

Morphology of Rhinencephalon and Hippocampal formation of the Bactrian Camel (*Camelus bactrianus*) with their adaptive features

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Abstract Detailed description of the brain size, rhinencephalon and hippocampal formation of the Bactrian camel is presented in our study. The brain weight of the Bactrian camel is 626 g averagely, and the encephalization quotient (EQ) value 1.3, indicating a high level of intelligence. The rhinencephalon is mature and well developed, accordant with the good olfactory sense. The hippocampus is relatively large, concomitant with the good ability of spatial memory. These anatomical features agree with the corresponding adaptive behaviors of the Bactrian camel and provide a morphological evidence of the camel to adapt to the acrid and semi-acrid environment.

Keywords Bactrian camel (*Camelus bactrianus*) · Rhinencephalon · Hippocampus formation · Adaptation · Indusium griseum (IG)

Introduction

The Bactrian camel lives in the acrid and semi-acrid area of the northwest China and Mongolia characterized by dense desert distribution, tremendous temperature differences between day and night, frequent and strong wind and extraordinarily low humidity. The Bactrian camel has evolved effective strategies to survive such environments, such as the appropriate structure of the kidney to increase the reabsorption of water (Chen and Wang 2002), capability to adjust body temperature to accommodate the drastic change of environmental temperature, (Zhao 1995), the slow respiratory rate to decrease energy consumption and thick wall of capillary blood vessel to reduce the influence of environmental temperature on body temperature (Schwartz and Dioli 1992). Despite these studies, rare attention has been paid to the brain. Friant and Hoest (1945) report the morphology of telencephalon of the Bactrian camel. The pattern of sulci and gyri of the brain of the Bactrian camel has been described in detail (Xie and Wang 2006). Both studies

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focus on the morphology primarily. In our study, we describe the detailed morphology of the rhinencephalon and hippocampus formation of the Bactrian camel and analyze the relationship of these two structures with the adaptive behaviors of the camel. On the one hand, we expect to provide a morphological basis for the comparative neuroanatomy. On the other hand, we try to seek more evidence about the adaptation of the camel to the arid and semi-arid environments, thus providing a scientific basis to protect the wild Bactrian camel and breed the domestic camel.

Materials and methods

Six heads of the adult Bactrian camel were collected from the slaughterhouse of the Right Alasan Banner Food Company in Inner Mongolia Autonomous Region of China. Perfusion and brain extraction were performed according to Xie and Wang (2006). Specimens were soaked in neutral formalin solution for about one month in order for complete fixation. Afterwards, samples were weighed, measured and observed. The EQ value was calculated according to Jerison (1970).

Results

Brain weight and EQ

Averagely, the brain weight of the Bactrian camel was 626 g and EQ value was 1.3 (Table 1).

Rhinencephalon

Observed ventrally (Fig. 1), the rhinencephalon consisted of a pair of olfactory bulbs, peduncles, tracts and piriform cortices symmetrically located in both hemispheres. The rhinal sulci, along the lateral surface of both hemispheres, clearly delimited the rhinencephalon from the neocortex.

Olfactory bulb, tracts and peduncle

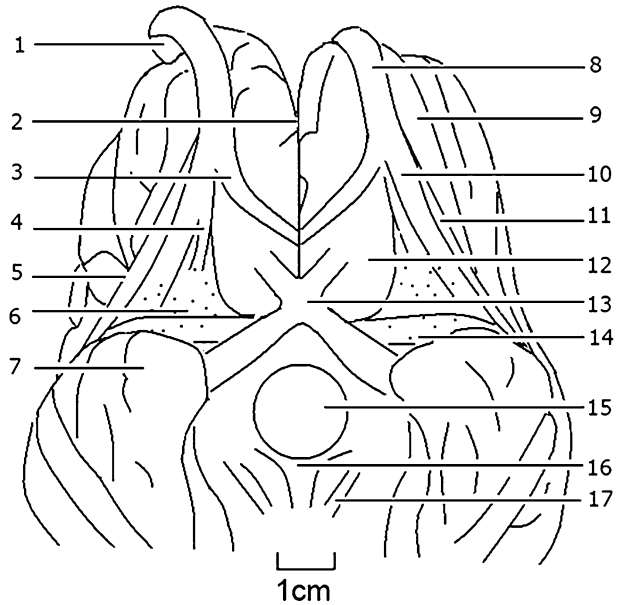
The olfactory bulb was the most anterior component of the rhinencephalon. The diameter of the widest region was 0.9 cm. It bent rostradorsally towards the orbital surface of the hemisphere. The olfactory peduncle was a bunch of wide fiber bundle about 0.9 cm long. It stretched rostrally to the bulb and split into two olfactory tracts caudally. The olfactory tract

Table 1 Brain weight and EQ

Animal taxa	Brain weight (g)	EQ
Bactrian camel	626	1.3
African elephant*	4200	1.3
dromedary camel*	762	1.2
Ox*	490	0.5
Horse*	510	0.9
Sheep*	140	0.8

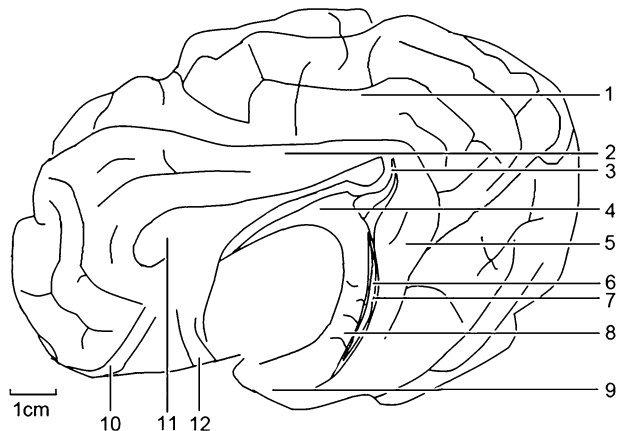
*Data from Roth and Dicke (2005)

Fig. 1 Ventral view of rhinencephalon. 1. Olfactory bulb; 2. Longitudinal fissure; 3. Medial olfactory tract; 4. Intermediate olfactory tract; 5. Lateral rhinal sulcus; 6. Anterior perforated substance; 7. Caudal piriform cortex; 8. Olfactory peduncle; 9. Neocortex; 10. Lateral olfactory tract; 11. Olfactory gyrus; 12. Olfactory tubercle; 13. Optic chiasma; 14. Diagonal gyrus; 15. Hypophysis; 16. Intercrural fossa; 17. Oculomotor nerve



consisted of the lateral and medial branches. They were about 0.4 cm and 0.18 cm respectively in width. The lateral tract stretched caudally to define the lateral border of rostral piriform cortex, until reaching the diagonal gyrus (Fig. 1). Between the lateral olfactory tract and lateral rhinal sulcus was the lateral olfactory gyrus. It started from a layer of grey matter covering the dorsal surface of the peduncle, and extended into the caudal piriform cortex. The medial olfactory tract deviated from the lateral branch at an angle of about 50 degree and extended to the rostral commissure area (Fig. 2). The intermediate tract was present. It stretched out from the crotches formed by lateral and medial tracts and terminated in the rostral perforated substance.

Fig. 2 Medial view of the telencephalon. 1. Neocortex 2. Cingulated gyrus 3. Fasciolar gyrus 4. Fimbria 5. Parahippocampal gyrus 6. The convolution on the floor of hippocampal gyrus 7. Hippocampal sulcus 8. Dentate gyrus 9. Caudal piriform cortex 10. Medial olfactory tract 11. Corpus callosum 12. Diagonal gyrus



Rostral piriform cortex

The lateral and medial olfactory tracts and the diagonal gyrus surrounded a triangular area, called rostral piriform cortex or olfactory trigone. The diagonal gyrus, about 0.2 cm wide, lay rostrally to the optic chiasm and extended from the caudal end of lateral olfactory tract to the rostral commissure area (Fig. 2). The lateral half of the cortex surface, termed anterior perforated substance, was pierced by holes for the passage of blood vessels. The medial half of cortex surface was convex in most individuals, termed olfactory tubercle.

Caudal piriform cortex

The caudal piriform cortex was delimited by diagonal gyrus rostrally and rhinal sulcus laterally. The caudal border was undistinguishable from the neocortex. The surface of the caudal piriform cortex was divided by small fissures. Viewed medially, the caudal piriform cortex was contiguous with the parahippocampal and dentate gyrus at the ventral end (Fig. 2).

Hippocampus formation

The hippocampus formation of the Bactrian camel consisted of hippocampus, dentate gyrus and parahippocampal gyrus. It lay ventrally to the lateral ventricle and dorsally to the diencephalons. This location made it invisible from the outer surface of the brain.

Parahippocampal gyrus

After removal of the brainstem and partial diencephalons, the medial and ventral surface of the hippocampus formation was exposed. Viewed medially (Fig. 2), the hippocampal sulcus separated the parahippocampal gyrus from the dentate gyrus. The collateral sulcus bounded the parahippocampal gyrus caudally. This sulcus was in parallel with the hippocampal sulcus. It extended dorsally to the caudal splenic fissure. The ventrolateral end of parahippocampal gyrus abutted on the caudal piriform cortex and neocortex. Extending dorsally, the parahippocampal gyrus broadened and gave off a short rostral branch. This rostral branch was separated from the main trunk by the caudal callosal sulcus and finally joined the fasciolar gyrus (Fig. 2). The main trunk extended along the splenium to join the cingulate gyrus.

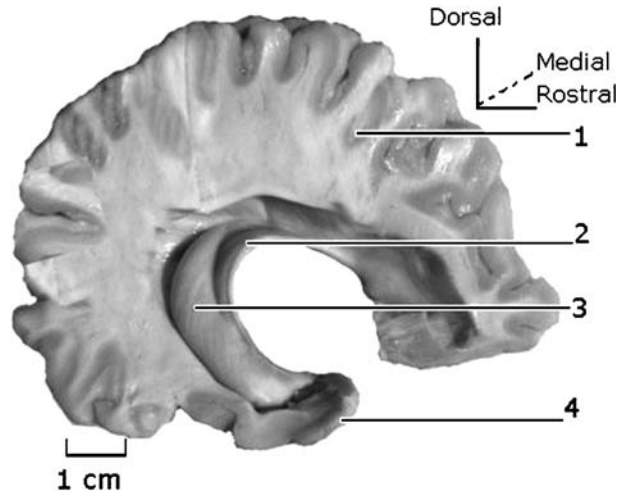
Dentate gyrus

The dentate gyrus was demarcated by the hippocampal sulcus caudally and formed a curved contour (Fig. 2). It was contiguous with the tubercle of the parahippocampal gyrus at the ventromedial end, was marked by three to four grooves transversely in the middle region and tapered gradually at the dorsolateral end to join the fasciolar gyrus. The diameter of its widest region was 0.4 cm.

Hippocampal fimbria

The fimbria was a smooth and flat white band attached to the concave surface of the hippocampus. It consisted of fibers from the alveus of hippocampus (Fig. 3). The fimbria

Fig. 3 Lateral view of hippocampus. 1. Neocortex 2. Fimbria 3. Hippocampus 4. Caudal piriform cortex



was small at the ventral end but the size gradually increased when extending dorsally. The widest region was about 1.2 cm.

Hippocampus

The hippocampus was recessed into the lateral ventricle with a 'C' shape (Fig. 3). The whole length was about 6.0 cm and the widest region 0.9 mm. It was contiguous with the caudal piriform cortex at the ventrolateral end. Like the dentate gyrus, it also tapered as it extended towards the dorsolateral end. Its surface was covered by a layer of white fibers, called alveus. These fibers accumulated on the concave edge of the hippocampus and formed the fimbria.

Convolution on the floor of hippocampal sulcus

A tiny convolution was observed on the floor of the hippocampal sulcus which join the fasciolar gyrus at the dorsal end(Fig. 2).

Discussion

EQ and intelligence

Intelligence may be defined by the speed and success of how animals solve problems to survive in their natural and social environments (Roth and Dicke 2005). The brain is considered to be the carrier of intelligence. The EQ, defined as the ratio between actual brain size and expected brain size for a given body weight, has been employed to assess the intelligence (Jerison 1970). Since a majority of mammals are expected to have an EQ of 1, a higher EQ than 1 may be associated with more than average intelligence (Martin 1990; McHenry 1988).

The EQ of Bactrian camel is 1.3 (Table 1). It is higher than that of the ox, horse and sheep, but close to that of the dromedary camel and African elephant, implying that the

Bactrian camel has a similar level of intelligence with the dromedary camel and African elephant, but higher than the ox, horse and sheep. Mammals with EQ near or above 2.0 like primates can make and use tools (Gordon 1966). Despite such observations in camels were rare, camels show good spatial memory and excellent ability of orientation in the desert even during sandy storm (Yuan et al. 2001). Associate learning was also recorded by Yuan et al. (2001). It is observed that captured young camels would come to people for food once hearing the bell after several accidental practices to associate the bell ring with food.

Rhinencephalon and olfaction

The rhinencephalon of Bactrian camel is well developed and almost covers the whole ventral surface of the cerebrum as Madeleine and colleagues (1944) described, characteristic of macromammals. The maturity of rhinencephalon is appropriately consistent with the acute olfaction of the camel. It is well-known that the camel could locate the water source from three miles away in the desert (Yuan et al. 2001), as is a unique survival skill for the camel. One volatile molecule that leads camels to water source has been identified (Gust et al. 2003). According to Chess et al. (1994), the receptor responding to the volatile molecule should be present in the sensory cells. Thus, it is very desirable to identify the receptor gene from the genome of the camel for the potential application of this gene.

Hippocampus and spatial memory

The hippocampus of the Bactrian camel is about 6.3 cm in length and 0.9 cm at its widest point. It is of approximately the same size with that of the human (Zhu 2002) and elephant (Shoshani et al. 2006). However, the relative size of hippocampus to the cerebrum in Bactrian camel is extraordinarily larger than in the human and elephant, suggesting a good ability of spatial memory. This is also in accordance with the report that food-hoarding birds using spatial memory to relocate their caches have a larger hippocampus than non-hoarding species (Garamszegi and Eens 2004). Other studies show the similar relationship of hippocampus size with spatial memory (Krebs et al. 1990; Healy and Krebs 1992, 1996; Hampton et al. 1995; Basil et al. 1996). Spatial memory is very important for orientation, especially in the desert. Behavioral reports also suggest the good spatial memory of Bactrian camel. It has been reported that abandoned camels succeed to return home from 600 Km away (Yuan et al. 2001). In another report, a camel leads a girl home during sandy storm at night (New Capital Newspaper 2006). In all, these observations have demonstrated a good spatial memory of the camel.

Hippocampal formation and IG

The IG is an extremely thin, narrow layer of gray substance on the dorsal surface of the corpus callosum and extends to the fasciolar gyrus (McClure 1983). It is usually considered as a poorly developed portion of the hippocampus and a nonfunctional structure of the brain (Künzle 2004). In our observation, the parahippocampal gyrus, dentate gyrus and the convolution at the bottom of hippocampal sulcus are connected with IG by the fasciolar gyrus. In mouse, the entorhinal area and olfactory bulb has direct projection to the IG (Adamek et al. 1984). In hedgehog tenrec, the IG receives specific afferents from the entorhinal cortex, anterior and posterior piriform cortices and a few fibers from the olfactory bulb and the dentate hilus (Künzle 2004). And projection from hippocampus to IG

is also identified in rats (Jinno et al. 2007). These studies, on the one hand, agree with our observation of the connection between hippocampal formation and the IG. On the other hand, they suggest a active functional activities of the IG. More attention should be paid to studying this neglected area.

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