The Brain – Evolution, Structure and Function

In: Herzing D & Johnson CM (eds) 2015. *Dolphin Communication and Cognition* (p. 3-18), MIT Press, Cambridge, Mass.

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<u>Introduction</u>

In the past three decades new research has uncovered the large complex cetacean brain which forms the neurobiological basis for the considerable cognitive abilities of dolphins and whales. Furthermore, the evolutionary history of cetacean brains is a powerful example of the way that brain structure-function relationships can follow a complicated pattern of divergence and convergence at different levels. The study of cetacean brains has revealed that the human brain is not the only brain that has undergone significant increases in size and complexity. Cetacean brains have as well, but have done so by taking a different neuroanatomical path to complexity than primate brains, and, although not the only one, they may be the most compelling example of an alternate route to intelligence on par with that of humans.

<u>The Evolution of Large Brains in Cetaceans</u>

The most recent terrestrial ancestor of cetaceans, *Pakicetus sp.*, looked somewhat like a medium-sized dog and stood on the hooved feet of its ungulate ancestors (Gingerich & Uhen, 1998). Pakicetus was a member of the first cetacean suborder, Archaeoceti, which originated about 52.5 million years ago (Ma) (Bajpai & Gingerich, 1998; Gingerich & Uhen, 1998) and lasted until the end of the Oligocene epoch (23 Ma) (Fordyce, 2004; Uhen, 2010). Pakicetus possessed a rather average brain in absolute and relative size (Marino, 2002). Archaeocete brains changed relatively little over the course of the first 15 million years of adaptation to a fully aquatic lifestyle (Marino, McShea, & Uhen, 2004), disproving a longstanding belief that cetacean brains became large and complex as a direct result of adaptation to an aquatic existence (see Tartarelli & Bisconti 2006 for further discussion). All of the evidence taken together suggests that the behavioral profile of archaeocetes – even those who were fully aquatic - was probably not fundamentally different from that of *Pakicetus*.

Dramatic environmental changes at the Eocene-Oligocene boundary (around 35 Ma) coincided with the emergence of Neoceti ("new cetaceans") which includes the two modern suborders Odontoceti and Mysticeti (Fordyce, 2003; Geisler, McGowan, Yang, & Gatesy, 2011; Uhen, 2010). And with the Neoceti came the earliest detectable changes in cetacean brain size and structure (Marino, McShea, & Uhen, 2004).

Because most of the data on cetacean brain evolution comes from odontocetes, extrapolations to mysticetes should be made conservatively, bearing in mind that both suborders adapted early on to two very different behavioural niches, which then led to differences in modern brain structure. But modern mysticetes and odontocetes also share several characteristics of brain evolution, including hemisphere elaboration, level of cortical folding, and neocortical architecture which show they are on a par with each other in terms of complexity (Oelschlager & Oelschlager, 2002; Hof & van der Gucht, 2007). Recent results suggest the difference in relative brain size between odontocetes and mysticetes is largely due to a higher rate of body mass evolution in mysticetes and decreases in body mass at the origin of odontocetes, resulting in a complete grade-shift between the two (Montgomery et al., 2013).

Because brain and body size are positively correlated (that is, brains, as are all other organs, larger in larger bodies) brain size is often

expressed as an Encephalization Quotient or EQ (Jerison, 1973) which is a value that represents how large or small the average brain of a given species is compared with other species of the same body weight. Thus, EQ accounts for brain: body allometry. An EQ of one means brain size is average for that species, less than one means the brain is smaller than expected for its body size, and greater than one larger than expected. For example, modern human EQ is 7.0 – our brains are 7 times larger than one would expect for a species of our body size.

The first major change in odontocete relative brain size was due mainly to a significant decrease in body size along with a rather more moderate increase in absolute brain size. This combination of changes drove the EQ levels of these early Neoceti groups significantly beyond the range of the archaeocetes. Recent findings suggest that cetacean brain and body mass evolved under strong directional trends to increase through time, but decreases in EQ were widespread as well (Montgomery et al., 2013).

The average EQ for archaeocetes was about 0.5, below average, while that of the early odontocetes soared to 2.0, above average, with, importantly, no overlap in EQ across the two groups (Marino, McShea, & Uhen, 2004). Modern cetacean brains are among the largest of all mammals in both absolute mass and in relation to body size. The largest

brain on earth today, that of the adult sperm whale (*Physeter macrocephalus*), at 8000g (Marino, 2002) is about 60% larger than the modern elephant brain and six times larger than the human brain. All modern odontocetes possess above-average encephalization levels compared with other mammals. Numerous odontocete species possess EQs in the range of 4 to 5, that is, they possess brains 4 to 5 times larger than one would expect for their body weights. There is strong evidence for a directional trend in increasing brain size and in decreasing body mass but little evidence for a directional trend in increasing EQ per se (Montgomery et al., 2013). However, lineage-specific selection led to some cetaceans, such as the Delphinoidea (porpoises, oceanic dolphins and toothed whales) becoming very highly encephalized (Marino, 1998) with some possessing EQs in a range second only to those of modern humans (Marino, 1998). Moreover, cetacean, or, at least, odontocete, brain evolution appears to have been in stasis for the past 15 million years (Marino, McShea, & Uhen, 2004).

Along with their modest size, archaeocete brains were characterized by small elongated cerebral hemispheres ending rostrally in large olfactory peduncles and bulbs (Edinger, 1955).

Figure 1 here

As mentioned earlier, their brain morphology was almost indistinguishable from that of the Pakicetids and many other predatory terrestrial species of the time. However, after the initial change in relative size, Neoceti cetacean brains underwent a number of structural and organizational evolutionary modifications with important functional consequences. The signature changes occurring in odontocetes were the substantial hyperproliferation and reorganization of the cerebral hemispheres, enlargement of auditory processing areas, development of a unique neocortical architecture, and reduction of olfactory structures with a re-proportioning of associated limbic and paralimbic regions. These changes, along with many others, placed odontocetes on an unusual evolutionary trajectory that would result in brains that are among the most massive, complex and sophisticated in the animal kingdom and engendering numerous hypotheses and debates about the ultimate drivers of cetacean brain evolution.

<u>Drivers of cetacean brain evolution</u>

Archaeocetes underwent several changes in body structure and physiology during their period of adaptation to a fully aquatic lifestyle.

Skull elongation and the migration of the nares to the top of the head, called "telescoping", produced significant changes in the architecture of the cranium over time. Archaeocetes also began the pattern of change in dentition from heterodonty to, ultimately, homodonty in odontocetes and baleen in mysticetes. In addition, changes in jaw and ear bone structure indicated these early whales developed increased underwater directional hearing abilities. But there is no evidence for echolocation in archaeocetes (see Uhen, 2007 for a review). Finally, as mentioned, fossil cranial morphology indicates they still possessed olfactory abilities. What we do know is that the emergence of the Neoceti from the archaeocetes around 35 million years ago signaled a host of significant transformations that were probably accompanied by dramatic changes in behavioral ecology. Discussion and debate about the ultimate causes of the initial major shift in cetacean brain evolution which occurred with the Neoceti have been ongoing for decades. Hypotheses proposed to explain the large brains of modern cetaceans in ways independent of increased cognition (Manger, 2006) have been refuted (Marino et al., 2008) and there is currently no support for this type of explanation. Rather, the scientific consensus is that large brain size is evidence of, or necessary for, the behavioral complexity and cognitive abilities observed in cetaceans (Marino, 2002; Simmonds 2006; Marino et al., 2007).

One hypothesis as to why the brain: body relationship shifted in odontocetes is that selection associated with the evolution of echolocation drove increases in EQ (through moderate brain size increases and more dramatic body size decreases) (Marino, McShea, & Uhen, 2004; Montgomery et al., 2013). The few Oligocene odontocetes whose inner ears have been studied in detail resemble the ears of modern odontocetes (Fleischer, 1976; Luo & Eastman, 1995), suggesting they were specialized for hearing high-frequency sounds. However, there is still some uncertainty about whether the earliest odontocetes had inner ears specialized for the high-frequency hearing used in echolocation (Geisler, McGowan, Yang, & Gatesy, 2011). Furthermore, it should be noted that although high frequency hearing is a prerequisite for echolocation it does not, by itself, provide information about how echolocation is used, i.e., if it shifted from a basic sensory system for navigation and hunting to one utilized in more complex ways in, for instance, social interactions. Echolocation was likely embedded within a suite of characteristics which signaled a change in behavior in early odontocetes.

At the time of the major shift in brain:body allometry in early cetaceans there was a cooling in temperate to polar latitudes, triggering changes in biodiversity and productivity in oceanic food chains (Salamy & Zachos, 1999). These changes must have led, in turn, to changes in

behavioral ecology (foraging opportunities and predation risk, for instance) (Lindberg & Pyenson, 2007) which drove further cognitive and social changes. In odontocetes, the moderate increase in brain size was matched by the evolution of a novel echolocation-related nasofacial muscle complex (Fordyce, 2002, 2003) and concurrent changes in ear structures associated with echolocation (Fleischer, 1976). Heterodonty was replaced entirely by long rows of pronglike uniform teeth adapted for grabbing and gulping whole prey items. Taken together, the decreased body size, homodonty, changes in skull and ear bone morphology, and brain enlargement all lead to evidence for a new echolocating niche for the early odontocetes. These early odontocetes were – in a phrase - fast and sleek and possessed new and enhanced sensory-perceptual abilities, leading to sophisticated levels of intelligence in modern species (Marino, 2011; Marino et al., 2008).

The environmental changes that occurred about 35 million years ago spurred a different set of physical and behavioural adaptations in mysticetes that led to the development of baleen, filter-feeding and large body size. Explanations for why two different suborders emerged so early on in cetacean evolution await further data and analysis. Nevertheless, modern mysticetes evince many of the same sophisticated cognitive capacities as odontocetes (Whitehead, 2011).

Modern Cetacean Brain Structure and Organization

Modern cetacean brains are not only very different from that of their ancestors but they are also highly unusual compared with other mammals. Speaking broadly, there are two different levels of evolutionary change which can occur: 1) Direct Selection: adaptation to specific selection pressures, 2) Indirect Selection: accommodation of other structures to those directly-selected adaptations, including allometrically-driven changes. Some of the changes that occurred in cetacean brain evolution were direct adaptations to specific pressures in the physical and social environment. A notable example is the increase in size of auditory brain structures to allow for an increase in processing of high frequency sound. That is, the emerging function of increased sensitivity and range in auditory processing most likely came under direct selection pressure. Second, changes in auditory brain structures and functions necessitated modifications in other components of the brain to accommodate those specific changes. For example, other sensory functions may be modified to accommodate the burgeoning auditory capacity or there may be changes in more general functions, i.e., sensory integrative processes,

which represent broader cognitive modifications. Brain size and structure

drive "universal" allometric changes in all brains as well, that is, changes

throughout the brain which allow for the maintenance of critical

neurobiological parameters, such as connectivity or speed of neural

transmission. For instance, when brains enlarge over evolutionary time

they do not simply become larger versions of the smaller form. When

brains enlarge they do so by changing their general architecture to

maintain connectivity over longer distances by increasing modularization

of functional areas. Therefore, brains cannot enlarge without also

reorganizing, thus creating new areas and new features simply to maintain

the same level of connectivity as in a small brain. And it is important to

keep in mind that the modern cetacean brain, like any other brain, is a

product of all of these processes.

Development of Auditory Structures

Counter to popular belief, with the exception of river dolphins (who

are almost blind), cetaceans have acute vision in and out of water (Mass &

Supin, 2009). As is well known, cetaceans are highly reliant on audition

and all brain structures associated with hearing, including the auditory

nerve, auditory midbrain regions and cortical projection zones are massive

in cetaceans and, particularly, odontocetes. Generally, auditory structures are relatively larger in odontocetes than mysticetes because of the odontocete ability to echolocate (Oelshlager & Oelshlager, 2002). Likewise, the primary and secondary auditory projection zones on the cerebral surface are extensive (Supin, Mukhametov, Ladygina, Popov, Mass, & Poliakova,1978).

One of the most intriguing and informative aspects of enhanced auditory processing in cetaceans is the evidence that they have integrated this perceptual system into the general cognitive domain in a way that may be unprecedented in the animal kingdom. For instance, echolocation in odontocetes may have evolved initially as a sensory device to provide information about the environment and objects in it. The large brains of odontocetes were initially used, at least partly, for processing this entirely new sensory modality. But, experimental evidence and behavioural field observations suggest echolocation plays a role in more highly integrated cognitive processing and communication in modern odontocetes. For instance, echolocation sounds are often produced simultaneously with other sounds that are communicative in nature and many authors have noted that sonar provides an efficient way to keep track of a moving social group over distances (Jerison, 1986; Ridgway, 1986; Wood & Evans, 1980). Therefore, the initial function (which was likely navigation and

hunting) may have evolved into an increasingly complex cognitive-behavioral feature with more "global" impact on odontocete lifestyle. In support of this idea, Herman, Pack, and Hoffman-Kuhnt (1998) and Pack and Herman (1995) have shown that bottlenose dolphins are capable of cross-modal integration, that is, recognizing complex objects through echolocation which they have only seen and visa versa. These findings indicate that audition and vision have been so well-integrated that echolocation involves the capacity for higher-order mental representation.

Re-proportioning of Limbic and Paralimbic Structures

Olfaction in cetaceans has been severely reduced in mysticetes and entirely lost in odontocetes. Fetal odontocetes possess small olfactory structures (Buhl & Oelschlager, 1988; Marino, Murphy, Gozal, & Johnson, 2001) that typically regress completely by birth. Infrequently, a short olfactory peduncle is found in adult sperm whales and northern bottlenose whales (*Hyperoodon ampullatus*) (Oelschlager & Oelschlager, 2002). Olfaction in adult mysticetes is vastly reduced; unlike odontocetes, as adults they maintain small olfactory bulbs, a thin olfactory peduncle, and an olfactory tubercle (Oelschlager & Oelschlager, 2002).

The limbic system is an evolutionarily old and highly conserved set of structures which supports a variety of functions, including memory, emotional processing, and olfaction. It includes the hippocampus, amygdala, mammillary bodies and the various structures of the limbic cortex. Limbic structures most intimately connected with olfaction, i.e., the hippocampus, fornix and mammillary bodies, have been greatly reduced in cetaceans (Jacobs, McFarland, & Morgane,1979; Morgane, Jacobs, & McFarland, 1980).

Despite a reduced hippocampus (a structure typically involved in memory in other mammals), the cetacean limbic system features a large amygdala (Schwerdtfeger, Oelschlager, & Stefan, 1984) and extremely well-developed cortical limbic lobe and entorhinal region above the corpus callosum (Marino, Murphy, Gozal, & Johnson, 2004; Oelschlager & Oelschlager, 2002), creating a highly-elaborated paralimbic region. There are dense connections between paralimbic structures and the amygdala in mammals in general. Broadly, the paralimbic region connects limbic and "higher-order" cortical structures and the degree of elaboration may be related to the complexity of ways emotions are integrated with "higher order" thought processes. The fact that cetaceans possess a reduced hippocampus and well-developed paralimbic region adjacent to the limbic system suggests that there may have been a transfer of memory functions

from the olfactory-based hippocampus to "higher-order" cortical regions. This hypothesis is consistent with the fact that cetacean learning, memory, and spatial navigation abilities (all "hippocampal" functions) are sophisticated and robust (Marino, 2008).

Enlargement and Re-arrangement of Cerebral Hemispheres

The cetacean forebrain represents a radical departure from the lobular architecture of many mammal brains, including that of humans. Instead of lobes, cetacean brains are organized into three concentric tiers of tissue that include the limbic, paralimbic and supralimbic regions. In addition to its unusual organization the cetacean forebrain is among the most highly convoluted of all mammals, revealing that there was a substantial increase in neocortical surface area and volume in cetacean evolutionary history. One measure of convolution is the 'gyrification index', which compares neocortical surface area to total brain weight. The index for modern humans is approximately 1.75. Known gyrification indices for odontocetes range from 2.4 – 2.7, substantially exceeding that of modern humans (Ridgway & Brownson, 1984). The gyrification index is positively correlated with brain mass across the mammals and cetacean (as well as human) brains appear to be consistent with this pattern.

The pattern of elaboration of the neocortex (the evolutionarily newest region of the forebrain) in cetaceans has resulted in a highly unusual configuration of sensory-motor processing regions as well. The map of sensory projection regions (the cortical regions that receive sensory information) in the cetacean brain stands in striking contrast to that of other large-brained mammals. In primates, for instance, the visual and auditory projection regions are located in the occipital and temporal lobes, respectively. This means that visual information is first processed in the cortex in the back of the brain (occipital region) and auditory information on the side of the brain (temporal region). An expanse of nonprojection or association cortex intervenes between these two regions. Therefore, in primates, for instance, in order to be integrated, visual and auditory information must be sent from primary and secondary projection zones to this intervening cortex. In cetaceans, by contrast, the visual and auditory projection zones are located in the parietal region atop the hemispheres and are immediately adjacent to each other. They are not separated by association cortex.

This arrangement of cortical adjacency is unusual in such a large brain and demonstrates that not only is the surface map of the cetacean neocortex different from most mammals but the relationship between the visual and auditory processing areas is closer than in most mammals.

Cetaceans possess a vast expanse of non-projection, or association

cortex, for even higher-order cognitive information processing, which lies

outside of the visual-auditory region in the remaining temporal and

occipital regions. This idiosyncratic pattern of visual-auditory adjacency

allows for highly developed cross-modal sensory processing abilities in

cetaceans (Herman, Pack, & Hoffman, 1998; Pack & Herman, 1995) and

the vast expanse of association cortex suggests complex higher-order

mental functions.

Figure 2 about here

The Cetacean Neocortex Revisited

Early neuroanatomical studies of cetacean neocortex appeared to

show that cortical regions are homogeneous and fairly simple in

architecture (Gaskin, 1982; Kesarev, 1971). These data led to a view

labeled the "initial brain hypothesis", which engendered much confusion

and debate about how a relatively "primitive" brain could be the basis of

the considerable cognitive and behavioral complexity observed in

cetaceans (Glezer, Jacobs, & Morgane, 1988). But more recent studies,

using more sophisticated histological methods, reveal a very different

picture, providing evidence for substantial neocortical complexity in both odontocetes and mysticetes (Hof, Chanis, & Marino, 2005; Hof & Van der Gucht, 2007). The cellular architecture of various regions of the cetacean neocortex is characterized by a wide variety of organizational features, i.e. columns, modules, layers, that are associated with complex brains. Furthermore, the various regions of the neocortex are well differentiated. Studies continue to support this more informed view of cetacean brains as comparable in complexity to other mammal, and possibly even human, brains.

Whereas there appears to be a high degree of organizational complexity throughout the cetacean neocortex some regions are especially elaborated. The cingulate and insular cortices (both part of the paralimbic system) in odontocetes and mysticetes are extremely well developed (Hof & Van Der Gucht, 2007; Jacobs, McFarland, & Morgane, 1979) and the expansion of these areas in cetaceans is consistent with high-level cognitive functions such as attention, judgment and social awareness (Allman, Watson, Tetrault, & Hakeem, 2005), Moreover, recent studies show that the anterior cingulate and insular cortices in larger cetaceans contains a type of projection neuron, known as a spindle cell or Von Economo neuron (Hof & Van Der Gucht, 2007). Von Economo neurons are highly specialized projection neurons thought to be involved

in neural networks subserving aspects of social cognition (Allman, Watson, Tetrault, & Hakeem, 2005); they have been found in humans and great apes (Allman Watson, Tetrault, & Hakeem, 2005) as well as elephants (Hakeem, Sherwood, Bonar, Butti, Hof, & Allman, 2008). It is important to note that, although spindle cells are thought to play a role in adaptive intelligent behavior, there is no consensus on their specific purpose. However, the presence of these neurons in cetaceans is, at the very least, not inconsistent with the complex cognitive abilities found in this group.

Despite general similarities in level of cellular and organizational complexity, there are striking differences in the specific connectivity patterns of cetacean brains and primate, including human, brains. Specifically, cetacean neocortex is characterized into five layers instead of the six typical of primates and many other mammals. Cetacean neocortex possesses a very thick layer I in combination with the absence of a granular layer IV. In primates, a granular layer IV is the primary input layer for fibers ascending from the midbrain to the cortex and this layer is also the source of important connections within the neocortex. However, since granular layer IV is absent in cetaceans, information comes into the cetacean neocortex through a different pathway than in most other mammals (Glezer, Jacobs, & Morgane, 1988). The prevailing view is that

the thick Layer I is the primary layer receiving incoming fibers in cetaceans. All of this rearrangement of input means that the way information gets to the cortex and is distributed is distinctly different in cetaceans from primates and other mammals. More importantly, the vastly different connectivity patterns of primate and cetacean brains are another compelling example of two distinctly different evolutionary trajectories taken towards neurological and behavioural complexity.

Implications for intelligence in dolphins and whales

There is strong evidence that the initial dramatic change in cetacean brain size and organization was correlated with striking transformations in behavioral ecology in cetaceans. Cetacean brains are massively elaborated but in very different ways than the brains of other mammals, including primates. Despite these striking differences in neuroanatomical organization, particularly at the neocortical level, cetaceans and primates (as well as other species) exhibit very similar cognitive and behavioral capacities, implying a high level of convergence in the factors that led to the evolution of brain and intelligence in cetaceans and primates.

One of the most striking examples of cognitive convergence between dolphins and primates is self-recognition. Bottlenose dolphins

have convincingly demonstrated that they use a mirror to investigate their own bodies, showing that they have a sense of self (Reiss & Marino, 2001). These findings are consistent with additional independent evidence for self-awareness, self-monitoring, and metacognition in dolphins (see Marino et al., 2008 and Simmonds, 2006, for recent reviews). In particular, the presence of a highly elaborated cingulate and insular cortex in cetacean brains is consistent with the idea that these animals are highly sophisticated and sensitive in the emotional and social domains. Moreover, it is not outside the realm of possibility that some cetacean species possess levels and dimensions of social-emotional sophistication not achieved by other animals, including humans.

<u>Future Directions</u>

Future directions in our study of cetacean brains and intelligence require taking into account the current evidence for sophisticated cognitive, emotional and social abilities in cetaceans. Taken together with the poor welfare of many cetaceans in captivity, this current knowledge calls for a new paradigm of noninvasive and field-based research on cetaceans (Marino and Frohoff, 2011). There is still much to be done in the domain of understanding patterns of brain evolution in cetaceans within a phylogenetic context. These kinds of studies can be done with

fossil specimens. Additionally, sophisticated histological and imaging methods make possible increasingly more profound analyses of neuroanatomical complexity in cetaceans. These kinds of studies require the availability of postmortem brains from individuals who die of natural death or may need to be euthanized. There is currently little cooperation between captive marine mammal facilities and scientists in terms of sharing these materials when they become available. This situation should change as there are so many questions about cetacean brains that could be answered by facilitating access to postmortem material.

In terms of behavior, long-term field studies and statistical modelling of behavior in the natural-setting are currently at the forefront of delivering ongoing information about cetaceans and, needless to say, these are important approaches to our continued study of cetaceans.

In an applied domain, conservation measures that do not take into account the known psychological complexity of these animals will do little to alleviate suffering on an individual level. As such, there needs to be more integration of the basic science on who cetaceans are and conservation efforts and a greater emphasis on individuals in efforts to protect cetaceans. Finally, beyond all of these suggestions the main point is that our scientific understanding and current knowledge of cetacean brains and cognitive abilities demands we develop a new ethic of respect

and co-existence with them, requiring changes in human behavior as we

move into the future.

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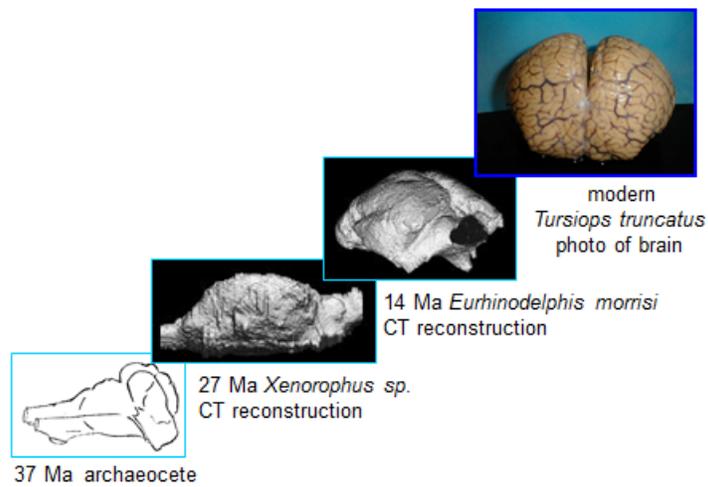
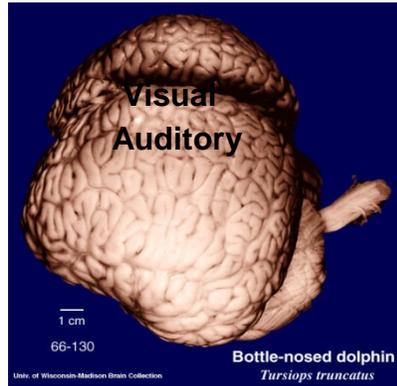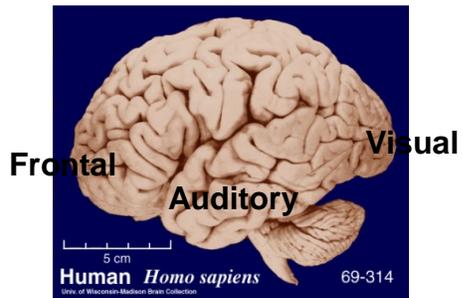Figure 1. Evolution of cetacean brains from archaeocetes to modern species.

Figure 2. Neocortical projection regions in human and dolphin brain.