On the Brain of the Sperm Whale (Physeter Catodon L.)

BY

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During the Antarctic expedition on board the Japanese whaling factory ship "Nissin Maru No. 1" in the season of 1949–50, I have undertaken to investigate the brain of the Sperm whale upon the following points.

(I) Brain weight
(II) Macroscopical observation on the cerebral hemispheres especially on the fissures and the gyri
(III) Cytoarchitecture of the cerebral cortex

The brain weight (I) was surveyed on the deck, while the other studies (II and III) were later performed at the Brain Institute, University of Tokyo, upon materials fixed in formalin.

In the Antarctic Ocean we captured none of female and infantile Sperm whales but only males of over 40 feet length. During the expedition the Nissin Maru could get 172 Sperm whales, in which only 7 (4.1%) were sexually immatured.

(I) Brain weight

The brain was taken out from the huge cranium, using such tools as chisel, gimlet or hatchet, after the bone was cut by a bone-saw into a block properly shaped for extraction of the brain, or after sagittal sectioning of the cranium into halves, two separated parts of the brain were gathered.

The brain weight was measured with the steelyard (the measure limit: 100 g), without stripping off the pia mater, because the brain substance is too soft to isolate it safely from the pia mater.

As the spinal cord was usually transected at the occipital condyles, its upper part, more rostral than the place of the IV cervical nerve roots, was attached to the brain.

The brain weights of 16 Sperm whales, of which the average body length is 49.8 feet, are shown in Table 1. This average body length is nearly equal to that (49.9 feet) of the total (172) Sperm whales captured. The brain of No. 3 (*1) weighed very light (6.4 kg); as the

Table 1. Brain weights, measured fresh, of 16 Sperm whales

Date of Measurement	No. of the Sperm whale	Brain weight (kg)	Body length (feet)	Brain weight (kg) / Body length (feet)
5/XII, 1949	1	8.0	50	0.160
〃 〃	2	7.0	49	0.142
〃 〃	3	6.4 *1	54	0.118
〃 〃	4	7.3	49	0.148
7/XII, 〃	5	7.7	50	0.154
〃 〃	6	7.0	52	0.134
9/XII, 〃	7	8.7	54	0.161
11/XII, 〃	98	9.2 *2	49	0.187
〃 〃	99	8.6	46	0.186
12/XII, 〃	108	9.0	51	0.176
〃 〃	110	8.0	49	0.163
14/XII, 〃	122	7.0	49	0.142
15/XII, 〃	123	8.0	54	0.148
〃 〃	125	7.0	51	0.137
〃 〃	153	8.0	51	0.156
〃 〃	154	8.2	49	0.167

cranium of this individual was fragile, the whale was estimated as a very old one, while the most heavy brain of No. 98 (*2) belonged to an individual, which seemed to be in full maturity, as the brain substance and the cranium were felt very hard.

Naturally I had an interest in knowing the ratio of the brain weight to the body weight, but it was impossible to determine the latter; moreover, even during the short season from beginning till end of December the Sperm whales increased considerably in the body weight, as they eat much food in the meantime; therefore the body weight varied to a high degree.

On the other hand, the ratio of the brain weight (kg) to the body length (feet) was easy to determine. Its individual difference was great, between 0.118 as minimum and 0.187 as maximum, the average being 0.154. We know that the brain weight bears no direct ratio to the body length. *Considering the fact that the Sperm whales caught* in the Antarctic are all males and almost all of them are fully matured, the difference in question seems to have some relation to the degree of senility.

It should be noted here that scarcely any reference has ever been made to the brain weights of the Sperm whale, though those of some Mystacoceti and of other Odontoceti have been sometimes studied. But even in these cases they were surveyed under different conditions as to fixation, its duration, the meninges contained or not, and the age, often including embryos.

Guldberg reported the brain weight of a Blue whale of 60 feet length, measured fresh inclusive the pia mater, arachnoides, and blood, as 6700 g, and the dura mater and rete mirabile of it as 3050 g. He said also that the brain fixed a few weeks in alcohol of a Blue of 64 feet length weighed 4673 g, and that the brain of a Fin whale together with the dura mater and rete miriable was 13680 g, after 8 weeks' fixation in alcohol. According to him, the brain weight had been measured by Knoch and Hunter in Balaenoptera rostrata, by Scoresby and Rudolphi in Balaena mysticetus, and by Eschricht in Megaptera boops. After all, we know in the literature Guldberg's only one case, when the fresh brain was measured in a whale of over 50 feet length; other reports concerned always the weights after fixation, or the brain of smaller whales, mostly of dolphins and porpoises. The brain weights measured by me in Physeter seem to be, though they are quite difficult to compare, heavier than those of Mystacoceti of over 50 feet length.

According to Guldberg, the brain weight loses about 1/3 after fixation in alcohol. I myself fixed pieces of the cerebral cortex of the Sperm whale in 10% and 20% formalin and followed how they change in weight by fixation; the results are shown in Table 2. I reached the opinion that the ratio of increase is smaller as the size of the fixed material is larger and the increase stops nearly after 29 hours' fixation. In cases of such large materials as the cetacean brain the permeation of the fixing fluid occurs quite uncertainly and incompletely, for example we found that after 7 months' fixation in 10% formalin the brain of the Sperm whals showed very few infiltration of the fluid

Table 2. Changes of the weight of brain substance during fixation in formalin solution (200 cc)

	in 10% formalin		in 20% formalin	
Weight before fixation	21.5g	15.0g	9.8g	39.4g
After 24 hours' fixation	29.2g	21.0g	13.2g	50.0g
After 29 hours' fixation	31.2g	21.0g	13.2g	51.2g
After 98 hours' fixation	31.0g	22.0g	13.2g	51.0g
Ratio of increase	44%	46%	34%	29%

even in the relatively small outlined brain stem; therefore I think the weight after fixation is quite unreliable.

Now that the brain weights reported in the present paper include pia mater, blood vessels and the cranial nerves of various lengths are attached, they can never be said to represent the genuine weight of the brain substance itself. There can be errors of about 500 g.

(II) Macroscopical observation on the brain especially on the gyri and the fissures of the cerebral hemisphere

1) Weight, volume and dimensions

The brain of a Sperm whale of 50 feet length was examined in details. It weighed 8.2 kg inclusive of the pia mater, which was attached to medial and basal parts of the hemisphere and to the brain stem.

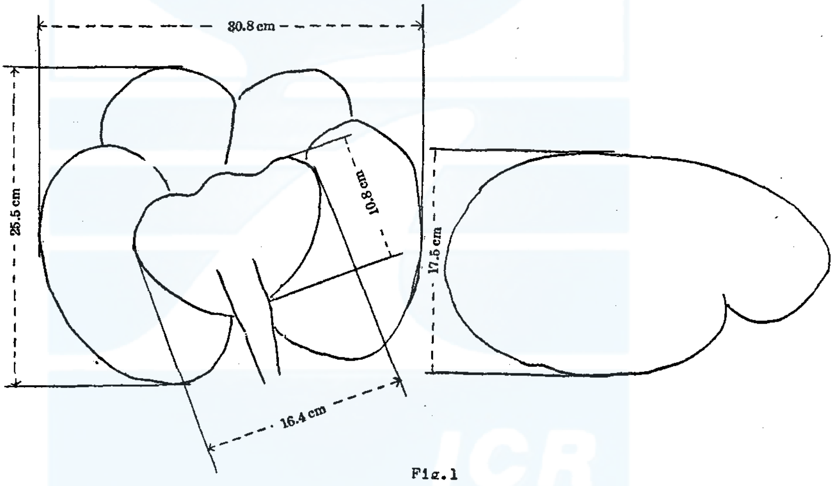

Fig. 1. Size of the brain of a Physeter.

The volume of the whole brain measured by the displacement of water is 8050 cc. The specific gravity as the whole is therefore 1.01. The brain was deformed to a certain degree during fixation in formalin. Especially the basal surface was pushed by the bottom of the vase and the vertical axis was shortened, while the transversal and sagittal axis became larger. Because of the deformation the following data must be a little different from the size of the brain in the living state (fig. 1).

Sagittal axis: 25.5 cm. This is the longest distance between the frontal and occipital extremities. The difference between both hemispheres is very slight (left 25.4 cm, right 25.5 cm).

Transversal axis: 30.8 cm, with some asymmetry. The right hemisphere 15.8 cm; the left one 14 cm. It was already pointed out by GULDBERG and RAWITZ in Mystacoceti that the right hemisphere is broader than the left.

Vertical axis: 17.5 cm. This must be smaller than in the living animal, as mentioned above.

The ratio between the sagittal and the transversal axis is 0.822 : 1, the latter surpassing the former. In the Mystacoceti (Balaenoptera sibbaldi, B. rostrata and B. musculus etc.) the ratio comes very near to 1 : 1. Therefore, the Sperm whale is extraordinarily brachycephalic.

The cerebellum is 10.8 cm sagittally and 16.4 cm transversally.

2) **Brain stem and cranial nerves** (fig. 2, 4 and 8)

In addition to the above mentioned specimen, I could use the brain of another Sperm whale for the morphological observation of the brain stem and cranial nerves. Viewed from antero-basal (fig. 4 and 8) the telescoping of the brain is quite remarkable; that is, the axis of corpus callosum is directed at a right angle to the axis from midbrain to pons and the latter axis forms again nearly a right angle with the axis from pons to the upper part of the spinal cord. The spinal cord shows in its upper part a very unusual spatulate bending. It runs at first along the occipital edge of the cerebral hemisphere, reaching far above the surface of the hemisphere (fig. 2).

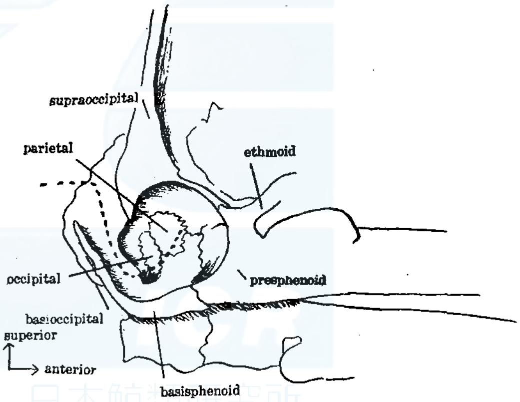

Fig. 2. Peculiar bending of the axis of brain stem (dotted line) projected to the lateral surface.

Cranial nerves:

The olfactory bulb and tract could not be seen. But in the other brain of the same species we noticed a mere trace of the nerve, which begins from the olfactory area and runs together with a very small vein along the olfactory fissure.

The oculomotor nerve appears as a few small roots, ventro-medial to the cerebral peduncle and is immediately gathered into one bundle running ventrolateralwards.

On the basal surface of the brain:

The olfactory area (=substantia perforata anterior), relatively large and swollen, has a shallow transversal furrow, and lies between the under surface of the frontal lobe and the optic nerve. Its frontal edge, differently than in Mystacoceti, is not divided into ecto- and entorhinal fissures and borders mediad on the frontal lobe by a very shallow sulcus.

The cerebral peduncle is composed by two masses of fibers, the one running from dorso-lateral to ventro-medial, the other from dorsal to ventral, a furrow showing the border between the two. The size of them are different between both sides; on the right the ratio is 1 to 3, on the left on the contrary the former protrudes like a boal occupying about 2/3 of the whole peduncle. Besides on the left side the tractus peduncularis transversus of a transversal Y-form is seen, but no such a tract exists on the right side.

On the ventral surface of medulla oblongata we see a pair of olivary eminences, along the outside of which one or two small groups of longitudinal fibers (pyramidal tract) run uphead and seem to cross at the caudal end of medulla oblongata.

Up to the present the brain stem and cranial nerves of the Sperm whale have not been reported by any authors, though many works have been published on those of Mystacoceti and other Odontoceti (HUNTER, v. BAER, BRUNS, RAPP, MAJOR, HERBERT, BEAUREGARD, HASWELL, WILLIAM, GULDBERG, RAWITZ, MILLER, LANGWORTHY and ADDISON etc.). Among them the works of GULDBERG and RAWITZ on Balaenoptera rostrata and that of LANGWORTHY on Tursiops truncatus are especially interesting for comparison with the Sperm whale.

All of the Mystacoceti are said to have small olfactory bulb and tract, while the Odontoceti can be grouped into two; one group (embryo of Beluga, Hyperodon and Phocaena communis) having mere traces of them, and the other (Globicephalus melas, Delphinus delphis) showing no residue of them. The Sperm whale belongs from my observations to either of them, but more possibly to the latter group.

In Mystacoceti the oculomotor nerve comes out from the interpeduncular fossa, while in the Sperm whale it is a little apart from this fossa.

The two division of the cerebral peduncle above mentioned and the existence of tractus peduncularis transversus have never been heard of the cetacean brains.

3) **Gyri and fissures** (fig. 3–10)

The configuration of the cerebral hemispheres of the Sperm whale looks at first very much complicated, but after a closer inspection, we recognize in the gyri and fissures a certain regularity which bears some definite resemblances to that in carnivores or ungulates.

Since GULDBERG published his classical work on the brain of the whalebone whales (1885), almost all of the workers have adopted his nomenclatures. On the dorsal surface of the hemisphere pretty parallel and more lateral to the interhemispherical fissure (Fit) the lateral fissure (F 1) runs and on the inner and outer sides of this we see F. endolateralis (F enl) and the F. ectolateralis (F ectl). About at middle of the lateral surface the F. sylvia is surrounded semicircularly by the the F. ecto- and F. suprasylvia and the anterior surface has F. olfactoria, F. coronalis and F. praesylvia.

My own observations will be described in the order of anterior, posterior, inferior, dorsal and medial surfaces of the hemisphere and such terms as "frontal", "occipital", "temporal", will be limited only to the places quite near to each pole, because boundaries between the lobes can scarcely be determined in this whale.

A) **Fissures**

a) **Dorsal surface** (fig. 3)

Nearly all of the fissures run here in sagittal direction without any large transversal fissures.

i) F. praesylvia (F pr)

Though it is not quite sure whether this fissure corresponds to that of carnivores and ungulates, I adopted this name considering its situation in relation to the whole hemisphere.

This fissure is asymmetrical, for on the right its anterior end lies lateral to the olfactory fissure, while on the left it is medial to this and moreover, on the right its posterior end does not reach the medial surface, while on the left it reaches almost the F. splenialis.

ii) F. cruciata (F cr)

In carnivores and ungulates this fissure courses quite transversely. But in the whales nobody has remarked about it, except LANGWORTHY, whose reference is but very insufficient. In the Sperm whale the F. cruciata runs almost parallel to the posterior part of the F. praesylvia and enters the medial surface. Its frontal part is not directed transversally, but compared with other fissures, it is the most oblique

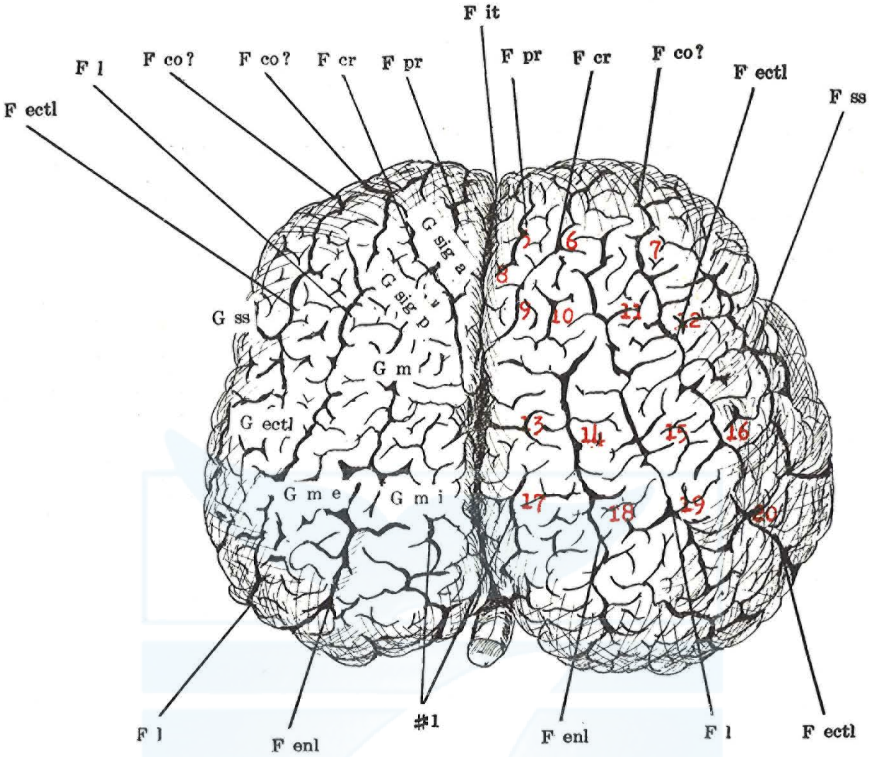

Fig. 3. Dorsal view of the Physeter brain

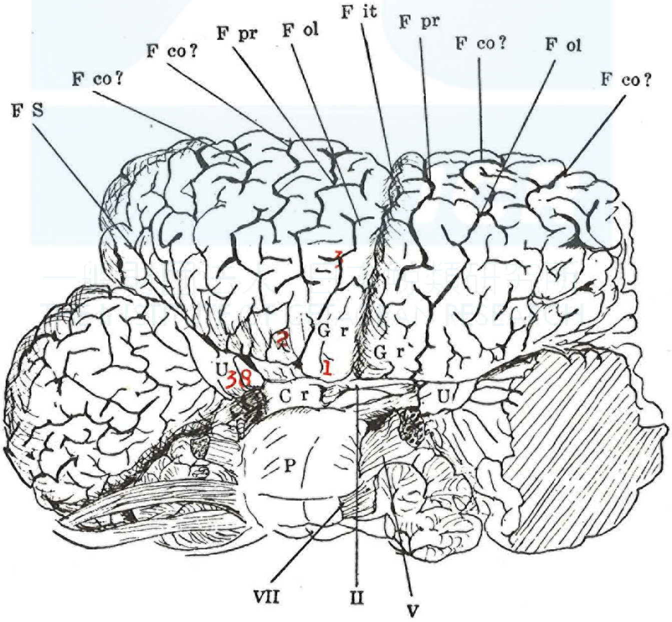

Fig. 4. Antero-basal view of the Physeter brain

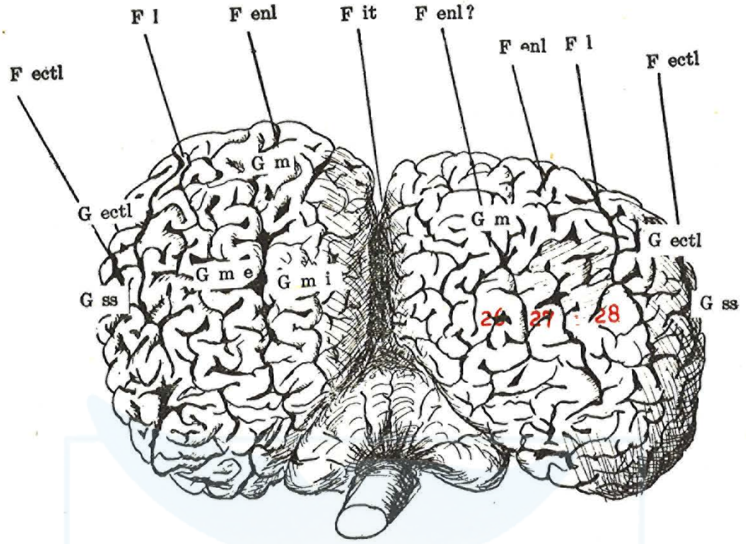

Fig. 5. Posterior view of the Physeter brain

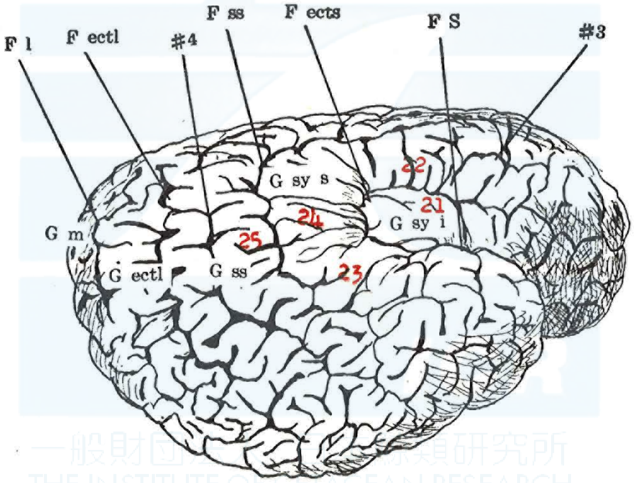

Fig. 6. The right cerebral hemisphere of Physeter, seen obliquely from postero-lateral

to the median plane, when it enters the medial surface, and continues to the F. suprasplenialis (fig. 9 and 10). RICHARD named a fissure probably corresponding to it "scissure endolatérale" in Globicephalus melas, but I take it for certain that this name should be given to a fissure, which lies along the F. lateralis and is other than the one now in question.

iii) F. endolateralis (F enl)=F. confinis (GULDBERG)

This is a large nearly straight fissure between the pallial margin (Mantelkante) and the F. lateralis. On the right side it is interrupted at one place and runs around the occipital lobe to reach the basal surface after a long course, while on the left side it goes without interruption to the neighbourhood of the occipital pole, assuming there a complicated figure.

According to GULDBERG, this fissure is always present in Phocaena communis, either combined with F. splenialis or bent into the medial surface, but no such combination or bending was seen in the Sperm whale.

iv) F. lateralis (F 1)

This very large and uncrooked fissure is located about at middle between the ecto- and endolateral fissures. It runs quite symmetrically for a long distance along the lateral occipital part up to the lateral temporal portion. Though GULDBERG and RAWITZ pointed out in B. musculus and B. rostrata that its frontal end often continues to F. coronalis and F. praesylvia, as this continuance occurs in carnivores, in the Sperm whale there are no direct connections between them.

v) F. coronalis. (F. co)

We can locate this fissure only with much difficulty. It is very asymmetrical. On the left two crooked fissures run to the frontal surface after being interrupted by F. lateralis and F. ectolateralis, while on the right a fissure which is continuous with F. cruciata and ectolateralis reaches the anterior surface after being cut on the way as on the other side. TURNER mentioned some variations of the F. lateralis: it is continuous either with F. cruciata (Dictyles, a kind of Ungulata) or with F. lateralis (cats etc.); in some other animals it continues to neither of them. There are also individual differences.

In addition there are between the F. endolateralis and the interhemispherical fissure short fissures which run symmetrically (fig. 3, # 1). Other small quite asymmetrical fissures do not seem to be of much significance.

b) **Lateral surface** (fig. 6 and 7)

Around the F. sylvia three semicircular fissures are arranged concentrically in the order from outside F. ectosylvia, F. suprasylvia and F. ectolateralis. Their forms are rather near to a circle than to a key, as this is the case in carnivores and ungulates.

vi) F. ectolateralis (F. ectl)

This is a quite symmetrical, large, very clearly defined sulcus, running from antero-medial of the frontal lobe to postero-basal of the temporal lobe, nearly parallel to F. lateralis.

vii) F. suprasylvia (F ss)

On the left, the frontal end of this fissure continues directly to about the middle of F. sylvia, while on the right it starts from a lateral part of the frontal lobe and runs parallel to F. sylvia, from which it is completely apart (fig. 6 and 7).

viii) F. ectosylvia (F ects)

This also is different between both halves; on the left it is directly connected with F. sylvia. Quite a long and distinct fissure, a little asymmetrical, runs along with F. suprasylvia and F. ectosylvia parallel to them. On the left a short sulcus connects F.

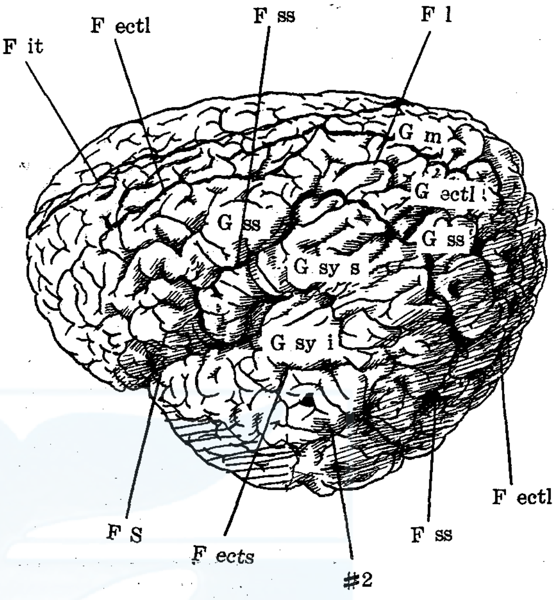

Fig. 7. The left cerebral hemisphere of Physeter: Lateral view

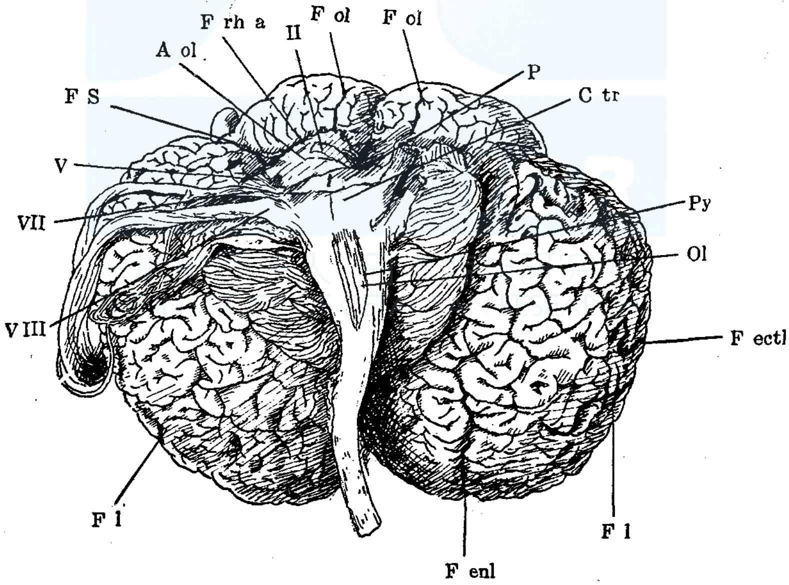

Fig. 8. Basal view of the posterior part of the Physeter brain

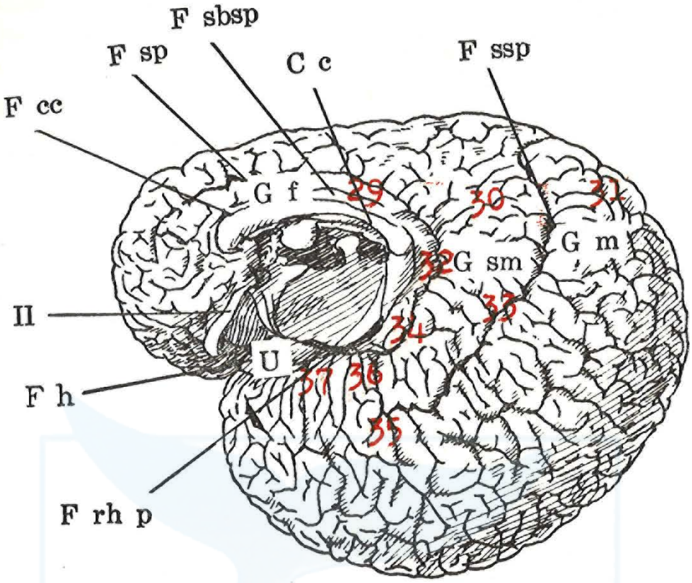

Fig. 9. The right cerebral hemisphere of Physeter, seen obliquely from postero-medial

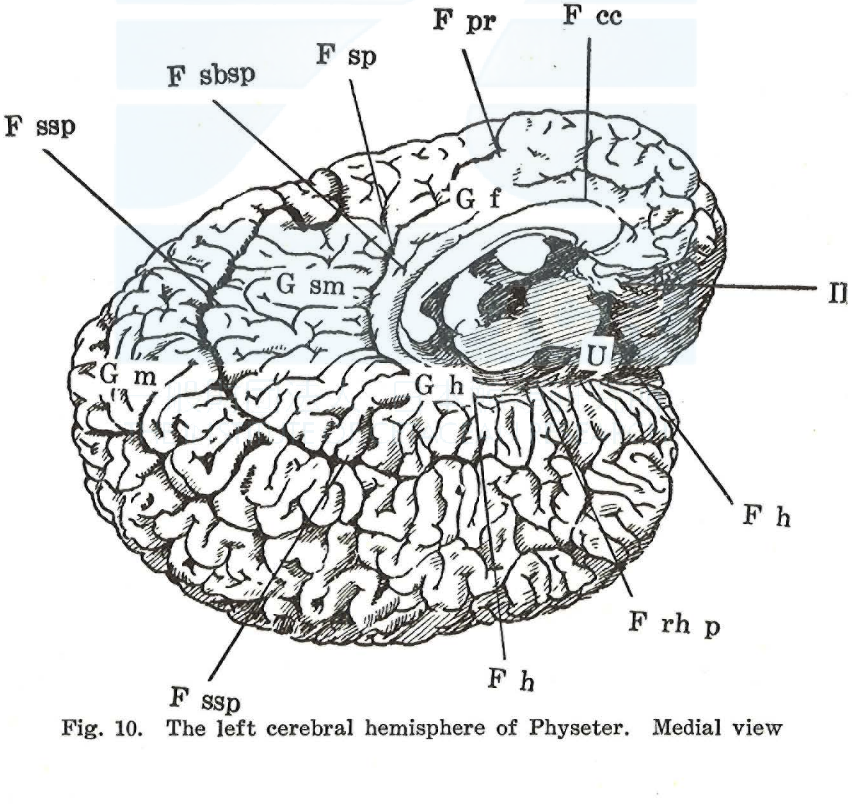

Fig. 10. The left cerebral hemisphere of Physeter. Medial view

suprasylvia with F. ectosyivia in the temporal lobe (fig. 7, #2), while on the right in the lateral part of the frontal lobe a short sulcus runs between these two fissures (fig. 6, #3) and besides a long distinct sulcus courses from the frontal lobe to the temporal lobe (fig. 6, #4).

iv) F. sylvia (F S).

This is nearly symmetrical on both sides.

c) **Posterior surface** (fig. 5)

No symmetry is seen here. Especially the right shows very irregular sulci of very complicated form. On the left we see parallel to the pallial margin the endolateral, the lateral, and the ectolateral fissures run side by side, while on the right the endolateral, fissure is not found, but the lateral and the ectolateral fissures are present in the lateral border. On both sides sulci of the region between the pallial margin and the lateral fissure show very complicated curving and bending, except the left F. endolateralis, which courses very distinctly as mentioned above.

d) **Medial surface** (fig. 9 and 10)

x) F. suprasplenialis (F ssp)

This long fissure shows no great difference between both sides. It starts from F. cruciata and runs to about middle of the medial temporal surface in a large semicircular form. It gives off many small sulci at right angles. As discussed before, this corresponds in my opinion to F. suprasplenialis observed by GULDBERG in the Fin whale and differs from "scissure endolatérale" mentioned by RICHARD in Globicephalus melas. TURNER' reported this fissure in Balaenoptera rostrata. But nobody seems to have found its continuance to F. cruciata. In carnivores and ungulates it is connected with F. splenialis or intercepted from this by a gyrus; so there is a possibility that the fissure in question corresponds to F. splenialis, but as a more probable F. splenialis is observed in a more basal region, I identified it to F. suprasplenialis.

xi) F. splenialis (F sp)

On both sides it begins from near the frontal pole and runs on the medial surface as if encircling the corpus callosum up to the gyrus hippocampi, which is at the medio-anterior end of the temporal lobe and united there with F. rhinica posterior.

xii) F. corporis callosi (F cc)

It demarcates the upper margin of the corpus callosum and its hinder part runs from the splenium along the medial border of the temporal lobe to the uncus, where it continues to F. hippocampi.

xiii) F. subsplenialis (F sbsp)

This nearly straight fissure lies between F. splenialis and F. corporis callosi, and shows at the frontal end some asymmetry; on the right it is bent semicircularly around the genu corporis callosi, but on the left it begins from dorsal of the genu. On the medial surface no fissure, which seems to correspond to the calcarine, was observed.

e) **Anterior and basal surface** (fig. 4 and 8)

xiv) F. olfactoria (F ol)

It runs from the medial part of the anterior F. rhinalis almost parallel to the pallial margin, and behaves somewhat asymmetrically; on the right it lies medial to F. praesylvia, having few branchings, while on the left it is lateral to this fissure and shows a longer course with many side branches. As previously mentioned, owing to absence of the olfactory tract, the anterior F. rhinalis is not divided into two parts, in- and outside.

The *uncus is subdivided into three portions* by *F. hippocampi* and another shallow sulcus in the medial part of the posterior F. rhinalis.

Till now I have related only comparatively well defined fissures, while many others of more irregular, very complicated forms are present on the basal temporal and occipital surface.

B) Gyri

On the dorsal and lateral surface, bordered by the above named fissures, broad gyri are arranged concentrically around the posterior end of F. sylvia in the following order, from the median margin of the pallium to the Sylvi's fissure: G. medialis interna, G. medialis externa, G. ectolateralis, G. suprasylvius, G. sylvius inferior. Generally speaking, those gyri show at their terminal parts very complicated figures pari passu with irregularity of the fissures. They show also some notable asymmetries. The gyri, which border the obliquely directed F. cruciata from anterior and posterior, must be called G. sigmoideus anterior and G. sigmoideus posterior in analogy to the cases in carnivores. In the left hemisphere the G. medialis is divided on the posterior surface into internal and external portions owing to the presence of a distinct F. ectolateralis, while in the right such a division does not take place.

On the medial surface there are G. submedialis and G. fornicatus demarcated by F. suprasplenialis, F. splenialis and F. corporis callosi etc. The G. fornicatus is narrowed remarkably when it extends around the splenium and continues then to G. hippocampi, terminating in a swollen form (uncus). Besides we can see also G. dentatus and Fimbria hippocampi behind the medial part of uncus.

Medial to the olfactory fissure lies on the anterior surface G. rectus, which shows some differences between both sides owing to the asymmetry of F. praesylvia. The configuration in the lateral frontal surface is quite irregular.

A number of anatomists have hitherto studied the fissures and gyri in the cetacean brains, especially Guldberg worked on Balaenoptera musculus, Balaenoptera sibbaldi and Phocaena communis, Rawitz on Balaenoptera rostrata, Richard on Globicephalus melas, and Turner on Monodon and Balaenoptera rostrata, and the similarities to carnivores and ungulates have been very often acknowledged.

According to my own observation the fissures and gyri of the Sperm whale are also similar to those of Mystacoceti, and of other Odontoceti. But I met with following several points, somewhat different from the mentioning of the foregoers.

As to F. cruciata, Langworthy slightly referred to this in Tursiops truncatus, but no one has remarked its continuance to F. suprasplenialis. In the Sperm whale I found F. suprasplenialis in direct connection with F. cruciata.

The F. coronalis is very differently connected with other fissures according to the kinds of animals, sometimes with F. suprasylvia, with F. lateralis, or with F. cruciata, while its continuance to F. cruciata has been reported neither in Cetacea nor in carnivores. Also in my Sperm whale one hemisphere had two fissures probably corresponding to it, but their direct connection with F. cruciata was not seen.

The presence of F. olfactoria in the Sperm whale is interesting, for it has not been reported in Odontceti, carnivores and ungulates. It is likely that this fissure is present only in such animals as Primates, and Mystacoceti, which have the largely developed hemisphere and are at the same time microsmatic.

The direct continuance of F. corporis callosi to F. hippocampi is not known in pig, cow, horse and baleen whales, though it occurs in the elephant seal and man etc.; from this fact, considering also the relations previously mentioned of F. cruciata and F. coronalis, the Sperm whale seems to have more similarity to carnivores rather than to ungulates.

Two divisions of the uncus has been mentioned in some ungulates and it forms wrinkles divided by several fissures in the polar bear, while three divisions of it were found only in this whale.

(III) Cytoarchitecture of the cerebral cortex

1) Method. Materials fixed in formalin were cut into pieces of 1–3 cm thickness. Then by freezing 20–40 μ sections were prepared, put in 90% alcohol or acid alcohol, containing 10% of concentrated acetic acid and preserved about 24 hours in 37–38°C. After washing in water they were stained with 1% thionin for about half an hour at 40°C. Then they were washed in water again, and differentiated in alcohol.

2) Results

i) General observation

From various parts of the right cerebral hemisphere 38 pieces of the cortex with underlying white matter were cut off at regular and about equal intervals (1–8 of fig. 3, 4, 5, 6, 9 and photo A, B, C).

Compared with the cortex of other mammalia it is noteworthy in this whale that the nerve cells are scarce and their differentiation in 6 layers is not fully developed.

Especially the development of the layers IV, V and VI is comparatively poor and in most places the layers IV and V are not well distinguishable from each other and so the cortex seems to have only 5 cell-layers.

Each of the layers will be described in the following.

Layer I, Lamina zonalis:

This layer is very inconstant in thickness (0.24–0.80 mm); the thickness is different also between top and sides of a gyrus.

Here a number of glia cells are dispersed and though scarce, small round nerve cells are observed. Besides, though it is of great rarity, we see sometimes large nerve cells of 10/30 μ (the largest diameter along the cortical surface, the largest diameter vertical to the cortical surface) (9, 13). This layer is sharply distinguished from the next deeper layer.

Layer II, Lamina granularis externa:

Of all layers this is the narrowest (0.08–0.20 mm), but very densely populated with cells and clearly distinguishable; most of the cells are either round granular or pyramidal, of the size 5/15–18/20 μ, and are arranged regularly. This layer is present in all places examined.

Layer III, Lamina pyramidalis externa:

This is well discerned from the more superficial layer but its border against the deeper layer is indistinct. Generally it is thick (0.4–0.6 mm), has scattered granular cells of various size (9/15–24/18 μ) and pyramidal cells exist in a larger number. The deeper within this layer, the larger become the cells, the form of which is mostly polygonal or triangular, though sometimes large round cells are also seen and the density of them is different according to the places observed.

Layer IV, Lamina granularis interna:

The granular cells, whose presence characterizes this layer in other mammalia, are not especially gathered here. Though in the deeper portion comparatively large cells are flocked together, I am not sure whether they really belong to this layer.

Layer V, Lamina pyramidalis interna:

The *thickness* (*0.2–0.4 mm*) *is nearly constant in all places.* There are comparatively large cells (about 18–24/30 μ) mostly of polygonal or pyramidal form, and they are much crowded. In some places this layer has giant pyramidal cells constituting a very clear layer, while in other places, where no such cells are present, it is difficult to determine the border against the more superficial layers.

Layer VI, Lamina multiformis:

It is 0.8–1.0 mm thick. Here are scattered relatively large pyramidal, round or stellate cells of 18–24/30–24 μ and many other forms.

ii) As the next step I tried to know the structural localization of the cortex, examining, if any, the peculiarity of each place.

a) Anterior and dorsal surface (1–4 of fig. 4, 3–20 of fig. 3, photo. A and B)

Giant pyramidal cells are present from the lower end of G. rectus to the anterior part of G. medialis on the dorsal surface and up to the frontal part of F. ectolateralis on the lateral surface. Especially on and near G. sigmoideus (5, 9, 8, 14) most of them are gathered. It reminds us of area 4 (praecentralis gigantopyramidalis) of BRODMANN. Further backward as well as foreward they become sparse.

At G. sigmoideus posterior (9) cells increase in number and form a clear layer in the deeper portion of the layer III (IV ?). Further backward at G. medialis interna (13) this layer becomes indistinct. Still further back near the occipital pole (17, 18) no giant pyramidal cells are found in the part corresponding to the layer IV (V ?) but relatively large granular cells are present forming a sheet.

At G. rectus (1) and near the *frontal* pole (3, 4) the layer IV can be observed only with difficulty and the layer II becomes thinner. On the whole, nerve cells of the cortex are few in number and giant pyramidal cells are shrunken to angular forms.

The anterior part of G. ectolateralis (3, 4) is similar in structure

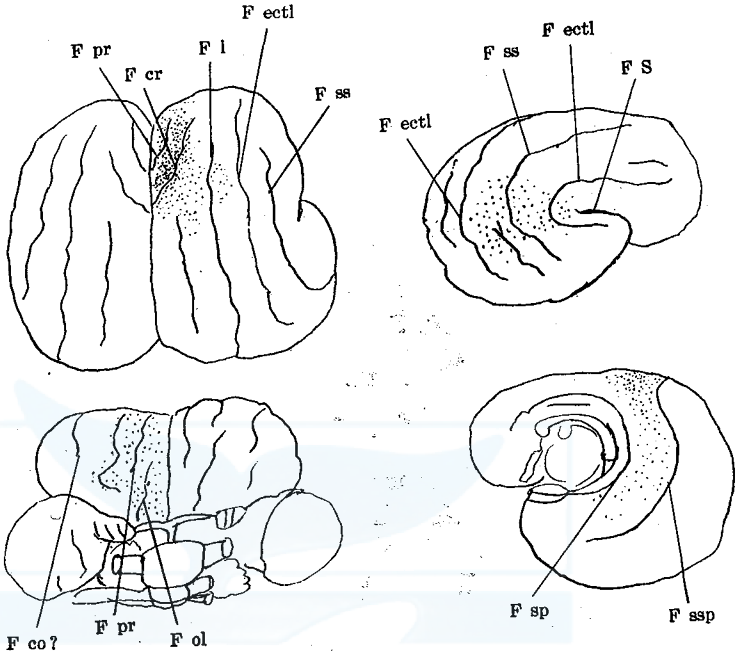

Fig. 11. Distribution of giant pyramidal cells in the right cerebral hemisphere of Physeter: The dots represent the cells in question

to G. sigmoideus, though the number of nerve cells is here somewhat less. G. suprasylvius contains no giant pyramidal cells.

From these observations I came to the opinion that the places, where giant pyramidal cells are present, probably representing the motor area, are in the Sperm whale not restricted within narrow limits but extend widely in the hemisphere.

They are most abundant on the anterior and posterior sides of G. sigmoideus, and dispersed both towards frontal and occipital. Also in the layer IV (V?) cells tend gradually to become dense from F. cruciata backward. The layer II becomes thinner in the frontal part and cells decrease in number, as we go more frontal. But further back than F. cruciata scarcely any change occurs. Generally speaking, cells in all layers tend to increase in number as we examine further backwards.

b) Posterior surface (26, 27, 28 of fig. 5, photo. B 27)

Three places near the occipital pole were studied, with the result that cells are numerous here, especially in the layer IV (or V) they are abundant and large in size. This finding reminds us of the striate area, though it was impossible to observe macroscopically neither the intracortical white stria nor the calcarine fissure.

c) Lateral surface (21–25 of fig. 6, photo. B 23)

Both of the superior and inferior G. sylvius and a part of G. suprasylvius were studied. In the antero-dorsal part of G. sylvius superior no giant pyramidal cells are present, while they appear on the lateral basal part of this gyrus and the cells are generally larger.

In the superior and inferior G. sylvius giant pyramidal cells are seen here and there, and cells of the layer III are also comparatively numerous.

d) Medial surface (28–37 of fig. 9, photo. B 29, C 30, 32)

G. submedialis, G. fronicatus and G. hippocampi were examined. The upper frontal part of G. submedialis (30) has densely arranged giant pyramidal cells, and the layers II and III are thick, having many cells. This part resembles G. sigmoideus posterior.

In the postero-basal part (33) many large round cells are assembled in the layer IV (V). Further lower (35) this layer shows middle sized pyramidal cells.

In G. fornicatus (29) each layer is narrow and in the layer V large round nerve cells are gathered densely, forming a special sheet.

G. hippocampi (32, 34, 37) has a quite particular structure; that is, the layers II and IV are thick and crowded with cells. Most cells of the layer IV are polygonal or pyramidal. In the extremely thin layer III small cells are scattered.

Uncus (38 of fig. 4, photo. C 38) is of an extraordinary cytoarchitecture; here only 3 layers are discerned, the first layer of which resembles the layer I of other regions and the second layer, though not very much different from the layer II of other regions, is comparatively thick and has many cells. The third layer contains very few cells of round or pyramidal form.

Considering the colossal bulk of the cortex and the very complicated fissures and gyri of the cetacean cerebral hemisphere, it must be of much interest to know the cytoarchitecture especially its difference according to regions. Though I desired at first to make a map upon the structural differences of the whole cortex, the fulfillment had to be postponed to a later occassion, for the present study was limited to only 38 places in one hemisphere. Meanwhile my object was directed to the determination of cortical regions, which might correspond to the so-called motor area, to the striate aera, or to the superior temporal area of the human brain, but the result is yet far from success, for the macroscopical orientation of these places is very difficult and moreover the cytoarchitecture of the cetacean cortex is very insufficiently differentiated.

Till today the cerebral cortex of the cetacea has been histologically studied by several authors, among whom MAJOR's work on Balaenoptera musculus, RAWITZ's on Balaenoptera rostrata and Phocaena communis and LANGWORTHY's on Tursiops truncatus are worthy of special reference.

MAJOR observed quite in details the cytoarchitecture at several places chosen from Gyri sylvius, suprasylvius, ectosylvius and medialis, and stated consequently that the frontal lobe is quite similar to the temporal lobe, while the occipital lobe only is a little different in structure as the cells are here smaller. Besides, the cells are pyramidal in the layers I, II, III and the layer IV is not clearly discriminated, while the layer V consists of spindle cells. Chronologically MAJOR's report is previous to BRODMANN's famous work on the localization of the cerebral cortex, and so it did not tell about the formation of 6 cell-layers.

In my opinion, the layers IV and V of MAJOR, are of much doubtful existence, and as giant pyramidal cells were seen in the deeper portion of the layer III in his classification, which I believe is corresponding to our layer V, I can not agree with MAJOR, so far as he said that the layer III has pyramidal cells, as I observed there round and polygonal cells too. As to the fact that in the frontal lobe and in the temporal lobe giant pyramidal cells are extensively observable, I agree with him (fig. 11).

RAWITZ examined only three parts of the cetacean cerebral cortex and stated that it is of a primitive, quite unusual structure, and that there is no differentiation of cell layers as seen in other mammals.

LANGWORTHY researched 16 places quite minutely. He discussed much on the thickness of the layer I, though he did not refer to the conditions of fixation. Deeper than the layer II he named each layer as supragranular, granular, infragranular, and polymorphic. He tried to determine motor area, sensory area, striate area and temporal area as in other mammalia, but he did not seem to have minded much about the complicatedness of the gyri, and identified F. cruciata, F. calcarina and other fissures relatively easily, and spoke even the physiological function of these areas. I endeavoured to compare LANGWORTHY's observations on the "striate area" of his nomination to my findings in the cortical region, which looks macroscopically like corresponding to his (36 of fig. 9) and further on another place of the occipital pole (27), and found that cells of the layer IV are increased the most noticeably in (27) than in the "striate area" of LANGWORTHY.

One point, in which I agree completely with him, is as also with MAJOR, that giant pyramidal cells exist quite in wide areas beginning from the anterior end of the frontal lobe.

It is a much discussed problem, which fissure in other mammalia the central fissure of Primates corresponds to. And most of the previous authors have identified it either with F. cruciata, with F. praesylvia or with F. coronalis, etc. BYCHOWSKY took F. coronalis for it on the histological basis, that in front of this fissure giant pyramidal cells are found while they are absent in the posterior. In the Sperm whale I can not find such a fissure as showing a clear borderline upon the histological structure. I want to say only that giant pyramidal cells are present the most densely in F. cruciata; it seems to be the centre of their existence (fig. 11).

As to the division of the whole cortex into granular and agranular ones which ECONOMO tried and recently BAILEY reported in the human brain, I can't say anything definite in the Sperm whale, because the layer IV is not well differentiated and moreover my microscopical observations are limited to only a relatively few cortical localities. But so far as my own results are concerned, the granular cortex exists near the occipital pole, on G. sigmoideus posterior and on the latero-basal portion of G. suprasylvius and on G. sylvius etc., while the agranular cortex is seen anterior to F. cruciata and in the antero-dorsal portion of F. ectolateralis. And further to determine the giganto-pyramidal area within the agranular cortex was impossible as the gian pyramidal cells are so extensively distributed in the cortex of the Sperm whale, as I stated above.

Résumé

Following observations were made on the brain of the Sperm whale caught in the Antarctic Ocean.

1) The average brain weight of 16 male whales (body length of 46–54 feet) is 7.8 kg, that is heavier than that of Mystacoceti (over 50 feet).

The ratio of the brain weight (kg) to the body length (feet) is 0.154 as average and this ratio seems to decrease in senility.

2) Measurement and macroscopical study on the brain of a Sperm whale (50 feet long)

a) The ratio of the sagittal axis to the transversal axis is 0.822 : 1 ; that is extremely brachycephalic.

b) The olfactory bulb and tract do not exist.

c) The cerebral peduncle is divided in two parts and the tractus peduncularis transversus is present.

d) On the ventral surface of medulla oblongata small pyramidal tracts are seen.

e) F. cruciata continues directly to F. suprasplenialis.

f) Differently from Mystacoceti, F. rhinalis is not divided into two, medial and lateral, parts.

g) F. corporis callosi is continuous with F. rhinalis posterior.

h) F. olfactoria is present.

i) Uncus is divided into three parts by two shallow sulci.

3) Cytoarchitecure of the cerebral cortex

a) The formation of 6 layers is not clearly observed. As it is difficult to discriminate between the deeper portion of the layer III and the layers IV and V, it seems that only 5 layers exist.

b) Giant pyramidal cells are found quite extensively from the lower end of the frontal lobe till the anterior part of G. medialis, spread on the outside from the anterior part of G. ectolateralis and on the inside till G. submedialis. Especially in G. sigmoideus anterior and posterior they are the most densely gathered.

c) In the vicinity of the occipital pole the layer IV (V?) becomes thicker, having more and larger cells.

d) In the frontal lobe cells of each layer decrease in number, as one observes more forewards.

e) Though it is difficult to divide the cortex into granular and agranular ones, in general F. cruciata seems to show the borderline, for further anterior from this the cortex becomes more agranular, while further posterior it gets more granular.

It is a pleasure to record my indebtedness to Prof. T. Ogawa for his constant guidance and encouragement. My thanks are also due to Ass. Prof. T. Kusama for help and advice on various aspects of this subject.

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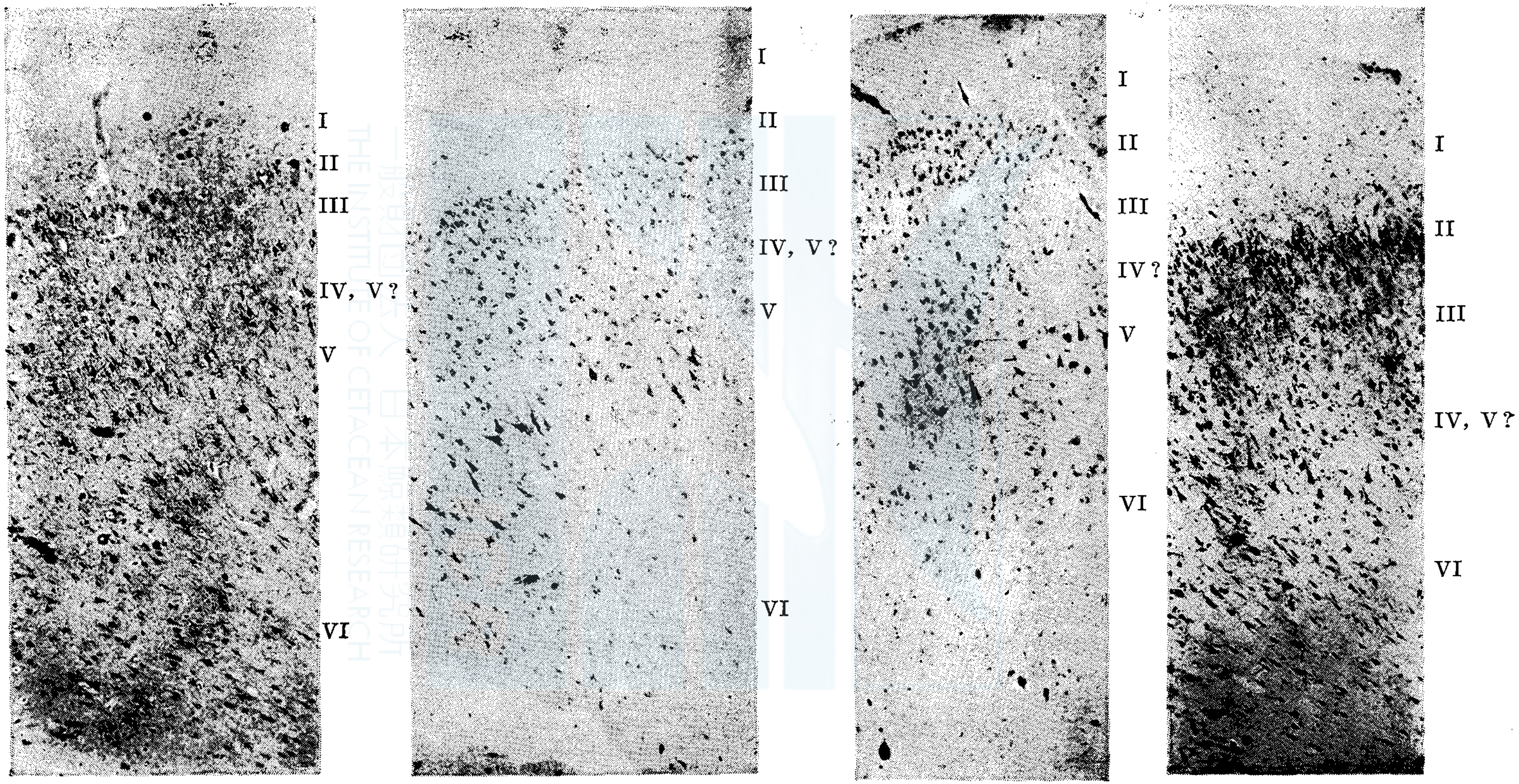
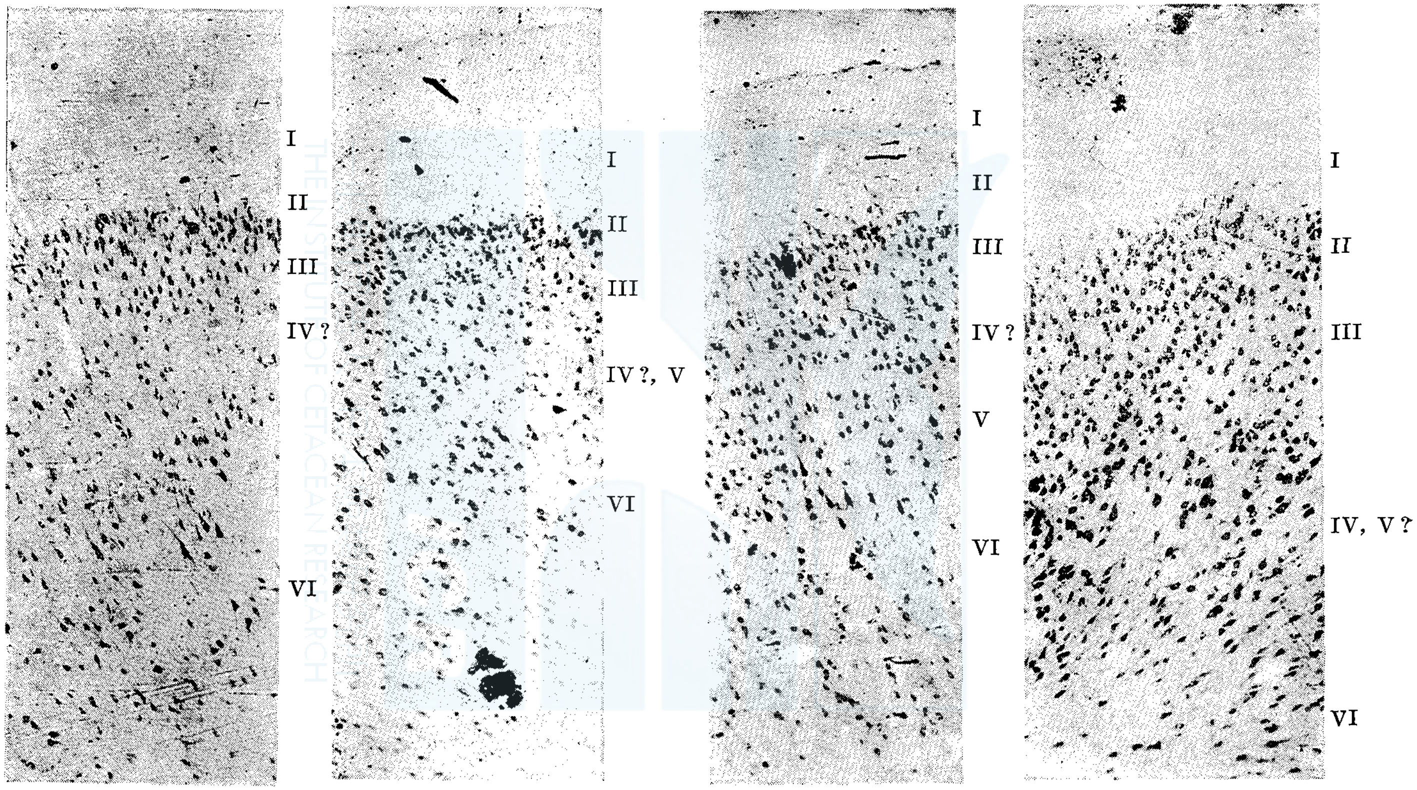
Abbreviation for all figures

A ol	Area olfactoria
C tr	Crus cerebri
Ge cc	Genu corporis callosi
Ol	Olive
P	Pons
Py	Pyramidal tract
Sp cc	Splenium corporis callosi
U	Uncus gyri hippocampi
II	Fasciculus opticus
V	N. trigeminus
VII	N. facialis
VIII	N. statoacusticus
F co	Fissura coronalis
F cr	F. cruciata
F cc	F. corporis callosi
F ectl	F. ectolateralis
F ects	F. ectosylvia
F h	F. hippocampi
F it	F. interhemisphaerica
F l	F. lateralis
F ol	F. olfactoria
F pr	F. praesylvia
F rh a	F. rhinica anterior
F rh p	F. rhinica posterior
F S	F. sylvia
F sp	F. splenialis
F ssp	F. suprasplenialis
F ss	F. suprasylvia
G ectl	Gyrus ectolateralis
G f	G. fornicatus
G h	G. hippocampi
G m	G. medialis
G m i	G. medialis interna
G m e	G. medialis externa
G r	G. rectus
G sig a	G. sigmoideus anterior
G sig p	G. sigmoideus posterior
G sm	G. submedialis
G ss	G. suprasylvius
G sy s	G. sylvius superior
G sy i	G. sylvius inferior



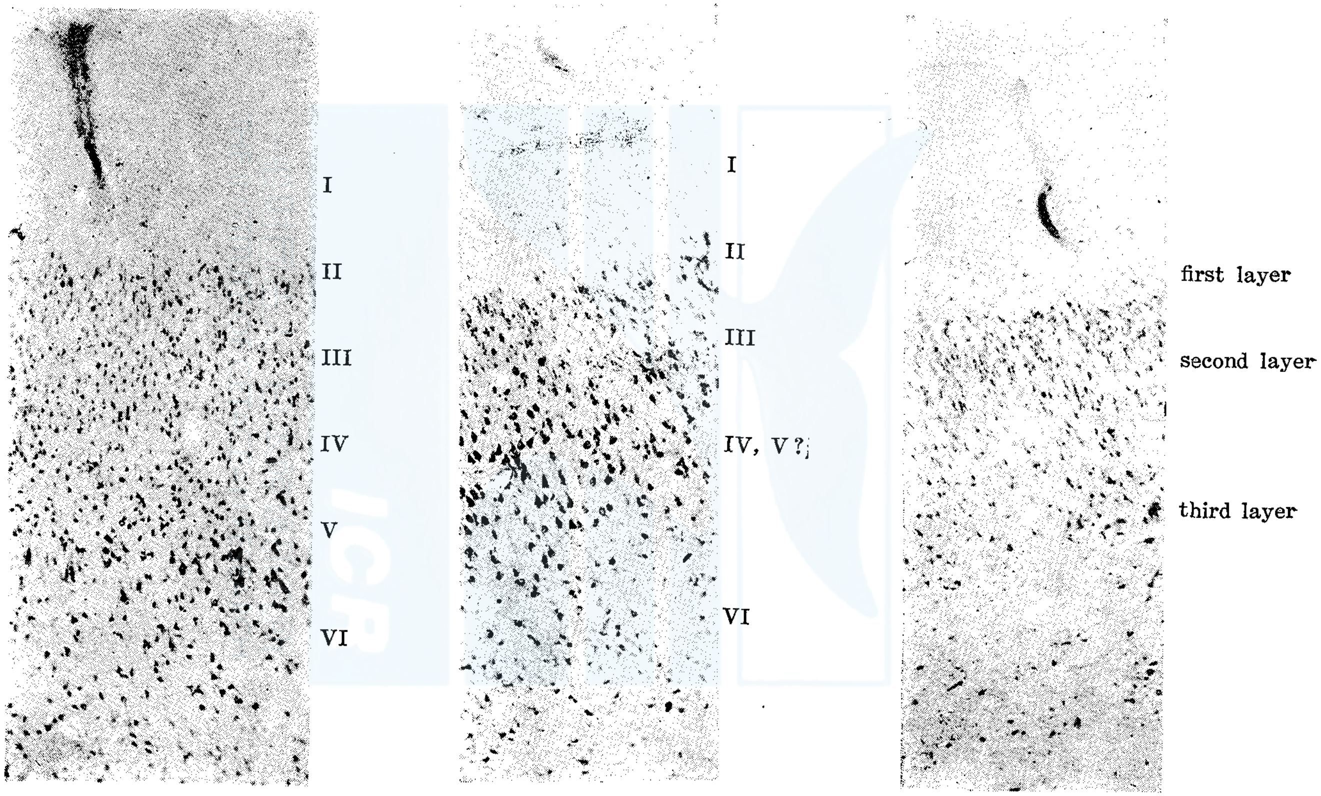
1 5 9 13

Photo. A....Cell layers of the cerebral cortex (1, 5, 9, 13) of Physeter.



14 **17** **23** **27**

Photo. B....Cell layers of the cerebral cortex (14, 17, 23, 27) of Physeter.



30 32 38

Photo. C....Cell layers of the cerebral cortex (30, 32, 38) of Physeter.