On the Acoustic System in the Cetacean Brains

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Introduction

It was first pointed out by Spitzka (1886) and a little later by Ziehen and Kükenthal (1893) that the acoustic system in the brains of the Cetacea is very well developed. Hatschek and Schlesinger (1902) referred to it in their study of the brain stem of a Delphinus. Later, Hofmann (1908) investigated the superior olive of a few kinds of dolphins and the inferior colliculus was studied in the same group of animals by Valeton (1908). Recently Langworthy (1932) examined the whole brain of Tursiops truncatus both macroscopically and microscopically, concluding that its acoustic system is in a high stage of development. It should be noted here that only the Odontoceti, mostly the dolphins, have been studied so far in this respect and scarcely any reference has ever been made to the acoustic system of the baleen whales, nor has there been any comparative study between Odontoceti and Mystacoceti regarding this system.

One of the reasons which prompted us to our present study is, apart from the comparative anatomical interest, the desire to estimate the auditory sense of the sperm whale and various Mystacoceti, at least as far as it is possible through the study of their brain stems. We are sure it is of practical importance to know about the sharpness of hearing in those whales, which are the chief objectives of the present-day whaling enterprise.

Six kinds of whales are studied in our present work: of the dolphins, Lagenorhynchus obliquidens Gill and Tursio borealis Peale, of other Odontoceti, Kogia breviceps Blainville (pigmy sperm whale) and Physeter macrocephalus Lesson (sperm whale, cachalot); of the Mystacoceti, Balaenoptera borealis Lesson (sei whale) and Balaenoptera acuto-rostrata Lacépède (little piked whale). Serial sections of the brain stems of these six animals, all stained by the Pal-carmin method, have been examined with the object of studying the structures in the acoustic system, of determining the difference between Odontoceti and Mystacoceti with references to the acoustic system of other mammals.

The Lagenorhynchus in our present study is an embryo of about 70 cm length, which corresponds, judging by the degree of myelinization in its brain stem, nearly to the newborn human infant. The Tursio is an embryo of about 45 cm length, whose brain stem is in the same stage of development as that of 7 months old human embryo. In this Tursio embryo the myelinization of nerve fibers belonging to the acoustic system has just started, while most of other fibers in the brain stem remain as yet unmyelinated. The very rare brain of Kogia breviceps was collected by T. OGAWA at Shiogama, Miyagi Prefecture on June 7th, 1936. The details on this specimen were already reported in "Botany and Zoology" Vol. 7, No. 7 (published by Yokendo, Tokyo. July, 1938). The brain stem of Physeter macrocephalus is not in perfect condition and the serial sections are limited only to the levels from the oral part of pons to the caudal part of mid-brain. Serial sections of the brains of two Mystacoceti are complete, in Balaenoptera borealis in transverse section and in B. acuto-rostrata in sagittal section. All the brain stems of four Odontoceti are sectioned transversely.

The details of our acquisitions will be reported later in another paper, and only summary of our work is presented here due to the limitation of space.

Results (summarized)

1. "Telescoping" of the dolphin's brain stem.

One of the most characteristic features in the brain stem of dolphins is the caudal shift of its dorsal structures. This peculiarity is not so apparent in the caudal part of oblongata, but on the level near the caudal end of pons, the axis of the brain stem seems to bend dorsally, presenting a curious topographical relation, as in one transverse section of the brain stem one sees in the ventral part structures belonging to the oral proximity of oblongata, in the dorsal part those of mid-brain and in the middle part structures corresponding to the pontile level.

Strangely enough, this unusual feature seems to have been overlooked by many researchers who have studied the brain stem of dolphins. Either no notice has been taken of it, or it was simply dismissed as a result of oblique section. As a matter of fact, however, this is very important in evaluating the structures in the brain stem of dolphins, and we would like to emphasize it.

In 1923 MILLER described a phenomenon called "telescoping" of the Cetacean skulls. According to him, the maxillary bone as well as the frontal bone is elongated caudally, one over the other, coming in contact with the occipital. The above mentioned shift in the brain stem of dolphins seems to have an intimate relation with this unusual configuration of the skull and we wish to use the term "telescoping" also for the brain stem of dolphins. Meanwhile it is as yet impossible for us to decide whether or not the telescoping of dolphin's skulls is directly responsible for the telescoping of the brain, as no remarkable shift of structures is to be seen in the brain of other whales such as Kogia, Physeter and Balaenoptera, even though MILLER's phenomenon is also present in the skulls of these animals.

The brain stem of dolphins is narrow from side to side and broad in ventrodorsal direction. This is also one of its characteristics.

LANGWORTHY said that the whole brain of Tursiops is foreshortened in its anteroposterior extent and widened laterally due to change in the conformation of the skull. This is true, in our opinion, as far as the cerebral hemispheres are concerned, but in the brain stem, especially in its caudal part, the transverse dimension is remarkably small. It is of interest to note here that the entire oblongata in dolphins, when considered in its topographical relation to the skull, seems to be caudally shifted, as both cochlear and vestibular roots run orocaudally to reach the brain stem in its lateral part. The cerebellar flocculus surrounds the ventrolateral surface of oblongata and pons, and the nucleus ventralis of the cochlear nerve lies buried deep between flocculus and the brain stem. The cochlear root approaches the brain stem obliquely and enters the oral part of the ventral nucleus.

2. Dolphins and sperm whales.

Though both dolphin and the sperm whale including Kogia, belong to the Odontoceti, many differences are observed in their acoustic systems, in all probability due to the above mentioned peculiar form of the brain stem at the side of dolphins. There is nothing, however, to indicate the existence of an essential difference between them.

In the case of Kogia, the ventral nucleus of the cochlear nerve protrudes from the ventrolateral part of the oral end of oblongata. Its caudal half is ventrally exposed to the view owing to the absence of flocculus over its ventral surface, while its oral half lies covered by the fibers of brachium pontis. The cochlear and vestibular nerves enter the nucleus in its medial part, as is generally the case in the mammals. The ventral nucleus is as well developed as that of Lagenorhynchus, and it is hard to decide which is more prominent.

In Odontoceti, the corpus trapezoides, which emerges medially from the ventral nucleus, is in a very good state of development; its transverse fibers occupy in Lagenorhynchus more than half (60%) of the dorsoventral length of the raphe, and in Kogia, a little less than the half (43%). The same applies to Held's tract, which runs quite separated from the trapezoidal body and joins this in the median line, where it forms the dorsal part of the trapezoidal body.

Massive fibers emerge from the dorsal half of the ventral nucleus in the fetal dolphins, seemingly ending in the superior olive of the same side. In Kogia it is hard to distinguish this group of fibers, probably because its myelinization is in a far advanced stage. In his study of myelinization in the cochlear system of man, dog, cat, rabbit and rat, one of us (Ogawa, 1936) observed the same kind of homolateral trapezoidal fibers as in the fetal dolphins.

Noteworthy difference is found regarding Monakow's striae acusticae. Those of Lagenorhynchus consist of a great number of fibers, which form a compact bundle, while in Kogia they are made of much fewer fibers. This should not be interpreted as an essential difference, because Monakow's tract also arises from the ventral nucleus of the cochlear nerve and is nothing but a part (pars dorsalis) of the trapezoidal body. In the same way Held's tract should be considered as its intermediate part. In Odontoceti no trace of the dorsal nucleus of the cochlear nerve, i. e. tuberculum acusticum, was observed.

One of the most impressive features in the brain stem of Odontoceti is the remarkable development of the superior olive. We need not enter into details about this nucleus of dolphins, as it is fully described by Hofmann, who studied it in Phocaena communis and Delphinus delphis, and also by Langworthy, who investigated that of Tursiops truncatus.

Partition of superior olive in two parts, pars lateralis and pars medialis, is hardly recognizable in Lagenorhynhus. It is almost the same with Tursio. Immature myelinization of the fetal brains is probably responsible for it. The superior olive of Kogia is relatively larger than that of dolphins. In fact no larger superior olive can be found in all the whales we have investigated. Distinctly divided in two parts, the pars lateralis is disproportionately bigger than the pars medialis. The nucleus as a whole presents a very light colored aspect, as there are relatively few myelin-stained fibers within it. The pars medialis is much smaller, its oral end lying more backward than that of the pars lateralis. It should be noted here that this caudal position of pars medialis is an exception to HOFMANN'S conclusion in his comparative anatomical study of the superior olive, inasmuch as he says that in many animals he studied the pars medialis is invariably found to be on a more oral niveau than the pars lateralis.

The trapezoidal nucleus is very well developed both in Kogia and in Lagenorhynchus, with only the following difference: in the latter, probably owing to the narrowness of the brain stem this nucleus borders on the median line, while in the former, there is some space between the nucleus and the raphe. Needless to say, this does not mean an intrinsic difference. A part of the trapezoidal nucleus is found wedged between the superior olive and the lateral lemniscus, protruding into the dorsomedial part of the latter. This is common to both of the Odontoceti.

One of the similarities between Kogia and dolphins is the vastness of the lateral lemniscus. That it is very large in dolphins has already been known, but in Kogia and Physeter it is strikingly larger. The term "colossal" can safely be used in describing it. One is easily led to imagine a malformation of the brain stem. The nucleus of the lateral lemniscus and the inferior colliculus with its brachium are also proportionately large. The medial geniculate body is completely merged in the posterior part of the optic thalamus, and even though its hugeness can easily be surmised, we were unable to measure its actual size.

Generally speaking, much similarity is observed in the acoustic system of Kogia and dolphins. Remarkable development of the ventral nucleus of of the cochlear nerve, corpus trapezoides, HELD's tract, trapezoidal nucleus, superior olive, lateral lemniscus with its nucleus and the nucleus colliculi caudalis is quite unique among all the mammals. MONAKOW's striae acusticae are more prominent in dolphins. Kogia and Physeter may well be said to surpass dolphins in the development of the superior olive, the lateral lemniscus and the inferior colliculus.

3. Odontoceti and Mystacoceti.

In the topographical relation of a great many structures in the brain stem, Balaenoptera has much in common with Kogia, presumably because there is no telescoping in their brain stem. At first sight, it seems as if Balaenoptera is more akin to Kogia than to Lagenorhynchus in their acoustic systems. Further investigation, however, reveals the existence of an intrinsic difference between them.

The ventral nucleus of the cochlear nerve and the corpus trapezoides are very well developed in Balaenoptera. The latter occupies in Balaenoptera borealis 40% of the raphe and in B. acuto-rostrata 47%, coming very close to that of Kogia (43%). In Balaenoptera there is not a vestige of HELD'S tract and MONAKOW'S striae acusticae are poorly developed.

The most significant difference is observed between Balaenoptera and Odontoceti in the development of the superior olive. That of B. borealis is very small, and it looks very dark as it has many myelinated fibers among the nerve cells. The pars lateralis of the superior olive in Kogia is disproportionately large compared with the pars medialis, or with the pars lateralis of Balaenoptera. That of B. borealis appears on the oral one third of the facial nucleus, terminating on the level of the oral proximity of this nucleus (orocaudally 4 mm, transversely 4 mm), while that of Kogia begins on the middle level of the facial nucleus and reaches the transitional part of the superior olive to the lateral lemniscus (orocaudally 5 mm, transversely 6 mm). The pars medialis of the superior olive in Kogia is small and disappears on a more caudal level, while in Balaenoptera it is fairly long in orocaudal direction, outstripping its pars lateralis by 4.5 mm. Histological difference of the superior olive between Odontoceti and Balaenoptera seems also to be of importance. As has been mentioned before, the superior olive of Kogia presents a very light colored aspect, as there are relatively few nerve fibers among its cells, while in Balaenoptera it is very dark on account of abundant fibers within the gray substance.

Meagre development of the superior olive in Balaenoptera in spite of its large trapezoidal body seems to indicate that a great number of the latter's fibers reach the lateral lemniscus without interruption, relatively a small part of it terminating in the superior olive. It is also conceivable that some of the trapezoidal fibers come directly from the cochlear root and end in the trapezoidal nucleus. This nucleus is fairly well developed in Balaenoptera but not so well as that of Odontoceti. A small part of the trapezoidal nucleus, which lies in Odontoceti between the superior olive and the lateral lemniscus, is not observed in Balaenoptera. The lateral lemniscus is as well developed as in most other mammals but falls short of Odontoceti in its size. The inferior colliculus of Balaenoptera with its brachium is above the average of mammals in its development but poorer in comparison with that of Odontoceti. The medial geniculate body is fairly large, but its inner structure does not seem to be in good differentiation, as we see neither any trace of an incisure on its lateral surface, nor any difference between the peripheral and the deeper regions in its ventral part.

Considered as a whole, there is a remarkable difference between Mystacoceti and Odontoceti in the development of the superior olive and the lateral lemniscus. We are not at present in a position to say what functional meanings these structures have in the auditory sense, but judging from the degree of development of intracerebral structures in the acoustic system, we may assume that Odontoceti must be more acute of hearing. In this respect Mystacoceti seem to be inferior to Odontoceti.

4. Man and Balaenoptera.

Inferiority of the acoustic sense of Balaenoptera to that of Odontoceti does not necessarily imply the bluntness of hearing in the former, as structures of the acoustic system developed in Balaenoptera are by no means below the average of mammals. Balaenoptera bears at least one resemblance to man in that the superior olive is very small compared with the well developed trapezoidal body. In this respect there seems to be something in common between Homo and Balaenoptera in their auditory sense. At the same time one should not forget the fact that Balaenoptera's superior olive as well as its trapezoidal body is in a slightly better state of development than that of man and the trapezoidal nucleus occupies a large area, while in man this nucleus is hardly recognizable.

5. The corpus ponto-bulbare of Essick, the dorsal nucleus of the cochlear nerve and the dorsal nucleus of the lateral lemniscus.

The corpus ponto-bulbare, first fully described by Essick, is hardly known to exist except in the human brains. Certainly there is no trace of it in dolphins, but in Kogia it is very well developed and is also distinctly recognized in Balaenoptera. When in 1933 Wilson described the brain stem of Balaenoptera borealis, he mistook this gray matter for the ventral nucleus of the cochlear nerve (Journ. Comp. Neurol. Vol. 58, No. 2, p. 455, fig. 18), and the space left blank just lateral to "tpz" in his illustration also belongs to it. The fibers intimately related to the ponto-bulbar body are attached to the lateral and the medial sides of the ventral nucleus both in Kogia and Balaenoptera. In B. borealis, these fibers run dorsalward parallel to the corpus restiforme, forming the most lateral of three bundles directly lateral to this body. Each of these bundles seems to have a significance of its own.

In the study of the acoustic system of whales, due attention should be paid to the existence of corpus ponto-bulbare.

The existence of the nucleus dorsalis nervi cochleae, i. e. tuberculum acusticum, in whales is very doubtful. We could not locate it in Odontoceti and found only a rudimentary one in Balaenoptera. According to Fuse, a partial fusion of the dorsal nucleus of the cochlear nerve to the ventral nucleus occurs sometimes in higher animals. In this connection the question arises whether or not the pars dorsalis of the ventral nucleus we observed in dolphins is to be considered as the dorsal nucleus itself. But our reasons for assuming the non-existence of the dorsal nucleus in Odontoceti are as follows.

In dolphins the ventral nucleus is divided in two parts, pars dorsalis and pars ventralis, while in Kogia it is divided in pars lateralis and pars medialis. The fact that the dorsal and ventral parts of the former correspond respectively to the lateral and medial parts of the latter is out of question, as the cause of this topographical difference lies certainly in the general form of the brain stems. In dolphins the brain stem is broad in ventrodorsal direction and narrow transversely, while in Kogia it is quite the opposite. Had the dolphin's brain stem been shaped just like that of Kogia, the ventral nucleus of the cochlear nerve might have been divided in pars lateralis and pars medialis as in Kogia. As it is, with its topographical relation to the cerebellar flocculus and to Monakow's striae acusticae being duly considered, we cannot identify in dolphins the dorsal part of the ventral nucleus with the dorsal nucleus of other mammals.

Next we wish to call attention to the so-called dorsal nucleus of the lateral lemnicus, which is located both in Kogia and Lagenorhynchus, just ventral to the nucleus of the inferior colliculus and seems to be closely connected with "fibrae perforantes". This nucleus remains very small among all other very well developed cochlear structures, and so it is very doubtful that this tiny gray matter has anything to do with the cochlear system. Probably it has some other functional significance. In Balaenoptera no trace of this nucleus is to be seen.

VALETON, in her comparative-anatomical study of the inferior colliculus, found a fiber group of small calibre in the lateral lemniscus of Phocaena communis emerging from its dorsomedial part. Some of it are believed to reach as far as the contra-lateral inferior colliculus by way of velum medullare anterius and some of it to run dorsally along the medial margin of the inferior colliculus until they disappear near the commissure of the inferior colliculus. Described in details as they were, we can not in any way locate such a fiber group in Lagenorhynchus. Some finely myelinated fibers are observed by us to arise out of the dorsomedial part of the lateral lemniscus in Lagenorhynchus. These fibers either pass through the brachium conjunctivum or over it to reach the central gray matter, where most of them disappear with only a small portion of them reaching as far medial as the surface of the fourth ventricle. They represent no doubt VALETON's fibrae marginales (loc. cit. p. 30 a. 59). In cachalot we saw several thick bundles of the same calibre pass through the brachium conjunctivum and reach the central gray matter dorsal to the fasciculus longitudinalis medialis, where they bend suddenly ventralward. In Kogia the existence of such fibers is not so clear, while in Balaenoptera borealis a thick bundle goes into velum medullare anterius ofter crossing the trochlear root. We could not decide whether or not this bundle has anything to do with the acoustic system.

6. Nuclei of the vestibular nerve, especially the DEITERS' nucleus.

In all the cetacean brains studied here, meagre development of the vestibular nuclei as a whole stands out in striking contrast to the very well developed cochlear nuclei. In Lagenorhynchus, the vestibular root is barely one tenth of the cochlear one in thickness.

In studying the vestibular system of whales, due consideration should be given to the existence of a part of the vestibular root, so-called tractus solitarius acustici of Lewandowsky, which runs, apart from the main tract, dorsally along the lateral margin of the restiform body. The cells of the Deiters' nucleus lie scattered along this root, a few of them reaching as far ventral as the ventrolateral margin of the restiform body.

The nucleus triangularis of Kogia and Balaenoptera occupies a smaller area than that of Lagenorhynchus, as in them the central gray matter of the fourth ventricle is more limited in space. This fact, however, should not be considered as showing some definite difference in vestibular function, as the nucleus triangularis is not limited to the vestibular nerve in its function.

The spinal tract of the vestibular nerve is very meagre in Lagenorhynchus and its fiber bundles are in a looser arrangement. In Kogia and Balaenoptera this tract occupies a far wider area and its fibers are massively collected. Except in Lagenorhynchus, the Bechterew's nucleus is hardly recognized in whales, a finding quite contrary to Kaplan's, who found this nucleus very well developed both in Phocaena and Balaenoptera. Incidentally it should be mentioned that according to Kaplan, this nucleus in whales is the shortest one of all animals in orocaudal direction, though it occupies a broad area on a transverse section.

In our opinion, of all the vestibular nuclei only the Deiters' nucleus is very well developed in whales. In Lagenorhynchus, Kogia, and Balaenoptera, the cells of this nucleus are scattered in a peculiar way and similarly distributed. They first come into view in the lateral part of the spinal tract of the vestibular nerve which caps the restiform body. Next some appear along the lateral vestibular root lateral to the restiform body. Soon they become most abundant in the lateral part of the spinal tract and also in the gray matter directly dorsal to it. Medium large cells belonging to the Deiters' nucleus are seen mostly in the dorsomedial part of the spinal tract and the adjacent gray matter. Only a few large cells are observed here. The cells of the Deiters' nucleus are numerous in number and widely distributed transversely, but is of short duration in orocaudal direction (in Kogia only 2 mm). Only a few cells of the Martin's nucleus are seen in Kogia and Balaenoptera borealis in the ventral part of the spinal tract medial to the restiform body.

The tractus vestibulo-spinalis is very prominent in Lagenorhynchus and Tursio, due probably to the immature development of other fiber tracts in the brain stem. It arises, as a collection of massive fibers, from the dorsolateral part of the Deiters' nucleus, and arches down ventrally until it reaches the ventromedial part of the reticular formation. This tract is fairly distinct in Kogia, but in Balaenoptera it is hardly distinguishable.

Resumé

1. Structures of the acoustic system were comparatively studied in serial sections of the brain stems of six kinds of whales (Lagenorhynchus, Tursio, Kogia, Physeter, and two species of Balaenoptera).

2. In dolphins, the dorsal·structures of mid-brain, pons and oblongata are remarkably shifted caudally. This phenomenon, to which the term, "telescoping" of the brain stem may be applied, is peculiar to dolphins. It is also noteworthy that the brain stem of dolphins is narrow transversely and broad dorsoventrally.

3. No "telescoping" of the brain stem was observed in Kogia, Physeter and Balaenoptera. Its form in these animals is broad transversely and narrow in dorsoventral direction, being hardly different from the brain stem of other mammals in general.

4. In Odontoceti (dolphins, Kogia, and Physeter), the ventral nucleus of the cochlear nerve, corpus trapezoides, superior olive, trapezoidal nucleus, lateral lemniscus with its nucleus, nucleus et brachium colliculi caudalis are all in a very good stage of development. They are overwhelmingly large compared with other structures in the brain stem. Monakow's striae acusticae are well developed in dolphins, but less prominent in Kogia. The Held's tract is highly developed both in dolphins and other toothed whales. The superior olive and the lateral lemniscus of Kogia and Physeter are larger than those of dolphins, probably the largest among all mammals.

5. In Balaenoptera the ventral nucleus of the cochlear nerve and the corpus trapezoides are fairly well developed, but the superior olive is small in size and the trapezoidal nucleus, large as it is, falls short of that of Odontoceti. This is one of the remarkable differences between Odontoceti and Mystacoceti. The superior olive of Balaenoptera presents a far darker aspect, as this nucleus contains many myelinated fibers. Their lemniscus lateralis with its nucleus is somewhat retarded in its development compared with that of Odontoceti. The nucleus of inferior colliculus is fairly large

but inferior to that of Odontoceti in its dimensions. MONAKOW's striae acusticae are meagre in development and no HELD's tract was observed in Balaenoptera.

6. That there is noteworthy difference between Odontoceti and Mystacoceti in their acoustic sense is easily surmised through the study of their brain stems. The acoustic sense of Odontoceti seems to be sharp and to have reached a peculiar stage of development which is quite unique among all the mammals. The acoustic sense of Mystacoceti, though probably not inferior to that of land-living animals in acuteness, seems to be very different from that of Odontoceti. Discussions on the Mystacoceti's acoustic sense through the study of that of Odontoceti are in no way justified.

7. The corpus ponto-bulbare of ESSICK is very well developed in Kogia and in a slighter degree in Balaenoptera. In observing the end nuclei of the cochlear nerve, the existence of this gray matter should always be borne in mind.

8. Of all the vestibular nuclei only the DEITERS' nucleus is well developed in the whales we have studied. The cells of this nucleus are widely distributed in a peculiar way, a part of it lying lateral to the restiform body. The vestibulo-spinal tract is most prominent in the brains of fetal dolphins. It also seems to be well developed in Kogia and Balaenoptera, but in these animals the myelinization of fibers in the brain stem is far advanced and the vestibulo-spinal tract is not so sharply distinguished from adjacent structures.

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List of abbreviations in figs. 1—14

bc ……Brachium conjunctivum
bck ……Decussatio brachiorum conjunctivorum
brp ……Brachium pontis
cc………Crus cerebri
cgm……Corpus geniculatum mediale
ci ………Colliculus caudalis
cibr ……Brachium colliculi caudalis
coch……N. cochleae
comci …Commissura colliculi caudalis
cpb ……Corpus pontobulbare
cpbf……Fibers belonging to Corpus pontobulbare
crs ……Corpus restiforme (restiform body)
cs………Colliculus rostralis
ctr ……Corpus trapezoides
fs………Fasciculus solitarius
hl………Fasciculus longitudinalis medialis
Ht ……HELD's tract
ll ………Lemniscus lateralis
Msa……MONAKOW's striae acusticae
nci ……Nucleus colliculi caudalis
nll ……Nucleus lemnisci lateralis
np………Nuclei pontis
ntr ……trapezoidal nucleus
nv ……Nucleus ventralis n. cochleae
nvd ……pars dorsalis } Nucleus ventralis n. cochleae
nvv ……pars ventralis }

om ……Nucleus olivae accessorius medialis
osup …Superior olive (Nucleus olivaris metencephali)
osupl …pars lateralis } superior olive
osupm…pars medialis }
sgc ……Stratum griseum centrale
sn………Substantia nigra
tds ……Tractus spinalis n. vestibuli
tsves …Tractus solitarius n. vestibuli
tts ……Tractus tectospinalis
tvs ……Tractus vestibulospinalis
ves ……Redix n. vestibuli
IIIr ……Radix n. oculomotorii
IVr ……Radix n. trochlearis
Vsp……Tractus spinalis n. trigemini
Vr ……Radix n. trigemini
Vsens…Nucleus terminalis n. trigemini
VIr ……Radix n. abducentis
VIIg……Genu (internum) n. facialis
VIIn……Nucleus originis n. facialis
VIIr……Radix n. facialis
VIII……N. statoacusticus (N. vestibuli+N. cochleae)
X ……N. glossopharyngicus et n. vagus
Xr ……Radix n. vagi
XIIr……Radix n. hypoglossi

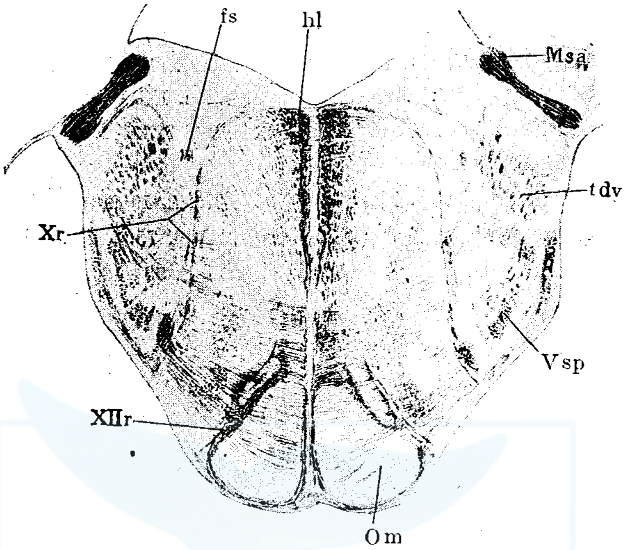

Fig. 1. Lagenorhynchus (x 3)

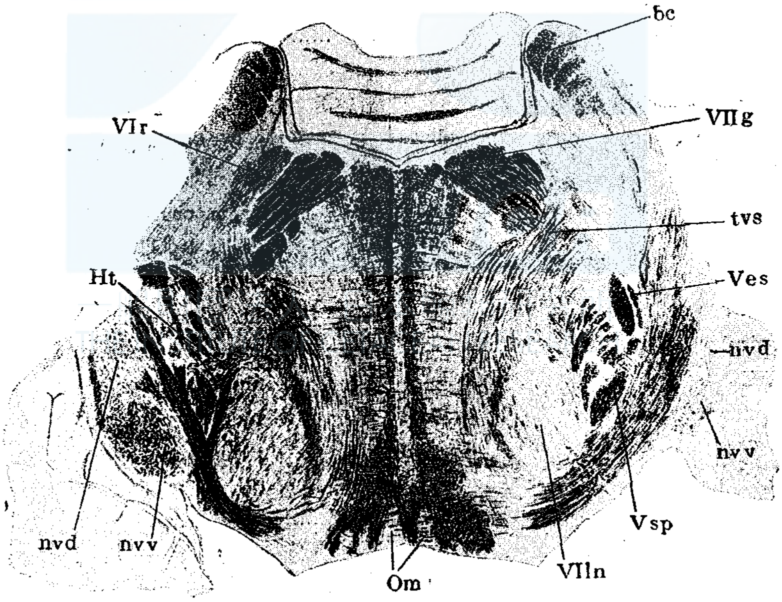

Fig. 2. Lagenorhynchus (x 3.7)

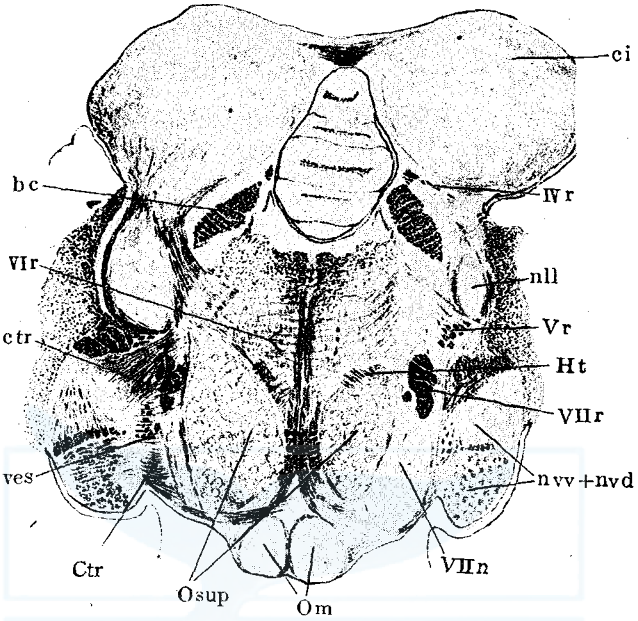

Fig. 3. Lagenorhynchus (x 2.6)

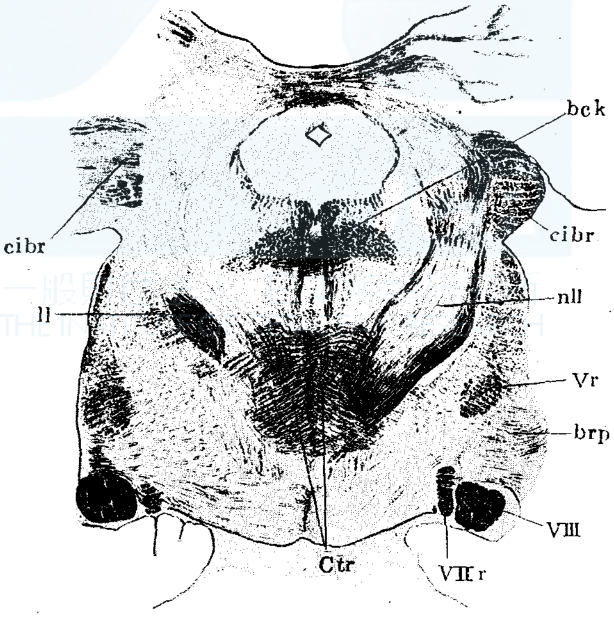

Fig. 4. Lagenorhynchus (x 2.2)

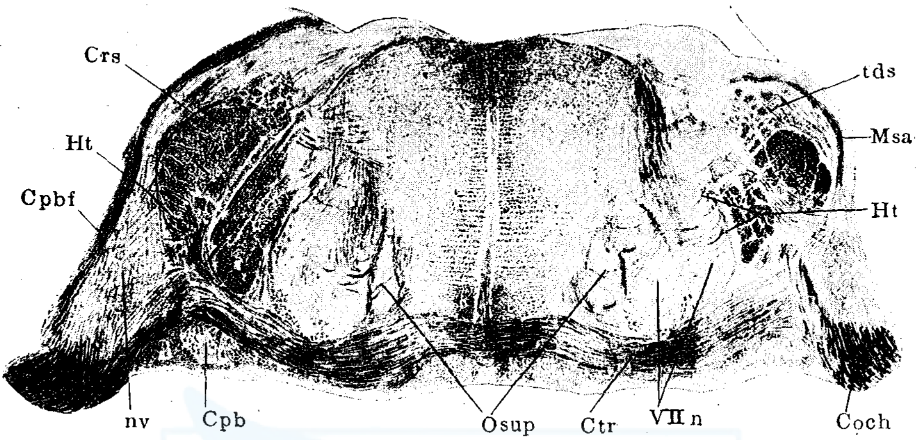

Fig. 5. Kogia (x 6.8)

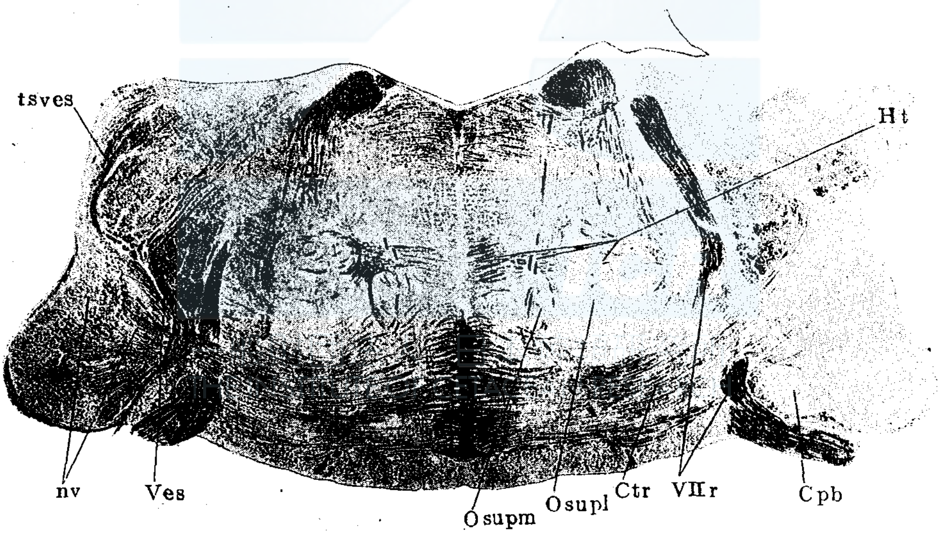

Fig. 6. Kogia (x 3.5)

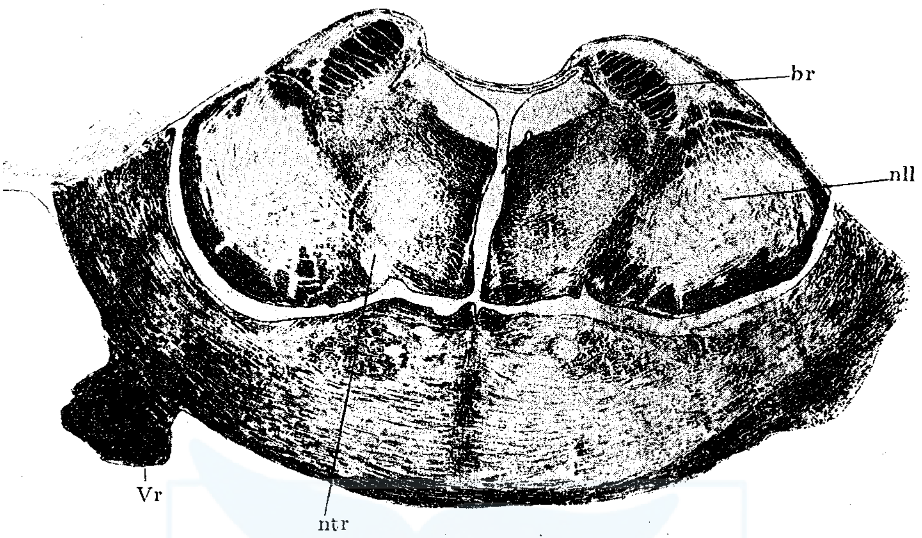

Fig. 7. Kogia (x 3.2)

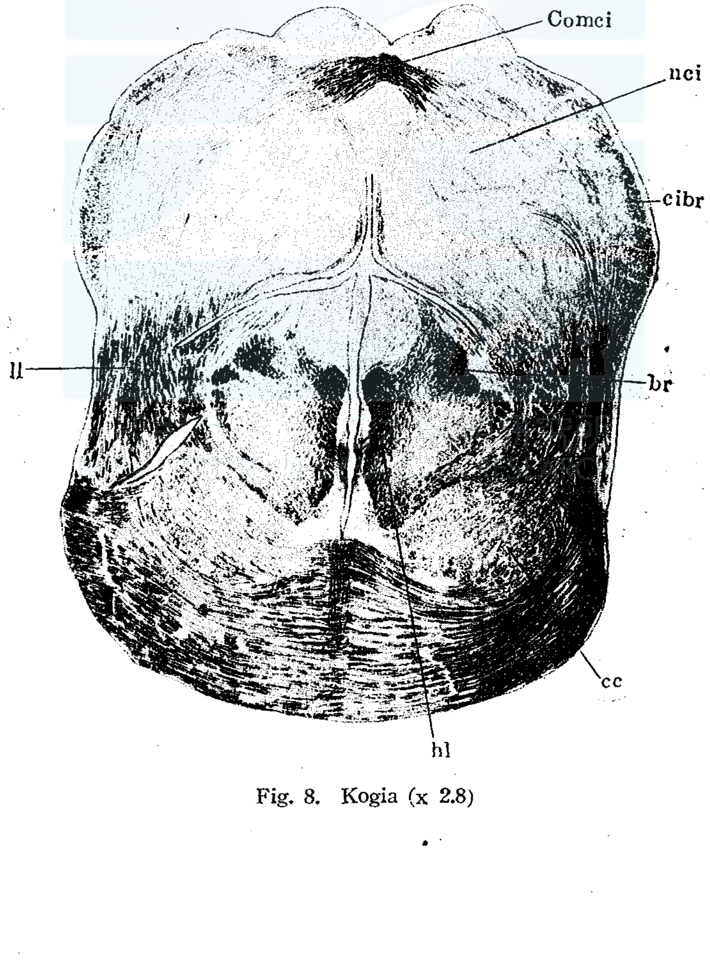

Fig. 8. Kogia (x 2.8)

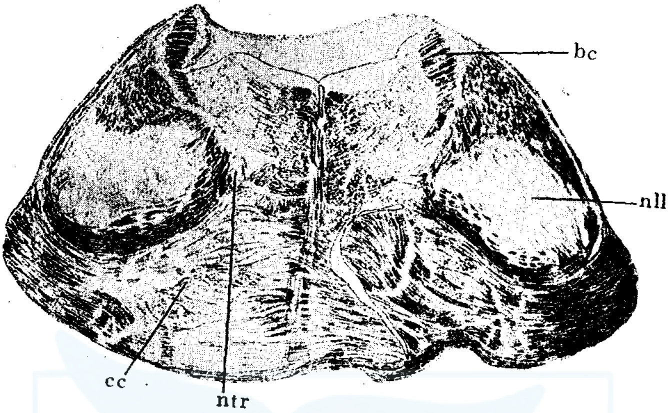

Fig. 9. Physeter (x 1.6)

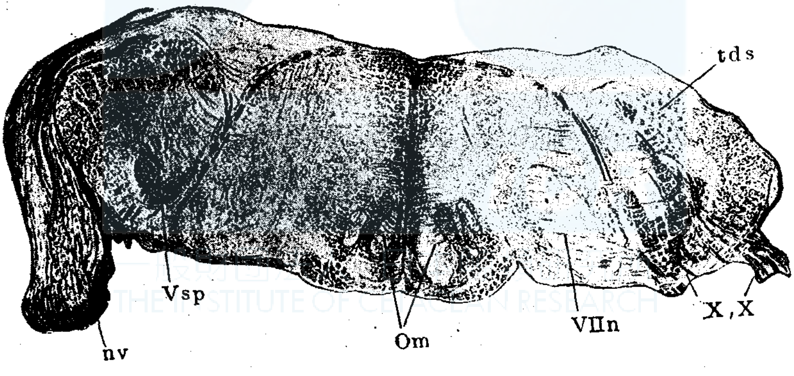

Fig. 10. Balaenoptera borealis (x 2)

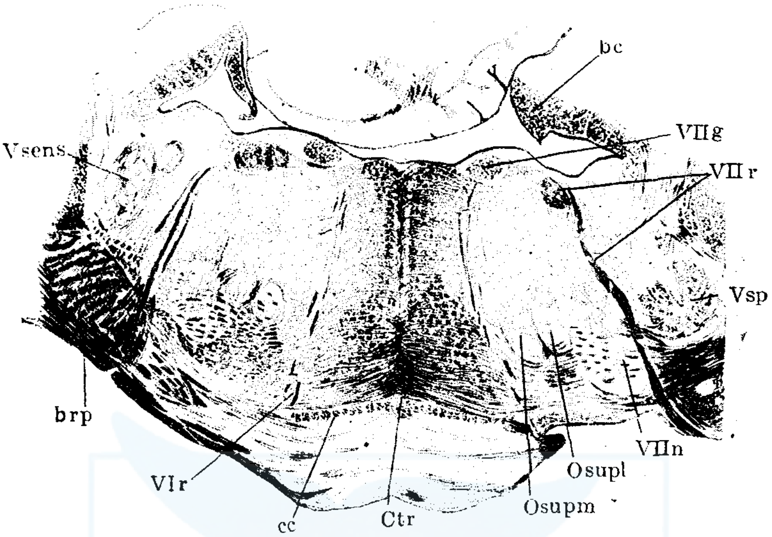

Fig. 11. Balaenoptera borealis (x 1.9)

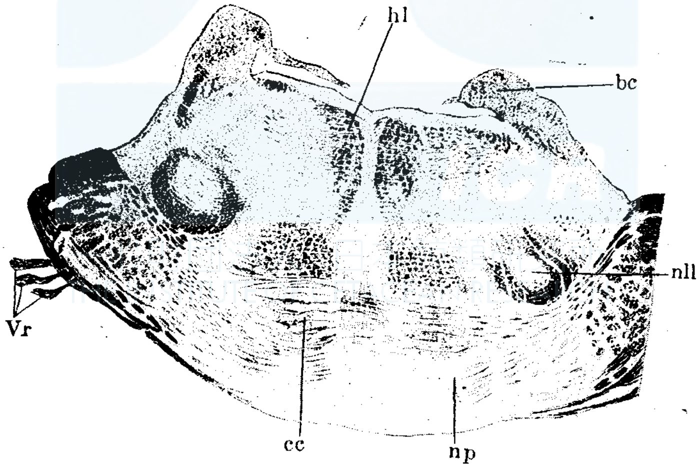

Fig. 12. Balaenoptera borealis (x 1.4)

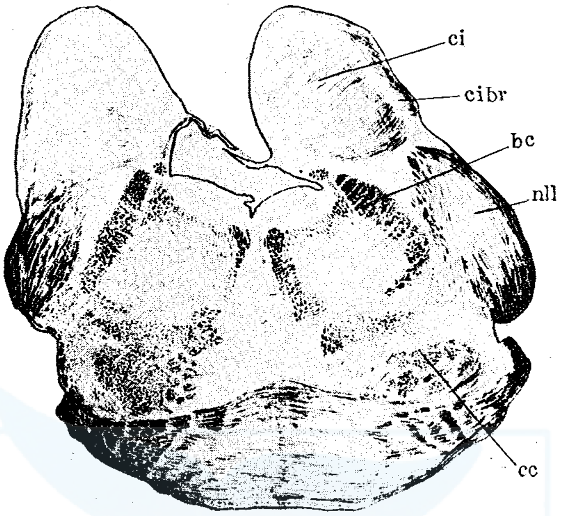

Fig. 13. Balaenoptera borealis (x 1.8)

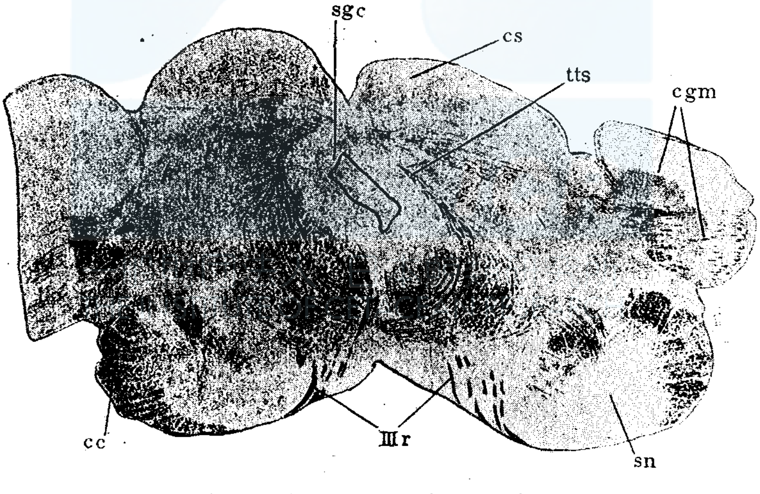

Fig. 14. Balaenoptera borealis (x 1.6)