

Trajectories and Constraints in Brain Evolution in Primates and Cetaceans

G. Tartarelli · M. Bisconti

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Abstract A negative allometric relationship between body mass (BM) and brain size (BS) can be observed for many vertebrate groups. In the past decades, researchers have proposed several hypotheses to explain this finding, but none is definitive and some are possibly not mutually exclusive. Certain species diverge markedly (positively or negatively) from the mean of the ratio BM/BS expected for a particular taxonomic group. It is possible to define encephalization quotient (EQ) as the ratio between the actual BS and the expected brain size. Several cetacean species show higher EQs compared to all primates, except modern humans. The process that led to big brains in primates and cetaceans produced different trajectories, as shown by the organizational differences observed in every encephalic district (e.g., the cortex). However, these two groups both convergently developed complex cognitive abilities. The comparative study on the trajectories through which the encephalization process has independently evolved in primates and cetaceans allows a critical appraisal of the causes, the time and the mode of quantitative and qualitative development of the brain in our species and in the hominid evolutionary lineage.

Keywords encephalization quotient · Delphinidae · human evolution · cortex · allometry

Introduction

Body size (BM) and brain size (BS) are important and strictly related biological factors of species. Body dimensions impose severe physiological and ethological constraints on living vertebrates while brain size is linked to the capabilities of a species to acquire and process

G. Tartarelli (✉)
Scuola Normale Superiore di Pisa, Piazza dei Cavalieri, 6, 56100 Pisa, Italy
e-mail: tartarelli@sns.it

M. Bisconti
Dipartimento di Scienze della Terra, Università degli studi di Pisa, Via Santa Maria, 53,
56126 Pisa, Italy
e-mail: bisconti@dst.unipi.it

sensorial information and transmit motor signals. The relationship between these two variables is non-linear, but allometric.

An allometric equation of this type

$$y = bxa(1)$$

(in our case, $y = \text{BS}$, $x = \text{BM}$, $b =$ allometric coefficient, $a =$ slope)

can be empirically calculated for any vertebrates group (e.g., birds, reptiles, fishes, etc. or lower taxonomic ranks) as for all vertebrates.

Generally, the equation describes the relation between these two variables with high reliability if the taxonomic rank is taken into account. The calculated value of the exponent of the power function ranges from 0.6 to 0.8. There is no agreement among researchers about the meaning of such an exponent; in fact, some authors suggested that it should simply reflect a surface area vs. volume relationship ($a \cong 0.67$), while others hypothesized that it represents a basal metabolic rate (BMR) vs. volume relationship (for which the available data best fit if $a \cong 0.75$); alternatively, it may in some way be related to both [12, 22, 26]. Based on this relation, it can be inferred that small vertebrates exhibit comparatively bigger brains than larger ones. Some species show a particular deviation from average brain/body ratio exhibited by the higher taxonomic rank used for comparison. To better describe this deviation, Jerison [12] proposed to define an encephalization quotient (EQ) = BSr/BSe , where BSr is the brain size recorded for a given species and BSe is the expected brain size for a species of a given weight. It is important to say that, for Jerison [12],

$$\text{EQ}(\text{mammals}) = \text{brain weight}/0.12 (\text{body weight})^{0.67}$$

while in Martin's view,

$$\text{EQ}(\text{mammals}) = \text{brain weight}/0.059 (\text{body weight})^{0.76}.$$

Other authors derived this quotient in different ways from different data sets (for this reason, caution must be used when comparing EQs from different sources).

A quotient greater than 1 indicates that actual brain mass is greater than predicted, while quotients lower than 1 indicate the opposite. Modern humans have the highest EQ (7.4–7.8, if we consider the cat as reference mammal with EQ=1, which is to say that our brain is more than 7 times larger than the expected ratio for mammals of the same weight). This value is the highest not only among Primates, but also among all vertebrates. Some species of modern odontocetes have EQs values of higher than 4.

The mean of EQ values ([12]; Jerison [13]) in modern odontocetes (mean EQ=2.56, range 0.58–4.56) exceeds the mean of modern non-human anthropoid primates (mean EQ=2.0, range 1.02–3.2).

It is interesting to note that the EQ has increased in most vertebrate groups during the course of the Cenozoic and this increase accelerated very quickly in the human evolutionary lineage in the last 5 Myr ([10]; Tartarelli, this volume). In the past, this fact, together with the peculiarity of the very high EQ detectable in our species, supported the use of EQ as preferred indicator of overall intelligence of a species. At present, other indicators such as the absolute or relative size of the cerebral cortex, and cortical neuron number or density have been proposed.

Why did cetaceans and primates, in general, diverged so markedly from the mean trend of all other mammals? How can we explain the different EQ distributions in these groups? How should we interpret the EQ of these groups in biological terms?

To explore the problems raised by these questions, we reviewed some data about primate and cetacean BS and BM.

Cetaceans

Cetacean Brains Cetaceans are usually regarded as very intelligent marine mammals. Lay people and scientists share this view because cetaceans are able to demonstrate complex behaviours and reach goals that depend on the understanding of sophisticated command sequences. In recent times, field studies of cetacean societies revealed a variety of intra- and inter-group relationships depending on such complex abilities as recognition of single individuals through individual sound repertoire in some odontocetes, coordinated hunting techniques in both odontocetes and mysticetes, communication through complex vocal repertoires (which some authors have assimilated to music) that differ from population to population (especially in mysticetes), self-recognition in mirrors by odontocetes, cultural transmission of vocal repertoires (documented in mysticetes) and, possibly, cultural transmission of behaviours (suggested on the basis of mitochondrial DNA in both odontocetes and mysticetes) (e.g., [4, 11, 23, 29, 30]).

The cerebral structures enabling cetaceans to coordinate such complex functions have been investigated from both neuroanatomical and citoarchitectonical points of view. Cetacean brain is highly gyrencephalic with well-developed temporal and frontal lobes. Brain organization differs in odontocetes and mysticetes in that in odontocetes the olfactory lobe and the olfactory nerve become atrophic and disappear during the late ontogeny, and the connection between the brain cavity and the narial cavity is obliterated by an overgrowth of the mesethmoid [24, 25]. In mysticetes, the connection between the brain cavity and the narial cavity is maintained over the whole life of individuals, thus the olfactory lobe and the olfactory nerve can continue their usual work. From a citoarchitectonical view, it has been shown that the density of neural cells in cetacean brains is lower than that observed in human brains [17].

Brain Size in Cetaceans The size of cetacean brains depends largely upon the body size of the species under consideration, reflecting some allometrical relationship [7]. In absolute terms, a dolphin brain is obviously smaller than rorqual brain; however, when dolphin and rorqual brains are compared in the context of Mammalia, it appears that the dolphin brain is comparatively larger than the rorqual brain. This difference can be seen in a regression analysis of brain size vs. body size in the whole Mammalia, from which it is evident that the brain of a giant blue whale (*Balaenoptera musculus*, the largest rorqual) is smaller than expected based on its enormous body size; in contrast, the brain of a bottlenose dolphin (*Tursiops truncatus*) is much larger than expected in relation to its body size (Table 1 and Fig. 1 for raw data and plot, respectively).

As discussed above, the ratio between brain size and body size is known as encephalization quotient (EQ). The regression analysis of mammalian EQs (as plotted in Fig. 1) shows that a group of four species of odontocetes includes the most encephalized mammals (with the exception of *Homo sapiens*): *Sotalia fluviatilis*, *Lagenorhynchus obliquidens*, *Delphinus delphis*, and *T. truncatus* [18]. All of them belong to the family Delphinidae, have small and middle-sized bodies, live in groups, and use high-frequency sounds to echolocate and communicate over short distances (see [33] for a detailed account).

Table 1 Body weights (in kg) and brain weights (in g) for 70 mammal species

Species	Body weight (kg)	Brain weight (g)
Arctic fox	3.38	44.5
Owl monkey	0.48	15.5
Mountain beaver	1.35	8.1
Cow	465	423
Grey wolf	36.33	19.5
Goat	27.66	115
Roe deer	14.83	98.2
Guinea pig	1.04	5.5
Vervet	4.19	58
Chinchilla	0.43	6.4
Ground squirrel	0.1	4
Arctic ground squirrel	0.92	5.7
African giant pouched rat	1	6.6
Lesser short-tailed shrew	0	0.14
Star-nose mole	0.06	1
Nine-banded armadillo	3.5	10.8
Tree hyrax	2	12.3
North American opossum	1.7	6.3
Asian elephant	2,547	4,603
Big brown bat	0.02	0.3
Donkey	187.1	419
Horse	521	655
European hedgehog	0.79	3.5
Patas monkey	10	115
Cat	3.3	25.6
Galago	0.2	5
Genet	1.41	17.5
Giraffe	529	680
Gorilla	207	406
Grey seal	85	325
Rock hyrax (<i>Heterohyrax brucei</i>)	0.75	12.3
African elephant	6,654	5,712
Water opossum	3.5	3.9
Rhesus monkey	6.8	179
Kangaroo	35	56
Yellow-bellied marmot	4.05	17
Golden hamster	0.12	1
Mouse	0.02	0.4
Little brown bat	0.01	0.25
Slow loris	1.4	12.5
Okapi	250	490
Rabbit	2.5	12.1
Sheep	55.5	175
Jaguar	100	157
Chimpanzee	52.16	440
Baboon	10.55	179.5
Desert hedgehog	0.55	2.4
Giant armadillo	60	81
Rock hyrax (<i>Procavia habessinica</i>)	3.6	21
Raccoon	4.29	39.2

Table 1 (continued)

Species	Body weight (kg)	Brain weight (g)
Rat	0.28	1.9
Eastern American mole	0.08	1.2
Mole rat	0.12	3
Musk shrew	0.05	0.33
Pig	192	180
Echidna	3	25
Brazilian tapir	160	169
Tenrec	0.9	2.6
Phalanger	1.62	11.4
Tree shrew	0.1	2.5
Red fox	4.24	50.4
Human	62	1,320
Sperm whale	35,632	7,999.4
Bowhead whale	91,000	2,738
Fin whale	63,000	6,930
Bottlenose dolphin	700	1,600
Fat-free sperm whale	17,600	7,999.4 (50% fat)
Fat-free bowhead whale	72,600	2,738 (40% fat)
Fat-free fin whale	40,950	6,930 (35% fat)
Fat-free bottlenose dolphin	560	1,600 (20% fat)

Data from Stephan et al. [39] and Allison and Cicchetti [2].

In comparative terms, the EQs of these species fill the gap between the human EQ and the EQs of other mammals. In fact, while human EQ approaches 7, the highest EQ among the other mammals excluding delphinids is about 4 [12]. In the delphinid species cited above, the EQ values are about 5 – supporting the view that they are the most encephalized mammals with the exclusion of *H. sapiens* [18].

In contrast, the large baleen whales are among the less encephalized living mammals. Two possible explanations have been proposed for this observation. (1) As the brain size/body size relationship is non-linear, the low EQ of mysticetes could depend on an allometric growth trajectory in which brain growth is slower than body growth [7]. This means that large baleen whales should have smaller brains than small ones. Even though this generic allometric trajectory is well demonstrated in the whole Mammalia, it is not clear if it consistently applies to the whole suborder Mysticeti. (2) A methodological problem has been discussed in recent studies on brain measurements among cetaceans. In the large mysticetes, the fat superficial layer is much thicker than in all other mammals, but this layer does not receive any nerve; this means that a large part of the mysticete body is not directly represented in the brain. In turn, this means that in order to obtain a good comparison with other mammals, a fat-free estimate of body size should be considered in mysticetes. Otherwise, calculation of their EQs will be misled by this large amount of fat that increases body size by adding volume and weight not represented in the brain (see [17, 37]).

Spatial Organization in Cetacean Brain In the past century, several authors have addressed the problem of the origin of the hypercomplication of cetacean brains by suggesting that the land-to-water transition following the origin of the group required the development of newer abilities as well as different and more sophisticated systems for sensory treatment

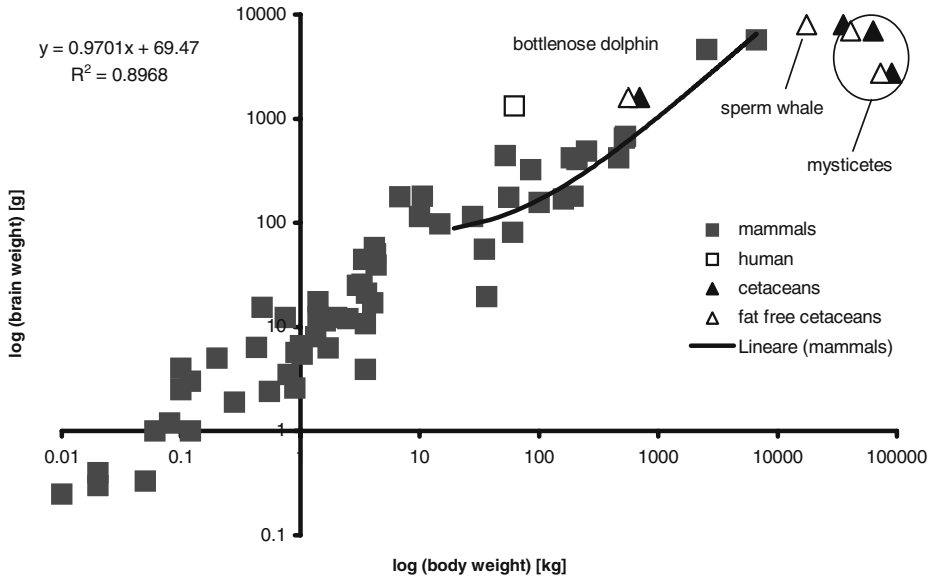


Fig. 1 Plot presenting the relationship between log (body size) vs. log (body weight). Filled squares represent EQ values for mammal species excluding man (open square) and cetacean (open and filled triangles). Filled triangles represent EQ values calculated including the total amount of fat in the body weight; open triangles represent EQ values calculated excluding fat from the body weight. Fat-free data are for cetaceans only. Numerical values are reported in Table 1. Regression line equation on the left superior corner. R^2 value suggests that the data are well fitted by the regression line

and movement control. Recent comparative analyses have shown that the situation is more complicated. Quantitative studies demonstrate that land-to-water transition did not trigger an explosive increase in brain size and did not result in a particular and detectable increase in the whole size of the brain of early, fully aquatic archaeocetes [9, 40]. However, some areas of the brain followed divergent theories. The cerebellum, for example, became larger in the early cetacean evolution, showing the development of large hemispheres but reduction of the vermis [17]. While the vermis is responsible of automatic control of equilibrium and posture in terrestrial animals, cerebellar hemispheres are responsible for automatic control of more complicated movements that, in the case of modern cetaceans, possibly include assistance in telencephalon-driven acrobatic swimming.

The cerebral structures responsible of sensory analysis underwent diverse evolutionary histories. Fossils show that over time there has been a strong reduction in the size of brain structures related to the treatment of olfactory inputs in both odontocetes and mysticetes. Possibly at the end of the Oligocene (about 25 million years ago), odontocetes completely lost the olfactory nerve and bulb upon reaching adulthood (while maintaining them in fetal and juvenile phases). The ontogenetic loss of the olfactory nerve, bulb and associated structures was thoroughly described in the sperm whale and in the common porpoise [24, 25]. In addition to the loss of cerebral structures related to olfaction, other parts of the odontocete brain were reduced during evolution. In particular, the archicortex (including the hippocampus) together with mammillar bodies and fornix were shown to be strongly reduced while the amygdala maintained its large size (possibly because it receives non-olfactory inputs). Marino [17] suggested that the general reduction of the limbic system is related to the loss of the olfactory structures. Archaeocete brain endocasts show that the olfactory structures were well developed up to at least the late Oligocene [40].

Cerebral areas directly related to the treatment of auditory information are particularly well developed and hypertrophied in cetacean brains ([17] and literature therein). The diameter of the vestibulocochlear nerve is relatively large, together with the primary auditory cortex and thalamic nuclei related to auditory processing (including pulvinar). Associative regions in the telencephalic hemispheres related to auditory stimulations and elaborations have been mapped and were revealed to be large and morphologically complex. The auditory sensory system is thought to be important in a cetacean's life for several reasons. Odontocetes use auditory signals in inter-individual communication and in determining spatial distribution of objects in the surrounding environment through sophisticated their echolocation capabilities. Mysticetes use auditory signals in long-distance inter-individual communication, but they do not possess physical characteristics that support echolocating capabilities. The evolution of osteological features, related to echolocation in odontocetes, were studied in fossil squalodontids [16]. These studies resulted in the observation that early odontocetes lacked the osteological characteristics related to echolocation, suggesting that this capability evolved at least during middle Miocene (approximately 15 million years ago). Unfortunately, comparative studies on the relative development of brain areas related to auditory processing in squalodontids are currently not available; they would certainly enhance our understanding of the origin of echolocating capabilities in odontocetes. Such a study would also illuminate a possible path toward the evolution of a large and complex brain as that found in odontocetes.

Surprisingly, inter-hemispherical connection systems are among the most reduced portions of cetacean brain [17]. Corpus callosum and fornix are particularly reduced in large-brained dolphins, and no other commissural structures can compensate for this reduction. It has been hypothesized that the reduction of interconnections allows whales to perform sleeping activities affecting only one hemisphere, thus maintaining vigilance with the active hemisphere.

Other enlarged brain portions include the basal nuclei and the telencephalic hemispheres. The total neocortical area of large-brained odontocetes exceeds that of humans and most of other mammals, documenting the presence of a highly complicated hardware for sophisticated cognitive output [32]. However, the height of the neocortex is approximately half of the height of human neocortex, suggesting that this wide neocortical area would not be able to provide high cognitive results. At present, there is no general consensus about what the cetacean brain should be able to do in terms of motional control, sensory analysis, and integrative functions. Field and behavioral studies strongly support a view of the cetacean brain as extremely complicated and able to produce sophisticated cognitive outputs, but anatomical and physiological works are not currently able to completely support this view.

Primates

Primate Brains The primates brain is characterized by features that distinguish it from those of other mammals. Part of the outstanding mental abilities of our species are a consequence of this basal architecture; this means that the principal differences existing between humans and other primate species are quantitative instead of qualitative. The primate visual cortex is particularly developed as a consequence of the importance (at different levels) of the sense of vision in the biology of the order.

Most of anthropoid species live in societies and spend much time in social intercourse. They have very complex communication strategies (implicating not only vision, but all

senses), and feeding research and acquisition strategies. Our closest relatives (chimpanzees, gorilla and orangutan) were used as models for the study of the human mind, because they show human-like capabilities such as self-recognition in mirror, abstract representation of the relations between objects, capacity to learn sign language, some states of consciousness, capacity to understand the mechanisms of tool use and toolmaking, etc. (e.g., papers in [8]).

Primate brains show a distinct temporal lobe separated from parietal and frontal regions by the Sylvian fissure. Interestingly, deep within this fissure is the presence of a large island of cortex (insula) under which a planar nuclear structure (claustrum) lies. Convolution of the brain varies considerably among primates (it is less variable in prosimians, more in great apes and men) and lateralization is somewhat developed. In a consistent way, the cortices of humans and great apes show high cortical neuron density and high thickness in comparison to other large brained mammals such as cetaceans and elephants [34, 35].

Brain Size in Primates In general, most primates have average brain sizes larger than those of other mammals, but there are several exceptions. Generally, anthropoids, whose Jerison's EQ ranges from 1.0 to 3.2 with a mean of about 2, show brains relatively larger than prosimians ($EQ \cong 1$), while the brains of great apes (except man) is larger than that of

Table 2 Encephalization quotients (EQ) of a number of Primate taxa

Taxa	EQ value
<i>Nasalis</i>	1.24
<i>Alouatta</i>	1.29
<i>Colobus</i>	1.41
<i>Aotus</i>	1.52
<i>Presbytis</i>	1.58
<i>Calicebus</i>	1.59
<i>Gorilla gorilla</i>	1.61
<i>Theropithecus</i>	1.61
<i>Macaca</i>	1.95
<i>Pithecia</i>	1.97
<i>Cercopithecus</i>	2.05
<i>Papio</i>	2.05
<i>Brachyteles</i>	2.17
<i>Erythrocebus</i>	2.19
<i>Chiroptotes</i>	2.27
<i>Cercocebus</i>	2.29
<i>Lagothrix</i>	2.29
<i>Pongo pygmaeus</i>	2.36
<i>Australopithecus afarensis</i>	2.44
<i>Ateles</i>	2.49
<i>Hylobates</i>	2.6
<i>Saimiri</i>	2.68
<i>Australopithecus africanus</i>	2.79
<i>Pan troglodytes</i>	3.01
<i>Paranthropus boisei</i>	3.22
<i>Paranthropus robustus</i>	3.24
<i>Cebus</i>	3.25
<i>Homo habilis</i>	4.31
<i>Homo erectus</i>	4.4
<i>Homo sapiens</i>	8.07

Data from Aiello and Dean [1].

monkeys only in absolute terms. Among the living non-human primates, the higher EQ value is found in capuchin monkeys (genus *Cebus*), for which recorded EQs range from 2.4 to 4.8. Our species shows the highest EQ of all primates, ranging from 7 to 8 (Table 2 and Fig. 2 for raw data and plot, respectively). Our high grade of encephalization is the result of an evolutionary process that started rather abruptly 2.5 Myr ago, which caused a strong increase in brain size at a nonconstant rate (Tartarelli, this volume).

According to Dunbar [5], it is possible to include the hypotheses proposed to explain the increase in brain size among primates into four classes: (1) epiphenomenal, (2) developmental, (3) ecological, and (4) social. The first two postulate that brain evolution is the result of the complex interaction of developmental processes instead of an external selective pressure. From an epiphenomenal point of view, primate brain evolution is simply the by-product of body size evolution; similarly, the evolution of different parts of the brain is the mere result of the whole brain evolution. Starting from the consideration that most of brain growth occurs before birth, the developmental hypothesis identifies in the maternal metabolic input the critical factor influencing brain development so that maternal energy constraints determine the energetic capacity available for fetal brain growth. The differences in brain size between the folivorous (smaller brains) and frugivorous (bigger brains) primate species could support this hypothesis since higher-quality diets enabled the frugivorous to invest more energy budget in fetal growth [21]. The ecological hypothesis explains the higher encephalization of the fruit eater species as a consequence of the need for more complex cognitive abilities (*ephemeral food supply hypothesis*), memory capacities (*mental map hypothesis*), and better sensorimotor coordination (*food extraction hypothesis*) to monitor the availability of a food supply highly dispersed in time and space and to extract it. The last class of hypotheses, the social ones, relate bigger brains to the high level of sociality shown by primates (with some exception in prosimians). Some

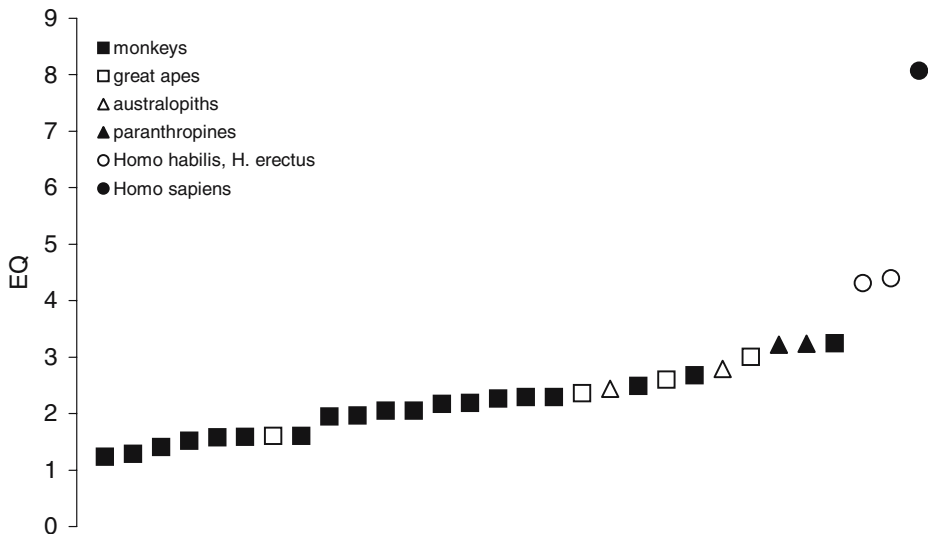


Fig. 2 EQs of some living and fossil primates including anthropoids, australopiths, paranthropines, and living and fossil humans. Note that apes' EQs (open squares) are not consistently higher than monkeys' EQs (filled squares). Note also the higher EQs of the genus *Homo* (filled and open circles). Adapted from Aiello and Dean [1] with modifications

correlations have been proposed between the total dimensions of the brain or one of its parts in particular (e.g., neocortex ratio) and group size, social structure and deception rates. This class of hypotheses are not mutually exclusive, and the primate brain size probably evolved as the result of constraints and selective forces acting in different ways on different brain regions [36].

Discussion [27]

The preliminary comparative analysis performed in our study shows the lack of a sole interpretative model able to explain the EQ distributions in primates and cetaceans. Analysis of fat-free data set for cetaceans showed little or no difference with respect to analysis based on total body weight (Fig. 1), suggesting that body composition should not have a significant impact on brain size.

The rate of brain size increase followed two different speeds in cetaceans and primates; in fact, while primates approached $EQ \sim 1$ by the end of the Eocene (33.7 Ma), cetaceans had already reached this value about 5 million years earlier, after the divergence of the odontocetes from the archaeocetes [19]. Cetacean EQ distribution is highly variable due to the emergence of large brains in an odontocete group, which occurred about 15 million years after the macroevolutionary process leading terrestrial cetaceans, such as *Pakicetus inachus*, to invade the water column during Early Eocene [19, 40]. There is no clear relationship between cetacean EQ and social complexity of groups, cultural behaviour, or other evident abilities of these marine mammals. In general, however, the cetacean brain is considered more complex than that of other marine mammals such as the extinct desmostylians and the living sirenians, which have more lissencephalic brains that probably resulted from an evolutionary process directed towards simplification of cerebral structures [20, 28]. The functional implications and the evolutionary path(s) of this supposed simplification have yet to be fully understood.

Among primates, the highest acceleration in the rate of brain increase occurred since Middle and Upper Pliocene. This acceleration affected two hominid lineages including the genus *Homo* and the genus *Paranthropus*. The parallel increase in EQs in paranthropines and humans was marked by different speeds: human EQ increase rate has risen more quickly than paranthropine EQ increase rate. It seems to be rather likely that dietetic constraints have influenced these rates, but some selective pressure towards higher EQs may have depended on evolution of more complex social structures and relationships [6, 41].

Future research on encephalization should focus on two distinct areas: (1) a fuller assessment of the impact of fat-free data set in the comparative evaluation of EQ in Mammalia (and, in consequence, in Primates and Cetacea); (2) a comparative study of the extension of brain areas and structures, such as the cerebellum, which should provide information about specific motor and/or cognitive capabilities in different species.

The evolution of sophisticated cognitive abilities remains a largely unresolved problem. A hypothesis that has been formulated long ago predicts that the complex cognitive abilities of humans are largely attributable to the disproportionate development of the cortex of the frontal lobes. A recent investigation on the relative size and allometry of the frontal lobe in humans and great apes demonstrated that a massive development of the cortex of the frontal lobe is shared by all living Hominoidea [38]. This means that other factors must have been involved in the evolution of complex cognitive abilities in the human lineage. Semendeferi

et al. [38] also suggested that there were no clear differences in the bauplan of human and great ape brains. It was also suggested that the advanced cognitive performance of the human brain was mainly due to enhanced interconnectivity [38]. However, as stated above, high interconnectivity did not play any crucial role in the evolution of complex cognitive abilities in cetaceans.

It is not yet clear how and why humans evolved large brains and complex behavioral patterns despite around one-and-a-half century of archaeological and anthropological studies. It is easy to imagine that the evolution of similar capabilities in animals other than humans is even more difficult to understand. Comparative studies on cognitive performances in different taxonomical groups can be of great help in obtaining a preliminary overview of the situation, eventually providing students with starting points for further and sharper researches. Comparisons of cetaceans and primates have been performed in the past 20 years, showing that only a small taxonomical sample of cetaceans displays an EQ comparable to that of humans. These include a few odontocetes belonging to the family Delphinidae whose brain has evolved into a larger size in the last 15 million years, about 10 million years after the functional loss of the olfaction in the toothed whales and about 30 million years after the invasion of the water column by stem cetaceans [19]. In toothed whales, a large brain has evolved primarily through the maintenance of large cerebellum and through the development of wider areas for receiving and processing auditory information. This occurred together with an increase in the size of basal nuclei and telencephalic hemispheres. In general, it can be said that large-brained odontocetes have brains with highly developed centers for automatic movement control (including automatic control of sophisticated movement sequences), highly developed centers for receiving and processing auditory information, and highly developed centers for integration in the telencephalon, but reduced inter-hemispheric connection systems and small-to-absent structures related to olfaction.

In about a century, the ontogeny of the cetacean brain has been clearly described but the genetic control of the process is yet largely unknown. The role of *Otx* genes, for example, is not known and the same is true about other key genes. The role of skull-vault segmentation genes described by, e.g., Iseki et al. [14, 15], is not observed in the highly modified skull structure of both odontocetes and mysticetes. The knowledge of the function of such genes during the development of cetacean skull would be very important because at least one of them is related to the position and probably to the extent of the cerebellum, a part which has been subject of wide expansion during cetacean evolution. Recent research efforts on cetacean development have been directed to understanding fin development and evolution [3, 31] and brain ontogeny, but they involved descriptive morphology and no molecular experiments have been carried out. Unavailability of high numbers of cetacean embryos will prevent such experiments from being carried out in the next several years. After this summary, it can be concluded that the sophisticated cognitive behaviors of cetaceans are performed under the control of a brain that is substantially different from that of humans. Self-recognition in the bottlenose dolphin is possible thanks to a set of hardware with few inter-hemispherical transfer of information and with less developed limbic structures than those of humans. In contrast, the observation of a marine landscape by a dolphin should be much richer in details due to its radar-like sound scanning of the environment. It is extremely difficult to even imagine what a dolphin or a whale would think about the world that it inhabits, or what happens in the brain of such an animal when it observes or hears the surrounding environment. The differences in brain architecture between humans and cetaceans make this task a speculative exercise without any scientific value. The point is

that we know that at least some cetacean species are able to behave in a way that appears extraordinarily similar to what we experience in our daily life when we see ourselves through a mirror. What we observe in cetacean behaviors is the final output of complex neural activities performed by a brain that is largely different from our brain in terms of spatial organization and architecture. In conclusion, we can reasonably think that when a dolphin recognizes itself through a mirror, it is doing that through mental processes different than our own. If this proves to be true (as it seemingly does), then we will be aware that complex and human-like cognitive abilities can be performed by minds that are vastly different from ours, minds shaped by selective forces generated in environments completely different from those where human evolution took place. And we will be aware that complex cognitive abilities can be convergently developed by different species with different brain structures after different evolutionary histories.

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