Morphology and Evolutionary Biology of the Dolphin (*Delphinus* sp.) Brain – MR Imaging and Conventional Histology

H.H.A. Oelschläger[a]   M. Haas-Rioth[a]   C. Fung[a]   S.H. Ridgway[b]   M. Knauth[c]

[a]Institute of Anatomy III (Dr. Senckenbergische Anatomie), Johann Wolfgang Goethe University, Frankfurt a.M., Germany; [b]Naval Marine Mammal Program and Department of Pathology, University of California, La Jolla, Calif., USA; [c]Department of Neuroradiology, Georg August University, Göttingen, Germany

Abstract

Whole brains of the common dolphin *(Delphinus delphis)* were studied using magnetic resonance imaging (MRI) in parallel with conventional histology. One formalin-fixed brain was documented with a Siemens Trio Magnetic Resonance scanner and compared to three other brains which were embedded in celloidin, sectioned in the three main planes and stained for cells and fibers. The brain of the common dolphin is large, with the telencephalic hemispheres dominating the brain stem. The neocortex is voluminous and the cortical grey matter thin but extremely extended and densely convoluted. There is no olfactory ventricular recess due to the lack of an anterior olfactory system (olfactory bulb and peduncle). No occipital lobe of the telencephalic hemisphere and no posterior horn of the lateral ventricle are present. A pineal organ could not be detected. The brain stem is thick and underlies a very large cerebellum. The hippocampus and mammillary body are small and the fornix is thin; in contrast, the amygdaloid complex is large and the cortex of the limbic lobe is extended. The visual system is well developed but exceeded by the robust auditory system; for example, the inferior colliculus is several times larger than the superior colliculus. Other impressive structures in the brainstem are the peculiar elliptic nucleus, inferior olive, and in the cerebellum the huge paraflocculus and the very large posterior interpositus nucleus. There is good correspondence between MR scans and histological sections. Most of the brain characteristics can be interpreted as morphological correlates to the successful expansion of this species in the marine environment, which was characterized by the development of a powerful sonar system for localization, communication, and acousticomotor navigation.

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Introduction

Among the Mammalia, the extant whales and dolphins have particularly large and complicated brains. This is most impressive in the smaller species of the delphinid toothed whales (Odontoceti) with an unexpectedly high brain mass which, in relation to body mass, is second only to that of the human [Schwerdtfeger et al., 1984; Oelschläger and Oelschläger, 2002; Manger, 2006].

The outstanding size of the dolphin brain can be understood by tracing odontocete evolution. Whales and dolphins, in general, share ancient small-brained carnivorous common ancestors with the hoofed animals (artiodactyls) that lived more than 50 million years ago [Van

Abbreviations used in this paper

I	left lateral ventricle	He	hemisphere	PIN	posterior interpositus nucleus
II	right lateral ventricle	I	insula	PL	parietal lobe
III	third ventricle	ic	internal capsule	Pu	putamen
IV	fourth ventricle	IC	inferior colliculus	Pul	pulvinar
2	optic nerve/chiasm	if	interpedundular fossa	SC	superior colliculus
7	facial nerve	IO	inferior olive	scc	sulcus corporis callosi
8	vestibulocochlear nerve	LGB	lateral geniculate body	scp	superior cerebellar peduncle
AC	amygdaloid complex	ll	lateral lemniscus	se	sulcus lateralis
aq	cerebral aqueduct	LL	lateral lemniscus nuclei	sec	sulcus ectosylvia
C	caudate nucleus	MAO	medial accessory nucleus of IO	SO	superior olive
CA	cornu ammonis	mcp	middle cerebellar peduncle	sp5	spinal tract of trigeminal nerve
cc	corpus callosum	MGB	medial geniculate body	ss	sulcus suprasylvius
cce	crus cerebri	ml	medial lemniscus	ssp	sulcus suprasplenialis
Cl	Claustrum	mt	medial tegmental tract	Sub	subiculum
Cer	cerebellum	oc	optic chiasm	T	thalamus
CG	central (periaqueductal) grey	OL	oval lobule	tb	trapezoid body
DG	dentate gyrus	OrL	orbital lobe	TB	nucleus of trapezoid body
E	elliptic nucleus	ot	optic tract	TL	temporal lobe
Ent	regio entorhinalis	OT	olfactory tubercle/ olfactory lobe	VA	nucleus thalamicus ventralis anterior
f	fornix	P	pons	VCN	ventral cochlear nucleus
FL	frontal lobe	pc	posterior commissure	Ve	vermis
GP	globus pallidus	pf	primary fissure	VL	nucleus thalamicus ventralis lateralis
H	hypothalamus	Pf	paraflocculus		

Grey matter (cortex and nuclei) in capitals, cortical sulci and fiber systems in lower case, ventricles in Roman figures and lower case, cranial nerves in Arabic figures.

Valen, 1966; Gingerich, 1998; Geisler and Luo, 1998; O'Leary, 2002]. There are indications that the adaptation of these ancestors to a habitat hostile to most mammals culminated in the formation of the sonar apparatus in toothed whales [Oelschläger, 1990, 2000; Au, 2000]. The latter combines a powerful auditory system [Ridgway, 1983, 1986, 2000; Ridgway et al., 1981; Ridgway and Au, 1999; Wartzok and Ketten, 1999; Nummela et al., 1999; Ketten, 2000; Kossatz, 2006; Breindl and Oelschläger, unpubl.] with a unique ensemble of nasal structures [epicranial complex, Cranford et al., 1996; Cranford, 2000; Huggenberger, 2004; Comtesse-Weidner, 2007, Prahl, 2007, Huggenberger et al., in press] responsible for the generation of ultrasound and sound signals for orientation and communication, respectively. As a result, central auditory structures of delphinids are, for the most part, extremely well developed, and this is true for every major division of the brain although not for every single auditory center [Zvorykin, 1963; Schulmeyer et al., 2000; Oelschläger and Oelschläger, 2002].

Although there are numerous publications on the histology of the bottlenose dolphin brain [*Tursiops truncatus;* e.g., Morgane and Jacobs, 1972; Morgane et al., 1980], only fragmentary information exists on the brain of the common dolphin [*Delphinus delphis;* e.g., Igarashi and Kamiya, 1972; Pilleri et al., 1980; Breindl and Oelschläger,

unpubl.]. Concerning modern imaging techniques, a series of papers have used MR scans and computer reconstructions to give insights into intact toothed whale brains [Marino et al., 2001a, b, c, 2002, 2003, 2004a, b]; however, these postmortem specimens often had some damage incurred in removal or storage and none compared the MR scans with histological sections from the same species.

We present high-resolution MR scans together with corresponding histological sections in order to show the detailed three-dimensional anatomy of the dolphin brain and methodological differences between the scans and the microslides (fig. 1–8) regarding the depiction of various structures. Such a synthetic approach has not been made up to now for whales and dolphins (cetaceans). In addition, some remarks will be made concerning the function and evolution of the dolphin brain and its structures.

Materials and Methods

We compare our MRI dataset of one common dolphin brain with microslides of three more *Delphinus delphis* brains, each sectioned in one of the three major planes, from the Pilleri Collection (Natural History Museum and Research Institute Senckenberg in Frankfurt am Main, Germany; see table 1).
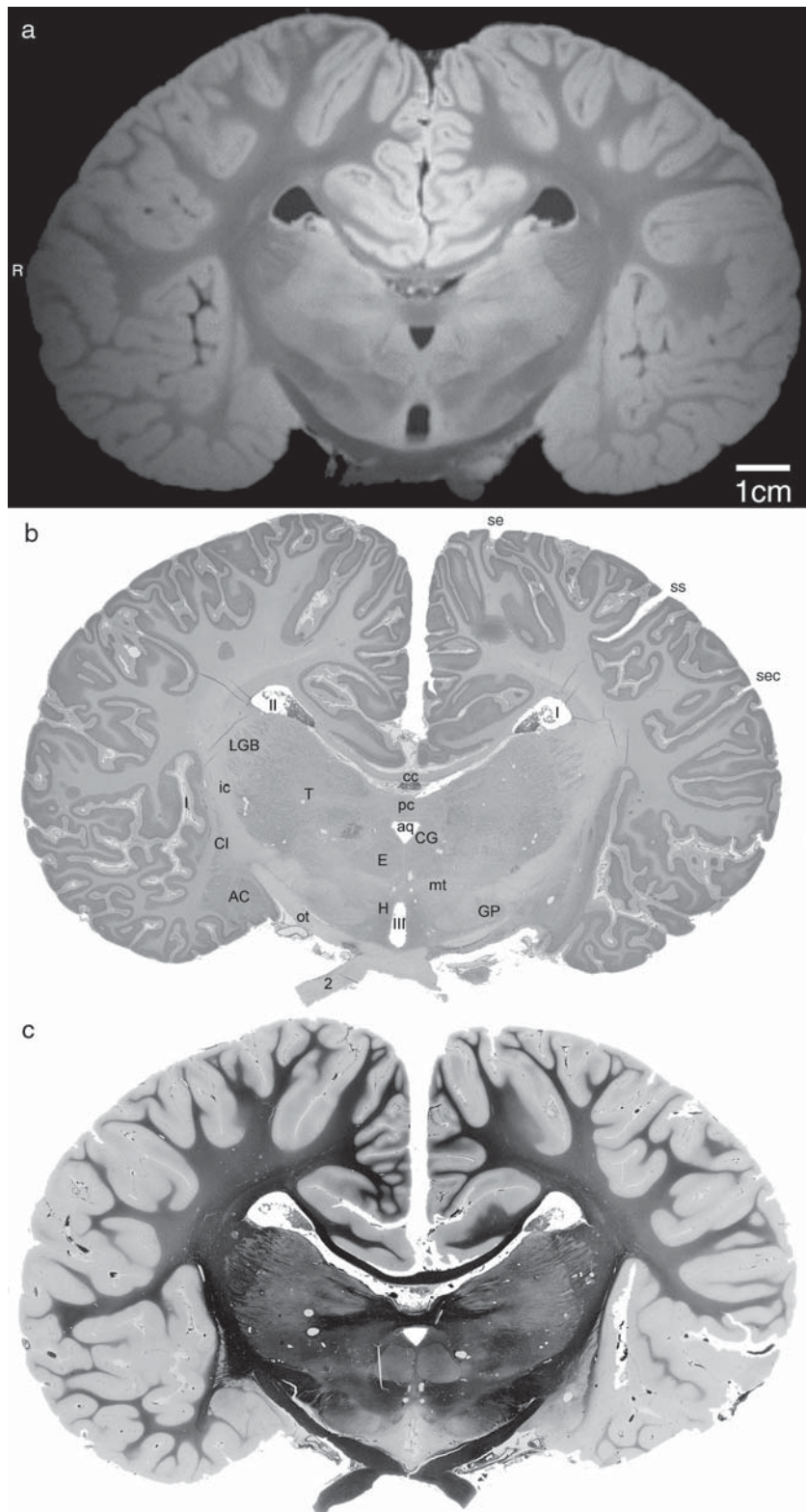
Fig. 1. *Delphinus delphis*. Total brains. Coronal MRI scan (**a**) and histological sections (**b**: cresyl violet, **c**: fiber stain). Level of the diencephalon with the insula (I), thalamus (T) and optic chiasm (not labeled). Scales in **a** 1 cm, the sections in **b** and **c** from other brains are enlarged to the same width and height, respectively (coronal section, sagittal section). For abbreviations see list.
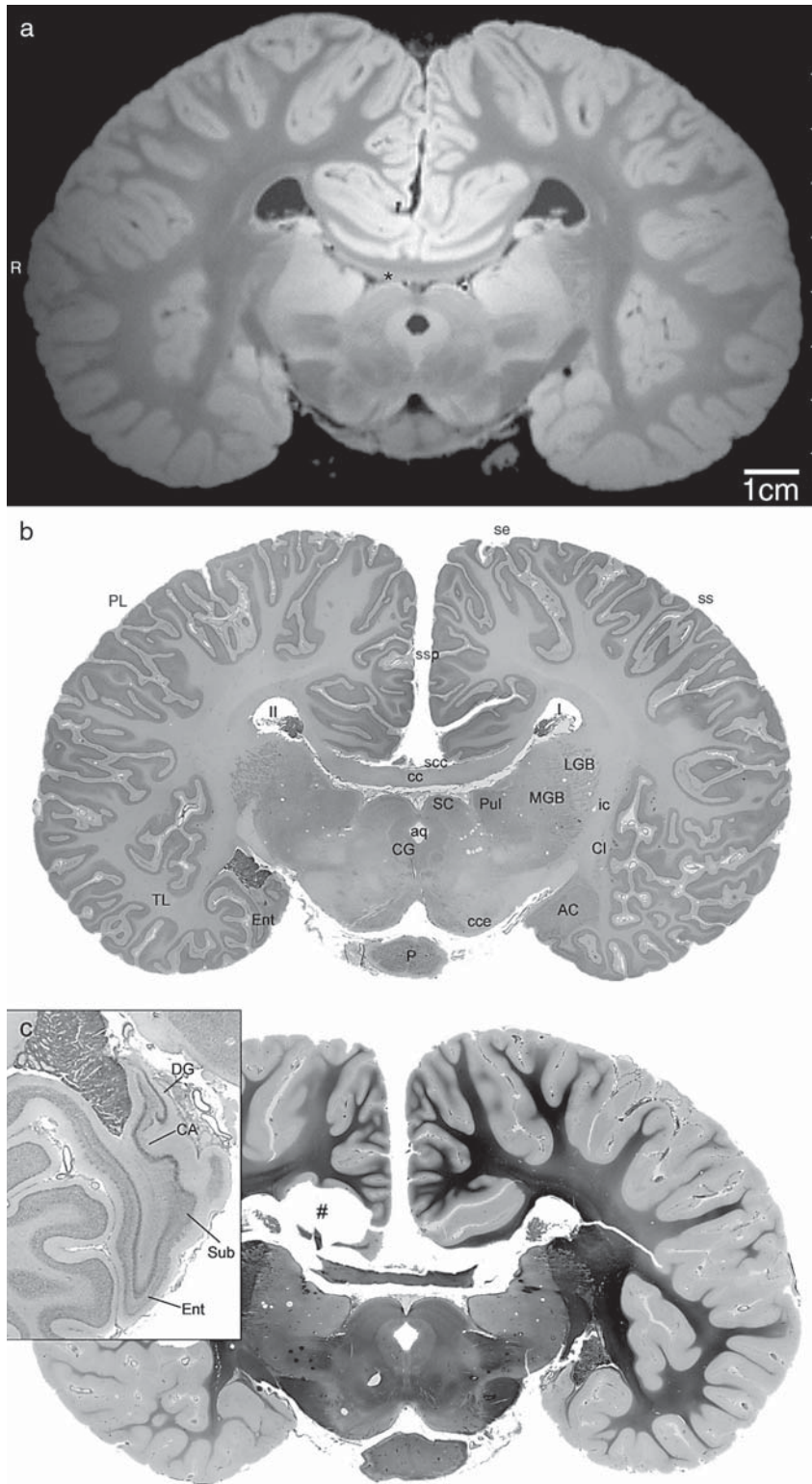
Fig. 2. *Delphinus delphis.* Anterior mesencephalon with the superior collicles (SC) and geniculate bodies (LGB, MGB). Inset: Enlarged detail of the hippocampus area (CA, DG, Ent, Sub) from adjacent section. Asterisk in **a**: fimbria hippocampi; #, artifact.
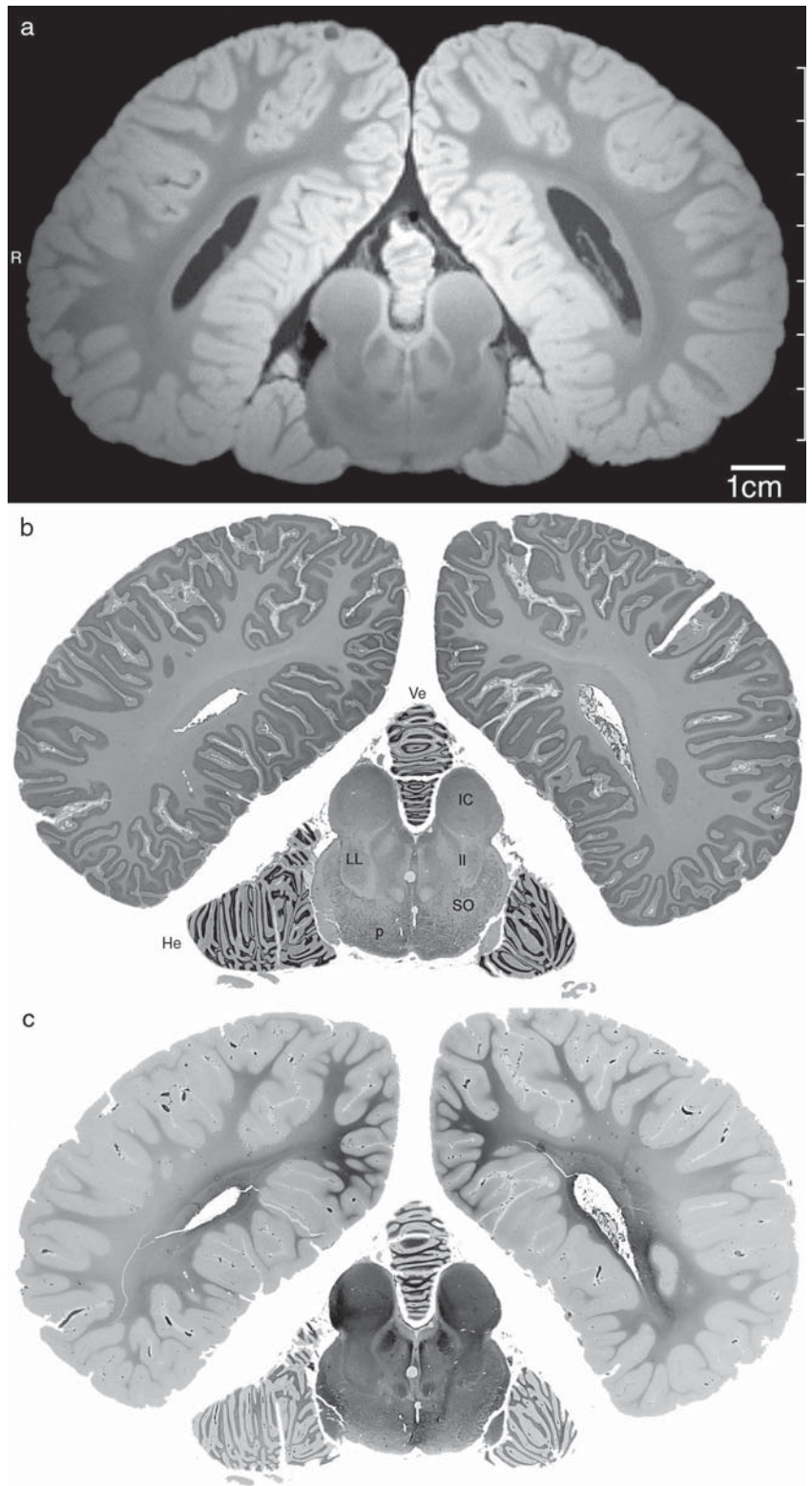
Fig. 3. *Delphinus delphis.* Posterior mesencephalon with the inferior collicles (IC), lateral lemnisci (LL, ll), pons (P), and the rostral extremities of the cerebellum (He, Ve).
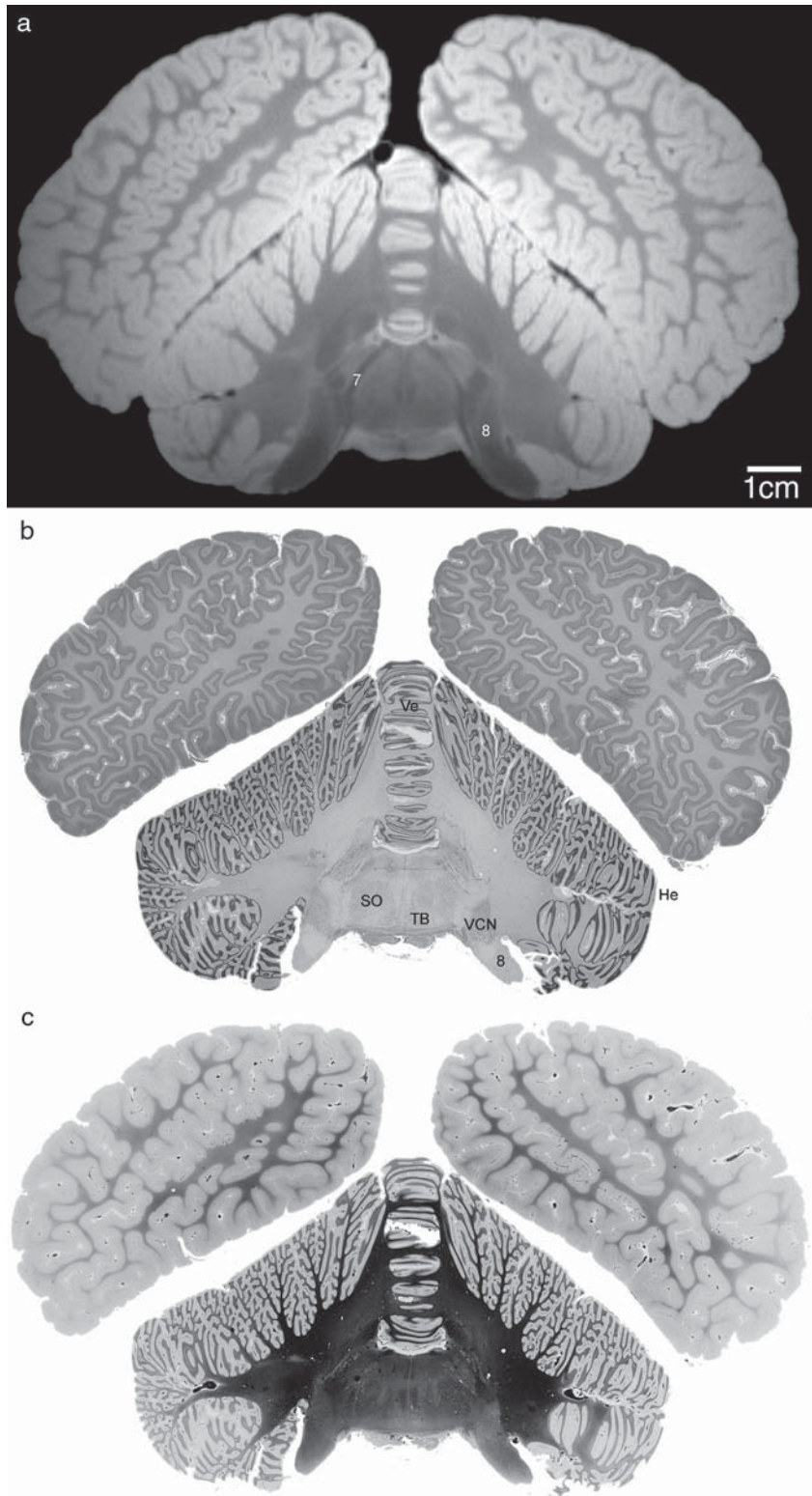
Fig. 4. *Delphinus delphis.* Anterior medulla oblongata with seventh and eighth nerves (7, 8), ventral cochlear nucleus (VCN), nucleus of trapezoid body (TB), superior olive (SO), and anterior part of cerebellum (He, Ve).
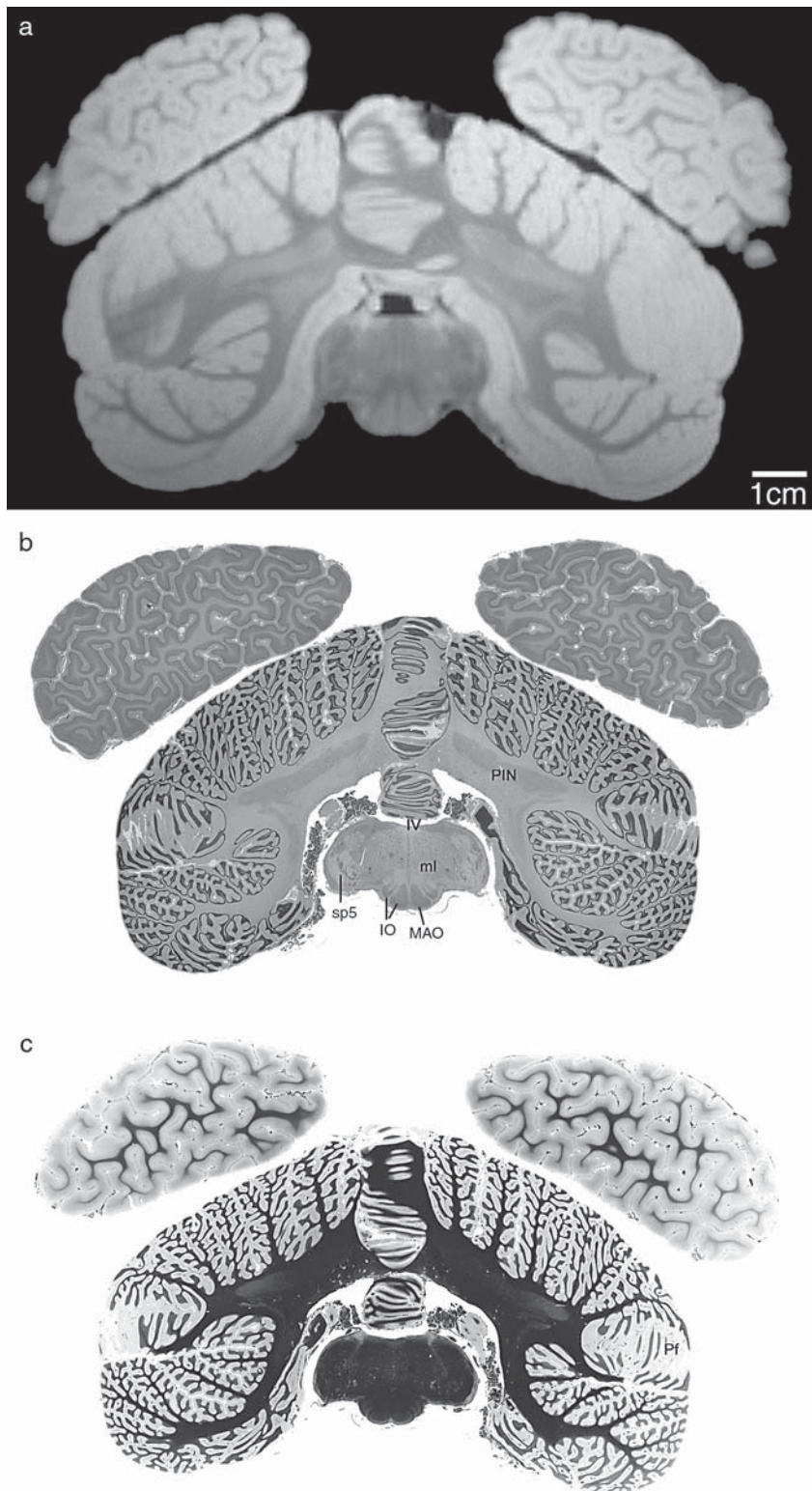
Fig. 5. *Delphinus delphis.* Posterior medulla oblongata with the inferior olives (IO) and the posterior part of the cerebellum with the posterior interpositus nucleus (PIN).
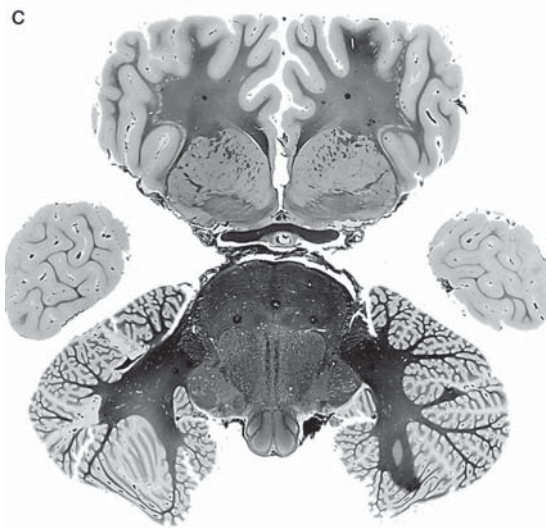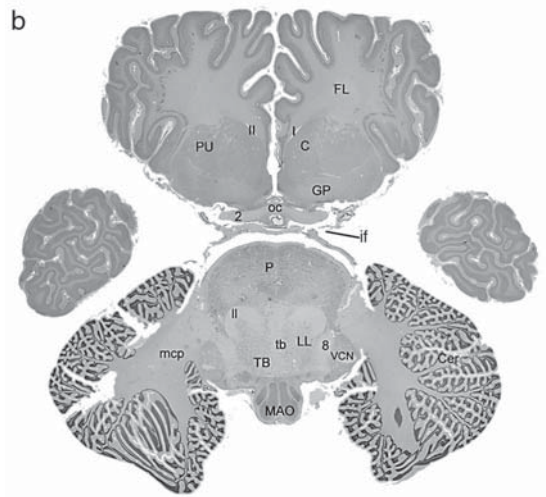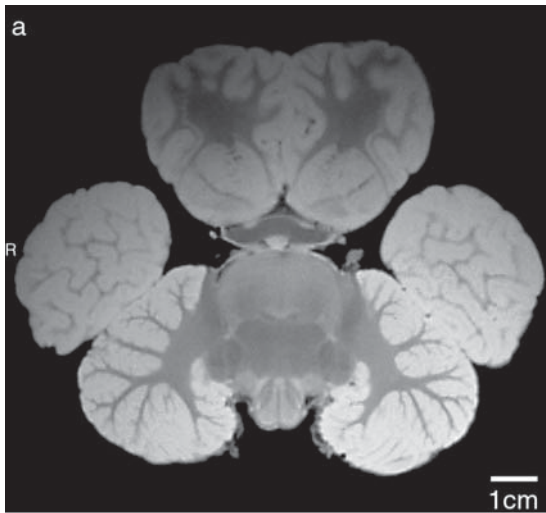
Fig. 6. *Delphinus delphis*. Horizontal scan and sections. Level of the basal ganglia (C, Pu), optic chiasm (oc), pons, trapezoid body and nucleus (tb, TB), middle cerebellar peduncles (mcp) and inferior olives (MAO).

Fig. 7. *Delphinus delphis*. Near-midsagittal scan and sections through the medial wall of the telencephalic hemisphere and the brainstem. White asterisk in **c**: commissural complex. Black dots in histologic sections: artifacts.

Dolphin Brain MR Imaging and Histology

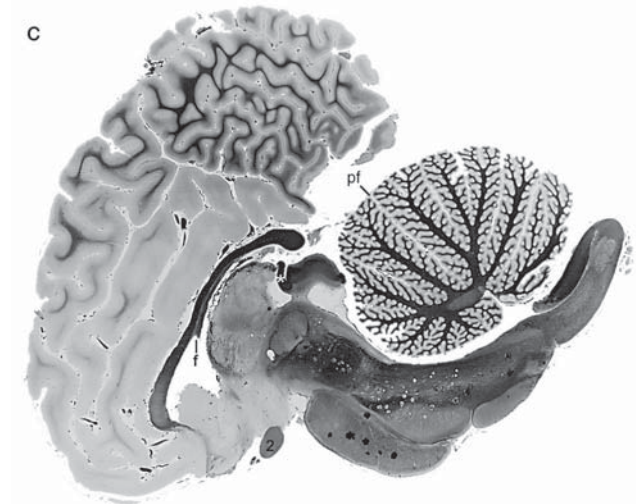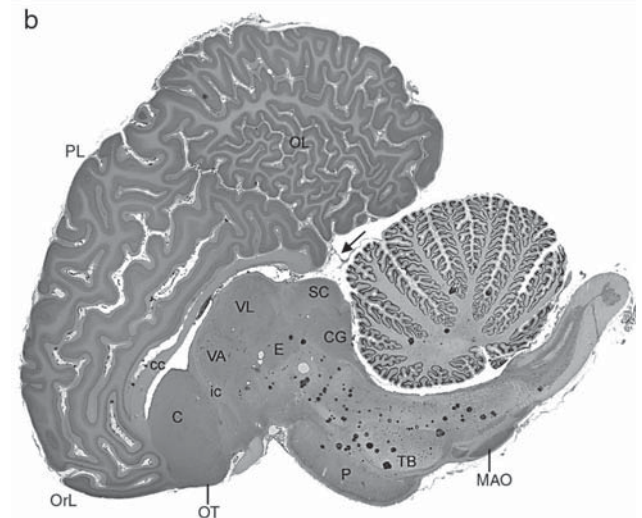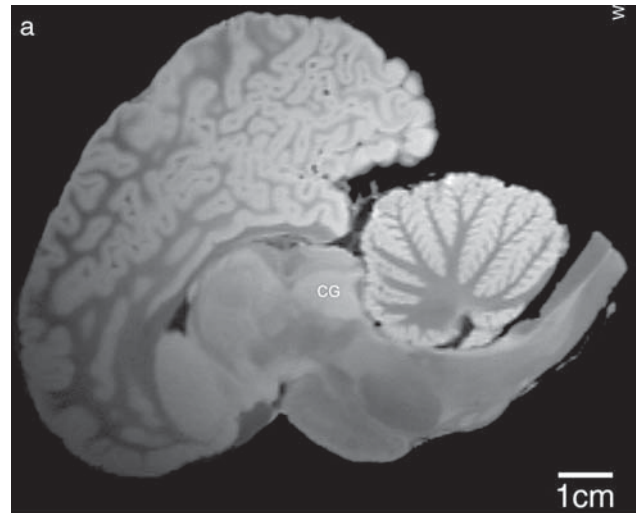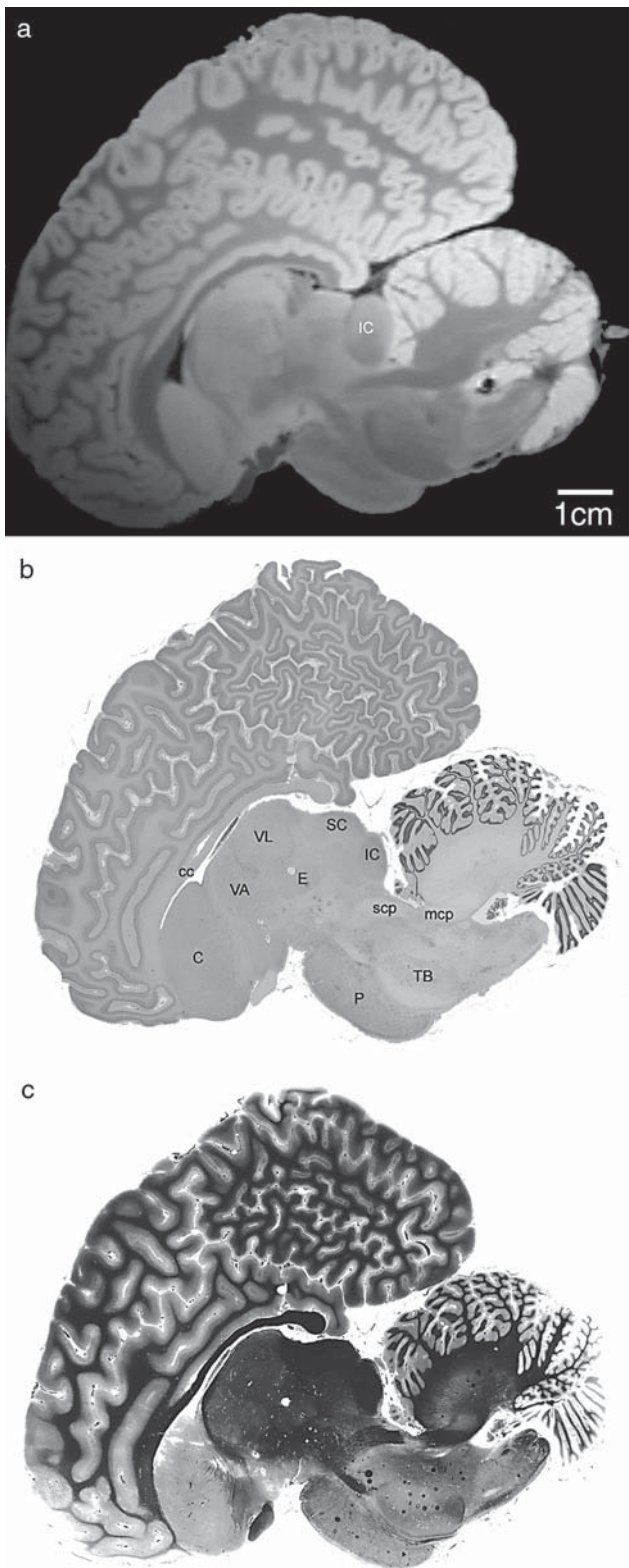**Fig. 8.** *Delphinus delphis*. Parasagittal scan and brain sections through the hemisphere and brainstem with the superior and inferior colliculus (SC, IC). For abbreviations see list.

The formalin-fixed brain used in MR tomography came from a stranded adult female common dolphin that was just over the average length at female sexual maturity of 160 cm [Perrin and Reilly, 1984]. Its brain mass taken fresh (757 g, table 1) is close to the average value in adult animals of this species (835.6 ± 79.9 g) relating to an average body length of 193.1 ± 5.8 cm for both sexes and an average body weight of 67.6 ± 11.7 kg [Ridgway and Brownson, 1984].

PD-weighted magnetic resonance (MR) images of the entire brain were acquired with a highfield MR scanner (3 Tesla; Siemens Magnetom Trio). A gradient echo imaging sequence (FLASH 3D) with the following protocol parameters was used: repetition time 11 ms, echo time 4.9 ms; flip angle 7°, slice thickness 0.5 mm, field of view 120 × 176 mm, matrix 240 × 352. Multiple repetitions of the imaging sequence were performed to improve the signal-to-noise ratio. Total scanning time was 16 h.

The resulting MR dataset was isotropic with a voxel size of 0.125 mm^3 and can be reformatted in any direction without loss of resolution.

Microslide Series

The three *Delphinus* brains (T375, T377 and T379) had been taken from specimens in the Mediterranean Sea in 1966, immersion-fixed in 10% buffered formalin solution, embedded in celloidin and sectioned in the coronal, sagittal, and horizontal planes at 35μm thickness. The sections were stained for cells (perikarya; cresyl violet) and for fibers [Weigert stain; Romeis, 1968]. In the coronal and horizontal planes, each 20th section was Nissl-stained and each 21st section stained for fibers, in the sagittal plane each 30th section for cells and each 31st for fibers.

For comparison, planes of the MR dataset could be adjusted appropriately to correspond to those predetermined in the 3 different series of histological sections.

Nomenclature and Labeling

Structures of the dolphin brain were labeled in cresyl violet sections from coronal, horizontal, and sagittal microslide series following the nomenclature of Ogawa and Arifuku [1948], Jansen and Jansen [1969], McFarland et al. [1969], Dailly [1972], Morgane and Jacobs [1972], Morgane et al. [1980], Pilleri et al. [1980], Schwerdtfeger et al. [1984], Oelschläger and Oelschläger [2002] as well as Terminologia Anatomica [1998] and Schaller [1992]. Structures of gray substance are in capitals, white substance and cortical sulci in lower case, cranial nerves in Arabic numerals and ventricular spaces in lower case and Roman numerals.

Results

General Aspects

The common dolphin brains investigated show all the features generally characteristic for adult dolphins (delphinids). In some size parameters they attain a level equal to or greater than that found in humans; in the following descriptions, such conditions are characterized as a mammalian 'extreme'. The term 'reduced' is reserved for fea-

Table 1. List of the dolphin brains investigated (MRI; serial sections, Nissl and fiber stained)

Delphinus delphis No.	ID number	Body length cm	Body mass kg	Brain mass fresh; g	Age	Sectional planes
1	Dd 9347B	168	49	757	adult	MRI
2	T 375	153	37	788	subadult	coronal
3	T 377	190	61	830	adult	horizontal
4	T 379	168	52	685	subadult	sagittal[a]

[a] Sagittal plane: only sections from the middle of the brain were mounted on slides and stained. Dd 9347B was judged an adult based on total body length because Perrin and Reilly [1984] indicated that females of this species mature at an average of 160 cm body length. The brain weight was taken fresh at necropsy after the animal stranded and died on a beach in Southern California.

tures that are small or minimally sized among the Mammalia. The dolphin brains are rather wide (brain width slightly larger than length) but seem to have flattened during the fixation process. Brain size is very large, the neocortex (including the underlying white matter) is voluminous, with the cortical grey matter thin but extremely expanded and folded into deep and complicated gyri and sulci (fig. 1–8). This is obvious across the whole surface of the telencephalic hemisphere, but particularly distinct are the main sulci (e.g., ectosylvian, suprasylvian, entolateral, and suprasplenial or limbic sulcus; fig. 1, 2: s, ss, se, ssp). The hemisphere does not show a defined occipital lobe [cf. Oelschläger and Oelschläger, 2002]; instead, the parietal lobe passes into the large temporal lobe (fig. 2: PL, TL). As in the bottlenose dolphin, the cortical surface in the dorsomedial part of the parietal lobe [paralimbic lobe; Morgane et al., 1980] shows a characteristic folding pattern which led to the term 'oval lobule' (fig. 7b: OL); this pattern, however, is less obvious in the MR slice (fig. 7a). In the rostral brainstem, the diencephalon is very much expanded in both width and height, the mesencephalon is wide and high and the pons and cerebellum are much pronounced (fig. 2, 3, 6–8). The cerebellum consists of a comparatively narrow vermis (Ve) and heavy hemispheres (He), each of the latter showing a very large paraflocculus (fig. 5c: Pf) and a minute flocculus (not shown). The caudal brainstem (medulla oblongata) is also well-developed, but it narrows quickly and turns dorsally to merge in the cervical spinal cord (fig. 5–8).

Ventricles

The ventricular system of the common dolphin (fig. 1, 2, 5) is organized as in other dolphins [e.g., bottlenose dolphin; McFarland et al., 1969]. In contrast to terrestrial mammals there are some interesting modifications that can be correlated with peculiar morphological and functional specializations of the brain (see Discussion). The lateral ventricles (l, ll) are semicircular, an olfactory recess is lacking, and a posterior horn is absent as is an occipital lobe of the hemisphere. The third ventricle (lll) is largely displaced by the extended fusion of the two thalami (intermediate mass, fig. 1; not labeled). There is no pineal recess and the pineal organ is also lacking. The cerebral aqueduct (fig. 2: aq) is tubular beneath the superior colliculi but nearly collapsed (fig. 3; not labeled) in the area of the very large inferior colliculi (IC) which are located more laterocaudally. The fourth ventricle of the dolphin (fig. 5) does not show any conspicuous specializations.

Telencephalon

Cortex. In the bottlenose dolphin *(Tursiops truncatus),* the motor and sensory areas can be attributed to several gyri of the neocortex and they are arranged in a pattern somewhat different from that in other mammals [cf. Nieuwenhuys, 1998; Supin et al., 2001; Oelschläger and Oelschläger, 2002; areas not shown in figures]. This sulcal pattern is also seen in the *Delphinus* brain (fig. 1, 2). In large-brained dolphins, the projection fields generally comprise most of the vertex of each hemisphere, and the auditory and visual areas, for the most part, are located between the ectosylvian and lateral sulci (fig. 1, 2: sec, se). The somatosensory field is found in the dorsal frontal lobe and the motor field adjacent to it near the frontal pole of the telencephalic hemisphere (not shown). For detailed analysis of the surface configurations of the dolphin brain we refer to Morgane et al. [1980].

Most allocortical areas of the dolphin (paleocortex and archicortex) are much less conspicuous than in other mammals (fig. 2, 7). The paleocortex as a whole seems to be relatively small in the dolphin which is typical for

toothed whales, in general. This is in correspondence with the reduction of the olfactory bulbs during early fetal development and the lack of olfactory peduncles (see Discussion). The area of the olfactory tubercle (fig. 7: OT) or olfactory lobe, which is large, shows a paradoxical situation (see below): in our brain specimens, no cortical plate was found here. The archicortex comprises the hippocampus and borders several cortical areas as transitional zones to the neocortex. As a major center within the limbic system of mammals, the hippocampus of *Delphinus* consists of three main parts: the cornu ammonis or hippocampus proper, the fascia dentata (dentate gyrus), and the subiculum (fig. 2c: CA, DG, Sub), but is as small as in other dolphin species. In correspondence with this, the fornix is rather thin (fig. 2a: asterisk, 7c: f; see below) and the mammillary bodies seem to be small (not shown). In contrast, the amygdaloid complex of the dolphin is very well developed (fig. 1, 2: AC) and the periarchicortical limbic areas [limbic lobe, Morgane et al., 1982], obviously corresponding to the cingular and parahippocampal gyri in other mammals [primates; Stephan, 1975], are also large. The cingular gyrus encompasses the medial surface of the telencephalic hemisphere between the sulcus corporis callosi and the suprasplenial sulcus or limbic cleft (fig. 2: scc, ssp) and extends onto the medial surface of the temporal lobe (entorhinal cortex, fig. 2b and inset: Ent).

Commissures. The corpus callosum (fig. 1, 2, 7, 8: cc), which unites isocortical fields located in the two large hemispheres, is remarkably thin even in the splenium, its posteriormost part. The fornix is flat and thin and attached to the corpus callosum (Fimbria fornicis; fig. 2a: asterisk; 7c: f). In MR scans it is seen as a narrow hyperintense band (Commissura fornicis) below the posterior half of the corpus callosum (see Discussion). The anterior commissure (not labeled in figures) is very thin in the dolphin both in absolute terms and with respect to brain size; this may be correlated with the strong regression of the olfactory system (no olfactory bulb or peduncle in adult animals, see below). The commissural complex [fig. 7c: asterisk; cf. Oelschläger and Kemp 1998] includes the well developed posterior commissure (fig. 1b: pc), which in part is more like a chiasm, as well as the habenular commissure which is situated dorsal to the pc (fig. 7, not labeled). The commissural complex stands subvertical like a plate below the splenium corporis callosi and between the thalami and the superior colliculi and is thus shown in transverse extension in figure 1b (pc) and in cross-section in figure 7c (asterisk).

Basal ganglia. The corpus striatum (fig. 6–8: C, Pu) is very large and bulges ventrally at the brain base like a watchglass (fundus striati). By this the residual cortex of the olfactory tubercle is maximally expanded and thus thin and sometimes incomplete (see Discussion). In our histological series, however, no paleocortical formation was found in this area under the microscope. The claustrum is large and seen as a pointed triangular structure in coronal sections medial to the subvertical insular gyrus; here, its base rests on the lateral part of the large amygdaloid complex and tapers dorsally along the internal capsule (fig. 1, 2: Cl, AC). As the planes of the coronal Nissl sections in figures 1 and 2 stand somewhat obliquely in the brain, more caudal details are shown on the left than on the right hand side. Thus, on the left hand side of figure 1b as on the right side of the corresponding section in figure 2b, the amygdaloid complex is shown in near-maximum cross-section between the internal capsule (ic) and the cortex of the temporal lobe (TL).

Diencephalon

The diencephalon is highly voluminous, with a very large thalamic complex that allows the macroscopic identification of single nuclei in our scans and sections (fig. 7: VA, VL). In figures 1 and 2 the optic nerve merges in the optic chiasm and optic tract (cf. fig. 1, 6–8: 2, ot), passing along medial to the amygdala and the insular region and heading for the lateral geniculate body (fig. 1, 2: LGB). The latter is distinct by its topography and characteristic texture, particularly in MR scans and fiber stained sections. As in other dolphins, the medial geniculate body (fig. 2: MGB) is much larger in *Delphinus* than the LGB, a fact which correlates well with the generally very strong development of the auditory system in these animals (e.g., inferior colliculus, fig. 3, 8: IC).

There were no traces of a pineal organ in our common dolphin brains. Close inspection of the three microslide series revealed that the meninges in the area concerned (behind the splenium corporis callosi) are intact (fig. 7b: arrow).

Brainstem

Below the posterior commissural complex (fig. 1b: pc, 7c: asterisk) and immediately lateral and ventral to the ventricular system (cerebral aqueduct, aq), the characteristic elliptic nucleus stands out as the rostralmost part of the mesencephalon (fig. 1, 7, 8: E). The nucleus is situated at the anterior end of and within the central gray (CG), rostral and dorsal to the oculomotor nuclear complex (not labeled). Ventrally, the surrounding sheath of fibers gives rise to the medial tegmental tract (fig. 1: mt) which runs to the anterior part of the medial accessory inferior

olive (fig. 5–7: IO, MAO). The identity of the elliptic nucleus and its potential functional implications are still under discussion.

In the histological sections (fig. 3b, c, 7c), the superior or rostral colliculus (SC) exhibits a laminar pattern which so far has not been analyzed in the dolphin. In corresponding MR scans (fig. 3a, 7a, 8a), this pattern is seen as a set of faint parallel lines (not labeled). In the mesencephalon as well as the pons area and somewhat less in the rostral medulla oblongata, the auditory system is very well developed (fig. 2–4, 6–8). The ascending auditory pathway is represented caudally by the thick cochlear nerve (8) and large ventral cochlear nucleus (fig. 4, 6: VCN) and the trapezoid body and nucleus (fig. 4, 6, 7: tb, TB); the latter can be seen at the surface of the brainstem between the bulging pons (P) and the inferior olivary complex (IO, MAO; see fig. 5, 7). The superior olive (SO) and the lateral lemniscus (ll) including its nucleus (LL) which merge in the inferior or caudal colliculus (fig. 3: IC) are located more rostrally. The latter is several times larger than the superior colliculus (fig. 2, 3), ovoid in shape, and stands upright in parasagittal sections (fig. 8); in figure 8a the inferior colliculus seems to show its maximal cross-sectional area. The quantitative neuroanatomy of the subcortical auditory system in the common dolphin was analyzed by Zvorykin [1963] (see Discussion).

Isolated areas of the cerebellum are shown in figure 3: medially the unpaired and narrow vermis (Ve) which protrudes between the two inferior colliculi (IC), and laterally the rostralmost extremities of the cerebellar hemispheres (anterior lobes, He). The pons is rather prominent, in correlation to the outstanding expansion of the neocortex and cerebellum (fig. 4–8). In figure 6 (horizontal scan and sections), the continuity and size correlation between the pons and the cerebellar hemispheres via the middle cerebellar peduncles (fig. 8: mcp) is obvious. In corresponding coronal sections (fig. 5), the large and band-like posterior interpositus nucleus (PIN) is seen extending within the cerebellar white matter. In figures 4 and 5 the telencephalic hemispheres are decreasing in size and the cerebellum becomes the dominant structure (compare fig. 6b: Cer). The cerebellar hemispheres are very large and bulge ventrally on both sides of the medulla (paraflocculus; fig. 5c: Pf).

The myelencephalon (medulla oblongata) is very large in the common dolphin compared to terrestrial mammals (see Discussion) because of the well-developed trigeminal and auditory systems. Figure 4 shows the very large ventral cochlear nuclei and thick eighth nerves (VCN, 8). In dolphins, the diameter of the vestibulo-cochlear nerve is maximal among all cranial nerves and the number of cochlear fibers is much larger than in the human (compare the small number of vestibular nerve fibers, see below). In contrast to its ventral counterpart, the dorsal cochlear nucleus is minute or lacking (not shown). The facial nerve, which is well-developed in dolphins (fig. 4a: 7), seems to have a moderate diameter in comparison with the dominant vestibulocochlear nerve (compare fig. 4, 6: 8). The inferior olives (fig. 5, 6, 7: IO, MAO) are well-developed, particularly the medial accessory subnuclei (MAO), and both are in contact with each other in the midline.

MR Imaging and Conventional Histology of the Dolphin Brain

The most obvious characteristic of dolphin brains, their considerable size, is particularly due to the large volume of the telencephalic hemisphere and the neocortex, respectively. The cortical layer (gray matter) is relatively thin but extremely extended and convoluted. The size and topography of the brain structures are nearly identical when comparing the same image size in MR scans and in corresponding celloidin sections even though coming from different animals. Obviously, similar shrinkage effects occurred in the gray and white matters during histological processing. Liquor-filled spaces of the ventricular system, however, are for the most part somewhat smaller in the histological sections, but this has only a moderate effect on volume shrinkage as a whole. Therefore the architecture of the brain can be analyzed easily by comparing the data from MR scans and from histological sections at the same size. On the other hand, in MR slices of the fixed dolphin brain, the cortical sulci are extremely narrow and their width is only slightly increased in the sections due to dehydration during the histological process. In MR slices, therefore, the deepest parts of the narrow sulci do not show because of a lack of resolution (compare fig. 1a and b).

MR images (fig. 1a–8a) acquired with the specified MR sequence render gray matter (cortex, nuclei) as hyperintense (brighter) areas and white matter (fiber material) as hypointense (darker) areas [cf. Nagara et al., 1987; Vullo et al., 1996; Schumann et al., 2001; Beaulieu, 2004]. This situation is found throughout the brain so that, to some extent, the scans show a situation which is complementary to the sections stained for cells (fig. 1b–8b) and thus more or less analogous to the fiber stain (fig. 1c–8c). However, there are differences between the MR scans and the sections stained for fibers with respect to the visualization of some brain structures (fornix, inferior collicu-

lus, facial nerve, see below). As a standard, the original topographical relationships of the MR scans can help determine artifacts in the microslide series due to the histological procedure leading, e.g., to disruptions and other alterations in the tissue. On the other hand, the identity of structures found in MR scans can be confirmed by their microscopic evaluation at some magnification in the sections with respect to histology and cytology (not shown here). Thus the combination of the three methods (MRI, cell, and fiber stain) and the comparison of the scans and sections offer the reliable identification of any brain part and thus an understanding of the three-dimensional configuration of the brain structures in question.

Discussion

Ventricles and Fiber Tracts
The lateral ventricles are semicircular in shape as in terrestrial (ungulate and carnivore) mammals [Nickel et al., 1984; Dyce et al., 1991; Schaller, 1992]; this is due to the extreme 'rotation' of the telencephalic hemispheres during ontogenesis [Nieuwenhuys, 1998] and the development of a very large temporal lobe. At the same time, the lateral ventricles are much foreshortened in dolphins which might be correlated with the so-called 'telescoping' of the brain and the neurocranium (braincase), respectively [Miller, 1923; McFarland et al., 1969; Morgane and Jacobs, 1972]. On the other hand, the olfactory recess is lacking in the adult correlated with the loss of the anterior olfactory system (olfactory bulb and peduncle) as are also the occipital horn of the lateral ventricle and the occipital lobe of the hemisphere, respectively [Jansen and Jansen, 1969; Oelschläger and Oelschläger, 2002].

The actual diameters of fiber tracts and cranial nerves in *Delphinus* can be taken from MR scans of the intact brain specimen. Thus, for example, the corpus callosum is indeed extremely thin in dolphins with respect to brain size indicating that in these animals both cerebral hemispheres may have a larger degree of independence from each other than in other mammals [Ridgway, 1986; Tarpley and Ridgway, 1994]. The anterior (rostral) commissure is so thin and inconspicuous that it cannot be identified macroscopically either in the MR scans or in the histological sections. In the bottlenose dolphin, its cross-sectional area is minute in comparison with the optic nerve [Morgane et al., 1980]. This might be due to the weak development of paleocortical structures in the dolphin [Addison, 1915; Nieuwenhuys, 1998]. In terrestrial mammals (domestic animals), this commissure inter-

connects the olfactory bulbs and areas in the piriform lobes of both telencephalic hemispheres [piriform and entorhinal cortex, amygdaloid complex; Stephan, 1975; Nickel et al., 1984; Schaller, 1992; Nieuwenhuys, 1998]. At the macroscopic level of our preparations, the fornix (fimbria hippocampi) is most obvious in MR scans as a hyperintense narrow stripe below and attached to the corpus callosum (fig. 2a, 7c: f). Here the two fornices exchange fibers in the so-called commissura fornicis or commissura hippocampi [Schaller, 1992; Nieuwenhuys, 1998; Terminologia Anatomica, 1998]. The representation of the commissural complex in the epithalamus [consisting of the posterior (syn. caudal, epithalamic) and the habenular commissures; Oelschläger and Kemp, 1998] is ambiguous in our figures of the dolphin brain (fig. 1a–c): it is obvious in the MR scan and Nissl stain but shows maximal contrast in the fiber stain preparation. In figure 7, the slice and sections (a–c), respectively, do not exactly fit one another due to technical reasons. Whereas the section with the fiber stain is mediosagittal and shows the fibers of the commissural complex in maximal condensation, the MR scan and the Nissl stain are parasagittal.

In some areas, the fiber content of nuclear structures may help to delimit the latter from neighboring structures. Thus, for example, the lateral geniculate body is clearly distinct from the thalamus as well as from the medial geniculate body and pulvinar in both the MR scans and fiber stain sections because of its characteristic pattern of diffuse hypointense fiber bundles (fig. 1a, c) as was shown histologically for the bottlenose dolphin [*Tursiops truncatus;* Morgane and Jacobs, 1972]. In the harbor porpoise, this pattern is much less obvious [Jelgersma, 1934; Revishchin and Garey, 1993]. Also, sections stained for fibers may show some details more clearly than MR slices as, for example, in the case of the elliptic nucleus (fig. 1, 7: E) and the inferior olivary complex (fig. 6: MAO) which are connected by the strong medial tegmental tract [fig. 1: mt, cf. Oelschläger, in press]. On the other hand, the inferior colliculus in figure 8 is more obvious in the MR scan. Examples of aberrant fiber tract representation are the optic nerve (fig. 1a: 2) which is extremely hypointense and the facial nerve which, in MR slices, can easily be distinguished from the vestibulocochlear nerve (fig. 4a: 7, 8).

Cortex and Nuclei
Regarding the size of the common dolphin brain, the highly convoluted neocortex (gray and white matter) is by far its largest component. Interestingly, whereas in larger

dolphins of about the same body mass, the surface of the neocortex exceeds that of the human, its volume percentage (gray and white matter) in the total brain seems to be somewhat smaller [Elias and Schwartz, 1969; Ridgway and Brownson, 1984; Ridgway, 1986, 1990; Manger, 2006]. The smallest and most generalized [plesiomorphic; Hennig, 1966, Wägele, 2004] dolphins (Ganges river dolphin, *Platanista gangetica;* La Plata dolphin, *Pontoporia blainvillei*) equal non-human simian monkeys in the average volume percentage of the necortex [Schwerdtfeger et al., 1984]. Concerning the size index of the neocortex with reference to body mass and the situation in generalized mammals, these two plesiomorphic dolphins rank between the prosimians and the non-human simian monkeys [Schwerdtfeger et al., 1984]. Only scarce data on the neocorticalization in larger marine dolphins are available so far. Here, the neocortex (gray matter) was reported to attain about 42% of the total brain volume (bottlenose dolphin), a percentage somewhat lower than in the human [47.5%; Haug, 1969, 1970].

Although the gyral pattern of the cetacean neocortex bears some general resemblance to that in carnivores and ungulates [cf. Oelschläger and Oelschläger, 2002], the localization of the neocortical sensory fields, however, shows marked differences [Morgane et al., 1986; Nieuwenhuys, 1998; Supin et al., 2001; not shown in our figures]. Within the neocortex of porpoises and dolphins (harbor porpoise, *Phocoena phocoena; Tursiops truncatus*) investigated so far with the methods of electrophysiology, the auditory fields are particularly large [Sokolov et al., 1972; Ladygina and Supin, 1977, 1978; Morgane et al., 1986; Popov et al., 1986; Supin et al., 2001].

Concerning the histological appearance of the neocortex, these projection fields seem to differ only slightly from each other as it has been shown in the bat neocortex [Morgane et al., 1986; Glezer et al., 1988]. Therefore, their delineation requires highly sophisticated quantitative methods: Recently, the La Plata dolphin *(Pontoporia blainvillei)* has been investigated stereologically concentrating on the primary and secondary auditory fields [Fung et al., 2005].

In the bottlenose dolphin, these auditory cortical areas are obviously larger than the other sensory cortical fields together [cf. Oelschläger and Oelschläger, 2002]. This fact correlates well with the sensory dominance of hearing and the massive development of the ascending auditory pathway in toothed whales [common dolphin: Zvorykin, 1969; Ridgway and Au, 1999; La Plata dolphin: Schulmeyer, 1992, Schulmeyer et al., 2000; Breindl and Oelschläger, unpubl.].

The olfactory bulb and tract are lacking in adult dolphins, and the bulb is only present in the late embryonic and early fetal stages of toothed whales [Oelschläger and Buhl, 1985a, b; Buhl and Oelschläger, 1988; Oelschläger and Kemp, 1998]. Obviously, the evolutionary transformation of the upper respiratory tract into a high-energy and high-frequency biosonar transmitter implicated the loss of the nasal part of the rhinencephalon in odontocetes [Ridgway and Au, 1999; Oelschläger and Oelschläger, 2002; Oelschläger, in press].

In the bottlenose dolphin, the cortex of the olfactory tubercle cannot be discriminated easily from the adjacent diagonal band and piriform cortex ['olfactory lobe'; cf. Jacobs et al., 1971; Morgane and Jacobs, 1972]. Moreover, there seems to exist a paradoxical correlation between the rather large area of the olfactory tubercle [Filimonoff, 1965: common dolphin] and the quality of its paleocortical layer. Thus the latter gives the impression that it is maximally expanded due to the considerable growth of the underlying striatum (fundus striati). Concomitantly, the paleocortex of the tubercle might have been reduced in these anosmatic animals leading to a partial exposition of the striatum at the basal surface of the brain [Addison, 1915: common dolphin; Breathnach, 1953: harbor porpoise]. This situation, to some degree, seems to parallel that in the microsmatic human [Stephan, 1975] concerning the reduction of the olfactory system and the large size of the striatum. In our microslide series of common dolphin brains no cortical layer could be found covering the fundus striati.

There were no traces of a pineal organ in our common dolphin brains as was reported for an early fetus of the narwhal [*Monodon monoceros;* Holzmann, 1991]. In some toothed whales [e.g., bottlenose dolphin, McFarland et al., 1969; Morgane and Jacobs, 1972; sperm whale, *Physeter macrocephalus*, cf. Oelschläger and Kemp, 1998] a pineal organ was found to be present up to the adult stage.

The hippocampus in *Delphinus* (fig. 2) seems to be as small and as little convoluted as in the bottlenose dolphin [Addison, 1915; Filimonoff, 1965; Morgane et al., 1982; Morgane and Jacobs, 1986] and the fascia dentata (dentate gyrus) is minute. The small diameter of the columna fornicis is coincident with the fact that the hippocampus is considerably reduced in cetaceans in comparison with terrestrial mammals and this is also true for the mammillary body, particularly in toothed whales. In contrast, other components of the limbic system [amygdaloid complex, limbic lobe (gyrus cinguli, gyrus parahippocampalis)] are large or at least well developed [Morgane et al.,

1980; Oelschläger and Oelschläger, 2002]. This means that non-olfactory afferent systems, and particularly the auditory (sonar) system, are responsible for the large size of the amygdaloid complex and might play a major role in the orientation and navigation of these animals [Ridgway, 1986, 1990; Ridgway and Au, 1999; Oelschläger, in press].

Among mammals the elliptic nucleus has been found so far only in cetaceans [and perhaps in the elephant; Precechtel, 1925; Kruger 1966]. It was reported to represent the hypertrophied nucleus of Darkschewitsch [perhaps including the nucleus Edinger-Westphal; Hatschek and Schlesinger, 1902; Ogawa, 1935b; De Graaf, 1967; Dailly, 1972; Nieto, 1989; Holzmann, 1991]. The elliptic nucleus is rather characteristic in MR scans and fiber stained sections because of its inclusion in a sheath out of white matter. From here, the large elliptic nucleus sends a strong projection via the medial tegmental tract (fig. 1: mt) to the well-developed rostral medial accessory inferior olive (fig. 5–7). Both nuclei obviously show a positive size correlation with the paraflocculus in the cerebellar cortex of the hemisphere and the posterior interpositus nucleus within the white matter [Oelschläger, in press].

The size of the common dolphin cerebellum is considerable, in accordance with massive descending cortical fiber systems and the well-developed pontine nuclei which serve as their main relay to the cerebellar cortex, particularly to the area of the very large paraflocculus. Thus, in dolphins a correlation seems to exist between the impressive expansion of the neocortex, the size of the ventral pons, and the dimensions of the cerebellum, a phenomenon also known from the ascending primate series [Schwerdtfeger et al., 1984; Matano et al., 1985; Stephan et al., 1988].

Adult common dolphins of about 75 kg have slightly smaller cerebella than humans of the same body mass [Blinkov and Glezer, 1968; Pilleri and Gihr, 1970; Rilling and Insel, 1998; Marino et al., 2000]. However, because total brain mass is lower in the dolphin, the percentage of the cerebellum in the total brain is higher than in the human. In comparison to primates, the size index [Stephan, 1967; Stephan et al., 1981] of the cerebellum in the La Plata dolphin, presumably the most generalized (plesiomorphic) marine odontocete, is higher than the average indices of prosimians and simian monkeys [Schwerdtfeger et al., 1984].

Whereas the dolphin vermis is relatively narrow in comparison to that of land mammals, the cerebellar hemispheres are very large, particularly the posterior

lobes [Jansen, 1950; Breathnach, 1960; cf. Oelschläger and Oelschläger, 2002]. The paraflocculus is by far the largest component of the cerebellar hemisphere, a fact that seems to correlate with the considerable size of the inferior olive (medial accessory nucleus) and the enormous size of the posterior interpositus nucleus [Ogawa, 1935a]. In contrast, the flocculonodular lobe (vestibulocerebellum) is extremely small [Morgane and Jacobs, 1972] which reflects the rudimentary condition of the vestibular system (see below).

As for dolphins, the intimate coupling to the extremely large auditory system in acousticomotor processing seems to explain, at least to some degree, the impressive size of their cerebellum [Oelschläger, in press]. Recently, it was suggested [Ridgway, 2000] that the cerebellum of odontocetes might be involved in rapid processing of acoustic stimuli with respect to the localization of objects in water, a medium in which sound is transmitted almost five times faster than in air.

The ascending auditory pathway of dolphins predominantly consists of very large to extremely large nuclei and strong fiber tracts [La Plata dolphin, harbor porpoise: Schulmeyer, 1992; Schulmeyer et al., 2000; common dolphin: Zvorykin, 1963, 1969; striped dolphin (*Stenella coeruleoalba*): Hosokawa et al., 1969; Breindl and Oelschläger, unpubl.; Oelschläger, in press]. In contrast, the vestibular system (semicircular canals, vestibular nerve, vestibular nuclei) is much reduced in toothed whales [Gray, 1907; Yamada, 1953; Yamada and Yoshizaki, 1959; Jansen and Jansen, 1969; Pilleri and Gihr, 1970; Gao and Zhou, 1995; Lindenlaub and Oelschläger, 2000; Spoor et al., 2002; Kossatz, 2006; Kern et al., unpubl.]. Some auditory nuclei, however, are small and even strongly reduced [Schulmeyer, 1992; Schulmeyer et al., 2000]. The latter situation, for example, is found in the dorsal cochlear nucleus, which is minute and sometimes not found in dolphins [Osen and Jansen, 1965; De Graaf, 1967]. In terrestrial mammals (e.g., cat) this nucleus is involved in integrating information about sound localization (somatosensory input on pinna position) and in the elimination of auditory 'artifacts' caused by changes in the position of the head and pinnae during their orientation towards a sound source [Schulmeyer et al., 2000; Young and Davis 2002]. Because dolphins have no outer pinnae and a much restricted head mobility, this nucleus is rudimentary [Schulmeyer et al., 2000]. An analogous but less extreme situation is found in seals which have much reduced outer ears and dorsal cochlear nuclei [Hall et al., 1974].

The superior olive of dolphins (fig. 3) is very large. In the common dolphin (brain mass about 800 g) it is as voluminous as the ventral cochlear nucleus, 150 times larger than in the human and contains 15 times more neurons [Zvorykin, 1963]. In the plesiomorphic La Plata dolphin, with a body mass of about 35 kg and a brain mass of 220 g and thus low encephalization [Schwerdtfeger et al., 1984], the superior olive is about 50 times larger than in the human [Schulmeyer, 1992]. Apart from a volume increase during evolution, whales and dolphins seem to have modified the typical structure of the mammalian superior olive, which consists of a medial and a lateral subnucleus. Cytological analysis in the La Plata dolphin and harbor porpoise using silver stain preparations and including synapse morphology indicate that in these two species only one nuclear unit exists which should be homologous to the lateral superior olive of the terrestrial mammals. In large toothed whales [North Atlantic bottlenose whale, *Hyperoodon ampullatus*, killer whale, *Orcinus orca;* De Graaf, 1967] as well as in baleen whales (fin whale, *Balaenoptera physalus*, minke whale, *Balaenoptera acutorostrata*) there are two distinct superior olivary nuclei and the medial nucleus is larger. Moreover, the superior olivary complex as a whole is larger in toothed whales than in baleen whales [De Graaf, 1967]. How these differences in the structure of the superior olive are correlated to hearing function in the various whales and dolphins awaits further investigation. The same is true concerning the morphology and very large size of other components of the ascending auditory pathway (e.g., lateral lemniscus, inferior colliculus).

Conclusions

Comparison with cell- and fiber-stained serial sections reveals that modern MR technical equipment and adequate settings provide excellent macroscopic scans from dolphin brain specimens. Apart from the fact that with this non-invasive method repeated documentation can be performed and that the scans can be manipulated in order to provide optimal contrast for the identification and delimitation (segmentation) of individual target structures, further analysis of the data set is possible by the determination of any sectional plane and slice orientation, respectively. All these advantages make MR documentation a powerful tool for quick analysis of whole brains and their macroscopic structures.

In our study, we give an overview of the three-dimensional topography of key structures within the common

dolphin brain and their main characteristics. Such a synthetic approach has not been made up to now for cetaceans. The methodology presented here helps establish a realistic impression of the shape, dimensions, and composition of these large brains and to identify whatever structure is of interest for the understanding of cetacean neurobiology and evolution. Concerning these criteria, brain morphology in the common dolphin corresponds nicely to the situation in other small delphinids and particularly that of marine species such as the bottlenose dolphin *(Tursiops truncatus)*. Potential qualitative and quantitative differences between the common dolphin and other delphinid brains regarding single components (e.g., structure and identity of the olfactory tubercle, the dorsal cochlear nucleus) and their neurobiological significance will have to be clarified using additional histological material.

It has been only recently that MR images could be obtained from living dolphins [Ridgway et al., 2006]. As equipment improves it will become easier to obtain superior images of the dolphin brain in situ and avoid the problems caused by the distortion of postmortem specimens due to damage, poor fixation, deterioration, and shrinkage. Because of its large size which is comparable to that of humans, the common dolphin *(Delphinus)* is an obvious choice for in situ scanning, and the basic information in the current study should be useful for future comparison.

The common dolphin brain shows the following major macroscopic characteristics known from other smaller toothed whales: 1. Brain slightly wider than long; 2. Very high volume of the neocortex and extremely extended but thin cortical gray matter; 3. Thin corpus callosum; 4. Peculiar pattern of surface configurations, e.g., folding of the neocortex; 5. No olfactory bulb and peduncle present in postnatal animals; 6. Extremely small hippocampus and archicortex, in general; 7. Very large basal ganglia, including the amygdaloid complex; 8. Large to extremely large size of many components of the auditory system; 9. Extremely strong development of the cerebellum.

The extreme reduction of the hippocampus in the dolphin is enigmatic. Here, the learning and memory processes seem to differ considerably from those in terrestrial mammals. The concomitant hypertrophy of the auditory system and cerebellum in toothed whales indicates that, apart from communication, these animals depend heavily on sound for three-dimensional navigation.

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