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Anatomy and Three-Dimensional Reconstructions of the Brain of the White Whale (*Delphinapterus leucas*) From Magnetic Resonance Images

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KEYWORDS

brain, neuroanatomy, cetacean, odontocete, white whale, Beluga, MRI

ABSTRACT

Magnetic resonance imaging offers a means of observing the internal structure of the brain where traditional procedures of embedding, sectioning, staining, mounting, and microscopic examination of thousands of sections are not practical. Furthermore, internal structures can be analyzed in their precise quantitative spatial interrelationships, which is difficult to accomplish after the spatial distortions often accompanying histological processing. For these reasons, magnetic resonance imaging makes specimens that were traditionally difficult to analyze, more accessible. In the present study, images of the brain of a white whale (Beluga) Delphinapterus leucas were scanned in the coronal plane at 119 antero-posterior levels. Fromthese scans, a computer-generated three-dimensional model was constructed using the programs VoxelViewand VoxelMath (Vital Images, Inc.). This model, wherein details of internal and external morphology are represented in three-dimensional space, was then resectioned in orthogonal planes to produce corresponding series of "virtual" sections in the horizontal and sagittal planes. Sections in all three planes display the sizes and positions of such structures as the corpus callosum, internal capsule, cerebral peduncles, cerebral ventricles, certain thalamic nuclear groups, caudate nucleus, ventral striatum, pontine nuclei, cerebellar cortex and white matter, and all cerebral cortical sulci and gyri.

Odontocetes (toothed whales, dolphins, and porpoises) have undergone a number of evolutionary modifications from their terrestrial ancestral state. Among these changes was a major increase in relative brain size. Several modern odontocete species possess encephalization levels second only to modern humans when brain-body allometry is taken into account (Ridgway and Brownson, 1984; Marino, 1998). An arguably equally dramatic transformation of odontocetes occurred in the anatomical structure and organization of their brains. Compared with many other mammalian brains, odontocete brain morphology is unusual in many respects. Researchers have stated that "…the lobular formations in the dolphin brain are organized in a pattern fundamentally different from that seen in the brains of primates or carnivores" (Morgane et al., 1980). Because of the fifty-five to sixty million year divergence between cetaceans and other mammals, odontocete brains represent a blend of early mammalian features along with unique derived characteristics (Ridgway, 1986, 1990; Glezer et al., 1988; Manger et al., 1998). The differences between odontocete and other mammalian brains of similar size are present at the level of cortical cytoarchitecture and immunohistochemistry (Garey et al., 1985; Garey and Leuba, 1986; Glezer and Morgane, 1990; Hof et al., 1992, 1995; Glezer et al., 1990, 1992a,b, 1993, 1998), cortical surface morphology (Jacobs et al., 1979; Morgane et al., 1980; Haug, 1987), noncortical structures and features (Tarpley and Ridgway, 1994; Glezer et al., 1995a,b), and ontogenesis (Oelschlager and Buhl, 1985; Buhl and Oelschlager, 1988; Oelschlager and Kemp, 1998).

Fig. 1. Ventral surface of a three-dimensional digital reconstruction of the whole brain and labeled schematic illustration of the same image.

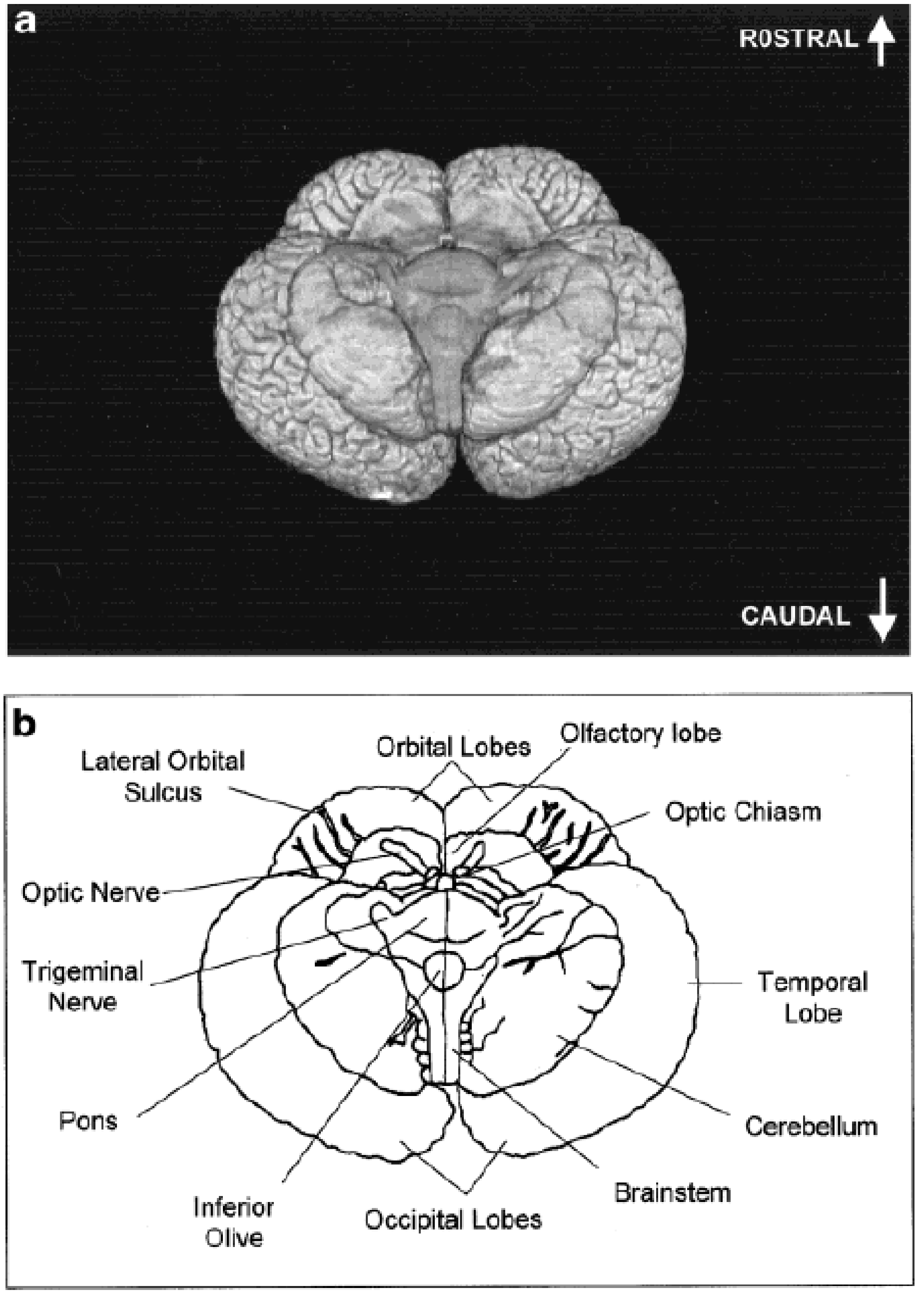


Fig. 2. Three-dimensional digital reconstructions of the whole brain and resectioning to produce "virtual" horizontal sections.

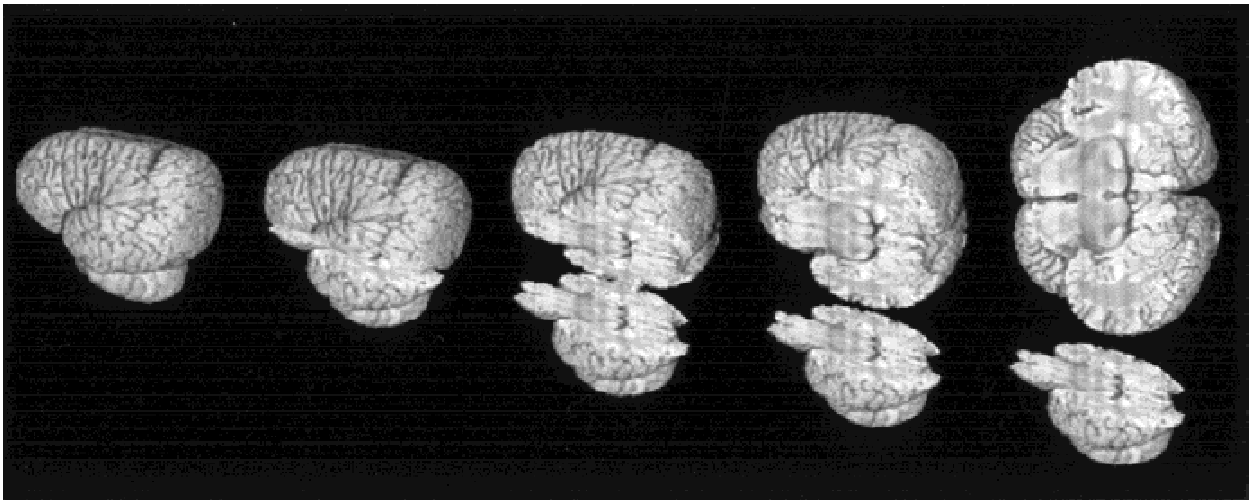
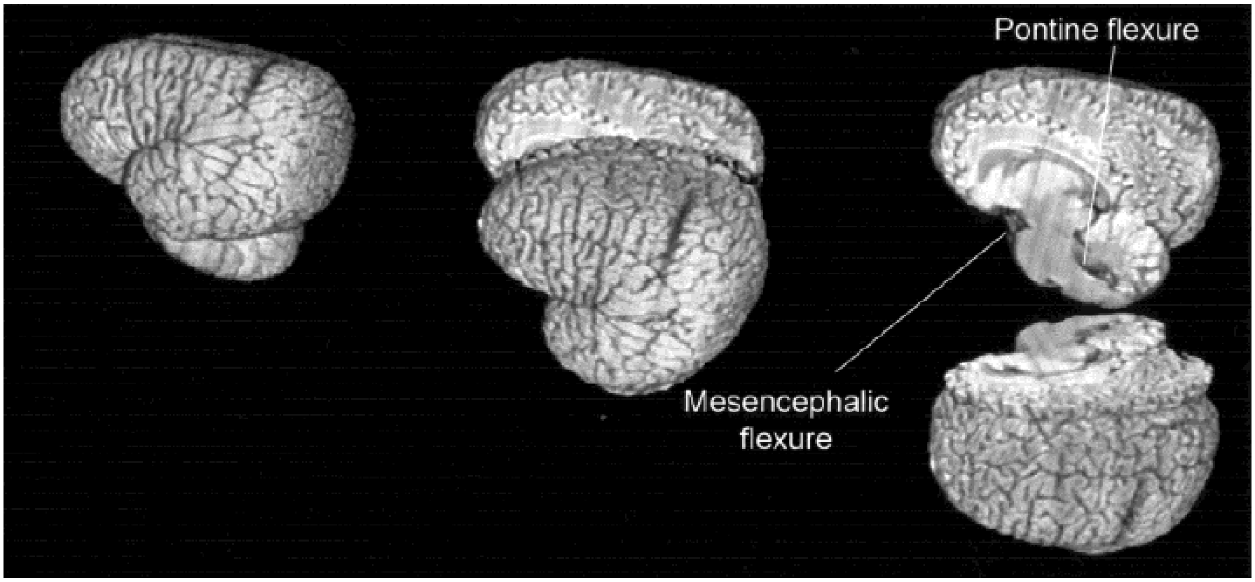


Fig. 3. Three-dimensional digital reconstructions of the whole brain and resectioning to produce "virtual" sagittal sections.



Although there are a number of published descriptions of cetacean neuroanatomy (see Morgane et al., 1986; Ridgway, 1990; for reviews of this literature) there are only a handful of studies in which morphometric analyses were conducted in a systematic way permitting quantitative comparative analysis with other mammals (Jacobs et al., 1984; Johnson et al., 1984; Schwerdtfeger et al., 1984; Garey and Leuba, 1986; Johnson et al., 1994; Tarpley and Ridgway, 1994; Manger et al., 1998; Marino, 1998). Furthermore, with the exception of Morgane et al. (1980), Ridgway and Brownson (1984), Haug (1987), and Tarpley and Ridgway (1994) there are no systematic anatomical descriptions of whole cetacean brains and substructures at the qualitative level. There currently exists no comprehensive cetacean neuroanatomical atlas either in paper or electronic format on which to base studies of cetacean brain organization and function. This situation is mainly due to the time and practicality associated with the preparation of such large brain specimens. Magnetic resonance imaging (MRI) offers a means of observing the internal structure of the brain where traditional procedures of embedding, sectioning, staining, mounting, and microscopic examination of thousands of sections are not practical. Furthermore internal structures can be analyzed in their precise spatial interrelationships, which is difficult to accomplish after the spatial distortions often accompanying histological processing. This study presents an anatomically-labeled three-dimensional atlas, created from MRI images, of the brain of one of the most behaviorally studied odontocetes, the white whale (*Delphinapterus leucas*).

MATERIALS AND METHODS

Specimen

The specimen is the postmortem brain, fixed in 10% buffered formalin, of an adult female white whale (*Delphinapterus leucas*) who died of natural causes. The whale had been involved in several behavioral studies including studies of its hearing (Awbrey et al., 1988). At death, the brain was extracted from the skull, weighed, and placed in neutral buffered formalin for 4 years before scanning. Fresh brain weight was 1,871 g. Fixed brain weight was 1,755 g at the time of scanning.

Magnetic Resonance Imaging

The brain was removed from the fluid and placed in a head coil ventral side down. Images of the entire brain were acquired in the coronal plane at 119 antero-posterior levels with a 1.5 T Siemens scanner (slice thickness = 1.3 mm, slice interval = 1.3 mm, isotropic 1 mm voxels, MPRAGE sequence, field of view = 240 mm, matrix = 256 x 256). The scanning was done by Richard Buxton, PhD at the University of California, San Diego.

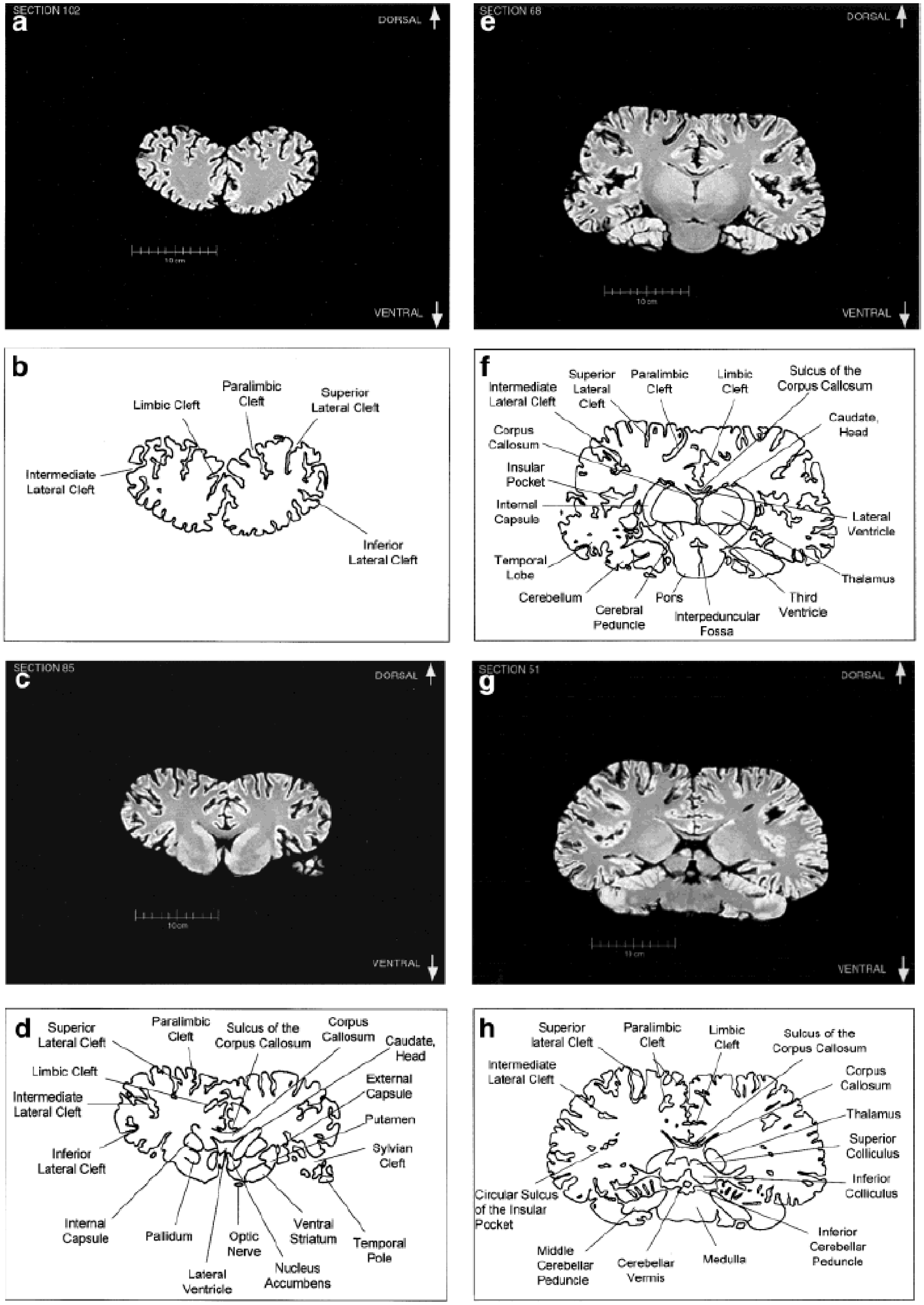
Three-Dimensional Reconstruction and Reformatting

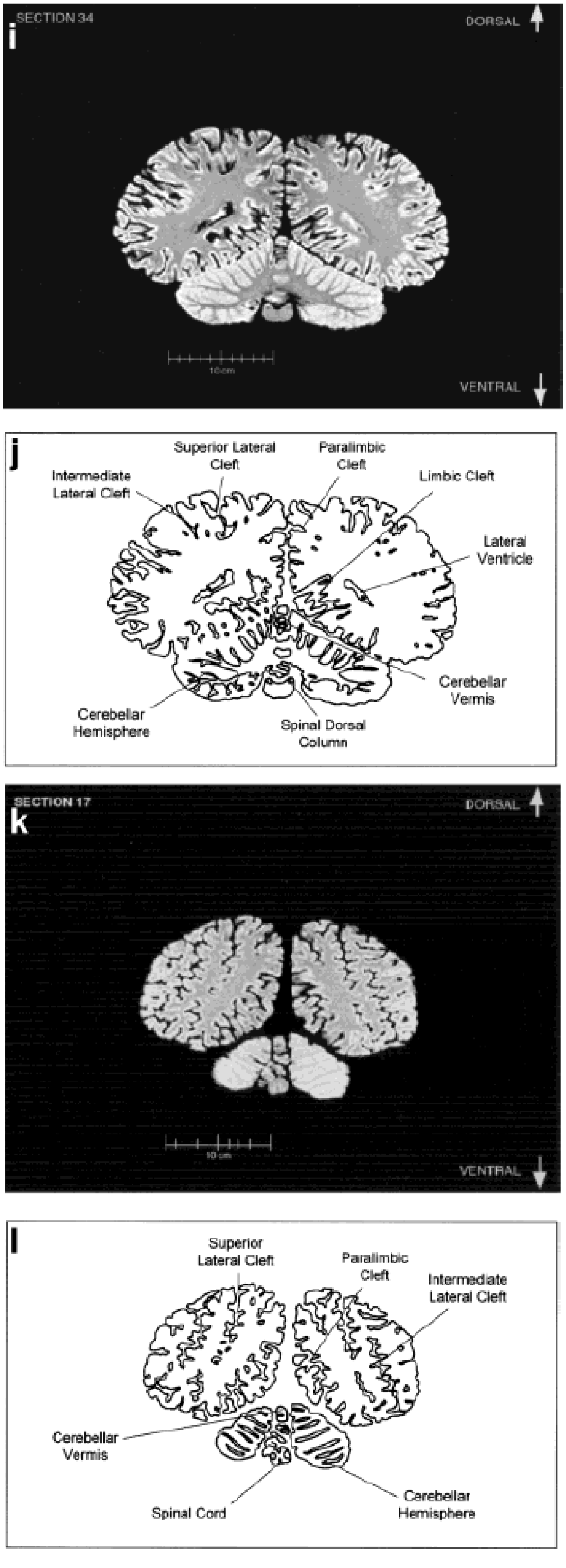
Computer-generated three-dimensional reconstruction images were created by Timothy L. Murphy, using the software programs VoxelView and VoxelMath programs (Vital Images, Inc.) at the Laser Scanning Microscopy Laboratory at Michigan State University, Joanne Whallon, Director. The 3D rendered model, wherein details of internal and external morphology are represented in three-dimensional space, was then digitally resectioned in orthogonal planes to produce corresponding 0.9375 mmthick “virtual” sections in the horizontal (163 “virtual” sections) and sagittal (236 “virtual” sections) planes.

Anatomical Labeling and Nomenclature

All identifiable anatomical structures of the white whale brain were labeled in the originally-acquired coronal plane images as well as in the images from the “virtual” sectioned brain in the sagittal and horizontal planes. The nomenclature used is from Morgane et al. (1980). As a guide to the identification of structures, the MRI scans and the sections from the three-dimensional reconstruction of the whale brain were compared with the few published illustrations (or images of real stained) sections through the white whale brain and photographs of the whole brain (Yablokov et al., 1964; Morgane et al., 1980). They were also compared with similar MRI scans and “virtual” sections and three-dimensional reconstructions from the scans of brains of bottlenose dolphins (*Tursiops truncatus*) (Morgane et al., 1980). All were compared with complete alternate series of sections from brains of bottlenose dolphins, stained, respectively, for cell bodies (Nissl method), and for myelinated fibers in the same three orthogonal planes (coronal, sagittal, and horizontal). These stained section series are from the Yakovlev-Haleem collection at the National Museum of Health and Medicine and the Welker collection at the University of Wisconsin-Madison.

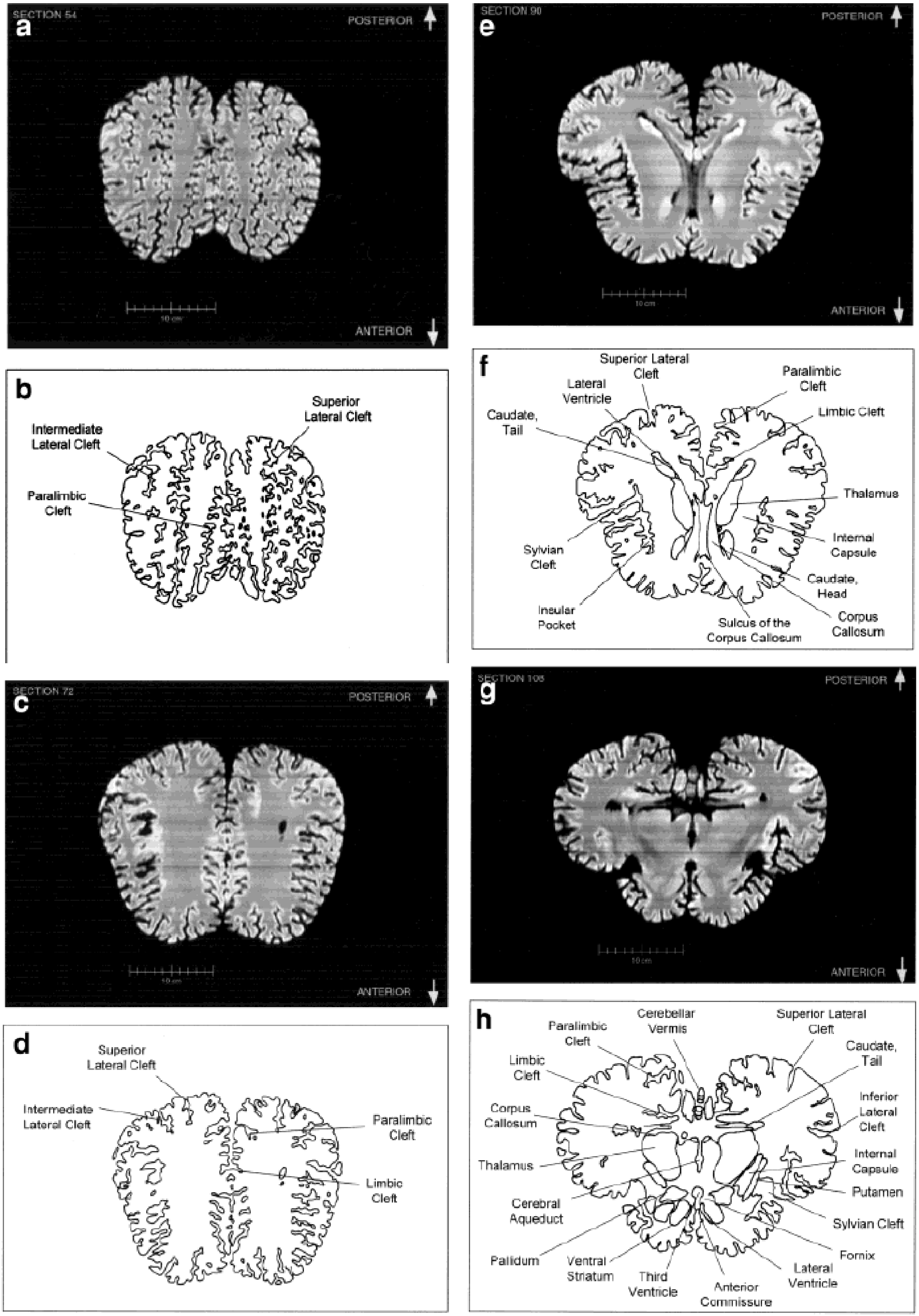
Fig. 4. Rostral-to-caudal sequence of originally-acquired 1.3 mm-thick coronal brain sections in 22 mm intervals and labeled schematic illustrations of each section.

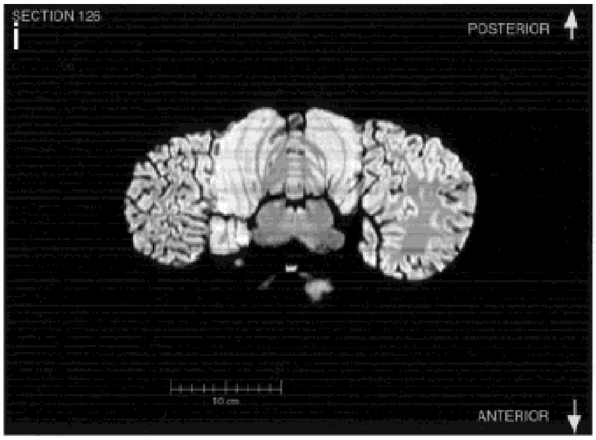


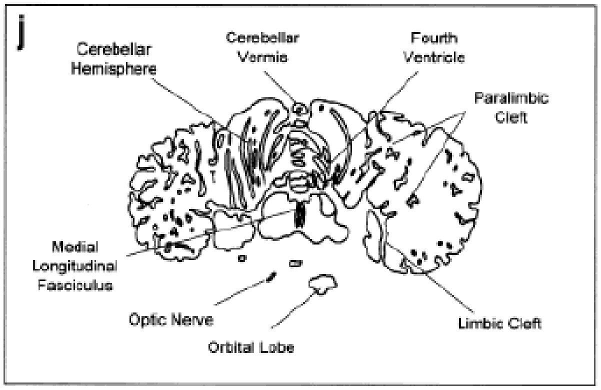


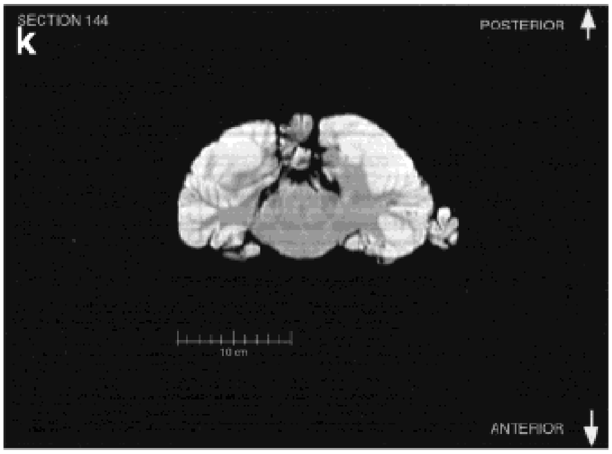
SECTION 34
i
DORSAL
10cm
VENTRAL
j
Superior Lateral Cleft
Paralimbic Cleft
Intermediate Lateral Cleft
Limbic Cleft
Lateral Ventricle
Cerebellar Vermis
Cerebellar Hemisphere
Spinal Dorsal Column
SECTION 17
k
DORSAL
10 cm
VENTRAL
l
Superior Lateral Cleft
Paralimbic Cleft
Intermediate Lateral Cleft
Cerebellar Vermis
Spinal Cord
Cerebellar Hemisphere

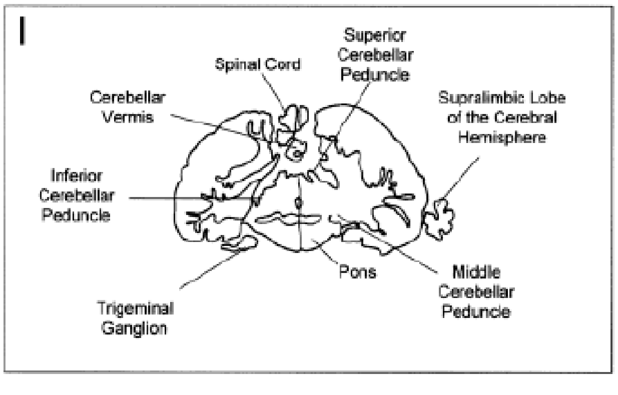
Fig. 5. Dorsal-to-ventral sequence of reconstructed 0.9375-mm thick horizontal brain sections and labeled schematic illustrations of each section.




SECTION 126
i
POSTERIOR
10 cm
ANTERIOR


j
Cerebellar Hemisphere
Cerebellar Vermis
Fourth Ventricle
Paralimbic Cleft
Medial Longitudinal Fasciculus
Optic Nerve
Orbital Lobe
Limbic Cleft


SECTION 144
k
POSTERIOR
10 cm
ANTERIOR


l
Spinal Cord
Superior Cerebellar Peduncle
Cerebellar Vermis
Supralimbic Lobe of the Cerebral Hemisphere
Inferior Cerebellar Peduncle
Pons
Middle Cerebellar Peduncle
Trigeminal Ganglion

RESULTS

Three-Dimensional Reconstruction

Three-dimensional reconstructions of the white whale's whole brain were produced from the original scans in the coronal plane. Figure 1 displays an image (or view) of the posterior-ventral surface of a computer-generated three-dimensional reconstruction of the whole brain and a labeled illustration of the image. Figures 2 and 3 also display three-dimensional reconstructions of the whole brain and the brain digitally recut in the horizontal and sagittal planes, respectively. These three-dimensional reconstructions clearly display many noted characteristics of the cetacean brain that diverge from most other terrestrial mammalian brains (Morgane et al., 1980). The foreshortened orbital lobes are evident in Figure 3 as is the pronounced bitemporal width of the brain in Figures 1 and the last "virtual" cut in Figure 2. The labeled "virtual" cut in Figure 3 shows the mesencephalic and pontine flexures reminiscent of brainstem flexure patterns in the embryonic state of most terrestrial mammals. These flexures remain present in adult cetacean brains.

Anatomically-Labeled Two-Dimensional MRI Sections

Figure 4a–l displays a rostral-to-caudal sequence of originally-acquired 1.3 mm-thick coronal MRI brain sections at 22 mm intervals along with a labeled schematic illustration of each section. Figure 5 displays a dorsal-toventral sequence of reconstructed "virtual" horizontal sections (0.9375 mm thick) and a labeled schematic of each section. Figure 6 displays a lateral-to-medial sequence of reconstructed "virtual" sagittal sections, also 0.9375 mm thick, through the left hemisphere at 18.75 mm intervals (with the last two images 10.3 mm apart) and a labeled schematic for each section.

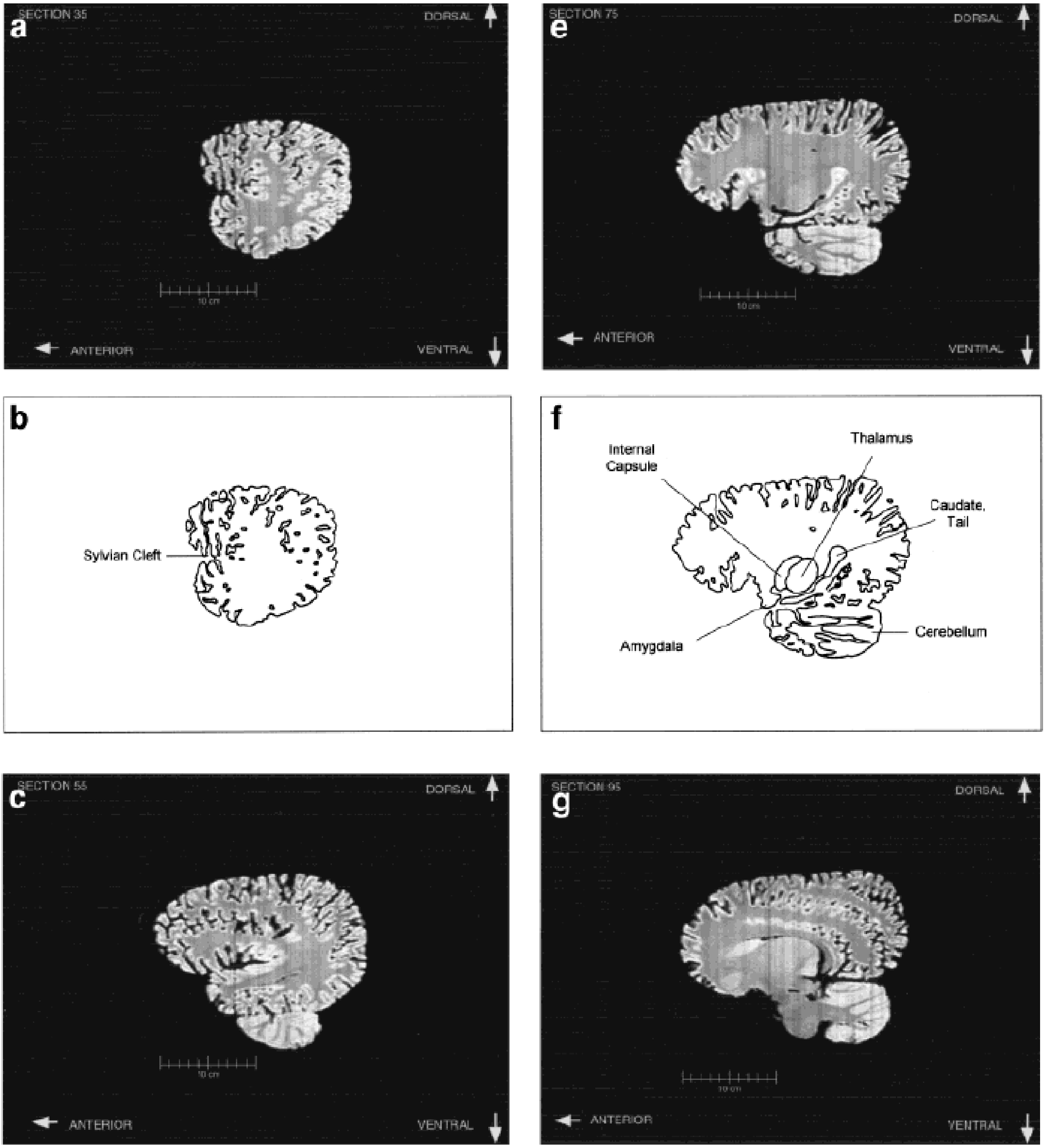
The high level of convolution of the cortex is evident in almost all of the figures. The extreme depth and density of cortical sulci are particularly evident in Figure 6 (c–f). These images also display an orbital-to-occipital gradient of increased sulcation concordant with the increased elaboration of the occipital-parietal region over the orbital region. This occipital-parietal elaboration is evident in Figure 6 (g–j) in the striking triple-tiered arrangement of limbic, paralimbic, and supralimbic arcuate cortical lobules divided by the deep limbic and paralimbic clefts. This specific combination of occipital-parietal organization and elaboration is distinct from other mammals.

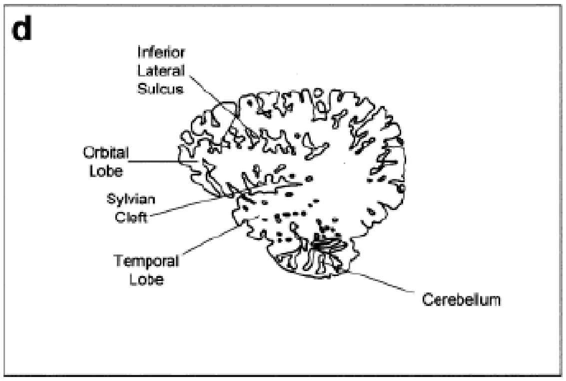
In contrast to the distinctive cortical features, the odontocete brain generally resembles other mammalian brains on a subcortical level. The volumetric proportions of various subcortical features, however, reveal even more of the distinctive adaptations and allometric rearrangements associated with odontocete evolution. As seen in Figure 1, the olfactory bulbs are absent. In contrast, auditory processing areas are enlarged (though visual structures are not necessarily reduced). These include the proportionately large inferior colliculus compared with the superior colliculus as seen most clearly in Figure 4 (g,h).

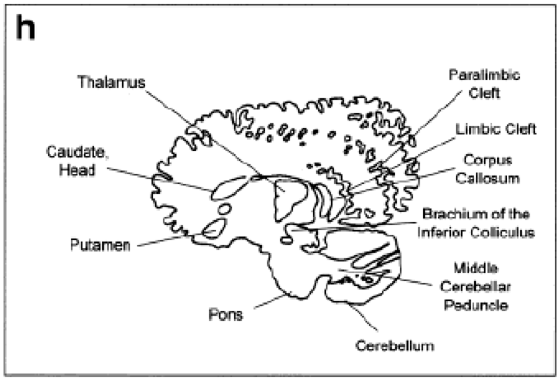
In keeping with behavioral and electrophysiological evidence for a high degree of hemispheric independence (Viamonte et al., 1968; Mukhametov et al., 1977; Mukhametov, 1984), the corpus callosum is small relative to the massive hemispheres, consistent with quantitative findings in other odontocete species and qualitative observations of the white whale brain (Tarpley and Ridgway, 1994). This is apparent in most of the figures but particularly in Figure 6 (g–l).

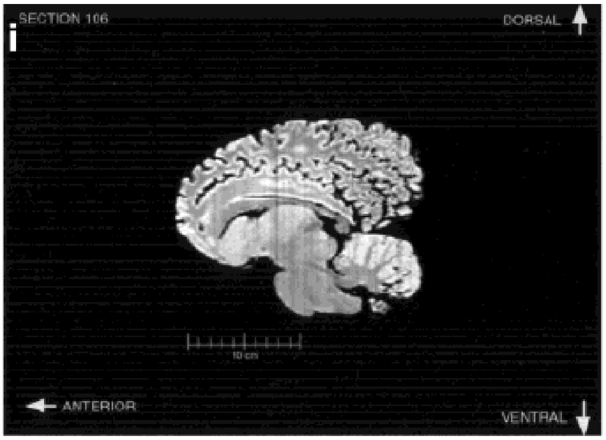
The cerebellum is large relative to the hemispheres. This is especially evident in Figure 4 (g–j), and Figure 5 (i,j), and also in the sagittal images. As shown in Figure 4 (e,f) the cerebral peduncles are high on the lateral surface of the caudal diencephalon and through the entire midbrain, rather than on the basal inferior or ventral surface as in most mammals. The basal surface is instead occupied by a large mass of gray matter that appears to be continuous with the ventral striatum and the dorsal and ventral pallidum of the forebrain reaching from these structures to the pontine nuclei caudally. The approximation of apparent basal ganglia and pons may be a consequence of the flexing of the diencephalon and the midbrain bringing the brain stem into contact with the basal forebrain, or it may represent a specialized development of the basal ganglia.

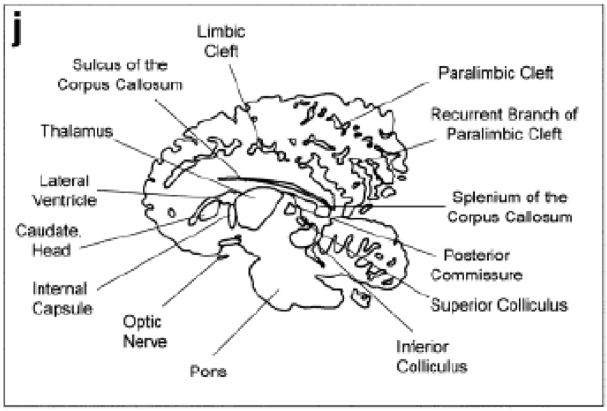
Fig. 6. Lateral-to-medial sequence of reconstructed 0.9375 thick sagittal sections and labeled schematic illustrations of each section.

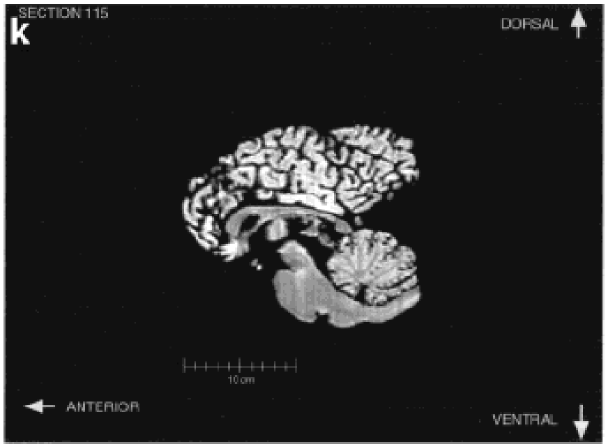



d
Inferior Lateral Sulcus
Orbital Lobe
Sylvian Cleft
Temporal Lobe
Cerebellum


h
Thalamus
Caudate, Head
Putamen
Pons
Paralimbic Cleft
Limbic Cleft
Corpus Callosum
Brachium of the Inferior Colliculus
Middle Cerebellar Peduncle
Cerebellum


SECTION 106
i
DORSAL
10 cm
ANTERIOR
VENTRAL


j
Limbic Cleft
Sulcus of the Corpus Callosum
Thalamus
Lateral Ventricle
Caudate, Head
Internal Capsule
Optic Nerve
Pons
Paralimbic Cleft
Recurrent Branch of Paralimbic Cleft
Splenium of the Corpus Callosum
Posterior Commissure
Superior Colliculus
Inferior Colliculus


SECTION 115
k
DORSAL
10 cm
ANTERIOR
VENTRAL

DISCUSSION

This study presents the first MRI-based, anatomically labeled, three-dimensional atlas of the brain of the white (beluga) whale (*Delphinapterus leucas*). In addition, we have constructed three-dimensional models of the white whale brain and produced “virtual” horizontal and sagittal sections from these original images. These reconstructed images allow for the visualizing of a range of distinctive white whale brain features from various orientations by preserving the gross morphological and internal structure of the specimen. Because there are none of the distortions associated with histological processing, we have a more realistic view of the brain as it was in situ.

Many cortical features are easily identified from the original MRI scans and “virtual” images. These include the distinctive lobular formations, gyral and sulcal patterns, and general gradient of elaboration in the parietal, occipital, and temporal regions. Subcortical allometry, including that of both gray and white matter structures, is easily assessed as well. Our findings are consistent with what has been noted in the few existing histological studies of the odontocete brain. Moreover, because we are able to preserve the internal structure of the specimen, neuroanatomical studies of brains from MRI set the stage for much-needed accurate and reliable morphometric analyses of various brain structures in odontocetes. These studies are underway.

Evolutionary Considerations

There is a deep evolutionary divergence of the Order Cetacea (of which Odontoceti is a suborder) from other mammalian lines. Furthermore, cetacean evolution is characterized by distinctive environmental pressures associated with a fully aquatic existence versus a terrestrial lifestyle. These related attributes make the comparative study of structure-function relationships in cetacean brains, compared with those of other mammals, uniquely valuable for improving our understanding of the parameters of mammalian brain evolution.

The brain of the white whale as revealed in this study is characterized by similar morphological trends as those found n the bottlenose dolphin and other cetaceans (Morgane et al., 1980). Although there are differences among cetacean brains, these differences are relatively minor compared with the striking dissimilarities to brains of other mammals. The most obvious difference between cetacean brains and those of other mammals is in the gross morphological configuration of the whole structure and the lobules of the cerebral hemispheres. These are well-visualized in MRI scans. Evolution of overall brain shape in cetaceans may have been partly due to migration of the blowhole and telescoping of the skull, i.e., antorbital elongation and postorbital compression. This in turn may account for the distinctive construction of the midbrain, i.e., the corticopontine, corticobulbar and corticospinal fibers travel high on the lateral surface whereas the ventral surface is occupied by a large continuous mass of gray matter extending from the diencephalon rostrally to the pontine nuclei caudally. There may be distinctive organizational features of the basal ganglia that also contribute to this uniquely cetacean architecture.

There is also adequate evidence that many of the anatomical changes in the cetacean brain represent changes in function, e.g., loss of olfactory structures and enlargement of acoustic structures. Similar, convergent changes in function, along with their neuroanatomical correlates, are observed in several brains of unrelated clades, such as many bats and primates (Johnson et al., 1984, 1994). In general, the cetacean brain possesses some common mammalian features in combination with specialized and highly unusual features, the function of which we have barely begun to understand.

CONCLUSIONS

If we are to eventually understand the functional significance of this mosaic of typical mammalian and uniquely cetacean features, the structural organization of the cetacean brain must be further elucidated. This can be rapidly and effectively accomplished by MRI-based studies of neuroanatomy. In comparison, already-existing data from the more traditional methods of sectioning and staining are very time-intensive, expensive, and vulnerable to spatial distortion compared with the data acquired by MRI. Studies like the present one are crucial for establishing the structural basis of and templates for future functional studies using non-invasive neuroimaging techniques to investigate the neurobiological basis of cetacean cognition and behavior.

ACKNOWLEDGMENTS

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