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A magnetic compass guides the direction of foraging in a bat

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Abstract

Previously, two studies have provided evidence that bats can use magnetic field cues for homing or roosting. For insectivorous bats, it is well established that foraging represents one of the most fundamental behaviors in animals relies on their ability to echolocate. Whether echolocating bats can also use magnetic cues during foraging remains unknown, however. Here, we tested the orientation behavior of Chinese noctules (*Nyctalus plancyi*) during foraging in a plus-shaped, 4-channel apparatus under different magnetic field conditions. To minimize the effects of spatial memory on orientation from repeated experiments, naïve bats were tested only once in each experimental condition. As expected, under geomagnetic field and a food resource offered conditions, the bats significantly preferred to enter the channel containing food, indicating that they primarily relied on direct sensory signals unrelated to magnetic cues. In contrast, when we offered food simultaneously in all four channels and minimized any differences in all other sensory signals available, the bats exhibited a clear directional preference to forage along the magnetic field direction under either geomagnetic field or a magnetic field in which the horizontal component was rotated by 90°. Our study offers a novel evidence for the importance of a geomagnetic field during foraging.

Keywords Geomagnetic field · Bats · Foraging orientation · A plus-shaped channel apparatus · Magnetic orientation

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Introduction

A growing number of studies have shown that the geomagnetic field represents an important physical reference for the orientation and navigation of animals both terrestrial and marine (Dubrov 1978; Wiltschko and Wiltschko 1995, 2005; Walker et al. 1984, 2003; Holland et al. 2006, 2010; Cresci et al. 2017). Foraging is vital for survival, growth, and reproductive success of all animals (Danchin et al. 2008). Similar to migration or homing, foraging requires goal-oriented behaviors in both known and unknown territories. For insectivorous bats, laryngeal echolocation represents the primary tool of detecting and locating prey (Metzner and Müller 2016). However, echolocating bats cannot locate food solely relying on echolocation when echoes from food sources overlap with the echoes from the background (or "clutter") (Schnitzler and Kalko 2001). Under those circumstances, bats need to include additional sensory cues, such as odor or prey-generated sounds to find the food source (Griffin 1958; Bell 1985; Schmidt et al. 1988; Hessel and Schmidt 1994; Jones et al. 2016). In addition, bats generally have highly developed spatial learning and memory, which enables them to navigate and forage in a much more

efficient manner (Schnitzler et al. 2003; Speakman et al. 1989; Rose et al. 2016). Long-tongued bats, *Glossophaga soricina*, for example, rely on spatial memory to relocate previously rewarded feeding areas (Carter et al. 2010; Thiele and Winter 2005; Rose et al. 2016).

In the past decade, a few studies have addressed the possibility that birds may use magnetic cues to seek food. For example, pigeons were trained to associate a local distortion of the magnetic field with food, enabling them to use this magnetic anomaly to locate visually hidden food objects (Thalau et al. 2007). Pigeons can also be conditioned to discriminate differences in magnetic field inclination to find a food reward (Mora et al. 2014). These studies indicate that pigeons can use magnetic cues to find and locate food sources after training reinforcement. Recently, two independent studies provided evidence that bats also can instinctively use a magnetic compass for homing or roosting

(Holland et al. 2006; Wang et al. 2007), even without training. It remains unknown, however, if a magnetic compass is also involved in the orientation of foraging bats. If so, it would be useful for bats to be able to learn the compass heading of locations, where the food supply is abundant, so the bats could fly back and forth to these foraging sites more efficiently.

To investigate if foraging in bats can also be affected by the presence of a magnetic field, we tested inexperienced Chinese noctules (*Nyctalus plancyi*) in a simple plus-shaped channel apparatus (see "Methods" for details). In addition to using food-related sensory cues (such as prey-generated sound and olfaction) or locating the food source by echolocation, we investigated whether these bats would also use a magnetic field for orientation when searching for food (Fig. 1a) (for details, please see "Methods"). We measured how many of the experimental bats entered each of
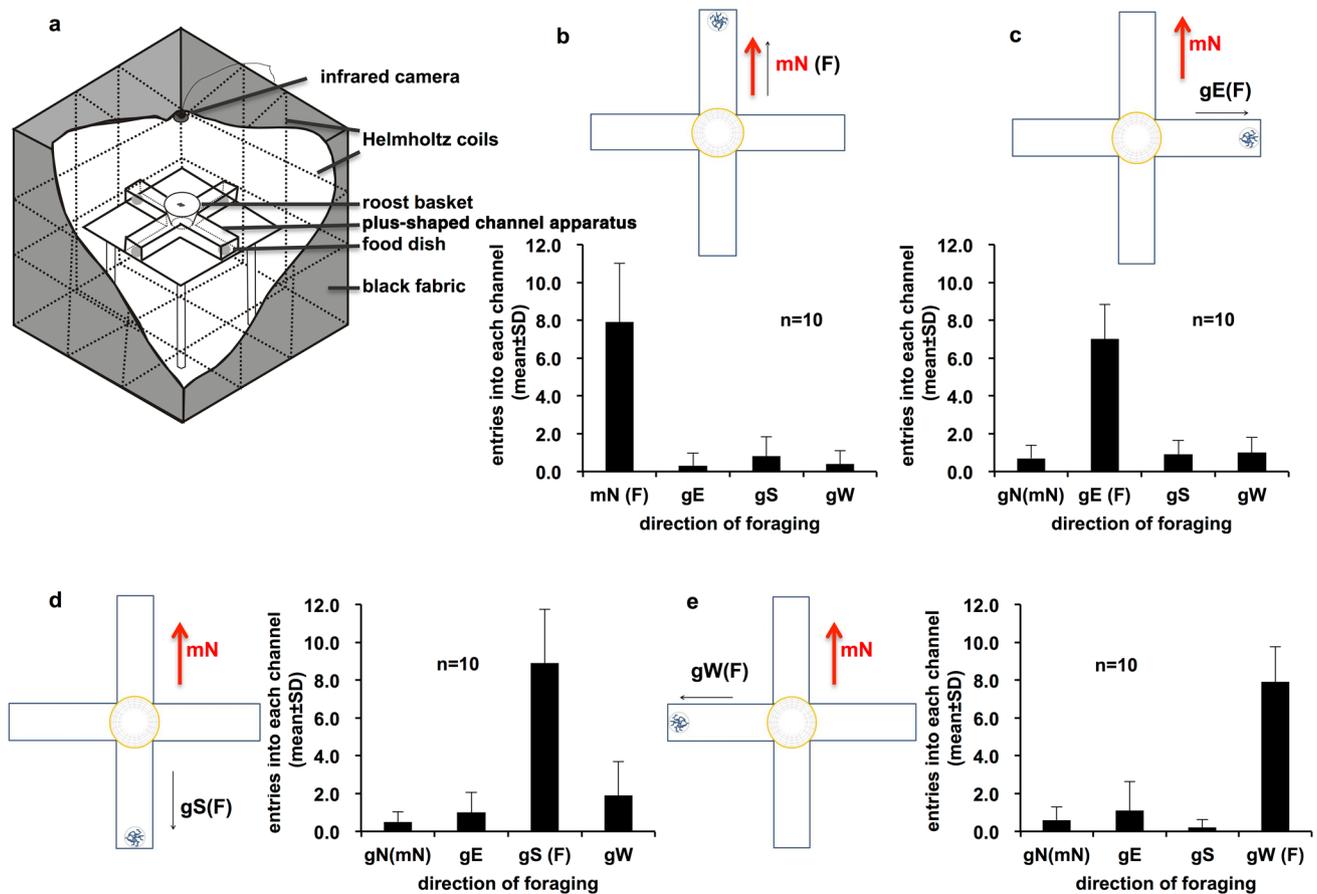
Fig. 1 Setup of the plus-shaped channel apparatus and results of the "one-food condition" (food provided in one channel only; empty food dishes in the remaining three channels; for details, please see "Methods"). **a** Illustration of the experimental setup. The device is centered on a wooden table inside a custom-built Helmholtz coil. An inverted plastic basket (open bottom and top) was positioned in the center of the four channels to allow the bats to roost during the experimental session. An infrared camera was centered directly above the top of the basket to monitor the behavior of the bats. **b–e** Average results of the "one-food condition" for all ten bats given as mean ± SD in the natural GMF and for all four locations at which the food dish was positioned. **b** Food in channel facing gN (mN). **c** Food in channel facing gE. **d** Food in channel facing gS (mS). **e** Food in channel facing gW. gN (gE, gS, gW) direction of geographic north (east, south, west), mN direction of magnetic north, F location of food

the four channels under two different experimental conditions. First, a single food source was offered in one channel under a natural geomagnetic field ("one-food condition"), i.e., only one of the four dishes in each channel was filled with mealworms (the channel in which food was presented was changed pseudo-randomly); the other three remained empty. This represented a condition, where the presence or absence of food provided an obvious, directly food-related sensory cue for the orientation of the animals. In the second experimental condition, equivalent food supplies were offered simultaneously in all four channels under a natural geomagnetic field (GMF) as well as the horizontal component of the magnetic field artificially rotated clockwise 90° ("four-food condition"). This second condition provided no differences in sensory cues for any particular position of the food source; the only cue available was the direction of the magnetic field. As expected, in the first paradigm, i.e., the one-food condition, bats clearly preferred the channel in which the food was located, indicating that they were mainly responding to food-generated sensory cues and that the direction of the GMF did not play any role in their directional preference. In contrast, in the second paradigm, i.e., the four-food condition, the bats instead exhibited a consistent direction of orientation with respect to the magnetic field for both the natural GMF and a magnetic field in which the horizontal component had been changed.

Materials and methods

Experimental animals

The bats used here, Chinese noctules (*Nyctalus plancyi*), a migratory species, were collected close to their roost sites in Tianjin suburban areas (China) at the end of September 2014 using mist nets. A total of ten adult male bats with an average weight of 30.5 ± 1.2 g and an average body length of 8.3 ± 0.4 cm were collected (note that only male bats were caught to minimize any potential impact on the population). All bats were housed in a room located in the basement of the Biogeomagnetism Laboratory at the Institute of Geology and Geophysics, Chinese Academy of Sciences in Beijing. The room was maintained at a constant temperature and relative humidity (22 ± 1 °C; $60 \pm 1\%$), and the bats had ad libitum access to food and water. The light was on a 12:12 h dark/light cycle. The housing room provided sufficient space (2.5 m $\times 4$ m) for bats to fly freely. Additional environmental enrichment in form of several wooden perches and plants were added. The health of the bats was determined at least once per day. The experiments were conducted in a separate room located in the same basement of the Biogeomagnetism Laboratory from March to September 2015 and 2016, a time during which these bats are still active at the collection site

and do not yet undergo hibernation. No bats were injured and no harmful manipulations were carried out.

Plus-shaped channel apparatus

We built a plus-shaped channel apparatus that contained an inverted basket in the center and four channels pointing to the geographic north (gN), east (gE), south (gS), and west (gW), respectively (Fig. 1a). The four channels were identical in size and material. The length of each channel was 25 cm. All materials were made from plastic to prevent any interference with the magnetic fields tested and to allow for easy cleaning. The inverted basket resembled a cone and had two openings, one at the top (to allow for camera observation) and one at the bottom (to allow the bats to enter the cross-shaped channels apparatus). The diameters of the top and bottom openings of the basket were 10 cm and 25 cm, respectively, and the basket's height was 23 cm above the channels. A food dish was positioned at the end of each channel. It was 4 cm tall, which prevented the mealworms from escaping. Different numbers of dishes were filled with food (same size live mealworms) depending on the experimental paradigm tested (see below). Each individual bat was released from the basket and had to move downwards into an arm of the apparatus to get food. The behavior of all bats was video-recorded with an infrared camera (DS-2CC502P-IPT, Hangzhou, China) and digitally stored on a computer.

Magnetic field

Homogeneous magnetic fields were produced with custom-made tri-axial Helmholtz coils (Firester 1996; Li 2004). The coil system was composed of three pairs of orthogonally aligned square coils, each with a diameter of 1.5 m. Each pair of coils was independently controlled by a DC power supply (DaHua Electronic Corporation, Beijing, China), which could generate a magnetic field in one specific axis (X, Y, or Z). This coil system provided a uniform net magnetic field ($60 \times 60 \times 60$ cm), covering the same area in which the basket, and the four channels were located.

The coil system was covered with thick black fabric to block out virtually all external light (< 0.03 lx) to mimic nocturnal conditions and to ensure that the bats could not rely on their eyesight and use any external landmarks for orientation. The power supplies of the coils were placed in a neighboring room to minimize noise. Before testing each magnetic condition, the stability and homogeneity of the magnetic field were verified using a three-axes fluxgate magnetometer (Applied Physics Systems, Mountain View, California). The intensity and inclination of the natural (local) GMF in the laboratory were 51.3 ± 0.3 µT and $60.6 \pm 0.2°$, respectively. In the "one-food condition", the power supply was switched off and the bats were only

exposed to the natural geomagnetic field (GMF). For the four-food conditions, bats were exposed to the natural GMF and an artificial magnetic field for which the horizontal component was rotated 90° clockwise relative to the natural GMF, pointing to the geographic east and west. Natural and artificially altered magnetic fields had the same intensity and inclination.

Behavioral test

To eliminate the effects of spatial memory for locating food that could have been acquired in the previous experiments, each of the ten bats was tested only once under each experimental condition. All bats were tagged with different plastic bands for individual identification. The day before the experimental session started, the test animals were offered only water (no food) to motivate them to seek food during the experiment. The bats were placed in a wooden transport box and were transported to the experimental device. At the start of each trial, a single bat was pseudo-randomly selected and placed at the top of the inverted basket. At the end of each trial for each bat, the entire experimental device was thoroughly cleaned using cotton balls soaked with 75% alcohol to eliminate any odor or traces of feces or urine left from the previous experiment. Furthermore, to minimize possible differences of intra-channel cues or odors between the four directions, the apparatus was pseudo-randomly rotated (+90°, +180°, or −90°) between trials.

As briefly outlined above, two types of experiments were performed and each bat underwent both types of tests. First, to test for the general effects of food-related sensory cues on food localization and how it was affected by the natural GMF, food was located in only one channel under the natural GMF ("one-food condition"). The magnetic north–south direction was always aligned with the geographic north–south direction. Only one channel contained a food dish at its end with 8 g of mealworms. The other three channels contained empty food dishes. All food dishes were alike and made from the same batch of products. Each bat underwent four tests in which the food was placed pseudo-randomly at the end of the geographic north-, east-, south-, or west-facing channel. Each test lasted from 5:00 p.m. on the first day to 8:00 a.m. on the next day and was recorded in its entirety by video (see above).

Subsequently, to specifically test for magnetic field effects, equal amounts of food were located simultaneously in all four channels ("four-food condition"). To ensure that the mealworms in each of the dishes produced similar amounts of noise when moving around in the food dishes, the mealworms in each dish were equal in weight and size.

Two different magnetic field conditions were pseudo-randomly performed for each bat during two sessions: one under the natural GMF and the other under an artificial

magnetic field in which the horizontal component was rotated clockwise by 90°. Between the experimental runs under the two magnetic field conditions, each individual bat was allowed to recover for at least 7 days under the normal GMF to minimize any potential disturbance from the last magnetic field condition tested.

Data analysis

Orientation data were collected only after the bats moved down from the top portion of the basket into a channel of the plus-shaped channel apparatus, and this was tallied as one orientation data point. During one test session, the bats would typically move several times between the different channels and the basket, with the number of movements differing for each bat (Supplemental Tables S1, S2). The number of moves in and out of the channels, the corresponding entry times of each channel, and the direction of the channels from the basket were obtained from the video recordings. They yielded the orientation data for the foraging behavior of each individual bat for each experimental session (i.e., one night). For comparison, the orientation data of entering the different channels for each bat (#1–10) are shown in Supplemental Tables S1 and S2, and are also given as percentage relative to the total number of entries for individual bats (Figs. 2, 4).

Analysis of variance (ANOVA) followed by Student–Newman–Keuls test or Dunnett's test was used for multiple comparisons among more than two groups. An independent-sample T test assessed differences between the local GMF group and the group undergoing the artificial magnetic field in which the horizontal component was changed by 90°. p values of < 0.05 were considered significant.

Results

All individuals were pre-tested without any food present ("no-food condition"). In the absence of any food in any of the four channels of the testing setup, seven individual bats remained in the inverted basket and did not enter any of the channels of the apparatus. Of the three bats that actually did enter the plus-shaped channel apparatus, they did so from one to three times. However, they returned to the inverted basket virtually immediately, i.e., after only a few seconds, and remained in the basket for any subsequent testing. These behaviors indicated that the bats were not willing to enter any of channels under no-food conditions. Therefore, this did not allow us to use the no-food condition as a control.

In the one-food condition, food was offered at the end of only one of the four channels under the natural GMF. This condition was chosen to examine the relative importance of sensory cues (e.g., smell, mealworm-generated sound,
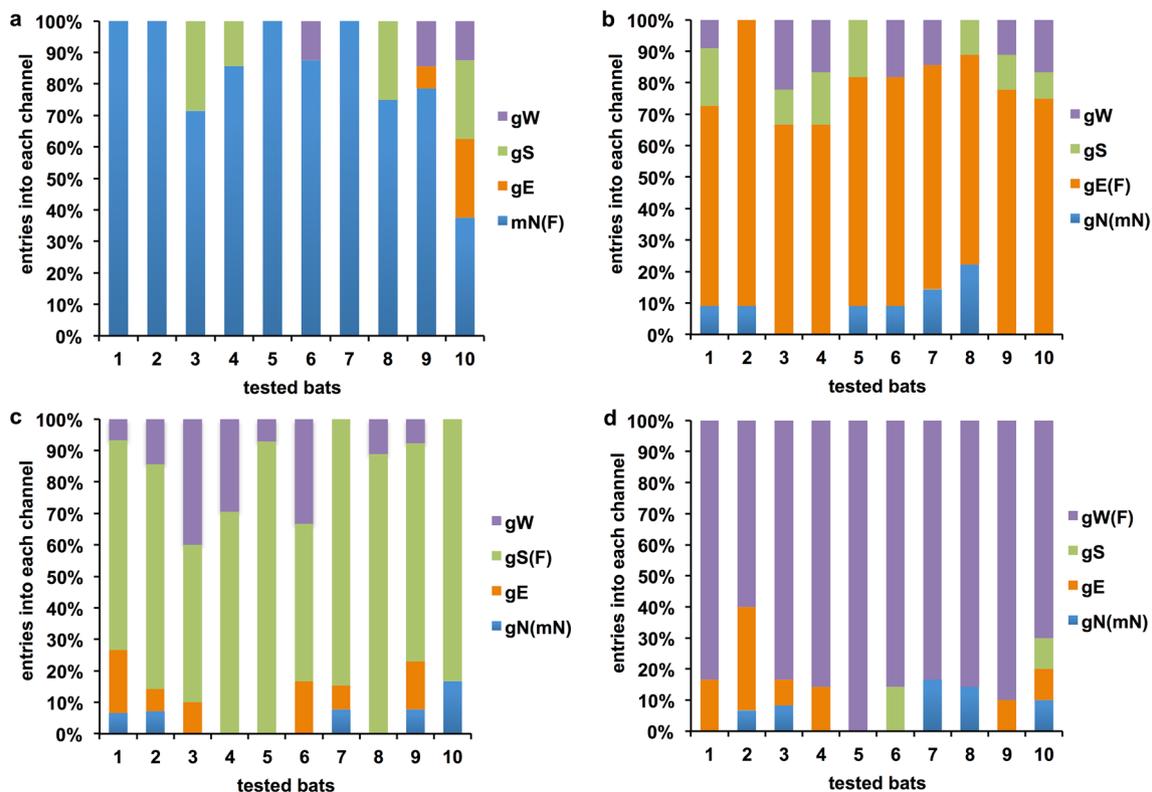
Fig. 2 Individual results (abscissa) of the "one-food condition" for each of the ten bats tested (#1–10, ordinate) in the natural GMF and for all four locations of the food dish (gN, gE, gS, gW, each marked with different colors; see legend in **a–d**). Abbreviations as in Fig. 1

echoes related to emitted echolocation pulses) emanating from the food versus that of the magnetic cues. In contrast, the four-food condition with food presented in all four channels under changing magnetic field conditions aimed at examining if/how a magnetic field would affect the orientation behavior during feeding (note that equal amounts of food were placed in all four channels, thus equally distributing any food-related sensory cues in all four directions; see "Methods" for more details). The magnetic fields tested were a normal GMF (magnetic north–south orientation aligned with geographic north–south direction) and a magnetic field for which the horizontal component was artificially changed clockwise by 90° (magnetic north–south direction aligned with geographic east–west direction). This second condition minimized and virtually eliminated directly food-related sensory cues differences among the four directions/channels and left only the direction of the magnetic field as potential source for orientation. The following will briefly outline the results of each of the experimental conditions.

Role of food-related sensory cues versus GMF ("one-food condition")

In this first experiment, food was presented pseudo-randomly in only one channel of any of the four directions

under a normal GMF (the food dishes positioned in the other three channels remained empty). As shown in Figs. 1 and 2 and Supplemental Table S1, all bats clearly preferred to enter the channel containing the food irrespective of its orientation relative to the normal GMF (average results for all bats given in Fig. 1 and results for each individual bat given in Fig. 2, Supplemental Table S1). Overall, the bats oriented themselves in the direction of the food source in more than 50% of the cases, and some individuals even chose to always enter the "food channel", resulting in a 100% performance rate (Fig. 2). It is worth noting that the first choice for foraging in each bat was the channel containing the food and not any of the channels containing no food. Individual bats entered the "food channel" 7–9 times during one experimental night, in contrast to entering to channels containing no food only 1–3 times or not at all (Fig. 2, Supplemental Table S1).

An ANOVA statistical analysis of the normalized data yielded a significant difference between the arm containing the food and the other three empty channels ($p = 0.000$). There is no difference between any of the choices of the three empty channels ($p = 0.148$).

In summary, this first set of experiments indicates that in the presence of food-related sensory cues (e.g., smell, mealworm-generated sound, and echoes related to echolocation

pulses emitted), the bats consistently oriented themselves towards the food source, rather than using the direction of the geomagnetic field.

Role of magnetic field orientation on the direction of foraging ("four-food condition")

This second experimental condition tackled the question of whether the alignment of the magnetic field affected the direction of the foraging behavior in these bats. We minimized the effects of food-related sensory cues by simultaneously presenting equal amounts of food in all four channels. We switched between exposing the bats to the normal GMF and an artificial magnetic field (same strength as the normal GMF) in which the alignment of the magnetic field was rotated 90° clockwise to coincide with the geographic east–west direction. The results were different from those of the one-food tests described above (Figs. 1, 2, Supplemental Table S1) and are given in Fig. 3 (average results for all bats) and Fig. 4 as well as Supplemental Table S2 (results for each individual bat).

Under the natural GMF condition, the mean number of entries into gN (mN), gE, gS (mS), and gW channels of all ten bats was 3.5 ± 2.4, 1.4 ± 1.4, 5.1 ± 2.5, and 1.6 ± 1.2, respectively. The mean percentage of bats choosing the N–S axis of the magnetic field was $75 \pm 10\%$. In contrast, the mean value of bats choosing the geographic E–W axis was $25 \pm 10\%$ (Fig. 3a, Table S2a).

When we artificially changed the alignment of the magnetic north to coincide with the geographic east direction by artificially rotating the horizontal axis of the magnetic field clockwise by 90º, the vast majority of bats also preferred the "new" magnetic north–south direction (which now coincided with the geographic east–west direction). The mean number of entries into the gN, gE (mN), gS, and gW(mS) channels of all ten bats was 1.9 ± 1.8, 5.4 ± 3.3, 1.4 ± 0.8, and 3.0 ± 1.8, respectively. The mean percentage of bats choosing the magnetic N–S axis of the magnetic field was $73 \pm 16\%$. In contrast, the mean value of bats choosing the geographic N–S axis was $27 \pm 16\%$ (Fig. 3b, Table S2b). A T test revealed significant differences between the percentage of bats choosing the N–S axis of the magnetic field compared with the percentage of bats choosing the other two
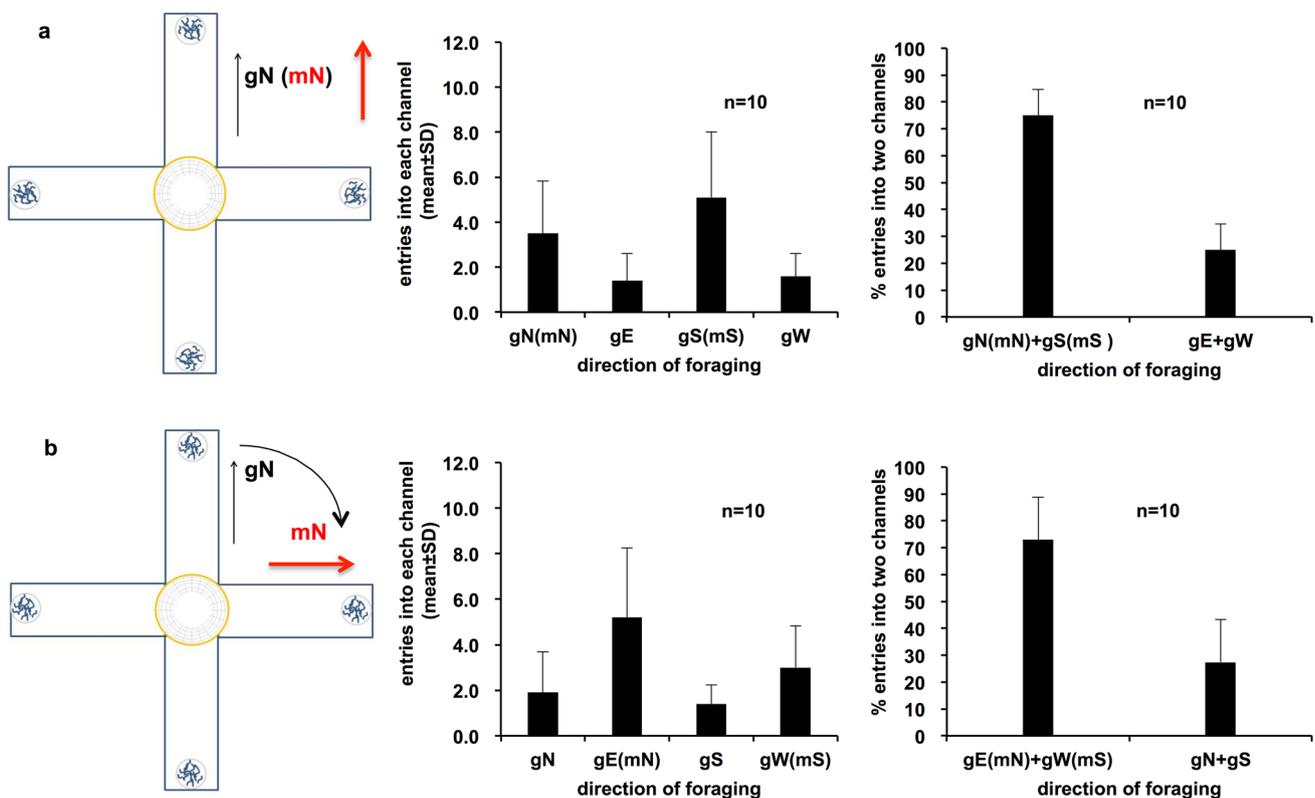
Fig. 3 Averaged results of "four-food condition". **a** Food presented in the natural GMF (as indicated in the left panel). **b** Food presented in a magnetic field with a horizontal component that was rotated clockwise by 90° relative to the natural GMF (see left panel). Center panels: mean number of entries into each channel for ten individuals (mean ± SD, abscissa). Right panels: relative frequency (% ± SD, abscissa) when the directions of foraging of gN and gS (left bars) and gE and gW (right bars) were pooled (average of all ten bats). Abbreviations as in Fig. 1
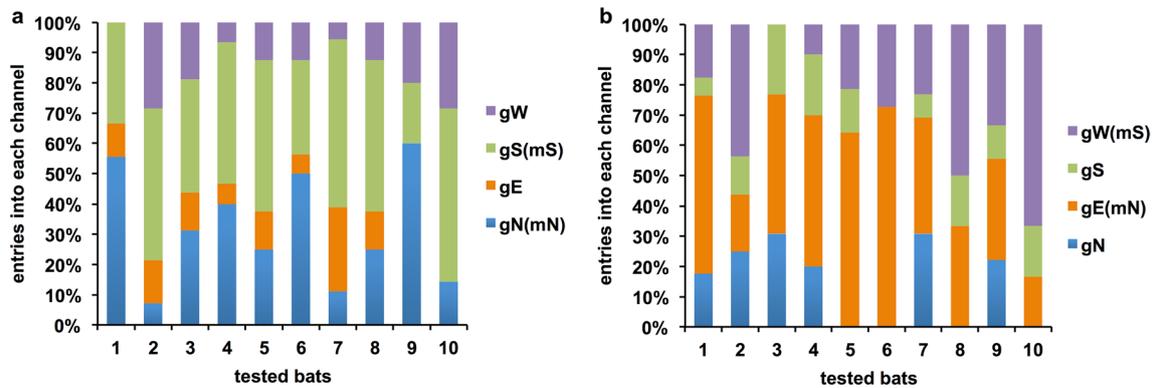
Fig. 4 Individual results (abscissa) of the "four-food condition" for ten individuals (#1–10, ordinate) for the two magnetic field conditions. **a** Natural GMF. **b** Magnetic field with a horizontal component rotated by 90° clockwise relative to the natural GMF. Abbreviations as in Fig. 1

directions, whether in the GMF group or when the magnetic field was artificially rotated clockwise by 90° ($p = 0.000$). There was no significant difference for bats choosing the magnetic north–south direction between the GMF group and the group in which the magnetic field was rotated clockwise by 90° ($p = 0.675$). In summary, these data clearly indicate that each bat preferred to enter the channel aligned with the direction of the magnetic field (mN or mS).

Discussion

These findings demonstrate that, as expected, in the presence of food-related sensory cues, such as smell, sound from moving mealworms, or echoes from echolocation pulses that the bats produced, the bats primarily relied on these direct sensory cues to locate the food source (one-food condition). On subsequent trials within the same experimental session, our results do not distinguish between the use of cues from the food source, and the use of spatial memory obtained from the first time of explorations to locate the food source in one test night. However, visual cues were eliminated, because the food sources were presented in complete darkness. In summary, in this paradigm, magnetic field cues did not appear to play any significant role for the foraging behavior of the bats.

In contrast, when we minimized food-related sensory cues by presenting equal amounts of food simultaneously in all four channels/directions ("four-food condition"), magnetic cues clearly affected the choice of the channel that the bats chose to get food. Our data indicate that there may be a hierarchy for different sensory cues during foraging in these bats depending on the circumstances of foraging.

What could be the biological significance of the use of magnetic compass information during foraging for bats that live in a three-dimensional environment/habitat? Under normal circumstances, there are several sensory cues available

for the bat to locate a food source, such as echoes from emitted sonar pulses, olfaction, vision, or spatial memory, and the order in which they are used by a bat mostly depends on the complexity of the background (Muchhala and Serrano 2015; Rydell and Eklöf 2003). Therefore, using food-related sensory cues to locate a food source appears to be the fastest and most efficient way, which is clear from our one-food test paradigm. The distance of 35 cm is an effective range of cue-directed search for bats in this study. When there were food resources offered in all four directions/channels, bats could get the food at any direction. However, the result showed that most bats chose the magnetic north–south direction and not the east–west direction. This may indicate that bats utilize a magnetic compass orientation whenever directional orientation is required.

Our findings clearly show that bats, like many of the other animals studied, can readily use the magnetic field as a source of directional ("compass") information in the context of foraging. We speculate that any directly food-related cues and the magnetic compass may be used over different spatial scales in any natural environment/habitat, rather than as alternative sources of directional information. The local food cues can guide bats for a direct approach of prey, while the magnetic compass cue may be used for directional orientation of targeting a specific location, where prey is abundant, and may be combined with local cues. Future research should address to what extent bats use a magnetic compass while foraging under natural conditions.

What is the mechanism for the detection of magnetic fields in bats? In our study, the majority of bats tested exhibited a bimodal distribution to mN and mS under two kinds of magnetic field conditions. In addition, we clearly showed that the bats actively followed the 90° rotation of the magnetic field direction. Based on our results, we could not distinguish between polarity-based and inclination/axis-based responses. However, the previous indirect evidence suggests that, in bats, a magnetite-based compass mechanism may be

involved (Holland et al. 2008; Tian et al. 2010), similar to that used by subterranean mole rats (Wegner et al. 2006).

Our results are based upon the performance of ten naive bats. When studying the navigation behavior of animals, it is better to consider whether animals are travelling for the first time or not. Once an individual bat has visited one or more foraging sites, the use of a magnetic compass would enable it to return directly to a previously visited foraging site or to follow a path that enables it to visit multiple foraging sites much more efficiently. To avoid the influence of prior memory on orientation from repeated experiments, we tested each animal only one time in each experimental condition. Although this number appears sufficiently high, especially in light of the clear outcome of our studies, future work will verify these results if more naïve, wild bats can be obtained (note that this species, such as many other bats, cannot be bred in captivity).

Author contributions LT, WM, and YP conceived the experiments and wrote the paper; BZ and JZ collected the animals and performed the experiments; HQ adjusted the experimental magnetic fields; and TZ and YC analyzed the behavioral data. All authors reviewed the manuscript and approved the final version submitted.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The Ethics Committee of the Chinese Academy of Sciences on Vertebrate Animals Experiments and the Institute of Geology and Geophysics Administrative Panel on Animal Care approved all experimental procedures. The collection of the bats was approved by the Institute of Geology and Geophysics, Chinese Academy of Sciences.

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