Neurosci Bull June 1, 2009, 25(3): 101-108. http://www.neurosci.cn
DOI: 10.1007/s12264-009-0311-y

·Original Article·

Analysis of magnetic elements in otoliths of the macula lagena in homing pigeons with inductively coupled plasma mass spectrometry

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Abstract: Objective The macula lagena in birds is located at the apical end of the cochlea and contains many tiny otoliths. The macula lagena is innervated and has neural projections to the brainstem, but its physiological function is still unclear. It remains disputable that it is because otoliths in the lagena are rich in elements Fe and Zn that birds can obtain geomagnetic information for homing. To clarify this issue, we carried out a study to determine whether or not otoliths in the lagena of homing pigeons are richer in magnetic elements than those in the saccule and the utricle. **Methods** The contents of ferromagnetic elements (Fe, Co, Ni) and other metal elements in lagenal otoliths of adult homing pigeons were precisely analyzed with inductively coupled plasma mass spectrometry (ICP-MS) of high sensitivity, and then they were compared with those in saccular and utricular otoliths (all the contents were normalized to Ca). **Results** In adult homing pigeons, the contents of ferromagnetic elements (Fe, Co, Ni) in lagenal otoliths were less than 0.7% (normalized to Ca element) and were the same order in magnitude as those in saccular and utricular otoliths. The content of Fe in lagenal otoliths was not significantly different from that in utricular otoliths and was even lower than that in saccular otoliths. The content of Co in lagenal otoliths was lower than that in saccular otoliths and higher than that in utricular otoliths. The content of Ni in lagenal otoliths was not significantly different from that in saccular otoliths and was higher than that in utricular otoliths. The contents of other metal elements Na, Mg, K, Al, Mn and Pb in lagenal otoliths were not significantly different from those in utricular and saccular otoliths. The contents of metal elements Zn, Ba and Cu in lagenal otoliths were lower than those in saccular otoliths. **Conclusion** The contents of magnetic elements in lagenal otoliths of homing pigeons are not much higher than those in utricular and saccular otoliths, which does not support the hypothesis that birds depend on high contents of Fe and Zn in lagenal otoliths for sensation of geomagnetic information. Similarities in morphology, element ingredient and element content between lagenal otoliths and utricular otoliths suggest that the two types of otolithic organs may play similar roles in sensing gravitational and acceleration signals.

Keywords: homing pigeons; lagena; otolith; magnetic element; saccule; utricle; inductively coupled plasma mass spectrometry

1 Introduction

The otoliths are tiny solid particles that cover the sensory epithelium surface of the utricle and the saccule in the membranous labyrinth of the vertebrate inner ear. They are composed of calcium carbonate, neutral polysaccharide, protein and trace elements. These otolithic organs constitute the vestibular system, together with three semicircular canals. Otoliths can pull the stereocilia of hair cells aside by shifting the otolithic membrane to stimulate hair cells, releasing neural transmitters to excite the nerve projecting to the central

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Article ID: 1673-7067(2009)-03-0101-08
CLC number: Q189
Document code: A
Received date: 2009-03-11

nervous system[1]. The saccular and utricular otoliths mainly sense gravitational and acceleration signals in mammals, but also sense acoustic signals in other lower species[2,3]. In lower vertebrates, such as the fish, the utricle is mainly involved in the balance function by sensing gravitational and acceleration signals[4], and the saccule is mainly involved in the auditory function by sensing acoustic signals[5]. During the course of evolution, the function of the utricle is conservative while the saccule gradually evolved into an organ specialized for balance sensation[6].

The macula lagena is another otolithic organ in the inner ear in non-mammalian vertebrates[7] and has distinct functions across species[8]. In the fish, the lagena is mainly involved in sensations of acoustic oscillations and orientation in the vertical plane. In the amphibian, the lagena is mainly involved in vestibular functions. In birds, the lagena is located at the apical end of the cochlea[9] (Fig. 1), which is highly innervated and has projections to the brainstem[10,11]. Currently, functions of the avian lagena are still unclear because of lack of detailed physiological studies. Some researchers speculate that the avian lagena is related to birds' navigation. The mechanism underlying homing ability of pigeons remains mysterious and one of the accepted opinions is that pigeons can detect geomagnetic information to find their way home[12,13]. The problem of this opinion is that no specific magnetic sensory receptor has yet been identified. One study analyzed the element ingredients of otoliths from the lagena, the saccule and the utricle in birds and fish using synchrotron radiation X-ray fluorescence spectroscopy (SR-XRF)[14], and found that the lagenal otoliths are rich in elements Fe and Zn. They conclud that the lagenal otoliths contain tiny magnetic particles, on which homing pigeons depend for sensation of geomagnetic information and navigation. However, this hypothesis is disputable since another group reported that the homing ability of pigeons was not impaired after their cochlea and lagena were extirpated[15].

To clarify whether homing pigeons depend on magnetic elements in lagenal otoliths for navigation, one of the key steps is to precisely determine whether the lagenal otoliths contain higher contents of magnetic elements than the saccular and utricular otoliths do. In the present study, we analyzed the contents of ferromagnetic elements (Fe, Co, Ni)[16,17] and other metal elements in lagenal otoliths of adult homing pigeons with inductively coupled plasma mass spectrometry (ICP-MS), and compared them with those in saccular and utricular otoliths. ICP-MS is one of the powerful tools for detections of trace elements and is superior to SR-XRF and energy dispersive microanalysis in detection sensitivity (at part per trillion level), elements distinguishing capacity and dynamic ranges. ICP-MS can be applied for precise isotopic analysis[18,19] and has become a preferred method for identifications of trace elements, thus it is widely used in the field of life sciences[18-20]. ICP-MS analysis for element ingredients of lagenal otoliths provides us with essential knowledge in

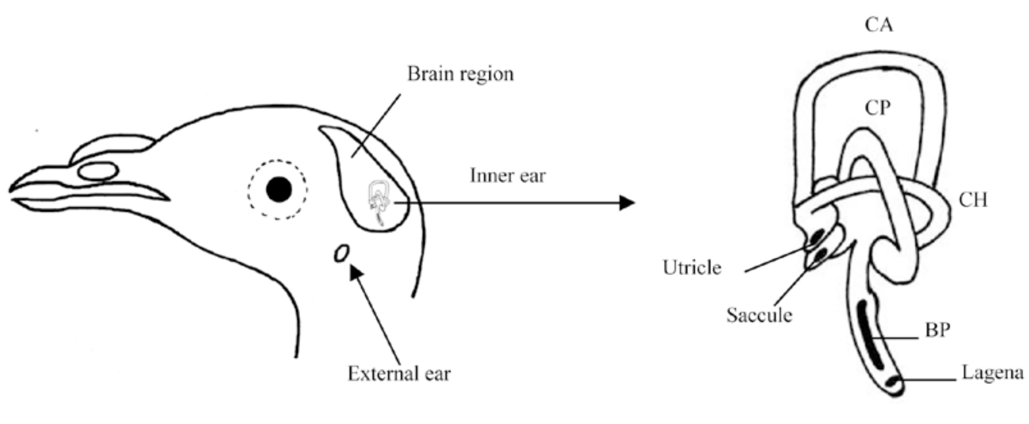

Fig. 1 Schematic descriptions of the pigeon inner ear in the skull (left panel) and the location of the macula lagena in the inner ear (right panel). BP, basilar papilla; CA, anterior canal; CP, posterior canal; CH, horizontal canal.

better understanding whether homing ability of pigeons is related to sensation for geomagnetic information by Fe and Zn in lagenal otoliths as well as the role of the lagena in the nervous system of birds.

2 Materials and methods

2.1 Collection and treatments of otolithic samples Twenty-five adult homing pigeons (Columba livia, aged from 1.5 to 4 years old, of either sex) were purchased from a local pigeon market. Otoliths in the lagena, saccule and utricle were collected separately. Given that the total weight of otoliths in each otolithic organ from a single pigeon was rather light (< 0.5 mg), otoliths in the same otolithic organ from 5 pigeons were mixed as one sample for ICP-MS analysis. HNO_3 with high purity was obtained by sub-boiling distillation of commercial MOS reagents. All solutions were prepared with Milli-Q water (18.2 MΩ·cm). The sample treatments were performed in a clean room of class 1000.

Adult homing pigeons were deeply anaesthetized with 20% urethane and decapitated. The heads were dissected into two parts in sagittal plane and the brain tissues were removed. Under a stereomicroscope, the lagena, saccule and utricle were isolated from the osseous and connective tissues of the skull respectively, with clean anti-magnetic forceps, and then they were rinsed with Milli-Q water for 3 times. The tegman was removed and otoliths were extracted into Teflon digestion vessels with caps. Digestion of the otolithic samples was carried out by carefully adding 1 mL 70% HNO_3 to the vessels. The vessels were then placed on a hot-plate at 140 ºC to allow evaporation of acid to dryness. 1 mL70% HNO_3 was added into the vessels again, followed by 4-h heating at 120 ºC on a hot-plate. Vessels were then uncapped. The sample-containing solutions were concentrated to around 0.5 mL at 140 ºC and then transferred into clean medical PET bottles, followed by dilution to 10 mL for ICP-MS analysis. A few otolithic samples without acid treatment were placed on copper disks for morphological studies with scanning electron microscopy (SEM).

2.2 Elements analysis ICP-MS is a powerful tool for trace element analysis, using inductively coupled plasma as its ion source. Fig. 2 shows the workflow of ICP-MS. The specific equipment for analysis of our sample solution was ELAN DRCII ICP-MS (Sciex/Perkin-Elmer). This instrument consists of a sample introduction system, an ICP torch, lens, a dynamic reaction cell (DRC), a quadrupole mass analyzer, a detector, a data acquisition and processing system, and a vacuum system. Operating parameters for ICP-MS are listed in Table 1. Before the sample test, the instrument was automatically optimized with the computer. A series of multi-element mixed standard solutions prepared from single-element standard solution (Alfa-Aesar) were analyzed to fit calibration curve. The standard material (United States Geological Survey) was tested for quality monitoring at intervals of every 10 samples. The sample solution was converted into aerosol via a nebulizer, and then introduced into the plasma torch. The plasma torch converted the aerosol into a stream of positively charged ions of low kinetic energy. Mass analyzer separated the ions according to their mass-to-charge ratios (m/z). Then the detector quantized ions emerging from the mass analyzer and determined the contents of elements based on

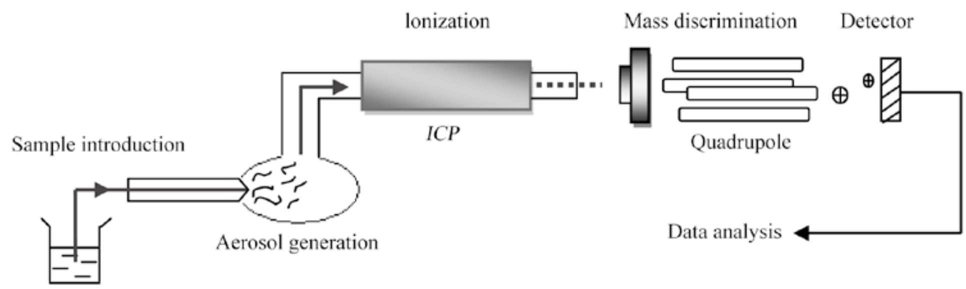

Fig. 2 Schematic diagram shows the workflow of inductively coupled plasma mass spectrometry (ICP-MS).

Table 1. Operating parameters of Elan DRCII ICP-MS

Parameter	Value
Nebulizer gas flow rate (L/ min)	0.93
Auxiliary gas flow rate (L/ min)	1.2
Plasma gas flow rate (L/ min)	15
Autolens	Open
RF power (W)	1150
Scanning mode	peak hopping
Replicates	5
Oxide and doubly charged ions	ratio CeO^+/Ce^+ measured < 1.5%, ratio Ba^{2+}/Ba^+ measured < 1.5%

the peak intensity.

2.3 Detection sensitivity and precision of ICP-MS The blank solution (2% HNO_3) was measured for 11 times continuously in the mode of single-point peak-hopping and 3 second integration time. Detection sensitivity was determined as 3 times of the standard deviation of blank solution. Detection sensitivity for the analyzed elements was up to 1 ng/L. Relative standard deviation (RSD) of standard solutions from 9 parallel tests was no more than 3%.

2.4 Data analysis $CaCO_3$ accounts for 96.2% of otolith weight and normalization of element contents in otoliths to Ca can effectively reduce inter-sample variance[21]. So, the contents of ferromagnetic elements (Fe, Co, Ni) and other metal elements in the lagenal, saccular and utricular otolith samples of adult homing pigeons were normalized to the content of Ca in the corresponding samples. Within-subject *ANOVA* was performed to compare the contents of these elements in lagenal otoliths with those in the saccular and utricular otoliths.

3 Results

3.1 Morphologies of lagenal, utricular and saccular otoliths SEM of otoliths with the connective tissue removed and with no acid treatment was performed using an environmental scanning electron microscope (XT 30ESEM-TMP, Philip Inc.). Otoliths in the lagena of homing pigeons were found to be typically cylindrical with triangular pyramid shaped ends (Fig. 3A and B), and the length of lagenal otoliths was around 10 μm. Similar findings in chicken lagenal otoliths were reported previously[9]. We also observed morphologies of the saccular and utricular otoliths in homing pigeons with SEM and found that their shapes resembled that of lagenal otoliths (Fig. 3C and D).

3.2 Contents of ferromagnetic elements in lagenal otoliths Contents of the elements in lagenal, utriular and saccular otoliths of adult homing pigeons were normalized to Ca and the numerical values are summarized in Table 2. The contents of ferromagnetic elements (Fe, Co, Ni) in lagenal otoliths were less than 0.7% (normalized to Ca element) and were the same order in magnitude as those in saccular and utricular otoliths. Within-subject *ANOVA* analysis revealed that the content of Fe in lagenal otoliths was not significantly different from that in utricular otoliths (0.6713 ± 0.0558% *vs*. 0.5700 ± 0.0292%, $n = 5$, $P > 0.05$) and was even lower than that in saccular otoliths (0.6713 ± 0.0558% *vs*. 0.8233 ± 0.0429%, $n = 5$, $P < 0.01$). The content of Co in lagenal otoliths was lower than that in saccular otoliths (0.1740 ± 0.0187 % *vs*. 0.3150 ± 0.0087 %, $n = 5$, $P < 0.01$) and higher than that in utricular otoliths (0.1740 ±

Table 2. Contents of ferromagnetic elements and other metal elements (%) in pigeon otoliths analyzed with ICP-MS

elements	lagena(n = 5)	utricle(n = 5)	saccule(n = 5)
Fe	0.6713 ± 0.0558	0.5700 ± 0.0292	0.8233 ± 0.0429
Co	0.1740 ± 0.0187	0.1191 ± 0.0088	0.3150 ± 0.0087
Ni	0.0044 ± 0.0003	0.0031 ± 0.0001	0.0124 ± 0.0030
Na	1.5531 ± 0.1454	1.9776 ± 0.3125	2.6851 ± 0.5398
Mg	1.9056 ± 0.1707	1.7502 ± 0.0905	1.9495 ± 0.2627
Al	0.1109 ± 0.0270	0.1396 ± 0.0625	0.2765 ± 0.0824
K	1.9312 ± 0.2278	2.2774 ± 0.3820	2.7146 ± 0.6516
Mn	0.0170 ± 0.0025	0.0230 ± 0.0067	0.0169 ± 0.0020
Pb	0.0185 ± 0.0028	0.0150 ± 0.0041	0.0361 ± 0.0102
Zn	0.1170 ± 0.0195	0.1344 ± 0.0116	0.3193 ± 0.0486
Ba	0.0112 ± 0.0018	0.0102 ± 0.0017	0.0253 ± 0.0027
Cu	0.0080 ± 0.0015	0.0067 ± 0.0014	0.0124 ± 0.0013

$CaCO_3$ accounts for 96.2% of otoliths weight. Contents of elements are normalized to content of Ca. Data were presented as mean ± SEM.

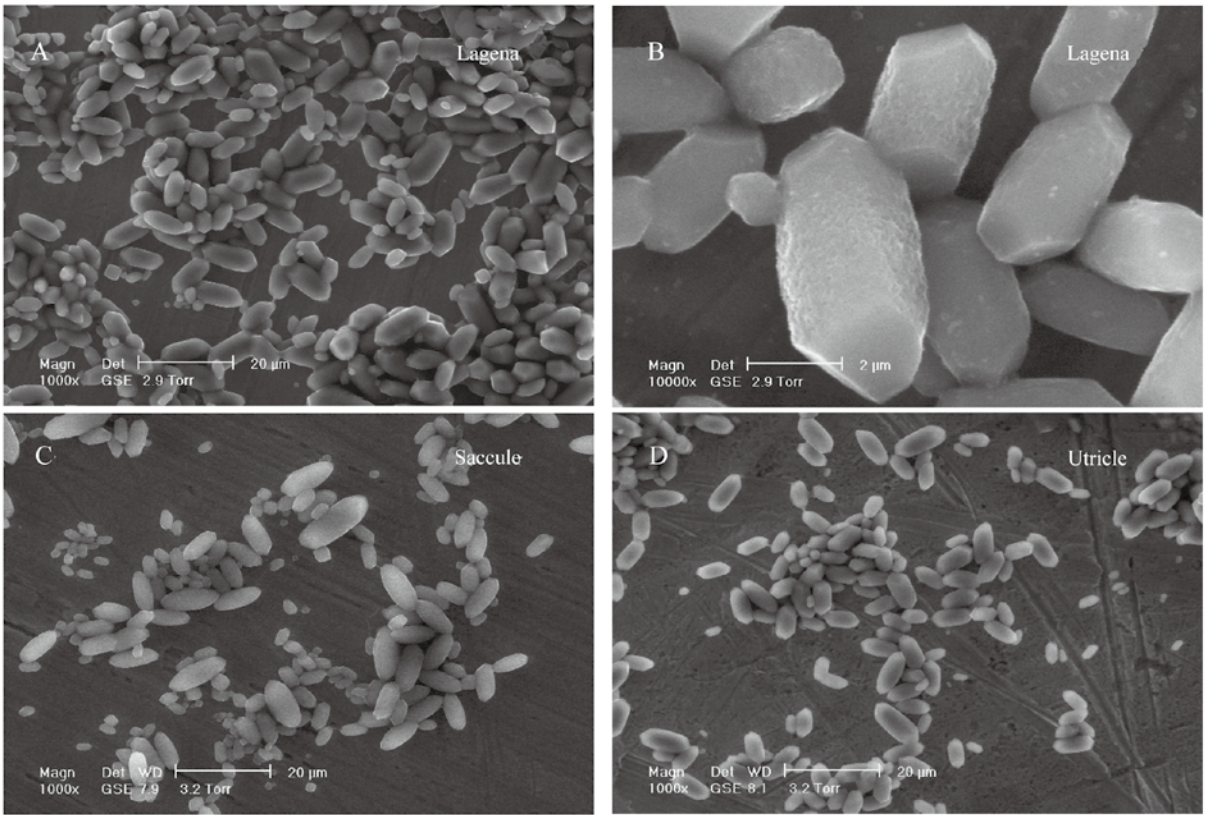

Fig. 3 Morphological observations of otoliths in homing pigeons using SEM. A: morphology of otoliths from the macula lagena at low magnification. Most of the lagenal otoliths in homing pigeons were typically cylindrical with triangular pyramid shaped ends, and the length of lagenal otoliths was around 10 µm; B: morphology of otoliths from the macula lagena at higher magnification; C: otoliths from the saccule showed similar morphological characteristics with that of lagenal otoliths; D: otoliths from the utricle also showed similar morphological characteristics with that of lagenal otoliths. Scale bar for A, C and D: 20 µm. Scale bar for B: 2 µm.

0.0187% *vs*. 0.1191±0.0088%, $n=5$, $P<0.01$). The content of Ni in lagenal otoliths was not significantly different from that in saccular otoliths (0.0044±0.0003% *vs*. 0.0124±0.0030%, $n=5$, $P>0.05$) and was higher than that in utricular otoliths (0.0044±0.0003% *vs*. 0.0031±0.0001%, $n=5$, $P<0.05$). Fig. 4A summarizes the results of statistical comparison of the contents of ferromagnetic elements (Fe, Co, Ni) in lagenal otoliths with those in utricular and saccular otoliths of adult homing pigeons.

3.3 Contents of other metal elements in lagenal otoliths As shown in Table 2, the contents of other metal elements Na, Mg, K, Al, Mn, Pb, Zn, Ba and Cu in lagenal otoliths were the same order in magnitude as those in saccular and utricular otoliths. Within-subject *ANOVA* analysis revealed that the contents of Na, Mg, K, Al, Mn and Pb were not significantly different from those in utricular and saccular otoliths ($P>0.05$) (Fig. 4B). The contents of Zn, Ba and Cu were not significantly different from those in utricular otoliths ($P>0.05$) and were lower than those in saccular otoliths (Zn, Ba: $P<0.01$; Cu: $P<0.05$, Fig. 4C).

4 Discussion

Our study demonstrates that the contents of magnetic elements in lagenal otoliths of homing pigeons are not much higher than those in utricular and saccular otoliths. Our findings do not support the hypothesis that birds depend on high contents of Fe and Zn in lagenal otoliths for sensation of geomagnetic information. In addition, we measured mag-

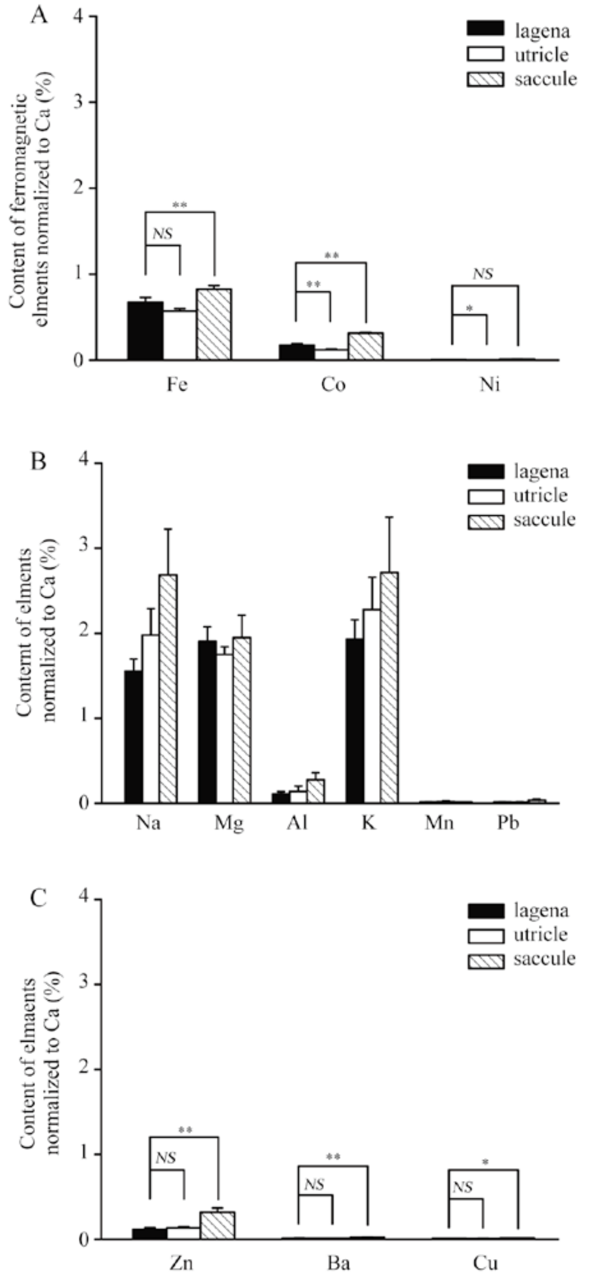

Fig. 4 Comparison of contents of metal elements in the macula lagena with those in the saccule and the utricle. A: contents of ferromagnetic elements Fe, Co, Ni were not particularly higher in the macula lagena than or were only slightly different from those in the saccule and those in the utricle; B: contents of other metal elements Na, Mg, K, Al, Mn, Pb in the macula lagena were not significantly different from those in the saccule or from those in the utricle; C: contents of other metal elements Zn, Ba, Cu in the lagena were not significantly different from those in the utricle, and were lower than those in the saccule. Data were expressed as mean±SEM. *P < 0.05; **P < 0.01; *NS*, no significant difference.

netic characteristics of lagenal otoliths in adult homing pigeons with Superconducting Quantum Interference Devices (SQUID, MPMS XL-7, Quantum Design), but did not discover any regular magnetic characteristics under available sensitivity and accuracy of this instrument (data not shown). Therefore, we speculate that the contents of ferromagnetic elements (Fe, Co, Ni) in lagenal otoliths of adult homing pigeons may be not high enough for the homing pigeons to detect geomagnetic information. Alternatively, these elements exist in otoliths as non-magnetic form. Our study does not suggest that homing pigeons depend on the lagena for sensation of geomagnetic information. One hypothesis believes that the beaks of homing pigeons are sensitive to magnetic stimulation[22,23].

Analysis of otoliths with SR-XRF by Harada *et al.*[14] showed that the lagenal otoliths are rich in elements Fe and Zn (the content of Fe normalized to Ca was around 0.7%), while the saccular and utricular otoliths rarely contain detectable Fe and Zn. However, our results in homing pigeon otoliths with ICP-MS are different from their findings. Firstly, we have detected the elements Fe and Zn not only in lagenal otoliths, but also in utricular and saccular otoliths. The contents of Fe and Zn in lagenal otoliths are the same order in magnitude as those in saccular and utricular otoliths, and even lower than those in saccular otoliths. Secondly, we have detected some metal elements that Harada *et al.* did not detect, including ferromagnetic elements Co and Ni. Contents of these elements in lagenal otoliths of homing pigeons are not much higher than those in utricular and saccular otoliths. These discrepancies are possibly caused by usage of different element analytical methods. SR-XRF depends on characteristic X-ray emitted after atoms are excited by high-energy particles for element discrimination, while ICP-MS uses inductively coupled plasma as ion source, separates the ions based on mass-to-charge ratio (m/z), and determines the contents of elements from the peak intensity. ICP-MS is more advantageous for trace analysis of multi-elements, owing to its excellent detection sensitivity (at part per trillion level), stability and discrimination capacity. In addition, it has simple spectra, wide linear dynamic ranges and multi-isotopic capability for most elements. These advantages make ICP-MS be the ideal technique for analysis of metal elements in biological samples.

Our experiment shows that lagenal otoliths of homing pigeons are similar to utricular and saccular otoliths in the following aspects. Firstly, the type of ferromagnetic elements and other metal elements contained in lagenal otoliths is the same as that in utricular and saccular otoliths. The content of each element in lagenal otoliths is the same order in magnitude as that in the other two kinds of otoliths in the vestibular system. The element contents in lagenal otoliths are close to those in utricular otoliths, and lower than those in saccular otoliths. Secondly, the lagenal otoliths are typically cylindrical with triangular pyramid shaped ends, similar in shape to saccular and utricular otoliths. These similar attributes of lagenal otoliths and those in the vestibular system in birds suggest that they may be crystallized with the same origin and their generation processes are similar. The lagena may play a similar role in sensing gravitational and acceleration signals as the utricle does. Current evidences from morphological and anatomical studies[8,11] indicate that the avian lagena mainly sends neural projections to the vestibular nuclei and the cerebellum, and at an obviously lesser extent to the auditory nuclei. It is also reported that lagenal hair cells are insensitive to sound signals[24]. The functions of the macula lagena in birds are still unclear. We speculate that the avian lagena has evolved to an organ which mainly performs vestibular functions, for the purpose of three-dimensional flight. However, further studies are needed to clarify the following issues. What is the role of the lagena in the avian nervous system? Why is the lagena preserved in birds, but lost in mammals during the evolution? Is the lagena related to homing pigeons' navigation?

Acknowledgements: ICP-MS analysis was performed in ICP-MS Laboratory, School of Earth and Space Sciences, University of Science and Technology of China. We thank Mr. Zhen-Hui HOU for his technical assistance. Scanning electron microscopy of otoliths was performed in Laboratory of Engineering and Material Science, University of Science and Technology of China. We thank Mr. Ming Gong and Mr. Fei Yu for their technical assistances. This work was supported by the National Natural Science Foundation of China (No. 30470560 and 30730041), the National Basic Research Program of China (No. 2007CB512306), and the Knowledge Innovation Project of Chinese Academy of Sciences (No. KSCX1-YW-R-36).

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信鸽瓶状囊耳石中磁性元素的电感耦合等离子体质谱分析

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摘要：目的 鸟类瓶状囊器官位于耳蜗的顶端，含有耳石并有神经支配，但其功能尚不清楚。有人认为瓶状囊的耳石中Fe、Zn等元素含量较高，使得鸟类能够感受地球磁场而具有导航能力，但对于这个假说目前还存在争议。为澄清这个争议，本研究分析成年信鸽瓶状囊耳石磁性元素的含量是否比内耳球囊和椭圆囊耳石更丰富。**方法** 应用具有高灵敏度和稳定性的电感耦合等离子体质谱法(ICP-MS)测定成年信鸽瓶状囊耳石样品中磁性元素Fe、Co、Ni以及其它金属元素的含量(以Ca含量作为基准的百分比含量)并同内耳的球囊和椭圆囊耳石中的这些元素的含量进行比较。**结果** 成年信鸽瓶状囊耳石中磁性元素Fe、Co、Ni的含量不足Ca元素的0.7%，与球囊和椭圆囊耳石中的含量为同一数量级。瓶状囊耳石中Fe的含量与椭圆囊耳石相比无显著性差异且低于球囊耳石；瓶状囊耳石中Co的含量低于球囊耳石，但高于椭圆囊耳石；瓶状囊耳石中Ni的含量与球囊相比无显著性差异，但高于椭圆囊耳石。瓶状囊耳石中其它金属元素Na、Mg、K、Al、Mn、Pb的含量与球囊和椭圆囊耳石相比无显著性差异，但Zn、Ba、Cu的含量低于球囊耳石。**结论** 结果表明成年信鸽瓶状囊耳石中磁性元素的含量极低而且不比内耳球囊和椭圆囊耳石更丰富，从而不支持信鸽因其瓶状囊耳石中含有较高的Fe、Zn等元素而能够感受地球磁场这一假说。信鸽瓶状囊的耳石与椭圆囊的耳石在形态、元素组成及含量水平上具有相似性，提示这两种耳石器官可能在感受重力和加速度信号中共同起作用。

关键词：信鸽；瓶状囊；耳石；磁性元素；球囊；椭圆囊；电感耦合等离子体质谱