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Neuroanatomical Structure of the Spinner Dolphin (*Stenella longirostris orientalis*) Brain From Magnetic Resonance Images

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KEYWORDS

spinner dolphin, brain, neuroanatomy, MRI, magnetic resonance imaging

ABSTRACT

High-resolution magnetic resonance (MR) images of the brain of an adult spinner dolphin (Stenella longirostris orientalis) were acquired in the coronal plane at 55 antero-posterior levels. From these scans a computergenerated set of resectioned virtual images in the two remaining orthogonal planes was constructed with the use of the VoxelView and VoxelMath (Vital Images, Inc.) programs. Neuroanatomical structures were labeled in all three planes, providing the first labeled anatomical description of the spinner dolphin brain.

The unusual brain of cetaceans evinces a unique combination of features that are generally dissimilar to those observed in other mammalian brains. These differences are found at the level of the cortical cytological and chemical architecture (Glezer and Morgane, 1990; Glezer et al., 1990, 1992a, b, 1993, 1995a, 1999; Morgane et al., 1990; Hof et al., 1992, 1995, 1999, 2000), cortical surface configuration (Jacobs et al., 1979; Morgane et al., 1980; Haug, 1969), and subcortical structure (Tarpley and Ridgway, 1994; Glezer et al., 1995b; Marino et al., 2000). Furthermore, cetacean brains are highly elaborated and convoluted, and exhibit hyperproliferation of the hemispheres in all regions but the frontal lobe (Morgane et al., 1980).

Magnetic resonance imaging (MRI) has become a valuable method for elucidating normal neuroanatomical structures (Marino et al., 2001a–c, 2002, 2003a, b) and neuropathologies (Ridgway et al., 2002) in several species within the cetacean suborder Odontoceti (i.e., toothed whales, dolphins, and porpoises). MRI allows the visualization of brain structures in a normal three-dimensional (3D) arrangement without histological artifacts and distortions. MRI-based neuroanatomical studies have elucidated a number of similarities and differences across odontocete brains (Marino et al., 2001a–c, 2002, 2003a, b).

Although our knowledge of odontocete brains is increasing, there is essentially no literature regarding the brain of the spinner dolphin (*Stenella longirostris*). *S. longirostris* is one of five recognized *Stenella*

species within the family Delphinidae. *S. longirostris* is a gregarious, deepwater species that subsumes several geographical varieties. The species is known for its habit of performing spectacular leaps and spins out of the water. Until now, however, the only published papers referring to the brain of *S. longirostris* have been limited to reports concerning the size of the whole brain and body (Marino, 2002) and the corpus callosum (Tarpley and Ridgway, 1994). There has been no neuroanatomical description of the spinner dolphin brain. In the present work we present the first MRI-based, anatomically-labeled, three-dimensional (3D) description of the brain of a spinner dolphin (*Stenella longirostris orientalis*).

MATERIALS AND METHODS

Specimen

The specimen examined in this study was the postmortem brain of a sexually immature though morphologically adult female eastern spinner dolphin (*Stenella longirostris orientalis*) (specimen #SJC-010). Mortality occurred in a tuna purse seine net in the eastern tropical Pacific Ocean. The total body length of the specimen was 164.8 cm, and the total body mass was 33.6 kg. Perrin (1975) reported that the total length of female spinner dolphins does not exceed 175 cm; thus, the current specimen was morphologically mature. The specimen was necropsied and the brain was collected within 2 hr postmortem. The whole-brain weight was 450 g at necropsy. A small biopsy (ca. 2 g) of tissue was removed from the convexity of the right hemisphere for contaminant and histopathology analysis. The brain was fixed immediately after necropsy in 10% neutrally buffered formalin, and the fluids were changed twice during the remainder of the research cruise.

MRI

T2-weighted MR images of the entire brain were acquired in the coronal plane (cross-sectional to the major axis of the brain) at 55 anteroposterior levels with a 1.5 T Philips NT scanner (Philips Medical System, The Netherlands) at Emory University School of Medicine. The scanning sequence included the following parameters: slice thickness = 2.0 mm, slice interval = 0 mm, time to repetition = 3000 msec, time to echo = 13 msec, number of signals averaged = 2, field of view = 160 mm, and matrix = 256 x 256 pixels.

3D Reconstruction and Reformatting

Computer-generated 3D reconstruction images were created with the use of the software programs VoxelView and VoxelMath (Vital Images, Inc., Plymouth, MN) at the Laser Scanning Microscopy Laboratory at Michigan State University. The 3D-rendered model was then digitally resectioned in orthogonal planes to produce corresponding virtual sections in the horizontal and sagittal planes. The dolphin brain possesses pronounced mesencephalic, pontine, and cervical flexures, and anteroposterior foreshortening of the forebrain, which gives it a forward rotated appearance in the cranium with respect to the beak-fluke axis. However, scanning was done with the brain removed from the cranium, and the alignment of the planes was adjusted so that it closely approximated coronal, horizontal, and sagittal planes in the human brain.

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). The MR images of the spinner dolphin brain were compared with published photographs and illustrations of the bottlenose dolphin brain from Morgane et al. (1980), as well as with published neuroanatomical atlases based on MRI scans of adult

odontocete brains (Marino et al., 2001b, c, 2002, 2003a, b). The scans were also compared with a complete alternate series of sections of bottlenose dolphin brains that were stained for cell bodies (Nissl method) and myelinated fibers in the same three orthogonal planes. These stained-section series were from the Yakovlev-Haleem collection at the National Museum of Health and Medicine at the Armed Forces Institute of Pathology, and the Welker collection at the University of Wisconsin–Madison.

Volumetric Estimate of the Whole-Brain Weight of the Specimen

We measured the full anteroposterior extent of the brain in coronal sections with the image analysis software program Scion IMAGE for Windows (PC version of NIH IMAGE), using manually defined areas from successive slices that were integrated to yield a volumetric estimate of brain size. We converted the total volume estimate to weight units by multiplying the volume by the specific gravity of brain tissue (1.036 g/cm^3) (Stephan et al., 1981).

RESULTS

Volumetric Estimate of the Whole-Brain Weight of the Primary Specimen

The average of two measurements of whole-brain volume based on MRI was 498.5. This value is not substantially different from the fresh brain weight at necropsy. It is lower than a published estimate of brain weight from a cranial volume of 660 g (Marino, 2002).

Neuroanatomical Description

Figure 1A–H show a posterior-to-anterior sequence of originally acquired 2.0-mm-thick coronal MR brain sections at 10-mm intervals, and a labeled schematic illustration of each section. Figure 2A–H display every ninth ventral-to-dorsal reconstructed horizontal section and a labeled schematic illustration of each section. Figure 3A–H show every sixth midline-to-lateral reconstructed sagittal section through the left hemisphere, and a labeled schematic illustration of each section.

General morphology. The figures display an excellent level of preservation of spatial relationships among the brain's structures in both the originally-acquired and reconstructed sections. Figure 3A and B show the mesencephalic and pontine flexures that resemble brainstem flexure patterns found only in the embryonic stage of terrestrial mammals. These flexures, which may be pedomorphic in nature, remain present in all adult odontocetes. Olfactory structures are absent, as is typical of adult odontocetes.

Telencephalon. Figures 1C, D, G, and H; 2G and H; and 3A–H display the highly convoluted neocortex. The limbic and paralimbic clefts, which divide the three concentric limbic, paralimbic, and supralimbic lobes, are observable in Figures 1D–H, 2F–H, and 3B and C, respectively. Basal ganglia structures, such as the caudate, putamen, pallidum, and internal capsule, are easily visualized in Figures 1G, 2D–F, and 3B–D. Figures 1G and 3B show the striatal fundus, where the caudate, putamen, and ventral striatum (including the nucleus accumbens) come together on the ventral surface of the hemisphere, which is a distinctive feature of cetacean brains. As is the case with other odontocete species (Morgane et al., 1980; Marino et al., 2001a, c, 2002a, b), limbic structures, such as the hippocampus, are quite small and difficult to delineate. However, also as in other odontocetes, the amygdala in *S. longirostris* (shown in Fig. 1F) is well developed. An interesting corollary feature to the small limbic system and corpus callosum is the elaborated cortical limbic lobe (periarchicortical field above the corpus callosum and the entorhinal cortex) (Oelschlager and Oelschlager, 2002; Marino et al., 2003b).

As is the case with other odontocetes (Tarpley and Ridgway, 1994; Marino et al., 2001a, c, 2002a, b; Oelschlager and Oelschlager, 2002), the corpus callosum in *S. longirostris* is relatively thin compared to the mass of the hemispheres. This is observable in Figures 1F and G; 2D, F, and G; and 3A and B.

Diencephalon. The odontocete diencephalon, including that of *S. longirostris*, is quite large (Marino et al., 2001a, c, 2002, 2003b). The massive thalamus can be seen in Figures 1E and F, 2E and F, and 3B–D. The impressive size of the thalamus in cetaceans is largely, though not exclusively, due to the massive pulvinar region, which contains the medial geniculate nucleus (auditory) and the lateral geniculate nucleus (visual). Although the lateral geniculate is not as large as the medial geniculate nucleus, it is very well developed nonetheless. The hypothalamus can be seen in Figure 1F.

Mesencephalon. The spinner dolphin mesencephalon, which consists of the tectal region, is characterized by an outstandingly large inferior colliculus (auditory tectum). The large inferior colliculus is typical of odontocetes, and it can be at least four times as massive as the superior colliculus (visual tectum). The massive inferior colliculus is observable in Figures 1D, 2D, and 3A. The commensurately large brachium of the inferior colliculus, which projects to the medial geniculate nucleus, protrudes rather laterally and can be seen in Figure 1E. The correspondingly large lateral lemniscus can be seen in Figures 2B and 3C.

Metencephalon and myelencephalon. As is characteristic of cetaceans, the spinner dolphin cerebellum is large and well developed. This is most evident in Figures 1A–D and 2A–D, and all of the sections in Figure 3. The combination of large cerebellar hemispheres and comparatively narrow vermis (an arrangement also typical of cetaceans) is best seen in Figures 1B–D and 2C–F.

The remainder of the hindbrain (the pons and medulla) is large and contains numerous well-developed nuclei. The size of these structures in relation to the rest of the brain is best seen in Figure 3A and B.

DISCUSSION

We have shown that the spinner dolphin brain is characterized by morphological trends similar to those found in other odontocetes (Morgane et al., 1980). This work presents the first series of MRI-based, anatomically-labeled images of the spinner dolphin (*Stenella longirostris*) brain. In accordance with our previous MRI-based studies of odontocete brains (Marino et al., 2001a–c, 2002, 2003a, b), the present study demonstrates the value of image-based analyses of postmortem cetacean brains. The images allow one to visualize the distinctive features of the dolphin brain from various orientations, while at the same time they preserve the spatial arrangement of structures in the specimen.

The spinner dolphin brain evinces many of the same proportions and spatial arrangements of midbrain structures found in other odontocetes. The auditory tectum (inferior colliculus) is particularly well developed. The thalamus is massive, and, consistent with the large auditory tectum, the medial geniculate nucleus is well developed. In general, the large size of the thalamus is in keeping with the massive neocortex.

As in other odontocetes, the cerebral hemispheres of the spinner dolphin show a distinctive, smooth-surfaced “lobe” (designated the “lobe desert” by Broca (1878)) on their ventral surface. The corpus striatum, caudate, putamen, accumbens, and ventral striatum all come together to make up the striatal fundus (Figures 1G and 3B). This feature is probably due to the absence of overlying olfactory regions plus the large size of the striatal nuclei, which in turn is due to the large size of the cerebral cortex that is being serviced by these striatal regions.

The spinner dolphin cerebellum appears to be quite well developed. This is consistent with the finding in other odontocete species that the large cerebellum averages approximately 15% of total brain size (Marino et al., 2000). This is particularly interesting in the context of the involvement of the cerebellum in motor coordination (for review see Paulin, 1993) and the spinner dolphin's prodigious acrobatic abilities.

Relative to most other mammals, the spinner dolphin cortex exhibits a high degree of gyrification. However, it does not appear to be as finely convoluted as the cortex of odontocetes with larger brains, such as the bottlenose dolphin (*Tursiops truncatus*) and the beluga whale (*Delphinapterus leucas*), in which the average brain weights are approximately three and four times, respectively, the mass of the average spinner dolphin brain. This is consistent with a previous study by Ridgway and Brownson (1984), who found a positive relationship between surface area and brain weight among odontocetes.

The relatively small hippocampus may be partly due to a reduction in olfactory function. However, in many species the hippocampus plays an important role in memory and spatial learning (O'Keefe and Nadel, 1978). Therefore, it may be that the highly elaborated and closely associated limbic lobe reflects the transfer of hippocampus-like functions from the hippocampal domain to other cortical regions (including the periarchicortical and entorhinal regions) in the course of cetacean brain evolution. In the light of the fact that spinner dolphins appear to rely heavily on spatial learning and memory in the context of foraging and social behavior, this intriguing evolutionary possibility deserves further exploration.

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Fig. 1. (A–H) Posterior-to-anterior sequence of originally acquired 2.0-mm thick coronal MR brain scans at 10-mm intervals and a corresponding labeled illustration of each scan.

Fig. 1. (continued)

Fig. 2. (A–H) Every ninth ventral-to-dorsal reconstructed horizontal MR scan and a corresponding labeled illustration of each scan.

Fig. 2. (continued)

Fig. 3. (A–H) Every sixth midline-to-lateral reconstructed sagittal MR scan through the left hemisphere and a corresponding labeled illustration of each scan.

Fig. 3. (continued)

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