

# The size and complexity of dolphin brains—a paradox?

STEFAN HUGGENBERGER

Zoological Institute II, University of Cologne, Weyertal 119, 50931 Köln, Germany

*Dolphin brain size with respect to body size ranks between that of apes and humans. The hypertrophic auditory structures, the large cerebrum with extended gyrification and the highly cognitive capabilities of toothed whales seem to be in paradoxical contrast to their thin neocortex with a plesiomorphic or pedomorphic cytoarchitecture. The total number of neurons in the delphinid neocortex is comparable to that of the chimpanzee (Primates), but, in relation to body weight, in the magnitude of the hedgehog (Insectivora) neocortex since cetaceans may be able to obtain larger body sizes than terrestrial mammals due to reduced gravitational effects in water. During evolution, dolphins may have increased the computational performance of their cytoarchitecturally 'simple' neocortex by a multiplication of relevant structures (resulting in a hypertrophic surface area) instead of increasing its complexity. Based on this hypothesis, I suggest that the evolution of the large dolphin brain was possible due to a combination of different prerequisites based on adaptations to the aquatic environment including the sonar system. The latter facilitated a successful feeding strategy to support an increased metabolic turnover of the brain and led to a hypertrophic auditory system. Moreover, the rudimentary pelvic girdle did not limit brain size at birth. These adaptations favoured the evolutionary size increase of the cerebral cortex in dolphins facilitating highly cognitive capabilities as well as precise and rapid sound processing using a 'simple' kind of neocortical cytoarchitecture.*

**Keywords:** neocortex; auditory system; toothed whales; cognitive capabilities.

Submitted 31 July 2007; accepted 2 December 2007; first published online 17 March 2008

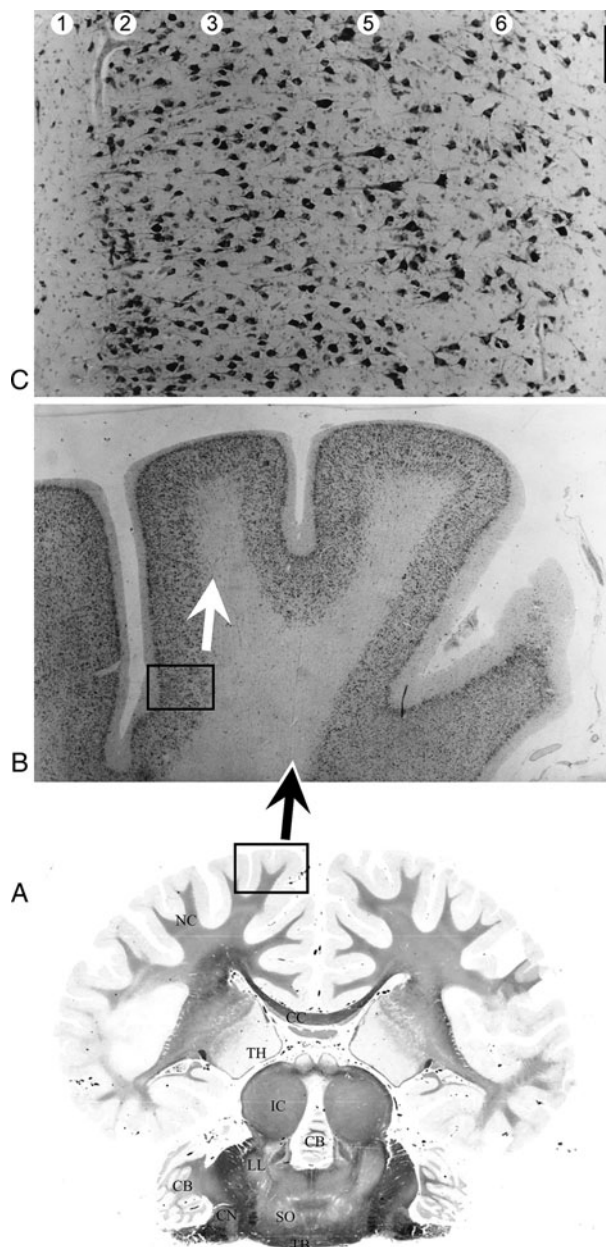
## INTRODUCTION

Several recent papers refer to the evolution and development of the large brain size of dolphins, ranking between that of apes and humans with respect to body size (Schwerdtfeger *et al.*, 1984; Deacon, 1990; Marino, 1998; Marino *et al.*, 2003, 2004; Hof *et al.*, 2005; Manger, 2006). The development of this high encephalization level of dolphins and other toothed whales (Odontoceti) has been correlated with social competition (Connor, 2007), a lengthened life span (Lefebvre *et al.*, 2006), water temperature during the Eocene–Oligocene transition period (Manger, 2006), and enhanced auditory processing (Oelschläger & Kemp, 1998; Ridgway & Au, 1999) as well as audiomotor navigation (Oelschläger, in press). Particularly impressive is the size and gyrification of the neocortex (isocortex) leading to a surface area surpassing that in humans (Ridgway & Brownson, 1979, 1984; Haug, 1987; Hof *et al.*, 2005; Marino, 2007; Oelschläger *et al.*, 2008).

Concrete functional implications of brain size, in general, and cortical expansion, in particular in dolphins are still enigmatic. However, the development of an underwater biosonar system in toothed whales during evolution led to profound modifications in the dolphin head (Rauschmann *et al.*, 2006). Here, the functional synthesis of the unique (hypertrophic) nasal complex representing the sound generator (Cranford *et al.*, 1996; Cranford & Amundin, 2004) with the structures of the peripheral and central auditory system in toothed whales (Oelschläger & Oelschläger, 2002) may have been a primary factor for the evolutionary size increase of the brain

as a whole (Oelschläger & Kemp, 1998; Ridgway & Au, 1999; Ridgway, 2000; Oelschläger, 2008; Oelschläger *et al.*, in press). Auditory structures in the dolphin's brain are generally large (Figure 1A; Breathnach, 1960; Bullock & Gurevich, 1979; Ridgway, 2000). The medial geniculate body is about seven times larger, the inferior colliculus twelve times and the lateral lemniscus 250 times larger in absolute terms than the equivalent structures in the human brain (Bullock & Gurevich, 1979). Thus, hypertrophic auditory structures may be the primary reason for the large brain in dolphins (Ridgway, 2000) and the cerebral cortex may have reached its great extension due to the increased acoustic input in modern dolphins (Langworthy, 1932; Wood & Evans, 1980; Ridgway, 1990, 2000). Accordingly, it was speculated that the hypertrophy of the dolphin brain results from the animal's need for greater precision and speed in processing sound due to the increased speed of sound in water compared to air (Ridgway & Au, 1999; Ridgway, 2000; Oelschläger & Oelschläger, 2002). This hypertrophy correlates with the large diameter of auditory nerve fibres (Bullock & Gurevich, 1979), the short latency in auditory brainstem responses (ABRs), and rapid temporal resolution of successive sounds (Mooney *et al.*, 2006 and references therein). Accordingly, Ridgway (1986, 2000) hypothesized that the specific neurons forming axes of echo delays (neurons tuned to discriminate target distance and azimuth) may take up considerable space in the cerebrum and could be a major reason for the great expansion of the neocortex in dolphins. This concept is supported by the observation that the ability to echolocate evolved in early toothed whales during the Oligocene period (Oelschläger, 1990; Fordyce & Muizon, 2001) in parallel to the increase of the size and scaling of their brain (Marino *et al.*, 2004; Manger, 2006).

**Corresponding author:**  
S. Huggenberger  
Email: st.huggenberger@uni-koeln.de



**Fig. 1.** Brain of a La Plata dolphin (*Pontoporia blainvillei*), transverse section 20  $\mu\text{m}$ . (A) Heidenhain-Woelcke stain, total slice width 7.61 cm; and (B & C) cresyl violet stain from the lateral cortical gyrus. The arrows and boxes indicate the approximate locations of the samples; note that the slice in (A) is slightly rostral to (B) and (C). Numbers indicate cortical layers. CB, cerebellum; CC, corpus callosum; CN, cochlear nucleus; IC, inferior colliculus; LL, lateral lemniscus; NC, neocortex; SO, superior olive; TB, trapezoid body. Scale bar: 100  $\mu\text{m}$ .

Further parameters that may have led to the development of a large neocortex in toothed whales may have been the highly cognitive capabilities allowing behavioural complexity and ambitious communication skills leading to strong social relationships (Connor *et al.*, 1998; Rendell & Whitehead, 2001; Marino, 2002; Simmonds, 2006; Connor, 2007). This could be shown, e.g. by the high learning and memory abilities of toothed whales (reviewed in Würsig, 2002), the ability of self-monitoring and self-recognition (Reiss & Marino, 2001; Herman, 2006), tool use (Krützen *et al.*, 2005), highly differentiated social behaviour (e.g. Acevedo-Gutiérrez, 2002; Tyack, 2002; Lusseau & Newman, 2004; Connor & Mann, 2006; Herman, 2006;

Connor, 2007), understanding of language-like instructions (reviewed in Herman, 2006) and cultural transmission (Rendell & Whitehead, 2001; Krützen *et al.*, 2005; Kuczaj *et al.*, 2007). Accordingly, toothed whales should be regarded as 'intelligent animals' (Simmonds, 2006) and the behaviour of dolphins is discussed as being metacognition (Browne, 2004).

In dolphins, the need for great precision and speed in processing sound, the highly cognitive capabilities, the hypertrophic cerebrum and the extended gyrification of the latter (see above references) seem to be in paradoxical contrast to the thin neocortical plate (grey matter), the plesiomorphic or paedomorphic lamination of the neocortex and the low density of neurons (Glezer, 2002; Oelschläger & Oelschläger, 2002). The neocortical grey matter is characterized by: (i) the widespread absence of layer IV; (ii) poor granulation with a predominance of large isodendritic stellate cells; (iii) well developed layers I and VI; (iv) an accentuated layer II; and (v) a high number of pyramidal neurons in layers II to VI (Figure 1B,C; Morgane *et al.*, 1990; Hof *et al.*, 2005 and references therein). These characteristics seem to represent a primitive mammalian brain (Glezer *et al.*, 1988). However, since the common ancestors of cetaceans and ungulates may have possessed layer IV granule cells (Deacon, 1990; Oelschläger & Oelschläger, 2002) at least the absence of this layer should represent a secondary condition in dolphins. Interestingly, cytoarchitectonical studies in several toothed whale species reveal clearly identifiable neocortical areas similar to those identified in other mammals (Fung *et al.*, 2005; Hof *et al.*, 2005) but the neocortex exhibits an unusual arrangement of sensory-motor areas (Glezer *et al.*, 1988; Morgane *et al.*, 1990).

## COMPARATIVE ASPECTS OF THE NEOCORTEX

Although neuron density is low in the dolphin neocortex (Figure 1C; Haug, 1987; Oelschläger & Oelschläger, 2002), the synaptic density is high (maximal number of synapses per neuron) and the absolute number of synapses in the neocortex is similar to that in humans (Glezer & Morgane, 1990; Morgane *et al.*, 1990; Oelschläger & Oelschläger, 2002). The total number of neurons in the neocortex of the bottlenose dolphin and the false killer whale (a delphinid species; Rice, 1998) is similar to that of the chimpanzee and clearly above that of the other mammals included in this study (rat, hedgehog, cat, rhesus monkey and horse) except the elephant and human (Table 1; Roth & Dicke, 2005). Interestingly, recent studies of the baleen whale (Mysticeti) brain demonstrate that the neocortex of these large mammals, although different in cytoarchitecture (Hof & van der Gucht, 2007) but comparably large in absolute terms (Oelschläger & Oelschläger, 2002), approximates the same high absolute neuron number as in dolphins (compared to rats and humans; Eriksen & Pakkenberg, 2007).

The brain weight of the chimpanzee is less than of the two dolphin species studied here and the latter are only surpassed by those in the elephant and the human (Table 1). Accordingly, the dolphins have more neocortical neurons in relation to their brain weight than the chimpanzee (and the elephant) but less than the rhesus monkey (Figure 2). The hedgehog and the rat have approximately the same number of neocortical neurons per gram brain weight as the human which is only surpassed by the cat. In relation

**Table 1.** Comparison of the total number of neocortical neurons with brain weight and body weight in different mammalian species.

Species	Total number of neo-cortical neurons ( $\times 10^6$ ) <sup>A</sup>	Brain weight (g) <sup>A</sup>	Body weight (g) <sup>B</sup>
Rat ( <i>Rattus norvegicus</i> , Rodentia)	15	2	250
Hedgehog ( <i>Erinaceus europaeus</i> , Insectivora)	24	3.3	930
Cat ( <i>Felis domestica</i> , Carnivora)	300	25	3300
Rhesus monkey ( <i>Macaca mulatta</i> , Primates)	480	88	6652
Horse ( <i>Equus caballus</i> , Perissodactyla)	1200	510	635000
Bottlenose dolphin ( <i>Tursiops truncatus</i> , Cetacea)	5800	1350	209000
Chimpanzee ( <i>Pan troglodytes</i> , Primates)	6200	430	48893
False killer whale ( <i>Pseudorca crassidens</i> , Cetacea)	10500	3640	1000000
African elephant ( <i>Loxodonta africana</i> , Proboscidae)	11000	4200	3505000
Human ( <i>Homo sapiens</i> , Primates)	11500	1450	57000

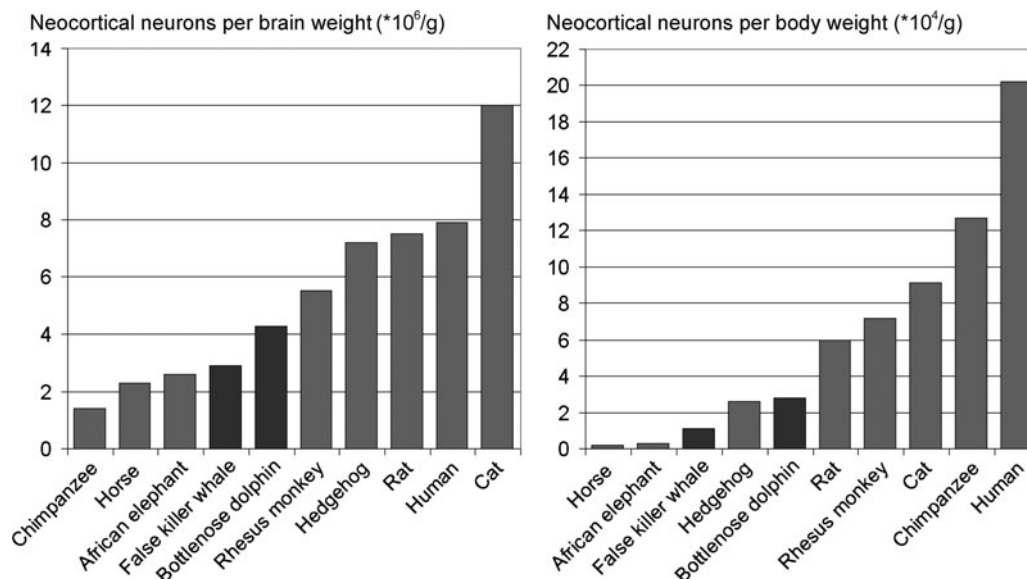
Data Sources: <sup>A</sup> Roth & Dicke (2005); <sup>B</sup> Spector (1956), Leatherwood & Reeves (1983), Marino (1998), Shoshani *et al.* (2006). Note that the total number of neocortical neurons was calculated using the method of Roth & Dicke (2005) but derived from Haug (1987).

to body weight, however, the neuron number in dolphins is in the range of the hedgehog which is lower than in the rat, rhesus monkey, cat, chimpanzee and human (Figure 2). This value is in contrast to the large absolute number of neurons in the dolphin neocortex due to their large body mass (Table 1) which is also true for the elephant and horse (Figure 2).

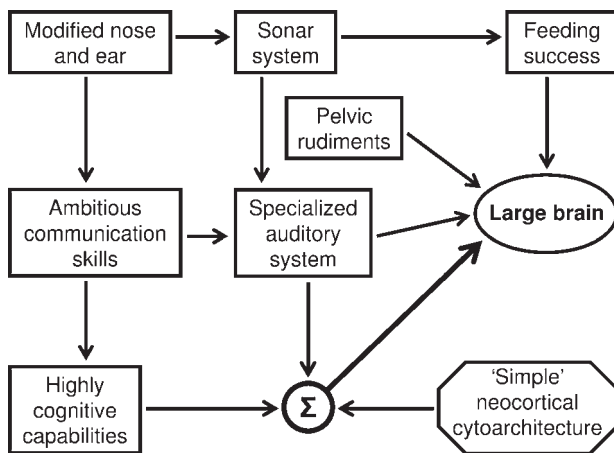
Due to the high absolute number of neurons contributing to the neocortical network as well as the high number of synapses in the odontocete neocortex (see above references) it is plausible that these morphological peculiarities are the prerequisite for the strong cognitive capabilities of dolphins (cf. Roth & Dicke, 2005). The low number of neocortical neurons in relation to body weight may be explained by 'aquatic weightlessness' (due to fewer gravitational constraints in the aquatic environment) allowing cetaceans to obtain larger bodies than terrestrial mammals, which suggests that the encephalization levels in many cetacean species are probably underestimated (Marino, 1998) and body weight may not be a useful reference for brain size (Harvey & Krebs, 1990).

#### INCREASE OF NEOCORTICAL SIZE INSTEAD OF COMPLEXITY

The cetacean cerebral cortex is probably unique and the lack of pronounced neocortical lamination, absence of layer IV, a thin neocortex, low neuronal density, and pyramidal cells in layer II, will probably all compromise the processing capacity of the mammalian neocortical network (Manger, 2006). A plausible alternative to compensate for these alterations in structure may be an increase in size of the dolphin brain. The ability to perform precise and fast sound processing and the highly cognitive capabilities may be made possible by an expansion or multiplication of a 'simple' neocortex (Figure 3; Glezer *et al.*, 1988) instead of the development of a more complex one. This was probably a neurobiological alternative to the situation in primates (Hof & van der Gucht, 2007; Marino *et al.*, 2007). Thus, during evolution, dolphins may have increased the computational performance of their brain by a multiplication of relevant structures (resulting in an enlargement of the neocortical surface area and a high number of neurons and synapses) instead of increasing its complexity. This potential



**Fig. 2.** Comparison of total cortical neurons in relation to brain weight (left) and body weight (right) of ten mammalian species belonging to seven different orders (based on data in Table 1). The two delphinid species are marked in darker grey.



**Fig. 3.** Diagram showing different parameters supporting the increase of brain size during dolphin evolution: feeding success, the absence of a pelvic girdle and the combination (indicated by  $\Sigma$ ) of a 'simple' neocortical cytoarchitecture with the development of highly cognitive capabilities and the need for precise and fast processing of sound for echo-orientation.

evolutionary trend, resulting in the large brain of extant dolphins, was advantageous due to two adaptations to the aquatic environment: (i) the feeding behaviour of toothed whales is highly successful since their ability to echolocate and communicate effectively allows them to fit in ecological niches not available to other marine vertebrates (Figure 3; Oelschläger, 1990; Fordyce & Muizon, 2001). Thus, the supply of a large brain, which is a considerable metabolic expense, should not be a limiting factor (McFarland *et al.*, 1979; Niven, 2005; Ridgway *et al.*, 2006; Connor, 2007); and (ii) toothed whales do not have a pelvic girdle. Instead, if developed at all, they have two small bones near the mid-sagittal plane, which are not fused (Adam, 2002), so that the shape and the size of the birth canal (apertura pelvis) may not limit head size at birth as is the case in humans (Figure 3; e.g. Ruff, 1995). In summary, the size of the dolphin brain does not seem to be in paradoxical contrast to the 'simple' neocortical architecture but rather the result of an evolutionary alternative solution to improve its computational performance. This alternative path was probably facilitated by the secondary adaptations of these mammals to the aquatic environment. Due to the general similarities of the toothed whale neocortex (Fung *et al.*, 2005; Hof *et al.*, 2005; Manger, 2006) and their monophyly (Fordyce & Muizon, 2001; Nikaido *et al.*, 2007) the hypothesis mentioned above may be true for all odontocetes.

## ACKNOWLEDGEMENTS

My sincere thanks go to Helmut H.A. Oelschläger (Institute of Anatomy III, Johann Wolfgang Goethe-University of Frankfurt am Main, Germany) for the donation of photographs of odontocete brain material under his care and I deeply appreciate his advice and assistance contributing to my understanding of cetacean anatomy. Sharon Meyen-Southard (Zoological Institute II, University of Cologne, Germany) kindly corrected the English style and two anonymous referees are thanked for their valuable comments on this paper.

## REFERENCES

- Acevedo-Gutiérrez A. (2002) Group behavior. In Perrin W.F. *et al.* (eds) *Encyclopedia of marine mammals*, San Diego: Academic Press, pp. 537–544.
- Adam P.J. (2002) Pelvic anatomy. In Perrin W.F. *et al.* (eds) *Encyclopedia of marine mammals*, San Diego: Academic Press, pp. 894–897.
- Breathnach A.S. (1960) The cetacean central nervous system. *Biological Reviews* 35, 187–230.
- Browne D. (2004) Do dolphins know their own minds? *Biology and Philosophy* 19, 633–653.
- Bullock T.H. and Gurevich V. (1979) Soviet literature on the nervous system and psychobiology of Cetacea. *International Review of Neurobiology* 21, 48–127.
- Connor R.C. (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B* 362, 587–602.
- Connor R.C. and Mann J. (2006) Social cognition in the wild: Machiavellian dolphins? In Hurley S. and Nudds M. (eds) *Rational animals?* Oxford: Oxford University Press, pp. 329–370.
- Connor R.C., Mann J., Tyack P.L. and Whitehead H. (1998) Social evolution in toothed whales. *Trends in Ecology and Evolution* 13, 228–232.
- Cranford T.W. and Amundin M. (2004) Biosonar pulse production in odontocetes: the state of our knowledge. In Thomas J.A. *et al.* (eds) *Echolocation in bats and dolphins*. Chicago: University of Chicago Press, pp. 26–59.
- Cranford T.W., Amundin M. and Norris K.S. (1996) Functional morphology and homology in the odontocete nasal complex: implication for sound generation. *Journal of Morphology* 228, 223–285.
- Deacon T.W. (1990) Rethinking mammalian brain evolution. *American Zoologist* 30, 629–705.
- Eriksen N. and Pakkenberg B. (2007) Total neocortical cell number in the mysticete brain. *Anatomical Record* 290, 83–95.
- Fordyce R.E. and Muizon C. de (2001) Evolutionary history of the cetaceans: a review. In Mazin J.M. and Buffrénil V. de (eds) *Secondary adaptation of tetrapods to life in water*, Munich: Verlag Dr Friedrich Pfeil, pp. 169–234.
- Fung C., Schleicher A., Kowalski T. and Oelschläger H.H.A. (2005) Mapping auditory cortex in the La Plata dolphin (*Pontoporia blainvilliei*). *Brain Research Bulletin* 66, 353–356.
- Glezer I.I. (2002) Neural morphology. In Hoelzel A.R. (ed.) *Marine mammal biology: an evolutionary approach*, Oxford: Blackwell Science, pp. 98–115.
- Glezer I.I., Jacobs M.S. and Morgane P.J. (1988) The "initial" brain concept and its implications for brain evolution in Cetacea. *Behavioral and Brain Sciences* 11, 75–116.
- Glezer I.I. and Morgane P.J. (1990) Ultrastructures of synapses and Golgi analysis of neurons in the neocortex of the lateral gyrus (visual cortex) of the dolphin and the pilot whale. *Brain Research Bulletin* 24, 401–427.
- Harvey P.H. and Krebs J.R. (1990) Comparing brains. *Science* 249, 140–146.
- Haug H. (1987) Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: a stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores, and one elephant). *American Journal of Anatomy* 180, 126–142.

- Herman L.M.** (2006) Intelligence and rational behaviour in the bottlenosed dolphin. In Hurley S. and Nudds M. (eds) *Rational animals?* Oxford: Oxford University Press, pp. 439–468.
- Hof P.R., Chanis R. and Marino L.** (2005) Cortical complexity in cetacean brains. *Anatomical Record* 287A, 1142–1152.
- Hof P.R. and Gucht E. van der** (2007) Structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). *Anatomical Record* 290, 1–31.
- Krützen M., Mann J., Heithaus M.R., Connor R.C., Bejder L. and Sherwin W.B.** (2005) Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Science of the United States of America* 102, 8939–3943.
- Kuczaj S.A., Makecha R., Trone M., Paulos R.D. and Ramos J.A.** (2007) Role of peers in cultural innovation and cultural transmission: evidence from the play of dolphin calves. *International Journal of Comparative Psychology* 19, 223–240.
- Langworthy O.R.** (1932) A description of the central nervous system of the porpoise (*Tursiops truncatus*). *Journal of Comparative Neurology* 54, 437–499.
- Leatherwood S. and Reeves R.R.** (1983) *The Sierra Club handbook of whales and dolphins*. San Francisco: Sierra Club Books.
- Lefebvre L., Marino L., Sol D., Lemieux-Lefebvre S. and Arshad S.** (2006) Large brains and lengthened life history periods in odontocetes. *Brain, Behavior and Evolution* 68, 218–228.
- Lusseau D. and Newman M.E.** (2004) Identifying the role that animals play in their social networks. *Proceedings of the Biological Sciences* 271 (Suppl. 6), 477–481.
- Manger P.R.** (2006) An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biological Reviews* 81, 293–338.
- Marino L.** (1998) A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior and Evolution* 51, 230–238.
- Marino L.** (2002) Convergence in complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* 59, 21–32.
- Marino L.** (2007) Cetacean brains: how aquatic are they? *Anatomical Record* 290, 694–700.
- Marino L., McShea D. and Uhen M.D.** (2004) The origin and evolution of large brains in toothed whales. *Anatomical Record* 281A, 1247–1255.
- Marino L., Uhen M.D., Pyenson N.D. and Frohlich B.** (2003) Reconstructing cetacean brain evolution using computed tomography. *Anatomical Record* 272B, 107–117.
- Marino L. et al.** (2007) Cetaceans have complex brains for complex cognition. *PLoS Biology* 5, e139. doi:10.1371/journal.pbio.0050139.
- McFarland W.L., Jacobs M.S. and Morgane P.J.** (1979) Blood supply to the brain of the dolphin, *Tursiops truncatus*, with comparative observations on special aspects of the cerebrovascular supply of other vertebrates. *Neuroscience and Biobehavioral Reviews* (Suppl. 1), 93.
- Mooney T.A., Nachtigall P.E. and Yuen M.M.L.** (2006) Temporal resolution of the Risso's dolphin, *Grampus griseus*, auditory system. *Journal of Comparative Physiology* 192A, 373–380.
- Morgane P.J., Glezer I. and Jacobs M.S.** (1990) Comparative and evolutionary anatomy of the visual cortex of the dolphin. In Jones E.G. and Peters A. (eds) *Comparative structures and evolution of cerebral cortex*, New York: Plenum Press, pp. 215–262.
- Nikaido M., Piskurek O. and Okada N.** (2007) Toothed whale monophyly reassessed by SINE insertion analysis: the absence of lineage sorting effects suggests a small population of a common ancestral species. *Molecular Phylogenetics and Evolution* 43, 216–224.
- Niven J.E.** (2005) Brain evolution: getting better all the time? *Current Biology* 15, R624–R626.
- Oelschläger H.A.** (1990) Evolutionary morphology and acoustics in the dolphin skull. In Thomas J. and Kastelein R.A. (eds) *Sensory abilities of cetaceans*. New York: Plenum Press, pp. 137–162.
- Oelschläger H.H.A.** (in press). The dolphin brain—a challenge for synthetic neurobiology. *Brain Research Bulletin*.
- Oelschläger H.H.A., Haas-Rioth M., Fung C., Ridgway S.H. and Knauth M.** (2008) Morphology and evolutionary biology of the dolphin (*Delphinus* sp.) brain—MR imaging and conventional histology. *Brain Behavior and Evolution* 71, 68–86.
- Oelschläger H.H.A. and Kemp B.** (1998) Ontogenesis of the sperm whale brain. *Journal of Comparative Neurology* 399, 210–228.
- Oelschläger H.H.A. and Oelschläger J.S.** (2002) Brain. In Perrin W.F. et al. (eds) *Encyclopedia of marine mammals*, San Diego: Academic Press, pp. 133–158.
- Rauschmann M.A., Huggenberger S., Kossatz L.S. and Oelschläger H.H.A.** (2006) Head morphology in perinatal dolphins: a window into phylogeny and ontogeny. *Journal of Morphology* 267, 1295–1315.
- Reiss D. and Marino L.** (2001) Mirror self recognition in the bottlenose dolphin: a case of cognitive convergence. *Proceedings of the National Academy of Science of the United States of America* 98, 5937–5942.
- Rendell L. and Whitehead H.** (2001) Culture in whales and dolphins. *Behavioral and Brain Sciences* 24, 309–382.
- Rice D.W.** (1998) *Marine mammals of the world: systematics and distribution* (Special Publication no. 4, Society for Marine Mammalogy). Lawrence: Allen Press.
- Ridgway S.H.** (1986) Physiological observations on dolphin brains. In Schusterman R.J. et al. (eds) *Dolphin cognition and behavior: a comparative approach*, Hillsdale NJ: Lawrence Erlbaum Associates, pp. 31–59.
- Ridgway S.H.** (1990) The central nervous system of the bottlenose dolphin. In Leatherwood S. and Reeves R. (eds) *The bottlenose dolphin*, New York: Academic Press, pp. 69–97.
- Ridgway S.H.** (2000) The auditory central nervous system of dolphins. In Au W.W.L. et al. (eds) *Hearing by whales and dolphins*, New York: Springer, pp. 273–294.
- Ridgway S.H. and Au W.W.L.** (1999) Hearing and echolocation: dolphin. In Adelman G. and Smith B.H. (eds) *Elsevier's encyclopedia of neuroscience* 2nd edn, New York: Elsevier Science, pp. 858–862.
- Ridgway S.H. and Brownson R.H.** (1979) Brain size and symmetry in three dolphin genera. *Anatomical Record* 193, 664.
- Ridgway S.H. and Brownson R.H.** (1984) Relative brain sizes and cortical surface areas of odontocetes. *Acta Zoologica Fennica* 172, 149–152.
- Ridgway S.H. et al.** (2006) Functional imaging of dolphin brain metabolism and blood flow. *Journal of Experimental Biology* 209, 2902–2910.
- Roth G. and Dicke U.** (2005) Evolution of the brain and intelligence. *Trends in Cognitive Sciences* 9, 250–257.

- Ruff C.B.** (1995) Biomechanics of the hip and birth in early *Homo*. *American Journal of Physical Anthropology* 98, 527–574.
- Schwerdtfeger W.K., Oelschläger H.A. and Stephan H.** (1984) Quantitative neuroanatomy of the brain of the La Plata dolphin, *Pontoporia blainvillei*. *Anatomy and Embryology* 170, 11–19.
- Shoshani J., Kupsky W.J. and Marchant G.H.** (2006) Elephant brain—Part I: gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin* 70, 124–157.
- Simmonds M.P.** (2006) Into the brains of whales. *Applied Animal Behaviour Science* 100, 103–116.
- Spector W.S.** (1956) *Handbook of biological data*. Philadelphia and London: Saunders.
- Tyack P.L.** (2002) Behavior, overview. In Perrin W.F. *et al.* (eds) *Encyclopedia of marine mammals* San Diego: Academic Press, pp. 87–94.
- Wood E.G. and Evans W.E.** (1980) Adaptiveness and ecology of echolocation in toothed whales. In Busnel R. and Fish J. (eds) *Animal sonar systems*, New York: Plenum Press, pp. 381–426.
- and
- Würsig B.** (2002) Intelligence and cognition. In Perrin W.F. *et al.* (eds) *Encyclopedia of marine mammals* San Diego: Academic Press, pp. 628–637.

**Correspondence should be addressed to:**

Stefan Huggenberger  
Zoological Institute II  
University of Cologne  
Weyertal 119  
50931 Köln  
Germany  
email: st.huggenberger@uni-koeln.de