

Cetacean Brain Evolution: Multiplication Generates Complexity

Lori Marino
Emory University, U.S.A.

Over the past 55-60 million years cetacean (dolphin, whale, and porpoise) brains have become hyperexpanded so that modern cetacean encephalization levels are second only to modern humans. At the same time, brain expansion proceeded along very different lines than in other large-brained mammals so that substantial differences between modern cetacean brains and other mammalian brains exist at every level of brain organization. Perhaps the most profound difference between cetacean and other mammalian brains is in the architecture of the neocortex. Cetaceans possess a unique underlying neocortical organizational scheme that is particularly intriguing in light of the fact that cetaceans exhibit cognitive and behavioral complexity at least on a par with our closest phylogenetic relatives, the great apes. The neurobiological complexity underlying these cognitive capacities may involve the extreme multiplication of vertical structural units in the cetacean neocortex.

The origin and evolutionary history of cetaceans (dolphins, whales, and porpoises) has been the topic of vigorous scientific discussion for decades. The mammalian order Cetacea comprises one extinct and two living suborders. The Eocene suborder, Archaeoceti, contained approximately thirty (described) genera (Thewissen, 1998) and survived from the early Eocene, around 53 million years ago (mya) until the late Eocene, around 38 mya (Bajpai & Gingerich, 1998; Barnes et al., 1985; Uhen, 1998). Of the modern suborders (i.e., Neoceti), Mysticeti (comprising eleven living species of baleen whales) are first found in the fossil record in the latest Eocene (Mitchell, 1989), and Odontoceti (comprising sixty-six living species of toothed whales, dolphins, and porpoises) are first found in the fossil record in the early Oligocene (Barnes et al., 1985). Longstanding molecular evidence (Gatesy, 1998; Milinkovitch et al., 1998; Nikaido et al., 1996; Shimamura et al., 1997) and more recent morphological evidence (Geisler & Uhen, in press; Gingerich et al., 2001; Thewissen et al., 2001) confirm a phylogenetic link between cetaceans and artiodactyls (even-toed ungulates). Figure 1 shows the phylogenetic relationships among cetaceans, artiodactyls, and primates.

Along with the major transformations in body form and physiology that occurred during cetacean evolution a less obvious but equally significant transformation occurred in brain size and brain morphology. Evidence for this outcome comes from both examination of fossil endocranial morphology and comparisons of modern cetacean neuroanatomy with other mammals.

Studies of Fossil Endocranial Size and Morphology

Several estimates of cetacean brain mass from endocranial casts have provided strong evidence that the first suborder of cetaceans, the archaeocetes,

possessed brains that were quite similar in relative size to that of their purported ancestors (Edinger, 1955; Gingerich, 1998) and significantly smaller, also with regard to body size, than many of their modern counterparts (Breathnach, 1955; Dart, 1923; Gingerich, 1998; Marino et al., 2000a; Marples, 1949). The most reliable brain volume estimates for archaeocetes from the limited sample of fossil cetacean endocasts and endocranial volumes suggest an approximate range from 485 cc for *Saghacetus osiris* to 2620 cc for the large *Basilosaurus isis* (Gingerich, 1998). The estimated adult brain weights for two relatively well-known archaeocete species, *Dorudon atrox* and *Zygorhiza kochii* are 944.3 g and 738.2 g, respectively (Marino et al., 2000a).

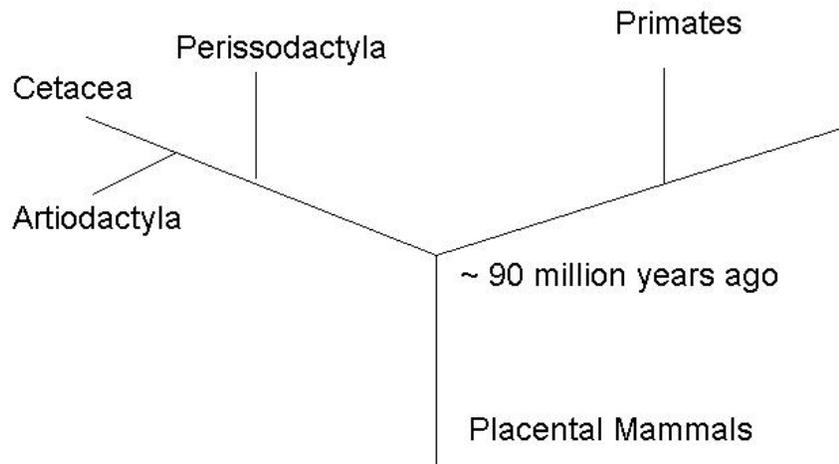


Figure 1. Phylogenetic relationships among cetaceans artiodactyls and primates.

Cetaceans became highly encephalized throughout the course of their evolution. A useful way to represent the level of encephalization obtained by a species or taxonomic group is with an Encephalization Quotient (EQ). EQ is a measure of observed brain size relative to expected brain size derived from a regression of brain weight on body weight for a sample of species. EQ measures how much larger or smaller a species' total brain size is from what would be expected solely on the basis of brain-body allometry. EQ values are essentially residuals from the regression line with values standardized as one, less than one, and greater than one for relative brain sizes that are average, below average, and above average, respectively. The absolute value of EQ varies with the reference group (Harvey & Krebs, 1990). The EQ values reported in this paper are based on the parameters of a regression equation derived by Jerison (1973).

Although estimates of brain size indicate that some archaeocetes had very large brains, archaeocetes possessed below-average EQ values ranging from 0.25 to 0.49 (Marino, 2002; Marino et al., 2000a). Various morphological features of fossil cetacean endocasts have also been noted in the literature, including cerebral asymmetry (Stefaniak, 1993), lobular morphology (Czyzewska, 1988; Edinger, 1955; Kellogg, 1936; Stefaniak, 1993) the relative size of major structures (Czyzewska, 1988; Edinger, 1955; Kellogg, 1936; Stefaniak, 1993), and imprints of cranial nerves (Czyzewska, 1988; Edinger, 1955; Kellogg, 1936). These kinds

of observations, when interpreted cautiously, reveal that there were significant morphological changes in cetacean brains during their evolution.

In a recently completed large-scale study of fossil cetacean endocranial morphology using Computed Tomography (CT)-based data, my colleagues and I have been able to describe and quantify substantial evolutionary changes in cetacean brain size and morphology (see Marino et al., 2003a, for a review of methods). Ongoing analyses of these brain size and morphology data, when registered to our best phylogenetic reconstructions, will provide the most comprehensive and quantitatively rigorous analyses of cetacean brain evolution to date. Preliminarily, these analyses reveal that there was a considerable increase in encephalization after the transition from archaeocetes to several modern forms. Later cetacean brains became highly elaborated and considerably different from the brain of Archaeoceti. Archaeocete brains possessed relatively small cerebral hemispheres, were vertically flattened and elongated in overall shape, and ended, rostrally, in well-developed olfactory peduncles (Figure 2a). Over time, cetacean cerebral hemispheres became considerably larger and more complexly convoluted. Also, olfactory structures regressed and the entire brain became foreshortened antero-posteriorly while maintaining prominent mesencephalic and pontine flexures. This pattern of elaboration gives the modern cetacean brain a globular shape. Cerebral enlargement, however, mainly took place in the parietal, temporal, and occipital regions with relatively less elaboration of frontal areas (Figure 2b).

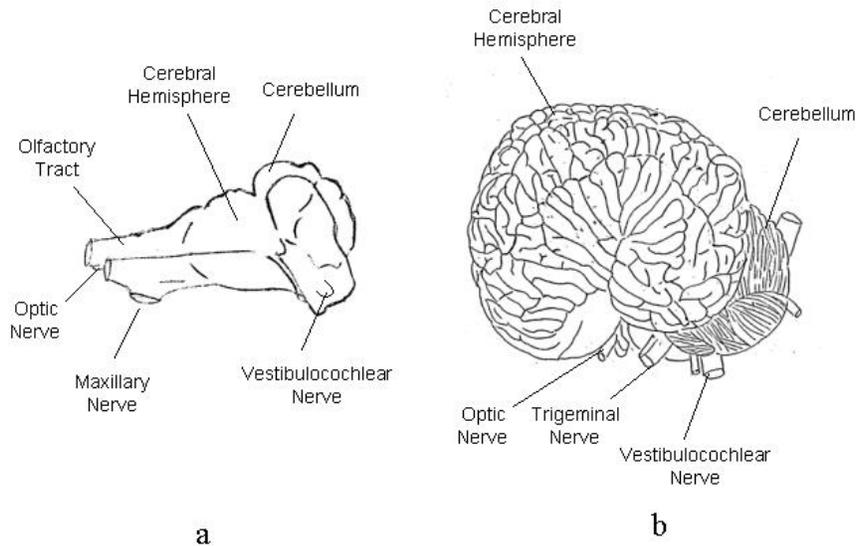


Figure 2. Illustrations of the brain of an archaeocete from a natural endocast (a) and the brain of a modern dolphin (b) with major structures labeled.

Comparative Studies of Brain Size Among Modern Groups

Comparative studies of modern cetaceans provide data for inferring the past through comparisons of modern species. There is a range of brain weights and encephalization levels among modern cetaceans, as there is in any taxonomic group. Modern odontocete adult brain weights range from 221 g for the Franciscana dolphin (*Pontoporia blainvillei*) to 8028 g for the sperm whale

(*Physeter macrocephalus*; Marino, 2002). The EQs of modern odontocetes range from 0.58 to 4.56 with a mean of 2.56 (Table 1). (The sperm whale (*Physeter macrocephalus*), with an EQ of 0.58, is the only known odontocete with an EQ considerably below 1 and is an example of a species with a disproportionately large body for which the measure of EQ is not particularly meaningful.)

Table 1
Known EQ Values for Modern Odontocete Species.

Species	EQ
Family Ziphiidae (Beaked and Bottlenose whales)	
<i>Mesoplodon mirus</i> (True's Beaked Whale)	1.97
<i>Mesoplodon europaeus</i> (Gervais' Beaked Whale)	2.11
<i>Mesoplodon densirostris</i> (Blainville's Beaked Whale)	1.39
<i>Ziphius cavirostris</i> (Cuvier's Beaked Whale)	0.92
Family Physeteridae (Sperm whales)	
<i>Physeter macrocephalus</i> (Sperm Whale)	0.58
<i>Kogia breviceps</i> (Pygmy Sperm Whale)	1.78
<i>Kogia simus</i> (Dwarf Sperm Whale)	1.63
Family Monodontidae (Beluga and Narwhal)	
<i>Delphinapterus leucas</i> (Beluga or White Whale)	2.24
<i>Monodon monoceros</i> (Narwhal)	1.76
Family Platanistidae (Freshwater dolphins)	
<i>Lipotes vexillifer</i> (Chinese River Dolphin)	2.17
<i>Inia geoffrensis</i> (Amazon River Dolphin)	2.51
<i>Platanista gangetica</i> (Ganges River Dolphin)	1.55
<i>Pontoporia blainvillei</i> (Franciscana Dolphin)	1.67
Family Phocoenidae (Porpoises)	
<i>Phocoena phocoena</i> (Harbor Porpoise)	3.15
<i>Phocoenoides dalli</i> (Dall's Porpoise)	3.54
Family Delphinidae (Oceanic Dolphins)	
<i>Tursiops truncatus</i> (Bottlenose Dolphin)	4.14
<i>Lagenorhynchus obliquidens</i> (Pacific White-sided Dolphin)	4.55
<i>Delphinus delphis</i> (Common Dolphin)	4.26
<i>Grampus griseus</i> (Risso's Dolphin)	4.01
<i>Globicephala melaena</i> (Long-finned Pilot Whale)	2.39
<i>Stenella longirostris</i> (Spinner Dolphin)	3.24
<i>Orcinus orca</i> (Killer Whale)	2.57
<i>Sotalia fluviatilis</i> (Tucuxi Dolphin)	4.56

Note. EQs are based on the formula derived by Jerison (1973).

In comparison, EQs of modern nonhuman anthropoid primates range from 1.02 to 3.21 with a mean of 2.0 (Marino, 1995, 1998). The EQ of modern humans is 7.0 (Marino, 1995; Marino, 1998). The modern odontocete values reveal that

some odontocetes have achieved a level of encephalization second only to modern humans and significantly higher than any of the modern nonhuman anthropoid primates. The high-end of the EQ range in odontocetes is occupied by several delphinid species with EQs above 4.0. These include the Tucuxi dolphin (*Sotalia fluviatilis*), the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), the common dolphin (*Delphinus delphis*), the bottlenose dolphin (*Tursiops truncatus*), and Risso's dolphin (*Grampus griseus*) with EQs of 4.56, 4.55, 4.26, 4.14, and 4.01, respectively (Marino, 2002)

The brains of modern mysticetes are also very large. For instance, the brain of the largest cetacean, the adult blue whale (*Balaenoptera musculus*) has been measured at approximately 7085 g. However, the EQs of mysticetes are all substantially below one (Marino 2002) because mysticetes have undergone extraordinary increases in body size without allometric increases in brain size. Therefore, EQ is not particularly meaningful in mysticetes because the general rules about brain and body relationships that underlie EQ do not hold for this group. Furthermore, the large size, high cortical convolutional index and highly derived morphology of mysticete brains establish that these brains have indeed undergone substantial enlargement and elaboration during the course of their evolution (Oelschlager & Oelschlager, 2002).

In addition to examining total brain size it is important to identify which specific structures and systems became enlarged and, regressed during the course of cetacean evolution. This information can inform us about how the relative importance of various functions changed throughout cetacean evolution. Studies of fossils can only offer information on surface morphology and size. Comparative studies of modern species are, therefore, critical for obtaining a level of morphological detail not attainable from fossil endocasts.

One of the more obvious morphological changes that occurred in cetacean brain evolution that is also highly detectable in fossils is the regression of olfactory system structures. Olfactory peduncles and bulbs were visibly well-developed in archaeocetes (Edinger, 1955). Fetal odontocetes possess small olfactory structures (Buhl & Oelschlager, 1988; Marino et al., 2001) that regress completely by birth. In modern adult odontocetes olfactory structures are completely missing except for the infrequent appearance of a short olfactory peduncle in adult sperm whales (*Physeter macrocephalus*) and northern bottlenosed whales (*Hyperoodon ampullatus*; Oelschlager & Oelschlager, 2002). Adult mysticetes have maintained small olfactory bulbs, a thin olfactory peduncle, and an olfactory tubercle (Oelschlager & Oelschlager, 2002). However, even in mysticetes the olfactory system has clearly regressed substantially.

In addition to olfactory structures, the limbic system in modern (and particularly odontocete) cetaceans, is exiguous compared with terrestrial mammals. Specifically, the hippocampus (archicortex), fornix, and mammillary bodies are all unusually small (Jacobs et al., 1979; Morgane et al., 1980; Oelschlager and Oelschlager, 2002). This condition is, in all likelihood, related to reduction in olfactory function. Nevertheless, as in humans, the amygdala is large and well-developed in cetaceans. The preservation of the amygdala is obviously due to the maintenance of substantial nonolfactory sources of input to this structure.

It is not possible to directly determine how developed the limbic system was in archaeocetes because these internal structures are not visible on endocasts.

Therefore, we cannot be absolutely certain that the small size of limbic structures in modern cetaceans is due to regression from a well-developed condition or a maintenance of initial structures without elaboration relative to the rest of the brain. However, the fact that archaeocetes had well-developed olfactory peduncles and bulbs strongly suggests that archaeocete limbic systems were well developed and that the condition in modern cetaceans is the result of regression of the limbic system over time.

An interesting corollary feature to the small limbic system is the extremely well-developed cortical limbic lobe (periarchicortical field above the corpus callosum and the entorhinal cortex) in cetaceans (Marino et al., 2003b; Oelschläger & Oelschläger, 2002). This juxtaposition of a vastly reduced archicortex and a highly elaborated periarchicortical/entorhinal zone leads to intriguing questions about whether there was a transfer of hippocampuslike functions from the olfactory-based hippocampal domain to other cortical regions, including periarchicortical and entorhinal regions.

Another notably undersized structure in cetacean brains is the corpus callosum, the main body of connectivity between the two hemispheres. Tarpley and Ridgway (1994) found that corpus callosum midsagittal area in delphinids was considerably smaller in relation to brain mass than in other mammals and that dolphins with larger brains possessed relatively smaller corpora callosa. Therefore, larger brains (in larger species) maintain less interhemispheric connectivity. The human and killer whale (*Orca orcinus*) corpora callosa, for example, possess the same crosssectional area despite the fact that the killer whale brain is over five times the weight of a human brain (Ridgway, 1986). As others have suggested, the relatively weaker interhemispheric connections in cetacean brains may facilitate the unihemispheric sleep patterns exhibited by cetaceans. It is also noteworthy that in cetaceans, as well as in other large-brained mammals, the relatively small size of the corpus callosum is not compensated for by enlargement of other commissures (Tarpley & Ridgway, 1994).

Despite the regression of several olfactory and limbic features, the cetacean brain is characterized by a hyperproliferation of tissue in other regions. Among those structures that are highly elaborated in cetacean brains are those related to the processing of auditory information. This feature of cetacean brains has been given considerable attention in the literature and can be summarized as follows. The diameter of the vestibulocochlear nerve in cetaceans is prodigious and, although the exact proportions of auditory to vestibular fibers are not agreed upon, it is composed of mainly auditory components (Oelschläger & Oelschläger, 2002). The ventral cochlear nucleus, trapezoid bodies, lateral lemniscus, and inferior colliculi are all greatly enlarged in comparison with terrestrial mammals. In odontocetes the inferior colliculus, which can be four times the size of the superior colliculus (Marino et al., 2003), projects to the large medial geniculate nucleus in the thalamus (which is massive itself, particularly in the pulvinar region). Primary auditory cortex, which receives afferent thalamic projections, has been electrophysiologically mapped in cetaceans and is located on the vertex of the hemisphere in the suprasylvian gyrus immediately lateral to the visual cortex. Secondary auditory cortex lies lateral to the primary auditory field in the medial ectosylvian gyrus (Supin et al., 1978). An interesting feature of the dolphin brain is the adjacency among the sensory cortical projection regions. This is a peculiar

arrangement for brains as large as those of cetaceans. The extent of neocortical areas involved in more integrated levels of auditory processing is not known but there is an extensive hemispheric field of “association” cortex that remains unmapped. It is clear that the elaboration of the auditory system in cetaceans occurred after they adopted an aquatic existence but answers to questions of when and how auditory elaboration occurred in cetacean evolution are largely unknown. What is apparent is that auditory functions were not, in any obvious way, elaborated at the expense of visual functions (Ridgway, 1990). (The only examples of reduced visual function in cetaceans are found among the Platanistidae, the freshwater dolphins. All species within this family appear to have well-developed auditory, including echolocatory, abilities.)

Another augmented region of the cetacean brain is the hindbrain, including pons, medulla oblongata, and cerebellum. Several brainstem nuclei are extremely large (Oelschlager & Oelschlager, 2002) and the cerebellum, which averages about 15% of total brain size in several odontocete species, is relatively larger than in humans and other primates (Marino et al., 2000b). The cetacean cerebellum contains two voluminous highly convoluted hemispheres and a relatively narrow vermis. The regions of the hemispheres that are among the most hypertrophied in odontocetes are the paraflocculus and paramedian lobules (Breathnach, 1960; Jansen & Jansen, 1969; Ridgway, 1990). There is evidence from natural endocasts that archaeocete cerebella were large in proportion to the rest of the brain (Edinger, 1955; Kellogg, 1936). Although the cerebellum of early cetaceans may have been well developed, more comprehensive morphometric analyses are needed to determine just how extensively the cerebellum changed in relative size during cetacean evolution.

Most notable among the regions of enlargement in the cetacean brain is the neocortex. The telencephalon is arranged into three concentric tiers of tissue comprising limbic, paralimbic, and supralimbic regions. The high degree of cortical gyrification in many cetacean brains and resulting neocortical surface area of approximately 3745 cm² is unsurpassed among mammals, including humans (2275 cm²; Elias & Schwartz, 1969; Ridgway & Brownson, 1984). Therefore, from both the point of view of total brain size and neocorticalization cetacean brains are highly elaborated. However, the cetacean neocortex is relatively thin with a width between 1.3 and 1.8 mm, as compared with the 3.0 mm thick human neocortex (Haug, 1969; Kesarev, 1971; Ridgway & Brownson, 1984). This combination of extreme surface area and narrow cortical width in cetaceans betrays a unique underlying neocortical organizational scheme that has been the focal point of longstanding and unresolved controversy about the computational capacities of the dolphin brain. It is to this discussion that we turn next.

Comparative Studies of Brain Organization and Morphology in Modern Groups

The study of cetacean neocortex has been limited to a few species and a subset of neocortical areas. However, there is a certain combination of shared characteristics that, despite variation across species, can be identified as distinctly cetacean. The cetacean brain has apparently exploited a highly conserved neocortical organizational scheme to evolve an extremely elaborated brain capable

of complex cognitive processing. The maintenance of a conservative neocortical theme is thought to be due to the early divergence of cetaceans from other mammal lineages. The large cetacean neocortex represents a striking alternative to the forms of elaboration one sees in other large brains, such as those of primates. For this reason, the cetacean brain is uniquely valuable for revealing the wide range of structural and functional possibilities that the mammalian neocortex can express. The major features of cetacean neocortical architecture that have been the focus of much attention are the following.

The topography of the primary and secondary neocortical projection zones in cetaceans is strikingly different from many other large mammals. As mentioned earlier, the functionally distinct somatosensory and motor regions, and the visual and auditory fields, exhibit an organizational pattern known as cortical adjacency. That is, the projection zones lie adjacent to one another with no cortex intervening between them. Furthermore, these zones are all clustered in the rostral region of the brain and, as a result, the visual and auditory areas occupy the lateral convexity cortex. Nonprojection regions, (i.e., “association” cortex), occupies the substantial field of surrounding tissue in the temporal, occipital, and posterior parietal regions. This arrangement is dissimilar to that found in primates and other large mammals. In primates, for instance, the projection regions are separated by intervening nonprojection cortex that cause the auditory and visual projection regions to occupy temporal and occipital areas, respectively. Some investigators have remarked that the cetacean pattern of projection zones is reminiscent of the positions of projection zones in mammals considered to be less derived, such as basal Insectivora (Glezer et al., 1988). Apart from the question of whether modern insectivores are “primitive,” this observation is based on a superficial similarity between the cetacean and insectivore pattern. The striking feature of the arrangement of projection zones in cetacean brains, which Glezer et al. (1988) also recognize, is the expansive field of nonprojection or “association” cortex that apparently occupies the remainder of the large hemispheres. This feature is not found in insectivores. Moreover, there is evidence from the highly developed nature of the thalamic pulvinar in cetaceans that the nonprojection or integrative neocortical regions in cetaceans are vast (Morgane et al., 1986).

Regarding lamination patterns, cetacean sensory neocortex possesses five layers (but see below). It is characterized by a very thick layer I that contains apical dendrites of extraverted pyramidal cells from a highly accentuated layer II (Glezer et al., 1988; Morgane et al., 1988). The strong pyramidalization of layer II is also a key feature of cetacean neocortex (Morgane et al., 1988). It has been suggested that, in cetaceans, the entirety of thalamocortical afferents feed into the thick layer I and through the extraverted neurons of layer II to deeper levels (Glezer et al., 1988; Morgane et al., 1990). Layer I also possesses large calretinin-containing neurons (Hof et al., 1999). In general and not surprisingly, the chemoarchitecture of the cetacean neocortex is dissimilar in many respects to that of primates and very similar to that of their closest phylogenetic relatives, artiodactyls (Glezer et al., 1999; Hof et al., 1999).

One of the most salient features of cetacean neocortex is the general lack of granularity, which is due primarily to the absence of (or, at best, barely identifiable) granular layer IV. Morgane et al. (1988) identified two types of visual cortex in the bottlenose dolphin. Heterolaminar cortex appears to contain a very

meager layer IV. In homolaminar cortex, however, layer IV is entirely absent. To most investigators, the overall dysgranularity of cetacean neocortex is one of the most striking and primary features signifying the conservative nature of cetacean neocortex. The general dysgranularity of the cetacean neocortex is viewed as evidence that cetaceans diverged from the mammalian line prior to the neocortical granularization trend evinced in other mammals. Furthermore, the general lack of layer IV in cetaceans has important implications for afferentation patterns. In primates and other mammals some afferent connections come through layer I to dendritic connections from layer II neurons while other specialized thalamocortical afferents synapse directly on layer IV. In cetaceans the majority of afferents appear to go through the very thick layer I to synapse *en passage* on extraverted neurons of layer II (Glezer et al., 1988). A small portion of afferents go to layers III and V as well (Garey & Revishchin, 1989; Revishchin & Garey, 1990). Some investigators view the segregation of afferents to layer IV and layer I to be a later evolutionary development than the pattern evinced in cetacean neocortex (Kesarev et al., 1975; Morgane et al., 1986; Glezer et al., 1988; Morgane et al., 1990). Therefore, according to this view, the cetacean neocortex has expanded on a highly conserved theme that almost entirely misses a stage of cortical evolution found in many other mammals.

Despite the importance of the evolutionary status of layer IV in cetacean neocortex the nature of this condition in cetaceans is far from settled and there still remain many critical unanswered questions about this feature in cetacean neocortex. For instance, there is some evidence suggesting that, in cetaceans, layer IV may be present in young animals and subsequently regress during maturation. Garey et al. (1985) observed a rudimentary granular layer IV in the visual cortex of an 18-day old bottlenose dolphin. Granularity in this layer was scarcer but still detectable in a 3-year old dolphin, and, apparently, absent in an adult. This finding speaks, albeit indirectly, to the question of whether the lack or scarceness of layer IV granular cells in cetacean neocortex is primary (conserved), that is, due to cetaceans not having attained a granular stage of neocortical evolution, or, secondary (derived), that is, due to cetaceans losing layer IV (and re-organizing thalamocortical inputs) throughout their evolution. Although ontogenetic-developmental patterns are not direct windows onto evolutionary processes, evolutionary-developmental (or, “evo-devo”) studies of cetacean neocortex are critically needed for determining the evolutionary status of layer IV and other characteristic features of cetacean neocortex.

In addition to the above characteristics, several researchers have remarked on the relative uniformity of the cetacean neocortex on both a cytoarchitectural (Morgane et al., 1988, 1990) and chemoarchitectural level (Hof et al., 1995, 1999, 2000). Also, the presence of numerous “transitional” types of neurons has been noted (Garey et al., 1985; Kesarev et al., 1977; Morgane et al., 1986). Despite the relative homogeneity of cetacean neocortex and, specifically, relatively weak lamination patterns, there is adequate evidence for another level of organization in the cetacean neocortex that depends on integration of nonhorizontal modules. Morgane et al. (1988, 1990) reported the presence of cytoarchitectonic vertically oriented columns in both homolaminar and heterolaminar visual cortex of the striped dolphin, *Stenella coeruleoalba*. The authors noted that these columns were more highly conserved than those in other mammals. Also, in a study of insular

cortex in the bottlenose dolphin, Manger et al. (1998) reported distinct cellular clumps or modular subdivisions that are different from the vertical columns noted by Morgane and his colleagues. Furthermore, Glezer et al. (1999) reported the prevalence of calretinin and calbindin-immunoreactive neurons over parvalbumin-immunoreactive neurons in dolphin neocortex and noted that, given the role of calretinin and calbindin neurons in inhibiting intracolumnar signals, the preponderance of vertical flow of inhibition along the columnar axis over laminar or horizontal flow is a chemoarchitectural indicator of strong verticality in cetacean neocortex.

Therefore, as in other mammals, non-laminar modularity imposes another level of complexity on the cetacean neocortex. The cetacean brain, however, represents the most highly developed version of a particular kind of expansion that involved an enormous multiplication of these modules and, consequently, the level of nonlaminar connectivity in the neocortex. This extreme expansion of the quantity of uniform units and connections in the cetacean neocortex is a special way of achieving computational complexity that represents an alternative to the evolutionary route taken by other large mammals, including primates. Morgane et al. (1990) remarked on the intriguing nature of the cetacean neocortex with the following:

“...we are dealing with a very unique situation of a massive cerebral cortex, in many cases considerably larger than in the human brain, but one in which the fundamental cortical structural plan is similar to that of smaller, more conservatively organized brains such as seen in basal insectivores and bats. Computationally, such a cortex is of special interest in that the total number of functional cortical modules may be very great but the fundamental organization is one of relative simplicity compared to those of more progressive terrestrial mammalian forms.”

Here Morgane et al. use the term *progressive* to refer descriptively to the kind of neocortex that primates possess and it would be a mistake to interpret their remark as implying that the cetacean brain is more primitive or simpler than primate brains. On the contrary, as mentioned before, the level of encephalization in many cetaceans is exceeded only by modern humans and the anatomical evidence demonstrates that, despite building on an apparently conservative laminar theme, cetacean brains are highly derived and elaborated overall. However, in the final analysis, brain complexity is revealed by the cognitive and behavioral complexity of an organism. In the case of cetaceans, the cognitive-behavioral literature demonstrates that cetacean intelligence is on a par with that of many primates.

Cetacean Brains and Cognition

Evidence points to a striking degree of convergence between primates and cetaceans in terms of the complexity, diversity, and flexibility of cognition and behavior across many domains. This level of cognitive convergence might be unexpected on the basis of their deep phylogenetic divergence, adaptation to very different physical environments, and divergent neuroanatomical evolution but, on the other hand, expected on the basis of general levels of encephalization and neocortical elaboration.

It should be noted that an overwhelming majority of experimental research on cognition and behavior in cetaceans has focused on the bottlenose dolphin, *Tursiops truncatus*, with a relatively small proportion of studies on other odontocetes such as the killer whale, *Orcinus orca*, the beluga whale, *Delphinapterus leucas*, and a tiny subset of other odontocete species. Therefore, as in any taxonomic group, one should expect cognitive and behavioral differences across cetacean species. However, the sizeable literature on the bottlenose dolphin can serve as an indication or “existence proof” of cognitive and behavioral abilities in cetaceans in general. Furthermore, the more extensive literature on behavioral ecological and social complexity in natural populations from a wider range of odontocetes and mysticetes is congruent with indications of a high-level intelligence from the experimental literature.

Bottlenose dolphins have demonstrated sophisticated capacities in the realms of memory (Mercado III et al., 1998, 1999), innovation (Braslau-Schneck, 1994), vocal and behavioral mimicry (Braslau-Schneck, 1994; Herman, 2002a; Reiss & McCowan, 1993; Richards et al., 1984; Xitco, 1988), and abstract rule comprehension and formation (Herman et al., 1994; Mercado III, 1998). These capacities appear to be at a level typically only demonstrated by great apes and humans.

Bottlenose dolphins have also demonstrated extensive capacities in the ability to understand an artificial (i.e., human devised) communication system based upon symbols and rules. Competence in comprehension of symbolic references and rule-based sequences appears to be limited to great apes, bottlenose dolphins, and an African Grey Parrot (Pepperberg, 1999). Only three species have demonstrated the capacity to understand that symbol or “word” order has meaning. These are a bonobo (Savage-Rumbaugh et al., 1993), a common chimpanzee (Premack, 1976), and bottlenose dolphins (Herman, 2002b). Although the comparability of primate and cetacean (as well as avian) studies of artificial communication system comprehension must be carefully considered, it is interesting that only these very few species have been able to meaningfully participate in such studies and also demonstrate compelling, if not definitive, capacities within the context of these studies. The fact that studies of comprehension of artificial communication systems can only be attempted with these very few species suggests that they all have converged toward a level of cognitive complexity that allows them to understand a simple symbolic and rule-based system of communication.

Another exceedingly rare capacity demonstrated by bottlenose dolphins is mirror self-recognition, which is a component of the more general capacity for self-awareness. Self-awareness refers to the ability to think about one’s own behavior, physical make-up, and, thoughts and feelings. Up until recently, mirror self-recognition had been demonstrated only in humans and great apes (see Povinelli et al., 1997, for a review of this literature) but not monkeys or lesser apes (Anderson & Roeder, 1989; Bayart & Anderson, 1985; Hyatt, 1998; Shaffer & Renner, 2000; Suarez & Gallup, 1986).

Reiss and Marino (2001) reported the first conclusive evidence of mirror self-recognition in a nonprimate species, the bottlenose dolphin. In a series of controlled variations of the procedures used with primates, both dolphins in our study used a mirror to investigate parts of their bodies that were marked (Figure 3).

These findings revealed, once again, that dolphins possess cognitively complex capacities that are found in only a small subset of primates with highly elaborated brains. Bottlenose dolphins also show related capacities in the domains of awareness of one's own body parts and behavior (Herman et al., 2001; Mercado et al., 1998, 1999).

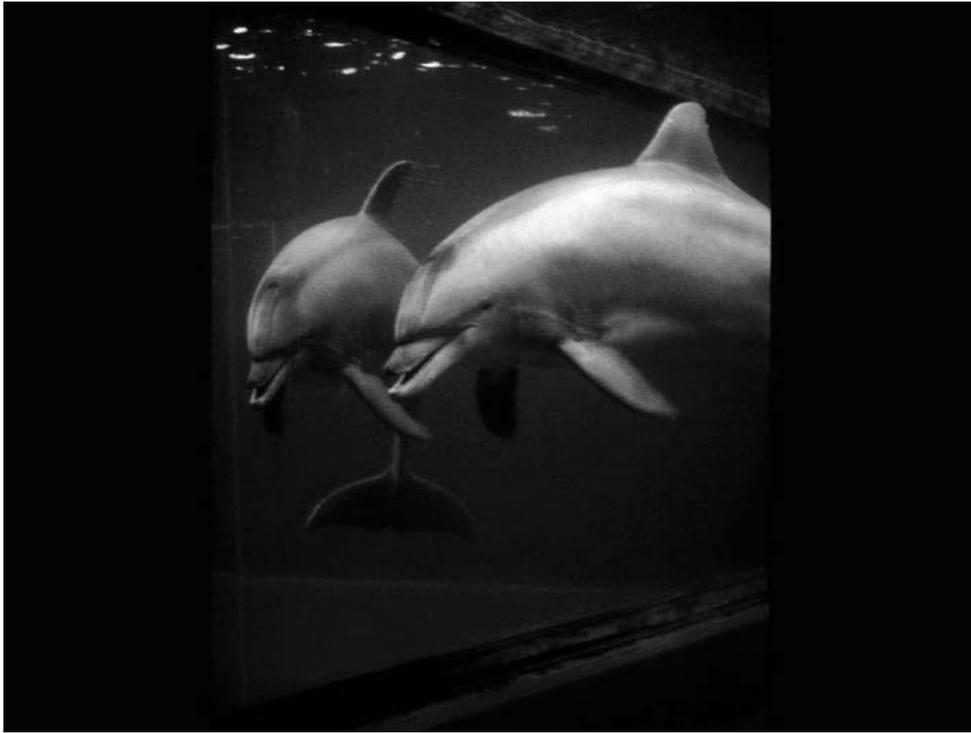


Figure 3. Bottlenose dolphins use mirrors to investigate marks on their bodies. Photograph by D. Reiss.

Many investigators have hypothesized that the cortical circuitry of the prefrontal cortex in humans and great apes is the necessary neuroanatomical substrate for self-recognition and other dimensions of self-awareness (Keenan et al., 2000; Miller et al., 2001; Stuss et al., 2001). The Reiss and Marino findings show that dolphins are capable of mirror self-recognition despite possession of unelaborated frontal lobes (or homologous frontal lobe structures) and an overall cortical organizational pattern that is very different from that of primates. This finding challenges the view that self-awareness is specific to primate frontal lobe architecture and suggests that self-awareness could be more of a holistic property of brains of any species that achieve a certain threshold of elaboration regardless of how that elaboration occurred.

Furthermore, the excellent performance of dolphins on tasks that rely on sophisticated memory abilities leaves open the interesting question of how cetaceans possess such high-level memory capacities while possessing a highly reduced hippocampus. In general, the importance of examining the cognitive and behavioral capacities of cetaceans and primates within the context of their respective neuroanatomies is that it affords the opportunity to resolve questions

about the specificity of neurobiological configurations underwriting cognitive complexity.

Summary

In summary, neuroanatomical studies of cetacean brains reveal that they are highly elaborated from the ancestral condition. Neocortical organization, based on extreme repetition of a relatively conserved pattern, is a radical departure from the brains of other large mammals. This situation is intriguing in light of the fact that there is abundant evidence for high-level convergent cognitive abilities between dolphins and primates.

References

- Anderson, J. R., & Roeder, J. J. (1989). Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror-image stimulation. *Primates*, **30**, 581-587.
- Bajpai, S., & Gingerich, P. D. (1998). A new Eocene archaeocete (Mammalia, Cetacea) from India and the time of origin of whales. *Proceedings of the National Academy of Sciences USA*, **95**, 15464-15468.
- Barnes, L. G., Domning, D. P., & Ray, C. E. (1985). Status of studies on fossil marine mammals. *Marine Mammal Science*, **1**, 15-53.
- Bayart, F., & Anderson, J. R. (1985). Mirror-image reactions in a tool-using adult male *Macaca tonkeana*. *Behavioural Processes*, **10**, 219-227.
- Braslau-Schneck, S. (1994). *Innovative behaviors and synchronization in bottlenosed dolphins*. Unpublished Master's Thesis, University of Hawaii, Honolulu.
- Breathnach, A. S. (1955). Observations on endocranial casts of recent and fossil cetaceans. *Journal of Anatomy*, **89**, 533-546.
- Breathnach, A. S. (1960). The cetacean central nervous system. *Biological Reviews*, **35**, 187-230.
- Buhl, E. H., & Oelschläger, H. A. (1988). Morphogenesis of the brain in the harbour porpoise. *Journal of Comparative Neurology*, **277**, 109-125.
- Czyzewska, T. (1988). Natural endocranial casts of the whales *Pinocetus polonicus*, from the Pinczow Limestones (Middle Miocene; southern slopes of the Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **38**, 46-49.
- Dart, R. (1923). The brain of the Zeuglodontidae (Cetacea). *Proceedings of the Zoological Society of London*, **42**, 615-654.
- Elias, H., & Schwartz, D. (1969). Surface areas of the cerebral cortex of mammals determined by stereological methods. *Science*, **166**, 111-113.
- Edinger, T. (1955). Hearing and smell in cetacean history. *Monatschrift für Psychiatrie und Neurologie*, **129**, 37-58.
- Garey, L. J., Winkelman, E., & Brauer, K. (1985). Golgi and Nissl studies of the visual cortex of the bottlenose dolphin. *Journal of Comparative Neurology*, **240**, 305-321.
- Garey, L. J., & Revishchin, A. V. (1989). Localization of thalamic neurons innervating the visual cortex of the lateral gyrus in the porpoise. *Doklady Akademii Nauk SSSR*, **305**, 1482-1486.
- Gatesy, J. (1998). Molecular evidence for the phylogenetic affinities of cetacea. In J. G. M. Thewissen (Ed.), *The emergence of whales* (pp. 63-111). New York: Plenum Press.
- Geisler, J. H., & Uhen, M. D. (in press). New fossils corroborate a close relationship between hippos and whales. *Journal of Vertebrate Paleontology*.
- Gingerich, P. D. (1998). Paleobiological perspectives on Mesonychia, Archaeoceti, and the origin of whales. In J. G. M. Thewissen (Ed.), *The emergence of whales* (pp. 423-449). New York: Plenum Press.
- Gingerich, P. D., ul Haq, M., Zalmout, I.S., Khan, I.H., & Sadiq, M. (2001). Origin of whales from early artiodactyls: Hands and feet of Eocene Protocetidae from Pakistan. *Science*, **293**, 2239-2242.
- Glezer, I. I., Jacobs, M. S., & Morgane, P. J. (1988). Implications of the 'initial brain' concept for brain evolution in Cetacea. *Behavioral and Brain Sciences*, **11**, 75-116.
- Glezer I. I., Hof, P. R., & Morgane, P. J. (1999). Comparative analysis of calcium-binding

protein-immunoreactive neuronal populations in the auditory and visual systems of the bottlenose dolphin (*Tursiops truncatus*) and the macaque monkey (*Macaca fascicularis*). *Journal of Chemical Neuroanatomy*, **15**, 203-237.

Haug, H. (1969). Vergleichende, quantitative untersuchungen an den gehiren des menschen, des elefanten und einiger zahnwale. *Medizinsche Monatschrift*, **23**, 201-205.

Harvey, P., & Krebs, J. R. (1990) Comparing brains. *Science*, **249**, 140-146.

Herman, L. M. (2002a). Vocal, social, and self-imitation by bottlenosed dolphins. In C. Nehaniv & K. Dautenhahn (Eds.). *Imitation in animals and artifacts*. (pp. 63-108). Cambridge, MA: MIT Press.

Herman, L. M. (2002b). Language learning. In W. F. Perrin, B. Wursig, & H. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 685-689). San Diego, CA: Academic Press.

Herman, L. M., Pack, A. A., & Wood, A. A. (1994). Bottlenose dolphins can generalize rules and develop abstract concepts. *Marine Mammal Science*, **10**, 70-80.

Herman, L. M., Matus, D. S., Herman, E. Y. K., Ivancic, M., & Pack, A. A. (2001). The bottlenosed dolphins (*Tursiops truncatus*) understanding of gestures as symbolic representations of its body parts. *Animal Learning and Behavior*, **29**, 250-264.

Hof, P. R., Glezer, I. I., Revishchin, A. V., Bouras, C., Charnay, Y., & Morgane, P. J. (1995). Distribution of dopaminergic fibers and neurons in visual and auditory cortices of the harbor porpoise and pilot whale. *Brain Research Bulletin*, **36**, 275-284.

Hof, P. R., Glezer, I. I., Conde, F., Flagg, R. A., Rubin, M. B., Nimchinsky, E. A., Vogt Weisenhorn, D. M. (1999). Cellular distribution of the calcium-binding proteins parvalbumin, calbindin, and calretinin in the neocortex of mammals: phylogenetic and developmental patterns. *Journal of Chemical Neuroanatomy*, **16**, 77-116.

Hof, P. R., Glezer, I. I., Nimchinsky, E. A., & Erwin, J. M. (2000). Neurochemical and cellular specializations in the mammalian neocortex reflect phylogenetic relationships: Evidence from primates, cetaceans, and artiodactyls. *Brain, Behavior and Evolution*, **55**, 300-310.

Hyatt, C. W. (1998) Responses of gibbons (*Hylobates lar*) to their mirror images. *American Journal of Primatology*, **45**, 30-311.

Jacobs, M. S., McFarland, W. L., & Morgane, P. J. (1979). The anatomy of the brain of the bottlenose dolphin (*Tursiops truncatus*). Rhinic lobe (rhinencephalon): the archicortex. *Brain Research Bulletin*, **4**, 1-108.

Jansen, J., & Jansen, J. K. S. (1969). The nervous system of cetacea. In H. T. Anderson (Ed). *Biology of marine mammals* (pp. 175-252). New York: Academic Press.

Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York: Academic Press.

Keenan, J. P., Wheeler, M. Gallup, Jr., G. G., & Pascual-Leone, A. (2000) Self-awareness and the right prefrontal cortex. *Trends in Cognitive Science*, **4**, 338-344.

Kellogg, R. (1936). *A review of the Archaeoceti*. Washington, DC: Carnegie Institution of Washington.

Kesarev, V. (1971). The inferior brain of the dolphin. *Soviet Science Review*, **2**, 52-58.

Kesarev, V. (1975). Homologization of the cerebral neocortex in cetaceans. *Arkhiv Anatomii, Histologii I Embriologii*, **68**, 5-13.

Kesarev, V., Malofeyeva, L., Trykova, O. (1977). Ecological specificity of cetacean neocortex. *Journal Hirnforschung*, **18**, 447-460.

Manger, P., Sum, M., Szymanski, M., Ridgway, S., & Krubitzer, L. (1998). Modular subdivisions of dolphin insular cortex: Does evolutionary history repeat itself? *Journal of Cognitive Neuroscience*, **10**, 153 – 166.

Marino, L. (1995). *Brain-behavior relationships in cetaceans and primates: Implications for the evolution of complex intelligence*. Unpublished Ph.D. Thesis, State University of New York at Albany.

Marino, L. (1998). A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior, and Evolution*, **51**, 230-238.

Marino, L., Uhen, M.D., Frohlich, B., Aldag, J.M., Blane, C., Bohaska, D., & Whitmore, Jr. F.C. (2000a). Endocranial volume of mid-late Eocene archaeocetes (Order: Cetacea) revealed by computed tomography: Implications for cetacean brain evolution. *Journal of Mammalian Evolution*, **7**, 81-94.

Marino, L., Rilling, J. K., Lin, S. K., & Ridgway, S. H. (2000b). Relative volume of the cerebellum in the bottlenose dolphin and comparison with anthropoid primates. *Brain, Behavior, and Evolution*, **56**, 204-211.

Marino, L., Murphy, T. L., Gozal, L., Johnson, J. I. (2001) Magnetic resonance imaging

and three-dimensional reconstructions of the brain of the fetal common dolphin, *Delphinus delphis*. *Anatomy and Embryology*, **203**, 393-402.

Marino, L. (2002). Brain size evolution. In W. F. Perrin, B. Wursig, & H. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 158-162). San Diego, CA: Academic Press.

Marino, L., Uhen, M. D., Pyenson, N. D., & Frohlich, B. F. (2003a). Reconstructing cetacean brain evolution using computed tomography. *New Anatomist*, **272B**, 107-117.

Marino, L., Pabst, D. A., McLellan, W. A., Sudheimer, K., and Johnson, J. I. (2003b). Magnetic resonance images of the brain of a dwarf sperm whale (*Kogia simus*). *Journal of Anatomy*. **204**, 57-76.

Marples, B. J. (1949). Two endocranial casts of cetaceans from the Oligocene of New Zealand. *American Journal of Science*, **247**, 462-471.

Mercado III, E., Murray, S. O., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1998). Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): repletion of arbitrary behaviors using an abstract rule. *Animal Learning and Behavior*, **26**, 210-218

Mercado III, E., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1999). Memory for action events in the bottlenosed dolphin. *Animal Cognition*, **2**, 17-25.

Milinkovitch, M.C., Berube, M., & Palsboll, P.J. (1998). Cetaceans are highly derived artiodactyls. In J. G. M. Thewissen (Ed.), *The emergence of whales* (pp. 113-131). New York: Plenum Press.

Miller, B. L., Seeley, W. W., Mychack, P., Rosen, H.J., Mena, I., & Boone, K. (2001). Neuroanatomy of the self-evidence from patients from frontotemporal dementia. *Neurology*, **57**, 817-821.

Mitchell, E. D. (1989). A new cetacean from the late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 2219-2235.

Morgane, P. J., Jacobs, M. S., & McFarland, W. L. (1980). The anatomy of the brain of the bottlenose dolphin (*Tursiops truncatus*). Surface configurations of the telencephalon of the bottlenose dolphin with comparative anatomical observations in four other cetacean species. *Brain Research Bulletin*, **5**, 1-107.

Morgane, P. J., Jacobs, M. S., & Galaburda, A. (1986). Evolutionary morphology of the dolphin brain. In R. J. Schusterman, J. A. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 5-59), Hillsdale, NJ: Erlbaum.

Morgane, P. J., Glezer, I. I., & Jacobs, M. S. (1988). Visual cortex of the dolphin: an image analysis study. *Journal of Comparative Neurology*, **273**, 3-25.

Morgane, P. J., Glezer, I. I., & Jacobs, M. S. (1990). Comparative and evolutionary anatomy of the visual cortex of the dolphin. In E. G. Jones & A. Peters (Eds.), *Cerebral cortex*, Vol. 8b (pp. 215 – 262). New York: Plenum Press.

Nikaido, M., Rooney, A. P., & Okada, N. (1996). Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: hippopotamuses are the closest extant relatives of whales. *Proceedings of the National Academy of Sciences USA*, **96**, 10261-10266.

Oelschlager, H. A., & Oelschlager, J. S. (2002) Brains. In W. F. Perrin, B. Wursig, & H. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 133-158). San Diego, CA: Academic Press.

Pepperberg, I. M. (1999) *The Alex studies*. Cambridge, MA: Harvard University Press.

Povinelli, D. J., Gallup, G. G., Eddy, T. J., Bierschwale, D., Engstrom, M. C., Perilloux, H. K., & Toxopeus, I. B. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behavior*, **53**, 1083-1088.

Premack, D. (1976). *Intelligence in ape and man*. Hillsdale, NJ: Erlbaum.

Reiss, D., & Marino, L. (2001) Mirror self recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences USA*, **98**, 5937-5942.

Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology*, **107**, 301-312.

Revishchin, A. V., & Garey, L. J. (1990). The thalamic projection to the sensory neocortex of the porpoise, *Phocoena phocoena*. *Journal of Anatomy*, **169**, 85-102.

Richards, D. G., Woltz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and labeling of objects by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology*, **98**, 10-28.

Ridgway, S. H. (1986). Physiological observations on dolphin brains. In J. A. Thomas & F.

- G. Wood (Eds.), *Dolphin cognition and behavior* (pp. 31-59). Hillsdale, NJ: Erlbaum.
- Ridgway, S. H. (1990). The central nervous system of the bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 69-100). San Diego, CA: Academic Press.
- Ridgway, S. H., & Brownson, R. H. (1984). Relative brain sizes and cortical surface areas of odontocetes. *Acta Zoologica Fennica*, **172**, 149-152.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K., Williams, S., & Rumbaugh D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, Serial No. 233, **58**, 1-254.
- Shaffer, V. A., & Renner, M. J. (2000). Black-and-white colobus monkeys (*Colobus guereza*) do not show mirror self-recognition. *International Journal of Comparative Psychology*, **13**, 154-160.
- Shimamura, M., Yasue, H., Ohshima, K., Abe, H., Kato, H., Kishiro, T., Goto, M., Munechika, I., & Okada, N. (1997). Molecular evidence from retroposons that whales form a clade within even-toed ungulates. *Nature*, **388**, 666-671.
- Stefaniak, K. (1993). Natural endocranial cast of a delphinid (Cetacea, Delphinidae) from the Pinczow Limestones (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **43**, 116-119.
- Stuss, D. T., Gallup, Jr., G. G., & Alexander, M. P. (2001). The frontal lobes are necessary for "theory of mind". *Brain*, **124**, 279-286.
- Suarez, S. D. & Gallup, G. G. (1986) Social responding to mirrors in rhesus macaques (*Macaca mulatta*): Effects of changing mirror location. *American Journal of Primatology*, **11**, 239-244.
- Supin, A. Y., Mukhametov, L. M., Ladygina, T. F., Popov, V. V., Mass, A. M., & Poljakova, I. G. (1978). Electrophysiological studies of the dolphin's brain. Moscow, Russia: Izdatel'ato Nauka.
- Tarpley, R. J., & Ridgway, S. H. (1994). Corpus callosum size in delphinid cetaceans. *Brain, Behavior, and Evolution*, **44**, 156-165.
- Thewissen, J. G. M. (1998). Cetacean origins. In J. G. M. Thewissen (Ed.), *The emergence of whales* (pp. 451-464). New York: Plenum Press.
- Thewissen, J. G. M., Williams, E. M., Roe, L. J., & Hussain, S. T. (2001). Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature*, **413**, 277-281.
- Uhen, M. D. (1998). New protocetid (Mammalia, Cetacea) from the late middle Eocene Cook Mountain Formation of Louisiana. *Journal of Vertebrate Paleontology*, **18**, 664-668.
- Xitco, M. J. (1988). *Mimicry of modeled behaviors by bottlenose dolphins*. Unpublished Master's Thesis. University of Hawaii, Honolulu.

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