

**CYTOARCHITECTONIC STUDIES OF THE CEREBRAL CORTEX
OF THE HARBOUR PORPOISE, *PHOCOENA PHOCOENA*
(LINNÉ, 1758)**

GÜNTHER BEHRMANN

Alfred Wegener Institute for Polar- and Marine Research
D-2850 Bremerhaven, Germany

INTRODUCTION

Dolphins are very agile and clever; they play, "speak", and help swimmers in distress at sea. Dolphins and also harbour porpoises have a highly developed echolocation system, and orientate themselves by the echo of their sounds. Dolphins have a highly sensible touch sense, and all other senses like mammals. The limbic layer of the dolphin brain has much more folds and windings than human brains. In view of its architecture the dolphin's brain is the highest developed brain of all mammals. But up to this day the level of efficiency of the dolphin's brain is unknown. This paper is an attempt to find out the mode of operation of the harbour porpoise's brain compared to the human and other dolphin's brains.

MATERIAL AND METHODS

Two brains of beaching harbour porpoises were analysed. The first head was fully dissected in slices nearly 5 mm thick, then fixed in formalin, dehydrated and embedded into synthetic resins by the method of von HAGENS (1976). After removing the second brain out of the skull, it was immediately fixed in formalin. Later this brain was cleaned and then photographs were taken from all sides. From each gyrus sections were removed, dissected in histological slices 10 or 15 μm thick, and stained by toluidin/eosin, hematoxilin/eosin, and by the Golgi staining method. For electron microscopical studies, slices of 50 nanometers were used, contrasted in using leadnitrate/natriumcitrate and uranylacitrate. Finally 2400 slices were used for description of the cytoarchitecture in the cortical fields.

All measurements together of the cortical thickness, the laminar thickness, and the sizes of cells, sum up to fifty, which allows to establish a good mean value. Standard deviations of the neuronal numerical density in cubic millimeters have been calculated on the basis of five measurements of one square millimeter in horizontal direction.

Following the branches of the Corona radiata and the deep clefts (Fissurae), the lobes and the lobules were located. In using the maps of human brains (BRODMANN 1909; KLIMA, 1975; BERTOLINI & LEUTERT, 1982) and maps of dolphin brains

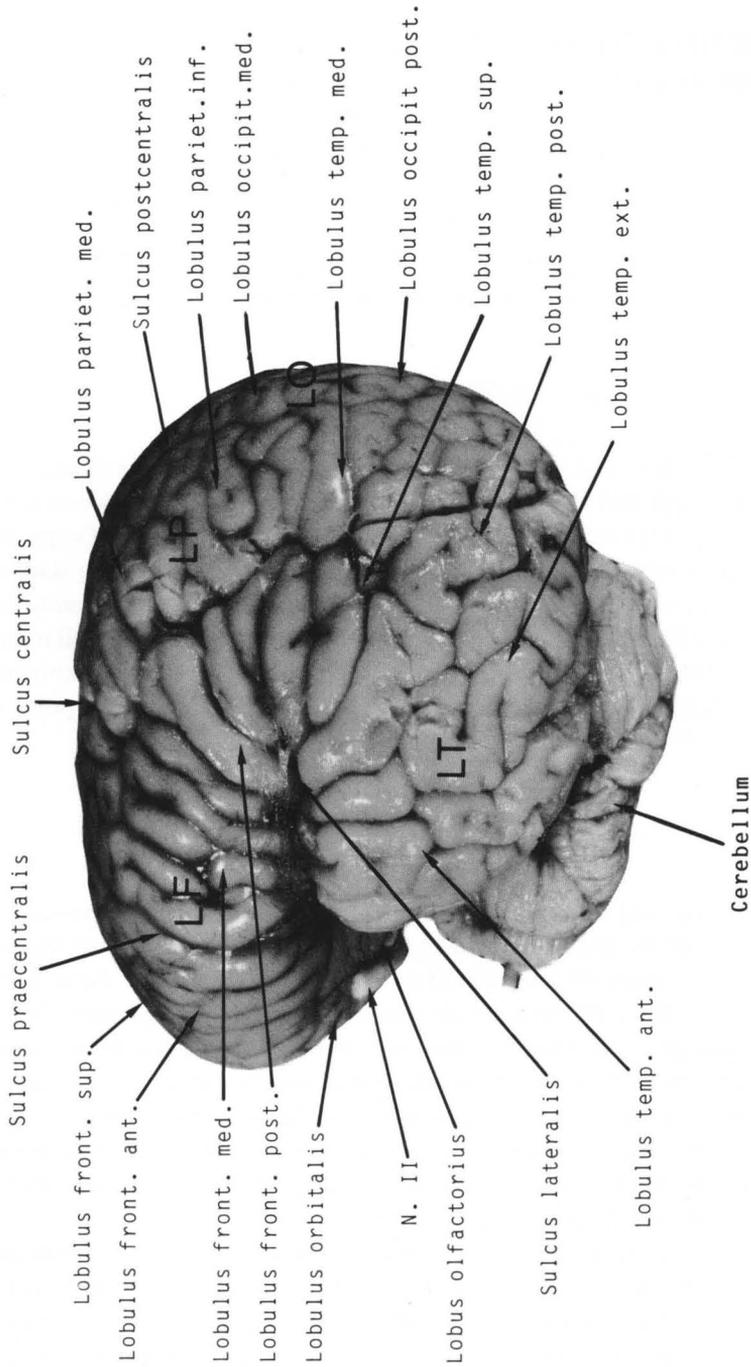


Fig. 1 — The left hemisphere of the telencephalon of the harbour porpoise. Lobus frontalis (LF), Lobus occipitalis (LO), Lobus parietalis (LP), Lobus temporalis (LT).

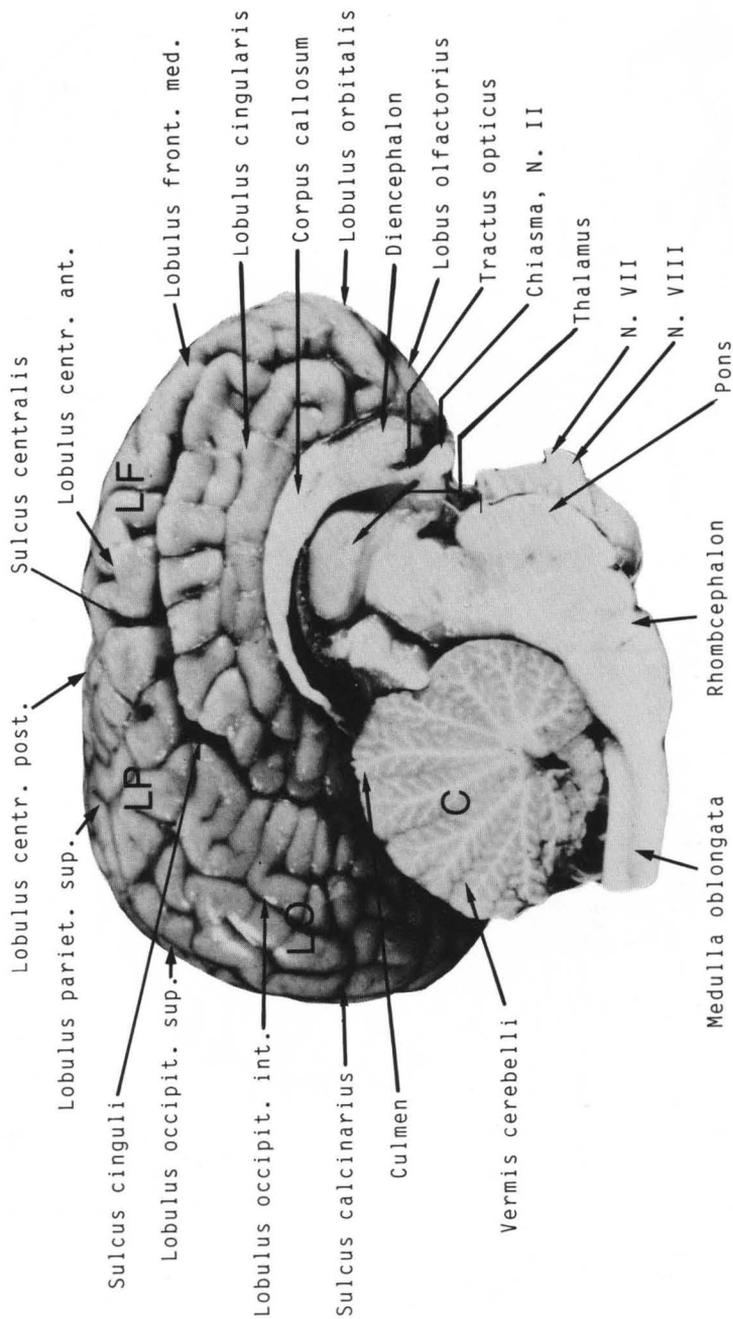


Fig. 2 — Medial view of the left hemisphere of telencephalon. Cerebellum (C), Lobus frontalis (LF), lobus occipitalis (LO), Lobus parietalis (LP).

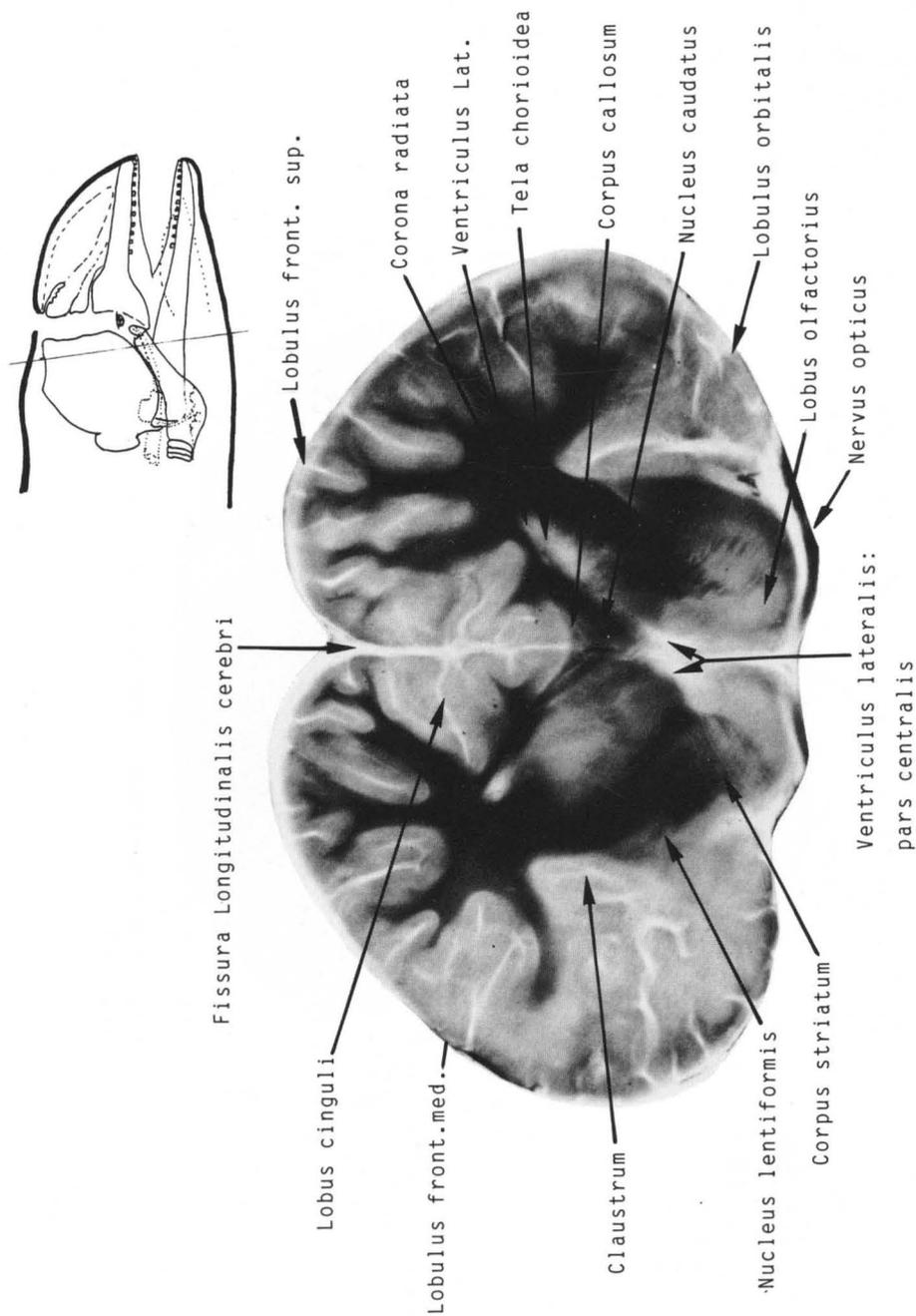


Fig. 3 — A brightened cross section through the Lobus frontalis. Such slices were used to find out the borders of the lobes, the lobules and the clefts.

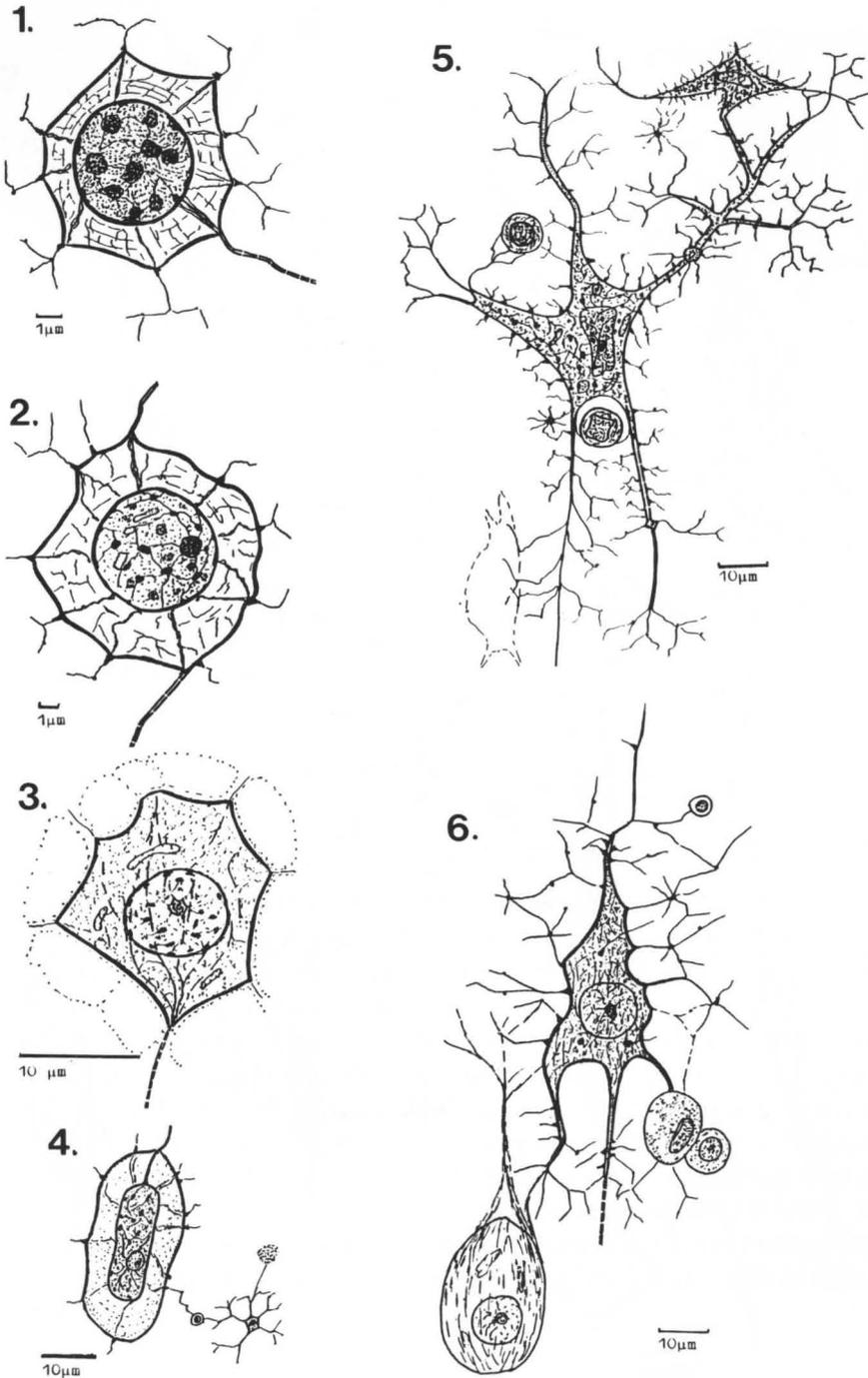


Fig. 4 — Granular cells (1., 2., and 3.), cell of Cajal (4.), polymorphous neuron (5.), small pyramidal cell (6.).

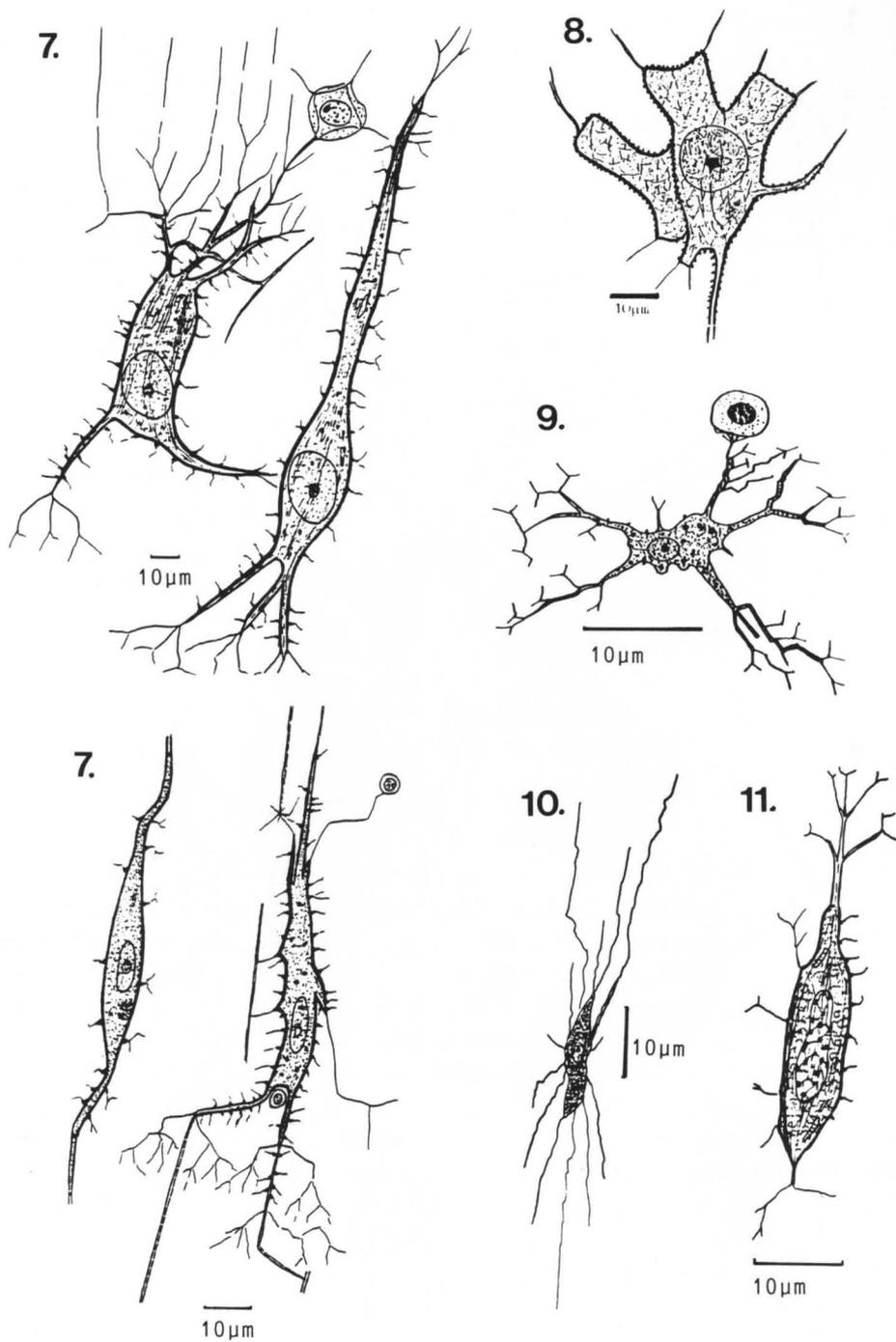


Fig. 5 — Various forms of gigantic pyramidal cells (7.), protoplasmic astrocyte (8.), fibrous astrocyte (9.), basket cell (astrocyte) (10.), glia cell of Hortega (11).

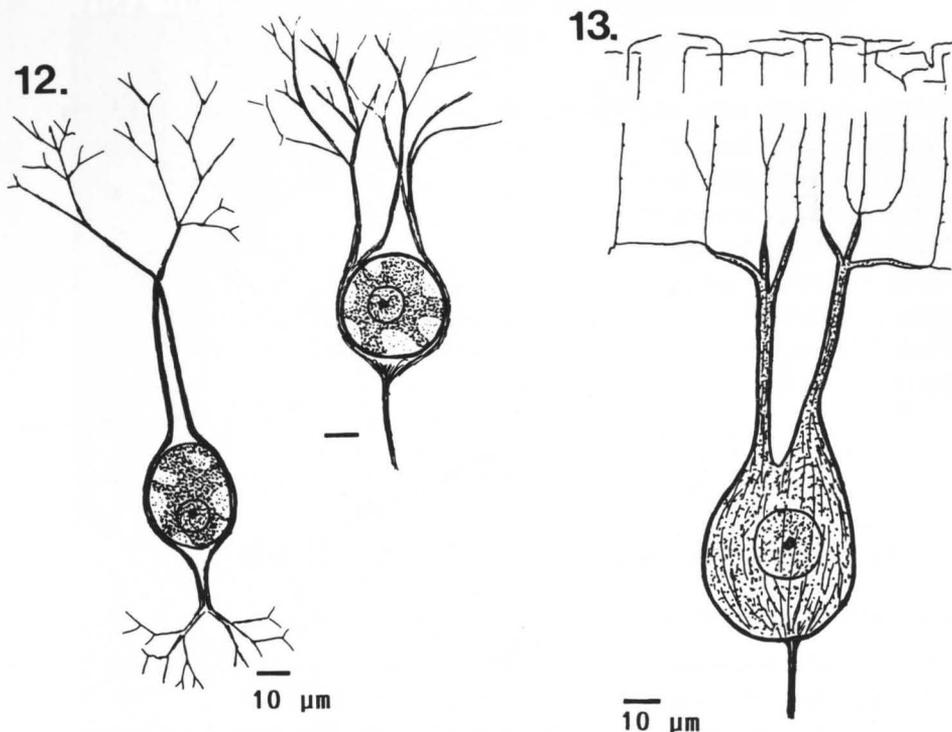


Fig. 6 — Interfascicular oligodendroglia cells, (12.), macro-oligodendroglia cell (13.).

(MORGANE *et al.*, 1980; MORGANE *et al.*, 1982), the architecture of the harbour porpoise brain was identified (Fig. 1, 2 and 3). The nerves end in the neurons and glial cells, which are accumulated in cortical layers (BRODMANN, 1909). The layers in the cortex are distinguishable in the accumulation of the single nerve and glial cells, and in their mixing proportion. To identify the layers of the cortex, first the morphology of the neurons and the glial cells has to be known (Fig. 4, 5 and 6).

After the identification of the single layers and their thicknesses, gyri with a nearly comparable cytoarchitecture were combined in area, and gyri with a comparable cytoarchitecture were combined in fields. The results of this examination were compared with cytoarchitectonic studies of the human cortex (BRODMANN, 1909; CREUTZFELDT, 1983; *et al.*), and with cytoarchitectonic studies of toothed whales (KESAREV, 1970; MORGANE *et al.*, 1982, 1986; PILLERI *et al.*, 1968; SOKOLOV *et al.*, 1972).

THE TERMINOLOGY OF THE ARCHITECTURE AND CYTOARCHITECTURE OF THE BRAIN

- Lobus = limbic lobe, large part of the brain, for example Lobus frontalis
 Lobulus = subdivision of the large part, for example Lobulus front. med.
 Gyrus = fold of the brain
 Sulcus = cleft between the folds
 Fissura = deep cleft between the lobes
 Polus = pole of the lobe
 Area = cortical plate with nearly homogeneous cytoarchitecture
 Field = subdivision of the plate with a homogeneous cytoarchitecture
 Sector = a small section in the field.

RESULTS

1. The morphology of the neurons and glial cells

Fig 4 and fig. 9, granular cells:

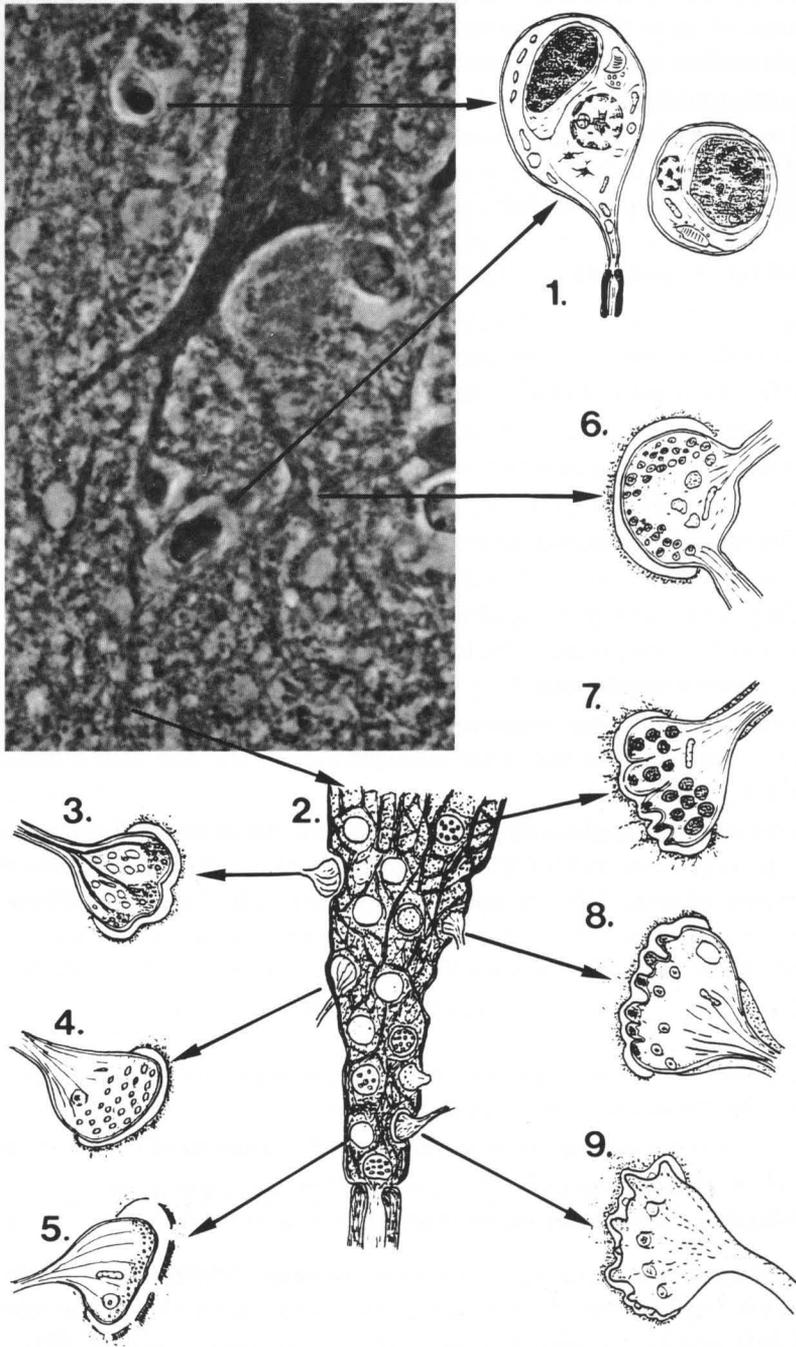
1. Cells with a diameter of 7—10 μm . The nuclei have a diameter of 2,5—3 μm , large dark chromatin granules and a dark nuclear sap.
2. Roundish cells with a diameter of 8—10 μm . The nuclei have a diameter of 3—3,5 μm , small dark granules, and a clear nuclear sap.
3. Roundish cells with a diameter of 12—15 μm . The nuclei have a diameter of 7—10 μm , fine granules, and a greyish nuclear sap.
4. Longish cells of Cajal have a length of up to 30 μm . The nuclei are also longish, have a length of up to 20 μm , dark granules, and a light nuclear sap.

Fig. 4 and fig. 5, neurons:

5. Multiforme neurons. The cell bodies have an extension of up to 65 μm . The nuclei are irregular, have a light nuclear sap and fine chromatin granules.

Fig. 7 — The foot of a large pyramidal cell in layer 6 of field 10, accompanied by blood-brain-barriers, stained by Golgi, 1000 \times .

1. Blood-brain-barriers control the change of matter into and out of the brain (Leonhardt, 1985). The lower part (axon hill) of a large pyramidal cell, and its synapses., 3.000 \times .
2. The axon hill 7.000 \times .
Where the synapses are lost, the pores got empty. The forms of the synapses:
3. Special form, 30.000 \times .
4. Synapse typ I of Gray, 30.000 \times .
5. Synapse typ II of Gray, 30.000 \times .
6. Synapse "en passant", 50.000 \times .
Synapses in function:
7. Synapse with large dark vesicles, 50.000 \times .
8. Synapse with light vesicles, 50.000 \times .
9. Surface of the synapse.



6. Small pyramidal cells are situated vertical to the surface of the brain and have a length of up to 80 μm . The roundish nuclei have a diameter of up to 12 μm and a light nuclear sap. Small pyramidal neurons dominate in the 2nd and 4th layer.
7. Gigantic pyramidal cells. The cell bodies can have a length of up to 250 μm , and together with their associated nerves an extension of some millimeters. The oval nuclei have a clear nuclear sap and a diameter of up to 25 μm . The gigantic pyramidal cells differ in their form and can be barrel-shaped and spindle like.

Fig. 5 and fig. 6, glial cells (neurogliaform cells):

8. Protoplasmatic astrocyte. The processes of the cell bodies are short. The cells can have an extension of 70 μm . The roundish nuclei, with a clear nuclear sap and fine chromatin granules, have a diameter of up to 20 μm (fig. 11).
9. Astrocytes (basket cells). The cells have an extension of up to 12 μm . The nuclei are dark and have a diameter of up to 3 μm .
10. Fibrous astrocytes. Out of the dark, spindle like cells with a length of up to 20 μm , nerve fibres extend to more than 150 μm . The oval nuclei are some lighter and have a length of up to 5 μm .
11. Hortega glial cells (macroglial c.). The longish cells have a length of up to 40 μm and a light plasma. The longish nuclei have a length of up to 13 μm and large chromatin granules.
12. Interfascicular oligodendroglia cells (fig. 11). The roundish cells have a diameter of nearly 50 μm . The nuclei are arranged eccentricly, and have a diameter of nearly 12,5 μm .
13. Macro-oligodendroglial cells (gigantic glial cells, BRODMANN, 1909; spiny stellate neurogliaform cells, CREUTZFELDT, 1983)). The longish cells have an extension of up to 250 μm , and their associated very long nerve fibres extend into the first layer below the surface. The roundish nuclei have a diameter of up to 15 μm . Such glial cells are characteristic in motoric areas (BRODMANN, 1909).

Only the named neuro- and glial cells were used to distinguish the cortical layers of the telencephalon of the harbour porpoise.

II. *The cortical lamination and the equipment in the single areas and fields of the telencephalon (Fig. 14)*

The cortical limbic formation has in the examined brain a thickness of 1,5 to 3 mm. The areas and the fields are distinct in number and accumulation of the single neurons and glial cells. In the cerebellar cortex, the greyish substance is arranged in layers (L), which differ in their outfit with neurons and glial cells.

THE OLFACTORY AREAS

Olfactory fields differ from all other cortical areas by the first layer; they have distinctly more granular cells. The olfactory field 1 contains five layers:

- L. 1, 200—300 μm granular cells (1—4),
- L. 2, 150 μm polym. neurons (5), small and gigantic pyramidal cells (6 and 7),
- L. 3, 150 μm granular cells (2 and 3), oligodendroglia cells (12), astrocytes (9),
- L. 4, 100 μm polym. neurons and small pyramidal cells,
- L. 5, 1 mm oligodendroglia cells (12) and spindle cells.

The fields 15, (Fig. 13 A) 23 and 25 have also many granular cells in the first layer, therefore they could belong to the olfactory system. The three fields have only three layers with a degenerated equipment.

The equipment of field 15:

- L. 1, 450 μm granular cells (1—4),
- L. 2, 250 μm polym. neurons, small pyramidal cells and some gigantic pyramidal cells, situated horizontally to the surface,
- L. 3, 1 mm granular cells and single spindle cells.

Field 25 it in its equipment like field 23, but the cerebellar cortex is thinner than in field 15.

The equipment of field 23:

- L. 1, 200 μm granular cells,
- L. 2, 100 μm polym. neurons, small pyramidal cells, gigantic pyramidal cells in oblique direction, and oligodendroglia cells (12),
- L. 3, 1 mm small pyramidal cells and single small spindle cells.

VISUAL AREAS

Around the occipital pole, all animals have visual fields, also the harbour porpoise. By electrophysiological experiments LADYGINA et al. (1974) and SOKOLOV et al. (1972) have proved the existence of visual centres in the occipital, parietal and frontal areas.

The equipment of field 20 (Fig. 8 and fig. 13 B), surrounding the occipital pole:

- L. 1, 400 μm some granular cells,
- L. 2, 200 μm small pyramidal cells, small spindle cells, astrocytes (9 and 10),
- L. 3, 300 μm single granular cells, oligodendroglia cells (12), astrocytes (basket cells 9)
- L. 4, 250—400 gigantic pyramidal cells,
- L. 5, 300 μm polym. neurons, small pyramidal cells,
- L. 6, 350 μm large spindle cells, granular cells.

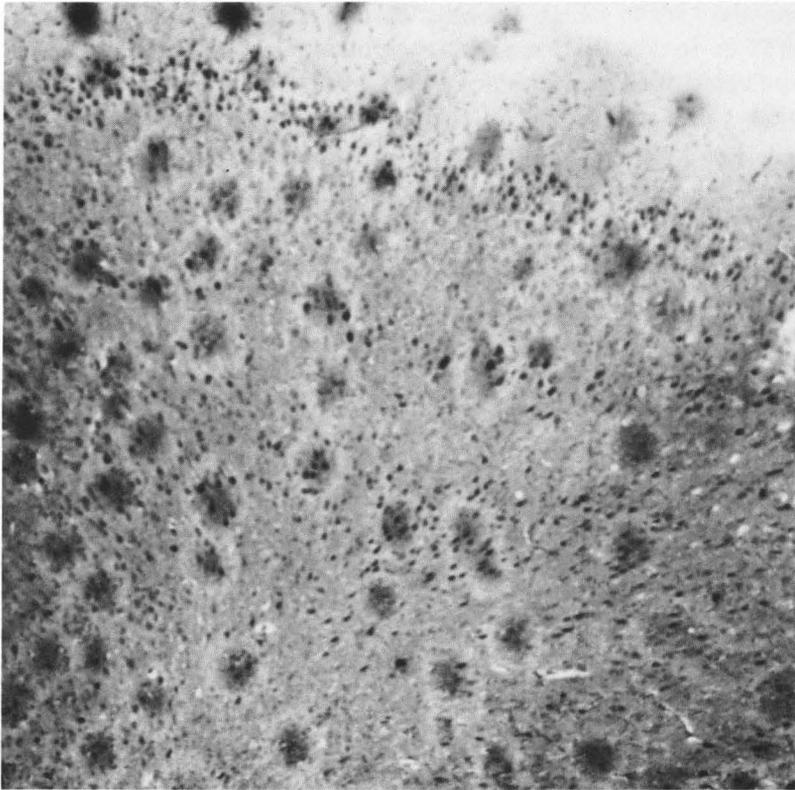


Fig. 8 — The cortical lamination of the visual field 20 with six layers. Tuloidin/eosin, 100 \times .

The characteristics of this visual field are small spindle cells in layer 2, and large spindle cells in layer 6 (Fig. 10). Such characteristics were identified in the caudal part of field 22, and in field 26.

MOTORIC AREAS

Characteristic for motoric areas large oligodendroglia cells (13), and the high accumulation of gigantic pyramidal cells (BRODMANN, 1909). Fields with such cells are the field 4 in the frontal lobe, and the field 14 in the temporal lobe. Characteristics of these fields are two layers accumulated by gigantic pyramidal cells, a remarkable accumulation of astrocytes (basket cells) in the 3rd layer, and large oligodendroglia cells (13) in the 5th layer.

The equipment of field 4 (Fig. 13 C):

- L. 1, 400 μ m few granular cells,
- L. 2, 100 μ m small pyramidal cells, polim. neurons, astrocytes,
- L. 3, 50 μ m granular cells, astrocytes and oligodendroglia cells (12),

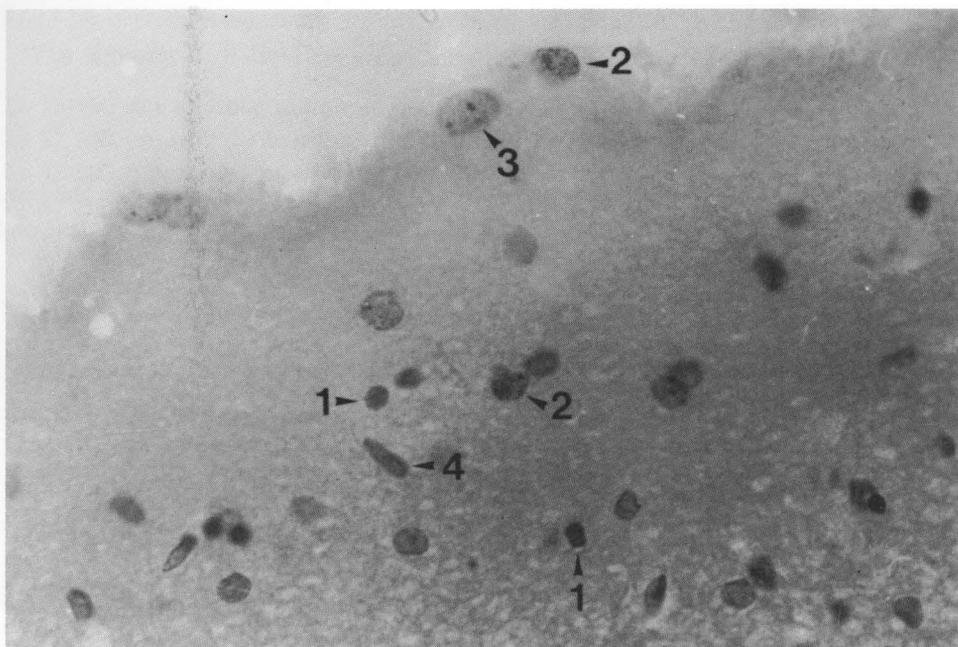


Fig. 9 — The first layer of the field 20 with a poor granulation. Tuloidin/eosin, $400\times$. 1, 2, and 3 granular cells, 4 cell of Cajal.

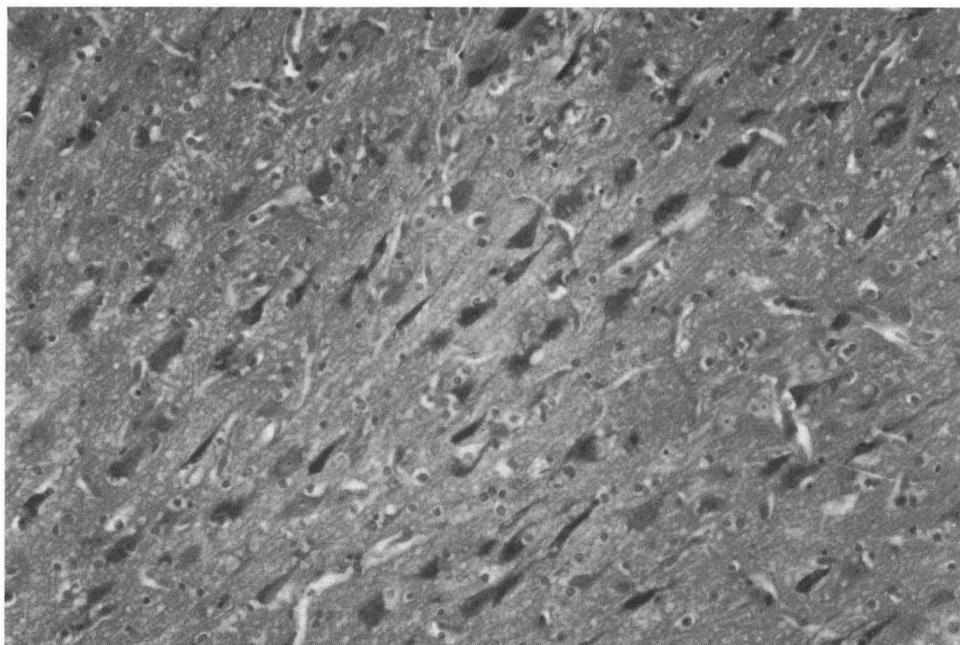


Fig. 10 — Layer 6 of field 20, with large spindle like cells and pyramidal cells.

- L. 4, 400 μm large pyramidal cells, granular cells,
- L. 5, 250 μm granular cells, oligodendroglia cells (13),
- L. 6, 800 μm large pyramidal cells,
- L. 7, 400 μm spindle cells, granular cells.

An area with the same equipment, but only with 6 layers, was located in the temporal lobe and contains the fields 17 and 18. The outward borders are unclear and mixed with structures typical for the adjoining fields.

The equipment of the wide centre of this area:

- L. 1, 350 μm few granular cells,
- L. 2, 100 μm polym. neurons, small pyramidal cells,
- L. 3, 350 μm astrocytes, granular cells and oligodendroglia cells (12),
- L. 4, 250 μm gigantic pyramidal cells, astrocytes,
- L. 5, 200 μm granular cells, oligodendroglia cells (13),
- L. 6, 350 μm small pyramidal cells, spindle cells.

At the caudal border of field 18 spindle cells are added to layer 3. At the dorso-rostral borders of field 17 single gigantic pyramidal cells are situated.

The best developed lamination was detected in field 10. In the comparable area of the bottle-nosed dolphin, LADYGINA *et al.* (1974) discovered by electrophysiological examination an auditory centre. With two layers accumulated by macro-oligodendroglia cells (13), this field shows motorical and acoustical characteristics.

The equipment of field 10 (Fig. 13 E):

- L. 1, 450 μm granular cells,
- L. 2, 150 μm polym. neurons, small pyramidal cells astrocytes,
- L. 3, 100 μm granular cells, oligodendroglia cells (12),
- L. 4, 150 μm astrocytes, small pyramidal cells and polym. neurons,
- L. 5, 100 μm granular cells, astrocytes, oligod. c. (12),
- L. 6, 250 μm gigantic pyramidal cells,
- L. 7, 300 μm granular cells, macro-oligodendroglia cells (13),
- L. 8, 400 μm polym. neurons, small pyramidal cells,
- L. 9, 1 mm granular and spindle cells.

Other fields with a accumulation of macro-oligodendroglia cells (13):

The boundary between the fields 20 and 22 is diffuse and cannot be correctly determined. In the rostral part of field 22 the layers are clearly separated.

The equipment of field 22:

- L. 1, 400 μm granular cells,
- L. 2, 150 μm polym. neurons, small pyramidal cells,
- L. 3, 300 μm granular cells, astrocytes and oligodendroglia cells (12),
- L. 4, 200 μm granular cells, astrocytes oligodendroglia cells (13),
- L. 5, 300 μm gigantic pyramidal cells,
- L. 6, 600 μm spindle cells, oligodendroglia cells (12).

Field 24 is clearly separated from its surroundings.

The equipment of field 24:

- L. 1, 450 μm granular cells,
- L. 2, 150 μm polim. neurons, small spindle cells, astrocytes,
- L. 3, 200 μm granular cells, oligodendroglia c. (12),
- L. 4, 200 μm gigantic pyramidal cells,
- L. 5, 300 μm granular cells, oligodendroglia cells (13),
- L. 6, 150 μm polim. neurons, small pyramidal cells,
- L. 7, 300 μm large and small spindle cells.

Field 5, comparable to the regio praecentralis (BRODMANN, 1909) of humans and animals, represents the motoric center of the whole body (CREUTZFELD, 1983). With the exception of two folds, this field has five layers of distinct thicknesses.

The equipment of field 5:

- L. 1, 400 μm , few granular cells,
- L. 2, 100 μm polim. neurons, small pyramidal cells,
- L. 3, 100 μm granular cells, oligodendroglia cells (12), astrocytes,
- L. 4, 200 μm polim. neurons, small pyramidal cells,
- L. 5, 1 mm polim. neurons, small pyramidal cells, spindle cells, and single gigantic pyramidal cells.

In the sector of field 5, which in the comparable sector of the human cortex represents the lips and legs, the amount of neurons in the 2nd and 4th layer is clearly reduced.

AUDITORY AREAS

By electrophysiological examinations SOKOLOV *et al.* (1972) and LADYGINA *et al.* (1974) discovered auditory centres in the parietal lobe of dolphins. The comparable region (Lobulus pariet. med.) of the harbour porpoise cortex has seven layers.

The equipment of the field 7:

- L. 1, 300 μm granular cells,
- L. 2, 200 μm polim. neurons, small pyramidal cells, astrocytes (9),
- L. 3, 200 μm granular cells, oligodendroglia c. (12),
- L. 4, 250 μm gigantic pyramidal cells, astrocytes,
- L. 5, 300 μm granular cells, oligodendroglia c. (13),
- L. 6, 450 μm polim. neurons, small pyramidal cells,
- L. 7, 1 mm polim. neurons, small spindle cells.

Characteristic of this field is the great density of oligodendroglia cells (12) in the layer 3 (Fig. 12). In a segment of a horizontal section of one square millimeter, nearly 1600 glia cells with a diameter of nearly 30 μm are installed. The same density of oligodendroglia cells (12) as in layer 3 and 5 was found in field 10.

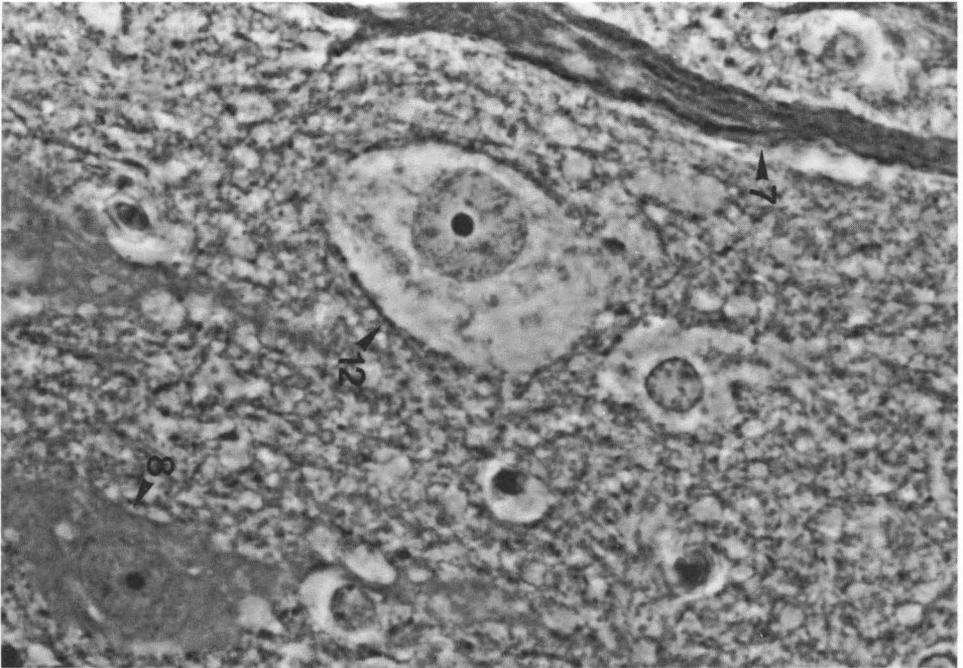


Fig. 11 — The layer 6 of field 12. Golgi, 1000 \times . Gigantic pyramidal cell (7.), protoplasmic astrocyte (8.), oligodendroglia cell (12.)

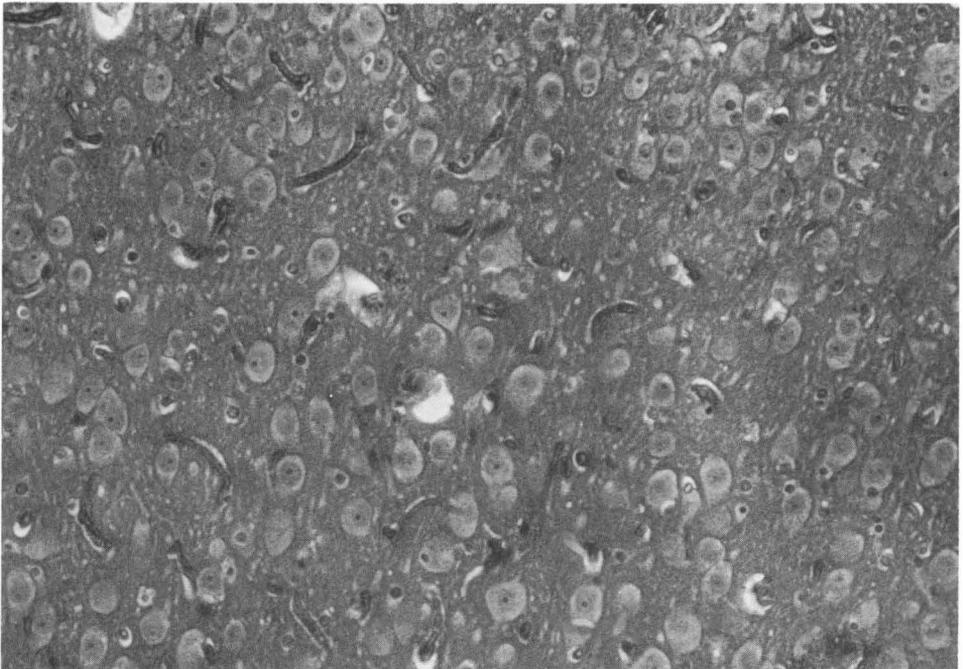


Fig. 12 — Horizontal section through the third layer of field 4, with a high density of oligodendroglia cells (12.). Tuloidin/eosin, 400 \times .

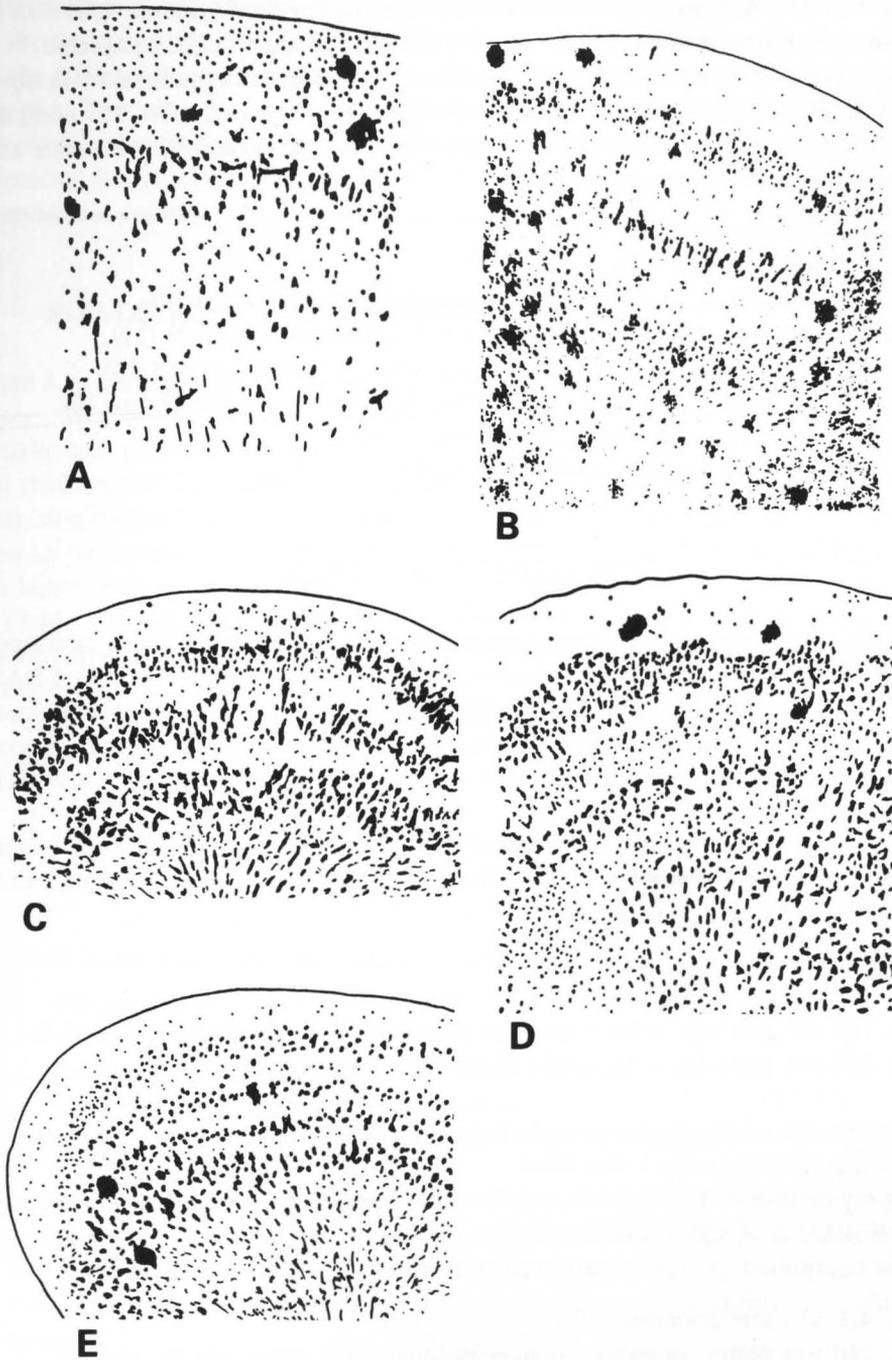


Fig. 13 — Pattern of the lamination in field 15 (A), field 20 (B), field 4 (C), border between field 16 and 17 (D), field 10 (D).

Field 21 of the regio cingularis also has a high density of oligodendroglia cells in the layer 3. But with only five layers this field has no significant equipment.

The second auditory centre, proven by electrophysiological examinations in other dolphins (SOKOLOV *et al.*, 1972), was located in the temporal lobe. The comparable field 12 of the harbour porpoise has a mixed character, and shows acoustic and somatosensorial characteristics.

The equipment of field 12:

- L. 1, 400 μm granular cells,
- L. 2, 150 μm polim. neurons, small pyramidal cells, astrocytes (9),
- L. 3, 300 μm granular cells, astrocytes (10), oligodendroglia cells (12),
- L. 4, 350 μm gigantic and small pyramidal cells, astrocytes (9 and 10),
- L. 5, 250 μm polim. neurons, small pyramidal cells, astrocytes (9 and 10),
- L. 6, 500 μm gigantic and small pyramidal cells,
- L. 7, 400 μm granular and small spindle cells.

SOMATOSENSORY AREAS

Caudally of the central cleft (Sulcus centralis), in the cortex of all highly developed mammals a somatosensory area is situated (BRODMANN, 1909; PENFIELD & RASMUSSEN, 1950; CREUTZFELDT, 1983). Therefore this area was first examined. In its lamination field 6 is not homogeneous, but often five layers are clearly discernible. Characteristical for this field is the accumulation of astrocytes 8, 9, and 10 in the layers 2, 3, and 4.

Of interest are the deviations from the standard lamination of field 6. In a small sector, comparable to the field of the human cortex which represents the lips, only four layers exist as follows:

- L. 1, 400 μm any granular cells,
- L. 2, 150 μm polim. neurons, small pyramidal cells,
- L. 3, 100 μm granular cells, astrocytes (9 and 10), oligodendroglia cells (12),
- L. 4, 500 μm granular cells, single oligodendroglia cells (12).

Only the sector which represents in the human cortex the legs and feet has three layers. There the cortex is only 1 mm thick.

Highly developed is the sector, which in the human cortex represents the tongue (PENFIELD & RASMUSSEN, 1950).

The equipment of this somatosensory sector:

- L. 1, 400 μm few granular cells,
- L. 2, 250 μm polim. neurons, small pyramidal cells, astrocytes (9, and 10),
- L. 3, 200 μm granular cells, oligodendroglia cells (12), protoplasmatic astrocytes (8),
- L. 4, 250 μm polim. neurons, small pyramidal cells, fibrous astrocytes (10),
- L. 5, 200 μm granular cells, oligodendroglia c. (12),
- L. 6, 250 μm polim. neurons, small spindle cells.

A somatosensory centre discovered by electrophysiological examination is located in the frontal cortex of dolphins (SOKOLOV *et al.*, 1972). The comparable field 3 in the harbour porpoise cortex has besides somatosensory also motorical characteristics. The cortex has in this field a thickness of 3 mm, and in the fifth layer many macro-oligodendroglia cells (13). Field 2 of the harbour porpoise has a somatosensory character. In the comparable centres of other dolphins SOKOLOV *et al.* (1972) found a motorical centre.

FIELDS WITH AN INDEFINABLE CYTOARCHITECTURE

Field 8 in the parietal lobe has the cortex with a thickness of 2 mm and only three layers, without pyramidal and spindle cells. The presence of astrocytes and oligodendroglia cells (12) indicates a connection to the somatosensory system. With a cortical thickness of 2,5 mm field 9 has five layers. Single macro-oligodendroglia cells (13), single gigantic pyramidal cells, and single large spindle cells indicate a connection to the optical system. In field 11, the cortex has a thickness of 2,5 mm, and six layers with motorical and acoustic characteristics.

Field 13 has five layers; the cortex is 2 mm thick and has a motorical character. Somatosensory acoustic characteristics were found in field 16. The lamination has a thickness of 2,5 mm, and five layers.

Very poor of neurons and glia cells is field 19. In the cortex with a thickness below 2 mm only three layers are present, as follows:

- L. 1, 450 μm granular cells,
- L. 2, 250 μm polym. neurons, small pyramidal cells,
- L. 3, 1 mm oligodendroglia cells (12), polym. neurons, granular cells.

Field 21 in the regio cingularis has five layers:

- L. 1, 400 μm granular cells,
- L. 2, 150 μm polym. neurons and small pyramidal cells,
- L. 3, 400 μm astrocytes, granular cells, oligodendroglia cells (12),
- L. 4, 250 μm gigantic and small pyramidal cells,
- L. 5, 800 μm polym. neurons, granular cells, small spindle cells.

Five layers and a thickness of nearly 2,1 mm has field 26. In layer 5 single large spindle cells were detected, but the equipment of the other layers is not comparable to the visual fields.

Field 28 in the regio cingularis has also no significant characteristics, it looks as follows:

- L. 1, 400 μm granular cells,
- L. 2, 200 μm polym. neurons, small pyramidal cells, astrocytes,
- L. 3, up to 1,5 mm polym. neurons, granular cells, astrocytes, oligodendroglia cells (12), small spindle cells.

DISCUSSION

For the identification of the architecture of the harbour porpoise telencephalon, and the cerebral orientation, maps of human beings and of cetaceans were used. The comparison of human and cetacean brains showed that the brains of all cetaceans have a greater number of folds. The folding of the brain, and with it the enlargement of the cortical surface, increased during evolution. A primitive brain contains only some folds, highly developed mammal brains however have many folds. Cetacean brains have more folds than human brains. If we postulate that the folding of the brain is an indication of its phylogenetic development, we have to accept, that the cetacean brain is the most advanced brain of all mammals. This is supported by different kind and numerous density of synapses of neurons. But it is also assumed that the configuration of a brain has no influence on its efficiency.

The efficiency of the brain first depends on numerical density of the neurons and glia cells, and secondly on the nervous connection. A critical examination of the nervous equipment of the brain leads to different interpretations. After cortical studies of dolphin brains KESAREV *et al.* (1977) stated that dolphin brains have a primitive cortical equipment, and a poor lamination over the entire cortical surface.

PILLERI (1962) and PORTMANN (1963) found in the brain of marine mammals an equipment, very similar to human brains. MORGANE *et al.* (1982) stated: "Nevertheless, as a whole, the limbic lobe in dolphin is a massive formation with the total number of cells being considerably greater than in the limbic lobe formations in primates, including man."

Differences also exist in regard to the cortical lamination. KESAREV *et al.* (1977) and MORGANE *et al.* (1980, 1982) noted the lack of layer 4, and supposed a duplication of layer 3 or 5. PILLERI *et al.* (1968), and MORGANE *et al.* (1986) however found the fourth layer. This demonstrates that it is very difficult to identify the cortical laminae of cetaceans in using the method of BRODMANN (1909).

The time of separation of the cetaceans and the other mammals is still not exactly known, but it happened more than 60 million years ago. Therefore both have very few phylogenetical relations. Their cortical fields and the cortical lamination are not fully comparable. Therefore in this description a consecutive numbering was used. The cortical field numbers of the harbour porpoise are not identical with the numbers in human cortical fields, as used by BRODMANN (1909). The equipment of the individual cortical layers of the harbour porpoise is different to the equipment of the cortical layers in the human cortex. In general, the first layer of toothed whales has fewer granular cells, and the second layer has more neurons (small pyramidal cells) than the same layer in the human cortex. The numerical density of nerve cells in the human cortex is 10.000 to 30.000 per cubic millimeter (LEONHARDT, 1985). Studies of the packing density of neurons in the dolphin limbic cortex led to an estimate in distinct parts of 5.600 to 105.000 per cubic millimeter (GAREY & LEUBA, 1986; MORGANE *et al.*, 1986). The numerical density of neurons in the visual cortex of the harbour porpoise is 6.400—40.000 per cubic millimeter. This is less than GAREY & LEUBA (1986) found in the visual cortex of the *Tursiops truncatus*. In

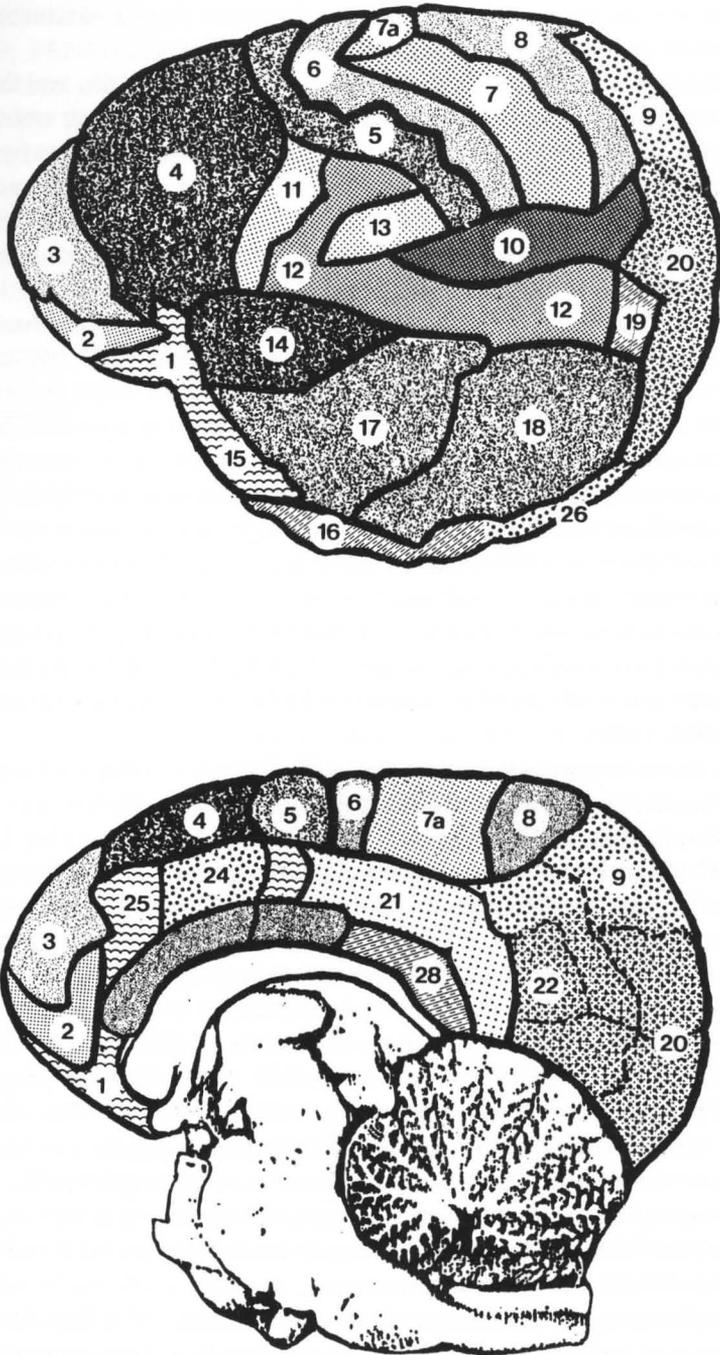


Fig. 14 — The cytoarchitectonic fields in the telencephalon of the harbour porpoise.
 Fields of the olfactory system: 1, 15, 23, 25.
 Fields of the optical system: 2, 9, 18, 20, 22, 26.
 Fields of the acoustic system: 7, 9, 10, 11, 12, 13, 16, 17, 18, 21.
 Fields of the motoric system: 3, 4, 5, 10, 11, 12, 13, 14, 16, 17, 18, 21.
 Fields of the somatosensory system: 2, 3, 6, 7, 8, 9, 11, 16, 28.

all examined cortical layers of toothed whales the largest density of neurons and glia cells was found in the second layer.

The ramification of the neurons, the connection between the cells, and the accumulation of synapses at the neurons, is comparable to the human nervous system (Fig. 7).

At present it is not possible to draw a conclusion on the intelligence by the archi- and cytoarchitecture of the brain. In spite of this fact, an attempt is made to compare human, dolphin and porpoise cortices, as this is a matter of great interest. For better understanding the Annex to the numbers of the human cortical fields, the letter "B" (BRODMANN, 1909) is added.

The olfactory regions in the nose of the harbour porpoise have a function, and are connected by the Nervus trigeminus to the brain (BEHRMANN, 1989). The smell nerves are totally reduced, and rudiments of the olfactory bulbi are rare (OELSCHLÄGER & BUHL, 1985). The olfactory field 1, (Fig. 14) is situated in the same area as in other mammals, and has five layers, and the density of neurons and glia cells is not reduced. Especially the first layer which has nearly 9.500 granular cells per cubic millimeter, has the largest density of the entire harbour porpoise cortex, where there are maximal 6.400 granular cells per cubic millimeter present. The same density of granular cells in the first layer was counted in field 15 comparable to the olfactory areas of primitive mammals (MORGANE, 1986), and in fields 23 and 25. But these fields have a reduced lamination and a poor nervous equipment. The harbour porpoises can smell, but like human beings only through a degenerated nose (BEHRMANN, 1989).

Only two harbour porpoise cortical fields have a visual cortex. A visual lamination, as in human visual fields, described by PORTMANN (1963), was located in the lobuli occipit. post. and in the caudal sector of the lobuli occipit. int. In the comparable field 17 (B) of the human cortex (calcarine type) nine layers are installed. In the occipital area of the common dolphin (*Delphinus delphis*) KESAREV et al. (1977) found seven layers. In the visual fields of the harbour porpoise never more than six layers are present. This demonstrates, that the optical system is not so well developed as in a human or a common dolphins brain. It is clearly visible in the field which is comparable to field 19 (B) of the human cortex (CREUTZFELDT, 1983), and in which the centre of colour view is situated. In the harbour porpoise brain this field is poor of neurons and has a degenerated equipment. Also poorly developed is the nervous equipment of field 11, comparable to the field 8 (B) of the human cortex, in which the centre of eye-movement is situated (CREUTZFELDT, 1983). Better developed is field 24 with seven layers and motorical characteristics. In the comparable field 32 (B) of the human cortex exists a centre of head and eye movements (CREUTZFELDT, 1983).

By electrophysiological localizations LADYGINA et al. (1974) identified a secondary visual area in the frontal and parietal lobes of dolphins. In the comparable fields of the harbour porpoise motorical and somatosensory equipment is contained.

By electrophysiological studies SOKOLOV et al. (1972) and LADYGINA et al. (1974) found an auditory area in the parietal and in the temporal lobe of dolphins. The comparable areas of the harbour porpoise are the fields 7, 10 and 12. The com-

parable fields of the human cortex contain acoustic and speech centres (OJEMANN *et al.*, 1979; PENFIELD & ROBERTS, 1959). Characteristic of acoustic fields in the human cortex is the great density of oligodendroglia cells in the fifth layer (BRODMANN, 1909). This agrees with the comparable layer of the harbour porpoise, but the third layer of the acoustic and motoric-acoustic areas of the harbour porpoise has the same outfit (Fig. 12). Toothed whales have a fine audition (FLEISCHER, 1982; BEHRMANN, 1988), which is reflected in the cortical lamination of the acoustic fields of the harbour porpoise. The cortex of field 10 has with nine layers the largest extension. In the comparable cortical human fields 41 (B), 42 (B) and 52 (B) auditory centres are located (CREUTZFELDT, 1983; PENFIELD & RASMUSSEN, 1950). The human cortical field 22 (B) and the ventral part of field 6 (B) are comparable to the field 12 of the harbour porpoise. These are in human brains centres of word and music melody understanding (CREUTZFELDT, 1983). The fields 17 and 18 of the harbour porpoise are comparable to the field 21 (B) of the human cortex, and are centres of acoustic attention (CREUTZFELDT, 1983). Very broad in its extension is field 16 of the harbour porpoise. The comparable field 20 (B) of the human brain contains a centre of sounds and music understanding. The cortical lamination and the density of neurons of the harbour porpoise in this field demonstrates that the audition system is very highly developed, higher than the human audition system (NACHTIGALL, 1986). Typical for the motoric areas are large pyramidal cells and large oligodendroglia cells (BRODMANN, 1909). The field 4 of the Lobulus front. med. of the harbour porpoise cortex is situated in an area which BRODMANN (1909) named "Area gigantopyramidalis". The lack of a layer of granular cells like in the comparable fields 4 (B) and 6 (B) observed by BRODMANN (1909), could not be pointed out in the motoric cortex of the harbour porpoise. Significant for the motoric area of the harbour porpoise is, besides the high accumulation of gigantic pyramidal cells in the fourth and sixth layer. The high density of large oligodendroglia cells (13) in the second and fifth layer. In fields of toothed whales comparable to fields 4 and 14 of the harbour porpoise, MORGANE *et al.* (1986) found motoric centres. By two layers with gigantic pyramidal cells, these motoric fields have a better equipment than the comparable human cortical fields 4 (B), 6 (B), and 8 (B). The motoric fields in the frontal lobe of the human cortex, represents the labyrinthal positions and the movable perceptions of head and body (CREUTZFELDT, 1983).

The Regio praecentralis (BRODMANN, 1909) represents the motoric centre of the entire body. The equipment of the cortical layers in field 5 of the harbour porpoise is comparable to the equipment of the human field 1 (B). However, two small sectors are different from the standard lamination: in one small sector of field 5, comparable to the sector which represents the mouth and the lips, and in the sector which represents the legs in the human cortex (PENFIELD & RASMUSSEN, 1950), the numerical density of neurons and glia cells in the second and fifth layer is distinctly reduced. The motionless lips and the lack of legs is clearly expressed in the equipment of the respective cortical sectors.

Also clearly recognizable is the importance of the tongue in the somatosensory system. The field 6 of the harbour porpoise is comparable to the Regio postcentralis,

field 1 (B), in the human cortex (BRODMANN, 1909). Deviations from the standard lamination was found in two sectors. Only four layers exist in the sector of field 6, which in the human cortex represents the oral region (PENFIELD & RASMUSSEN, 1950). The second sector is located in a region which in the human cortex represents the tongue (PENFIELD & RASMUSSEN, 1950). In this sector the layers are bigger and the accumulation of neurons is higher. The tongue of the harbour porpoise contains many kinds of nervous end corpuscles (BEHRMANN, 1988, 1990), which is reflected in the cortical equipment.

Field 7 (B) in the human cortex coordinates the sensory movement of the legs and the body. The extension of the comparable field 7a of the harbour porpoise is smaller. The other somatosensory fields of the harbour porpoise are situated in regions comparable to somatosensory human cortical fields (BRODMANN, 1909; CREUTZFELDT, 1983).

SUMMARY

The olfactory system of the harbour porpoise is reduced but has a function. The visual system of the harbour porpoise is badly developed, and its inferior to the one of dolphins and human beings. However the acoustic system is highly developed. With the equipment of the speaking centre, the harbour porpoise should be able to speak. The extension of motorical areas demonstrates the high agility of the harbour porpoise. The cytoarchitecture of the motorical fields demonstrate the high efficiency of the motorical system, which is much better developed than the human motorical system. By the important accumulation of free nerve endings, and the large collection of nervous end corpuscles, in the integument, the harbour porpoise has the highest sensibility of all mammals. This is not reflected in the somatosensory areas. The equipment of the somatosensory fields are comparable to those in dolphins and humans.

The study of the structural organization of the limbic cortex of the harbour porpoise confirms the assertion of PORTMANN (1963), and his results are comparable to the findings in other dolphins.

However at present it is not possible to make any declaration about the efficiency of the brain by its neural equipment.

ACKNOWLEDGMENTS

I am indebted to Professor Dr. W. Schultz and the staff of the Institut für Haustierkunde of the University of Kiel for the collection of the material. I also owe thanks to Professor Dr. G. Pilleri from Bolligen, Switzerland, and to Mrs Dr. Chr. Manteuffel and Mrs. Dr. A. Schmidt of the University of Bremen for reviewing the manuscript.

I thank Dr. G. Giermann of Alfred Wegener Institute in Bremerhaven editing the English text.

REFERENCES

- BEHRMANN, G. 1988 — The peripheral nerve ends in the tongue of the harbour porpoise *Phocoena phocoena* (Linné, 1758). *Aquatic Mammals* 14.3, 107—112.
- BEHRMANN, G. 1989 — The olfactory regions in the nose of the harbour porpoise *Phocoena phocoena* (Linné, 1758). *Aquatic Mammals* 15.3, 130—133.
- BEHRMANN, G. 1990 — The tuberous organs of the harbour porpoise *Phocoena phocoena* (Linné, 1758). *Aquatic Mammals* 16.1, 33—35.
- BERTOLINI, R. & LEUTERT, G. 1982 — *Atlas der Anatomie des Menschen* 3. Verlag Georg Thieme, Leipzig.
- BRODMANN, K. 1909 — *Vergleichende Lokalisationslehre der Großhirnrinde*. Verlag J.A. Barth, Leipzig.
- CREUTZFELDT, O.D. 1983 — *Cortex Cerebri*. Springer Verlag, Berlin, Heidelberg, New York, Tokyo.
- FLEISCHER, G. 1982 — Hörmechanismus bei Delphinen und Walen. *Deutsche Gesellschaft für Hals-, Nasen-, Ohrenheilkunde*, 30, 123—130.
- GAREY, L.J. & LEUBA, G. 1986 — A quantitative study of the neuronal and glia numerical density in the visual cortex of the Bottlenose Dolphin. *Journal of Comparative Neurology* 247, 491—496.
- HAGENS, G. v. 1979 — Emulsifying resins for plastination. *Der Präparator* 25.2, 43—50.
- KESAREV, V.S. 1970 — Certain data on neuronal organization of the neocortex in the dolphin brain. *Arkh. Anat. Gistol. Embriol.* 59, 71—77.
- KESAREV, V.S., MALOFEYEVA, L.I. & TRYKOVA, O.V. 1977 — Structural organisation of the cerebral neocortex in cetacean. *Archiv Anat. Gistol. Embryologii* 73, 23—30.
- KLIMA, M. 1975 — *Anatomie des Menschen* 1. Kosmos Taschenatlas. Frankh'sche Verlagshandlung Stuttgart, 1—70.
- LADYGINA, T.F. & SUPIN, A.I. 1974 — Evolution of the cortical areas of the brain in terrestrial and aquatic mammals. In: *Morphology, physiology and acoustics of marine mammals*. Academy of Science of the USSR, Moscow, 6—15.
- LEONHARDT, H. 1985 — *Histologie, Zytologie und Mikroanatomie des Menschen*. Georg Thieme Verlag Stuttgart/New York.
- MORGANE, P.J., JACOBS, M.S. & MACFARLAND, W.L. 1980 — The Anatomy of the brain of the Bottlenose Dolphin (*Tursiops truncatus*). Configurations of the telencephalon of the Bottlenose Dolphin with comparative anatomical observations in four other cetacean species. *Brain Research Bulletin* 5, Supple. 3, 1—107.
- MORGANE, P.J., MACFARLAND, W.L. & JACOBS, M.S. 1982 — Limbic lobe of the Dolphin Brain. *Journal f. Hirnforschung* 23, 465—552.
- MORGANE, P.J., JACOBS, M.S. & GALABURDA, A. 1986 — Evolutionary aspects of the cortical organisation in dolphin brains. In: *Research on Dolphins*, eds. BRYDEN & HARRISON. Clarendon Press Oxford, 71—98.
- NACHTIGALL, P.E. 1986 — Vision, audition and chemoreception in dolphins and other marine mammals. In: *Dolphin cognition and behavior: a comparative approach*, (eds. R.J. SCHUSTERMAN, J.A. THOMAS & F.G. WOOD). Lawrence Erlbaum Association, Publishers, Hillsdale, New Jersey, 79—113.
- OELSCHLÄGER, H.A. & BUHL, E.H. 1985 — Development and rudimentation of the peripheral olfactory system in the harbour porpoise *Phocoena phocoena* (Mammalia: Cetacea). *Journal of Morphology* 184, 351—360.
- OJEMANN, G. & MATEER, C. 1979 — Human language cortex: Identification of the common sites for sequencing motor activity and speech discrimination 6.4/2, 205—211. eds. O.D. GREUTZFELD, J. SCHEICH & Chr. SCHREINER, 6.4/2, 205—211.
- PENFIELD, W. & RASMUSSEN, A.I. 1950 — *A clinical study of localization of function*. Mac Millan, New York.
- PENFIELD, W. & ROBERTS, L. 1959 — *Speech and brain-mechanisms*. Princeton University Press, Princeton, New Jersey.
- PILLERI, G. 1962 — Die zentralnervöse Rangordnung der Cetacea (Mammalia). *Acta anat.* 51, 241—258.
- PILLERI, G. 1963 — Zur vergleichenden Morphologie und Rangordnung des Gehirns von *Delphinapterus (Beluga) leucas*, Pallas (Cetacea, Delphinapteridae). *Rev. suisse. zool.* 70, 569—586.
- PILLERI, G., KRAUS, G. & GIHR, M. 1968 — The structure of the cerebral cortex of the Ganges dolphin. *Zeitschrift f. mikroskopische anatomische Forschung* 79, 373—388.
- PORTMANN, A. 1963 — Welche Tiere besitzen die differenziertesten Gehirne? *Umschau H.* 18, 563—566.
- SOKOLOV, V.E., LADYGINA, T.F. & SUPIN I.A. 1972 — Localization of sensory zones in the dolphin's cerebral cortex. *Doklady Akademii Nauk SSR*, 202, 490—493.