

Florida State University Libraries

2021

Are cetaceans neuroanatomically sophisticated? Absolute brain size may be the key.

Dean Falk

Preprint.



Are cetaceans neuroanatomically sophisticated? Absolute brain size may be the key.

Dean Falk
Department of Anthropology
Florida State University
60 N Woodward Ave
Florida State University
Tallahassee, FL 32306

dfalk@fsu.edu

Back in the day when John Lilly (1915-2001) had become famous for, among other things, giving LSD to dolphins to facilitate human-dolphin communication, I asked my mentor Leonard Radinsky (1937-1985) if he thought dolphins were exceptionally intelligent. After thinking for a moment, he answered with a succinct, *“I think they’re overrated.”* It is in fond memory of Len that the following analysis is offered.

Comparative measures of relative brain size (RBS) in primates and cetaceans, including encephalization quotients (EQ), are frequently used to support the claim that cetaceans are extremely intelligent. Some scholars go so far as to assert that cetaceans “rank near the top of any list measuring neuroanatomical sophistication, next to great apes, humans, and elephants.”¹ Below, I analyze mean adult brain and body masses for 58 cetacean and 76 primate species (Table 1)² and suggest that the large RBS of dolphins compared to humans may be due at least partly to an artifact of allometric scaling, and that absolute brain size, rather than RBS, might be a better indicator of cognitive abilities in cetaceans and primates.

TABLE 1

Species	Cetaceans, various authors	Brain Mass (g)	Body Mass (g)	RBS	RBS rank cet	Primates, Boddy 2012	Brain Mass (g)2	Body Mass (g)3	RBS	RBS rank prim
1	Platanista minor	164	18300	0.00896		Microcebus murinus	1.84	58.00	0.032	10
2	Neophocaena phocaenoides	468	32400	0.01444	8	Tarsius bancanus	2.70	77.60	0.035	5
3	Stenella longirostris	450	33600	0.01339	10	Galagoides demidoff	3.38	81.00	0.042	1
4	Neophocaena asiaeorientalis	422	34000	0.01241	13	Callithrix pygmaea	4.64	134.75	0.034	6
5	Pontoporia blainvillei	221	34890	0.00633		Cheirogaleus medius	3.34	179.67	0.019	
6	Cephalorhynchus hectori	644	38000	0.01695	2	Galago senegalensis	5.90	300.33	0.020	
7	Sotalia fluviatillis	688	42200	0.01630	4	Loris tardigradus	6.00	322.00	0.019	
8	Cephalorhynchus commersonii	748	43667	0.01713	1	Saguinus oedipus	9.64	327.14	0.029	12
9	Lagenorhynchus obscuris	886	58470	0.01515	6	Callithrix jacchus	7.73	347.45	0.022	
10	Platanista gangetica	295	59630	0.00495		Cheirogaleus major	6.80	450.00	0.015	
11	Stenella coeruleoalba	884	63500	0.01392	9	Nycticebus pygmaeus	7.80	480.00	0.016	
12	Delphinus delphis	797	65087	0.01225	14	Leontopithecus rosalia	13.05	512.38	0.025	
13	Lagenorhynchus albirostris	1126	67500	0.01668	3	Saimiri sciureus	23.35	578.70	0.040	2
14	Phocoena spinipinnis	597	68040	0.00877		Saimiri oerstedii	22.45	605.00	0.037	4
15	Cephalorhynchus heavisidii	763	71000	0.01075		Saguinus geoffroyi	14.27	634.67	0.022	
16	Lissodelphis borealis	1162	73000	0.01592	5	Nycticebus coucang	12.74	655.50	0.019	
17	Stenella attenuata	748	77000	0.00971		Aotus trivirgatus	16.04	701.68	0.023	

18	Phocoenoides truei	876	78400	0.01117		Saimiri boliviensis	24.06	750.00	0.032	8
19	Lipotes vexillifer	510	82000	0.00622		Callicebus moloch	19.00	900.00	0.021	
20	Sousa chinensis	1247	85000	0.01467	7	Perodicticus potto	12.07	929.33	0.013	
21	Stenella clymene	666	86000	0.00774		Eulemur rubriventer	24.90	1015.00	0.025	
22	Lagenorhynchus obliquidens	1137	89750	0.01267	11	Avahi laniger	10.49	1285.00	0.008	
23	Inia geoffrensis	632	90830	0.00696		Pithecia monachus	35.00	1500.00	0.023	
24	Phocoenoides dalli	834	98333	0.00848		Eulemur mongoz	24.03	1559.33	0.015	
25	Lagenorhynchus acutus	1200	120000	0.01000		Cebus albifrons	62.95	1620.00	0.039	3
26	Steno bredanensis	1542	123830	0.01245	12	Macaca sinica	58.15	1970.00	0.030	11
27	Lagenodelphis hosei	1103	124700	0.00885		Eulemur macaco	22.60	2086.17	0.011	
28	Feresa attenuata	1030	125000	0.00824		Lemur catta	21.63	2090.00	0.010	
29	Phocoena phocoena	1735	142430	0.01218	15	Cebus capucinus	70.14	2104.88	0.033	7
30	Kogia simus	622	168500	0.00369		Cebus apella	71.30	2589.00	0.028	14
31	Tursiops truncatus	1573	170480	0.00923		Cebus olivaceus	72.50	2684.50	0.027	15
32	Peponocephala electra	1392	206638	0.00674		Varecia variegata	31.20	2705.50	0.012	
33	Kogia breviceps	1012	305000	0.00332		Daubentonia madagascariensis	45.15	2800.00	0.016	
34	Grampus griseus	2387	328000	0.00728		Alouatta seniculus	45.50	2827.50	0.016	
35	Delphinapterus leucas	1921	498250	0.00386		Cercopithecus mona	67.00	3001.00	0.022	
36	Hyperoodon planifrons	2994	600000	0.00499		Macaca fascicularis	66.93	3109.45	0.022	
37	Mesoplodon bidens	1440	649000	0.00222		Ateles paniscus	108.96	3430.00	0.032	9

38	Mesoplodon europas	2149	732500	0.00293	Macaca nigra	97.50	3452.00	0.028	13
39	Mesoplodon densirostris	1463	767000	0.00191	Chlorocebus aethiops	64.13	3452.67	0.019	
40	Globicephala macrorhynchus	4166	900770	0.00462	Propithecus verreauxi	26.70	3480.00	0.008	
41	Mesoplodon mirus	2355	929500	0.00253	Cercopithecus cephus	76.00	3508.33	0.022	
42	Globicephala melas	2893	943200	0.00307	Macaca assamensis	90.50	3655.00	0.025	
43	Mesoplodon carlhubbsi	1860	1168000	0.00159	Lagothrix lagotricha	89.35	3905.00	0.023	
44	Monodon monoceros	2997	1578330	0.00190	Macaca nemestrina	110.00	4456.00	0.025	
45	Pseudorca crassidens	4307	2000000	0.00215	Macaca mulatta	87.99	4612.78	0.019	
46	Ziphius cavirostris	2004	2273000	0.00088	Cercocebus agilis	95.30	4700.00	0.020	
47	Orcinus orca	6052	3273000	0.00185	Alouatta caraya	50.70	5012.50	0.010	
48	Eubalaena australis	2750	12500000	0.00022	Lophocebus albigena	96.80	5125.00	0.019	
49	Eschrichtius robustus	4305	14329000	0.00030	Hylobates agilis	88.10	5528.75	0.016	
50	Megaptera novaeangliae	6100	30050000	0.00020	Hylobates lar	93.99	5550.00	0.017	
51	Physeter macrocephalus	8028	35833330	0.00022	Ateles geoffroyi	104.96	5774.00	0.018	
52	Balaenoptera borealis	4900	36666667	0.00013	Alouatta palliata	50.04	5952.00	0.008	
53	Physeter catadon	7818	37093000	0.00021	Hylobates muelleri	95.31	5954.88	0.016	
54	Balaenoptera edeni	3750	40000000	0.00009	Indri indri	38.30	6250.00	0.006	
55	Balaenoptera musculus	3636	50904000	0.00007	Cercopithecus mitis	75.00	6300.00	0.012	

56	Eubalaena japonica	2700	60793171	0.00004	Macaca maura	94.48	6846.00	0.014
57	Balaenoptera physalus	5100	62500000	0.00008	Procolobus badius	78.00	7000.00	0.011
58	Balaena mysticetus	2843	90000000	0.00003	Semnopithecus entellus	111.50	7010.00	0.016
59					Erythrocebus patas	100.20	7376.00	0.014
60					Pygathrix nemaeus	77.00	7500.00	0.010
61					Macaca arctoides	100.70	7630.00	0.013
62					Theropithecus gelada	130.00	7710.00	0.017
63					Ateles fusciceps	113.60	9026.50	0.013
64					Aotus lemurinus	113.50	9026.50	0.013
65					Trachypithecus francoisi	94.40	9100.00	0.010
66					Colobus angolensis	74.40	9670.00	0.008
67					Colobus guereza	83.90	10281.25	0.008
68					Macaca sylvanus	87.70	11200.00	0.008
69					Mandrillus sphinx	159.20	11500.00	0.014
70					Papio hamadryas	142.00	12020.00	0.012
71					Hylobates syndactylus	134.80	12172.00	0.011
72					Pan paniscus	329.70	39700.00	0.008
73					Pongo pygmaeus	341.99	54229.04	0.006
74					Pan troglodytes	354.81	60433.16	0.006
75					Homo sapiens	1250.43	65142.86	0.019
76					Gorilla gorilla	454.55	120975.00	0.004

Legend for Table 1: Relative brain size in 58 cetacean and 76 primate species. Brain and body sizes for primates from Boddy (2012); those for cetaceans are from Boddy (2012), Manger (2006), and Fox (2017). The 15 species with the largest RBS (1 = highest rank) occur among the smallest-bodied half of each order.

RBS is defined here as the ratio between brain mass and body mass (brain mass/body mass). Fig. 1A shows the typical ontogenetic brain growth curves for humans and chimpanzees. During the first year of life, brain size increases rapidly, and the rate of brain growth continues to decrease in subsequent years until adult brain size is reached. The human postnatal brain “spurt” is steeper than that of chimpanzees, which is why adult humans end up with brains that are over three times the size of adult chimpanzee brains. As can be seen, the curves plotting RBS against body size for different primate taxa in Fig. 1B are shaped inversely compared to ontogenetic curves. Despite their different positions relative to the vertical axis, the curves for the different taxa are similarly shaped, with humans on top.³

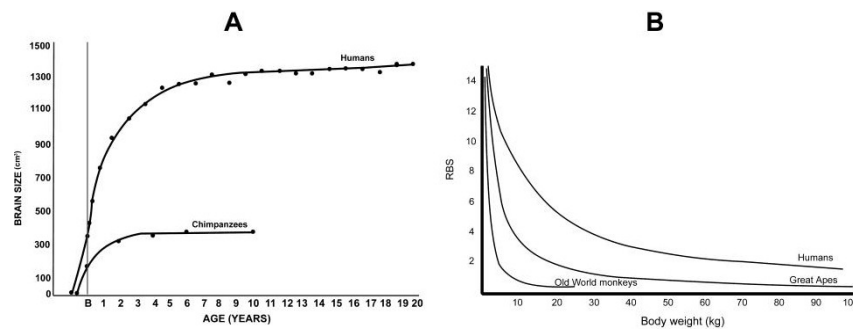


Fig. 1. Brain growth and relative brain size in primates. A: Typical ontogenetic brain growth curves for humans and chimpanzees (brain size versus age in years, B = birth). Brain size is in cubic centimeters, a traditional proxy for grams. B: RBS (brain mass/body mass) versus body mass for humans, great apes, and Old World monkeys. See Falk, 2007 for details.

These observations are not limited to primates. What is remarkable is that the shape of brain growth curves for individuals is the same as the shapes of the brain growth curves for species. As Harry Jerison notes: “The aspect that intrigues me is that the growth pattern during development of an individual animal generates an equation that is equally useful for describing relationships among adults of different species.”⁴ Thus, just as individual apes and humans have larger RBS than more mature (bigger-bodied) individuals in the same species, adults representing smaller-bodied species of primates usually have larger RBS compared to adults of larger-bodied species (Table 1).

But does RBS in cetaceans scale like that of primates? If one includes the largest species of cetaceans, the overall distribution scales in ways that depart from other mammals: “The relationship between brain size and body size in cetaceans is strongly nonlinear even after log-transforming each variable.”⁵ As noted long ago, one researcher considered two of the largest cetaceans available at that time, Megaptera and Balaenoptera, “as unusual, because of an excess amount of fat, so he calculates his rectilinear regression without them. Just at what point one should stop and say, ‘From such a body weight on, the animals all have too much inanimate weight to be considered,’ I cannot say.”⁶ Nonetheless, RBS in the first 47 cetacean species in Table 1 scales in a mammalian-typical inverse curve (Fig. 2). RBS is compared below in species from the two orders that are of similar body sizes, i.e., those located to the left of *Phocoena phocoena* (P.p.) in Fig. 2.

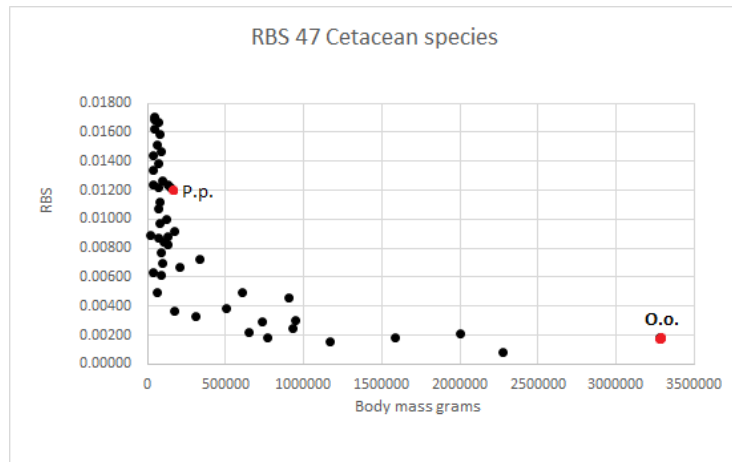


Fig. 2. Relative Brain Size (brain mass in grams/body mass in grams) for 47 species of Cetaceans. The largest is *Orcinus orca* (O.o.). Cetaceans that are smaller than *Phocoena phocoena* (P.p.) have body masses that overlap with those of great apes and humans (Fig. 3).

Comparisons of RBS in primates and cetaceans are provided here because this variable is more intuitively accessible than are residuals from log-transformed brain size/body size data and less subject to statistical artifacts.⁷ Fig. 3 plots mean adult RBS for 76 species of primates and the 29 smallest-bodied cetacean species (up to and including *Phocoena phocoena*) listed in Table 1. If one excludes *Homo sapiens* (H.s.), it is clear that the distribution of RBS for primates is shaped like the inverse brain growth curves for more restricted taxa of primates (Fig. 1B), as expected. Although the one obvious departure from the primate distribution is H.s., 30 of the 76 primate species have a mean RBS that is larger than the .019 RBS of H.s. (Table 1). At .040, for

example, mean RBS in the common squirrel monkey (*Saimiri sciureus*) exceeds that of H.s. Nevertheless, H.s. is clearly “encephalized” (i.e., has a RBS that is relatively large for its body size) compared not only to squirrel monkeys but to all other primates (Fig. 3).

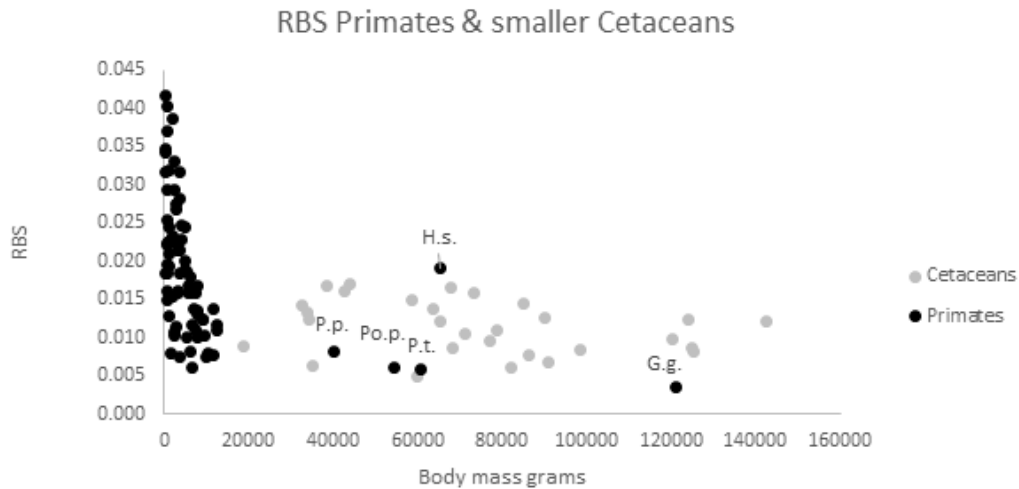


Fig. 3. Relative Brain Size (brain mass in grams/body mass in grams) for 76 primate species and 29 cetacean species. The entries represent average adults for each species (Table 1). The largest-bodied cetacean represents *Phocoena phocoena*. Most of the cetaceans are in the dolphin (*Delphinidae*) family. Abbreviations of four great apes and human: G.g., *Gorilla gorilla*; H.s., *Homo sapiens*; P.p., *Pan paniscus*; P.t., *Pan troglodytes*; Po.p., *Pongo pygmaeus*.

Because bigger primates tend to have absolutely larger brains but smaller RBS than smaller animals, and despite the fact that they are regarded as more intelligent than monkeys, the four great apes have among the smallest RBS for primates (Fig. 3, Table 1). In other words, RBS is smaller in great apes than monkeys because they occupy the bigger-bodied (right) side of the distribution for all primates (Fig. 3). Like primates, the cetacean species with the highest RBS are the smaller-bodied ones; the 15 species with the largest RBS (1 = highest) occur among the smallest-bodied half of each order (Table 1). The highest RBS among primates is .042 (*Galagoides demidoff*); the highest among cetaceans is .01713 (*Cephalorhynchus commersonii*). Thirty-eight of the 76 primate species have a RBS that is larger than the largest RBS in any cetacean.

Despite the fact that Fig. 3 shows that mean RBS in the smallest cetacean species is more variable and usually greater than the RBS averages for great apes of similar body sizes, one must

be careful about interpreting these data with respect to “neuroanatomical sophistication.” Unlike *Homo sapiens*’ position relative to the primate distribution for RBS, no cetacean species is located far above the general cetacean distribution for RBS. Elsewhere, I have hypothesized that the high RBS in H.s. is, indeed, related to neuroanatomical sophistication because of evolutionary and developmental factors associated with the brain spurt that characterizes our species during the first 1-2 years of life (Fig. 1A), when infants are acquiring and developing the distributed neural networks for language.⁸ Later in life (and also during hominin evolution), these linguistic networks pave(d) the way for the emergence of other advanced cognitive abilities associated with (among other things) music, mathematics, and reading. The extent of these abilities sets humans apart from all other mammals. It is not just the relative size of the brain (i.e., compared to other primates of approximately similar body sizes) that is associated with neurological sophistication in H.s. The brain’s wiring is at least as important, and neurological connectivity associated with cognitive processing is beginning to be understood from advanced functional imaging studies of living people. Because imaging of brain physiology in living dolphins⁹ and postmortem computed tomography and postmortem magnetic resonance studies of gross neuroanatomical features of cetacean brains are in their infancy,¹⁰ functional connectivity related to cognition in cetacean brains remains uncharted territory.

One approach for exploring the functional implications of high RBS in dolphins might be to investigate ontogenetic brain growth in the smaller and larger cetaceans and plot the curves separately, as was done for humans and chimpanzees in Fig. 1A. Do the dolphins that are closest to H.s. in Fig. 3 have a relatively steep rate of postnatal brain growth (brain spurt) compared to other species in their order, as humans do compared to chimpanzees (Fig. 1)? If so, what cognitive and social skills do infant dolphins acquire during the brain spurt, and might any of them (possibly related to audition) require extraordinary neurological processing? Do dolphins have any skills that are as far reaching as the ability of humans to perceive and generate frequencies of little bits of air and use them to understand and generate an infinite number of ideas from/to conspecifics?

No matter how social or self-aware (able to recognize themselves in mirrors, etc.) dolphins may be, and despite comparative cytoarchitectonic and gross neuroanatomical studies of the (very differently organized) brains of primates (including humans) and cetaceans, attempts to compare levels of neurological sophistication in dolphins, apes, and humans are, at best,

premature.¹¹ According to Jerison, the similar RBS of dolphins and humans indicates that their overall information-processing capacity is “about the same. Does this mean that dolphins are as smart as we are? I suppose that depends on what one means by smart. But it is a nonsense question. It should be obvious that all species use their processing capacity in species-typical ways.”¹² Jerison reasonably suggests that dolphins may be processing unusual amounts of auditory information.

Body size and absolute brain size are both better predictors of mental capacity and cognitive abilities than RBS in primates.¹³ As noted, great apes have bigger bodies and bigger brains than monkeys and are generally perceived as more intelligent than the latter, although RBS is smaller in apes. Could this also be true for cetaceans, in which case cognition in the largest ones, which have the largest brains, might be at least as interesting as that of the smaller-brained dolphins? In any event, the lack of one or more striking outlier for RBS in the cetacean distribution and the large range of variation for cetacean RBS compared to the narrow range for similarly-sized great apes suggest that ecological and physiological factors may have been important determinants of the RBS of dolphins.

Ecological factors related to cetacean body and brain sizes

Jerison notes “that cetaceans, evolving in a gravitationally odd environment, had different constraints on the size of their bodies than land mammals.”¹⁴ Indeed, gravity was relevant for primate and cetacean evolution generally: The smallest-bodied primates live in strictly arboreal habitats; larger-bodied primates shifted to less gravitationally-challenging (i.e., in terms of potentially fatal falls) semi-terrestrial habitats; and the largest hominins eventually shifted to the fulltime ground living that characterizes *Homo sapiens*.¹⁵ After the ancestors of cetaceans entered the ocean around 50 millions of years ago, some of them evolved large increases in body mass,¹⁶ likely in response to relaxed gravitational constraints combined with the availability of sufficient nutrition. Brain mass increased as well. Since most variation in mammalian brain size is ‘explained’ by body size,¹⁷ it is reasonable to speculate that increased body mass was initially targeted by natural selection in some cetaceans and that brain mass went along for the ride. (This would not have excluded cognition and its neurological substrates from also being potential targets to some degree.) Positing body mass as a prime target for natural selection as early cetaceans underwent adaptive radiation is consistent with Bergmann’s rule, since increased body

mass maximizes body volume relative to surface area, thus facilitating heat retention in cold aquatic habitats. Similarly, cetaceans' globular body shape and lack of long appendages likely promote heat retention (Allen's rule). Significantly, Bergmann's rule is known to apply to the global distribution of cetaceans, since interspecific body size strongly correlates with water temperature, with large-bodied species being favored in colder environments.¹⁸

A recent analysis¹⁹ dismisses the "thermogenesis hypothesis" that cetacean brains evolved to be large, at least partly, under pressure from water temperature,²⁰ and in the process mischaracterizes my radiator theory of hominin brain evolution as a proposition that "the brain served as a radiator to disperse heat," citing another source that incorrectly claims "according to the modern radiator theory the human brain developed starting as a refrigerator of itself."²¹ Because the high rate of metabolism in large human brains generates excessive heat, the radiator theory²² is based on the assumption that, as brains increased in size during hominin evolution, so did their thermolytic cooling needs. The hominin cranial radiator was conjectured to consist of an extensive network of tiny valveless veins that evolved in response to altered hydrostatic pressures that were exerted on blood vessels during selection for bipedalism—a network (not to be confused with the rete mirabile of carnivores and ungulates) that was exapted to cool the brain selectively under stressful thermal conditions. Although the concept of selective brain cooling in humans was controversial when I proposed the hominin radiator, its anatomical basis has since been demonstrated and imaged.²³ As detailed elsewhere, the radiator theory does not describe the human brain itself as either a cranial radiator or "refrigerator," as asserted by some. Rather, the radiator is a vascular network that is "viewed as an underlying and dynamic mechanism that helped regulate brain temperature and, as such, released thermal constraints that would otherwise have kept brain size in check...The radiator is therefore best viewed as a 'prime releaser'... not a prime mover of human brain evolution."²⁴ For natural selection to increase brain size, homeostatic mechanisms that can support the brain's presumably increased metabolic and thermal requirements need to be or become available.

Ridgway speculates that dolphin brains may also have a high rate of metabolism that necessitates a mechanism for cooling: "Cetaceans may have adapted special means for cooling. The entire blood supply of their brains passes through a large rete mirabile in the dorsum of the thorax and then into another rete system...before reaching the cranial vault...Such a configuration is well positioned to provide a counter-current heat exchange mechanism capable

of regulating temperature in blood reaching the brain.”²⁵ Cetacean brains have also evolved special features in cortical neurons and glia that increase their ability to generate heat.²⁶ Together, these cooling and heating adaptations hypothetically would have kept enlarging cetacean brains within safe temperature ranges via dynamic homeostatic processes that released thermal constraints that might, otherwise, have kept brain size in check. As noted, such physiological adaptations need not be viewed as prime movers of brain size evolution; rather, they may have developed on the coattails of behaviors (whatever they were) that were targeted by natural selection, ultimately, resulting in enlarged bodies and brains in many cetaceans.

Significantly, body size sometimes decreased during cetacean (and primate) evolution, and it is not always clear whether enlarged RBS in extant species is the result of increased brain size or decreased body size (phyletic dwarfism).²⁷ Because body size decreased during the evolution of some cetaceans including dolphins,²⁸ one hesitates to equate cognitively the right-side bigger-bodied (smaller RBS) part of the primate distribution with the left-side (larger RBS) part of the cetacean distribution (Fig. 3). In other words, it is not clear to what extent one may, or may not, rule out evolutionary reduction in dolphin body mass as a (non-cognitive) factor in their high RBS compared to the great apes, which experienced an evolutionary increase in body mass.

Like some birds and nonhuman primates, dolphins are, indeed, capable of social learning, imitation, and cultural innovation and transmission of certain behaviors.²⁹ Nonetheless, the conclusion that it “is certain now” that cetaceans “display cognitive skills surpassing any other animal” warrants close scrutiny.³⁰ As others have noted, cetaceans do not have hands and fingers. They rarely use, let alone make, tools, with the fascinating exception of sponge carrying in some individuals. Cetaceans lack rudiments of a material culture, unlike wild great apes that construct tree nests and use and sometimes make tools for extractive foraging. Regarding the social brain hypothesis to explain the high RBS in dolphins, many animals are social and most anthropoid primates including humans are remarkably so. (Highly intelligent orangutans, on the other hand, are relatively solitary.) Interestingly, humans with high-functioning autism (e.g., Asperger syndrome) who famously lack social skills, are known for their analytical, abstract, systematic thinking, which was/is crucial for the cognitive skills that, so far, appear to be unique to people. There is ample reason to believe that humanity’s repertoire of advanced cognitive skills depends largely on neurological substrates that initially evolved in conjunction with the emergence of symbolic grammatical language. Rather than sociality per se, an explanation for

RBS in some dolphins might best be sought by exploring their whistles and clicks, as Ridgway suggests when comparing *Stenella* and *Steno*.³¹ And what about the largest-bodied cetaceans that have the absolutely biggest brains on earth? I wonder what's on their minds!

¹ Fox, Kieran 2020 "The social cetaceans," *Inference* 5 (3); quotation p. 1.

² Brain and body masses listed in Table 1 are from (1) Table S1 of Boddy, A. M., M. R. McGowen, C. C. Sherwood, L. I. Grossman, M. Goodman, and D. E. Wildman. 2012. "Comparative analysis of encephalization in mammals reveals relaxed constraints on anthropoid primate and cetacean brain scaling." *J Evol Biol* 25 (5):981-94. doi: 10.1111/j.1420-9101.2012.02491.x.; (2) Table S1 of Fox, K. C. R., M. Muthukrishna, and S. Shultz. 2017. "The social and cultural roots of whale and dolphin brains." *Nat Ecol Evol* 1 (11):1699-1705. doi: 10.1038/s41559-017-0336-y; and (3) Table 1 of Manger, Paul R. 2006. "An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain." *Biological Reviews* 81 (2):293-338.

³ Falk, D. 2007. "Evolution of the primate brain." In *Handbook of Palaeoanthropology Vol. 2: Primate Evolution and Human Origins*, edited by W. Henke and I. Tattersall, 1133-1162. Springer-Verlag.

⁴ Jerison, Harry J. 2001. "Epilogue: The study of primate brain evolution: where do we go from here?" In *Evolutionary Anatomy of the Primate Cerebral Cortex*, edited by Dean Falk and Kathleen R. Gibson, 305-337. Cambridge, UK: Cambridge University Press; quotation p. 312

⁵ Fox, K. C. R., M. Muthukrishna, and S. Shultz. 2017. Quotation p. 1704; see also Fig. S5.

⁶ Count, Earl W. 1947. "Brain and body weight in man: their antecedents in growth and evolution: a study in dynamic somatometry." *Annals of the New York Academy of Sciences* 46 (10):993-1122; quotation p. 1056.

⁷ Growth curves described with the formula, $y=ax^b$ can be straightened by log-transforming the formula to $\log(y) = \log(a) + b*\log(x)$, in which b is the slope of the line and $\log(a)$ is its intercept. As is well known, comparing EQs (or other indices) that depend on residuals from such log-transformed linear regressions of brain size/body size data is highly influenced by the species that are included in the regression used to compute the indices/residuals. The slope (and intercept) of the basal regression changes with the composition of the basal group. Outliers in body size in a group of related species (i.e., the largest-bodied and smallest-bodied species) are subject to deflated and inflated indices, respectively, because a linear distribution of brain size versus body size in the taxonomic group under consideration (e.g., anthropoid primates) usually has a smaller slope than the more inclusive basal regression. The effect of this is that the largest species may be 'tilted' below the linear regression on the right, the smallest ones may fall above the regression on the left. This is why some view the supposedly low EQ of gorillas as a possible artifact. Many workers use some version of mouse-to-elephant regressions to compute various encephalization indices, which entails a certain amount of circularity if the basal regression

includes the taxa for which indices are being computed. Manger 2006, at least, uses a mammalian linear regression (slope = .718) that excludes cetaceans and primates to compute and compare EQs from the two groups. There are other problems with EQ analyses of cetaceans as discussed in Ridgway, Sam H, Kevin P Carlin, Kaitlin R Van Alstyne, Alicia C Hanson, and Raymond J Tarpley. 2016. "Comparison of dolphins' body and brain measurements with four other groups of cetaceans reveals great diversity." *Brain, behavior and evolution* 88 (3-4):235-257.

⁸ Falk, Dean. 2016. "Baby-the-trendsetter: Three evo-devo trends and their expression in Asperger syndrome." In *Costly and Cute: How Helpless Newborns Made Us Human*, edited by W. Trevathan and K. Rosenberg. Albuquerque, NM: University New Mexico Press; Falk, Dean. 2016. "Evolution of brain and culture: the neurological and cognitive journey from Australopithecus to Albert Einstein." *Journal of Anthropological Sciences* 94:1-14; Falk, Dean, and Eve Penelope Schofield. 2018. *Geeks, Genes, and the Evolution of Asperger Syndrome*: University of New Mexico Press.

⁹ Ridgway, S., D. Houser, J. Finneran, D. Carder, M. Keogh, W. Van Bonn, C. Smith, M. Scadeng, D. Dubowitz, R. Mattrey, and C. Hoh. 2006. "Functional imaging of dolphin brain metabolism and blood flow." *J Exp Biol* 209 (Pt 15):2902-10. doi: 10.1242/jeb.02348.

¹⁰ Kot, Brian Chin Wing, Henry Chun Lok Tsui, Tabris Chung, and Amy Pik Yan Lau. 2020. "Postmortem neuroimaging of cetacean brains using computed tomography and magnetic resonance imaging." *Frontiers in Marine Science* 7:775. doi: 10.3389/fmars.2020.544037

¹¹ Marino, L., C. Butti, R. C. Connor, R. E. Fordyce, L. M. Herman, P. R. Hof, L. Lefebvre, D. Lusseau, B. McCowan, E. A. Nimchinsky, A. A. Pack, J. S. Reidenberg, D. Reiss, L. Rendell, M. D. Uhen, E. Van der Gucht, and H. Whitehead. 2008. "A claim in search of evidence: reply to Manger's thermogenesis hypothesis of cetacean brain structure." *Biol Rev Camb Philos Soc* 83 (4):417-40. doi: 10.1111/j.1469-185X.2008.00049.x.

¹² Jerison, Harry J. 2001; quotation, p. 320.

¹³ Gibson, K.R. 2001. "Bigger is better: primate brain size in relationship to cognition." In *Evolutionary Anatomy of the Primate Cerebral Cortex*, edited by D. Falk and K. R. Gibson, 79-97. Cambridge, UK: Cambridge University Press. Deaner, R. O., K. Isler, J. Burkart, and C. van Schaik. 2007. "Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates." *Brain, Behavior and Evolution* 70 (2):115-24. doi: 000102973 [pii] 10.1159/000102973.

¹⁴ Jerison, Harry J. 2001; quotation, p. 307.

¹⁵ Falk, Dean. 2000. *Primate Diversity*. New York: W.W. Norton.

¹⁶ Montgomery, S. H., J. H. Geisler, M. R. McGowen, C. Fox, L. Marino, and J. Gatesy. 2013. "The evolutionary history of cetacean brain and body size." *Evolution* 67 (11):3339-53. doi: 10.1111/evo.12197.

¹⁷ Jerison, Harry J. 1991. *Brain Size and the Evolution of Mind: 59th James Arthur Lecture on the Evolution of the Human Brain*, James Arthur lecture on the evolution of the human brain 59. New York: American Museum of Natural History; see p. 54. Thus, whales and elephants have brains that are many times larger than those of humans, largely because they have enormous bodies.

¹⁸ Torres-Romero, Erik Joaquín, Ignacio Morales-Castilla, and Miguel Á Olalla-Tárraga. 2016. "Bergmann's rule in the oceans? Temperature strongly correlates with global interspecific patterns of body size in marine mammals." *Global Ecology and Biogeography* 25 (10):1206-1215.

¹⁹ Fox, 2020.

²⁰ Manger, Paul R, Nina Patzke, Muhammad Spocter, Adhil Bhagwandin, Karl Karlsson, Mads Bertelsen, Abdulaziz Alagaili, Nigel Bennett, Osama Mohammed, and Suzana Herculano-Houzel. 2020. "Amplification of potential thermogenetic mechanisms in cetacean brains." *bioRxiv*:1-32. See also Manger, 2006.

²¹ Falk, D. 1990. "Brain evolution in Homo: the "radiator" theory (target article)." *Behav Brain Sci* 13 (333-381); endnote 33 of Fox 2020; Olga Longo, "Hot Heads and Cold Brains: Aristotle, Galen and the 'Radiator Theory,'" *Physis: Rivista internazionale di storia della scienza* 33 (1996): 259–66.

²² Falk, Dean. 2007. "Constraints on brain size: The radiator hypothesis." In *The Evolution of Primate Nervous Systems*, edited by T.M. Preuss and J. H. Kaas, 347-353. Oxford: Elsevier-Academic Press; see especially Fig. 4.

²³ Zenker, W., and S. Kubik. 1996. "Brain cooling in humans--anatomical considerations." *Anat Embryol (Berl)* 193 (1):1-13. doi: 10.1007/BF00186829.

²⁴ Falk 2007. "Constraints on brain size..."

²⁵ Ridgway, et al. 2016; quotation p. 254.

²⁶ Manger et al. 2020.

²⁷ Smaers, J. B., R. S. Rothman, D. R. Hudson, A. M. Balanoff, B. Beatty, D. K. N. Dechmann, D. de Vries, J. C. Dunn, J. G. Fleagle, C. C. Gilbert, A. Goswami, A. N. Iwaniuk, W. L. Jungers, M. Kerney, D. T. Ksepka, P. R. Manger, C. S. Mongle, F. J. Rohlf, N. A. Smith, C. Soligo, V. Weisbecker, and K. Safi. 2021. "The evolution of mammalian brain size." *Sci Adv* 7 (18). doi: 10.1126/sciadv.abe2101.

²⁸ Montgomery et al. 2013.

²⁹ Rendell, Luke, and Hal Whitehead. 2001. "Culture in whales and dolphins." *Behavioral and brain sciences* 24 (2):309-324

³⁰ Fox, 2020; quotation p. 3. Fox cites Pryor, Karen, and Jon Lindbergh. 1990. "A dolphin-human fishing cooperative in Brazil." *Marine Mammal Science* 6 (1):77-82. However, the supposedly "cooperative" dolphin-human fishing is clearly opportunistic on the part of humans, and there is no evidence of intention on the part of the fish-herding/feeding dolphins to "cooperate." Similarly, the essay's assertion that the dolphin's ability to understand human pointing is unknown in primates is tenuous in light of recent research: Leavens, D. A. 2021. "The Referential Problem Space revisited: An ecological hypothesis of the evolutionary and developmental origins of pointing." *Wiley Interdiscip Rev Cogn Sci*:e1554. doi: 10.1002/wcs.1554. Nor is the "inventiveness" of some dolphins particularly surprising because (as with many trained animal performers) the novel motor behaviors emerged in response to shaping/training with food reinforcements: Pryor, Karen W, Richard Haag, and Joseph O'Reilly. 1969. "The creative porpoise: Training for novel behavior 1." *Journal of the Experimental Analysis of behavior* 12 (4):653-661.

³¹ Ridgway et al. 2016, p. 255.