RESEARCH ARTICLE

Bats Respond to Very Weak Magnetic Fields

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Abstract

How animals, including mammals, can respond to and utilize the direction and intensity of the Earth’s magnetic field for orientation and navigation is contentious. In this study, we experimentally tested whether the Chinese Noctule, Nyctalus plancyi (Vespertilionidae) can sense magnetic field strengths that were even lower than those of the present-day geomagnetic field. Such field strengths occurred during geomagnetic excursions or polarity reversals and thus may have played an important role in the evolution of a magnetic sense. We found that in a present-day local geomagnetic field, the bats showed a clear preference for positioning themselves at the magnetic north. As the field intensity decreased to only 1/5th of the natural intensity (i.e., 10 μT; the lowest field strength tested here), the bats still responded by positioning themselves at the magnetic north. When the field polarity was artificially reversed, the bats still preferred the new magnetic north, even at the lowest field strength tested (10 μT), despite the fact that the artificial field orientation was opposite to the natural geomagnetic field (P<0.05). Hence, N. plancyi is able to detect the direction of a magnetic field even at 1/5th of the present-day field strength. This high sensitivity to magnetic fields may explain how magnetic orientation could have evolved in bats even as the Earth’s magnetic field strength varied and the polarity reversed tens of times over the past fifty million years.

Introduction

Many animals rely on the Earth’s magnetic field for spatial orientation and navigation, especially migratory species of birds [1, 2] and pigeons [3], fish [4–6], insects [7, 8], sea turtles [9, 10], lobsters [11, 12], and bats [13, 14]. Nevertheless, it is poorly understood how they respond to changes of the geomagnetic field when the magnetic field strength is much weaker than at present-day, for example, during geomagnetic polarity reversals (the positions of magnetic north and magnetic south are interchanged) or geomagnetic excursion (a short-lived variation colatitude of the virtual geomagnetic pole is greater than 45 degrees from previous position).
The intensities of the present-day geomagnetic field vary between 23 μT at the equator and
66 μT at polar regions [15]. Paleomagnetic studies have shown that dipolar field intensity may
drop to 10% during geomagnetic polarity reversals or geomagnetic excursions [16–20]. Hence,
such dramatic changes of the strength and direction of the geomagnetic field may pose a signif-
icant challenge for the evolution of any magnetic orientation in organisms.

Recently, Winklhofer and co-workers found that the avian magnetic compass could be
tuned to respond to very low magnetic intensities, even down to 4 μT, indicating the consider-
able plasticity of the avian magnetic compass [21]. It is unknown, however, if mammals can
also detect such weak magnetic fields. Bats are the second most abundant order of mammals
and possess excellent flying skills. Similar to birds, many bats also migrate over large distances,
crossing over a wide range of latitudes where geomagnetic field strengths and directions vary.
Since bats originated in Laurasia in the early Eocene (52–50 Mya) [22], bats have experienced
tens to hundreds of geomagnetic polarity reversals and geomagnetic excursions [23–25]. Since
the last Brunhes-Matuyama reversal at 780 ka B.P., there were more than ten geomagnetic ex-
cursions [26]. Hence the question emerges if bats (and other mammals) could have responded
to the changes of the geomagnetic field in the past (and if they will be able to do so in the
future).

A pioneering study on magnetoreception in bats [13] found that big brown bats (Eptesicus
fuscus) used the Earth’s magnetic field as compass in displacement studies. An independent
laboratory investigation demonstrated that the Chinese noctule (Nyctalus plancyi), responded
to the polarity of the magnetic field while roosting [14]. Recent works revealed that bats could
calibrate their magnetic compass using polarization cues at sunset [27, 28]. These behavioral
data strongly suggest that bats use magnetic compass for orientation (during migration as well
as while roosting). Very limited data suggest that bats may have specialized sensory cells that
contain freely rotating magnetite (Fe3O4) particles, which may serve as magnetic sensors in bat
head [29, 30].

It is still unclear, however, whether bats can sense directional changes and weak field
strengths that were associated with either geomagnetic polarity reversals or geomagnetic excur-
sions. Therefore, in this study we attempted to tackle the enigmatic question if a bat can sense
weak geomagnetic fields. The Chinese noctule, Nyctalus plancyi, which is endemic to China, is
a fast aerial hawking bat that migrates to its breeding sites in March from unknown winter
roost each year [31, 32]. Our previous work [14] has demonstrated that N. plancyi uses a polar-
ity compass for orientation during roosting: the bats preferred to roost at the magnetic north
when exposed to an artificial magnetic field with twice the strength of the local geomagnetic
field (100 μT). As the magnetic north was reversed but field strength did not change, the bats
always followed the position of the altered magnetic north.

The present study extends this previous work by examining the ability of N. plancyi to detect
magnetic fields with very low intensities. Such high sensitivity would explain how bats could
have acquired and retained their magnetic sense during evolution when such low magnetic
field strengths and polarity reversals occurred numerous times. We found that the bats posi-
tioned themselves at the magnetic north at field strengths that were only 1/5th of the natural
geomagnetic field, and did so even when the polarity of the artificial field was reversed. The
conditions tested here are comparable to both present-day and ancient geomagnetic field fea-
tures. We briefly also discuss possible mechanisms underlying magnetoreception in bats.

Materials and Methods

The experiments were performed in the Biogeomagnetic Laboratory at the Institute of Geology
and Geophysics, Chinese Academy of Sciences, in Beijing from March to October 2013,
avoiding time periods during which the bats normally undergo torpor and hibernation. The bat species used in this study was the *N. plancyi*, which were collected from the Dule Temple in Tianjin (40°5’ N, 117°4’ E) at the end of September of 2012 using mist nets. After the completion of the experiments, all individuals were returned to their site of origin and released.

**Ethical statement**

The collection and experiment of the bats was approved by the Chinese Academy of Sciences and the administration of Dule Temple. The Ethics Committee of the Chinese Academy of Sciences on Vertebrate Animals Experiments and the Institute of Geology and Geophysics Administrative Panel on Laboratory Animal Care approved all experimental procedures.

**Magnetic field conditions**

Bats were maintained in a basement laboratory at constant temperature and relative humidity (22±1°C; 60±1%; temperature and humidity meter THG312, Oregon Scientific, Portland, Oregon) throughout the course of the experiments. Because the *N. plancyi* are highly social animals, we used a group of six individuals (all males) in all conditions tested (Logistical reasons limited us to a sample size of six bats). The mean body length of the bats was 8.6±0.4 cm and the mean weight 31.5±1.7 g. The weight of the bats was monitored daily to ensure that weight loss never exceeded 10% of the original weight. The group of six bats was placed into a round plastic basket (30 cm inner diameter, 30 cm inner height) with small holes in its sides. The holes provided for ventilation of the inside with fresh air and also allowed the bats to freely move around and hang from the uppermost sides of the basket. The top of the basket was covered with a transparent glass lid, allowing for continuous infrared camera monitoring of the bats (S1 Fig).

The schematic diagram of this experimental apparatus followed the one described in [14]. The round plastic basket was placed in the center of a homogeneous magnetic field, which was generated by a custom-made tri-axial square Helmholtz coil system [33, 34]. The coil system is composed of three pairs of orthogonally aligned square coils (D = 1.5 m). Each pair of coils is independently controlled by a DC power supply (DH1715-3, DaHua Electronic Corporation, Beijing, China), generating a magnetic field in one specific axis—X, Y or Z (the number of wire loops is 190, 114, and 228, respectively). This coil system provided a uniform net magnetic field in the coil center space no less than 45×45×45 cm. The coil system was covered with thick black fabric to block out any external light. The power supplies of coils were placed in a neighboring room to keep away any noise. The experimental setup was free of any human disturbance, ambient noise, or natural light (no acoustic or visual cues provided during the entire experiments). Roosting positions of the bats were automatically recorded via an infrared camera (DS-2CC502P-IPT, Hikvision Digital Technology Corporation, Hangzhou, China). Before each magnetic condition started, the stability and homogeneity of the designed magnetic fields produced at the position of the experimental basket were monitored using an APS 520 3-axis fluxgate magnetometer (Applied Physics Systems, Mountain View, California) for 3 consecutive days. Details of used magnetic fields are present in S1 Table.

**Experimental procedures**

The roosting behavior of the bats was recorded for 10 consecutive days for each magnetic field condition. During the experimental period, the bats were daily removed from the experimental basket at 6:40 p.m. every day for a period of 30 min and transferred into a holding cage where they were provided with food (mealworms) and water. Meanwhile, the experimental basket was thoroughly cleaned using water followed by 75% alcohol to eliminate any odor cues and
then returned to the coil system. After feeding, the bats were returned to the center at the bott-
tom of the cleaned experimental basket, starting an orientation record anew. Between each
magnetic field condition run, the bats were allowed to recover for 7 days in the local normal
geomagnetic field in order to eliminate any potential disturbance from the last tested magnetic
field condition.

We initially tested the roosting behavior of the bats under local normal geomagnetic field
condition (51 μT). Then, we tested the reversed polarity condition using the same strength
(51 μT). Next, we pseudorandomly examined the roosting position of the bats responding to
low field strengths, i.e., value of 1/3rd (17 μT), 1/4th (13 μT), or 1/5th (10 μT) of the local geo-
magnetic field and also to a polarity-reversed field at the weakest intensity (10 μT).

In this study, we repeated the exposure to 1/5th (10 μT) of the geomagnetic field twice and a
polarity-reversed field at this low intensity. We tested the bats in a natural geomagnetic field
experiment once more serving as additional control.

Statistics

All statistical analysis was conducted in MATLAB (Mathworks Inc.). We used a MATLAB
toolbox for Circular Statistics to analyze the data on the bats’ roosting positions [35]. The
upper rim of the basket was divided into 72 equal sectors marked by holes, which allowed us to
determine the angle of the bats’ roosting orientation with 5 degrees accuracy. The magnetic
north in the natural geomagnetic field was defined as zero degree, marked by the letter “N” on
the rim of the basket. In all trials, the position of the basket did not change, including during
the polarity reversals.

Due to their highly social nature, the bats usually clustered together when roosting. The an-
gular value of their roosting position was obtained by determining the angle at the center of the
cluster. If the bats happened to form more than 1 cluster by splitting up into several (no more
than 3) groups, which occurred only very rarely, the average angular value was derived by vec-
tor calculation. The data were discarded, however, if the bats were distributed over more or less
the entire surface of the basket or if they were continuously moving.

The data of the roosting position of the bat cluster was collected at 30 min intervals during
the experimental time. The daily session was ended by 30 min break for feeding and watering,
since the tested bats were removed from the experimental field, exposed to natural magnetic
field for 30 min, and the bats had to re-determine the orientation of the magnetic field after
being returned to the tested magnetic field condition (see Methods above). Therefore, we con-
sidered the daily data set obtained for each magnetic field condition as 10 independent repetitions.

We determined the distribution of the bats in the basket as circular means, which were ex-
pressed as vector mean values, not the classic arithmetic mean value [35]. Vector analysis then
yielded the mean direction of the entire group of bats for each magnetic field condition for
each 10-day testing period. The length of the vector mean indicated how concentrated the data
sample was around the mean direction (max. value is 1; for details, see rθ values in Table 1, and
S3 Table). We illustrated the distribution of the different angular orientation (12 angle bins)
graphically in a rose (theta) diagram, covering 30 degrees each. The results for replicated trials
at the lowest intensity 1/5th of the natural geomagnetic field strength are shown in S2 Fig. A
nonparametric Rayleigh test and a Watson U2 test assessed if the orientation was significantly
different from a random distribution (see p values in Table 1 and S3 Table) and compared the
mean directions of the bat clusters between different magnetic field conditions. The daily ori-
entation data for each magnetic condition were also assessed by a nonparametric Rayleigh test
(p values not shown).
Results

Fig 1 shows that *N. pancyi* in a magnetic field with natural strength preferred to roost near the magnetic north (0°). The mean direction in the natural geomagnetic field was 25°. When the polarity was reversed, the bats changed their roosting preference to the geographic south (162°), i.e. they remained at the (now new, artificial) magnetic north. The mean direction of the bats in both the natural geomagnetic field and the polarity-reversed field were significantly different from a random distribution and from each other (*p* < 0.05) (Table 1).

Fig 2 demonstrates that the bats statistically significantly preferred to roost at the magnetic north at 1/3rd, 1/4th, and 1/5th of the strength of the natural geomagnetic field. The lengths of

Table 1. Summary of the mean directions of the bat cluster and results of Rayleigh test for a preferred orientation in different magnetic fields.

| Field conditions      | No. data | a_b (°) | r_b    | p       |
|-----------------------|----------|---------|--------|---------|
| GMF                   | 394      | 25      | 0.53   | <0.001  |
| 1/3rd GMF             | 451      | 21      | 0.50   | <0.001  |
| 1/4th GMF             | 433      | 25      | 0.62   | <0.001  |
| 1/5th GMF             | 466      | 27      | 0.47   | <0.001  |
| Reversed_GMF          | 454      | 162     | 0.52   | <0.001  |
| Reversed_1/5th GMF    | 462      | 158     | 0.56   | <0.001  |

GMF: natural geomagnetic field strength.  
*a_b*: the mean direction  
*r_b*: the magnitude of the mean resultant vector  
*p*: a significant level. *p* < 0.05 indicating a preferred direction; *p* > 0.05 indicating random directions.

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the mean vectors, \( r_n \), were all >0.5, except for the case of the weakest field (Table 1). Under all magnetic field conditions, from natural down to 1/5\(^{th}\) and normal to reversed polarities, the tested bat’s roosted near the magnetic north. Although the direction data for the weakest intensity (1/5\(^{th}\) of the natural strength) appeared slightly more scattered than those for 1/3\(^{rd}\) and 1/4\(^{th}\) of the natural strength (Fig 2A–2C), statistical analysis indicated that the mean
directions under all three weak magnetic field conditions were not significantly different \( (p>0.05) \). When we reversed the polarity of the weakest field \( (\text{Fig 2D}) \), the mean direction of the bat cluster is 158°, indicating that the bats still preferred the (new, artificial) magnetic north at a statistically significant level.

This is further confirmed by repeat tests in the weakest field strength \( (10 \mu T) \) for normal polarity and reversed polarity \( (\text{S2 Fig}) \). Their a and r values are present in \text{S3 Table}.

All magnetic field conditions yielded results that were significantly different from random roosting behavior \( (\text{Table 1 and S3 Table}) \). All daily orientation data of the bats were also significantly different from a random distribution \( (p<0.05, p \text{ values not shown in S2 and S4 Tables}) \). Individual analysis of the daily orientation data for each magnetic condition also revealed a consistent preference for the magnetic north, only a few data deviating from the magnetic north. It is noteworthy, however, that the \( a_b \) and \( r_b \) values of the daily orientation data indicated that the bats did not remain at the exact same position throughout the entire day. Instead, they often moved around slightly, nevertheless always staying close to the magnetic north. These results clearly indicate a remarkable sensitivity of \textit{N. plancyi} to magnetic field strengths of only 10 \( \mu T \), which is only 1/5\textsuperscript{th} of the present-day local geomagnetic field value.

Although generally all bats eventually congregated at the magnetic north at even the weakest magnetic field strength tested, the time period that passed until the bats did so (the "response time") depended on the magnetic field strength. At field strength greater than 1/5\textsuperscript{th} of the natural strength, the bats began roosting near the magnetic north more quickly than at the lowest intensity. At a field strength of 1/5\textsuperscript{th} of the natural strength (either at the normal or the reversed polarity), the bats roosted at random positions on the rim of the basket \( (\text{S1D Fig}) \) for the first three experimental days, which did not allow us to determine preferred roosting angle. After that, the bats began to exhibit a clear preference for a particular orientation. Hence, we began data collection on the 4\textsuperscript{th} exposure day and continued for the subsequent 10 days.

Interestingly, we noted that every time either the field strength was changed and/or the field polarity was reversed, the bats also reduced their food intake for the first 1–3 daily exposures following the changes. Only after this initial period, the bats appeared to habituate to the changed magnetic condition and their food intake returned to normal.

**Discussion**

The results of the present study demonstrate a remarkable sensitivity of a migratory vespertilionid bat, the Chinese noctule \( (N. \textit{plancyi}) \), to magnetic fields as weak as 1/5\textsuperscript{th} of the natural geomagnetic field strength, i.e. 10 \( \mu T \). This sensitivity was evident in responses to the normal orientation of fields with different strength but also to a polarity-reversed field of even the weakest field strength. Under all tested magnetic field conditions, the bats always roosted near the magnetic north. This further corroborates the finding of polarity-based compass of \textit{N. plancyi} in our earlier study \[14\]. It remains unclear, however, what the benefits of roosting near the magnetic north might be.

This high sensitivity of the magnetic orientation in bats, the first of its kind in mammals, is comparable to that recently observed in birds \[21\]. This ability of bats and birds to detect even very weak magnetic fields may have important implications in how these animals cope with the significant geomagnetic field changes that occurred over their course of evolution. Based on the data presented here and our earlier study \[14\], \textit{N. plancyi} is able to detect field strengths ranging from 10 to 100 \( \mu T \). This allows them to orient themselves across the entire range of present-day global geomagnetic field strengths. The remarkable sensitivity to magnetic field strengths of only 10 \( \mu T \) indicates that these bats may have been able to orientate themselves even in the low field strengths that occurred during geomagnetic polarity reversal or excursion.
It may enable bats to use the Earth’s magnetic field coordinate for orientation and navigation, similar to that of sea turtles, lobsters, or pigeons [10, 11, 36].

Interestingly, numerous other mammals, such as cows, red foxes, or dogs, also appear to be able to sense magnetic fields and align their bodies along the magnetic north-south axis when they rest, hunt or defecate. The underlying mechanism and the purpose of this behavior remain unknown, however [37–40]. Finally, the prolonged delay in the response to the weakest magnetic field tested here (1/5th of the natural field strength, or 10 μT) suggests that this field strength may be close to the threshold of magnetoreception for these bats. Due to the technical difficulty to generate very stable magnetic fields with even lower-intensity, we refrained here from testing magnetic field strengths below 10 μT.

The physiological mechanisms underlying magnetoreception in bats and other animals are poorly understood. The most widely accepted hypotheses include photoreceptor-based and/or magnetite-based magnetoreception [41–43]. Because the location of any magnetite magnetoreceptor in bats is currently still unknown, we could not determine the potential role of magnetite particles in magnetic orientation, for example by pharmacologically blocking sites containing such magnetite particles, as performed in birds [21]. Nevertheless, the bats used here naturally roost in dark locations, such as in caves, during the day and only in the darkness of night emerge from their roost sites to forage. Hence it appears unlikely that a light-based mechanism of magnetoreception is at work here.

Several lines of evidence rather suggest a magnetite-based mechanism: First, magnetite-based magnetoreceptors should be able to detect both, direction and intensity of a magnetic field [44, 45]. We recently measured magnetic properties of the brain tissues of migratory as well as non-migratory bats using a “superconducting quantum interference device” (SQUID) magnetometer. Interestingly, the isothermal remanent magnetization acquisition results indicated that the amount of soft magnetic particles (magnetites) was higher in migratory than in non-migratory species, implying a magnetite-based reception mechanism [30]. Furthermore, Holland and co-workers used pulse-remagnetization experiments detecting primarily iron minerals indicating that the body of bats contains freely rotating magnetite particles [29]. Such a magnetite-based magnetoreception has also been suggested for different mole-rat species [46, 47].

In summary, our results hint at the possibility that migratory bats may have the potential to detect magnetic fields and potentially use them for orientation and maybe even navigation. We found for the first time that the magnetic sense in the Chinese noctule, N. plancyi, could even detect extremely weak magnetic field (10 μT). This could explain how magnetoreception was able to evolve over a period of time when the Earth’s magnetic field underwent numerous and dramatic weakenings of its field strength during geomagnetic reversals or excursions. However, the location of any magnetoreceptors, which are most likely magnetite-based, in mammals including bats and how they function remains unclear. Further histological and physiological studies may aid in determining where such magnetoreceptors are found and how they work.

Supporting Information

S1 Fig. Snapshots of the bat cluster in the experimental chamber while roosting in different magnetic fields.
(TIF)

S2 Fig. Angular histograms of roosting locations in replicated trials of the weakest field strengths (1/5th GMF, 10μT) and of reversed polarity at the weakest field strength.
(TIF)
S1 Table. Details of the magnetic field conditions tested.

S2 Table. Daily vector averages of the bat cluster for exposures to six different magnetic field conditions.

S3 Table. Summary of the mean directions of the roosting location of the bat cluster (ab in degrees) and results of Rayleigh test for a preferred orientation in replicated trials of lowest intensity magnetic fields (rb, p).

S4 Table. Daily vector averages for the bat cluster when exposed to the lowest magnetic field intensity. Data cover one complete exposure series (10 days).

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Author Contributions

Conceived and designed the experiments: LXT YXP. Performed the experiments: LXT JSZ BFZ. Analyzed the data: LXT YXP WM. Wrote the paper: LXT YXP WM.

References

1. Wiltschko R, Wiltschko W. Magnetic orientation in animals. Berlin, Heidelberg, New York: Springer Verlag; 1995.
2. Wiltschko W, Wiltschko R. Magnetic orientation and magnetoreception in birds and other animals. J Comp Physiol A. 2005; 191: 675–93. PMID: 15886990
3. Mora CV, Davison M, Wild JM, Walker MM. Magnetoreception and its trigeminal mediation in the homing pigeon. Nature. 2004; 432: 508–11. PMID: 15565156
4. Mann S, Sparks NHC, Walker MM, Kirschvink JL. Ultrastructure, morphology and organization of biogenic magnetite from Sockeye Salmon, Oncorhynchus-Nerka—Implications for magnetoreception. J Exp Biol. 1988; 140: 35–49. PMID: 3204335
5. Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR. Structure and function of the vertebrate magnetic sense. Nature. 1997; 390: 371–6. PMID: 20358649
6. Diebel CE, Proksch R, Green CR, Neilson P, Walker MM. Magnetite defines a vertebrate magnetoreceptor. Nature. 2000; 406: 299–302. PMID: 10917530
7. Vacha M. Laboratory behavioural assay of insect magnetoreception: magnetosensitivity of Periplaneta americana. J Exp Biol. 2006; 209: 3882–6. PMID: 16985204
8. Merlin C, Heinze S, Reppert SM. Unraveling navigational strategies in migratory insects. Curr Opin Neurobiol. 2012; 22: 353–61. doi: 10.1016/j.conb.2011.11.009 PMID: 22154565
9. Putman NF, Endres CS, Lohmann CMF, Lohmann KJ. Longitude perception and bicoordinate magnetic maps in sea turtles. Curr Biol. 2011; 21(6): 463–6. doi: 10.1016/j.cub.2011.01.057 PMID: 21353561
10. Lohmann KJ, Putman NF, Lohmann CMF. The magnetic map of hatchling loggerhead sea turtles. Curr Opin Neurobiol. 2012; 22: 336–42. doi: 10.1016/j.conb.2011.11.005 PMID: 22137566
11. Boles LC, Lohmann KJ. True navigation and magnetic maps in spiny lobsters. Nature. 2003; 421: 60–3. PMID: 12511953
12. Cain SD, Boles LC, Wang JH, Lohmann KJ. Magnetic orientation and navigation in marine turtles, lobsters, and molluscs: concepts and conundrums. Integr Comp Biol. 2005; 45: 539–46. doi: 10.1093/icb/45.3.539 PMID: 21676799
13. Holland RA, Thorup K, Vonhof MJ, Cochran WW, Wikelski M. Navigation: Bat orientation using Earth’s magnetic field. Nature. 2006; 444: 702. PMID: 17151656

14. Wang YN, Pan YX, Parsons S, Walker M, Zhang SY. Bats respond to polarity of a magnetic field. Proc R Soc B 2007; 274 (1627): 2901–5. PMID: 17848365

15. Finlay CC, Maus S, Beggin CD, Bondar TN, Chambodut A, Chernova TA, et al. International Geomagnetic Reference Field: the eleventh generation. Geophys J Int. 2010; 183: 1216–30.

16. Juárez MT, Tauxe L, Gee JS, Pick T. The intensity of the Earth’s magnetic field over the past 160 million years. Nature. 1998; 394: 878–81.

17. Zhu RX, Pan YX, Coe RS. Paleointensity studies of a lava succession from Jilin Province, northeastern China: Evidence for the Blake event. J Geophys Res. 2000; 105: 8305–17.

18. Valet JP, Meynadier L, Guyo Y. Geomagnetic dipole strength and reversal rate over the past two million years. Nature. 1993; 366: 234–8.

19. Altringham JD. Bats: biology and behaviour. New York: Oxford University Press; 1996.

20. Olson P, Hinnov LA, Driscoll PE. Nonrandom geomagnetic reversal times and geodynamo evolution. Earth Planet Sci Lett. 2014; 388: 9–17.
40. Hart V, Nováková P, Malkemper EP, Begall S, Hanzal V, Jezek M, et al. Dogs are sensitive to small variations of the Earth's magnetic field. Front Zool. 2013; 10: 80. doi: 10.1186/1742-9994-10-80 PMID: 24370002

41. Ritz T, Adem S, Schulten K. A model for photoreceptor-based magnetoreception in birds. Biophys J. 2000; 78: 707–18. PMID: 10653784

42. Kirschvink JL, Walker MM, Diebel CE. Magnetite-based magnetoreception. Curr Opin Neurobiol. 2001; 11: 462–7. PMID: 11502393

43. Wiltschko R, Wiltschko W. The magnetite-based receptors in the beak of birds and their role in avian navigation. J Comp Physiol A. 2013; 199 (2): 89–98. doi: 10.1007/s00359-012-0769-3 PMID: 23111859

44. Kirschvink J L, Gould J L. Biogenic magnetite as a basis for magnetic field detection in animals. BioSystems. 1981; 13: 181–201. PMID: 7213948

45. Davila AF, Winkloher M, Shcherbakov VP, Petersen N. Magnetic pulse affects a putative magnetoreceptor mechanism. Biophys J. 2005; 89: 56–63. PMID: 15863473

46. Wegner RE, Begall S, Burda H. Magnetic compass in the cornea: local anaesthesia impairs orientation in a mammal. J Exp Biol. 2006, 209: 4747–50. PMID: 17114407

47. Oliveriusova L, Nemec P, Kralova Z, Sedlacek F (2012). Magnetic compass orientation in two strictly subterranean rodents: learned or species-specific innate directional preference? J Exp Biol. 2012; 215: 3649–3654. PMID: 22855619