the task. The number of relocations before reaching criterion varied between four and 25, with the mean being 11.0 \pm 4.9 (s.d.). The birds that had been previously used in the tests for the biological window and were now, after a pause, reused for the Xylocaine series needed only 2.9 \pm 1.1 (s.d.) relocations to reach criterion again. The number of relocations between tests also varied between 1 and 9, with a mean of 1.8 \pm 1.2 (s.d.).

Testing for a functional window

In these series, two groups of chickens were tested in the control field (with the intensity of the local geomagnetic field) and in fields with the intensity 50% or 25% weaker and stronger. In all these fields, magnetic North was shifted by 90° to the East. Table 1 summarizes the percentage of correct choices and the number of chickens performing above average in the different experimental conditions; Table A1 in the Appendix gives the individual chicken's choices.

In the series varying magnetic intensity by 50%, the birds chose the screen in the correct magnetic direction or the screen directly opposite it in 78% of the tests in the control field, with each of the 12 individual chicks being above chance level (Sign test, $P < 0.001$; see Table 1). In the weaker and stronger fields, only 47% and 42% of the choices, respectively, were on the correct axis, with the choices in these two conditions not different from chance level (see Table 1). The difference between the performances in the three test conditions is significant (ANOVA, $F_{2,22} = 24.97$, $P < 0.001$), with significantly more choices of the correct axis in the control field than in the weaker or stronger fields (see Table 1). That is, the chickens showed significantly oriented search behaviour in the test field with intensity like the local

Table 1. Testing for a functional window: test at different magnetic intensities

Test condition	Tests per bird	Correct directional choices				Latencies (s) (means \pm s.d.)
		Percentage correct (mean \pm s.d.)	Individuals with >50% correct choices	Significant directional preference?	Different from C?	
C ₁ , intensity like geomagnetic field	5	78 \pm 13	12/12	***	C ₁	35.6 \pm 35.7
Intensity 50% decreased	5	47 \pm 16	6/12	n.s.	**	38.9 \pm 40.8
Intensity 50% increased	5	42 \pm 16	4/12	n.s.	**	52.6 \pm 68.9
C ₂ , intensity like geomagnetic field	5	72 \pm 16	12/12	***	C ₂	28.2 \pm 29.1
Intensity 25% decreased	5	75 \pm 21	11/12	**	n.s.	37.5 \pm 32.7
Intensity 25% increased	5	50 \pm 13	7/12	n.s.	*	29.6 \pm 31.1

C₁ and C₂ are the control tests of the two series; column 4 gives the number of individuals with more than 50% correct choices compared with the number of individuals tested; column 5 indicates whether there was a significant preference of the correct axis by the Sign test, indicating oriented behaviour (*** P <0.001; n.s., not significant); column 6 indicates whether the distribution of choices was significantly different from that in respective control conditions according to the F -test: * P <0.05; ** P <0.01. 'Latency' indicates the time, in seconds, between release of the chick and its scoring by moving behind a screen.

geomagnetic field but were not oriented in the two other fields (Fig. 1, top row).

In the other series, the intensity of the stronger and the weaker fields differed from that of the local geomagnetic field by only 25%. Here, 72% of the choices in the control tests were correct, and again all 12 individuals performed above chance level (Sign test, P <0.001). In the lower field, the chicks performed 75% correct choices, with 11 of the 12 chicks above chance level (Sign test, P <0.01), whereas only

50% of choices were correct in the higher field (see Table 1, lower section). This indicates that significantly oriented search behaviour occurred in the control field and in the 25% lower field but not in the 25% higher field (Fig. 1, bottom row). The difference between the three test conditions is significant (ANOVA, $F_{2,22}=5.526$, $P=0.011$), with significantly more correct choices in the control field and in the 25% decreased field than in the 25% increased field (see Table 1).

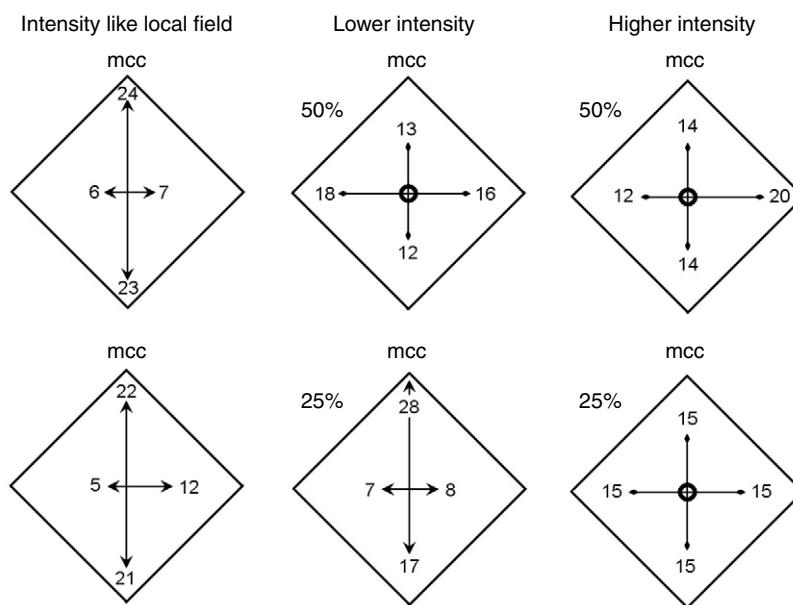


Fig. 1. Testing for a functional window: pooled number of choices of the four screens in magnetic fields with different intensities, with the direction of the magnetically correct choice (mcc) projected upward. Arrowheads indicate samples with a significant preference of an axis; rounded ends and a ring around the centre indicate random choices (for numerical data, see Table 1).

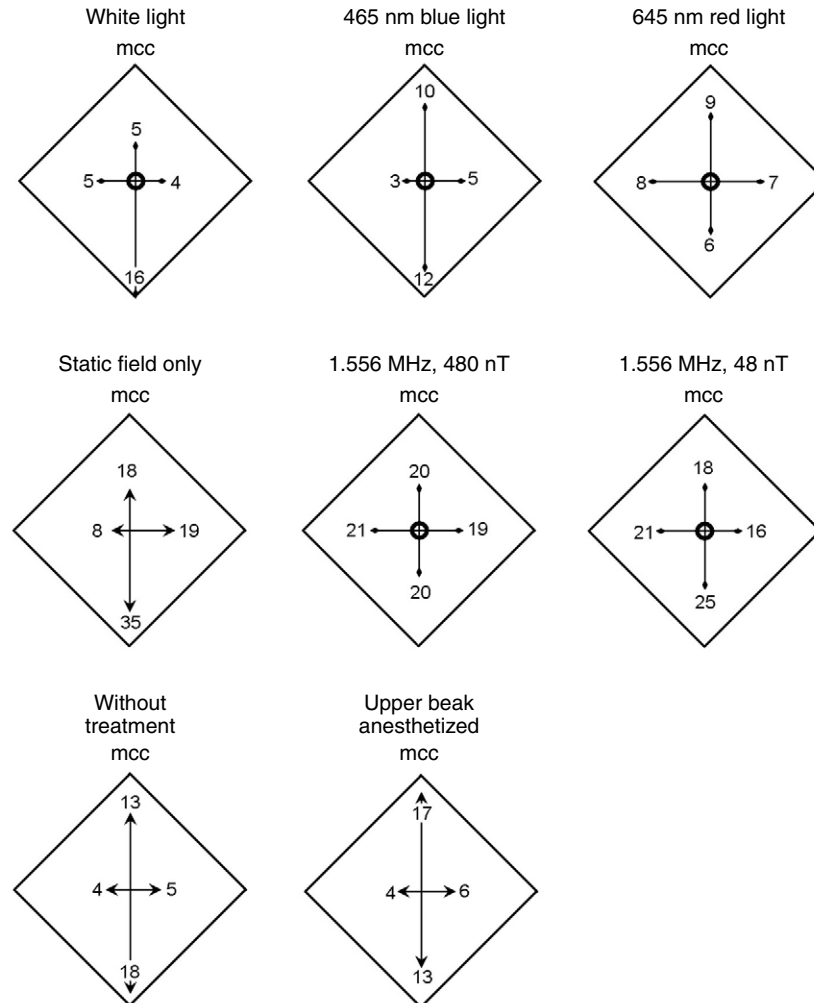


Fig. 2. Testing for the physical principle underlying the chickens' magnetic compass: pooled number of choices of the four screens in the control field (left column of diagrams) and various treatments, with the direction of the magnetically correct choice (mcc) projected upward. Arrowheads indicate samples with a significant preference of an axis; rounded ends and a ring around the centre indicate random choices. Top row, test under different light regimes; centre row, oscillating field of 1.566 MHz of two different intensities added; bottom row, iron-containing structures in the upper beak deactivated by local anesthesia (for numerical data, see Table 2).

The latencies, i.e. the time taken by the chickens from being released until reaching a screen and scoring, are included in Table 1. They vary greatly and do not differ between experimental conditions (50% series, $F_{2,22}=1.074$, $P=0.359$; 25% series, $F_{2,22}=0.421$, $P=0.662$).

These data demonstrate that the chickens' magnetic compass is restricted to a functional window, working only at total intensities equal or similar to that of the local geomagnetic field, with a decrease as well as an increase in magnetic intensity leading to disorientation. Interestingly, the functional window appears to be asymmetric with respect to the ambient geomagnetic field: its lower limit lay between 25 and 50% below the local field's intensity of $55.4 \mu\text{T}$, whereas the upper limit was less than 25% above this intensity.

Testing for the physical principle underlying the chickens' magnetic compass

The Radical Pair model (Ritz et al., 2000) predicted that magnetoreception would be light dependent and can be disrupted by high-frequency fields in the MHz range (for details, see Ritz et al., 2000; Ritz et al., 2004). In view of this, we tested the chickens under monochromatic blue and red light and subjected them to oscillating magnetic fields, a diagnostic tool for radical pair processes. Another potential mechanism of magnetoreception involves iron-based receptors (e.g. Kirschvink and Gould, 1981; Davila et al., 2003), and such receptors have been described in the upper beak of pigeons (Fleissner et al., 2003; Fleissner et al., 2007). Chickens have a similar arrangement of receptors in their upper beak (Fleissner et al., 2007); hence we also tested

Table 2. Testing for the physical principle underlying the chickens' magnetic compass

Test condition	Tests per bird	Correct directional choices				Latencies	
		Percentage correct (mean \pm s.d.)	Individuals with >50% correct choices	Significant directional preference?	Different from C?	Time (s) (mean \pm s.d.)	Different from C?
C ₃ , 'white' light	5	73 \pm 21	5/6	n.s.	C ₃	8.6 \pm 4.6	C ₃
465 nm blue light	5	73 \pm 30	5/6	n.s.	n.s.	24.3 \pm 11.1	n.s.
645 nm red light	5	50 \pm 24	2/6	n.s.	n.s.	51.3 \pm 21.4	***
C ₄ , static field only	10	66 \pm 14	5(3)/8	*	C ₄	55.2 \pm 48.4	C ₄
1.566 MHz, 480 nT	10	50 \pm 11	2(3)/8	n.s.	*	45.2 \pm 31.4	n.s.
1.566 MHz, 48 nT,	10	46 \pm 13	3(1)/8	n.s.	*	46.7 \pm 33.6	n.s.
C ₅ , no treatment	5	78 \pm 17	8/8	**	C ₅	22.9 \pm 31.7	C ₅
Local anaesthesia	5	75 \pm 18	8/8	**	n.s.	55.5 \pm 37.9	*

In the series with the oscillating fields, 10 tests per bird were tested; here, column 4 indicates the number of birds with more than 50% correct choices and, in parentheses, those with exactly 50% correct choices. For other explanations, see Table 1.

chicks whose upper beak was locally anesthetized in order to temporarily disable these receptors.

Testing for an effect of the wavelengths of light

For technical reasons, this test series had to be performed at the end of testing and could not be completed. Only six chickens were tested under monochromatic light and the distribution of their choices is given in Fig. 2, top row. Under white light and monochromatic 465 nm blue light, 73% of their choices were on the correct axis; under 645 nm red light, only 50% of the choices were correct, suggesting oriented behaviour under white and blue but not under red light. However, due to the small sample size of only six chicks, neither of the distributions differed from random (see Table 2), and they did not differ from each other (ANOVA, $F_{2,10}=1.811$, $P=0.213$). However, it should be noted that under white and blue light, five chicks performed above chance level, whereas only two chicks did so under red light (Table 2).

Testing for an effect of oscillating fields in the MHz range

Adding oscillating fields to the local geomagnetic field caused random searching (Fig. 2, middle row). While the chickens performed 66% of choices on the correct axis in the control field, with five of the eight birds performing above and three at chance level, the percentage of correct choices was only 50% in the 480 nT oscillating field. Even in the markedly weaker oscillating field of only 48 nT, the percentage of correct choices was only 46%, reflecting searches that were no longer oriented (Table 2). The difference between the three groups is significant (ANOVA, $F_{2,14}=7.144$, $P=0.007$), with significantly more choices on the correct axis in the control field than in the two oscillating fields (F -test, $P=0.015$ and $P=0.003$, respectively). The disorienting effect of the oscillating fields indicates a

disruption of the reception processes, thus identifying an underlying radical pair mechanism.

Testing for an effect of local anaesthesia of the upper beak

Anaesthesia of the upper beak did not affect the chicken's searching behaviour (Fig. 2, bottom row): 78% and 75% of the choices were on the correct axis, and all chickens performed above chance level, untreated as well as with the beak anesthetized (Table 2). There was no difference between the two test conditions ($F_{1,7}=0.030$, $P=0.867$). These findings speak against an involvement of iron-based receptors in the upper beak in providing the magnetic compass information the chicks rely on when searching for the correct screen.

The performance of the individual chicks in these three test series is given in Tables A2–A4 in the Appendix.

Table 2 also includes the latencies, i.e. the time required to score in the various experimental conditions. They vary greatly and indicate a surprising phenomenon: while there is no general difference between conditions where the chicken can orient and those where they cannot in the tests documenting the biological window and those with oscillating field, there are treatments that affect the latencies but not the directional choices. This is true for the local anaesthesia: while the chickens show a preference of the correct axis with and without treatment, they need significantly longer to choose when their upper beak is anesthetized ($F_{1,7}=6.631$, $P=0.037$). These longer latencies may be attributed to possible general discomfort of having a sensory input disrupted, even if it is not the one used for locating direction. The latencies also differ significantly under the different coloured lights (ANOVA, $F_{2,10}=14.504$, $P<0.001$). Here, the chicks take significantly longer under red light, where they appear to be disoriented, than under white and blue light ($F_{1,7}=28.366$, $P=0.0003$ and $F_{1,7}=11.314$, $P=0.0072$, respectively). It seems likely that the sudden exposure to a monochromatic environment may confuse the chicks, with red having a

stronger effect than blue because it additionally interferes with their ability to solve the task.

Discussion

Our findings reveal striking parallels between the magnetic compass of the domestic chicken and that of European robins.

The chickens' magnetic compass, like that of robins, works in a rather narrow functional window closely attuned to the intensity of the local magnetic field. For robins living in a local field of $\sim 46 \mu\text{T}$, the upper limit lies between $54 \mu\text{T}$ and $60 \mu\text{T}$, while the lower limit lies between $43 \mu\text{T}$ and $34 \mu\text{T}$; i.e. between an increase of 17–30% and a decrease of 7–26% (Wiltschko, 1978). It is not necessarily asymmetrical, as appears to be the case in the chickens, but without a systematic study we cannot tell whether the functional windows of the two species are truly different – the few intensity levels tested so far do not allow a meaningful conclusion.

The data in the other test series indicate that the same physical principles underlie the compass mechanism of both robins and chickens. The data obtained under monochromatic blue and red light from only six chicks do not allow a definite answer about a wavelength dependence of the chickens' magnetic compass. The average percentage of correct choices under the various light conditions, however, is in agreement with a wavelength dependence as found in European robins (Wiltschko, W. and Wiltschko, 1995; Wiltschko, W. and Wiltschko, 1999) and two other species of passerines, the Australian silveryeye, *Zosterops lateralis* (Wiltschko, W. et al., 1993), and the European garden warbler, *Sylvia borin* (Rappl et al., 2000). The chickens' response to the high-frequency field of 1.566 MHz, on the other hand, identifies their magnetic compass as a mechanism based on radical pair processes like that of robins (Ritz et al., 2004; Thalau et al., 2005; Wiltschko, W. et al., 2005). Here, the great sensitivity of the chickens is remarkable: an oscillating field of only 48 nT, i.e. less than 1/1000 of the local field's intensity, already disrupted oriented searching. The frequency used in this study, 1.566 MHz, represents the Larmor frequency in the local magnetic field of $55.9 \mu\text{T}$. A particularly sensitive resonance at the Larmor frequency indicates specific properties of the crucial radical pair (T.R. et al., manuscript in preparation). Robins also respond very sensitively to an oscillating field with the local Larmor frequency (T. Ritz, R. Wiltschko and P. Hore, manuscript in preparation), and this suggests an identical mechanism, with the same receptor molecule forming the radical pair in both species.

The non-involvement of the iron-based receptors in the upper beak is likewise a parallel to the magnetic compass of robins. Robins, too, remained well oriented with these receptors deactivated by local anesthesia and continued to prefer their migratory direction as when they were untreated. With robins, there is also evidence that applying the anesthetic in the way that it was applied in the present study can affect other responses, e.g. 'fixed direction' responses,

but it does not interfere with their inclination compass (Wiltschko, R. et al., 2007).

There is no direct evidence that the chickens' compass is also an inclination compass. The response of chicks was axial rather than unimodal – they preferred the correct screen and the one opposite to it, e.g. the ones in the North and the South over those in the East and the West (see Freire et al., 2005). Hence, reversing the vertical component – the diagnostic test for an inclination compass – could not be applied, because in case of axiality, a reversal in orientation does not become evident. Theoretical considerations, however, clearly indicate an inclination compass: the underlying mechanism was identified as a radical pair mechanism, and radical pair processes are not sensitive to polarity but respond only to the course of the field lines. The observed axially bimodal responses suggest that the chickens, in contrast to the robins, did not distinguish the two ends of the axis.

In summary, our analysis of the chickens' magnetic compass and comparison with the magnetic compass of robins points to an identical mechanism, namely a light-dependent inclination compass based on radical pair processes that works in a narrow functional window attuned to the local geomagnetic field. The same appears to be true for the magnetic compass of pigeons: it is also an inclination compass (Walcott and Green, 1974; Visalberghi and Alleva, 1978), probably with a similar light dependence as in robins (Wiltschko, R. and Wiltschko, 1998). This seems to suggest that it may be a mechanism common to all birds. Passerines and pigeons on the one hand and chickens on the other hand are not closely related. The galliformes belong to an ancient line of birds, which separated from the more modern lines of birds as early as the Cretaceous period (Cooper and Penny, 1997). Hence, the existence of the same type of magnetic compass mechanism in birds of both lineages implies that this type of compass is of great age and probably was already developed in the common ancestors of all modern birds.

The above considerations, together with the finding that the avian magnetic compass is well developed in a sedentary species such as the domestic chicken, indicate the ecological background of its development. In contrast to what is frequently stated, it has not been developed in connection with extended migrations. It must be assumed that it already existed before modern birds began to migrate. When some species began with seasonal movements, the existence of an efficient compass mechanism may have facilitated migration over extended distances. Originally, the magnetic compass developed most likely as a mechanism for orientation within the home range, to allow the birds fast and efficient movements between roosts, nest, feeding places, water, etc. – a function that it still serves today in non-migrants and in migrants outside migration. The finding that even domestic chickens, after thousands of years of domestication (Fumihito et al., 1996), still have a well-developed magnetic compass highlights the important role of this mechanism in birds' everyday navigation tasks.

Appendix: tables giving the directional choices of the chicks

Table A1. Testing for a functional window: choices in fields with a decrease and increase in intensity

Bird	Sex	Training direction	Magnetic North shifted 90° to geographic East					
			Intensity like geomagnetic field		Intensity decreased		Intensity increased	
			Choices*	%	Choices*	%	Choices*	%
<i>Choices in fields with a 50% decrease and increase in intensity</i>								
13	♀	E	S w e S N	60	N N S w w	60	w N e w N	40
14	♀	W	S S N S w	80	e w S N N	60	N e S N e	60
15	♂	N	E E W W W	100	W E n E n	60	s E E W s	60
19	♀	N	n E W E W	80	E n n n W	40	E W W s s	60
20	♂	E	S e N S N	80	w N e S S	60	N N e w e	40
21	♀	S	W E n n E	60	s E s W n	40	s s n s E	20
22	♂	W	S N S e S	80	e N w e S	40	e e w w S	20
24	♂	E	S w S S S	80	e e w N w	20	e N w S w	40
40	♀	S	W W W E s	80	E E s n n	40	W s W n W	60
41	♂	S	E n W W s	60	E n s W W	60	n n E W n	40
47	♂	W	e S N N S	80	w w S w w	20	e e N w S	40
50a	♀	N	W W E E W	100	E W s s W	60	n W s s E	40
N=12				Mean = 78%		Mean = 47%		Mean = 42%
<i>Choices in fields with a 25% decrease and increase in intensity</i>								
25	♀	W	e S N e N	60	N e S w N	60	e S N S e	60
26	♂	N	s E W E s	60	W E E s n	60	E E E n s	60
27	♀	E	S S N N S	100	S w S N w	60	S e N N w	60
28	♂	E	S S S w w	60	N S e S e	60	S e S e S	60
29	♀	S	W E E E s	80	W W W W W	100	n E s W n	40
32	♀	N	E W s E E	80	E n E W E	80	s W E W s	60
33	♂	W	e N S S N	80	N S S S S	100	w w S w S	40
42	♂	E	N e S N w	60	w S S S w	60	N w S e e	40
45	♀	S	W E n E n	60	E W W E W	100	E n n W W	60
46	♂	N	E E W E E	100	W E s E W	80	n s s s W	20
53	♂	S	s E E W s	60	W s W n s	40	s E W s s	40
54	♀	W	N N S w e	60	S S N S S	100	w S S N e	60
N=12				Mean = 72%		Mean = 75%		Mean = 50%

*Letters indicate the directions of the five choices, with capital letters indicating those on the correct axis and small letters indicating those on the other axis. The mean of the percentage of choices on the correct axis is given.

Table A2. Testing for the physical principle underlying the chickens' magnetic compass: choices under monochromatic blue and red lights

Bird	Sex	Training direction	Magnetic North = geographic East					
			'White' light		465 nm blue light		645 nm red light	
			Choices*	%	Choices*	%	Choices*	%
50a	♀	N	W W E E W	100	E n W s E	60	s n n W E	40
53	♂	S	s E E W s	60	E n E E W	80	s W n n E	40
56a	♂	W	S S S N w	80	N S N N N	100	w N e N w	40
51a	♂	S	n s n E E	40	E E E E s	80	W n E E E	80
49	♀	W	S S S e S	80	S S S N N	100	e N S N N	80
57	♂	E	e N N S w	60	S w w e w	20	e e e w S	20
N=6				Mean = 73%		Mean = 73%		Mean = 50%

For explanations, see Table A1.

Table A3. Testing for the physical principle underlying the chickens' magnetic compass: choices when high-frequency (HF) fields of 1.566 MHz are added to the static field

Bird	Sex	Training direction	Magnetic North = geographic East					
			Static field only		HF field, 480 nT added		HF field, 48 nT added	
			Choices*	%	Choices*	%	Choices*	%
36	♀	W	e S S S e e e e S S	50	N S e S w N w w w w	40	N S e S w N w w w w	40
35	♂	E	w S S e N S S N N N	80	S w N w w S e S w S	50	S N N S S e e e N w	60
44	♀	E	N e w S N N e N S N	70	e e w S N S e N e S	50	S S N e e S w N N e	60
56b	♀	S	W W n n n n E s W E	50	E n E n E n W E n E	60	s W W s W E W n E s	60
55	♂	S	W W E n W W s n E E	70	W W n n s s n W W W	50	W s n s E W n E n E	50
50b	♂	W	w w S S S N e S e e	50	e w S w e N N e S e	40	e N e e N e e S e S	40
45	♀	N	W s W W W W E s W W	80	W E E n E W E s W n	70	s s n n E s n W E s	30
51b	♀	N	W W n W W W E s E E	80	W n n W s s n W W n	40	n n n n n s E E n E	30
N=8			Mean = 66%		Mean = 50%		Mean = 46%	

For explanations, see Table A1.

Table A4. Testing for the physical principle underlying the chickens' magnetic compass: choices of chicks whose upper beak was locally anesthetized with xylocaine

Bird	Sex	Training direction	Magnetic North = geographic East			
			Without treatment		With local anesthesia	
			Choices	%	Choices	%
47	♂	W	e S N N S	80	S N e N w	60
46	♂	N	E E W E E	100	s E W E W	80
45	♀	S	W E n E n	60	E E E n s	60
50	♀	N	W W E E W	100	W s E s W	60
53	♂	S	s E E W s	60	E E W W W	100
54	♀	W	N N S w e	60	e N w S N	60
49	♀	W	S S S e S	80	N N S N N	100
56a	♂	W	S S S N w	80	w N S N N	80
N=8			Mean = 78%		Mean = 75%	

For explanations, see Table A1.

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