

Neuroanatomy of the Killer Whale (*Orcinus orca*) From Magnetic Resonance Images

LORI MARINO,^{1–3*} CHET C. SHERWOOD,^{4,5} BRADLEY N. DELMAN,^{6,7}
CHEUK Y. TANG,^{6,7} THOMAS P. NAIDICH,^{6,7} AND PATRICK R. HOF^{5,7–9}

¹Neuroscience and Behavioral Biology Program, Emory University, Atlanta, Georgia

²Center for Behavioral Neuroscience, Emory University, Atlanta, Georgia

³Living Links Center for the Advanced Study of Ape and Human Evolution, Yerkes
Regional Primate Center, Atlanta, Georgia

⁴Department of Anthropology and School of Biomedical Sciences, Kent State
University, Kent, Ohio

⁵Foundation for Comparative and Conservation Biology, Needmore, Pennsylvania

⁶Department of Radiology, Mount Sinai School of Medicine, New York, New York

⁷Advanced Imaging Program, Mount Sinai School of Medicine, New York, New York

⁸Department of Neuroscience, Mount Sinai School of Medicine, New York, New York

⁹New York Consortium in Evolutionary Primatology, New York, New York

ABSTRACT

This article presents the first series of MRI-based anatomically labeled sectioned images of the brain of the killer whale (*Orcinus orca*). Magnetic resonance images of the brain of an adult killer whale were acquired in the coronal and axial planes. The gross morphology of the killer whale brain is comparable in some respects to that of other odontocete brains, including the unusual spatial arrangement of midbrain structures. There are also intriguing differences. Cerebral hemispheres appear extremely convoluted and, in contrast to smaller cetacean species, the killer whale brain possesses an exceptional degree of cortical elaboration in the insular cortex, temporal operculum, and the cortical limbic lobe. The functional and evolutionary implications of these features are discussed. © 2004 Wiley-Liss, Inc.

Key words: killer whale; *Orcinus orca*; delphinid, cetacea; brain; MRI

Compared with other mammalian brains, the cetacean brain is, in many respects, highly unusual. Morgane et al. (1980: p. 105) state 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.” As there is a 55–60 million year divergence between cetaceans and the phylogenetically closest group, the artiodactyls, odontocete brains represent a blend of early mammalian and uniquely derived features (Ridgway, 1986, 1990; Glezer et al., 1988; Manger et al., 1998). Differences between cetacean and other mammalian brains of similar size have been found in cytoarchitecture and histochemistry (Garey et al., 1985; Garey and Leuba, 1986; Glezer and Morgane, 1990; Glezer et al., 1990, 1992a, 1992b, 1993, 1998; Hof et al., 1992, 1995, 1999, 2000), cortical surface configuration (Jacobs et al., 1979; Morgane et al., 1980; Haug, 1987), and subcortical structural morphology (Tarpley and Ridgway, 1994; Glezer et al., 1995a, 1995b).

The brains of a few cetacean species, particularly the bottlenose dolphin (*Tursiops truncatus*), have been studied relatively extensively. This is primarily due to the fact that bottlenose dolphins are popular in captivity and have been the focus of many long-term field studies. Therefore, much is known about their behavior, cognitive abilities, and social ecology. However, there is little neuroanatomical information on the brain of the largest Delphinid species, the killer whale (*Orcinus orca*), despite the fact that this species has

*Correspondence to: Lori Marino, Neuroscience and Behavioral Biology Program, Emory University, Atlanta, GA 30322. Fax: 404-727-0372. E-mail: lmarino@emory.edu

Received 5 February 2004; Accepted 11 May 2004

DOI 10.1002/ar.a.20075

Published online 14 October 2004 in Wiley InterScience (www.interscience.wiley.com).

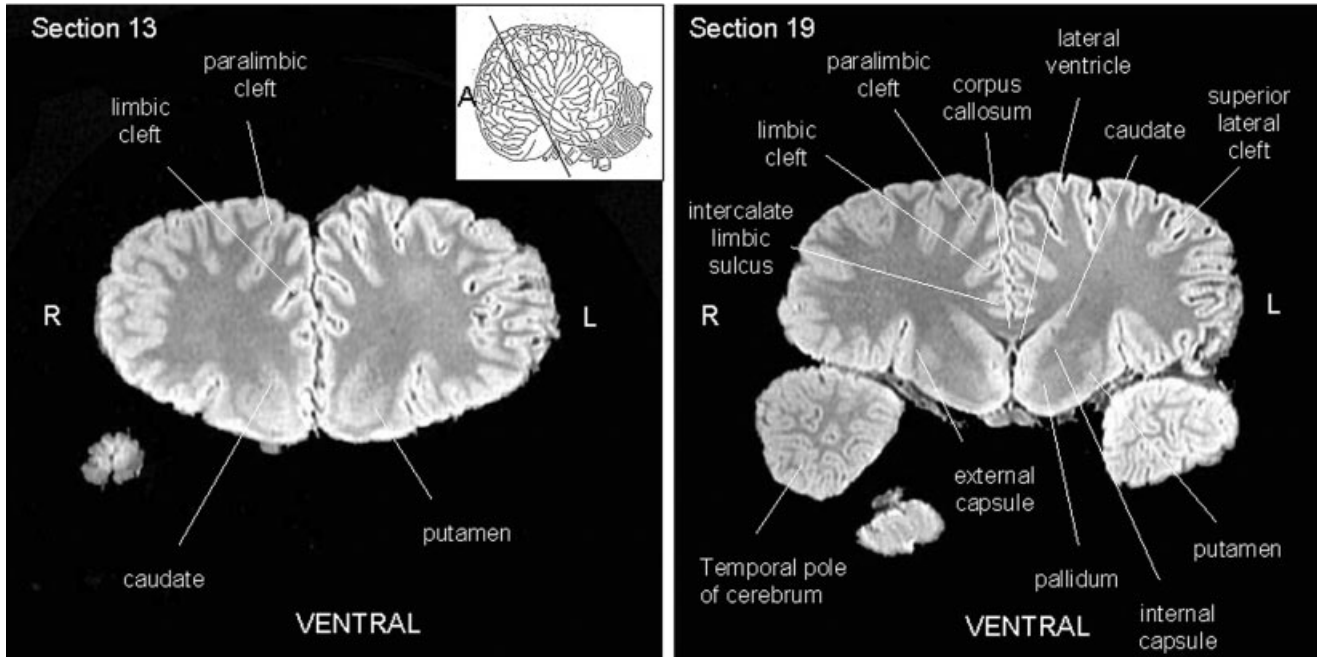


Fig. 1. Figures 1–10: Rostral-to-caudal sequence of anatomically labeled 2 mm thick coronal scans of the killer whale brain at 12 mm intervals. Section 13. L, left; R, right; A (inset), anterior.
Fig. 2. Section 19.

also been studied in captivity and in the field quite extensively. The lack of information on killer whale brains is likely due to the difficulties associated with preparing and examining such a large brain (approximately 5,000 g). Yet understanding killer whale neuroanatomy is important because, like the bottlenose dolphin, killer whales show evidence of many complex and unusual social, communicative, and cognitive capacities. These include learning-based cooperative foraging strategies (Baird, 2000), cultural variation and transmission (Rendell and Whitehead, 2001; Yurk et al., 2002), and possibly mirror self-recognition (Delfour and Marten, 2001). Therefore, if we wish to understand the neurobiological basis of such abilities, we will need to further our understanding of the brains of killer whales.

A few studies address the size of the killer whale brain (Pilleri and Gahr, 1970; Marino, 1998, 2002) or a specific brain structure such as the corpus callosum (Tarpley and Ridgway, 1994). There are, however, no published descriptions of the basic neuroanatomy of the killer whale. In the present study, we present the first labeled sequential description of killer whale neuroanatomy. The findings are based on magnetic resonance imaging (MRI) of a postmortem brain. As with previous MRI-based studies of other cetacean species (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b), this method offers the opportunity to observe the internal structure of the brain with little or no distortion and with atlas-level precision.

MATERIALS AND METHODS

Specimen

The specimen is the postmortem brain of an adult male killer whale (*Orcinus orca*). The brain was obtained shortly after death of natural causes and was immersion-fixed in a

large volume of 10% buffered formalin for an extended period of time.

Magnetic Resonance Imaging

Contiguous T2-weighted coronal and axial magnetic resonance images were acquired with a 1.5 T GE high-gradient MRI scanner equipped with 8.3 software at Mount Sinai School of Medicine. Coronal scans were acquired using TR = 500 msec and TE = 14.8 msec with an echo train of 2. Axial scans were acquired using TR = 700 and TE = 15 msec with an echo train of 2. Images are 2 mm thick with a matrix size of 512×512 and in-plane resolution of 32×32 cm yielding a voxel size of $0.63 \times 0.63 \times 2.0$ mm. Data were transferred electronically to eFilm (v1.5.3, eFilm Medical, Toronto, Ontario, Canada) for offline processing.

Anatomical Labeling and Nomenclature

All identifiable anatomical structures of the dolphin brain were labeled in the coronal and axial plane images. The MR images of the killer whale brain were compared with the published photographs and illustrations of the bottlenose dolphin brain from Morgane et al. (1980) as well as published neuroanatomical atlases based on MRI scans of other adult odontocete brains (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b). The labeling nomenclature follows that in the above sources.

RESULTS

General Morphology

Figures 1–10 display a rostral-to-caudal sequence of anatomically labeled originally acquired 2 mm thick coro-

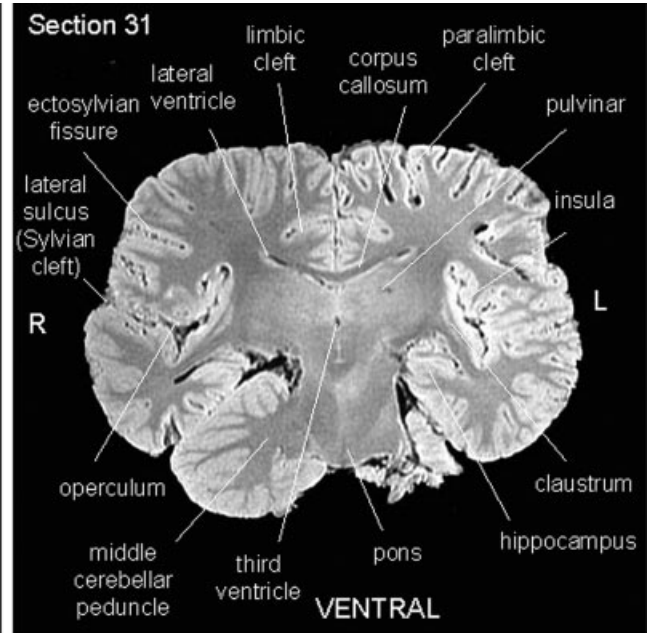
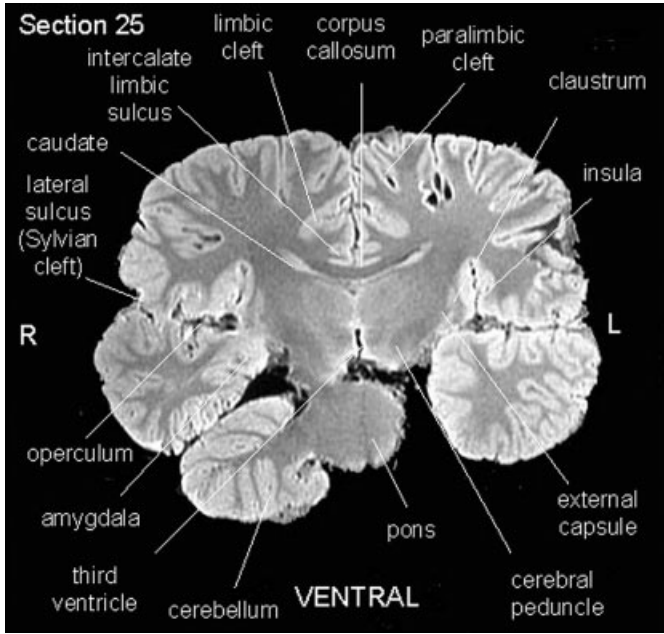


Fig. 3. Section 25.
 Fig. 4. Section 31.

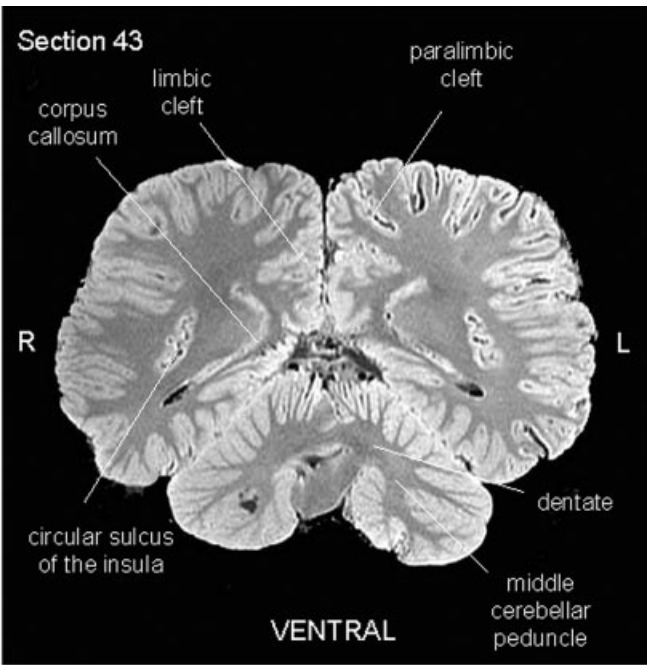
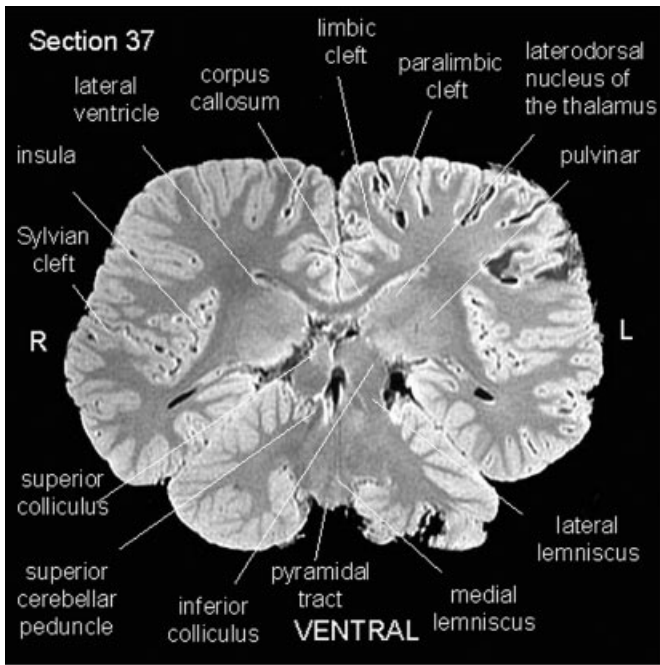


Fig. 5. Section 37.
 Fig. 6. Section 43.

nal scans at 12 mm intervals. Figure 1 also includes an inset diagram of an odontocete brain showing the approximate orientation of coronal sections. Figures 11–18 display a ventral-to-dorsal sequence of anatomically labeled originally acquired 2 mm thick axial scans at 20 mm intervals. Figure 11 also includes an inset diagram of an

odontocete brain showing the approximate orientation of horizontal sections. The figures show that the gross morphology of the killer whale brain is generally comparable to that of other odontocete brains (Morgane et al., 1980; Marino et al., 2001a, 2001b, 2002, 2003a, 2003b). The killer whale brain is characterized by extreme bitemporal

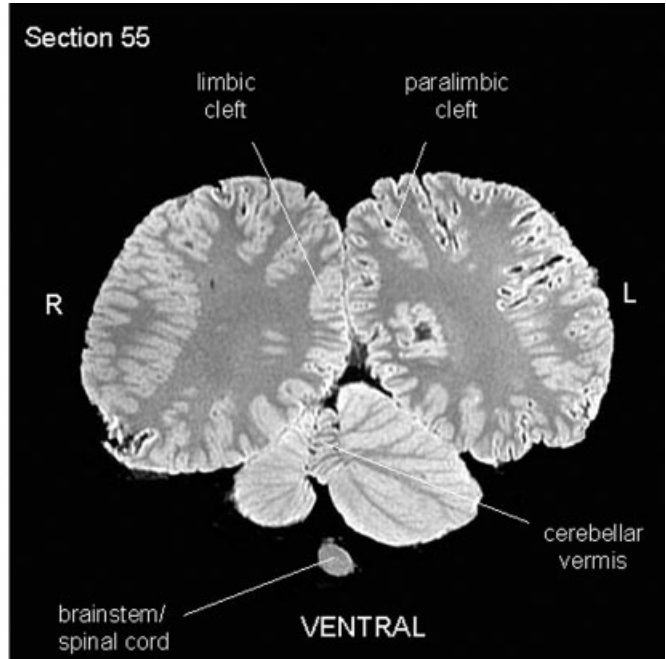
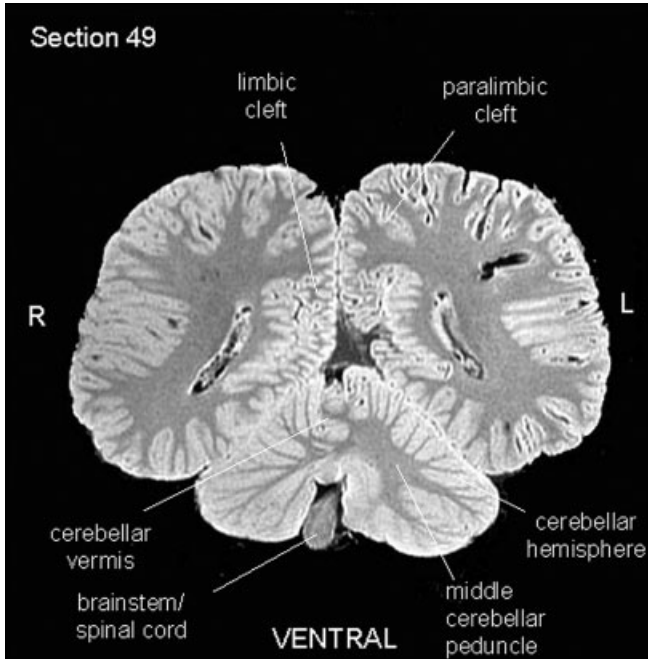


Fig. 7. Section 49.
Fig. 8. Section 55.

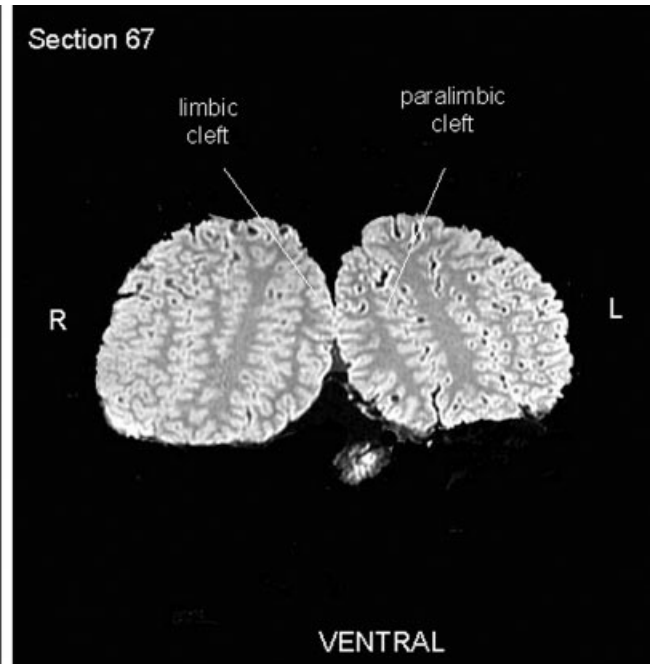
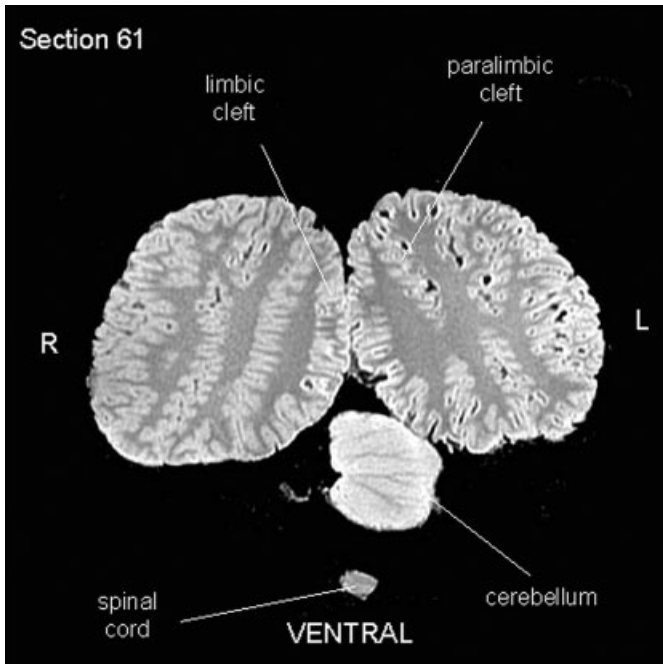


Fig. 9. Section 61.
Fig. 10. Section 67.

width, as seen most clearly in Figures 3–10 and 14–18, and is apparently highly convoluted. The killer whale shares with other odontocetes a three-tiered arrangement of limbic, paralimbic, and supralimbic arcuate cortical lobules divided by deep limbic and paralimbic clefts (Figs. 9, 10, 17, and 18).

Forebrain Anatomy

The most striking feature of the killer whale forebrain is the exceptional degree of cortical gyrification and sulcation, which is most apparent in Figures 3–10 and 15–18. Cortical complexity appears particularly extensive in the

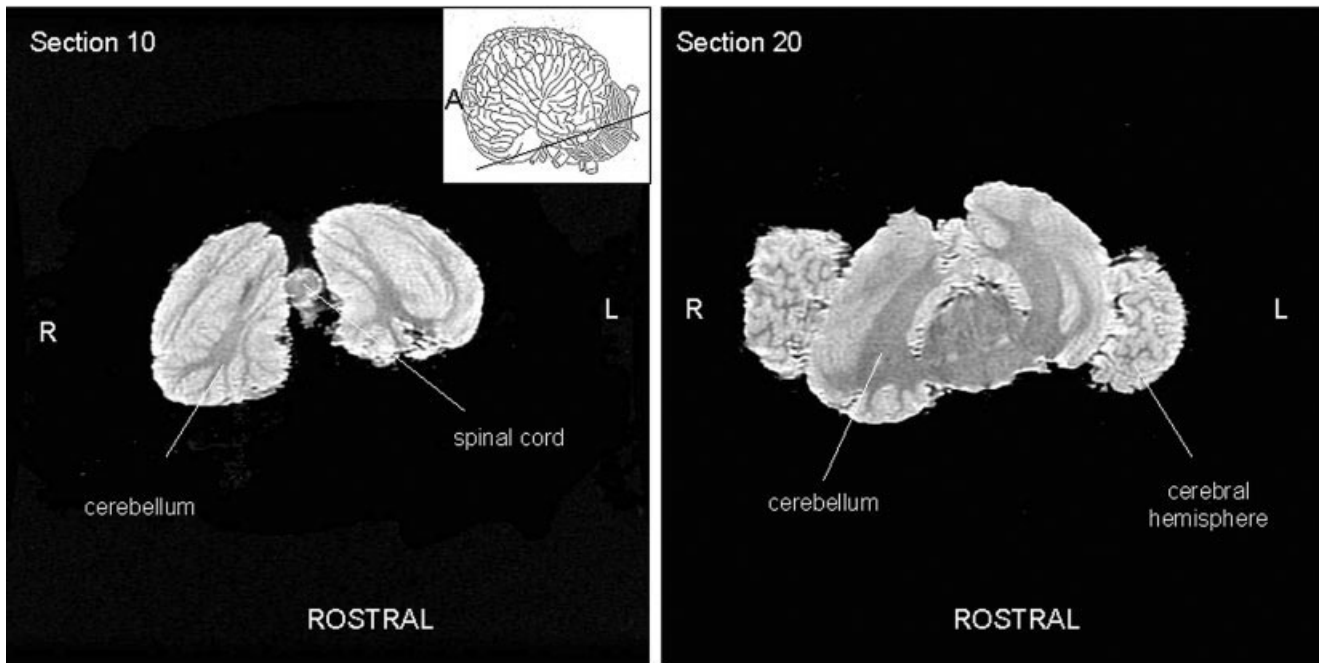


Fig. 11. Figures 11–18: Ventral-to-dorsal sequence of anatomically labeled 2 mm thick axial scans at 20 mm intervals. Section 10.

Fig. 12. Section 20.

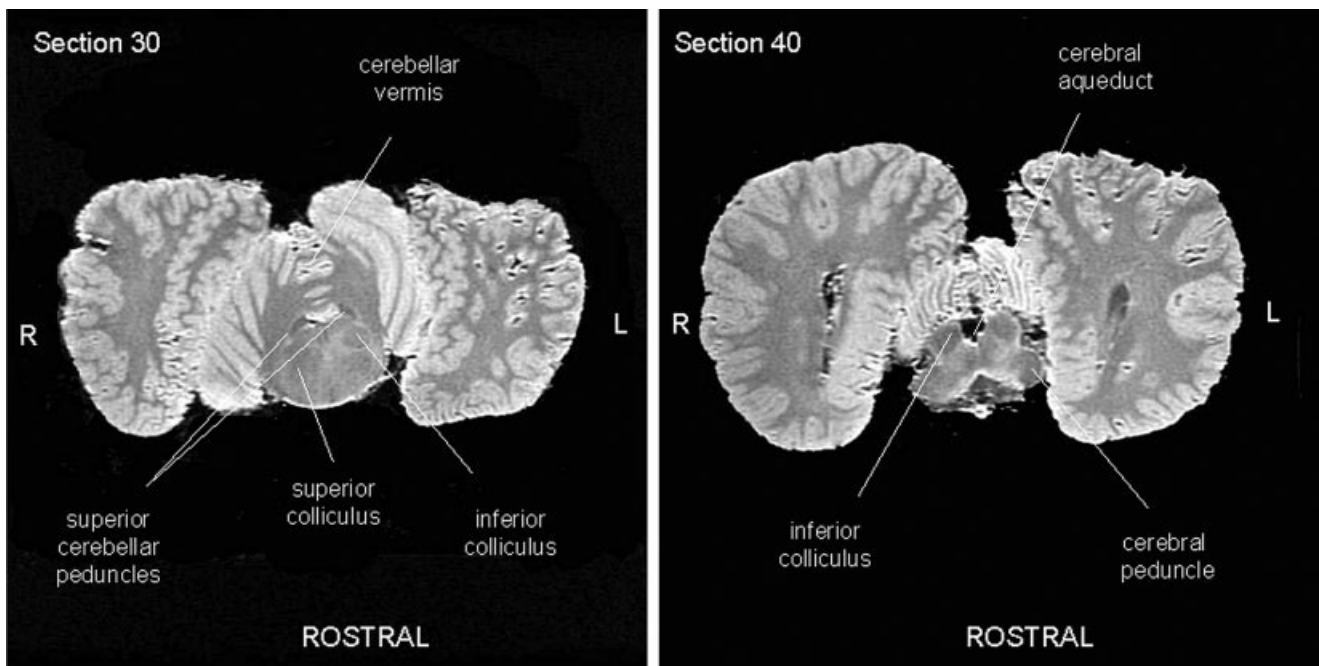


Fig. 13. Section 30.

Fig. 14. Section 40.

insular cortex (Figs. 4, 5, and 16), temporal operculum (Figs. 3 and 4), and the cortical limbic lobe (periarchicortical field above the corpus callosum and entorhinal cortex; Figs. 2–7, 16, and 17). An interesting corollary feature

to the small limbic system is the striking development of this cortical limbic lobe in cetaceans (Oelschlager and Oelschlager, 2002; Marino et al., 2003b). The thalamus also appears massive (Figs. 3–5, 15, and 16).

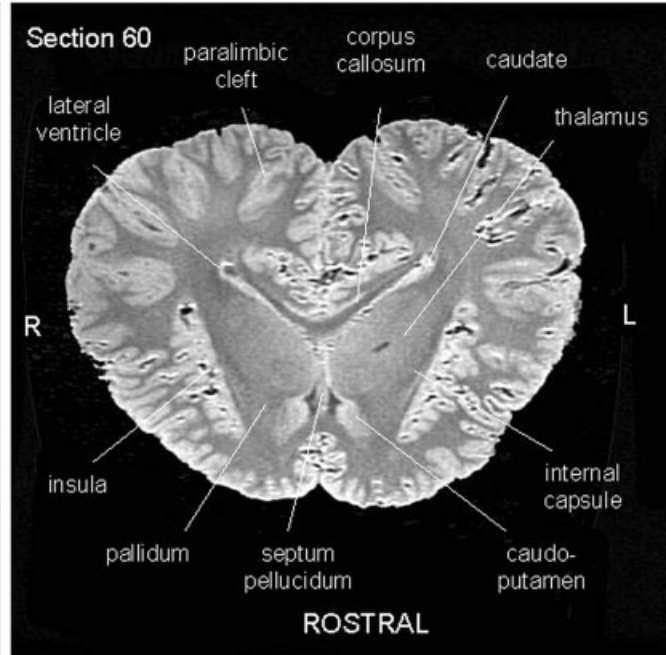
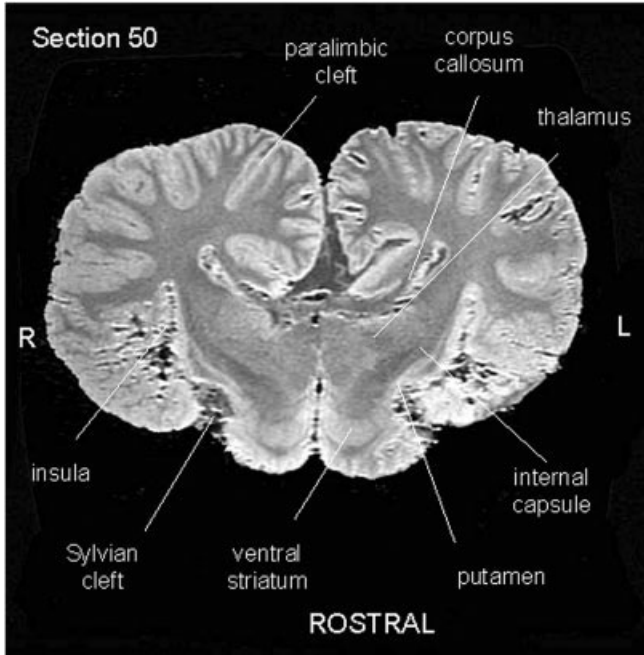


Fig. 15. Section 50.
Fig. 16. Section 60.

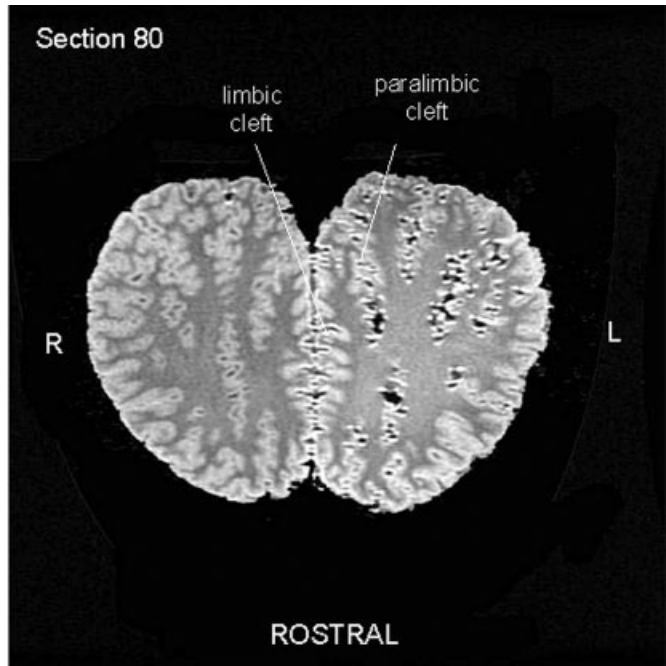
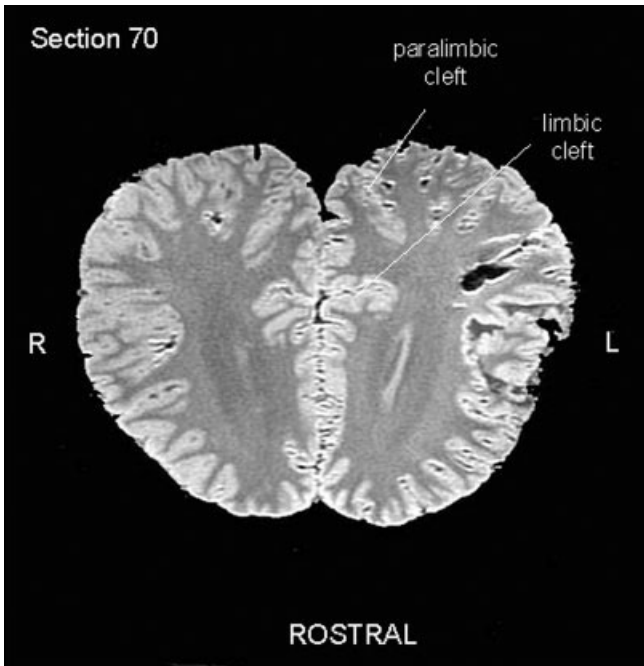


Fig. 17. Section 70.
Fig. 18. Section 80.

Consistent with findings in other odontocetes (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b), olfactory structures are absent in the killer whale brain and some limbic structures, particularly the hippocampus, are greatly reduced in size. In contrast, the amygdala appears well

developed (Fig. 3). All features of the basal ganglia that are found in other mammals are present in killer whale and other odontocete brains, including the caudate (Figs. 2, 3, and 16), putamen (Figs. 15 and 16), pallidum (Figs. 2 and 16), and internal capsule (Figs. 15 and 16).

The corpus callosum appears relatively small with respect to the mass of the hemispheres (Figs. 3–6, 15, and 16) despite the highly elaborated adjacent limbic field. This observation is consistent with findings in other odontocetes (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b).

Midbrain Anatomy

The killer whale brain demonstrates many of the proportions and spatial arrangements of midbrain structures found in other odontocetes. The tectum is well developed, particularly in the size of the inferior colliculus (Figs. 5, 13, and 14). As has been observed in other odontocetes (Marino et al., 2001a, 2002, 2003a, 2003b) and not in other mammals, the cerebral peduncle in the killer whale brain lies high on the lateral surface of the ventral midbrain (Fig. 3).

Hindbrain Anatomy

Figures 6 and 7 show the massive cerebellum in the killer whale brain as well as the narrow vermis relative to the cerebellar lobes. These features are typical of odontocetes (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b).

DISCUSSION

This article presents the first series of MRI-based anatomically labeled images of the brain of the killer whale. These images allow for the visualizing of the distinctive features of the brain of this species from two orientations by preserving the gross morphological and internal structure of the specimen.

Although a quantitative assessment was not made, the killer whale cerebral hemispheres appear more highly convoluted, possessing more surface area, than those of smaller species within the same family of delphinids such as the bottlenose dolphin (Marino et al., 2001a) and the common dolphin (*Delphinus delphis*) (Marino et al., 2002). The killer whale brain is also approximately 3.5 and 6.5 times more massive than that of the bottlenose dolphin and common dolphin brains, respectively. This pattern is consistent with Ridgway and Brownson (1984), who found a positive relationship between surface area and brain weight among odontocetes, including the killer whale, bottlenose dolphin, and common dolphin. Therefore, elaboration of cortical structures may represent the influence of scaling factors but quantitative assessments should be made to determine if nonscaling factors partially contribute to the variance. Additionally, although scaling factors may play a large role in accounting for the variance in cortex (or other brain structures for that matter), it is likely that there are real information processing consequences associated with increased convolutions of the cortex and other such scaling features in the brain.

The corpus callosum is an apparently relatively small structure in the killer whale brain. This observation is consistent with findings that corpus callosum midsagittal area in delphinids is considerably smaller in relation to brain mass than in other mammals and that dolphins with larger brains possessed relatively smaller corpora callosa (Tarpley and Ridgway, 1994). The inverse relationship between corpus callosum size and the size of the hemispheres is likely due to trade-offs between conduction velocities and brain metabolism (Shultz et al., personal communication).

The unusual lateral spatial position of the cerebral peduncle in the midbrain has been noted in other odonto-

cetes. It has been hypothesized that this arrangement is not only unique to cetaceans but due to the distinctive flexed posture of the midbrain in adult cetaceans (Marino et al., 2001a, 2002, 2003a, 2003b; Johnson et al., 2003). The proportions of the cerebellum in the killer whale brain are consistent with those in other odontocetes (Marino et al., 2001a, 2001b, 2002, 2003a, 2003b) as well as with the quantitative finding that the cerebellum makes up a significantly larger portion of the total brain mass in cetaceans than in primates (Marino et al., 2000).

The killer whale brain appears extremely elaborated in the insular cortex, surrounding operculum, and limbic lobe. The extremely well-developed limbic lobe is an interesting corollary feature to the small hippocampus. This finding is consistent with observations in other odontocetes (Morgane et al., 1980; Oelschläger and Oelschläger, 2002; Marino et al., 2003b) and is interesting in light of the fact that killer whales exhibit highly sophisticated ranging and distribution patterns that depend heavily on spatial memory skills (Baird, 2000). This juxtaposition of a vastly reduced archicortex and a highly elaborated periarchicortical zone leads to interesting questions about whether there was a transfer of hippocampus-like functions to other cortical, including periarchicortical, regions.

Finally, extreme development in the insular cortex and surrounding temporal operculum in the killer whale is intriguing. The insula mediates viscerosensation, gustation, and some somatosensation in most mammals. In humans, the frontal operculum is involved in speech. The topographical arrangement of cortical maps in cetaceans is very different from other mammals (Lende and Welker, 1972; Sokolov et al., 1972; Ladygina et al., 1978; Supin et al., 1978) and it remains a possibility that the insula and surrounding operculum are serving an entirely different purpose in the killer whale than in other mammals. However, one conjecture put forth by Morgane et al. (1980) suggests that, on the basis of architectonic evidence, the operculum may cortically represent trigeminal (rostrum) and glossopharyngeal (nasal respiratory tract) innervation. Given the fact that various sounds are modified by structures associated with the control of air flow through the nasal region, it is a speculative but not altogether unreasonable possibility that the cetacean operculum could serve a similar function as the speech-related opercular cortex in humans. In general, it would not be surprising to find that there are adaptive features of the killer whale brain associated with the evolution of complex communicative abilities given the highly complex social structure of this species (Baird, 2000; Rendell and Whitehead, 2001; Yurk et al. 2002). Others have suggested that the insular region surrounded by the operculum is related to specializations of the auditory cortex (Manger et al., 1998), though audition is obviously closely tied to communication. What is clear, however, is that because of its elaboration, the temporal opercular region of the killer whale and other odontocete brains should be the target of extensive future study.

ACKNOWLEDGMENTS

The authors thank Ilya I. Glezer and Peter J. Morgane for their generous donation of the specimen, John I. Johnson for advice and assistance with neuroanatomical identifications, and John C. Gentile for MRI technical assistance.

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