# Progress in Studies of Geomagnetic Navigation of Animals

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*The geomagnetic field may play a key role in orientation and navigation of many long-distance migratory animals. Taking homing and migrating birds as examples, this paper reviews recent progress in studies of geomagnetic "compass" of animals. Moreover, we propose to address two aspects in future geomagnetic orientation research: (1) what are the true components of the "map"? (2) What are the magneto-receptors and which brain areas acquire and process the geomagnetic field information?*

**Key words** geomagnetic orientation, birds, neurophysiology, magneto-receptors

It is well known that many birds seasonally migrate to a distant region every year, such as swallows. Some turtles and salmons also navigate long distances back home. The spiny lobsters are capable of returning to the collection site when they are displaced to unfamiliar locations. How do these animals determine position and direction to their destinations, in particular, in the open sea? Field and laboratory experiments indicate that some animals more or less rely on geomagnetic information in orientation and navigation.

Studies on avian navigation began at the end of the 19th century in order to explain birds' mysterious direction-sense. The earliest explanations for geomagnetic compass orientation were brought forward by two persons: von Middendorff[1] suggested that migrating birds determine direction according to magnetic meridian, which means the birds use magnetic compass in navigation. Viguier[2] pointed out the birds might use the total intensity and inclination of the geomagnetic field, which composed the magnetic "map" factors, to determine their position relative to home. But the first hypotheses were largely disregarded until 1968, the magnetic map effects have been found in European robins by W. Wiltschko[3]. The European robins which were placed in cages often tended to orient toward the side of the cage corresponding to the normal migration direction. This observation suggested a new approach to the elusive problem of migratory orientation. According to the special behavior, Emlen et al.[4] exploited a funnel apparatus which consisted of a blotting paper funnel, an ink pad base, and a screen top (a square of one-half inch mesh hardware cloth caps the funnel). A bird in migratory condition placed inside the bottom of the funnel finds itself surrounded by outwardly sloping walls of white blotting paper. At frequent intervals the bird hops forward onto the sloping white paper, only to slide back and continue its pointing and quivering. Such hops from an ink pad leave clear black prints on the blotting paper and it is the accumulation of these inked footprints which produces the orientation record of the bird's activity. Today the traditional Emlen funnel has been replaced by a computer-controlled version of the Emlen funnel which enables the experimenter to manipulate relevant orientation cues indoors. The Emlen funnel has been a very important tool in the study of bird orientation and navigation. In 1968, Wiltschko[5] used this apparatus to prove that European Robins made use of the magnetic field to detect the north direction.

Another direct evidence of birds' geomagnetic navigation is that pigeon's homing behavior can be affected by attached magnets. The experimenters divided pigeons into two groups: one group wore a magnet bar glued to the back, and the control group wore equally weighted brass bars. These pigeons were released from unfamiliar sites. Results indicated that the pigeons in the magnet-carrier group often resulted in disorientation under total overcast; while the pigeons in the control group succeeded in returning home, which strongly suggested the magnets did cause disorientation[6].

It should be pointed out that magnetic compass is a second compass mechanism available to birds. Generally, the Sun and the polarized light compass are the first choice[7]. But under total overcast, birds only rely on the magnetic compass and during the premigratory period, the birds also use the magnetic compass. So it is obvious that the magnetic field may play a key role in orientation and navigation of migrating birds.

How do the birds use the geomagnetic information? Kramer[8] proposed a "map-and-compass" model. This model describes homing as a two-step process: In the first step, the "map" step, the bird determines the direction to the goal as a compass course (in other words: the first step produces a specification equivalent to "south" or "west" in human terms); In the second step, the "compass" step, a compass is used to locate this course, that is into a specification of the type "this way" or "go there". Kramer's model still forms the main basis of our present concept on avian homing and navigation. But in this model, components of the "map" in the first step still remain entirely open. Coriolis force, magnetic vertical intensity and specific distributions of odors and so on have been proposed, but so far neither of them have been experimentally proved. The geomagnetic parameter cues are extensively regarded as the most likely component. We proposed that more experiments are needed in future to prove or deny any above navigational cues.

Although migrating birds have been proved to make use of the magnetic field in navigation by many behavioral experiments, the physiological basis of navigation and the mechanisms of magnetoreception remain unknown. Two types of potential magnetoreception mechanisms have been suggested over the past decades: one is magnetite-based magnetoreceptor and the other mechanism is based on photoreceptors forming radical-pair intermediates. Previous findings suggested that magnetite crystals in the upper beak of homing pigeons are the potential source of navigational map information[9]. Electrophysiologic recordings from this nerve indicated that the frequency of the nervous impulses modified by intensity changed of the magnetic field and this nervous connection maybe carry magnetosensory information from receptors in the beak to the brain[10]. This supports the magnetite-based mechanism. However, this mechanism is recently defied by other experiments. For example, no changes in magnetic alignment of magnetite receptors were observed in weak oscillating fields with frequencies higher than 100 KHz. Furthermore, Ritz et al.[11] found that Robins exposed to a 7 KHz oscillation field exhibited seasonally appropriate migratory orientation when the oscillation field was parallel to the geomagnetic field, but were disoriented when it was presented at a 24° or 48° angle. These results are consistent with a resonance effect on singlet-triplet transitions and suggest a magnetic compass based on a radical-pair mechanism. In the radical-pair mechanism, the magnetic field alters the dynamics of transitions between spin states, after the creation of a radical pair through a light-induced electron transfer. Through this pathway, birds can rapidly respond to the change of the geomagnetic field as the birds can "scan" the field. Molecular evidence further supports the radical-pair mechanism. The cryptochromes (CRYs) have been suggested as the most likely candidate class of molecules. Mouritsen et al.[12] show that one CRY1 and one CRY2 exist in the retina of migratory garden warblers and the gwCRY1 is concentrated in specific cells, particularly in ganglion cells, which also shows high levels of neuronal activity at night when garden warblers perform magnetic orientation. In addition, there seem to be striking differences in CRY1 expression between migratory and nonmigratory songbirds at night. Consequently, cytosolic gwCRY1 is well placed to possibly be the primary magnetic-sensory molecule required for light-mediated magnetoreception.

In general, little is known about the parts of the brain involved in processing navigational information, which requires combining multimodal input. Bingman et al.[13] summarized the potential role of some brain regions, in particular the hippocampal formation. From neuroanatomy of magnetoreception, Němec et al.[14] found that the superior colliculus contains neurons that are responsive to magnetic stimuli. But until now the neural substrate subserving magnetic orientation is largely unknown in vertebrates. We believe that in the future, the pathways of acquiring and processing geomagnetic information in animals will be uncovered by the combined efforts of biologists, physicists and other subject experts.

Recently, studies on geomagnetic navigations have been extensively involved in many passerines and non-passerines. Some similar important progress hasalso been made in other animals, for instance, spiny lobsters[15], sea turtle[16], ants[17] and blind mole rats living under the dark[18,19]. More animals are being experimentally examined whether or not to rely on the geomagnetic field in orientation and navigation.

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**References**

[1] Von Middendorff A. Die Isepiptesen Rußlands. Mém Acad Sci St Petersbourg VI Ser Tome, 1859, 8:1—143.

[2] Viguier C. Le sens de l'orientation et ses organes chez les animaux et chez l'homme. Rev Phil France Etranger, 1882, 14:1—36.

[3] Wiltschko W. Über den Einflu-2 statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). Zeitschrift Für Tierpsychologie, 1968, 25:536—558.

[4] Emlen S. T. et al. A technique for recording migratory orientation of captive birds. The Auk, 1966, 83:361—367.

[5] Wiltschko W. et al. Magnetic compass of European robins. Science, 1972, 176:62—64.

[6] Keeton W. T. Magnets interfere with pigeon homing. Proceedings of the National Academy of Sciences USA, 1971, 68:102—106.

[7] Able K. P. et al. Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarization. Nature, 1993, 364:523—525.

[8] Kramer G. Wird die sonnenhöhe bei der Heimfindeorientierung verwertet? Journal für Ornithologie, 1953, 94:201—219.

[9] Beason R. C., Nichols J. E. Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. Nature, 1984, 309:151—153.

[10] Fleissner G. et al. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. The Journal of Comparative Neurology, 2003, 458:350—360.

[11] Ritz T., Thalau P., Phillips J. B. et al. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. Nature, 2004, 429:177—180.

[12] Mouritsen H., Janssen-Bienhold U., Liedvogel M. et al. Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. PNAS, 2004, 101:14294—14299.

[13] Bingman V. P. et al. Neuroethology of avian navigation. In: Balda R P, et al. eds. Animal Cognition in Nature. San Diego: Academic Press, 1998. 201—222.

[14] Němec P. et al. Neuroanatomy of Magnetoreception: The Superior Colliculus Involved in Magnetic Orientation in a Mammal. Science, 2001, 294:366—368.

[15] Boles L. C. et al. True navigation and magnetic maps in spiny lobsters. Nature, 2003, 421:60—63.

[16] Lohmann K. J. et al. Geomagnetic map used in sea-turtle navigation. Nature, 2004, 428:909—910.

[17] Acosta-Avalos D. et al. Seasonal patterns in the orientation system of the migratory ant *Pachycondyla marginata*. Naturwissenschaften, 2001, 88:343—346.

[18] Burda H. et al. Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae, Rodentia). Experientia, 1990, 46:528—530.

[19] Kimchi T. et al. A subterranean mammal uses the magnetic compass for path integration. PNAS, 2004, 101:1105—1109.