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Histological Structure Difference of Dog's Olfactory Bulb Between Different Age and Sex

WEI Qin-guo, ZHANG Hong-hai*, GUO Bing-ran

（*College of Life Science, Qufu Normal University, Qufu* 273165, *China*）

Abstract: The purpose of this article is to detect sex and age difference in the structure of the olfactory bulb in dogs by histological methods. The thickness of the olfactory bulbs layers and its main cells were analyzed comparatively with the methods of HE-staining and statistics, through which we studied the development course of dogs' olfactory bulb and the structural differences which affect the olfaction in both males and females. The results showed that between both male and female juveniles and adult males and females, the difference in thickness of each layer is not significant. But the difference in quantity of mitral cells between adult males and females was significant. Meanwhile, the structure of every layer in juvenile dogs was apparent while the volume and the weight of adult dogs' olfactory bulb and each layer's width increased significantly. On the other hand, the density of each layer's cells decreased apparently. Our results demonstrated that the olfactory bulb developed with age, and the apparent differences in morphology and quantity of mitral cells between males and females may be one of the reasons leading to the sexual variations of olfactory sensitivity.

Key words: Histology; HE-staining; Olfactory bulb; Mitral cell

家犬嗅球组织学结构的性别和年龄差异

韦钦国，张洪海*，郭炳冉

（曲阜师范大学 生命科学学院，山东 曲阜 273165）

摘 要：用组织学方法研究家犬嗅球的结构，观察家犬嗅球内结构的性别和年龄差异，依据常规 HE 染色法及数理统计学原理对家犬嗅球各层宽度，主要细胞的数量进行比较统计学分析，探讨嗅球内部结构的发育过程以及性别差异对雌雄动物嗅觉差异的影响。结果表明：雌雄幼年家犬嗅球内各层结构差异不显著；成年家犬也表现出同样的结果，但是成年动物的僧帽细胞形态、数量差异极显著。分析发现，幼年家犬嗅球各层结构都已比较明显，成年家犬嗅球体积和重量明显增加，各层宽度明显变宽，各层细胞密度显著降低，说明嗅球也处在不断的发育完善过程之中。同时僧帽细胞的差异可能是造成雌雄动物嗅觉差别的原因之一。

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The sense of smell is a primal sense for dogs. From an evolutionary standpoint, it is one of the most ancient senses. But research on olfaction lags far behind research on vision and hearing as it is harder to study the olfactory system. In 1991, Linda Buck and Richard Axel discovered the family of transmembrane proteins that were believed to be the odor receptors and some of the genes that encode them. They cloned and characterized 18 different members of an extremely large multigene family that encodes the seven transmembrane proteins whose expression was restricted to the olfactory epithelium. This was a seminal breakthrough in our potential understanding of the olfactory system and they were awarded the Nobel Prize in 2004. Since then, many studies on the olfactory system have been conducted.

The olfactory bulb is the relay station in the passage of the olfactory signal's conduction. The main structure of the olfactory bulb includes olfactory nerve layer,

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* 通讯作者(Corresponding author) , E-mail: zhanghonghai67@126.com
第一作者简介：韦钦国(1982-), 男, 硕士, E-mail: qgwei2008@163.com

olfactory glomerular layer, external plexiform layer, mitral cell layer, internal plexiform layer and granule cell layer (Zhu, 2002). All of these layers are arranged very clearly and regularly in the olfactory bulb. These features of the olfactory bulb's structure make it easier for information processing, and they also provide a structural foundation for the spatial encoding of olfactory information.

According to classical research, the olfactory bulb includes four kinds of cells: mitral cell, granule cell, tufted cell and short axon cell (Colonnier, 1968). Of these neurons, the granule cell has long been known to be morphologically unusual for having no typical axon, and recent electron-microscopic studies have shown that it participates in unusual reciprocal synaptic connections with the mitral cells (Hirata, 1964; Andres, 1965; Rail et al, 1966). Mitral cells are the largest cells in the olfactory bulb, and they are also the major efferent neuron of the olfactory bulb as indicated by light microscopy (Cajal, 1911) and electron microscopy (Andres, 1965) studies. The dendrites of mitral cells can be classified into primary and secondary dendrites, and both of the smooth primary and secondary dendrites pass superficially into the external plexiform layer, but only the primary dendrites project down to the olfactory glomerulars (Mori et al, 1983; Orona et al, 1984). Within the glomerular the mitral cell dendrites are in synaptic contact with the olfactory nerves and also with the periglomerular cells, but elsewhere the only synapses on mitral cells are the "reciprocal synapses" with the granule cells. (Jackowski et al, 1978; Rall et al, 1966). Anatomical research has suggested that there are inhibitive synapses on mitral cells (Crespo et al, 2001). Mitral cells, as the major efferent neurons of the olfactory bulb, also play an important role on the conduction and modification of the olfactory signal. To carry out studies on them may preliminarily explain why dogs can distinguish so many odors. To find the difference between different sexes may supply reasons for explaining the sexual variance in smell sensitivity of dogs.

The impulse resulted from the binding of odor and olfactory receptors conduct to mitral cell's dendrites through olfactory receptor neurons' axons. From the mitral cells the message is sent directly to the higher levels of the central nervous system in the corticomedial amygdala portion of the brain (via the olfactory nerve tract) where the signal process is decoded and olfactory interpretation and response occurs. The granule cell would deal with the impulse during the course of the conduction from mitral cells to the central nervous system.

During the course of olfactory signal conduction, the olfactory receptor cells which express the same receptors from axons are bundled in groups of 10—100 to penetrate the ethmoidal cribriform plate of bone, reaching the olfactory bulb of the brain where they converge to terminate with post-synaptic cells to form synaptic structures called glomerulars. The glomerulars are connected in groups that converge into mitral cells. Physiologically, this convergence increases the sensitivity of the olfactory signal sent to the brain and achieves the goal of spatial encoding. Therefore the olfactory bulb plays an important role in information modification and encoding during the conduction of the olfactory signal.

As we all know, the sexual variation is the main difference in animals. And there are certain difference in smell sensibility between males and females (Koelega & Koster, 1974). Many studies on tissue and organ differences result from sexual variation have been conducted in recent years. However, there were few studies on structure difference in olfactory system between males and females, especially for dogs.

There are already many studies on the olfactory system at the cellular and molecular level. Dogs, which have a powerful sense of smell, belong to macrosmatic animals. Yet, the histological structure of dogs' olfactory bulb remains largely unknown.

In this paper, we detected sex and age differences in the structures of dogs' olfactory bulb by histological method. The thickness of olfactory bulb layers and its main cells, such as mitral cells and granule cells, were analyzed comparatively using HE-staining and statistics, through which we studied the development of dogs' olfactory bulbs and the structural differences which may affect olfaction in both males and females.

1 Materials and Methods

1.1 Subjects

In this study, we used three male and three female juvenile dogs (one month old) whose weight were 1.5±0.3 kg on average and three adult male and female dogs whose weight were 20±3.6 kg on average (fourteen months old). All dogs used in this study were healthy.

1.2 Methods

The dogs were anesthetized with Pentobarbital Sodium and then perfused with 4% depolymerized

paraformaldehyde. The heads were removed and the skull were opened to expose the olfactory bulb, and then fixed for an additional 48h at 4°C. The olfactory bulbs were taken out and weighed with electronic balance, and then dehydrated and embedded in paraffin using standard techniques. The olfactory bulb was sectioned in the largest coronal plane at 10 micrometers and the sections were mounted on slides. Alternate slides were stained for routine histological studies with hematoxylin and eosin. We chose the slides which were at the same position in the olfactory bulb to analyze and took photos, measured the thickness of each layer and the quantity of main cells per standard area (1000μm^2) by Motic Images Advanced 3.2. This software can collect these data automatically. The statistical analysis was carried out by SPSS 13.0, and the significance of differences was tested by *t*-test.

2 Results

We studied the difference of olfactory bulb structure between different ages and sexes. The results showed that there was no significant difference in the width of each layer of the olfactory bulb between males and females of juvenile dogs as well as adult dogs. However, there were significant differences in the morphology and quantity of mitral cells between male and female adult dogs. This might be one of the most important reasons for the difference of smell sensitivity between females and males. But there might be other factors that affect the difference of smell sensitivity. Further studies are needed to find the exact reason for this difference.

Tab. 1 Comparison of MOB's structure between juvenile and adult dogs of different sexes

Layers	Male juvenile （μm） (Mean±*SD*)	Female juvenile （μm） (Mean±*SD*)	*P*	Adult male （μm） (Mean±*SD*)	Adult female （μm） (Mean±*SD*)	*P*
ONL	236.09±121.62	220.81±54.65	*P*>0.05	469.45±209.14	454.55±200.51	*P*>0.05
GL	155.80±51.47	162.21±44.23	*P*>0.05	282.93±65.01	297.06±68.82	*P*>0.05
EPL	260.13±82.85	263.64±47.18	*P*>0.05	398.35±74.66	351.07±68.46	*P*>0.05
ML	107.27±20.95	110.32±17.44	*P*>0.05	154.34±28.94	157.06±25.75	*P*>0.05
IPL	75.62±16.62	75.95±13.35	*P*>0.05	87.79±18.21	87.96±19.18	*P*>0.05
GRL	604.08±73.37	602.83±37.40	*P*>0.05	673.52±132.47	662.59±160.45	*P*>0.05

MOB: main olfactory bulb; ONL: olfactory nerve layer; GL: olfactory glomerular layer; EPL: external plexiform layer; ML: mitral cell layer; IPL: internal plexiform layer; GRL: granule cell layer.

Tab. 2 Comparison of cell number of standard area in each layer of MOB between juvenile and adult dogs of different sexes

Layers	Male juvenile (Mean±*SD*)	Female juvenile (Mean±*SD*)	*P*	Adult male (Mean±*SD*)	Adult female (Mean±*SD*)	*P*
ONL	5.39±0.91	6.16±1.87	*P*>0.05	4.58±1.23	4.88±1.56	*P*>0.05
GL	8.89±1.59	11.08±1.97	*P*<0.01	6.41±1.23	7.03±2.24	*P*>0.05
EPL	2.93±0.96	3.25±0.43	*P*>0.05	2.22±0.72	2.64±1.04	*P*>0.05
ML	83.6±3.99	85.13±3.31	*P*>0.05	51.5±7.09	66.64±3.52	*P*<0.05
GRL	10.81±3.74	12.66±4.69	*P*>0.05	9.08±2.45	9.57±2.60	*P*>0.05

MOB, ONL, GL, EPL, ML, IPL, GRL are the same as Tab. 1. Standard area is 1000μm^2.
The number of mitral cells is the quantity of cells in each visual field.

Tab. 3 Comparison of the width of each layer of MOB and cell number in standard area between juvenile and adult dogs

Layers	Cells' number (Mean±*SE*)			Width of each layer(Mean±SE)		
	Juvenile	Adult	*P*	Juvenile	Adult	*P*
ONL	5.58±0.16	4.73±0.15	*P*<0.01	115.60±2.17	256.52±4.86	*P*<0.01
GL	9.47±0.25	6.72±0.19	*P*<0.01	156.60±0.91	290.13±1.19	*P*<0.01
EPL	3.01±0.11	2.43±0.10	*P*<0.01	260.61±1.43	372.99±1.38	*P*<0.01
ML	83.98±0.50	59.03±0.99	*P*<0.01	107.88±0.68	155.47±0.57	*P*<0.01
GRL	11.27±0.52	9.32±0.27	*P*<0.05	607.51±3.44	668.29±2.90	*P*<0.01

ONL, GL, EPL, ML, GRL are the same as Tab. 1.

The results also showed that there were significant differences in the olfactory bulb structure between adults and juveniles. The olfactory bulb's weight in adult dogs was much heavier than that in juvenile dogs (Fig.1). The olfactory bulb's each layers was much wider than that in juvenile dogs. The density of each layer's cells in juveniles was much higher than that in adults. All of these suggested that the olfactory bulb developed during the course of a dog's growth.

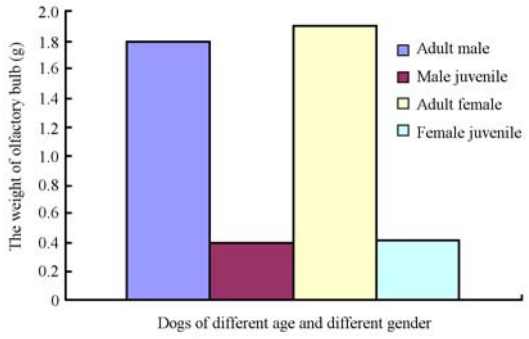

Fig. 1 Comparison of olfactory bulb's weight between dogs of different ages and sexes

2.1 Olfactory nerve layer (ONL)

The olfactory nerve layer, at the margin of the olfactory bulb, mainly consisted of axons that were bundled in groups of 10－100 by olfactory receptor neurons (Fig.2). The olfactory neurons contact with odors in the atmosphere, and conduct this signal to a certain quantity (2－3) and certain type of olfactory glomerulars by its axons through nerve impulses. It achieves the goal of olfactory information's spatial encoding during this course of conduction. We found that many bundles of fibers formed by olfactory neurons' axons reached glomerulars (Fig.2). The results of a t-test showed that there was no significant difference in olfactory nerve layer width between female and male juvenile dogs (P>0.05). The width of the olfactory nerve layer in male juvenile dogs was 236.09 μm on average and about 220.81 μm for female juveniles. There was also no significant difference in the olfactory nerve layer's width between adult female and male dogs (P>0.05). The width of the olfactory nerve layer in adult male dogs was 469.45 μm and 454.55 μm in adult female animals. However, the difference in the olfactory nerve layer's width and the cells' density in this layer between adult and juvenile dogs reached the significant level (P<0.01).The width of the olfactory nerve layer distributed unevenly in the olfactory bulb, and the widest position was at the apex of the bulb (Fig.2). The widest part of juvenile dogs' olfactory nerve layer was about 750 μm and about 1 200 μm in adult animals. The olfactory neurons in certain areas of the olfactory epithelium accept odorant information and conduct it to certain areas of the olfactory nerve layer according to the principal of space to space projection.

2.2 Olfactory glomerular layer (GL)

The olfactory glomerular layer at which the mitral cell dendrites are in synaptic contact with the olfactory nerves and also with the periglomerular cells, consists of glomerulars which are made up of the synapses described above. Oval olfactory glomerulars are arranged regularly in the olfactory bulb, and are surrounded by glial cells. Periglomerular cells which are distributed around the glomerulars are interspace neurons and they connected closely with glomerulars (Fig.3).

The olfactory information can be converged at this layer. The olfactory neurons' impulse was conducted to mitral cells, tufted cells and periglomerulars in this layer, through which the impulses could be modified. According to the result of a statistical analysis, there was no significant difference in the width of the olfactory glomerulars layer between male and female juvenile dogs. The average width of this layer in male juvenile dogs was 155.8 μm, and 162.21 μm for female animals. There was also no significant difference in the width of olfactory glomerulars layer between adult male and female dogs, but the width increased significantly with age. The average width of this layer in adult male dogs was 282.93 μm and 297.06 μm in female animals. On the other hand, the density of cells in this layer decreased significantly with age and there was also obvious difference in the quantity of cells in this layer between male and female juvenile dogs.

2.3 External plexiform layer (EPL)

This layer was mainly made up of the primary dendrites of mitral cells and tufted cells, tufted cells and nerve fibers. The tufted cells are distributed unevenly, and the cells increased in size closer to the mitral cell layer (Fig.4). The average width of the EPL was 262.13 μm for male juvenile dogs and 263.64 μm for female juvenile dogs. The result of a t-test demonstrated that the difference of the EPL's width between juvenile dogs of different sexes was not at the significant level (P>0.05). The average width of the EPL was 398.35 μm in adult male dogs and 351.07 μm in adult female dogs. There was no significant difference between them, but the

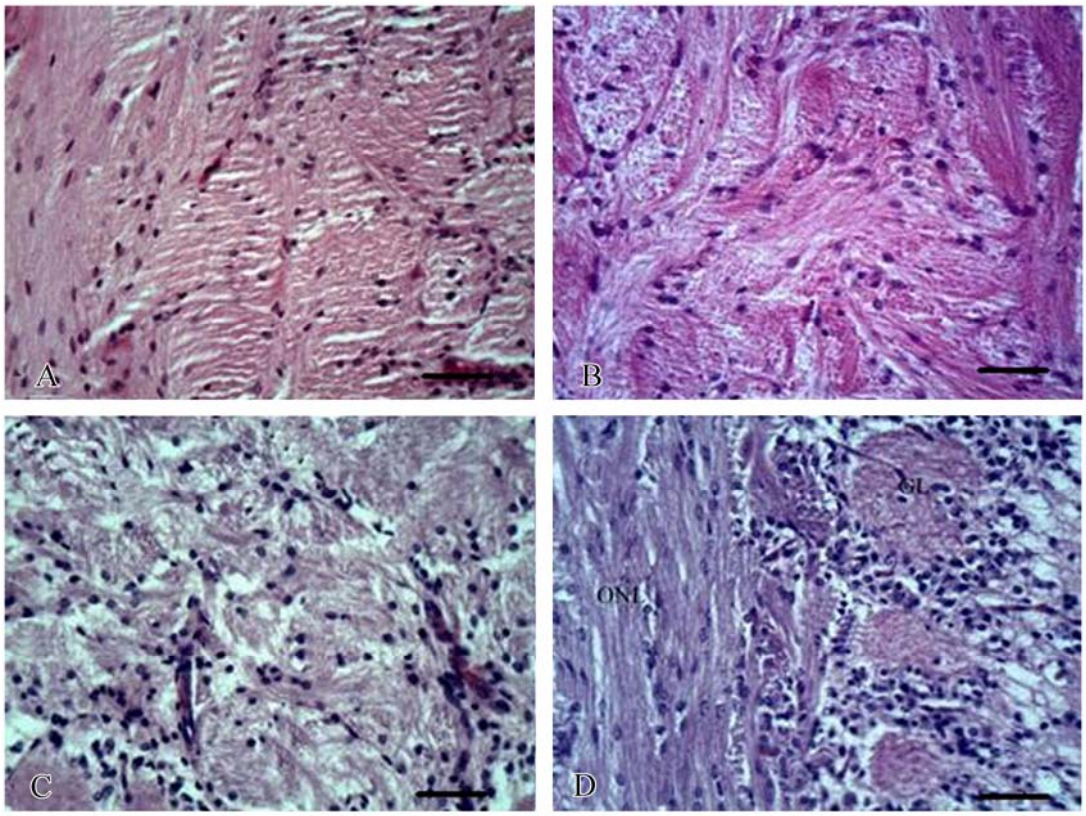

Fig. 2 ONL of dog's olfactory bulb HE (10×40)

A: Adult male; B: Adult female; C: Male juvenile; D: Female juvenile (ONL & GL).

ONL: olfactory nerve layer; GL: olfactory glomerular layer. Scale bar=50μm.

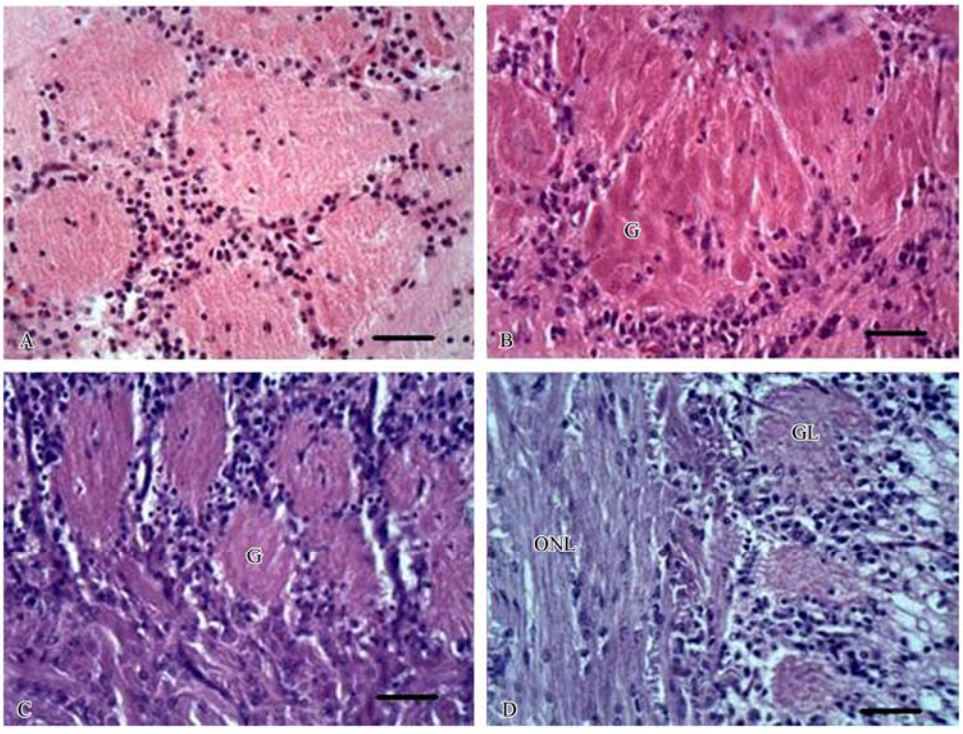

Fig. 3 GL of dog's olfactory bulb HE (10×40)

A, B, C, D, ONL, GL are the same as Fig. 2; G: glomerular. Scale bar=50μm.

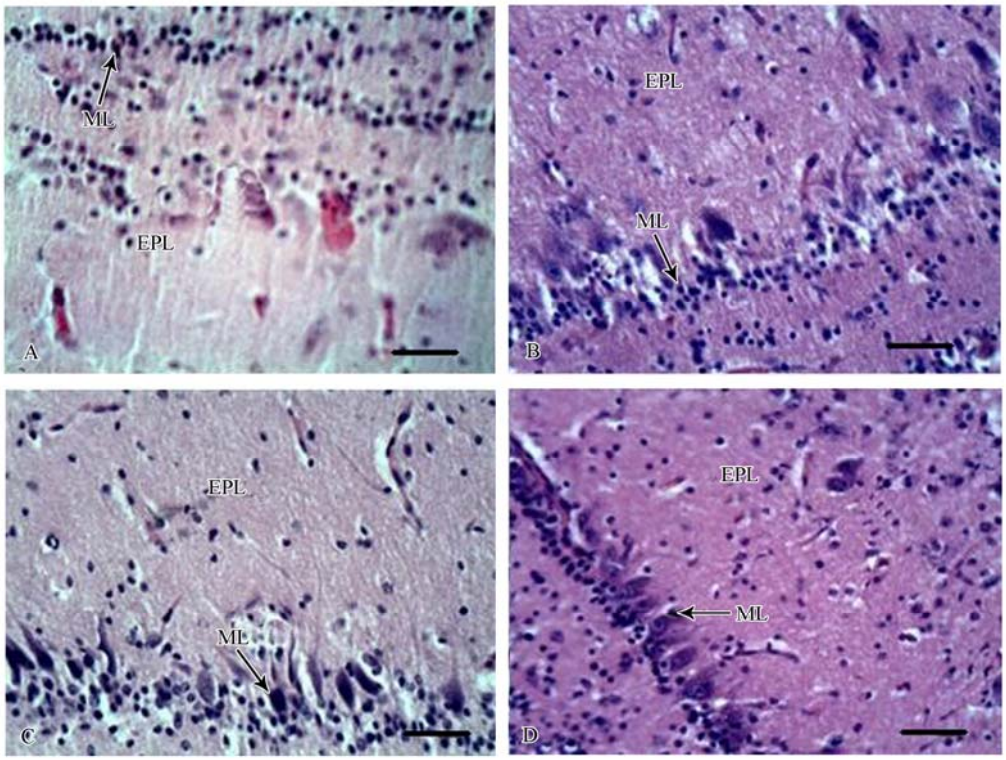

Fig. 4 EPL and ML of dog's olfactory bulb HE (10×40)

A, B, C, D are the same as Fig. 2; EPL: external plexiform layer, ML: mitral cell layer. Scale bar=50μm.

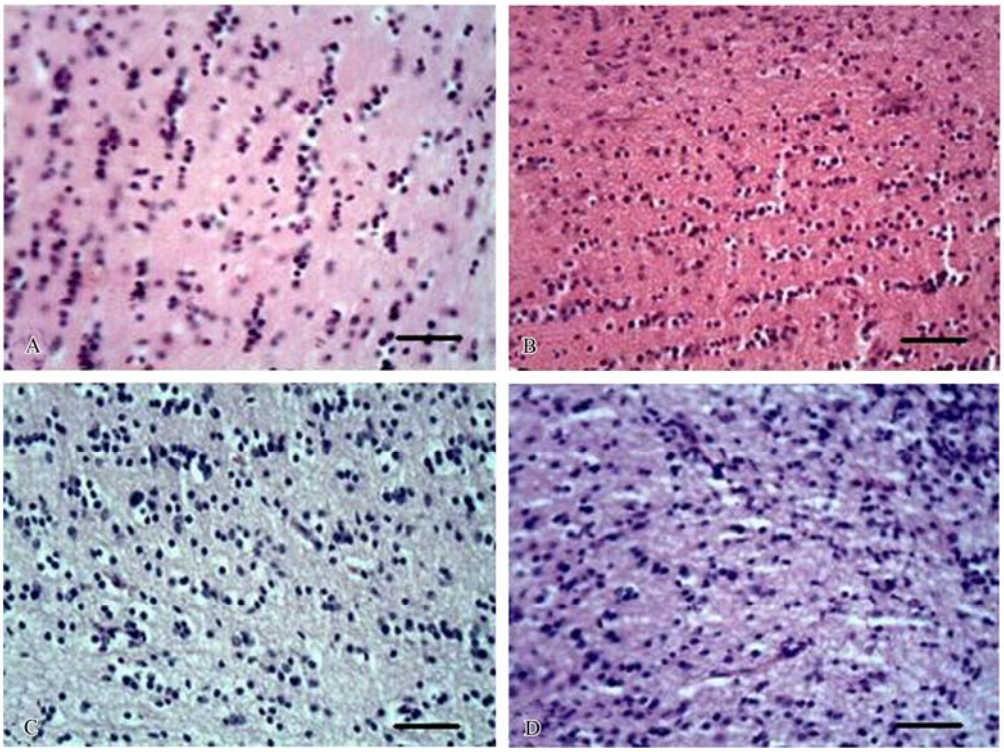

Fig. 5 GRL of dog's olfactory bulb HE (10×40)

A, B, C, D are the same as Fig. 2; GRL: granule cell layer. Scale bar=50μm.

width increased significantly with age. And there was significant difference in cells' density in this layer between adults and juveniles.

2.4 Mitral cell layer (ML)

This layer mainly included mitral cell bodies and their dendrites, tufted cells and a small quantity of granule cells. The pyramidal mitral cells are the largest cell in the olfactory bulb. The primary dendrites, which are somewhat larger than the secondary dendrites, extend more or less rapidly across the plexiform layer, and enter the glomerular formations in the superficial layer of the olfactory bulb (Fig.4). Mitral cells excite granule cells while granules inhibit mitral cells. This layer can unite the olfactory information during the course of signal efference. Mitral cells are the secondary olfactory neurons, and their axons project to the cortex of the central nervous system. The olfactory nerve axons are in synaptic contact with the mitral cell dendrites within the glomerulars, and the impulses are conducted to the mitral cells in this area. It had long been demonstrated that it is a kind of stimulant synapse modulated by γ-aminobutyrate (γ-GABA). The most important feature of mitral cells is that it is only in synaptic contact with olfactory nerves belonging to the same groups. As described above, olfactory glomerulars are arranged regularly in the olfactory bulb (Fig.3). Therefore, the same kind of olfactory nerves project to a certain area of the olfactory bulb, and this engenders the second spatial encoding.

Every mitral cell accepts a number of (25－100) axons belonging to the same kind of neurons, because of this, as long as one of these olfactory neurons is excited, it will excite the corresponding mitral cell. This feature enhances smell sensitivity. The mitral cell layer is a thin layer in the olfactory bulb, consisting of 1－2 layers of cells. There are also many tufted cells and granule cells in this layer. The average width of the ML was 107.27 μm in male juvenile dogs and 110.32 μm in female juvenile dogs. The result of a *t*-test demonstrated that there was no significant difference in the ML's width between dogs of different sexes ($P>0.05$).The average width of the ML was 154.34 μm in adult male dogs and 157.06 μm in adult female dogs. And there was also no significant difference between them ($P>0.05$). The width of the ML increased significantly during the course of a dogs' growth from juvenile to adult and the cells' density decreased obviously during this course.

Mitral cells are the main efferent cells in the olfactory bulb, and there was no significant difference in size and quantity between females and males in juvenile animals ($P>0.05$). The color of nucleoli of mitral cells is light and its brim is blurry in juvenile dogs. According to the results, there was a significant difference in the morphology of mitral cells between males and female adult dogs. Like its name, the morphology of females' mitral cells is mitral, and it also has obvious prominency and heavy color in nucleoli. The color of oval mitral cells in males is light. The difference in the quantity of mitral cells between males and females was significant ($P<0.01$). There were 51.5 cells on average in each visual field in males and 66.6 cells in females. This difference might be the reason for the difference in smell sensitivity between males and females as a result of the importance of mitral cells in the olfactory system.

2.5 Granule cell layer (GRL)

The granule cell layer takes up a large part of the olfactory bulb and is mainly made up of granule cells and their prominency. There are also some short axon cells in this layer. Round granule cells are the interspace neurons, and they are in synaptic contact with the mitral cells, tufted cells and short axon cells' axons and branches, among which the synapses with mitral cells are reciprocal synapses (Fig.5). The granule cells' dendrites are the key position that modulates the output of odor signal by the brain. The granule cells lie inside the olfactory bulb, and there are more of them than mitral cells. There were 11.8 cells per 1000 μm^2 on average in male juvenile dogs and about 12.7 cells in females. There was no significant difference in the quantity of cells between males and females ($P>0.05$). The density of granule cells was 9.08 cells per 1000 μm^2 on average in adult male dogs and 9.57 cells in females. The difference in the quantity of cells between males and females was not at a significant level ($P>0.05$). But there was significant difference in cells density in this layer between adults and juveniles. The width of the GRL was 604.08 μm in male juvenile dogs, 602.83 μm in female juvenile dogs, 673.52 μm in adult males and 662.59 μm in adult females. There was no significant difference between males and females according to the results of a *t*-test ($P>0.05$). From juvenile to adult, the width of the GRL increase noticeably while the quantity of cells decreased and the volume increased. This change may affect the development of the olfactory system.

3 Discussion

The olfactory bulb is the primary centrum of the olfactory system and it is the relay station in the passage of the olfactory system. We studied the olfactory bulb's structure comparatively through histological methods. According to the results from our studies, the structure of every layer in the olfactory bulb of juvenile dogs was already very developed. However, there were no significant difference in the structure of the olfactory bulb between males and females. The layer structure of the olfactory bulb in adult dogs was much clearer and the width of each layer was much wider than that of juvenile dogs. The density of cells in each layer was higher in juveniles than that in adults. There was no existent mechanism for explaining this decrease, and we presumed that this might has relation with the developmental and perfection course of olfactory bulbs of dogs. With the growth of dogs, the weight of the olfactory bulb increased. The quantity of mitral cells and granule cells decreased but they increased in size. All of these suggested that the olfactory bulb developed with the growth of the dog. There was no significant difference in the width of each layer between adult males and females. But there was a significant difference in the quantity and morphology of mitral cells between adult males and females. This difference might be one of the reasons for the difference in smell sensitivity between males and females.

The mitral cells are the largest cells in the olfactory bulb with primary and secondary dendrites which are nearly vertical and parallel to its somata respectively. The dendrites of mitral cells were incompletely surrounded by glial. The axons of mitral cells converge in bundles of fibers and come through the GRL. The conduction of impulses from olfactory receptor neurons to mitral cells and tufted cells depended on periodic occurrence and transverse inhibition (Laurent G. 1999; Jahr & Nicoll，1980). Mitral cells accept environmental excitation in the glomerulars through the input conduction of olfactory receptor neurons. And then, the active potential in M/T (Mitral & tufted) cells leads to the γ-GABA energy cycle and transverse inhabitation modulated by Glutaminesidechain. It has been suggested that this recurrent and transverse inhibition plays an important role in odor distinguishing, sense occurrence and the active synchronism of mitral cells (Segev, 1999). The transverse dendrites of M/T cells distributed in the most part of MOB (Mombaerts et al, 1996), suggests that the transverse inhabitation modulated by granule cells may control a large part of the MOB's activity. The conduction of active potentials in transverse dendrites of mitral cells may decide the scope of transverse inhabitation modulated by M/T cells.

Mitral cells are the relay station in the process of odor signal conduction in the olfactory bulb (Wang et al, 1998). Odor signals are conducted through olfactory neurons, mitral cells and granule cells to the cortex of the central nerves system and finally perceived by the animal. On the other hand, the granule cells could modulate the mitral cells. Mitral cells' quantity and its dendrites' scope decide the scope of which the odor molecule is chosen. Smell sensitivity can be enhanced by increasing the quantity of mitral cells. The wide distribution of the secondary dendrites of mitral cells suggested that they had a strong ability for modulating and processing olfactory information. The result of our experiments showed that there was a significant difference in the quantity and morphology of mitral cells between adult males and adult females, and this difference may explain the sex difference in smell sensitivity. We also found that the olfactory bulb developed during the course of a dogs' growth. However, the course of odor discerning and apperception is very complicated, and further research is needed to study the mechanism behind the intricate nerve network of the olfactory system.

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本刊主编张亚平院士入选中国改革功勋（贡献）人物候选名单

2008 年 9 月 3 日，《科学时报》刊登了由国家发改委指导，中国社科院城市发展与研究中心主办,《中国改革报》、新浪网特别支持的“中国改革与发展高峰论坛暨中国改革功勋(贡献)人物/中国改革贡献单位”推选活动候选人名单，本刊主编张亚平院士被荣誉推选为中国改革功勋(贡献)人物候选人

(http://www.sciencenet.cn/sbhtmlnews/2008/9/210578.html)。其评选活动结果有待关注。