MORPHOLOGICAL CHARACTERISTICS AND MYELINIZATION OF ACOUSTIC SYSTEM IN THE DOLPHINS (*STENELLA CAERULEOALBA*)

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The acoustic system in the cetacean brain is more developed than the other common mammals. Since ancient times, it has been well known that the cetaceans possess a remarkably fine sense of hearing. Anatomically, Spitzka (1880, 1886) was the first investigator who had noticed this characteristic that the whales, dolphins and porpoises have the largest auditory nerves in the animal kingdom. Hatschek and Schlesinger (1902) described the same characteristic of the brain stem in a *Dolphines*. Hofmann (1908) and Valeton (1908) investigated the brain of adult dolphins, the former observed especially the superior olivary nucleus, while the latter did also the inferior colliculus. In view of developmental neuroanatomy, Langworthy (1932) dealt with the brain of *Tursiops truncatus* and appraised its acoustic system as high grade of development. Ogawa and Arifuku (1948) referred to aforecited works and pointed out that the comparative study of this system between *Odontoceti* and *Mystacoceti* had never been done. Therefore myelinization of the acoustic system in the cetacean brains was studied by Ogawa and Arifuku. This work is very important for the comparative and developmental anatomy of the acoustic system. Recently Morgane and McFarland (1965) represented the neuroanatomical correlates of functional specializations in the dolphin (*Tursiops truncatus*), however no study as for the developmental neuroanatomy was performed.

The authors were much interested in the striking development of the acoustic nerve and its tract of the brain stem in the dolphins. For the past years one of the authors, Kamiya, has collected embryos of the dolphins (*Stenella caeruleoalba* Meyen) which came from Kawana, Shizuoka Prefecture.

Myelinization during the course of embryonal development is observed on these materials in order to make clear the development of the acoustic system. The collection contains such a series of the embryos that their body lengths are 42, 51, 61, 74 and 88.8 cm. Besides the three brains of adult *Stenella caeruleoalba* were provided. All the brain stems were embedded in celloidin and sectioned 30 or 50μ in thickness in frontal series. The sections stained by Weigert-Pal carmin method have been studied microscopically, sketched and photographed. The authors do not intend to go into the details of each internal view here due to the limitation of space, however the representative sections of the adult and embryonal materials are shown in Figs. 3 to 23. Some adult brain stems were disected and observed macroscopically, e.g.

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one of them is shown in Fig. 2. In the following pages the acoustic tract in the adult material will be shown in the first part for reference and myelinization in the embryonal stage will be represented in the next part. Intracranial disposition of the brain stem was shown already in the preceding report (Hosokawa and Kamiya 1965).

Acoustic system of the brain stem in the adult *Stenella Caeruleoalba*

The radix of the cochlear nerve enters the ventro-lateral part of the medulla oblongata (Figs. 1, 2 and 12). The pars vestibularis of the n. octavus is found just lateral to the radix cochlearis.

1. *Nucleus cochlearis ventralis* (*ventral cochlear ganglion*): This is large ganglion and subdivided into two parts, one is called the pars ventralis and the other is the pars dorsalis. The former is about 6 mm in width and 9 mm long, the latter lies over the former and is just shifted to cranial. Size of the each part is approximatly the same, but the latter is a little larger than the former. Both of them send forth the nerve fibers towords midline of the medulla oblongata, then most fibers make up the trapezoid body (Figs. 8 to 11). While the some fibers originated from the pars dorsalis run up as far as the level of the rostral border of the facial nucleus, moreover these fibers can be traced up to the homolateral superior olivary nucleus (Fig. 12).

2. *Stria acustica dorsalis* (*Monakow's striae acusticae*): This stria exhibits conspicuous development as compaired with the other mammals; i.e. about 5 mm thick (Fig. 7). It seems that the vast majority of the nerve fibers in the *Monakow*'s striae acusticae are originated from the pars dorsalis of the ventral cochlear ganglion.

3. *Tractus cochlearis intermedialis* (*Held's tract*): The *Held*'s tract consists of several thin bundles, which penetrate into the trigeminal nucleus of spinal tract. They pass through the trigeminal nucleus and the facial nucleus too, after that they enter the dorsal part of the superior olivary nucleus and some fibers crossing the median plane on each side are observed (Figs. 9 and 10). This tract is not seen to hang over the dorsal side of the inferior cerebellar pedunculus in the *Stenella caeruleoalba*.

4. *Corpus trapezoideum* (*trapezoid body*): In ventral view of the brain stem, this comes into our notice through the extremely thin layer of the pyramidal tract in the area about 1 cm between the caudal edge of the pons and the rostral end of the olive (nucleus olivaris accessorius medio-rostralis to be exact). It consists of the fibers come from pars ventralis and dorsalis of ventral cochlear ganglion (Figs. 9 and 10). These fibers contain the dispersed nerve cells and certain nucleus, i.e. the nucleus corporis trapezoidei. The caudal part of the trapezoid body is constituted with the majority of fibers come from the pars ventralis of the ventral cochlear ganglion and some from the pars dorsalis, but the rostral division of the body accepts fibers from the both parts.

5. *Nucleus corporis trapezoidei*: The nucleus is placed near the midline within the trapezoid body. The nerve cells are widly dispersed among the nerve fibers of the trapezoid body (Figs. 9 to 13). However they tend to accumulate near the

trapezoid body, consequently they make up a large cellular mass so-called trapezoid nucleus. The nucleus is penetrated with transvers fibers which run crossing the median plane on each side. The nucleus extends up to the level of the rostral end of the superior olivary nucleus (Fig. 16).

6. *Nucleus preolivaris lateralis*: This is found ventro-lateral to the superior olivary nucleus in the cross sections. The preolivary nucleus is located at the level where the radix of the facial nerve emerges from the medulla oblongata (Fig. 11). The nucleus contains such the nerve cells as similar to the cells in the nucleus corpris trapezoidei in shape. At the higher level nucleus corporis trapezoidei is replaced by the other nerve cells, but these cells are dispersed widly among the myelinated nerve fibers in such a manner as the elements in the nucleus pontis, therefore the nucleus preolivaris medialis dose not represent itself as a clear-cut nucleus.

7. *Nucleus olivaris superior*: This nucleus is very large in proportion to the size of the trapezoid body and has place near the facial nucleus (Figs. 9, 10 and 11). Comparing with Primates the location of the superior olivary nucleus in the dolphins is shown more medial. The fibers arising from this nucleus are traced up to inside of the nucleus lemniscus lateralis.

8. *Lemniscus lateralis*: In the cross sections of the pons through the cranial level, the largest tract which attracts our attention is the lateral lemniscus. This tract involved a large cellular mass namely the nucleus lemniscus lateralis and some accessory nuclei on its way to the inferior colliculus. The lemniscus is divided into two main tracts by these nuclei. One in lateral side to the nuclei is made with fibers come from the trapezoid body, the other is medial and consists of the tracts which come from the superior olive and others. In the lateral lemniscus are seen cellular masses which seem to give rise to commissural fibers that pass medially and cross the midline.

9. *Nucleus lemniscus lateralis*: It appears as conspicuous cell clusters in the lemniscus lateralis (Figs. 13 to 17). Shape of this large nucleus is oval and its long axis runs in parallel with the lemniscus. Traced up, the fibers from this nucleus is seen to pass upwards as the lemniscus and to enter the inferior colliculus.

10. *Nucleus lemniscus lateralis accessorius dorsalis*: The nerve cells representing strong carminophilic cytoplasma are found rostro-dorsal to the nucleus of lateral lemniscus (Figs. 14 to 17). This accessory nucleus is embedded in the lemniscus, so then it differs from the nucleus dorsalis lemniscus lateralis in previous reports. Because the latter has characteristic of the central gray matter in the brain stem and it should be observed as segregated nucleus from the main nucleus of lateral lemniscus. This accessory nucleus is seen to connect with the nucleus of lateral lemniscus in some sections, even though stainability of the cells differs from the latter one (Fig. 17).

11. *Nucleus lemniscus lateralis accessorius medialis*: Strong carminophils and the size of the nerve cells in this nucleus are similar to those of the cells in the nucleus of the lemniscus lateralis accessorius dorsalis. Both of them are embedded in the lateral lemiscus (Figs. 13 to 16).

12. *Colliculus inferior*: It is found as a large spherical mass which is twice as large as the superior colliculus in diameter (Figs. 16 and 17). The lateral lemniscus is entering the ventral part of the colliculus and sends great quantities of fibers into it. The commissura colliculi inferior is well developed and many fibers from the cells of the colliculus appear upon its lateral surface as the brachium of the inferior colliculus (Fig. 17).

13. *Brachium colliculi inferior*: From the inferior colliculus fibers pass laterally to form a broad band on the outer surface. This very thick band is the brachium of the inferior colliculus and it runs forward to the medial geniculate body (Figs. 17 and 18).

14. *Some peculiar nuclei except the acoustic system*: In ventral view of the medulla oblongata in dolphins the prominent olivary eminence is seen apparently, this mass consists of the nucleus olivaris accessorius medialis and a few nerve fibers. The atrophied feature of the nucleus of inferior olive is showed in these materials as well as in *Lagenorhynchus obliquidens*. Strictly speaking, this accessory nucleus may be divided into two parts (Fig. 3). The authors will call them the nucleus olivaris inferior accessorius medio-ventralis and medio-dorsalis, which will be discussed later on. The medio-ventral one is very large nucleus about 1.5 cm in orocaudal length in adult and the other one is found dorsal and just caudal to the former at the level of the lower hypoglossal radix. The medio-dorsal one has a hilus directed towards the midline and its carminophils is stronger than the other. They are divided into each other by myelinated nerve fibers and both nuclei can be seen at once in some sections (Fig. 3). Development of the pons in the dolphins is commonly very poor, though the corpus pontobulbare (*Essick*) is very well developed in these materials. Other peculiar nuclei are the nucleus ellipticus and nucleus interstitialis which show high development compared with the other mammals (Fig. 18).

Myelinization of acoustic system in the embryonal stage

No myelinated nerve fibers are seen in the whole brain of the *Stenella caeruleoalba* in an embryo of 42 cm body length. Stainability of the acoustic nerve is too faint to be demonstrated. The each fiber of *Monakow*'s striae acusticae, *Held*'s tract and the trapezoid body has not been stained by Weigert-Pal's method yet, nevertheless these tracts have been well developed so that their courses are recongnizable easily in contrast with the other tracts.

Myelinated fibers of acoustic system appear in a 51 cm long embryo (Figs. 19 to 21). In this stage the sequence of myelination from peripheral tracts reaches the lateral lemniscus though myelination of the lateral lemniscus never comes to perfection. *Monakow*'s striae acusticae and *Held*'s tract are stained most intensely and considerable fibers of the trapezoid body are myelinated too. The fibers between the inferior colliculus and the nucleus of lateral lemniscus are stained very slightly (Fig. 21). In the embryo length of 51 cm, the following tracts have been myelinated also; the fasciculus longitudinalis medialis, tractus tectospinalis, commissura ventralis alba and the tractus vestibulo-cerebellaris. The genu of facial nerve and the the other tracts, however, have never been stained at this stage yet (Fig. 20).

In a 61 cm long embryo, the lateral lemniscus is matured but the brachium colliculi inferior and the commissura colliculi inferior are not myelinated. The trigeminal nerve begins to myelinate in this stage, above all the pars minor is dominant over the pars major. The medial lemniscus and the superior cerebellar peduncle are not stained.

An embryo length of 74 cm is examined with great interest (Figs. 22 and 23). The brachium colliculi inferior becomes myelinized at last, accordingly the whole acoustic system up to the medial geniculate body is matured at this stage.

DISCUSSION

Recently the fact that the cetacean react to short radio wavelength was examined and observed (Kellogg and Kohler, 1952; Schevill and Lawrence, 1953; Fraser and Purves, 1954; Reysenbach de Hann, 1957, etc.). Anatomical observation of acoustic system in those animals have been done by many investigators as described in the opening paragraph. Moreover Riese (1936) and Romanes (1945) reported some observation about developmental anatomy of the whale's brains. However aspect of this system in *Stenella caeruleoalba* and its development have never been seen. The authors will make some comments on the previous reports and our observations.

State of telescoping (Miller, 1923) is observed at late embryonal stage in these materials. It seems that this phenomenon precedes the ossification of the skull itself. The dorsal cochlear ganglion is not found as has been in the other whales. The ventral cochlear ganglion is well developed and diveded into two parts in lieu of the absence of the dorsal one. The pars dorsalis of the ventral cochlear ganglion corresponds to the dorsal cochlear ganglion in the human brain, because the fibers of the *Monakow*'s striae acusticae mainly arise from the pars dorsalis. *Held*'s tract shows the peculiar course up to the upper nucleus in these materials. In the brains of human or some mammals, this tract is seen to hang over the dorsal side of the inferior cerebellar peduncle, however this tract of *Stenella caeruleoalba* pass through the trigeminal nucleus and does not hang over the peduncle. The trapezoid body is remarkably large in proportion to the size of the cochlear ganglion and it is seen as if naked bundles due to the extremely thin pyramidal tract. Natural atrophy of the pyramidal tract is understood anatomically, because of the absence of the extremities and their digits. The nerve cells in the trapezoid body are widly dispersed and they show similar size and stainability, therefore the preolivary and lateral preolivary nucleus are analogous to the nucleus of trapezoid body. The dorsal accessory nucleus of the lateral lemniscus is found in these materials. The nerve cells of this nucleus are intensely stained with carmin as well as the neurons of the medial accessory nucleus. Both of them belong to the acoustic system because they are embedded in the lateral lemniscus completely. Strikingly large inferior colliculus is dislocated just lateral and the vermis of cerebellum is hold between them in some parts (Figs. 15 and 23).

Pilleri reported that asymmetrization of the colliculi was found in *Eubalaena* *australis* (1964) and *Balaenoptera borealis* (1966). However the asymmetric construction of the inferior colliculus have never been seen in *Stenella caeruleoalba*.

Concerning the myelinization *Held*'s tract and *Monakow*'s striae acusticae are stained by Weigert-Pal method in a stage of the 51 cm length. The beginning of myelination in this system has been seen in a 45 cm long embryo of *Lissodelphis borealis* (Kamiya, 1962). In a little earliar stage of the 51 cm length of *Stenella caeruleoalba* it seems that the commencement of myelination takes place in the acoustic system. Ogawa and Arifuku (1948) described that *Monakow*'s striae acousticae was well developed in the dolphins, but less prominent in *Kogia breviceps* and the *Held*'s tract is highly developed both in dolphins and other toothed whales. The trapezoid body and the cochlear nerve take their myelin sheath at the same embryonal stage in the pigs, but this phenomenon is not so important. The problems awaiting solution are when myelination in this system takes place and mature itself. The ripe structure has been shown at an embryo length of 74 cm in this work. In a 70 cm long embryo of *Lagenorhynchus obliquidens* accomplishment of myelinization in acoustic system observed by Kamiya (1962). The systems of optic nerve and vestibular nerve are developed around the stage of myelination of acoustic nerve in these materials. The study on the development of the eye was reported in detail by Pillery (1964), however it is difficult to compare his observation with our data because of the difference in materials, e.g. sei whales and dolphins.

Peculiar development of the inferior olive have been noticed by a number of neuroanatomists; Williams, Kooy, Brunner, Kappers, Kuskens, Tsuru, etc. Hatschek and Schlesinger described the mediodorsal accessory olivary nucleus, as the chief nucleus of the olive. The authors insist that the medio-dorsal accessory olivary nucleus essentially differs from the medio-ventral one though both of them are found medial to the radix of the hypoglossal nerve. Because the nerve cells of the former are stained with carmin more stronger than those of the latter and myelination of the nerve fibers in the former is a little faster than the other in embryo. Making an additional remark, the authors are interested in the small size of the nucleus ambiguus in these materials, while it is shown that very large nucleus in *Balaenoptera borealis* (Hosokawa, 1950).

SUMMARY

This work has been studied with the myelination method in embryo (*Flechsig*) in order to make clear the embryonal development of the acoustic system in *Stenella caeruleoalba*. The brain stem was prepared into serial sections and stained by the Weigert-Pal carmin method. Microscopic study of the sections revealed that there were many remarkable differences in the development of various internal structures, therefore the representative sections of adult materials are showed and explained.

In an embryo of 51 cm body length myelinated fibers of the acoustic system appear and its myelination reaches up to the lateral lemniscus. The whole acustic system as far as the medial geniculate body is myelinated completly in an embryo length of 74 cm. Development of this system is considerable fast in view of its

myelinization. However it seems that the rate of its development tends to retard a very little.

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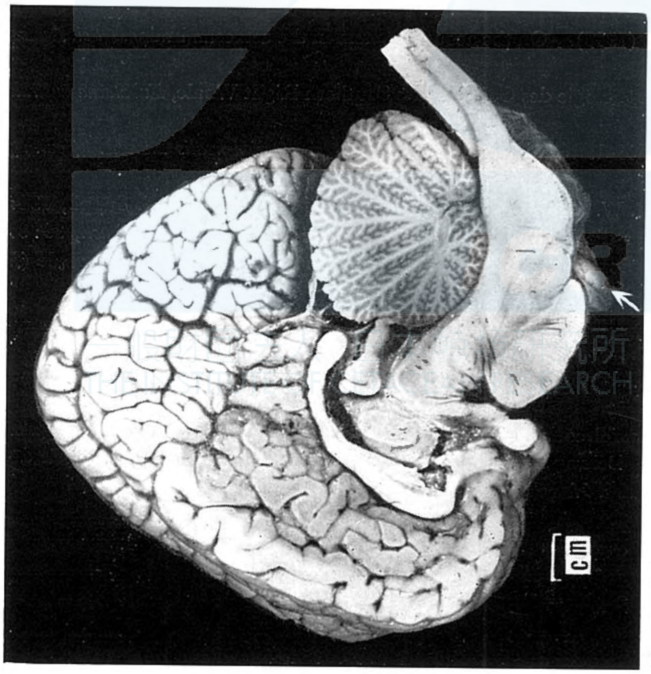

Fig. 1. Median section of the brain of the adult *Stenella caeruleoalba*. Arrow indicates the cochlear nerve.

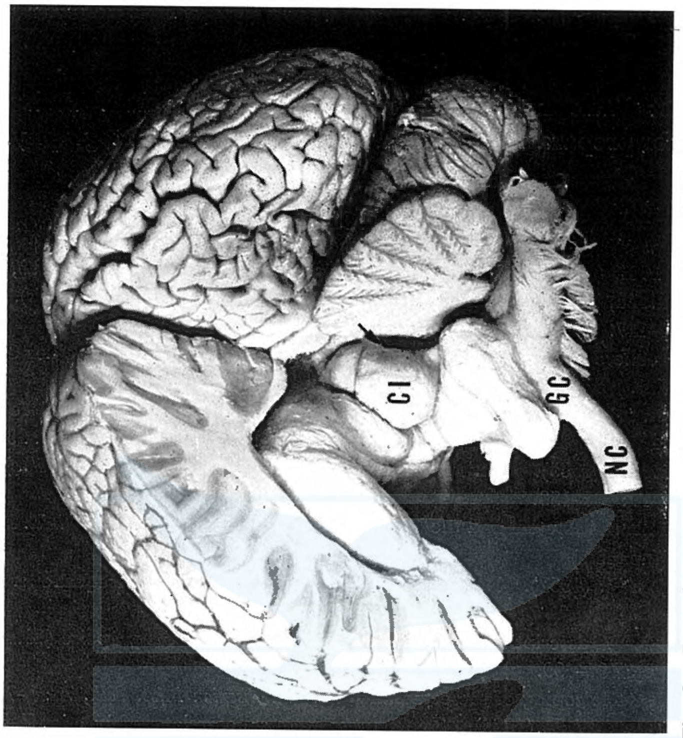

Fig. 2. Dorso-lateral view of the brain stem, the left hemisphere of the cerebellum was removed.
NC: Cochlear nerve, GC: Ventral cochlear ganglion,
CI: Inferior colliculus, Arrow: Commissure of the inferior colliculus.

Fig. 3. Section of medulla through the caudal end of the inferior olivary nucleus.

Fig. 4. Section of medulla through the middle of the inferior olivary nucleus.

Fig. 5. Section of medulla through at the rostal portion of the inferior olivary nucleus.

Fig. 6. Section through the rostral portion of medulla at the exit of glossopharyngeal nerves.

Fig. 7. Section through the medulla at the exit of the Monakow's striae acusticae.

Fig. 8. Section of medulla at the ventral cochlear ganglion.

Fig. 9. Section through the caudal end of trapezoid body.

Fig. 10. Section through the caudal portion of trapezoid body at the level of the facial nucleus.

Fig. 11. Section through the middle of trapezoid body at the level of genu of the facial nerve.

Fig. 12. Section through the cranial end of trapezoid body at the exit of radix of the facial nerve.

Fig. 13. Section through the caudal end of pons.

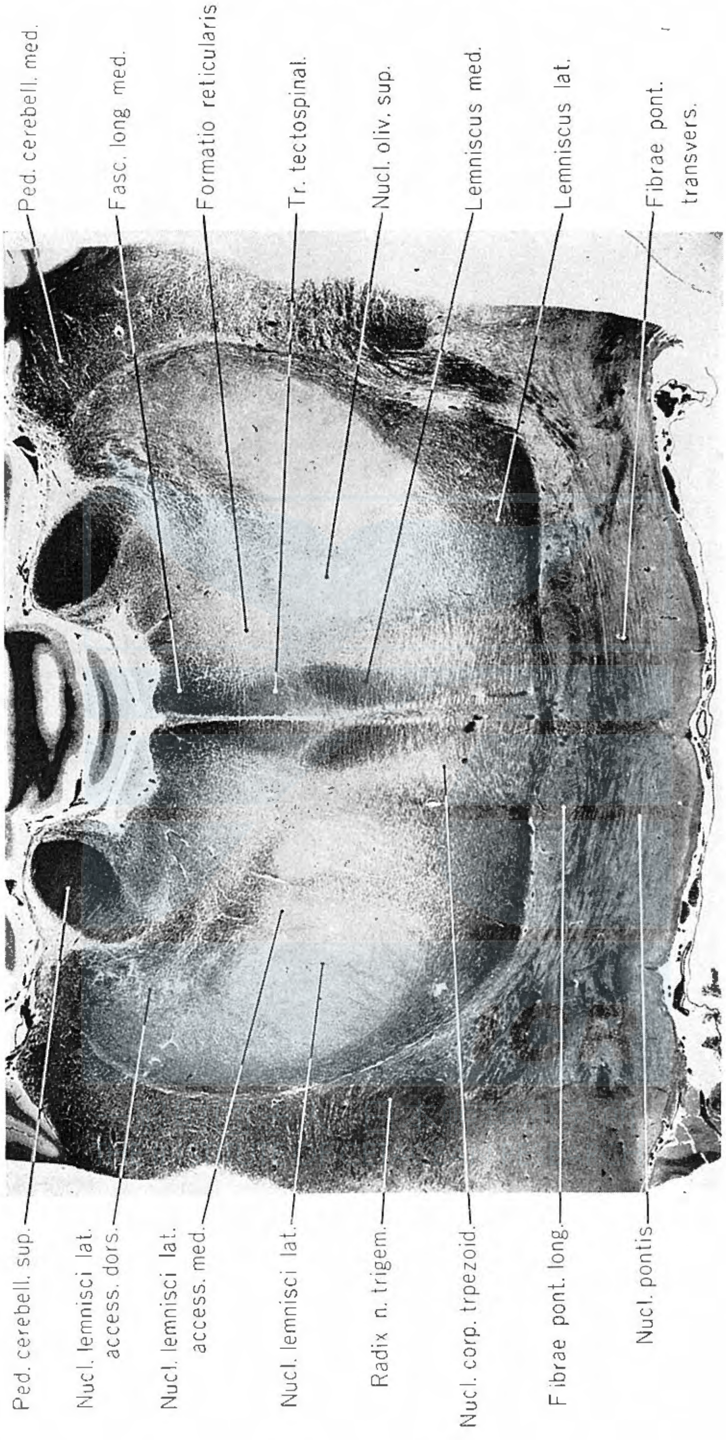

Fig. 14. Section through the middle of pons.

Fig. 15. Section through the inferior colliculus at the exit of radix of the trochlear nerve.

Fig. 16. Section through the middle of inferior colliculus.

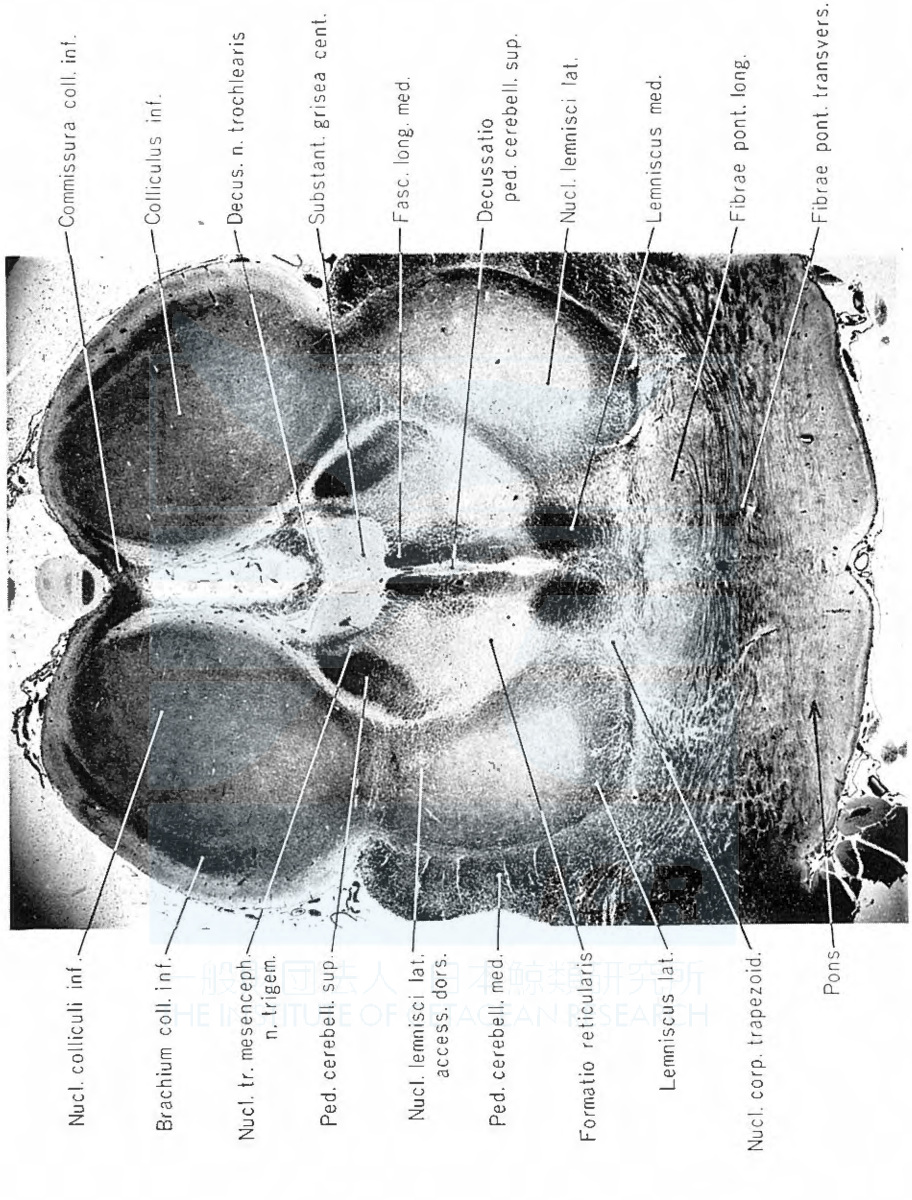

Fig. 17. Section through the middle of inferior colliculus at the level of commissure of inferior colliculus.

Fig. 18. Section through the superior colliculus, brachium of the inferior colliculus, nucleus of ellipticus, interstitial nucleus and optic tract.
* Fasciculus retroflexus (Meynerti).

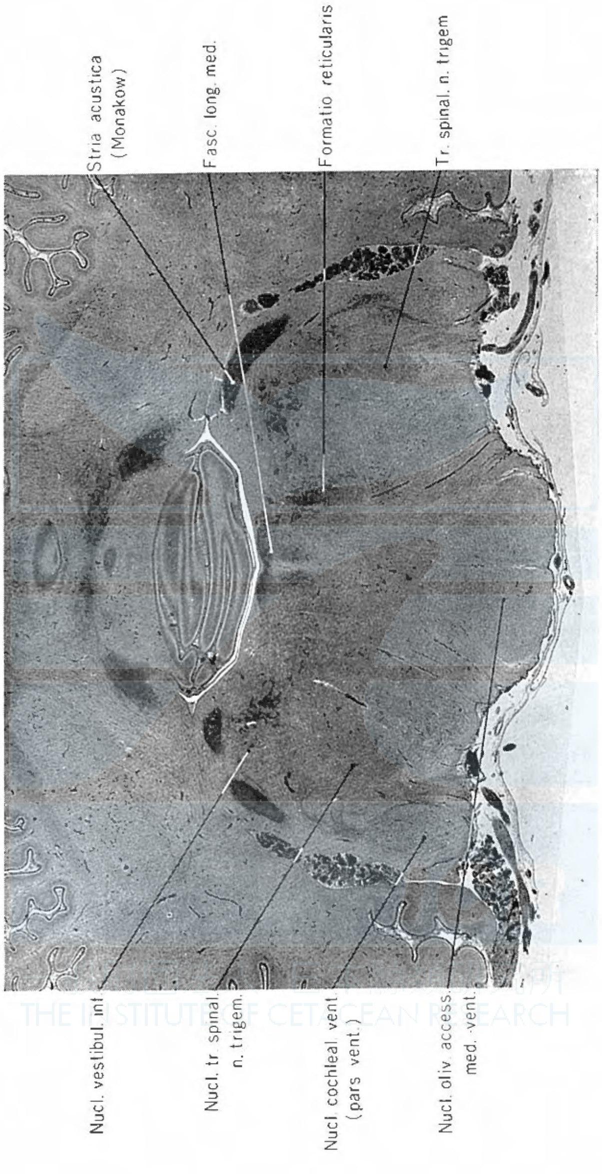

Fig. 19. Section of medulla in embryo 51 cm long, at the exit of the Monakow's striae acusticae.

Fig. 20. Section of medulla in embryo 51 cm long, at the level of the trapezoid body and cochlear nerve.

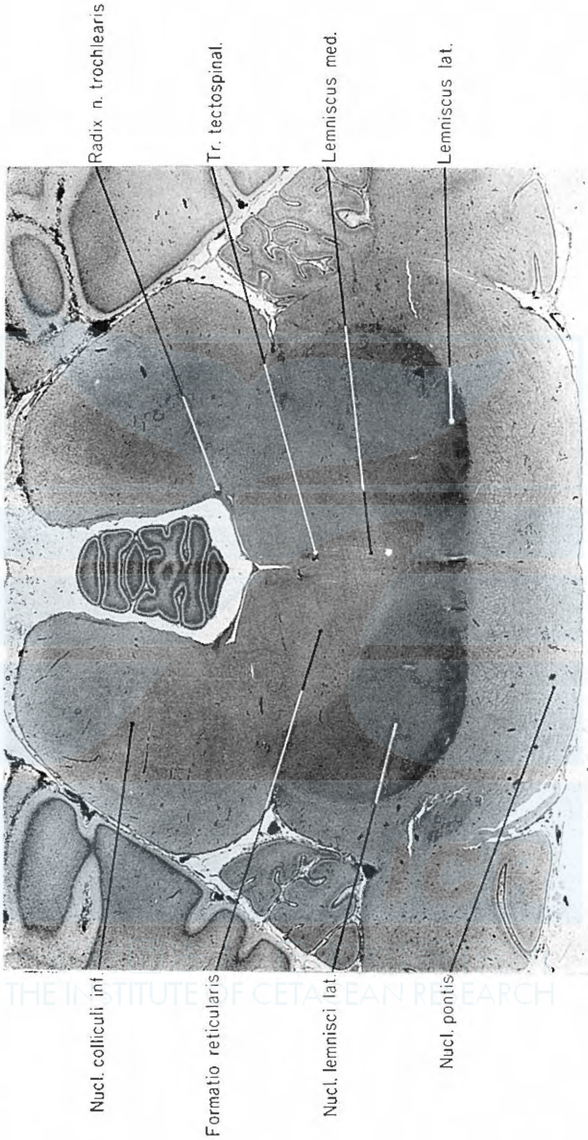

Fig. 21. Section of the midbrain in embryo 51 cm long, at the exit of the radix of trochlear nerve.

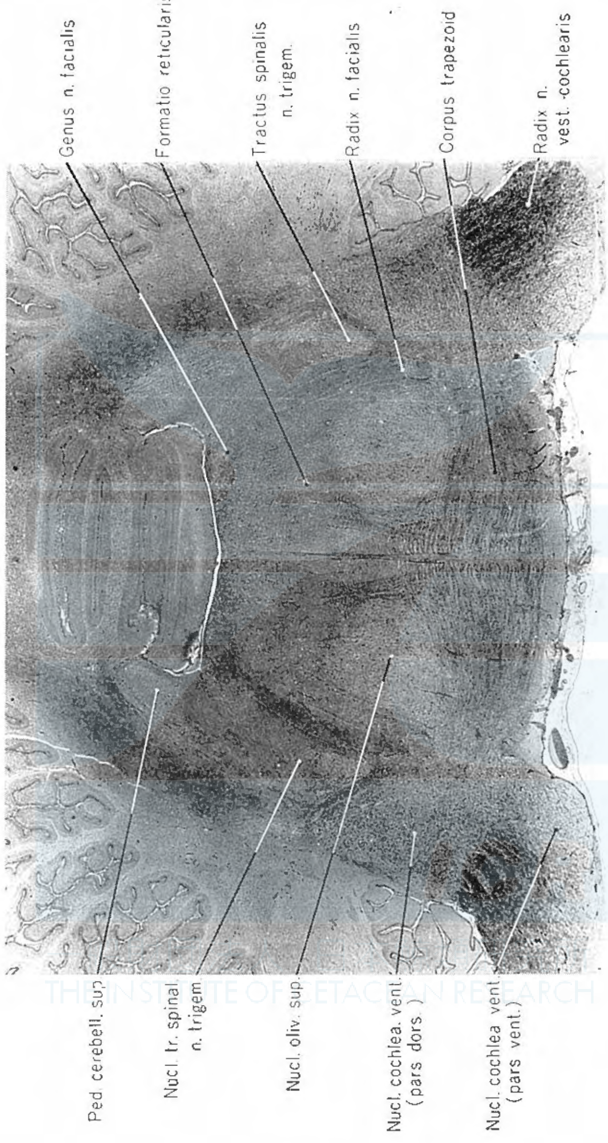

Fig. 22. Section of medulla in embryo 74 cm long, at the level of the trapezoid body and radix of cochlear nerve.

Fig. 23. Section of medulla in embryo 74 cm long, at the level of the nucleus of lateral lemniscus.