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The mechanism of the avian magnetic compass

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Abstract

The avian magnetic compass was analyzed by testing migratory birds, using their orientation as an indicator. These tests revealed some remarkable properties of the avian magnetic compass: (1) It is an 'inclination compass', (2) it is light-dependent, with (3) receptors located in the right eye. These characteristics are in agreement with the Radical Pair model proposed by Ritz et al. (2000). Using the same experimental set-up, we tested the model by 'behavioral spectroscopy', exposing migratory birds to radio-frequency fields of different frequencies and intensities. Such fields affected the orientation only when applied at an angle to the field lines. Tests with different frequencies led to an estimate of the life time of the crucial radical pair between 2-10 μ s. We also could identify an extremely sensitive resonance at the Larmor frequency, which implies specific properties of the radical pair. Cryptochromes, a blue-light absorbing photopigment, has been proposed to be the receptor-molecule; it has been found to be present in the retina of birds.

Keywords: Magnetic compass, inclination compass, Radical Pair model, Larmor frequency, cryptochrome

1. Introduction

The geomagnetic field is an omnipresent feature of the earth, with its poles close to, but not identical with the rotational poles. The field lines leave the earth at the southern magnetic pole, run around the earth, being horizontal at the magnetic equator, and re-enter it at the northern magnetic pole; hence they point upward in the southern and downward in the northern hemisphere. Magnetic intensity shows north-south gradients, ranging from about 65 μ T (microTesla) near the poles to below 30 μ T near the magnetic equator [1].

For animals able to perceive the geomagnetic field, it represents a reliable, always available source of navigational information. In particular, it indicates directions, providing them with a 'magnetic compass' [2].

2. The Avian Magnetic Compass

To demonstrate that an animal uses the geomagnetic field as a compass, one must show that its orientation depends on the direction of the ambient magnetic field and compare its behavior in the geomagnetic field with that in a field with magnetic north altered.

2.1. Demonstrating magnetic compass orientation in birds

First evidence for magnetic compass orientation in animals came from European Robins, *Erithacus rubecula* (Turdidae). This small passerine bird is a nocturnal migrant: it breeds all over Europe and the northern populations spend their winter in the Mediterranean countries. During migration season, their behavior is controlled by a spontaneous tendency to fly at night into their migratory direction - slightly west of south in autumn and slightly east of north in spring. This innate urge is so strong that even captive birds head into the respective direction in their cages, thus providing a solid baseline for experiments.

Migratory birds are tested in round cages, recording their spontaneous activity. The type of cage most commonly used today is funnel shaped, and its inclined walls are covered with special paper where the birds leave marks as they move, thus documenting the distribution of their movements. These marks are counted to obtain the direction in which the bird was heading. Within the limited space around the cage, the magnetic field can be altered with the help of coil systems in various ways.

Tested in a field with magnetic north shifted, but with the same intensity as the geomagnetic field (see 2.2), the robins responded with a corresponding shift in their headings (Fig.1). This clearly showed that they used the magnetic field for orientation [3]. Meanwhile, magnetic compass orientation has been demonstrated in a number of other birds species, in migrants based on their spontaneous directional preferences during migration, in non-migrants like Zebra finches, *Taeniopygia guttata* (Estrildidae), [4] and Domestic chickens, *Gallus gallus*, [5] using the method of directional training (for review, see [6]).

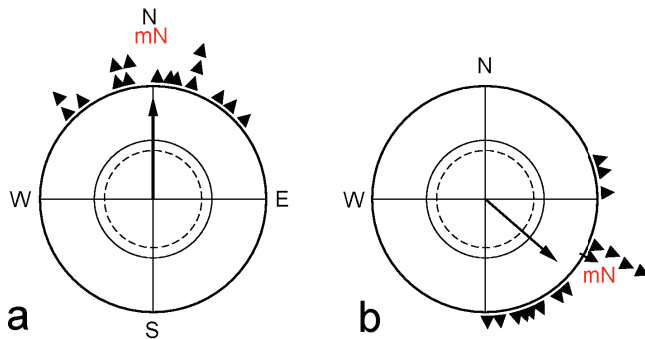


Fig.1. Orientation behavior of migrating European Robins in spring, tested in (a) the local geomagnetic field and (b) an experimental fields with magnetic North shifted by 120° to East-Southeast with the help of Helmholtz coils. mN, magnetic North. The triangles at the periphery of the circle mark mean headings of individual birds, the arrows represent the grand mean vectors with their lengths proportional to the radius of the circle. The two inner circles are the 5% (dashed) and the 1% significance border of the Rayleigh test indicating difference from a random distribution (after [3]).

2.2. Functional Properties of the Avian Magnetic Compass

Using migratory orientation as a criterion whether or not birds could obtain directional information from the magnetic field and how they interpreted this information, the functional properties of the avian magnetic compass were analyzed by testing birds in a variety of experimental magnetic fields, using the methods described above. It was found to differ from our technical compass in several important aspects:

A first important difference is that it is an 'inclination' compass. In a magnetic field with the vertical component inverted, birds reversed their headings, in spring preferring magnetic South instead of magnetic North, whereas they preferred the same direction as in the local geomagnetic field when both components were reversed [7]. These observations indicate that the functional principle of the robins' magnetic compass is fundamentally different from that of the technical compass: it does not respond to polarity, but instead relies on the axial course of the field lines, using their inclination to distinguish between the two ends (Fig.2). This means that the avian magnetic compass does not indicate magnetic North and South, a distinction based on polarity, but 'poleward', where the field lines are inclined to the ground, and 'equatorward', where they are inclined upward (Fig.2). The same type of mechanisms has been found in all other birds species tested for it so far [6].

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 our 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 intensities was decreased or increased by about 30%, indicating a narrow functional window [2,6]. The disorientation in higher fields was especially surprising, because it clearly showed that the loss of

orientation was not caused by the intensity getting below threshold. Further tests showed that the functional window is flexible and can be adjusted to intensities outside the normal functional range. Robins regained their ability to orient when they are exposed to lower or higher intensities, with an exposure of about 1 h at 92 μT sufficient to enable them to orient at this intensity [8]. At the same time, the birds did not lose their ability to orient in the local geomagnetic field. This adjustment 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 [2, 6].

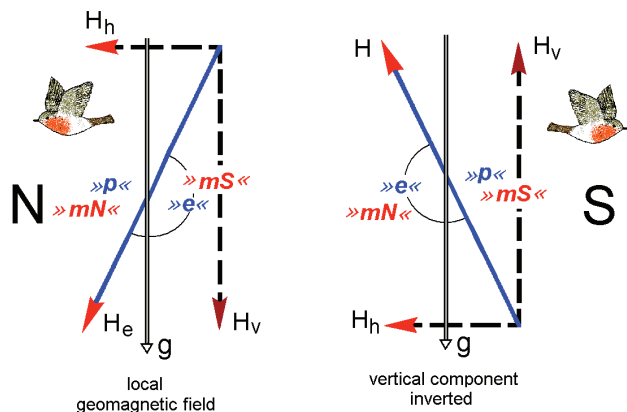


Fig.2. Schematic section through the geomagnetic field from the west to illustrate the functional mode of the inclination compass. N, S, North and South; H_e , vector of the geomagnetic field; H, vector of the experimental field, H_h , H_v , horizontal and vertical components of the magnetic fields, g, gravity vector. The arrow heads indicate the polarity of the fields, with »mN«, »mS«, indicating magnetic North and magnetic South, respectively. 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. The birds fly towards the directions that they assume to be their spring migratory direction.

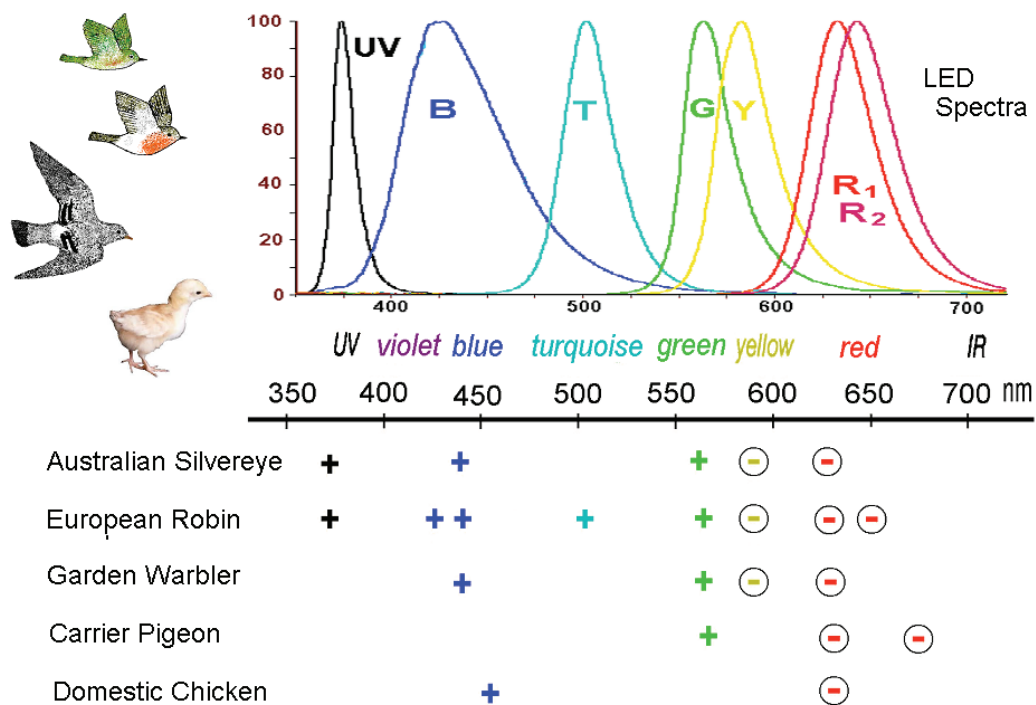


Fig.3. Wavelength dependency of the avian magnetic compass. Above: spectra of the light-emitting diodes used in the tests; below: orientation of five birds species tested, with + indication oriented behavior and \ominus indicating disorientation (data from [5, 9-13] and unpublished).

Another important characteristic of the avian magnetic compass is its light-dependency. Normal compass orientation requires light from the short-wavelength part of the spectrum. European robins and Australian silvereyes, *Zosterops l. lateralis*, are well oriented in their migratory directions under 373 nm UV, 424 nm blue, 502 nm turquoise and 565 nm green light. Under 590 nm yellow and beyond, they were disoriented (Fig.3), indicating that their magnetoreception system works no longer properly under longer wavelength [6, 9, 10]. This pattern seems to be common to passerine species [11], homing pigeons, *Columba livia f. domestica* [12], and domestic chickens [5].

The experiments mentioned above used low intensity monochromatic light of a quantal flux of about $7 \cdot 10^{15}$ quanta / s m² as found 45 min before sun rise and after sunset (only with UV, the intensity was about $0.7 \cdot 10^{15}$ quanta / s m², i.e. 1/10). Under monochromatic light of higher intensities and under bichromatic light, migratory birds no longer prefer their migratory direction [13]. However, birds are able to use their magnetic compass also under high light levels, provided the light is 'white', i.e. composed of a wide variety of different wavelengths - the magnetic compass can be used e.g. by homing pigeons in bright daylight.

3. The Mechanism underlying the Avian Magnetic Compass

A number of models for magnetoreception based on fundamentally different principles have been proposed, the three most prominent ones being (i) induction, (ii) processes involving magnetic material and (iii) interactions of chemical processes with the ambient magnetic field. Induction would be restricted to marine animals because it requires sea water as a surrounding medium with high conductivity; the other two models are more general and would also serve terrestrial animals and those living in fresh water. Here we focus on the third type of model, because experimental evidence supports the assumption that it applies to the magnetic compass of birds.

3.1. The Radical-Pair Model

The Radical-Pair model, first proposed in the 1980s [14] and detailed in 2000 by Ritz and colleagues [15], postulates a 'chemical compass' based on direction-specific interactions of specialized photopigments with the ambient magnetic field. We need not go into details here, as it is described and discussed comprehensively in the paper by Thorsten Ritz (this volume), but will just briefly summarize the points that are important for understanding the mechanism of the avian magnetic compass.

In the initial step, photon absorption leads to the transfer an electron. Donor and acceptor form singlet radical pairs, which, by interconversion, in part turn into triplet pairs. The magnetic field alters the dynamics of the transition so that the triplet yield depends on the alignment of the receptor-molecule in the ambient magnetic field (for details [15] and Ritz, present volume) – it can thus convey information on magnetic directions. To obtain this information, birds must compare the yields in different spatial directions. This requires orderly arrays of the specialized photopigments oriented in the various directions. Ritz and colleagues [15] hence suggested that the respective magnetoreceptors might be located in the eyes, because the required conditions could be met by their spherical shape and the arrangement of receptors: light is available, and radical-pair processes would generate characteristic activation patterns across the retina. These patterns would be centrally symmetric to the axis of the field lines and could enable animals to detect the direction of the magnetic field.

The radical pair model was very attractive for biologists, because it could readily explain the observed characteristics of the avian magnetic compass. A wavelength dependency would result from the absorption range of the photopigment involved, and since radical-pair reactions are axial rather than polar, the proposed mechanism would results in an inclination compass, ignoring polarity. The model can also explain the functional window and the ability to adjust to other intensities: the patterns formed on the retina not only depend on the direction, but also on the intensity of the magnetic field, with different intensities leading to somewhat different patterns. Yet the patterns would always retain their central symmetry with respect to the magnetic vector, so that birds, confronted with a new, unfamiliar pattern, could learn to interpret this pattern after a while.

But aside from accounting for the known characteristics of the avian magnetic compass, the model allowed a number of predictions that could be tested.

3.2. Testing the Model

When the radical pair model was first proposed, the location of the receptors mediating directional information from the magnetic field was not yet known. Meanwhile, we know that the prediction of Ritz and colleagues [15] are true. Experiments testing European 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 [16]: monocular birds that had to rely solely on their right eye were just as well oriented in their migratory direction as when they had both eyes open, whereas they were disoriented when they had to rely on their left eye alone. The same lateralization in favor of the right eye was found in Australian silvereyes [17] and domestic chickens [18].

The model allows another prediction that can be experimentally tested: if the relative singlet or triplet yield were crucial for magnetoreception, then interfering with the singlet-triplet interconversion should alter the output of the receptor markedly and thus should disrupt magnetoreception. Hence a diagnostic test aimed at obtaining more direct evidence for a radical-pair mechanism possibly underlying the avian magnetic compass made use of the fact that the singlet-triplet interconversion can be significantly affected by radio-frequency oscillating fields in the MHz range [15]. The effect of these fields would depend on their frequency and on their orientation with respect to the static background field. First critical tests were performed with migratory birds, again using orientation in migratory direction as an indicator whether or not the reception of magnetic compass information was disrupted. European robins, tested under the influence of radio-frequency fields of 7.0 and 1.315 MHz with an intensity of 480 nT were oriented when these fields were presented parallel to the geomagnetic vector, whereas they were disoriented when the same fields were presented at an angle to the geomagnetic field (Fig.4) [19,20]. This clearly shows that the observed effect of the radio-frequency fields was a specific one. Similar experiments with radio-frequency fields showed that two non-migratory bird species, domestic chickens and zebra finches, also have a magnetic compass based on radical-pair processes [5, 21].

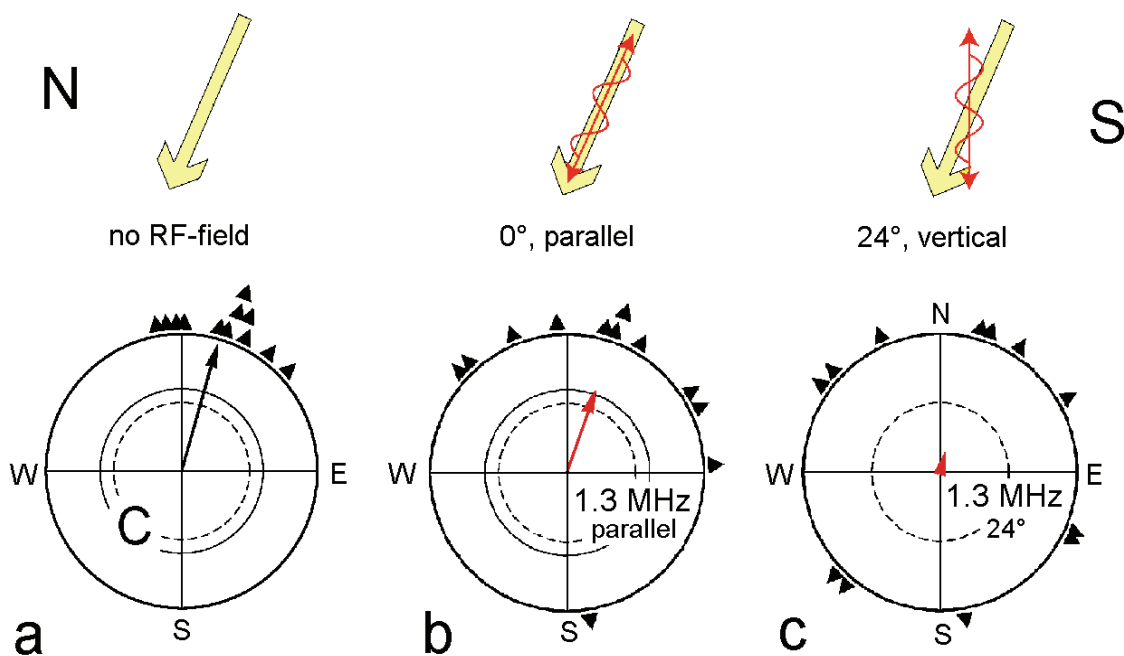


Fig.4. Orientation of European Robins in spring. (a) in the geomagnetic field alone (Control, C) and with radio-frequency fields added to the geomagnetic field in two different orientations (b, c). The *upper part* of the diagram illustrates the orientation of radio-frequency fields with respect to the geomagnetic field (open arrow) in the three test conditions; symbols in the circular diagrams as in Fig.1 (from [20], modified).

3.3. 'Behavioral Spectroscopy'

By exposing migratory robins to oscillating magnetic fields of different frequencies and intensities and again using their orientation as an indicator of whether or not they could derive directional information from the magnetic field under the given conditions, we were able to identify characteristic of the receptor molecule by behavioral means.

When we tested robins under oscillating fields of different frequencies with an intensity of 480 nT added to the geomagnetic field at an angle of 24° , we found that they were normally oriented in frequencies up 0.05 MHz. When exposed to 0.10 and 0.50 MHz, however, their behavior became axial, indicating that they had problems with obtaining directional information. From 0.65 MHz onward, they were disoriented (Fig.5). From these data, we could estimate the lifetime of the crucial radical pair to be in the range of 2-10 μs [22], a lifetime that appears to be sufficiently long to allow biological responses.

Testing robins at 0.65, 1.315 and 2.63 MHz at different intensities, we found a sharp resonance at 1.315 MHz, the Larmor frequency in the local geomagnetic field of about $46 \mu\text{T}$: while radio frequency fields of 150 nT no longer disrupted magnetic compass orientation at 0.65 and 2.63 MHz, a field of only 15 nT (roughly 1/3000 of the intensity of the local geomagnetic field) proved disruptive at 1.315 MHz. A shift of this resonance to 2.63 MHz when the static field was doubled to an intensity of $92 \mu\text{T}$ shows that this was indeed a resonance at the Larmor frequency (Fig.6) [22].

The occurrence of a strong resonance at the Larmor frequency is not a common feature of radical pairs; theoretical calculations indicated that such a resonance is to be expected only in rather special radical pairs [22], suggesting a specialized mechanism underlying the avian magnetic compass. It allowed theoreticians specific conclusions about characteristics of the crucial radical pair, which are discussed in detail by Thorsten Ritz in the present volume.

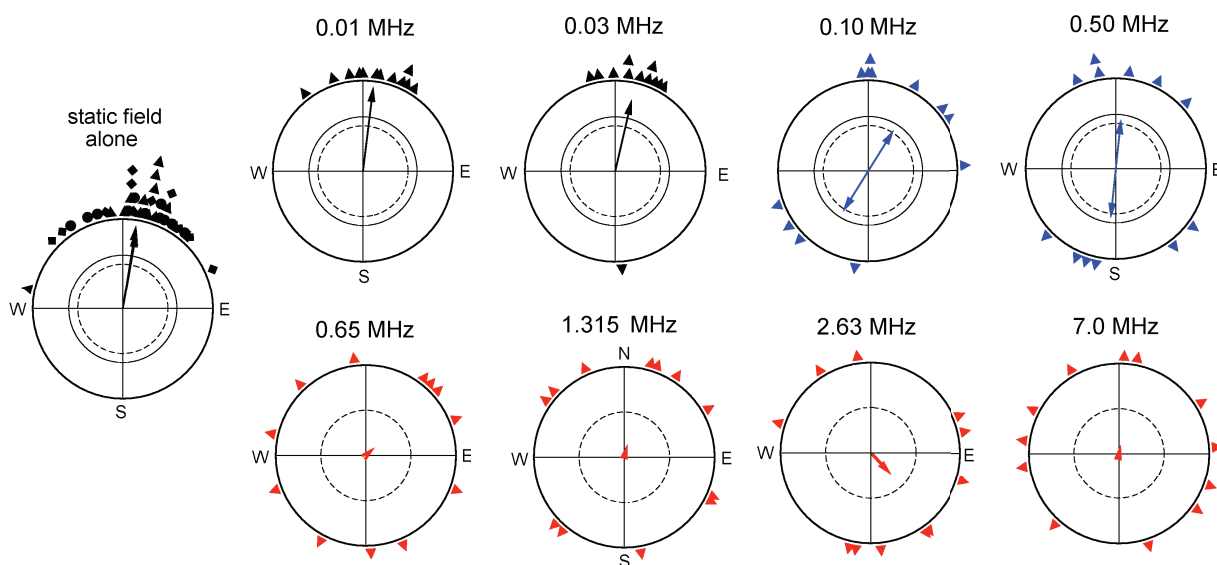


Fig.5 Orientation behavior of European robins in the geomagnetic field and with oscillating fields of different frequencies added, their intensity being 480 nT. Symbols in the circular diagrams as in Fig.1 (from [22]).

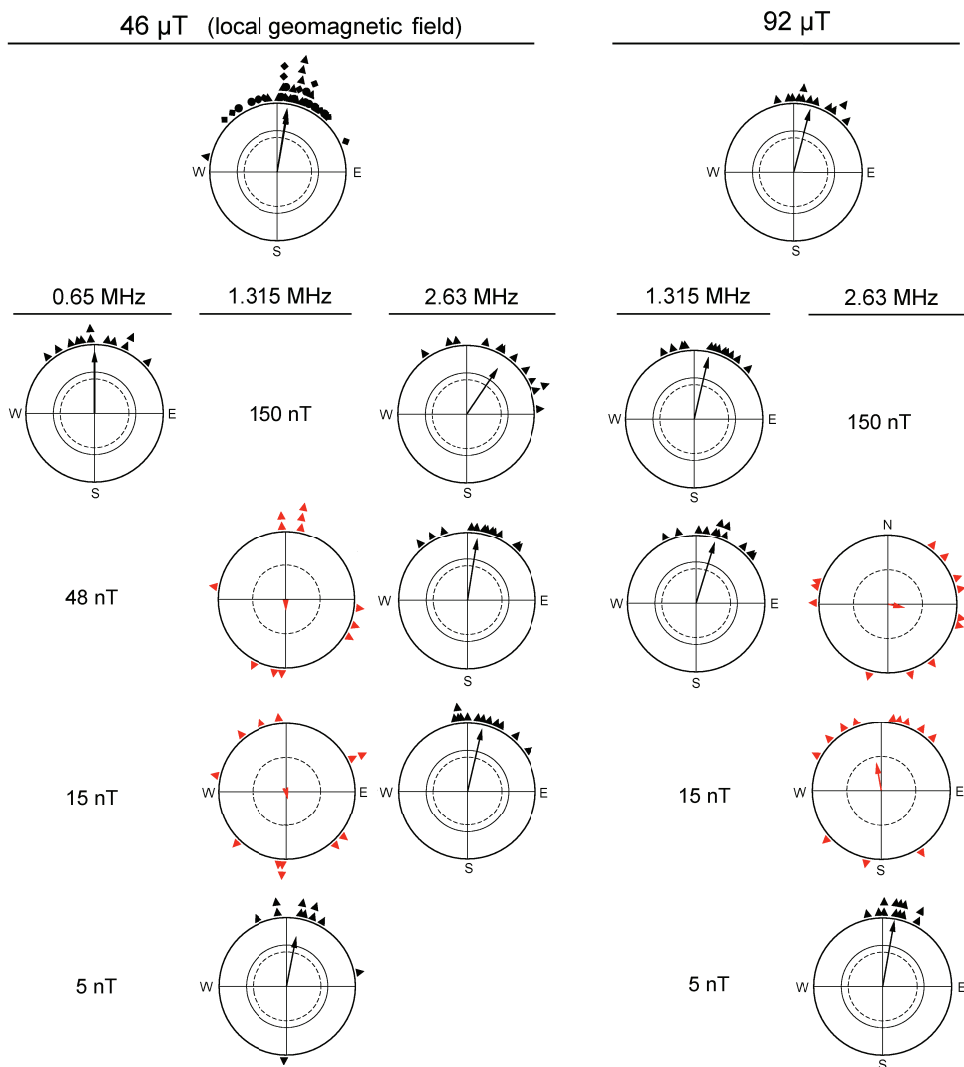


Fig.6. Orientation behavior of European robins in static fields and with oscillating fields of 0.65, 1.315 and 2.63 MHz with different intensities added. Symbols in the circular diagrams as in Fig.1 (from [22]).

3.4. The Receptor-Molecule

This leaves the question about the receptor-molecule. The opsins, the pigments mediating visual information, cannot be involved, because here, photon absorption leads to a change in configuration - they do not form radical pairs. Ritz and colleagues [15] therefore suggested cryptochromes, another class of photopigments that possess the chemical properties crucial for the model. These photopigments are known from plants, but also occur in animals where they are involved in the internal clock (see [23] for review). In vertebrates, they were found first in mammals, but also in chicken [24, 25] and passerine birds [26-28], where they occur in the retina, i.e. at a place where one would expect them if they were involved in magnetoreception (for review, see [29]).

Cryptochromes are blue-light receptors, with a flavin and a pterin as photoactive cofactors. During photoreduction, they absorb short-wavelength light and form radical pairs [30]; they also form radical pairs during re-oxidation, which might be the crucial reaction for the avian magnetic compass (see [22] and Ritz, present volume, for discussion). The lifetime of the cryptochrome radical pair is sufficiently long to allow biological interactions [29]. Cryptochromes thus possess the general properties required to be affected by magnetic field. Cryptochrome-controlled processes, like hypocotyl growth and anthocyanin accumulation in plant seedlings, have been found to be affected by magnetic fields [31]. However, to act as receptor molecule for the avian magnetic compass, all cryptochromes within one cell would have to be aligned in the same direction to act as a unit, and the different receptor cells would have to be positioned in a way that they represent all spatial directions to allow a comparison between these directions. A recent immunohistological study [32] found Cryptochrome 1a in ordered bands along the membrane disks in the outer segment of the ultraviolet/violet single cones in chickens and robins. The ultraviolet/violet cones are present all across the retina, thus being aligned in the different spatial directions. With this distribution, cryptochrome 1a fulfills the above-mentioned conditions of the Radical-Pair model, supporting the idea that it is indeed the receptor-molecule of the avian magnetic compass.

4. Conclusions

After the first discovery that birds can derive directional information from the geomagnetic field, their 'magnetic sense' remained enigmatic, and the lack of knowledge on magnetoreception caused considerable skepticism against magnetic orientation in general. In the last decade, however, starting with the publication of the radical-pair model, we have begun to understand the physical bases of avian magnetoreception: the magnetic compass of birds is based on a radical-pair mechanism, making use of a physical principle sciences has become aware of only in the second half of the 20th century. Direct evidence which receptor molecule forms the crucial radical pairs is still lacking, but indirect evidence accumulates indicating that it is a cryptochrome, in particular Cryptochrome 1a.

Altogether, a magnetic inclination compass has been shown in all bird species tested for it, which are more than ten species; light-dependency of this compass is indicated in five species (see Fig.3). An underlying radical-pair mechanism has so far been demonstrated in three bird species only, in domestic chickens and two passerines [5, 19, 21]. This is interesting, since chickens and passerines belong to two different lineages of birds that phylogenetically separated already 95 million years ago in the early Late Cretaceous [33]. Finding the same type of magnetic compass in these different species suggests that it evolved already in the Mesozoic in the common ancestors of birds and has been passed down to their modern-day descendants.

Acknowledgements

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