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The Magnetic Compass of Domestic Chicken, *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 chicken’s 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 towards higher intensities. Testing chickens under monochromatic 465 nm blue and 645 nm red light suggested a wavelength dependency, 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 anaesthesia of the upper beak, where iron-based structures have been described as potential magnetoreceptors, did not affect the number of correct choices, 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 chicken and small passerines use the same type of magnetic compass mechanism. This suggests that the avian magnetic compass 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*
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; 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 (W. Wiltschko & Merkel 1966).

Migratory behaviour of robins has also been used to analyze the functional properties of this compass mechanism and two surprising characteristics have become evident. Firstly, the robin's magnetic compass is an 'inclination compass', based on the (axial) course of the field lines and their inclination in space rather than on the polarity of the magnetic field (W. Wiltschko & 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 (W. Wiltschko 1968, 1978; W. Wiltschko et al. 2006).

Recent experiments have been focused on the physical mechanisms underlying the reception of magnetic compass information. The Radical Pair model (Ritz et al. 2000) proposed that the avian magnetic compass was 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 (i) magnetoreception should be light-dependent, and (ii) 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 and beyond, robins were disoriented (W. Wiltschko & Wiltschko 1995, 1999; Muheim et al. 2001). 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; R. Wiltschko et al. 2005). Magnetite, also found in birds in the ethmoid region and the upper beak (e.g. Beason & Brennon 1986; Hanzlick et al. 2000; Fleissner et al. 2003), on the other hand, does not seem to be involved in the processes providing passerine birds with compass information (e.g. Beason & Semm 1997; Munro et al. 1997; W. Wiltschko et al. 2006; R. Wiltschko et al., in prep.).

Meanwhile, a magnetic compass has been demonstrated in more than twenty species of birds (see R. Wiltschko & Wiltschko 1995 for summary; Bäckman et al. 1997; Gudmundson & Sandberg 2000). The vast majority are also 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 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 (see R. Wiltschko & Wiltschko 1995 for review). The only successful operant studies involved detection of changes in magnetic intensity and the presence or absence of a magnetic anomaly (Bookman et al. 1977; Mora et al. 2004; Thalau et al., in prep.) rather than magnetic directions. 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 this 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 by conditioning in an avian species that offered no suitable spontaneous directional behaviour.

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

**Material and Methods**

The experiments were performed in Armidale, NSW, Australia, during three testing periods. The series analyzing the biological window of the chicken's magnetic compass were begun in August 2005 and were completed in March 2006, when also the series testing for an effect of the local anaesthetic and of monochromatic lights took place, in part using the same chicks. The test series subjecting the chicken to high frequency fields was conducted in November 2005. Technical constrains and limits of time 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 55,400 nT, -62° inclination was undisturbed.

**Test animals, imprinting and housing**

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

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 10 days of age, 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 the 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 x 80 cm, 70 cm high) with wood shavings on the floor. At each corner, corresponding to magnetic North, South, East and West, were white screens (15 cm wide, 25 cm high) positioned perpendicularly to the centre, 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. 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 imprinting stimulus, 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 imprinting stimulus behind one of four screens, with an equal number of chicks trained to North, South, East and West, the series with the local anaesthetic being an exception. A chick was placed in the centre of the arena in a transparent plastic start cage (20 x 15 cm, 25 cm high) for 20 s next to the ball that had served as 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 approached to within 5 cm of the ball behind the screen, 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 minutes 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'. One minute after the chick had approached to within 5 cm of the ball, it was replaced in its home pen. If a chick failed to approach the ball within 3 minutes of release, it was replaced in the start cage and received a visual displacement trial before being replaced in its home pen. In order to take the axiality 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 approaching to within 5 cm of the screen concealing 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 and not used to determine whether criterion was reached.

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 of age. The procedure was similar to that used in the relocation trials, except for two aspects: (i) these tests were unrewarded, i.e. there was no ball behind the correct or the opposite screen, and (ii) 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 by 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 approached to within 5 cm of 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 the next test. If the chick failed to approach the ball within 3 minutes 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 tests conditions was randomised 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 anaesthesia 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 anaesthetic were performed one after the other (see below).

**Experimental conditions**

The experimental conditions 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 anaesthetic, we used three pairs of coils with their axes aligned horizontally in North-South, horizontally East-West direction and vertically. These coils could be operated independently to modify each component of the magnetic field separately. For the series testing 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° that allowed us to turn magnetic North to 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 make sure that the chicks were relying on the ambient magnetic field for locating the imprinting stimulus. This field with intensity like the local geomagnetic field (55,400 nT) 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:

(1) **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 27,700 nT and 83,100 nT, respectively. In the second part of the series, the intensity differences were 25%, with the respective intensities 41,600 nT and 69,300 nT.

(2) **Monochromatic lights.** To test for wavelength dependency of the chicken’s 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 light-emitting diodes (LEDs) mounted above the screens so that the light passed the 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 and 666 nm. The monochromatic lights were of about equal quantal flux, with the intensity of blue light in the arena being 0.60 W/m² and that of red light 0.45 W/m².
(3) **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.

(4) **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 hydrochlorid 2%, produced by AstraZeneca Pty Ltd., North Ryde, 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 twelve chicks were tested five or ten 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 ± 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 ($p' = \text{asin}(\sqrt{p}) \times 57.298$), as described by Sokal and Rohlf (1994), and analysed in a repeated measures ANOVA. The F-test was used to look for differences between the various test conditions.

**Results and Discussion**

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 4 and 25, with the mean ± SD 11.0 ± 4.9. The birds that, after a pause, were used in the Xylocaine series, needed only 2.9 ± 1.1 relocations to reach criterion again. The number of relocations between tests also varied between 1 and 9, with a mean of 1.8 ± 1.2.

**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. Table 1
summarises 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 field, only 47% and 42% of the choices, respectively, were on the correct axis, with the choices in these conditions two not different from chance (see Table 1). The difference between the performance 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 field (see Table 1). That is, the chickens showed significantly orientated searching behaviour in the test field with intensity like the local geomagnetic field, but were not oriented in the two other fields (Fig. 1, upper diagrams).

In the other series, the intensity of the stronger and the weaker field 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 searching behaviour occurred in the control field and in the 25% lower field, but not in the 25% higher field (Fig. 1, lower diagrams). 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).

The latencies, i.e. the time taken by the chickens from being released until reaching a screen and scoring, are included in Table 1, last columns. They vary greatly and do not differ between experimental conditions (50% series: \( F_{(2,22)} = 1.074, P = 0.359 \); 25% series: \( F_{(2,22)} = 0.421, P = 0.662 \). [IT WOULD BE INTERESTING TO SEE WHETHER LATENCY FOR CORRECT CHOICES WAS SHORTER THAN FOR INCORRECT CHOICES.]

These data demonstrate that the chicken's 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 observed window appears to be a somewhat asymmetric: its lower limit lay between 25 and 50% below the local field's intensity of 55 400 nT, whereas the upper limit was less that 25% above this intensity.

*Testing for the physical principle underlying the chicken's magnetic compass*

The Radical Pair model (Ritz et al. 2000) predicted that magnetoreception would be light-dependent and could be disrupted by high-frequency fields in the MHz-range (for details, see Ritz et
In view of this, we tested the chicken 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). Assuming a similar arrangement of receptors in chicken, we also performed tests with chicks whose upper beak was locally anaesthetized 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 the last testing period and could not be completed. Only six chickens were tested under monochromatic light and the distribution of their choices is given in Fig. 2, upper diagrams. Under 'white' light and monochromatic 465 nm blue light, 73% of their choices were on the correct axis; under 45 nm red light, only 50% of the choices were correct, suggesting oriented behaviour under 'white' and blue, but not under red. However, due to the small sample size of only 6 chicks, neither of the distribution tests differed from random (see Table 2, centre), and they do 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, centre).

Testing for an effect of oscillating fields in the MHz-range: Adding oscillating fields to the local geomagnetic field caused random searching (Fig. 2, centre). While the chickens performed 66% of choices on the correct axis in the control field, with 5 of the 8 birds performing above and 3 at chance level, the percentage of correct choices was only 45%, reflecting searching behaviour that was no longer oriented (Table 2, center). The difference between 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, lower diagrams): 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, lower section). 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 on which the chicks rely when searching for the correct screen.

The performance of the individual chicks in these three test series is given in the Tables A2 to A4 in the appendix.
Table 2, last columns, also include 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 which 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 alike, they need significantly longer to chose 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 are also significantly different 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 can be assumed that being suddenly in a monochromatic 'world' may be rather confusing for the chicks, with red having a stronger affect than blue because it additionally interferes with their ability to solve the task.

**General Discussion**

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

The chicken's 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 about 46,000 nT, the upper limit lay between 54,000 nT and 60,000 nT, while the lower limit lay between 43,000 and 34,000 nT, that is, between an increase of 17 to 30% and a decrease of 7 to 26% [CITE REFERENCE]. It is not necessarily asymmetric, as that of the chickens indicated in the present study, 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 underlyie both the compass mechanism of robins and that of chickens. The data obtained under monochromatic blue and red light from only six chicks do not allow a definite answer about a wavelength-dependency of the chicken's magnetic compass; the average percentage of correct choices under the various light conditions, however, are in agreement with a wavelength-dependency as found in European robins (W. Wiltschko and Wiltschko 1995, 1999) and two other species of passerines, the Australian silvereye, *Zosterops lateralis* (W. Wiltschko 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 the chicken's magnetic compass as a mechanism based on radical pair processes like that of robins (Ritz et al. 2004; Thalau et. al. 2005; R. Wiltschko 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 55,400 nT. A particularly sensitive resonance at the Larmor frequency indicates specific properties of the crucial radical pair (see in prep. for details). Robins also respond very sensitively to an oscillating field with the local Larmor frequency (in prep.), 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 anaesthesia and continued to prefer their migratory direction like untreated. With robins, there is also evidence that applying the anaesthetic the same way as it was applied in the present study can affect other responses, like 'fixed' direction responses, but it does not interfere with their normal magnetic inclination compass (R. Wiltschko et al., in prep.).

There is no direct evidence that the chicken's compass is 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. Indirect evidence, however, clearly indicates an inclination compass, as for any mechanism based on radical pair processes, would not be sensitive to polarity, but respond only to the axial course of the field lines.

Taken together, our analysis of the chicken's magnetic compass and the 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 was also found to be an inclination compass (Walcott and Green 1974; Visalberghi and Alleva 1978), probably with a similar light dependency as found in robins (R. Wiltschko et al. 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 at all closely related. The galliformes belong to an ancient line of birds, which separated from the more modern lines of birds as early as in 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, 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 non-migrating species like 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, and when some species began with seasonal movements, the existence of an efficient compass
mechanism may have facilitated covering extended distances. Originally, however, the magnetic compass must be assumed to have been developed as a mechanism for orientation within the home range, to allow the birds fast and efficient movements between nest feeding place, water etc., a function that it still serves today in non-migrants and migrants outside the migration seasons. The finding that even domestic chicken, after thousands of years of domestication (Fumihito et al. 1996) still has a well-developed magnetic compass points out the important role of this mechanism in the birds' everyday navigation tasks.

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To the Figures:

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

Fig. 2 Testing for the physical principle underlying the chicken's 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. Arrow heads indicate samples with a significant preference of an axis, rounded endings and a ring around the centre indicate random choices. Upper row: test under different light regimes; centre row: oscillating field of 1.566 MHz of two different intensities added; lower row: iron-containing structures in the upper beak deactivated by local anaesthesia (for numerical data, see Table 2).
Table 1. *Testing for a functional window: test at different magnetic intensities*

<table>
<thead>
<tr>
<th>Test condition: intensity</th>
<th>Tests per bird</th>
<th>mean ± SD</th>
<th>individuals with &gt;50% corr. choices</th>
<th>significant directional preference?</th>
<th>different from C?</th>
<th>mean ± SD</th>
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<tr>
<td>C1, like geomagnetic field</td>
<td>5</td>
<td>78 ± 13%</td>
<td>12 / 12</td>
<td>***</td>
<td>C1</td>
<td>35.6 ± 35.7</td>
</tr>
<tr>
<td>intensity 50% decreased</td>
<td>5</td>
<td>47 ± 16%</td>
<td>6 / 12</td>
<td>n.s.</td>
<td>**</td>
<td>38.9 ± 40.8</td>
</tr>
<tr>
<td>intensity 50% increased</td>
<td>5</td>
<td>42 ± 16%</td>
<td>4 / 12</td>
<td>n.s.</td>
<td>**</td>
<td>52.6 ± 68.9</td>
</tr>
<tr>
<td>C2, like geomagnetic field</td>
<td>5</td>
<td>72 ± 16%</td>
<td>12 / 12</td>
<td>***</td>
<td>C2</td>
<td>28.2 ± 29.1</td>
</tr>
<tr>
<td>intensity 25% decreased</td>
<td>5</td>
<td>75 ± 21%</td>
<td>11 / 12</td>
<td>**</td>
<td>n.s.</td>
<td>37.5 ± 32.7</td>
</tr>
<tr>
<td>intensity 25% increased</td>
<td>5</td>
<td>50 ± 13%</td>
<td>7 / 12</td>
<td>n.s.</td>
<td>*</td>
<td>29.6 ± 31.1</td>
</tr>
</tbody>
</table>

C1, C2, the control test of the two series; column 4 gives the number of individuals with more than 50% correct choices and, behind the dash, the number of individuals tested. 'significant directional preference' tells whether there was a significant preference of the correct axis by the Sign test, indicating oriented behaviour. The column 'different from C' indicates whether the distribution of choices was significantly different from that in respective control conditions by the F-test: **, p < 0.01; *, p < 0.05; n.s., not significant. 'Latency' indicated the time, in seconds, between release of the chick and its scoring by moving behind a screen.
Table 2. Testing for the physical principle underlying the chicken’s magnetic compass

| Test condition                  | Test per bird | mean ± SD     | chicks with >50% corr. choices | significant directional preference? | different from C? | latencies
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>correct directional choices</td>
<td></td>
<td></td>
<td></td>
<td>mean ± SD</td>
</tr>
<tr>
<td>C₃, ‘white’ light</td>
<td>5</td>
<td>73 ± 21%</td>
<td>5 / 6</td>
<td>n.s.</td>
<td>C₃</td>
<td>8.6 ± 4.6</td>
</tr>
<tr>
<td>465 nm blue light</td>
<td>5</td>
<td>73 ± 30%</td>
<td>5 / 6</td>
<td>n.s.</td>
<td>n.s.</td>
<td>24.3 ± 11.1</td>
</tr>
<tr>
<td>645 nm red light</td>
<td>5</td>
<td>50 ± 24%</td>
<td>2 / 6</td>
<td>n.s.</td>
<td>n.s.</td>
<td>51.3 ± 21.4</td>
</tr>
<tr>
<td>C₄, static field only</td>
<td>10</td>
<td>66 ± 14%</td>
<td>5 (3) / 8</td>
<td>*</td>
<td>C₄</td>
<td>55.2 ± 48.4</td>
</tr>
<tr>
<td>1.566 MHz, 480 nT</td>
<td>10</td>
<td>50 ± 11%</td>
<td>2 (3) / 8</td>
<td>n.s.</td>
<td>*</td>
<td>45.2 ± 31.4</td>
</tr>
<tr>
<td>1.566 MHz, 48 nT</td>
<td>10</td>
<td>50 ± 12%</td>
<td>3 (1) / 8</td>
<td>n.s.</td>
<td>*</td>
<td>46.7 ± 33.6</td>
</tr>
<tr>
<td>C₅, no treatment</td>
<td>5</td>
<td>78 ± 17%</td>
<td>8 / 8</td>
<td>**</td>
<td>C₅</td>
<td>22.9 ± 31.7</td>
</tr>
<tr>
<td>local anaesthesia</td>
<td>5</td>
<td>75 ± 18%</td>
<td>8 / 8</td>
<td>**</td>
<td>n.s.</td>
<td>55.5 ± 37.9</td>
</tr>
</tbody>
</table>

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