2011

Cetaceans and Primates: Convergence in Intelligence and Self-Awareness

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Abstract

Cetaceans (dolphins, porpoises and whales) have been of greatest interest to the astrobiology community and to those interested in consciousness and self-awareness in animals. This interest has grown primarily from knowledge of the intelligence, language and large complex brains that many cetaceans possess. The study of cetacean and primate brain evolution and cognition can inform us about the contingencies and parameters associated with the evolution of complex intelligence in general, and, the evolution of consciousness. Striking differences in cortical organization in the brains of cetaceans and primates along with shared cognitive capacities such as self-awareness, culture, and symbolic concept comprehension, tells us that cetaceans represent an alternative evolutionary pathway to complex intelligence on this planet.

KEY WORDS: Consciousness, Cetaceans, dolphins, porpoises and whales, self-awareness, astrobiology

1. Why Dolphins and Whales?

Cetaceans (dolphins, porpoises and whales) have been of great interest to the astrobiology community and to those interested in consciousness and self-awareness in animals. Given the likelihood that "water worlds" may be common in the universe (Goertzel and Combs 2010; Tyler, 2010), it is therefore possible that intelligent mammals and other creatures might evolve completely adapted to a life beneath the sea. The study of Cetaceans may provide a window into the evolution of consciousness in extraterrestrials who have evolved in water and not on land.

There is an early historical connection between the study of cetaceans and research on the possibilities for extraterrestrial intelligence beginning with the first scientific meeting on the search for extraterrestrial radio signals at Green Bank, West Virginia in 1961. The meeting participants included Frank Drake, Bernard Oliver and Carl Sagan, as well as renowned dolphin neuroscientist John Lilly (1969, 1987), who regaled the group with accounts of dolphin intelligence which so impressed them that they voted to call themselves the Order of the Dolphin. Despite the fact that some of Lilly's later work was controversial, he brought to light the large complex brain and sophisticated intelligence of dolphins. Moreover, the independent scientific evidence for complex intelligence in dolphins and whales continued to grow. The meeting was the starting point for the Drake Equation (a gross estimate of the number of habitable worlds) and an enduring involvement of cetacean research in the Search for Extraterrestrial intelligence (SETI).

There are, arguably, two, not entirely unrelated, ways in which dolphin research has played a role in astrobiology and SETI. First, the complex and unusual communicative capacities of dolphins, which includes whistles, clicks, echolocation and many other kinds of sounds, is considered by many in the SETI community as a model for probing the factors relevant to communication with an extraterrestrial. To be sure, no one in this domain views dolphins as extraterrestrials. However, they view human-dolphin communication efforts as a way to prepare for the issues that will need to be addressed in deciphering a complex extraterrestrial signal. These kinds of studies range from efforts to communicate with wild and captive dolphins (Herzing, 2010; Reiss and McCowan, 1993) to research using information theory to quantify the complexity within dolphin whistle repertoires, an approach that would be used if an extraterrestrial signal were to be found (McCowan et al., 1999, 2002). These research paths have continued to be productive in illuminating both basic information about dolphin communication and intelligence and its application to SETI.

The second way in which the study of dolphins is highly relevant to astrobiology has more to do with consideration of the evolutionary pathways that lead to highly complex communicative intelligences. The astrobiological para-

digm involves using Earth-based data to form hypotheses about what might be possible beyond Earth. Dolphin and whale evolution, in comparison to human evolution, is arguably an alternative way that intelligence and large complex brains have evolved on this planet.

Therefore, studies of dolphin and whale brains and intelligence allow us to probe questions about the evolution of complex intelligence and implications for evolution of awareness. I will focus on this approach in this paper.

2. Cetacean Evolution and Phylogeny

The modern order Cetacea consists of two suborders: Odontoceti (toothed whales, dolphins and porpoises) and Mysticeti (rorqual and baleen whales). Interestingly, the scientific fervor over dolphins and whales is based on knowledge of relatively few species (the bottlenose dolphin, the orca or killer whale, the beluga whale, humpback whale, for instance) among the seventy-seven species known. It is intriguing to consider the vast array of cetacean intelligence that remains unknown to us. The bottlenose dolphin (*Tursiops truncatus*) has been the focus of the most study and, as such, we know the most about this species. Therefore, in this paper the term "dolphin" will refer to this species unless otherwise specified.

The origin and evolutionary history of cetaceans represents one of the most dramatic transformations in the mammalian fossil record. The earliest cetacean, *Pakicetus*, was a medium-sized semi-aquatic mammal with carnivorous dentition (Gingerich and Uhen, 1998) is known from 50 million year old fossil evidence. The earliest odontocete specimen is found in the fossil record in the early Oligocene, about 32 million years ago (Fordyce, 2002). The earliest Mysticete is from the late Eocene, approximately 35 million years ago (Mitchell, 1989). Cetacean ancestry is closely tied to that of Artiodactyla, the suborder of even-toed ungulates; molecular and morphological evidence points to a a sister-taxon relationship between modern cetaceans and Hippopotamidae (Geisler and Theodor, 2009; Geisler and Uhen, 2003; Milinkovitch et al., 1998) although the two lineages diverged over 52 million years ago (Gingerich and Uhen, 1998).

3. General Characteristics of Cetaceans

Despite variability in morphology, behavior and ecology across the numerous cetacean species, there are certain features that are characteristic of cetaceans. Here I will focus upon those most relevant to intelligence, that is, ecology, life history, sensory-perceptual capacities, social behavior and communication.

Ecology Dolphins and whales have adapted to a wide range of habitats,

including open ocean, coasts, and rivers. Many of the larger odontocetes, such as the sperm whales, dive to depths of over 500 meters. Most odontocetes feed on fish or cephalopods and, in the case of orcas (killer whales) sometimes other marine mammals. Mysticetes are filter feeders and rely on krill and small fish.

Life history Life history has to do with how a species allocates time and resources to growth, reproduction and survival. Although there is variability across species, cetaceans share a life history strategy with other large-brained highly intelligent animals characterized by a long lifespan, long gestation period, and long juvenile period with substantial parental care of a relatively few singly-born offspring over the lifetime (Chivers, 2009). The longer lifespan and long periods of juvenile dependency are related to the importance of learning in the life of the individual; cetaceans, and other large-brained animals, spend a great deal of their time learning about both the physical environment and their social relationships.

Sensory-perceptual systems Audition (hearing) is the most important sensory modality for cetaceans. Auditory structures in odontocete brains are greatly enlarged (Ridgway, 2000) and although less is known about audition in mysticetes, it is clear that they rely heavily on hearing as well. Odontocete hearing is exceptional with a range of 40 to 150 kHz and 7 sensitivity far exceeds that of humans. They have also developed rapid temporal processing of auditory signals which is an integral part of echolocation. Echolocation, the highly specialized sensory-perceptual adaptation involving the emission of sounds and reception of echoes, is superbly refined in odontocetes as they use it for making very fine discriminations in very complex contexts (Au, 2009). Dolphins use echolocation for navigation, prey capture, avoidance of predators, communication and, it has been hypothesized, "communal cognition" (Jerison, 1986). Dolphins are also capable of cross-modal processing. Complexly shaped objects perceived through echolocation alone can be spontaneously recognised through vision alone, and vice-versa (Pack & Herman, 1995; Pack et al., 2002). Mysticetes do not echolocate and rely on lower frequency sounds for communication.

Though they rely heavily on sound to communicate, most cetaceans are able to see fairly well in both water and air. River dolphins are the exception given there is little use for vision in turbid river waters, so their eyes are greatly reduced. Cetaceans also use touch extensively with others in their group and there appear to be particularly sensitive regions on their body, e.g., blowhole area, genital area. A key feature of odontocetes is the complete loss of olfactory structures while mysticetes possess a reduced olfactory sense (Oelschlager and Oelschlager, 2002). Cetacean tongues contain fewer taste receptors than most land mammals and it is not known how well they can use taste, if at all (Thewissen, 2009).

Social Behavior and Communication Social behavior and communica-

tion are intimately connected and, as such, are discussed here together. Cetacean groups vary enormously in size across species and there are often many nested hierarchical levels of social organization that change in composition over time. Perhaps the most relevant aspects of cetacean social behavior for understanding their intelligence and awareness are that they are extremely group-oriented by nature (perhaps at a level not yet understood), maintain highly complex and dynamic social interactions, and possess cultures, i.e., learned traditions passed on from one generation to the next.

Dolphins live in large highly complex societies with dynamic differentiated relationships (Baird, 2000; Connor, 2007; Connor et al., 2000; Lusseau, 2007) that include long-term bonds, higher order nested alliances and cooperative networks (Baird, 2000;Connor, 2007; Connor et al., 2000) that are based upon learning and memory. These complex relationships and social roles are all mediated by an equally-complex system of communication. Cetacean communication includes body postures and movements. However, cetaceans are known for their reliance on acoustic information as the main modality for communication. Odontocetes make three distinct types of sounds: 1) burst pulses or clicks, which can be narrow or broad spectrum, 2) narrow-band frequency-modulated whistles, and 3) percussive sounds produced with the body. Mysticetes do not appear to echolocate and possess a very different repertoire of kinds of sounds, including low-frequency moans, short humps or knocks, chirps and whistles. Humpback whale songs are probably the most recognized and well known form of mysticete vocalization (Dudzinski et al., 2009).

In order to appreciate the complexity of cetacean communication it is important to consider the functional context of these sounds and the role they serve in their social life. A large proportion of vocal variation within cetacean species is likely the result of vocal learning (Rendell & Whitehead, 2001). There is evidence for individual-level variation in the whistle repertoires of dolphins (McCowan & Reiss, 2005). Bottlenose dolphins produce individually distinctive whistles that they apparently use to identify conspecifics (Sayigh et al., 1999; Tyack, 1999) and may also be employed as a cohesion call (Janik & Slater, 1998; McCowan & Reiss, 1995, 2001). Research described earlier, using information theory, has shown that the sequential order of whistles is an important feature of dolphin communication. Data from McCowan et al. (1999, 2002) suggests that at least for two-whistle sequences (second-order entropy) internal structure is present. This suggests there may be a syntactic component to the use of whistles in dolphin communication. Cetacean communication is intimately associated with culture as many cetacean cultural traditions often include acoustic conventions. Multifaceted cultures have been documented from field studies of orcas, sperm whales, bottlenose dolphins, humpback whales, and there is suggestive evidence for other species as well. These impressive cultural traditions involve

dialects, foraging sites, feeding strategies, and even tool use. For instance, orcas produce dozens of community, clan and pod-specific call types (Ford, 1991; Yurk et al., 2002). Studies of sperm whales have documented over 33 types of 'coda' vocalisations (rhythmic patterns of clicks) and shown that their use varies among social groups (Rendell & Whitehead, 2003) and there is even matching of codas in sperm whale vocal interactions (Schulz et al., 2008). Marcoux et al. (2007) found evidence for sympatric cultural clans of sperm whales. And cultural transmission of tool use has been documented among bottlenose dolphins, who use sponges to probe into crevices for prey (Krützen et al., 2005) and pass these skills to younger generations (Mann et al., 2008).

In summary, in addition to possessing a general life history pattern associated with strong reliance on learning, cetaceans exhibit complex social and communicative behaviors consistent with a sophisticated level of intelligence and awareness. The experimental work directly addressing intelligence and awareness, described next, supports that conclusion.

4. Cetacean Intelligence and Awareness

There is a large body of data from studies of captive dolphins demonstrating sophisticated cognitive abilities by dolphins and supporting field studies, described above, of apparently complex and sophisticated behavior. In these experimental studies dolphins exhibit prodigious capacities, extraordinary behavioral flexibility, and a profound sense of self.

In the realm of artificial language comprehension, concept formation, and behavioral innovation, dolphins excel. They learn and master not only the semantic features of artificial gestural and acoustic languages, but also the syntactic features (Herman, 1986 for a review; Herman et al., 1993). Human language gains its versatility and communicative power not just through the word, but through the sentence. In human language, syntax allows for the combination of words into an infinite number of possibilities. Herman et al. (1984) showed that dolphins can respond appropriately by situations that involve the use of several different syntactic rules creating thousands of unique sentences constructed from a finite 40-item vocabulary. Among nonhumans, only the great apes, particularly the bonobo (*Pan paniscus*), have shown this type of ability (e.g., Savage-Rumbaugh et al., 1993). Dolphins also possess an understanding of numerical concepts and can generalize these concepts to novel sets outside of the learned range (Killian et al., 2003). Dolphins demonstrate the ability to learn a variety of types of governing rules for solving abstract problems (Herman et al., 1994). For example, they can reliably classify pairs of objects as "same" or "different" (Mercado et al., 2000).

Dolphins have demonstrated an understanding of the abstract concept of "imitate" (Herman, 2002) and are one of the few species that can imitate both

arbitrary sounds and arbitrary behaviors (Richards et al., 1984; Reiss & Mc-Cowan, 1993; Herman, 2002). Dolphins can even spontaneously innovate, that is, create new behaviors upon request (Herman, 2006; Mercado et al., 1998).

In addition to showing impressive capacities in the communicative, social, and learning domains, dolphins are among the few species who, thus far, have shown convincing evidence of self-awareness in formal tests. Self-awareness is a sense of personal identity, i.e., what is commonly referred to as the subjective "I". At the bodily level self-awareness is typically labeled self-recognition, the ability to become the object of one's own attention in the *physical* realm. At a more abstract level self-awareness can take the form of robust *psychological continuity* over extended time. 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 further evidence for self-awareness and self-monitoring in dolphins and related cognitive abilities that likely underwrite the complex social patterns observed in many cetacean species. Body awareness has been demonstrated through the dolphin's ability to understand symbolic gestural references to her own body parts and the ability to use those body parts in ways (often novel) specified by the experimenter (Herman et al., 2001). Moreover, McCowan et al. (2000) provided evidence that bottlenose dolphins anticipate, monitor, organize, and modify goal-directed behavior on the basis of contingencies. Finally, awareness of one's own knowledge states has been demonstrated by dolphins reporting when they were "uncertain" about discriminations they were asked to make. They performed comparably to human subjects in the same study showing that they are able to access their mental states about how confident they are of completing a task and acting upon that knowledge appropriately. This is evidence of abstract "meta-knowledge" in dolphins (Smith et al., 1995).

Related to awareness of one's body and knowledge is the capacity to consider the perceptual and mental perspective of others. This capacity, called Theory of Mind, has, again, been evinced in only a few species thus far. And, again, one of them is the dolphin. Dolphins can spontaneously produce pointing (using rostrum and body alignment) to communicate desired objects to a human observer (Xitco et al., 2001), and appear to understand that the human observer must be present and attending to the pointing dolphin for communication to be effective (Xitco et al., 2004).

In summary, consistent with the evidence for considerable behavioral complexity in their natural communication systems and social lives, dolphins exhibit outstanding cognitive capacities in experimental situations and possess a sense of self and possibly a theory of mind. Although the bottlenose dolphin has been the subject of almost all of these formal studies there is every reason to hypothesize that, despite cognitive 13 variability across cetaceans, other species, particularly orcas and other odontoceties, would demonstrate similar

capacities. This body of behavioral evidence from both the field and the lab inevitably leads to intriguing questions about the kind of brain that would produce such a complex self-aware intelligence.

5. Cetacean Brain Evolution - An Alternative Pathway to Complex Intelligence

In the past three decades new research has shed light on the complexity of cetacean brains and has begun to lay bare the neurobiological basis for their considerable cognitive abilities. But the story about cetacean brain evolution is one that goes beyond an evolutionary tale about increased brain size. It is also a fascinating example of the way that brain structure-function relationships can follow a complicated pattern of evolutionary divergence and convergence. Studies of cetacean brains has revealed that the human brain is not the only brain that has undergone substantial increases in size and complexity. Cetacean brains have as well but along a different neuroanatomical trajectory, providing an example of an alternative evolutionary route to complex intelligence on earth.

6. The Massive Modern Cetacean Brain

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 sperm whale with an average weight of 8000g for adults (Marino, 2009), is about 60% larger than the elephant brain and six times larger than the human brain. Relative brain size is typically 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 average body weight. The EQ for modern humans is 7.0. Our brains are seven times the size one would expect for a species with our body size. Almost all 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. Many of these values are second only to those of modern humans and significantly higher than any of the nonhuman anthropoid primates (Marino, 1998). Figure 1 illustrates the relative EQ levels of several modern dolphin species and the great apes, including humans.
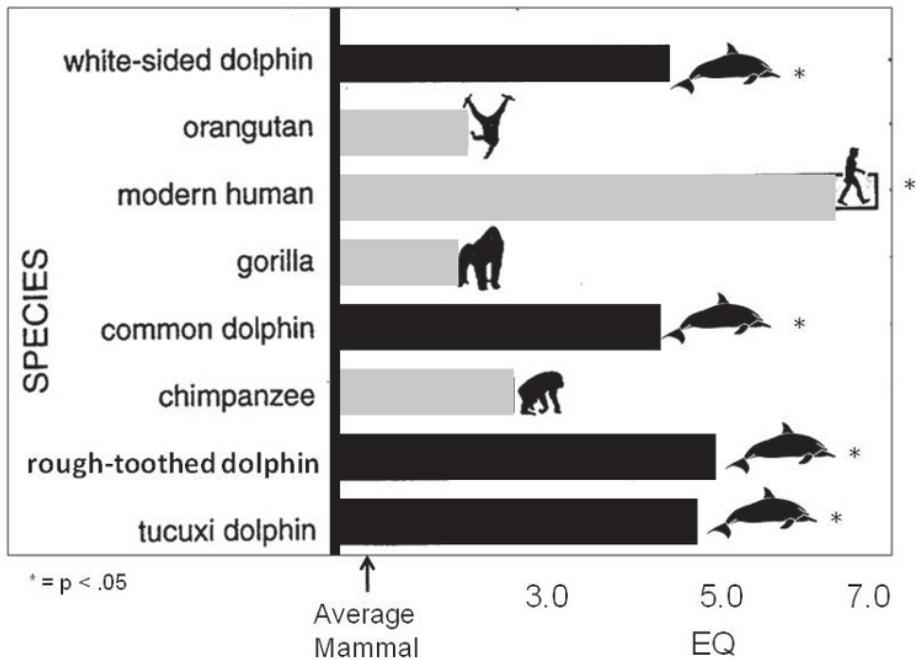
Figure 1. The relative EQ levels of several modern dolphin species and the great apes, including humans. An EQ of 1 (representing mammals with average brain sizes) is labeled for comparison.

EQs of mysticetes are all below 1 (Marino, 2009) because of an uncoupling of brain size and body size in very large aquatic animals. That is, very large animals, such as whales, tend to have smaller brains compared to their weight and this is exacerbated by "aquatic weightlessness". However, mysticete brains are large in absolute size and exhibit high degrees of cortical complexity confirming that mysticete brains have, in addition to odontocete brains, undergone substantial elaboration during the course of their evolution (Oelschlager and Oelschlager, 2009).

7. The Unique Cetacean Brain

The key point about cetacean brains from an astrobiological perspective is not only that they are greatly enlarged and, specifically, highly expanded in the cortical region (the structure involved in high-level processing of information, self-awareness, and generally, abstract intelligence), but represent a strikingly unique combination of cortical characteristics. Whereas subcortical neuroanatomy is shared across mammals (with variations in, mainly, the proportions of various structures), the massive expansion of the cetacean cortex occurred along a very different organizational route than that of other mammal brains (including humans).

Unlike the primate brain, which is organized around four lobes, the cetacean forebrain is arranged around three concentric tiers of tissue and includes an entirely unique region called the paralimbic cortex. The function of the paralimbic cortex in cetaceans is largely unknown and is another signpost of the radical departure of the cetacean brain from the general mammalian pattern. The cetacean forebrain is among the most highly convoluted of all mammals, indicative of a substantial increase in neocortical surface area and volume in cetacean evolution (Ridgway & Brownson, 1984).

The pattern of elaboration of the neocortex in cetaceans has resulted in a highly unusual configuration. 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, visual and auditory information must be sent to this intervening cortex from 16 the projection zones if they are to be integrated. In cetaceans, by contrast, the visual and auditory projection zones are located in the parietal region atop the hemispheres, that is, in a very different location than in primates and other large-brained mammals. Moreover, these areas are immediately adjacent to each other (Ladygina et al., 1978, Supin et al., 1978). This arrangement of cortical adjacency is unusual for such a large brain and reveals 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 or more highly integrated than in most large-brained mammals. This idiosyncratic pattern of visual-auditory adjacency may allow for the highly developed cross-modal sensory processing abilities in cetaceans discussed earlier. Outside of the borders of the primary sensory regions cetacean brains possess a vast expanse of nonprojection or association cortex for even higher-order cognitive information processing. Figure 2 illustrates the cortical surface configurations of the visual and auditory regions in cetacean brains and human brains.

Recent studies of cetacean neocortical cytoarchitecture reveal extensive neocortical complexity and variability in both odontocetes and mysticetes (Hof et al, 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, there is substantial differentiation across the various neocortical regions.

Whereas there appears to be a high degree of organizational complexity throughout the cetacean neocortex there are specific regions that are especially notable in their apparent degree of elaboration. The cingulate and in-
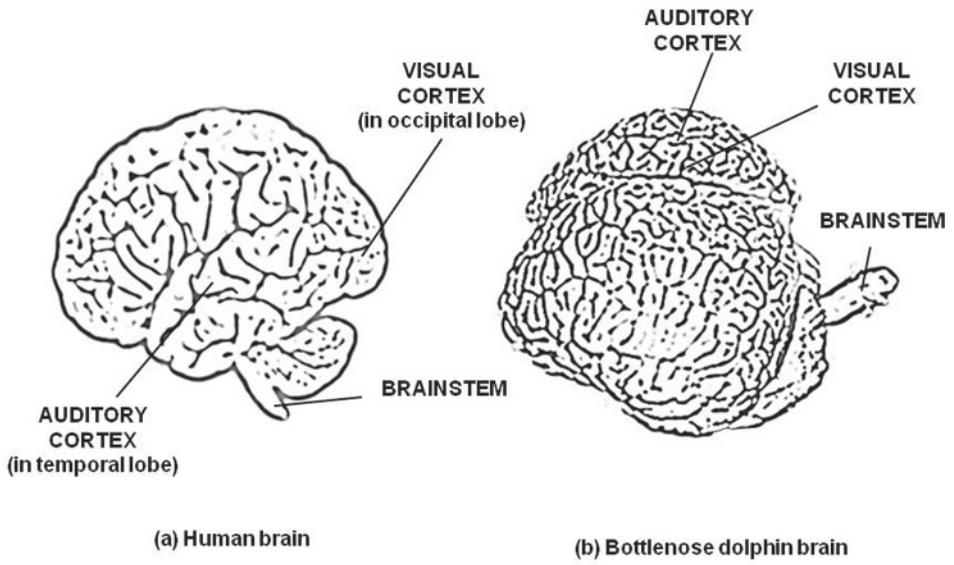
Figure 2. The cortical surface configurations of the visual and auditory regions in cetacean brains and human brains with hindbrain labeled for orientation.
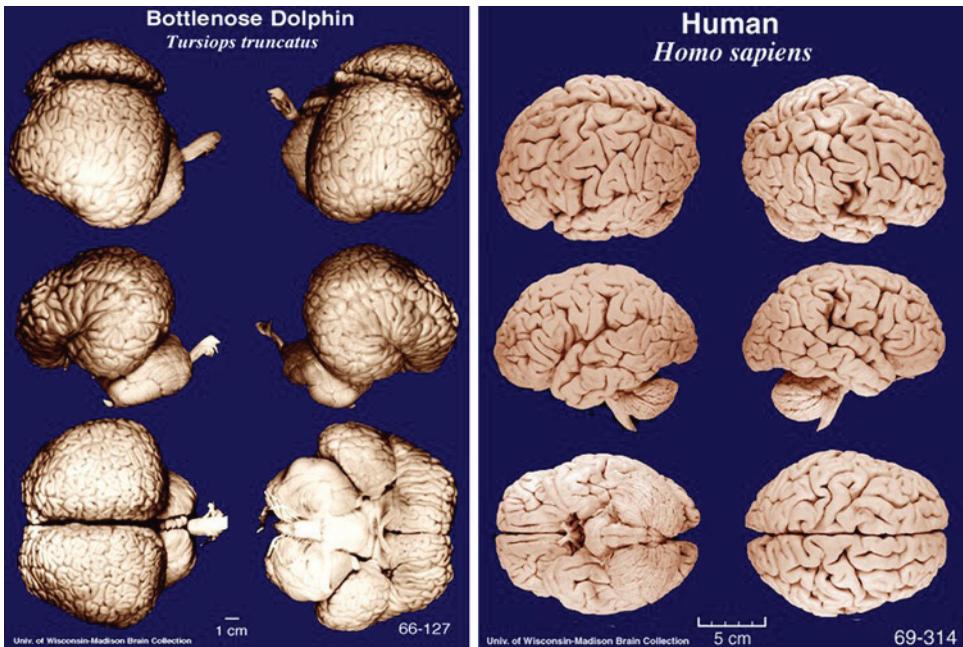

Figure 3. The Dolphin and Human brain.

sular cortices (both situated deeper within the forebrain) in odontocetes and mysticetes are extremely well developed (Hof & Van Der Gucht, 2007; Jacobs et al, 1979) and the expansion of these areas in cetaceans is consistent with high-level cognitive functions such as attention, judgment and social awareness (Allman et al, 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 specialised projection neurons considered to be involved in neural networks subserving aspects of social cognition (Allman et al, 2005) and have thus far been found in humans and great apes (Allman et al, 2005) and elephants (Hakeem et al, 2008). Spindle cells are thought to play a role in adaptive intelligent behaviour and the presence of these neurons in cetaceans is consistent with their complex cognitive abilities.

Despite similarities in level of complexity and in the presence of specialized neurons, e.g., Von Economo neurons, there is a fundamental distinction in cortical architecture between cetacean and primate brains that relates to a striking difference in connectivity patterns. Specifically, cetacean neocortex is characterized by 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 cortex. However, granular layer IV is absent in cetaceans and this has compelling implications for how information reaches the cetacean cortex and then gets distributed to other areas (Glezer et al, 1988). The current prevailing view is that the thick Layer I is the primary layer receiving incoming fiberss. This means that the way information gets to the cortex and distributed within the layers of the cortex in cetacean brains is distinctly different from primates and other mammals.

In summary, cetacean brains are organized around a very different theme than that of primates and other large-brained mammals. There are differences in the arrangement of the cortical project zones, in cytoarchitecture, and in the intra-cortical and input-output relations between the cortex and the rest of the brain. The very different connectivity patterns between primates and cetaceans is a compelling example of distinctly different evolutionary trajectories taken towards neurological complexity.

8. Implications for Astrobiology & Evolution of Extraterrestrial Consciousness

Cetaceans and primates (including humans, who have a typical primate brain) have very large brains that have expanded considerably over their re-

spective evolutionary histories. And they share many mammalian characteristics, including basic neuroanatomy; the brains are similar on the subcortical level as are all mammalian brains. But when one examines the evolutionarily newest structure of mammal brains, the cortex, one finds tremendous differentiation between the cortex of cetaceans and primates. These distinctions are fundamental to the way in which each cortex is contructed, the way it organizes and processes information, and the way it interacts with the rest of the brain. Yet, despite these divergent neuroanatomical evolutionary trajectories cetaceans and primates share a number of cognitive abilities that are found in only a few other animals. Therefore, cetacean-primates comparisons hold tremendous potential for astrobiological questions about the evolution of intelligence.

One of the ongoing debates within the astrobiology community has to do with contingency and convergence, that is, whether, if the "tape of life" were rewound, would complex intelligence evolve again on the earth. I argue that cetacean and primate intelligence is a case of cognitive convergence. Convergence (or homoplasy) involves the appearance of a similar feature in two or more distantly related species whose common ancestor lacked the feature (Nishikawa, 2002; Ridley, 1993). The greater the phylogenetic separation of the two species the stronger the case for convergence, or, in other words, the deeper the convergence. Evolutionary convergence can occur within any domain of biology, from chemistry to morphology to cognition. Cognitive convergence, specifically, is convergence in those processes that comprise the way an organism processes information. These processes include memory, learning mechanisms, sensory and perceptual processing, and levels of awareness. In a general way cognitive convergence refers to convergence in intelligence. Since it is arguably the case that the common ancestor of cetaceans and primates, who lived over 95 million years ago, did not possess many of these shared traits, e.g., self-awareness, symbolic language comprehension, culture, the existence of these traits in these two highly divergent groups of mammals represents a striking case of cognitive convergence. As such, the more we learn about these neuroanatomical differences in the face of shared intelligence the more we learn about the parameters that may shape the evolution of intelligence in general, that is, in an astrobiological context.

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