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# **Anatomy and Three-Dimensional Reconstructions of the Brain of a Bottlenose Dolphin (*Tursiops truncatus*) From Magnetic Resonance Images**

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## **KEYWORDS**

**magnetic resonance imaging, dolphin, brain, three-dimensional model**

## **ABSTRACT**

*Cetacean (dolphin, whale, and porpoise) brains are among the least studied mammalian brains because of the formidability of collecting and histologically preparing such relatively rare and large specimens. Magnetic resonance imaging offers a means of observing the internal structure of the brain when traditional histological procedures are not practical. Furthermore, internal structures can be analyzed in their precise anatomic positions, which is difficult to accomplish after the spatial distortions often accompanying histological processing. In this study, images of the brain of an adult bottlenose dolphin, *Tursiops truncatus*, were scanned in the coronal plane at 148 antero-posterior levels. From these scans a computer-generated three-dimensional model was constructed using the programs Voxel-View and 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 major neuroanatomical features such as the arrangement of cortical lobes and subcortical structures such as the inferior and superior colliculi, and demonstrate the utility of MRI for neuroanatomical investigations of dolphin brains.*

The bottlenose dolphin (*Tursiops truncatus*) is one of the most extensively studied cetaceans. In the past few decades, there has accrued a sizable body of literature on the ecological, behavioral, cognitive, physiological, and neurobiological characteristics of the bottlenose dolphin (e.g., Herman, 1986; Leatherwood and Reeves, 1990; Morgane et al., 1980; Reiss et al., 1997; Reynolds et al., 2000; Ridgway, 1990 for reviews). Yet, relative to our knowledge of many other mammals, we know very little about the bottlenose dolphin brain. Those few studies that have been done have provided data that have served as the basis for many intriguing hypotheses

about mammalian brain evolution (e.g., Glezer et al., 1988). These hypotheses will possibly never be explored until we understand how dolphin brain structure relates to function. Although a number of promising noninvasive functional brain imaging methods currently exist (e.g., functional magnetic resonance imaging), they rely upon a solid knowledge about brain structure and organization and the range within which brain morphometry varies across individuals. Therefore, neuroanatomical studies, particularly those based on imaging techniques, of the bottlenose dolphin form the crucial foundation for future functional imaging studies.

Compared to many other mammalian brains, the bottlenose dolphin brain is unusual in many respects. It has been 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, pp. 105). Because of the 55- to 60-million year divergence between cetaceans and other mammals, odontocete brains represent a blend of early mammalian features and uniquely derived characteristics (Glezer et al., 1988; Manger et al., 1998; Ridgway, 1986, 1990). The differences between dolphin and other mammalian brains of similar size have been noted at the level of cortical cytoarchitecture and immunohistochemistry (Garey et al., 1985; Garey and Leuba, 1986; Glezer and Morgane, 1990; Glezer et al., 1990, 1992a,b, 1993, 1998; Hof et al., 1992, 1995), cortical surface morphology (Haug, 1987; Jacobs et al., 1979; Morgane et al., 1980) and subcortical structures (Glezer et al., 1995a,b; Tarpley and Ridgway, 1994). These differences are also manifest during ontogenesis (Buhl and Oelschlager, 1988; Oelschlager and Buhl, 1985; Oelschlager and Kemp, 1998).

There are a number of published descriptions of bottlenose dolphin neuroanatomical characteristics [(see Morgane, et al., 1986; Ridgway, 1990; for reviews), Morgane et al. (1980), Ridgway and Brownson (1984), Haug (1987), and Tarpley and Ridgway (1994)]. There are, however, few detailed systematic anatomical descriptions of whole bottlenose dolphin brains and substructures at the qualitative or quantitative level. The most complete neuroanatomical descriptions of the bottlenose dolphin brain are arguably found in a series of monographs describing the anatomy of the rhinencephalon (Jacobs et al., 1979), telencephalon (Morgane et al., 1980), and insular formations of the limbic lobe (Jacobs et al., 1984) in the bottlenose dolphin. There has yet to be a published description of the bottlenose dolphin brain that contains sequential neuroanatomical images in three orthogonal planes because of the practical difficulties 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 anatomic positions, which is difficult to accomplish after the spatial distortions often accompanying histological processing. This study presents an anatomically-labeled three-dimensional description of the bottlenose dolphin brain based on a series of MRI images.

## **MATERIALS AND METHODS**

### *Specimen*

The specimen is the postmortem brain of an adult pregnant female bottlenose dolphin (*Tursiops truncatus*) that stranded in February 1999 at Long Beach, North Carolina (Field number WAM

545). The carcass was in exceptionally fresh condition (Smithsonian Condition Code 2; Geraci and Loundsbury, 1993) with no evidence of damage. Total body length was 246 cm and total body weight was 238 kg. The brain, which was extracted from the skull approximately 8 hr after the dolphin had died, was weighed and placed in 10% neutral buffered formalin, with the formalin being changed three times during the 39 days before scanning. Fresh brain weight was 1,378 g. A small plug of cortical tissue was removed from the right cortical hemisphere of the fresh brain for biopsy purposes.

### *Magnetic Resonance Imaging*

T2-weighted magnetic resonance (MR) images of the entire brain were acquired in the coronal plane at 148 antero-posterior levels with a 1.5 T Philips NT scanner (Philips Medical System, The Netherlands) at Emory University School of Medicine. Protocol parameters were: slice thickness 5 2.0 mm, slice interval 5 1.0 mm, Time to Repetition 5 3,000 msec, Time to Echo 5 22 msec, Field of view 5 200 mm, matrix 5 256 3 256 pixels.

### *Three-Dimensional Reconstruction and Reformatting*

Computer-generated three-dimensional reconstruction images were created using the software programs Voxel-View and VoxelMath programs (Vital Images, Inc.) at the Laser Scanning Microscopy Laboratory at Michigan State University. The three-dimensional 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 virtual section series in the horizontal (122 virtual sections) and sagittal (136 virtual sections) planes.

### *Anatomical Labeling and Nomenclature*

All identifiable anatomical structures of the dolphin 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 dolphin brain were compared to the published photographs and illustrations of the bottlenose dolphin brain from Morgane et al. (1980). All scans were also compared to a complete alternate series of sections stained, respectively, for cell bodies (Nissl method), and for myelinated fibers in the same three orthogonal planes (coronal or transverse, sagittal, and horizontal). These stained sections are from the Yakovlev-Haleem collection at the National Museum of Health and Medicine and the Welker collection at the University of Wisconsin-Madison.

### *Volumetric Estimate of Whole Brain Weight*

The full antero-posterior extent of the brain in coronal sections was measured with the image analysis software program Scion IMAGE for Windows (PC version of NIH IMAGE) using manually-defined areas from successive slices that are integrated to arrive at a volume estimate. The volume of the biopsied region was estimated and included. The entire volumetric estimate was converted to weight units by multiplying the volume by the specific gravity of brain tissue or 1.036 g/cm<sup>3</sup> (Stephan et al., 1981).

## RESULTS AND DISCUSSION

### *Volumetric Estimate of Whole Brain Weight*

The measured volume of the entire brain was 1363.13 cm<sup>3</sup>. The resulting estimate of whole brain weight was 1,412.20 g. This estimate is only 3% more than the fresh brain weight of 1,378 g and is not an atypical brain weight obtained with this method for an adult female bottlenose dolphin (Marino, 1998).

### *Three-Dimensional Reconstructions*

Computer-generated three-dimensional reconstructions of the bottlenose dolphin whole brain were produced from the original scans in the coronal plane. Figure 1a shows a dorsal view of the brain. Figure 1b shows the brain at an angle that exposes the left and right hemispheres as well as the anterior portion of the brain and some of the ventral structures, including the pons. These three-dimensional reconstructions clearly display many noted gross morphological differences between the cetacean brain and the brains of terrestrial mammals (Morgane et al., 1980). The reason the ventral side of the brain remains visible from the angle in Figure 1b is because of the foreshortened frontal or “orbital” lobes (Morgane et al., 1980). The foreshortened orbital lobes, as well as the pronounced bitemporal width of the brain, are apparent in Figure 1a,b.

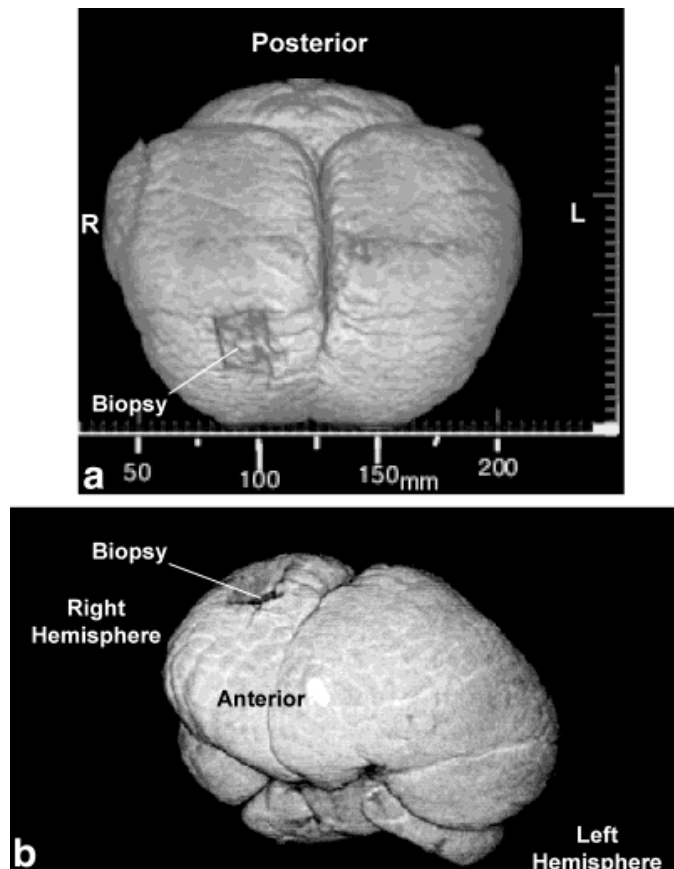
### **Anatomically-Labeled Two-Dimensional MR**

#### *Sections*

Figures 2–9 display a posterior-to-anterior sequence of originally-acquired 2.0 mm-thick coronal MR brain sections at 30 mm intervals, a labeled schematic illustration of each section, computer-generated cutaways shown at two orthogonal planes to the section, and a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section. Figures 10–17 display a ventral-to-dorsal sequence of reconstructed “virtual” horizontal sections (1.0 mm thick) at 14 mm intervals, a labeled schematic illustration of each section, computer-generated cutaways at two orthogonal planes to the section, and a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section. Figures 18–25 display a midline-to-lateral sequence of reconstructed “virtual” sagittal sections, also 1.0 mm thick, through the right hemisphere at 11 mm intervals, a labeled schematic illustration of each section, computer-generated cutaways of two orthogonal planes to the section, and a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section.

Figures 2–9 demonstrate the excellent level of preservation of the spatial relationships among the brain’s structures that has allowed for reconstruction in the horizontal and sagittal planes shown in Figures 10–17 and 18–25, respectively. All of the sagittally-oriented three-dimensional reconstructions and, in particular, Figure 18, show the mesencephalic and pontine flexures reminiscent of brainstem flexure patterns in the embryonic state of most terrestrial mammals. These flexures remain present in adult bottlenose dolphin brains and may represent pedomorphic features.

**Fig. 1.** Dorsal view (a) and antero-ventral view (b) of computer-generated three-dimensional reconstruction of the bottlenose dolphin brain.



#### **LEGEND**

**Figs. 2–9.** Posterior-to-anterior sequence of (a) originally-acquired 2.0 mm-thick coronal MR brain sections at 30 mm intervals, (b) a labeled schematic illustration of each section, (c) computer-generated cutaways shown at two orthogonal planes to the section, and (d) a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section.

**Figs. 10–17.** Ventral-to-dorsal sequence of (a) reconstructed “virtual” horizontal sections (1.0 mm thick) at 14 mm intervals, (b) a labeled schematic illustration of each section, (c) computer-generated cutaways at two orthogonal planes to the section, and (d) a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section.

**Figs. 18–25.** Midline-to-lateral sequence of (a) reconstructed “virtual” sagittal sections, also 1.0 mm thick, through the right hemisphere at 11 mm intervals, (b) a labeled schematic illustration of each section, (c) computer-generated cutaways of two orthogonal planes to the section, and (d) a computer-generated three-dimensional reconstruction of the whole brain showing a cutaway of each section.

Figure 2.

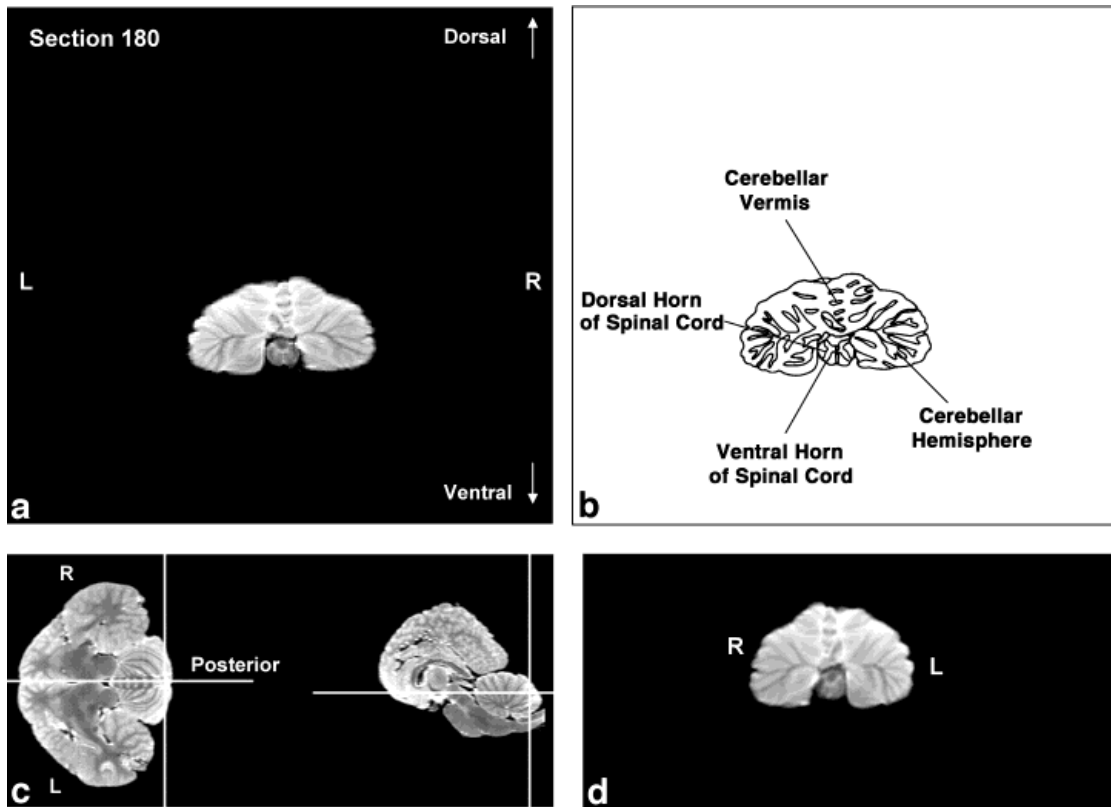


Figure 3.

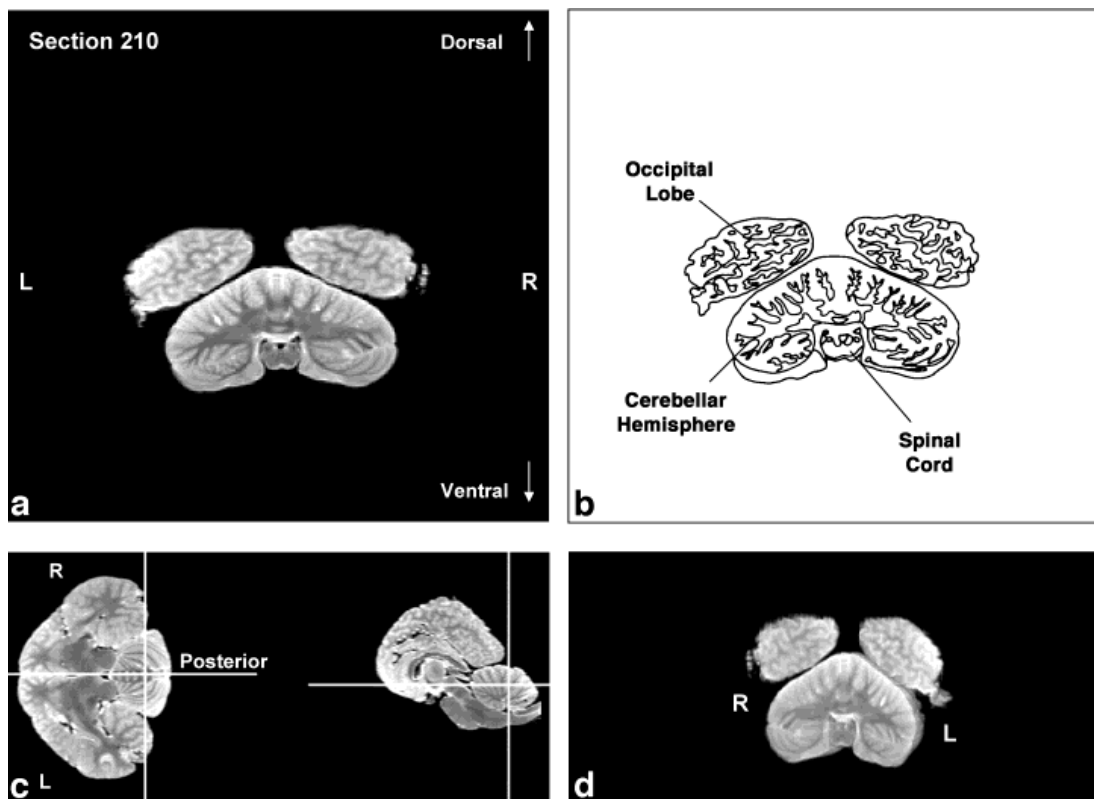




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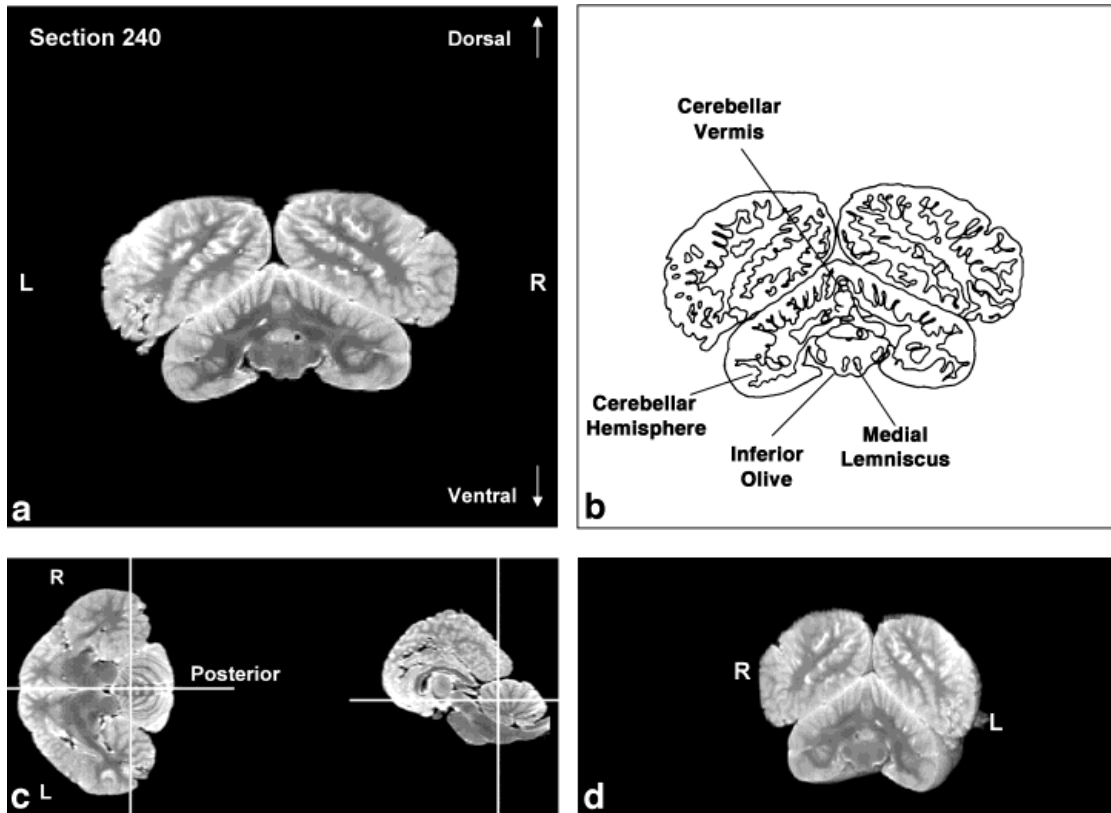


Figure 5.

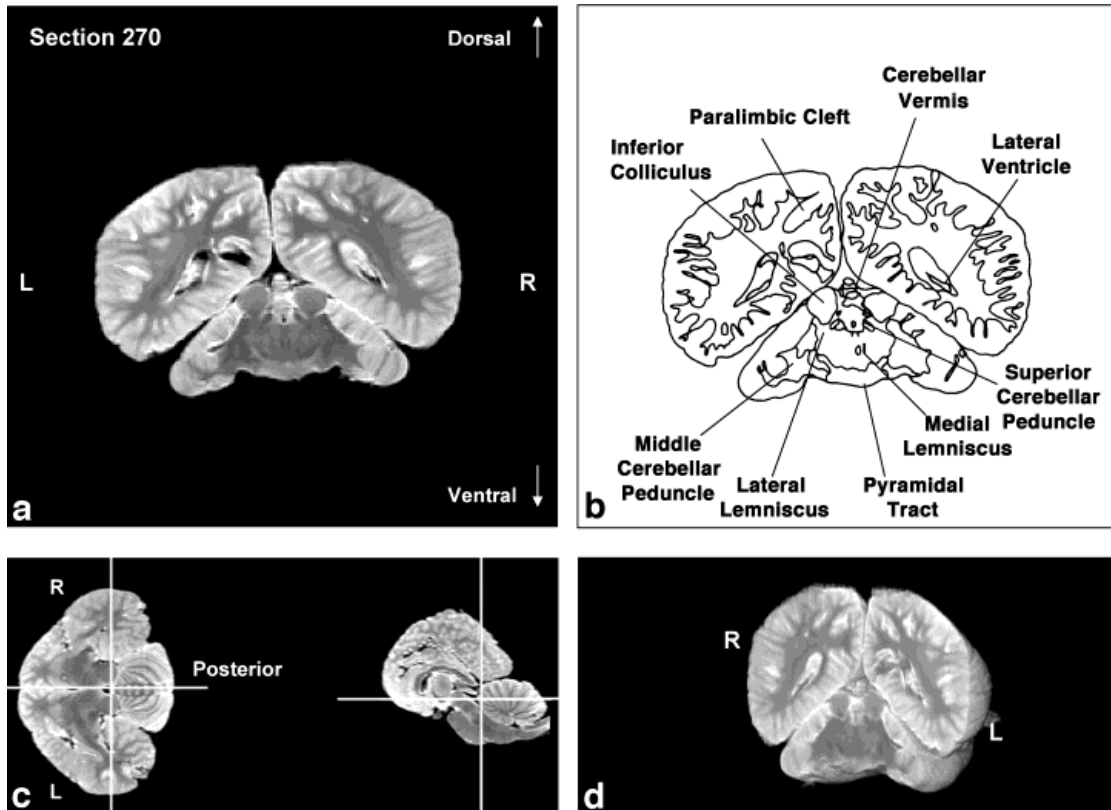


Figure 6.

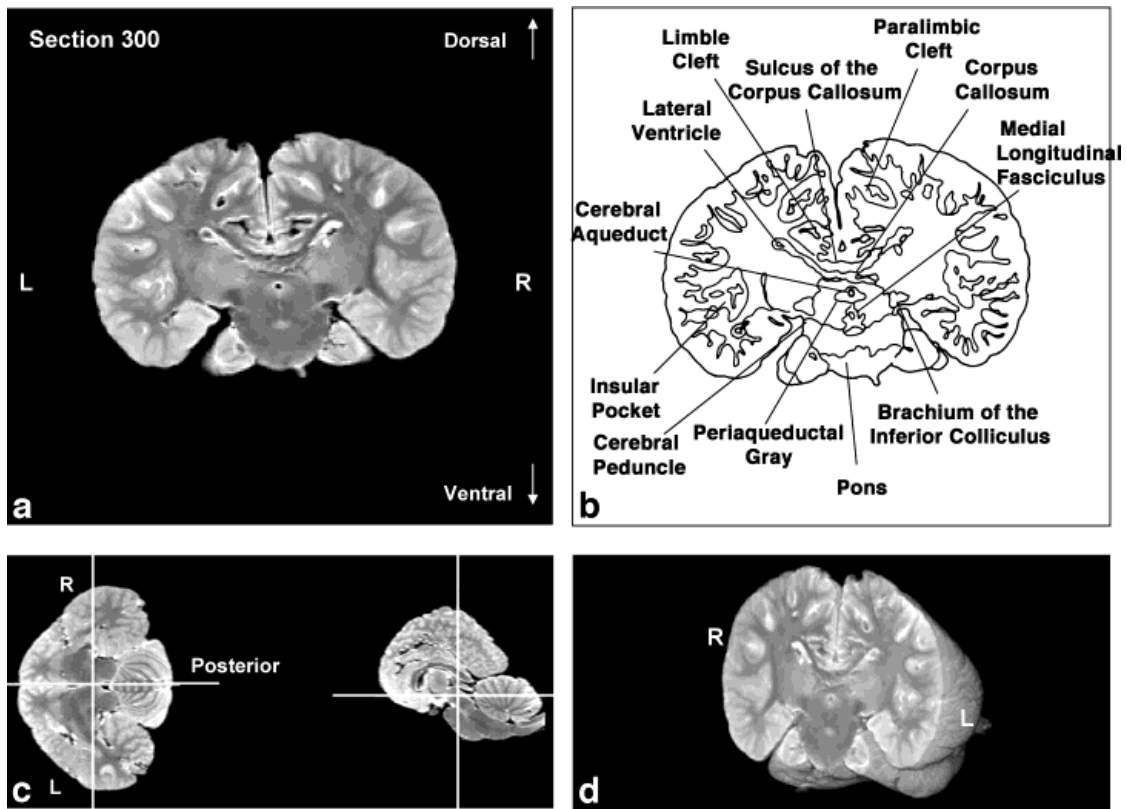


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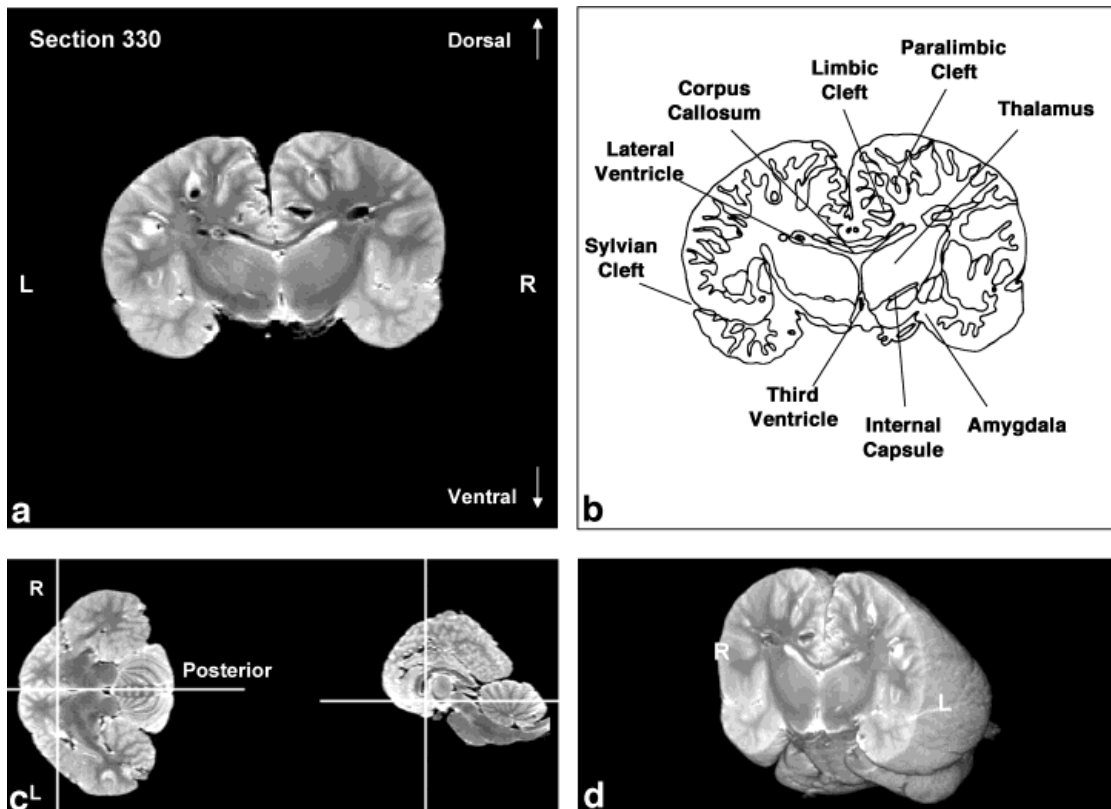


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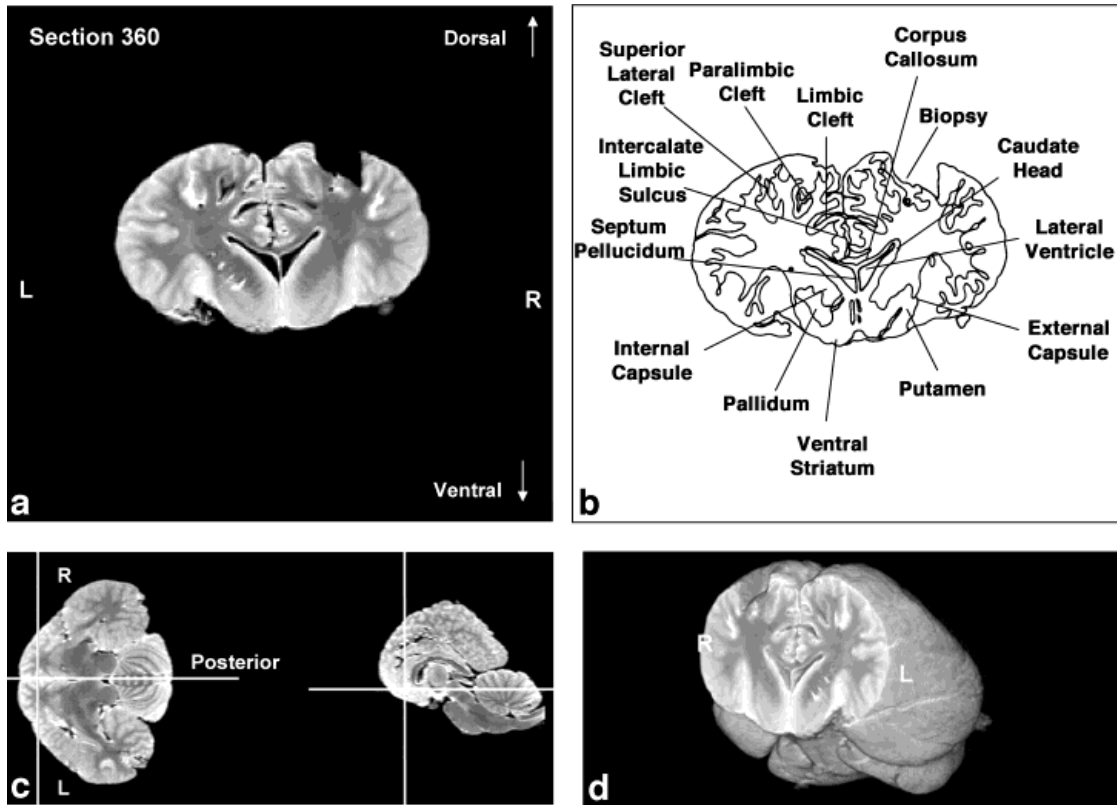


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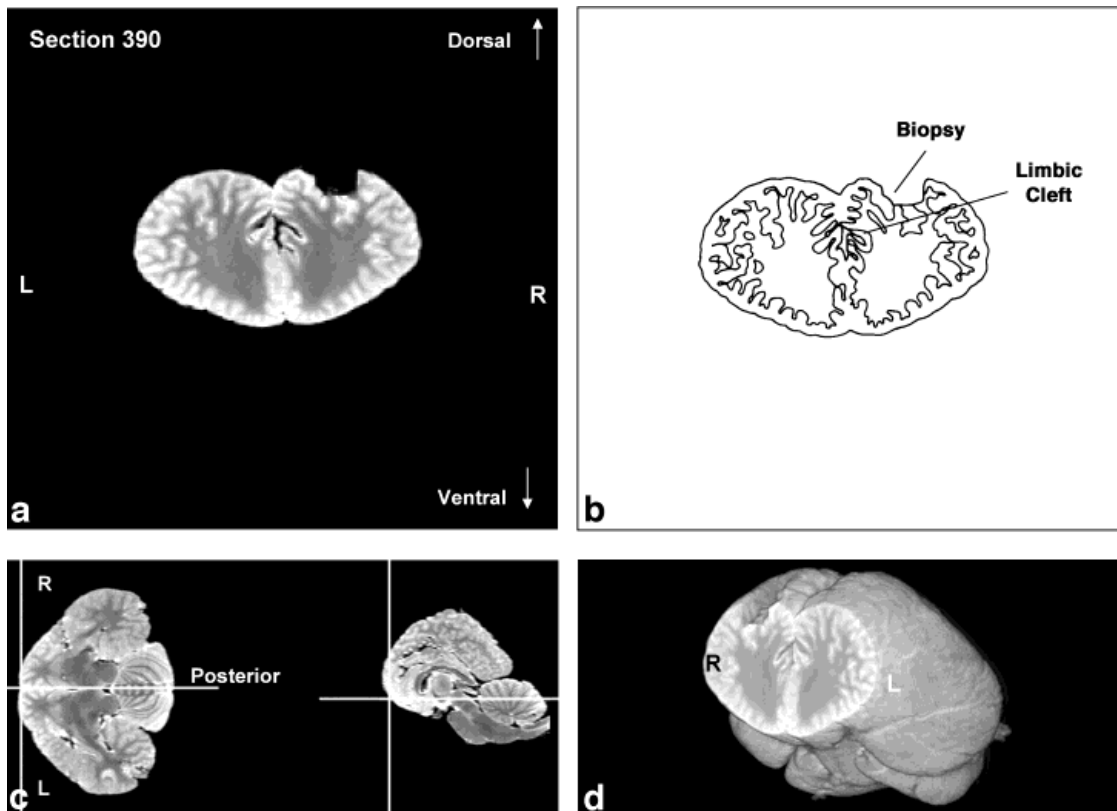


Figure 10.

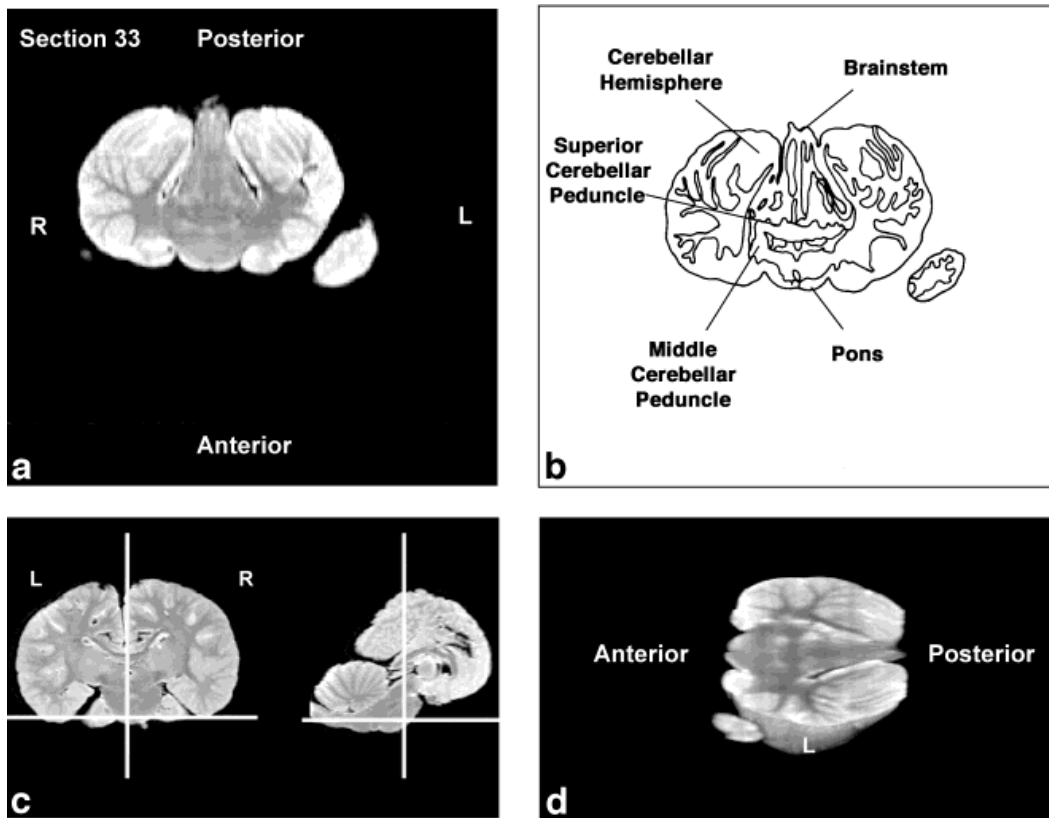


Figure 11.

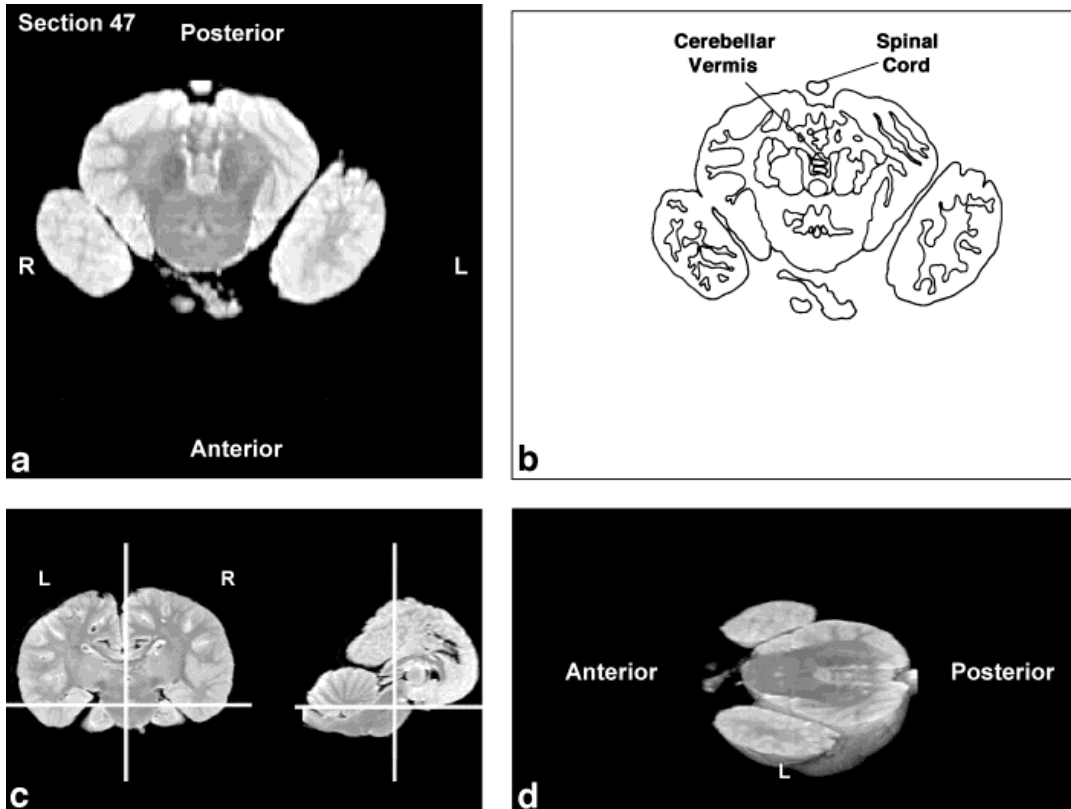


Figure 12.

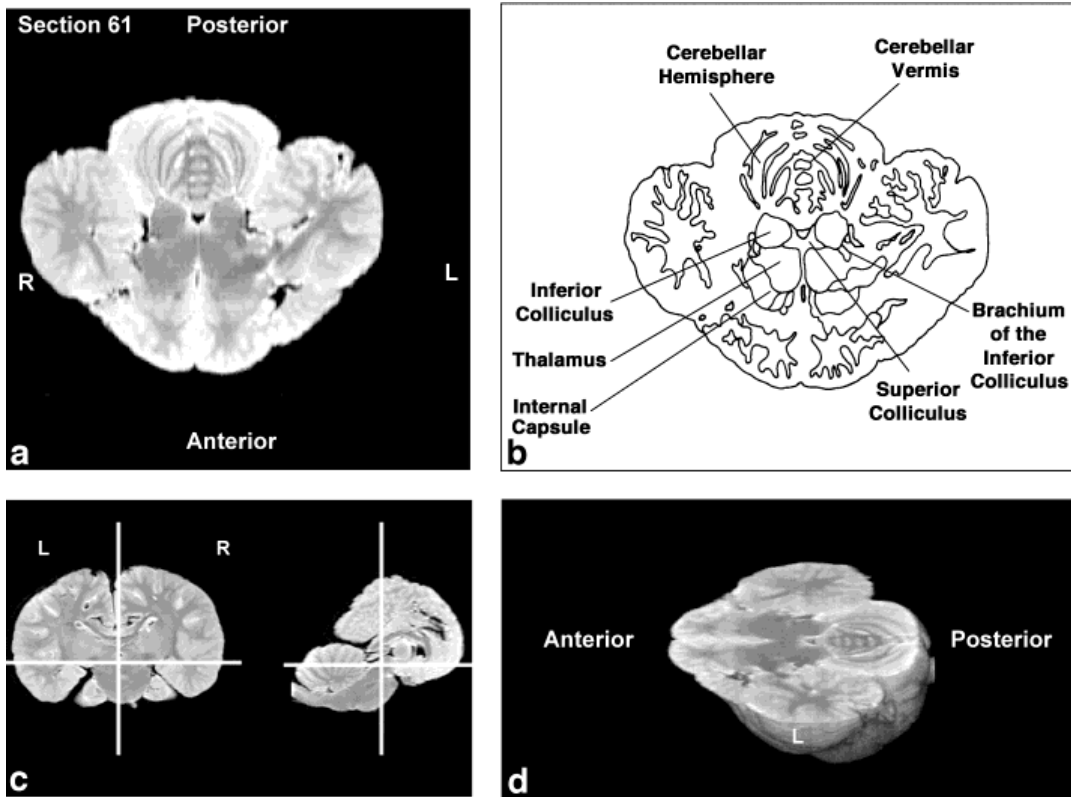


Figure 13.

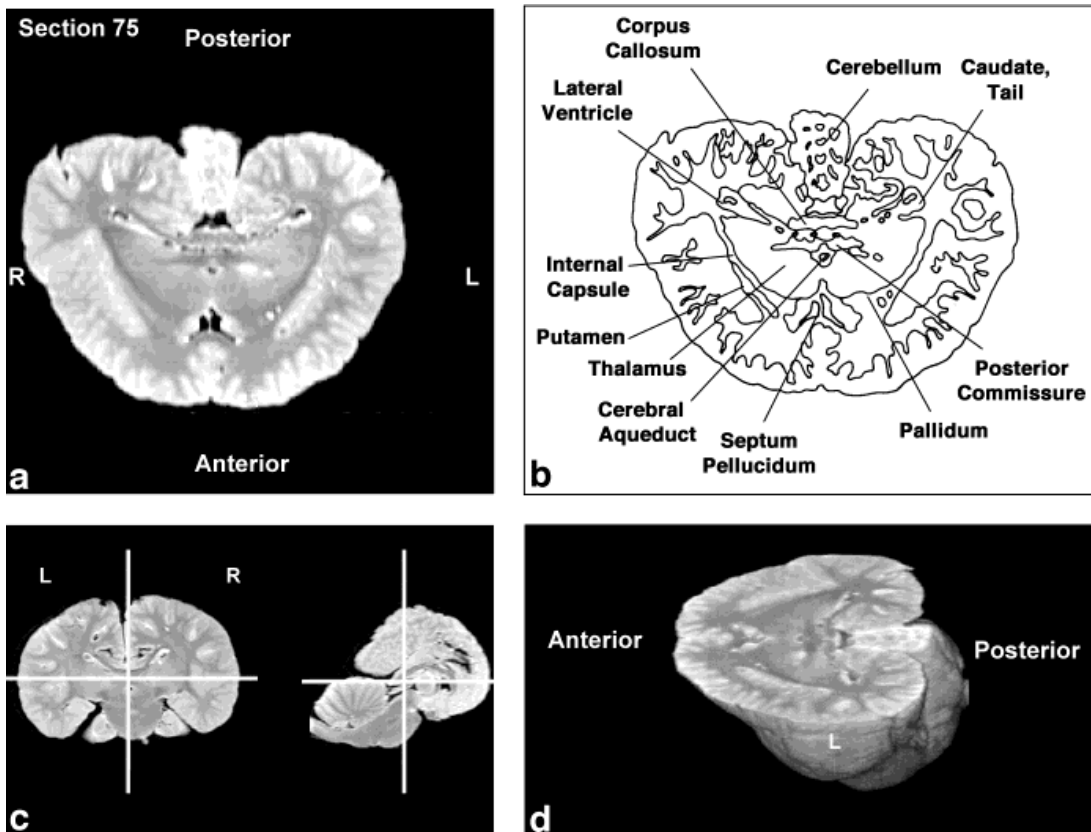


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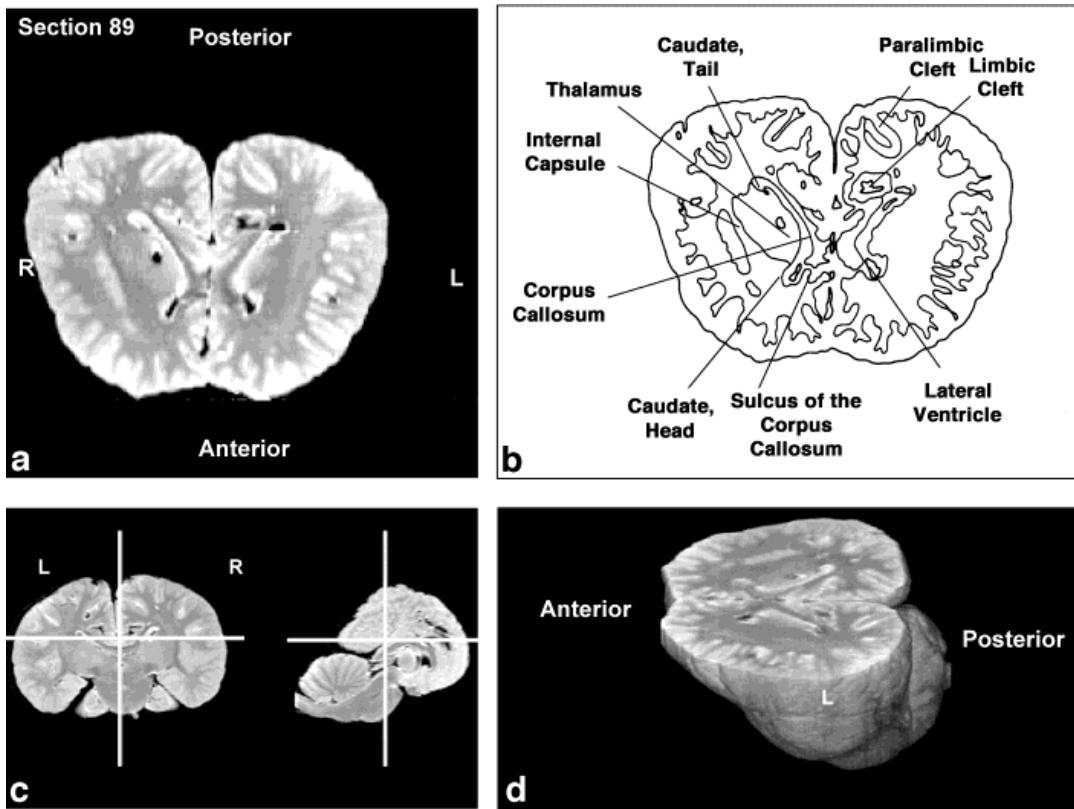


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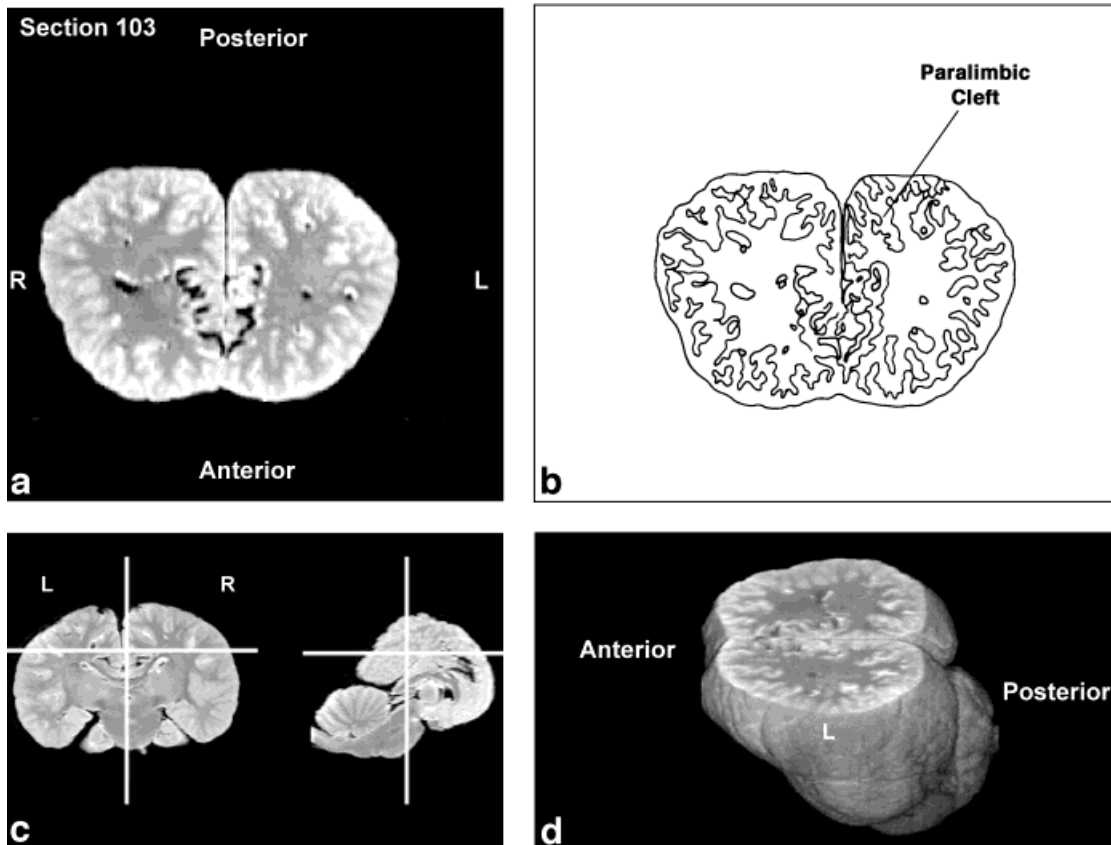


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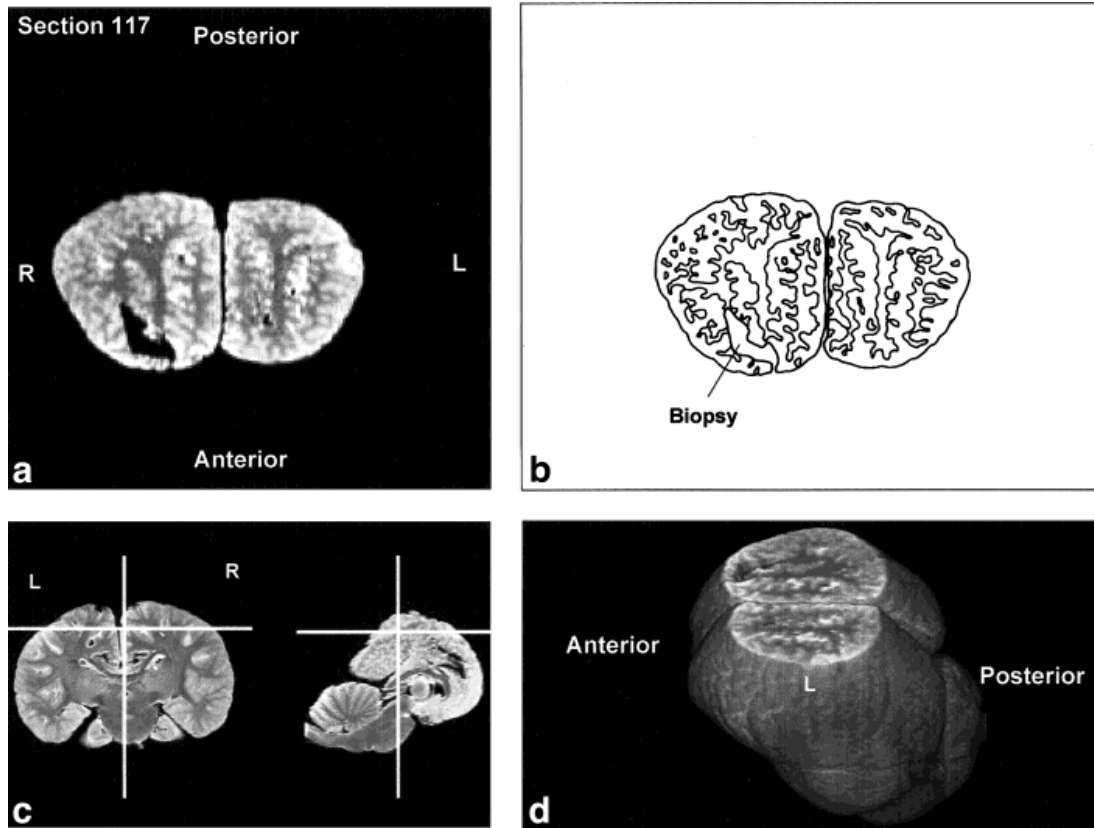


Figure 17.

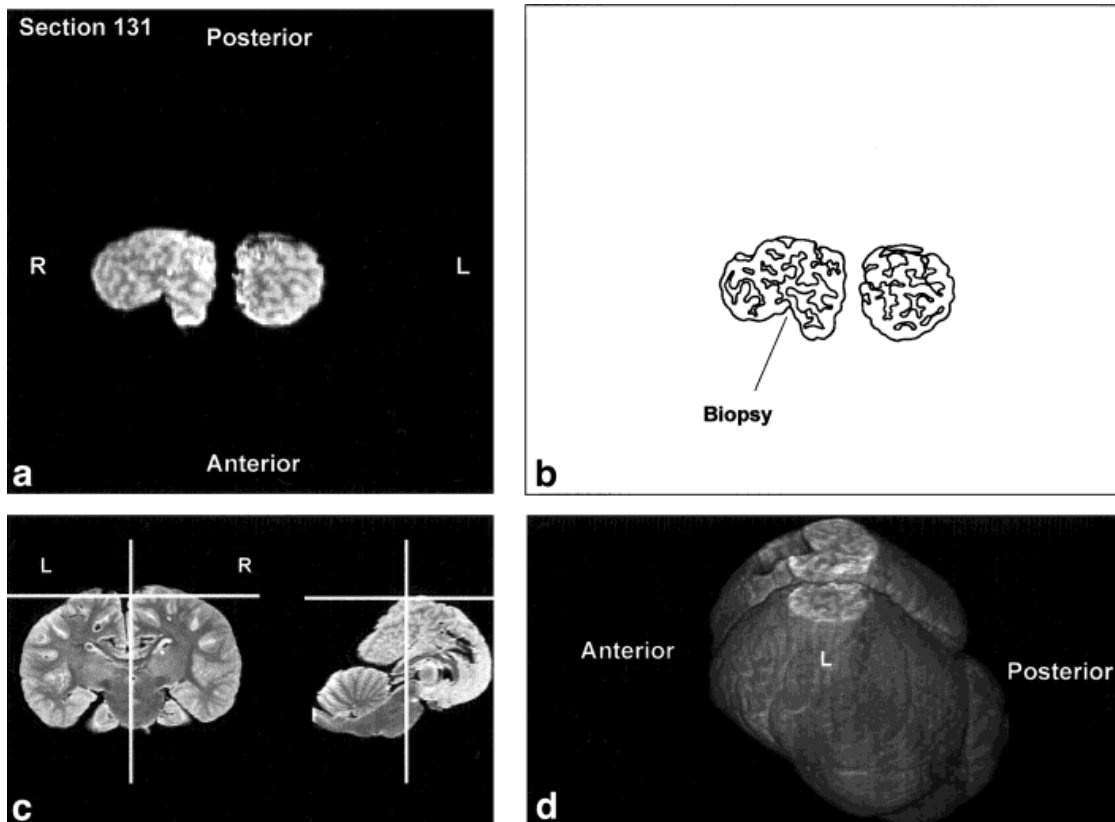


Figure 18.

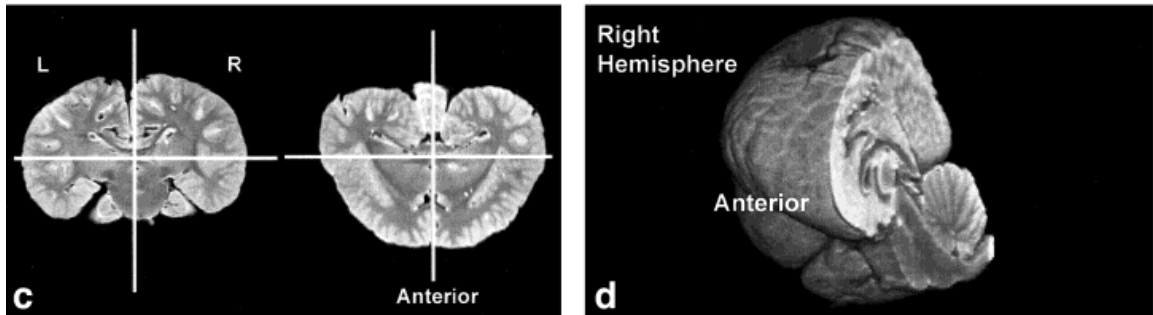
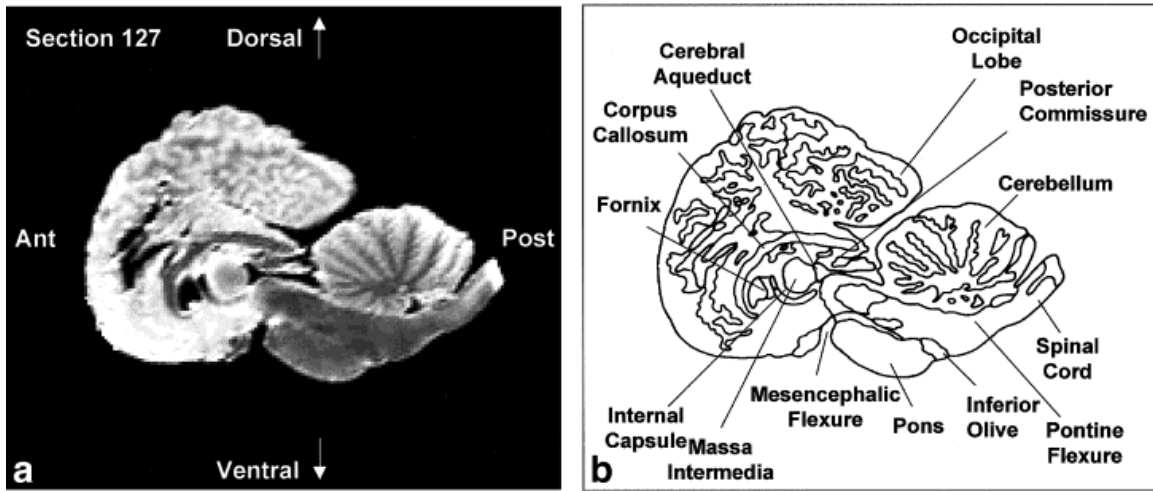


Figure 19.

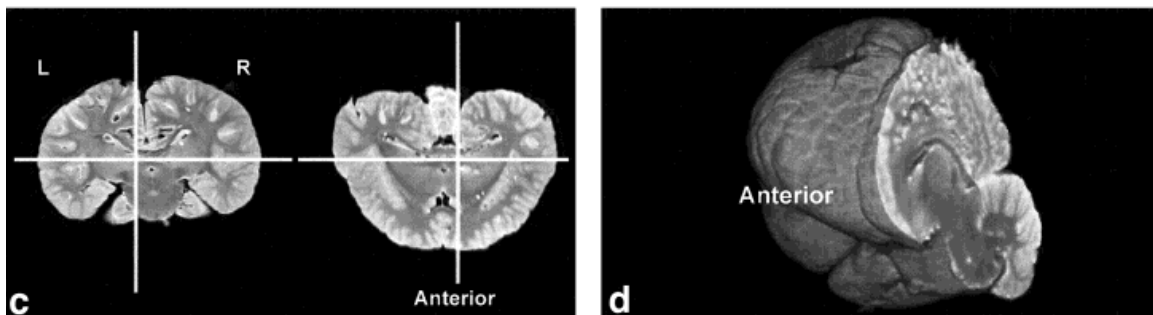
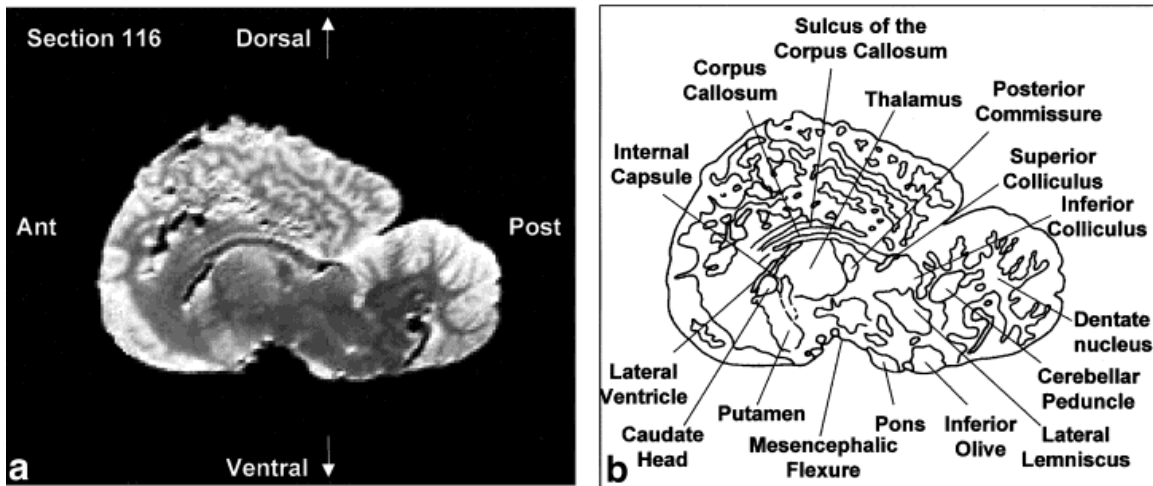




Figure 20.

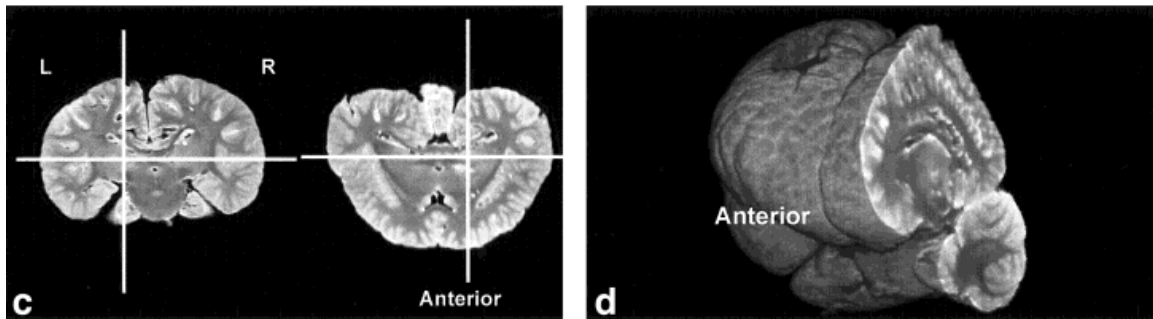
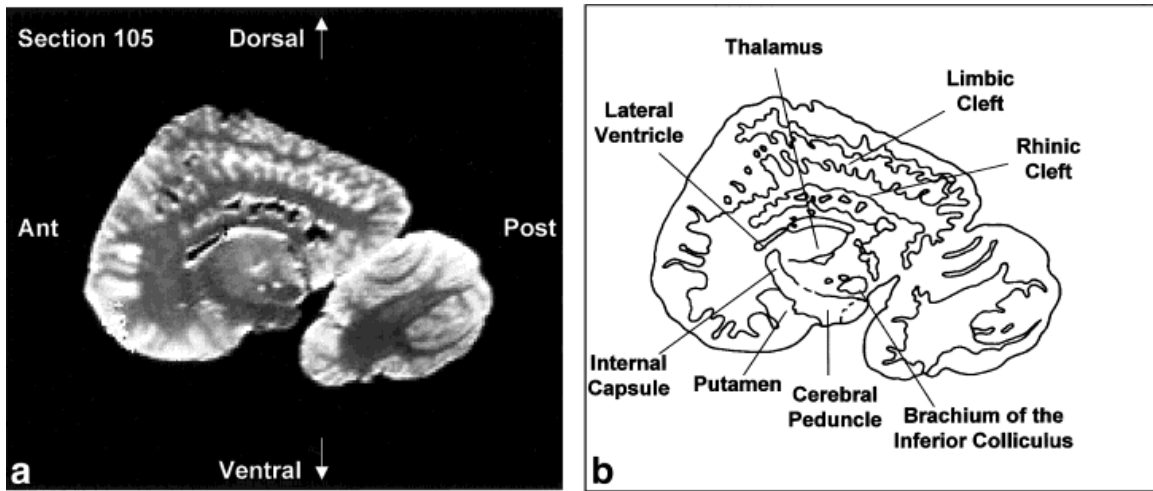


Figure 21.

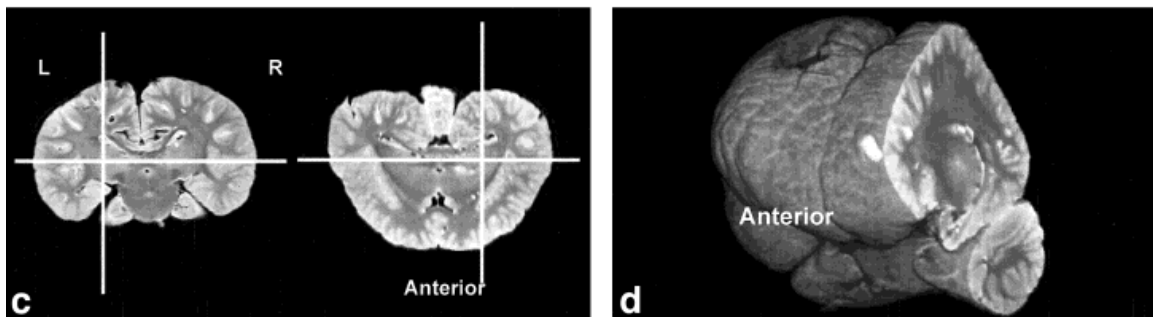
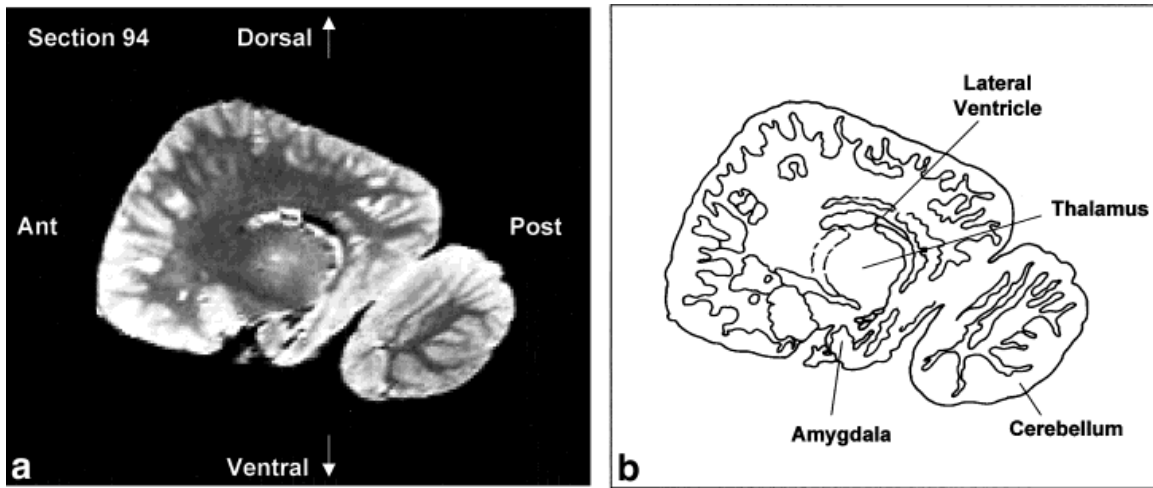


Figure 22.

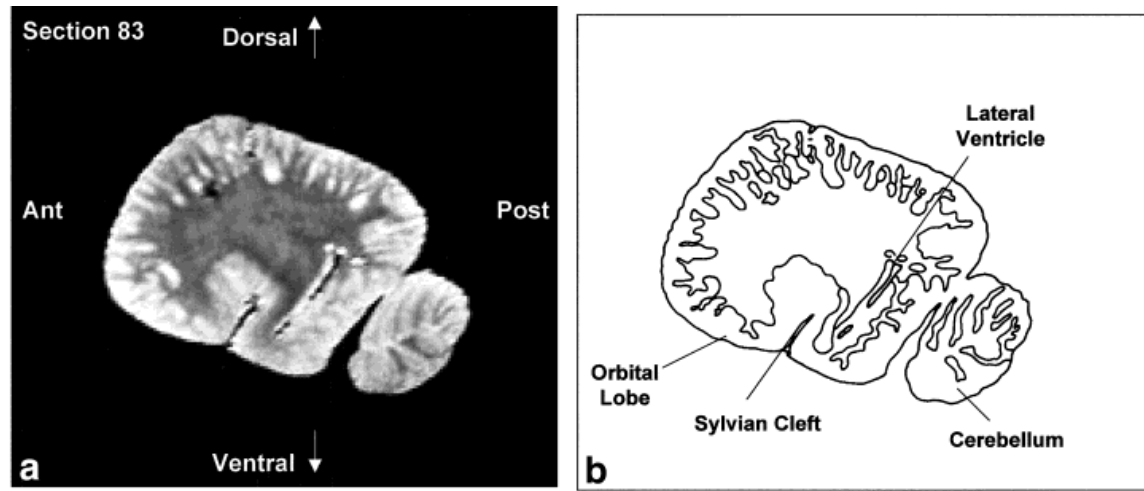


Figure 23.

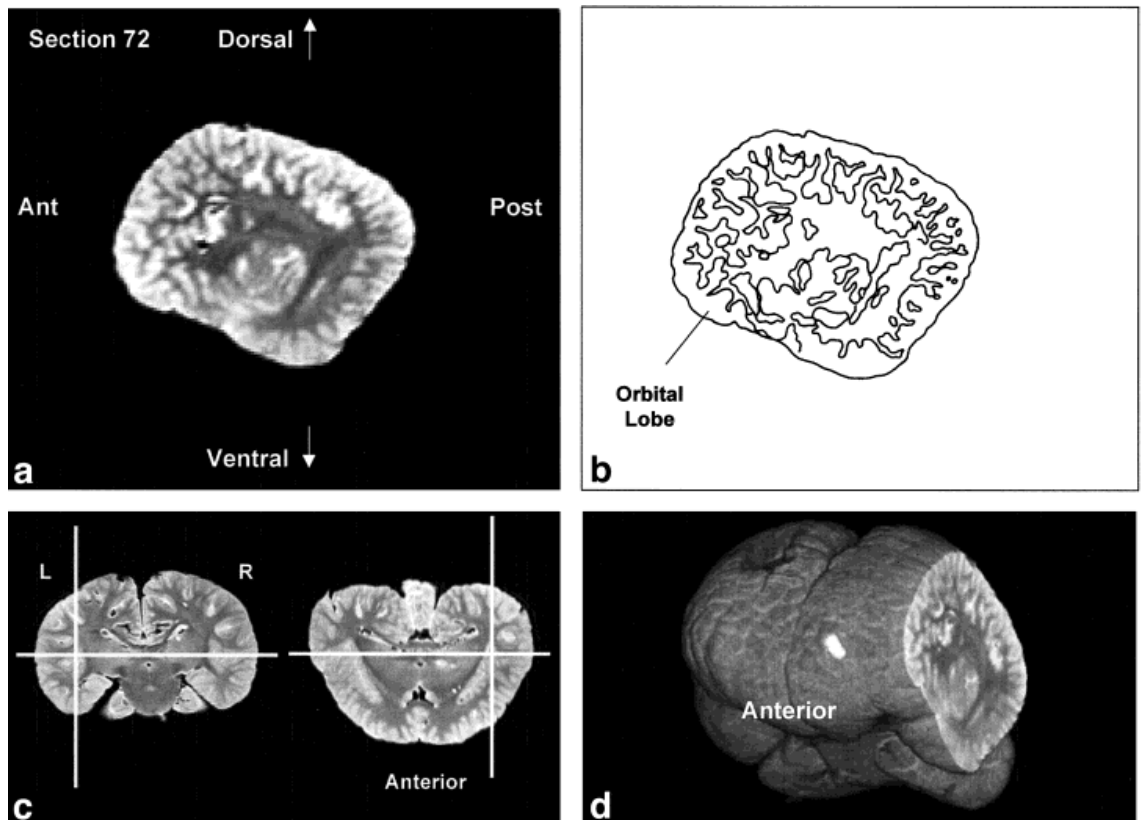


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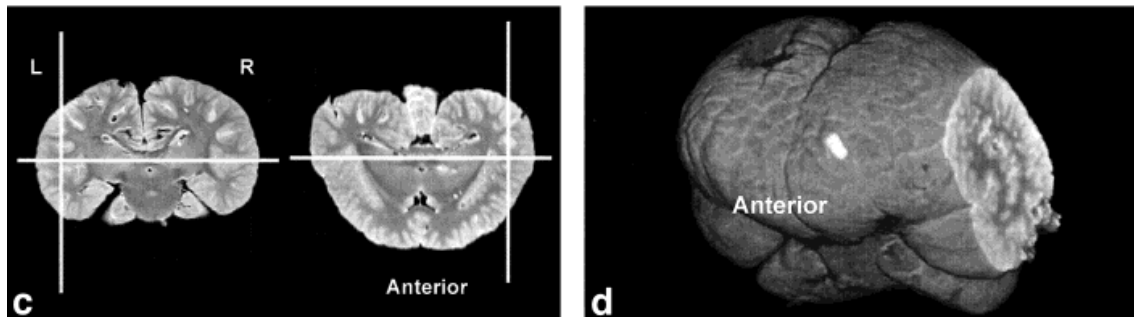
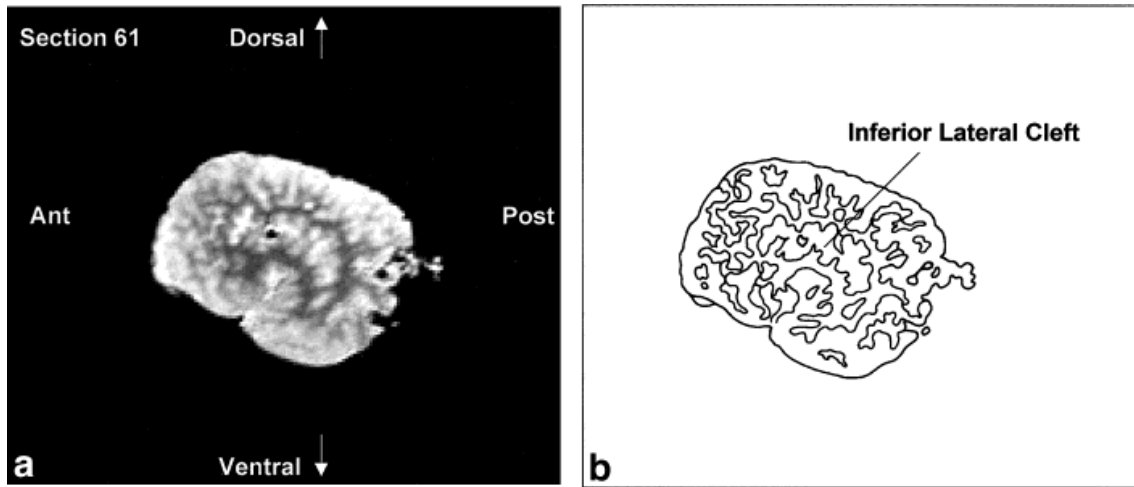
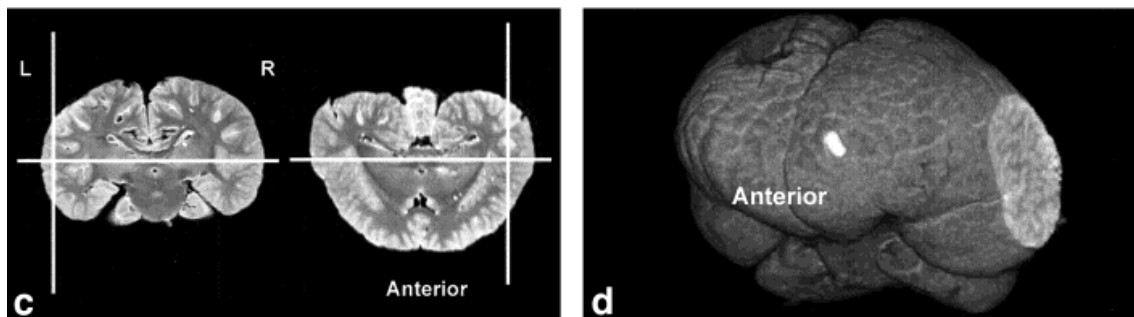
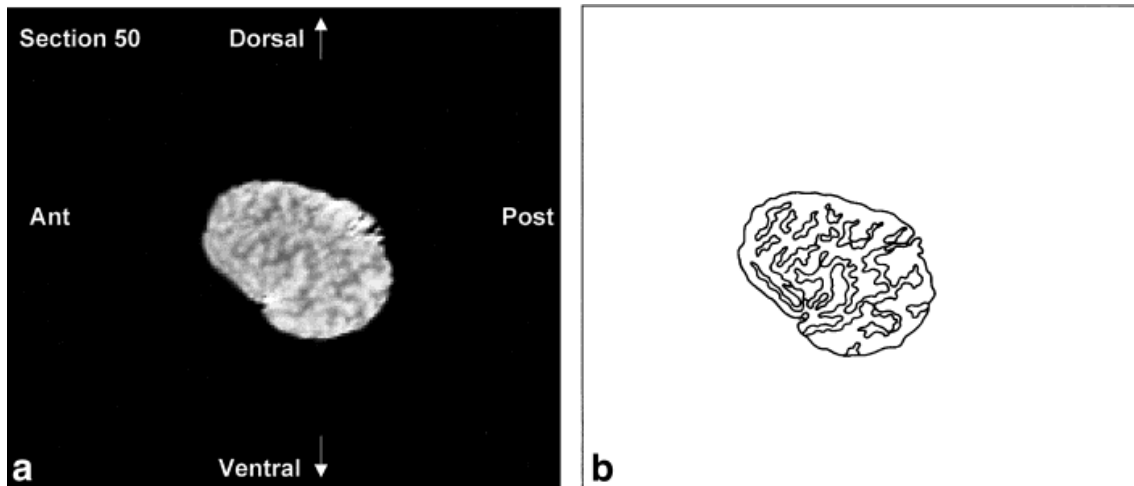


Figure 25.



The high level of cortical convolution is particularly clear in Figures 3–9, 13–17, and 18–25. The extreme depth and density of cortical sulci are particularly evident in Figures 19–23. Figures 18–20 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 20 in the three-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 but not unique to the bottlenose dolphin among the cetaceans (Morgane et al., 1980).

In contrast to the distinctive cortical features, the bottlenose dolphin brain generally resembles other mammalian brains on a subcortical level (Morgane et al., 1980). Despite the shared subcortical structures between dolphin brains and other mammal brains, however, the volumetric proportions of various subcortical features of the dolphin brain are quite different from those of terrestrial mammalian brains. These morphometric differences are expressions of different ecological histories between dolphins and terrestrial mammals. For instance, as seen in Figure 1b, the olfactory bulbs are absent. In contrast, auditory processing areas, such as the inferior colliculus, seen in Figures 5, 12, and 19, are enlarged, presumably because of the substantial amount of acoustic processing conducted by the dolphin. The enlargement of auditory processing structures is not, notably, accompanied by reduced visual structures, which suggests that vision is an important sensory-perceptual system in dolphins.

In keeping with the behavioral and electrophysiological evidence for a high degree of hemispheric independence (Viamonte et al., 1968; Mukhametov, 1984; Mukhametov et al., 1977), 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 (Marino et al., 2001; Tarpley and Ridgway, 1994). This feature is most apparent in the three planes in Figures 6, 7, 14, and 18–21.

The cerebellum is large relative to the hemispheres (Marino et al., 2000), as is especially evident in Figures 4, 5, 12, 18, and 19. As shown in Figure 6 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, which 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.

### *Evolutionary Considerations*

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 to those of other mammals, especially valuable for improving our understanding of the parameters of mammalian brain evolution.

There is abundant evidence for a phylogenetic link between cetaceans and ungulates (e.g., Milinkovitch et al., 1998) and evidence for a proposed sister-group relationship with the

hippopotamus (Gatesy, 1998). Given these affinities it is worth noting that there are similarities in cortical cytoarchitecture and neurochemistry between cetaceans and ungulates (Hof et al., 1999). It would be interesting to compare how these similarities (and differences) have been expressed at gross neuroanatomical levels in cetaceans and various ungulates. For instance, Hof et al. (1999) have noted the early physical maturity of the brain in both cetaceans and ungulates and the possibility that both brains may be characterized by a number of pedomorphic features.

The brain of the bottlenose dolphin as revealed in this study is characterized by similar morphological trends as those found in other cetaceans (Morgane et al., 1980). Although there are differences among cetacean brains, these differences are relatively minor compared to their 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 cranial transformation, 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 while 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.

## **CONCLUSION**

This article presents the first series of MRI-based anatomically-labeled sectioned images and three-dimensional reconstructions of the brain of the bottlenose dolphin. These images allow for the visualizing of a range of distinctive dolphin 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 coronal MRI scans and the “virtual” images in the horizontal and sagittal planes. 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. Our findings are consistent with what has been noted in the few existing histological studies of the bottlenose dolphin brain. Moreover, because we are able to preserve

the internal structure of the specimen, neuroanatomical studies of brains from MRI set the stage for increasingly accurate and reliable morphometric analyses of various brain structures.

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 process 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 to 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.

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