Occipital-Dural Muscle: A Specialized Myodural Bridge in Narrow-Ridge Finless Porpoise (*Neophocaena Asiaorientalis*)

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Abstract

A dense bridge-like tissue named the myodural bridge (MDB) connecting the suboccipital muscles and the spinal dura mater was originally discovered in humans. Recent studies have revealed that the MDB confirmed a universal existing normal anatomical structure in mammals which is considered being significant in physiological functions. Our previous investigations have confirmed the existence of MDB in the finless porpoises. We conduct this research to expound the specificity of the MDB in *Neophocaena asiaeorientalis* (*N.asiaeorientalis*). Five carcasses of *N.asiaeorientalis* with formalin fixation were used for this study. Two were used for head and neck CT scanning, three-dimensional reconstruction, and dissection of suboccipital region. One was used for P45 plastinated sheets observation. One was for histological analysis of suboccipital region. One was for Scanning electron microscopic study. The results showed that the MDB in *N.asiaeorientalis* is an independent muscle originated from the caudal border of occiput, directly extended through the posterior atlanto-occipital interspace and connected with the cervical spinal dura mater. Thus the MDB in *N.asiaeorientalis* is an independent and specialized muscle. Based on the origin and termination of this muscle, we could name it as 'Occipital-Dural Muscle'. And the direct pull on the cervical spinal dura mater might affect the circulation of the cerebrospinal fluid (CSF) by altering the volume of subarachnoid space of spine.

Introduction

In human body, the suboccipital region is a particularly intricate area that contains a bundle of connective tissue connecting the rectus capitis posterior minor (RCPmi) and cervical spinal dura mater (SDM) as an anatomical bridge. This bridge-type connection was firstly found in humans' atlanto-occipital interspace by Khan et al. [1], termed as the myodural bridge (MDB) by Hack et al. [2]. Subsequent studies revealed that the rectus capitis posterior major (RCPma), the nuchal ligament (NL), and the obliquus capitis inferior (OCI) also participated in the forming of MDB [3–8]. Furthermore, researchers investigated that the MDB existed in more mammalian taxa including *Macaca mulatta*, *Canis familiaris*, *Felis catus*, *Oryctolagus cuniculus*, *Ratus norvegicus*, *Cavia porcellus*, and *Indoasian finless porpoise* [9]. In addition, it was confirmed that this structure is also present in reptiles (*Crocodylus siamensis*) [10], and avifauna (*Columba livia* and *Gallus domesticus*) [11, 12]. This universal existence inferred that the MDB could be physiologically significant in both humans and other species. According to the morphology studies, the authors speculated that the MDB is related with the transmission of proprioception [13, 14]. Zheng et al. [15] and Xu et al. [16] proposed that the MDB could be an indispensable factor in modulating the dynamic circulation of the cerebrospinal fluid (CSF).

Narrow-ridged finless porpoise (*N. asiaeorientalis*) is one of the smallest cetaceans [17]. Since 2017, *Neophocaena asiaeorientalis* has been placed endangered by the IUCN [18]. Besides, A range of evidence revealed that finless porpoises is the most basal clade in existing porpoises of family *Phocoenidae* [19–23]. A previous study has confirmed the existence of the MDB in *Neophocaena phocaenoides*, yet the posterior Atlanta-occipital (PAO) membrane was not found [24]. In addition, the first three vertebrae in Finless Porpoise were fused [25–27] which resulted in the only remaining entrance of the MDB to the

SDM was the atlanto-occipital interspace. More interestingly, we found a muscle inserting through the atlanto-occipital interspace, and terminated at the SDM, which might perform the role of the MDB in *N.asiaeorientalis*. According to the morphological studies of the finless porpoise, the suboccipital triangle was much different from humans and other species, in which we could not find the obliquus muscle. Upon that, we initiated this research to investigate this muscle which insert the atlanto-occipital interspace in *N.asiaeorientalis*, figure out the relationship between this muscle and the MDB in humans, and infer the physiological function of it.

Materials And Methods

Analyzed specimens represent narrow-ridged finless porpoises (*N.asiaeorientalis*) that were killed incidentally in fishing nets or were found washed ashore. They were successively collected in Dalian with the permission from Chinese Authorities for Animal Protection. The study of these carcasses was approved by the Ethics Committee of Dalian Medical University. All of the collected dead bodies were conducted arterial perfusion through the aorta with 10% formalin solution. All methods were carried out in accordance with relevant guidelines and regulations.

Methods

CT three-dimensional reconstruction

Two specimens' heads and necks were continuously scanned by GE 128-row VCT, and dual phase serial computer tomography (CT) images were obtained, the slice thickness and pitch were set to 0.6mm. The images were analyzed for modeling and reconstruction in MIMICS software (MIMICS 18.0.0.525, Materialise, Leuven, Belgium).

Dissection of postoccipital region

Four specimens were dissected layer-by-layer at the posterior occipital region to expose the atlanto-occipital interspace. A dorsal midline incision was made at the neck, the skin, subcutaneous fascia, and superficial neck muscles were gradually removed to expose deep post-occipital musculature. Subsequently, the rectus capitis dorsalis (RCD) was detached from its cranial attachment carefully to reveal the other muscle lying deep. The musculature and other structures in the atlanto-occipital interspace along with a part of cervical spinal dura mater were isolated as tissue block by an electric handsaw. The tissue blocks were preserved for histology and scanning electron microscope. The photographic documentations were carried out by Canon 7D and 450D camera.

P45 sheet plastination

One specimen of *N.asiaeorientalis* was sliced in sagittal section for p45 sheet plastination. The P45 sections are semi-transparent, durable slices with a clear delineation of the tissue morphology including the connective tissues [28]. Anatomical structures in posterior occipital region and the connections between the postoccipital muscles and cervical spinal dura mater were observed. The experimental procedure of the technique is described as follow [29]:

Slicing.

The embalmed specimens of the head and neck were frozen at -70°C for two weeks and then embedded in polyurethane foam and frozen at -70°C again for two days. After freezing, 3 mm sagittal slices were made from side to side with a high-speed band saw.

Bleaching.

All the slices were rinsed overnight in cold running water, and afterwards, the slices were immersed in 5% dioxogen overnight.

Dehydration. After bleaching, the slices were dehydrated with 100% acetone by the freeze substitution method.

Casting and forced impregnation.

After dehydration, the casting mold was prepared. The slices were lifted from the acetone bath and placed between two glass plates. The molds were then filled with polyester (Hoffen polyester P45, Dalian Hoffen Bio-Technique Co. Ltd., Dalian, P. R. China.).

The filled mold was placed upright into a vacuum chamber at room temperature for impregnation. The absolute pressure was slowly decreased to 20, 10, 5, and 0 mm Hg, according to the rate of bubble releasing. The pressure was maintained at 0 mm Hg until bubbling ceased. The impregnation time lasted for more than eight hours.

Curing.

After the vacuum was released, the air bubbles within the sheets were checked and removed. The top of the mold was clamped with large fold back clamps, and the sheet was then ready for curing. The sheets were cured using a heated water bath and were placed upright in the water bath at 40°C for 3 days. After curing, the sheets were removed from the bath and cooled to room temperature in a rack. The slices were then removed from the flat chamber and covered appropriately with adhesive plastic wrap for protection. The sheets were then observed and photographed.

Histological study

Two tissue blocks were prepared containing the postoccipital musculature, the periosteum of the adjacent cervical vertebrae and the occiput, adjoining spinal dura mater, and spinal cord. After washed in running water overnight, these tissue blocks were dehydrated with ethanol in increasing grades, passed through xylene, infiltrated and then embedded in paraffin wax. A rotary microtome was used to cut 10- μ m-thick sections. Sections were mounted on the glass microscope slides, then rehydrated for Van Gieson (VG, picric acid and acid fuchsin) staining. The staining sections were analyzed and photographed under a Nikon Eclipse 80i light microscope, with the support of Nikon NIS image software.

Scanning electron microscopic study

Through layer-by-layer dissection, two tissue blocks were used for scanning electron microscope (SEM) study. After washing in running water overnight, the specimens were fixed with 2.5% glutaraldehyde in 0.1 M phosphate buffer at PH 7.3 for more than 2h. Then, the specimens were repeatedly washed in the buffer solution. They were subsequently dehydrated through a graded alcohol series, vacuum dried with 100% tert-butyl alcohol, and sputter-coated with platinum by ION SPUTTER JFC-1100 ion sputtering equipment. Tissues of the specimens were observed under a scanning electron microscope (model FEI QUANTA 200, voltage:20KV, manufacture: the Netherlands FEI company). Fibers connections were photographed, digitized and analyzed.

Results

CT three-dimensional reconstruction

The reconstructed 3D model of cranium and cervical vertebrae of the *N.asiaeorientalis* demonstrated that the atlanto-occipital interspace was broader compared with humans and some other terrestrial mammals, to the cervical dura mater. The first three cervical vertebrae merged into one unit. It was observed that either the spinous processes and the transverse processes fused as well (Fig. 1). Since the relationship of the bones were clearly demonstrated by 3D records, and it was also considered as a guidance of gross anatomy in this study.

Gross anatomy

With the fusion of the first three vertebrae, the obliquus muscle vanished in *N.asiaeorientlis*. A rectus muscle was found in the deep post-occipital region (Fig. 2). The cranial attachment of this rectus muscle was at occiput, while the caudal attachment was at the transverse process of the fused cervical vertebrae. This muscle was rectus capitis dorsalis muscle (RCD). Another muscle was found underneath the RCD, which originated from the occiput, and ended at spinal dura mater. We named it 'the occipital-

dural muscle' (Fig. 3). Yet the dorsal atlanto-occipital (DAO) membrane was not found in *N. aisaorientalis* during the dissection.

P45 sheets plastination

Median sagittal sections of the plastination sheets showed that all the fibers of the occipital-dural muscle extended into the atlanto-occipital interspace, attached to the cervical spinal dura mater ultimately (Fig. 4). The dorsal atlanto-occipital (DAO) membrane was not present throughout the observation of the sheets. In addition, we found a reverse angle between the cranial and spinal dura mater.

Histology

Through the histological analysis of VG staining, the relationship between the muscles, bony structures and cervical dura mater was clearly identified (Fig. 5). It was found that the proximal attachment of the RCD was on the occiput while the distal was the fused cervical vertebrae. All of the muscular fibers of the occipital-dural muscle inserted into the atlanto-occipital interspace, terminated and merged with the spinal cervical dura mater directly. Neither could we find the dorsal atlanto-occipital (DAO) membrane through the histological sections. The sections of VG staining showed that the occipital-dural muscle's muscular fibers were stained in yellow, while entering the atlanto-occipital interspace, the extending fibers turned to red, which revealed that the extended parts were collagenous fibers as muscle tendon.

Observation under scanning electron microscope

On the sagittal section, the cervical spinal dura mater was composed of multi-layer fiber bundles. Dorsal atlanto-occipital (DAO) membrane was absent in atlanto-occipital interspace under the scanning electron microscope either. It was found that the muscular fibers of the occipital-dural muscle extended through the atlanto-occipital interspace, arranged in parallel, ran caudally and merged with the cervical spinal dura mater at the end. According to the observation, we saw the tendon fiber of the occipital-dural muscle was knitted into the cervical spinal dura mater as a fusion (Fig. 6).

Discussion

The myodural bridge was described as a dense fibrous connection between the occipital-dural muscle and SDM by Hack et al. (1995) [2]. Subsequent studies enriched this definition stage by stage. Till now we have never found a species except the finless porpoises whose MDB was an isolated muscle, yet all of the muscle tendon finally terminated at the SDM. Meanwhile, the physiological significance of MDB was highly concerned in recent research. Sui et al. (2013) [30] and Zheng et al. (2014) [15] supported that the suboccipital muscles which connecting to the upper cervical spinal dura mater via MDB was proposed to provide power for cerebrospinal fluid (CSF) circulation. Thereby, Xu et al. [16] speculated that head

movement could be significant contributor to CSF dynamics in craniocervical junction, besides mentioned factor such as heartbeat [31, 32] and respiration [33–35].

Finless porpoises have a wide geographic range, distributing in shallow, costal water western Pacific and Indian oceans from the Persian Gulf to most of the Indo-Malay region and then northward through the waters of China (including the lower to middle reaches of the Yangtze River) to southern Japan and Korea [26, 36]. Narrow-ridge finless porpoises (*N.asiaeorientalis*), no dorsal fin, and more slender than other porpoise species, with a flexible neck. They have tubercles on its back from mid-back to tail, with a dorsal ridge anywhere from 0.2 to 1.2 cm wide [37]. Regarding marine mammals, our team confirmed that the MDB existent in the finless porpoises (*Neophocaena phocaenoids*) and the sperm whale recently [24, 38]. Like most of marine mammals, *N.asiaeorientalis* have to hold their breath and dive while foraging in aquatic habitats. During dives, they are up against extensive apnea apparently, similar as their related species, harbor porpoises [39, 40]. To tolerate that, the dive response turned into a crucial necessary trait, which consists of bradycardia and peripheral vasoconstriction. Through this response, cardiac output and organ perfusion would be diminished, while the transient cessation of respiration proceeding simultaneously [40–42]. However, aforementioned series of processes scarcely occurred in terrestrial mammals. That is, comparing to the terrestrial counterpart, marine mammals routinely confront challenges that stem from the dive response. Coincidentally, heartbeat and respiration were considered as crucial contributor to maintain the circulation of CSF, whereas marine mammals have to decrease.

Here we found the MDB in *N.asiaeorientalis* was isolated as an independent muscle that originated from the occiput, extended through the atlanto-occipital interspace, and terminated at the spinal dura mater. It was already confirmed that this muscle was found in *Neophocaena phocaenoids* without PAO membrane performing the job of intermediate junction [24]. Neither could we find any other termination except the SDM in *N.asiaeorientalis*. In other words, pulling the SDM might be the main job of the occipital-dural muscle in *N.asiaeorientalis*. During finless porpoises' diving time, the lower heart rate and suspended respiration could not afford the power source to maintain the CSF's circulation, and simultaneously, a specialized muscle objectively existed which can provide powerful traction force to the SDM by the relative movement between head and neck. Thus we could predict that this muscle in *N.asiaeorientalis* plays an indispensable role on the dynamic circulation of CSF. Moreover, this mechanism is steadily sustainable due to continuous body motion during the bottom-time of finless porpoises. Therefore, we can call this unique and special functional muscle as the occipital-dural muscle.

As subsequent research reported that myodural bridge universally existed in mammals [9], the MDB was considered as a highly evolutionary conserved structure. The myodural bridge of *N.asiaeorientalis* is the strongest and most specific one among the animals we have ever exam. Due to the absence of the PAO membrane, the occipital-dural muscle could insert the Atlanta-occipital interspace, attached to the dura mater directly. In addition, the scanning electron microscopic result revealed that the connection between the MDB and the dura mater is close-knit in *N.asiaeorientalis*, where the dense tissue of the MDB gradually fused with the SDM, and eventually became a part of the SDM.

In summary, all the evidence above supports that, MDB in *N.asiaeorientalis* works efficiently as an isolated muscle named the occipital-dural muscle. Unlike humans, this muscle directly connects with the SDM in *N.asiaeorientalis*, transmits the strong traction force to the SDM, by muscular contraction and relaxation. Furthermore, the mechanism is also highly related to sustainable relative movement between occiput and the fusion of the first three cervical vertebrae (Fig. 7). This mechanism is obviously more powerful and representative than that in humans and most of other species we have investigated before. Meanwhile, it enhances the credibility of the significant physiological function of MDB.

Declarations

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Author Contributions

Conceived and designed the experiments: HJS, SBY, NZ. Performed the experiments: ZXZ, JG, SBY, JXS, SWD. Analyzed the data: ZXZ. Drafting of the manuscript: ZXZ. Software: SZS, SWD, GJM, ZXZ. Illustration: ZXZ. Critical revision of the manuscript: HJS, NZ, CL.

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Figures

Figure 1

The 3D-reconstruction of bones in suboccipital region of the *N. asiaeorientalis*. Dorsal view of the suboccipital region. occi: occiput. *: the atlanto-occipital interspace. #: the fused spinous processes of the first three vertebrae.

Figure 2

Anatomical dissection of the suboccipital region of the N.asiaeorientalis. A: the superficial layer of suboccipital musculature. B: the deep layer of suboccipital musculature. occi: occiput. RCD: rectus capitis dorsalis. S.C.: semispinalis capitis. ODM: occipital-dural muscle.

Figure 3

The sagittal section dissection of suboccipital region of the *N.asiaeorientalis*. OCCl: occiput. RCD: rectus capitis dorsalis. ODM: occipital-dural muscle. ☒: the fused vertebral body of the first three vertebrae. ☒: the fused spinous process. △: the origination of the occipital-dural muscle. ▲: the termination of the occipital-dural muscle. ...: the boundary of the occipital-dural muscle. ↑: cerebral dura mater.

Figure 4

The sagittal section P45 plastination sheet of suboccipital region of the *N.asiaeorientalis*. OCCl: occiput. RCD: rectus capitis dorsalis. ODM: occipital-dural muscle. ☒: the fused vertebral body of the first three vertebrae. ☒: the fused spinous process. △: the origination of the occipital-dural muscle. ▲: the termination of the occipital-dural muscle. ...: the boundary of the occipital-dural muscle. ↑: cerebral dura mater.

Figure 5

Van Gieson (VG, picric acid and acid fuchsin) stained histological sagittal section of suboccipital region of the *N.asiaeorientalis*. The image was under 4× light microscope. RCD: rectus capitis dorsalis. ODM: occipital-dural muscle. SDM: spinal dura mater. a: fibers of muscle belly of the occipital-dural muscle. b: fibers of muscle tendon of the occipital-dural muscle.

Figure 6

The scanning electron microscope observation of the occipital-dural muscle and the spinal dura mater of the *N.asiaeorientalis* in atlanto-occipital interspace. A, B: connection between the MDB and the SDM. C: sagittal view of the tissue block. MDB: the myodural bridge. SDM: the spinal dura mater. M. fibers: muscular fibers of the occipital-dural muscle.

Occipital-Dural Muscle

A Specialized Myodural Bridge in Narrow-Ridge Finless Porpoise (*Neophocaena Asiaorientalis*)

Figure 7

The occipital-dural muscle directly pull the spinal dura mater (SDM), alter the volume of subarachnoid space of the spine, affect the circulation of the cerebrospinal fluid (CSF).