

Brain of the African Elephant (*Loxodonta africana*): Neuroanatomy From Magnetic Resonance Images

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ABSTRACT

We acquired magnetic resonance images of the brain of an adult African elephant, *Loxodonta africana*, in the axial and parasagittal planes and produced anatomically labeled images. We quantified the volume of the whole brain (3,886.7 cm³) and of the neocortical and cerebellar gray and white matter. The white matter-to-gray matter ratio in the elephant neocortex and cerebellum is in keeping with that expected for a brain of this size. The ratio of neocortical gray matter volume to corpus callosum cross-sectional area is similar in the elephant and human brains (108 and 93.7, respectively), emphasizing the difference between terrestrial mammals and cetaceans, which have a very small corpus callosum relative to the volume of neocortical gray matter (ratio of 181–287 in our sample). Finally, the elephant has an unusually large and convoluted hippocampus compared to primates and especially to cetaceans. This may be related to the extremely long social and chemical memory of elephants. © 2005 Wiley-Liss, Inc.

Key words: African elephant; brain; magnetic resonance imaging; hippocampus; corpus callosum

The order Proboscidea emerged in the late Paleocene epoch, approximately 60 million years ago (Sukumar, 2003). It was extremely successful, with a wide radiation of species of various shapes and sizes. However, after the extinctions at the end of the Pleistocene, only the two modern genera of elephants (*Loxodonta* and *Elephas*, the African and Asian elephants, respectively) remained. The lineages of these two genera first appear in the fossil record around 4–6 million years ago (Eggert et al., 2002; Sukumar, 2003). Figure 1 shows how the living elephants fit into the phylogeny of living mammals. The elephant is most closely related to the hyrax and to the sirenians (dugongs, manatees, and sea cows).

The African elephant, *Loxodonta africana*, is the largest living land mammal. It has a brain comparable in size and complexity to those of cetaceans and humans (Cozzi et al., 2001). This makes the elephant brain of

interest both because it is an extreme data point in studies of brain structure sizes or connectivity, and because elephants, like primates, are long-lived species possessed of a complex social structure (Payne, 2003; Sukumar, 2003). Recently, four hierarchical tiers of social organization were demonstrated in the African el-

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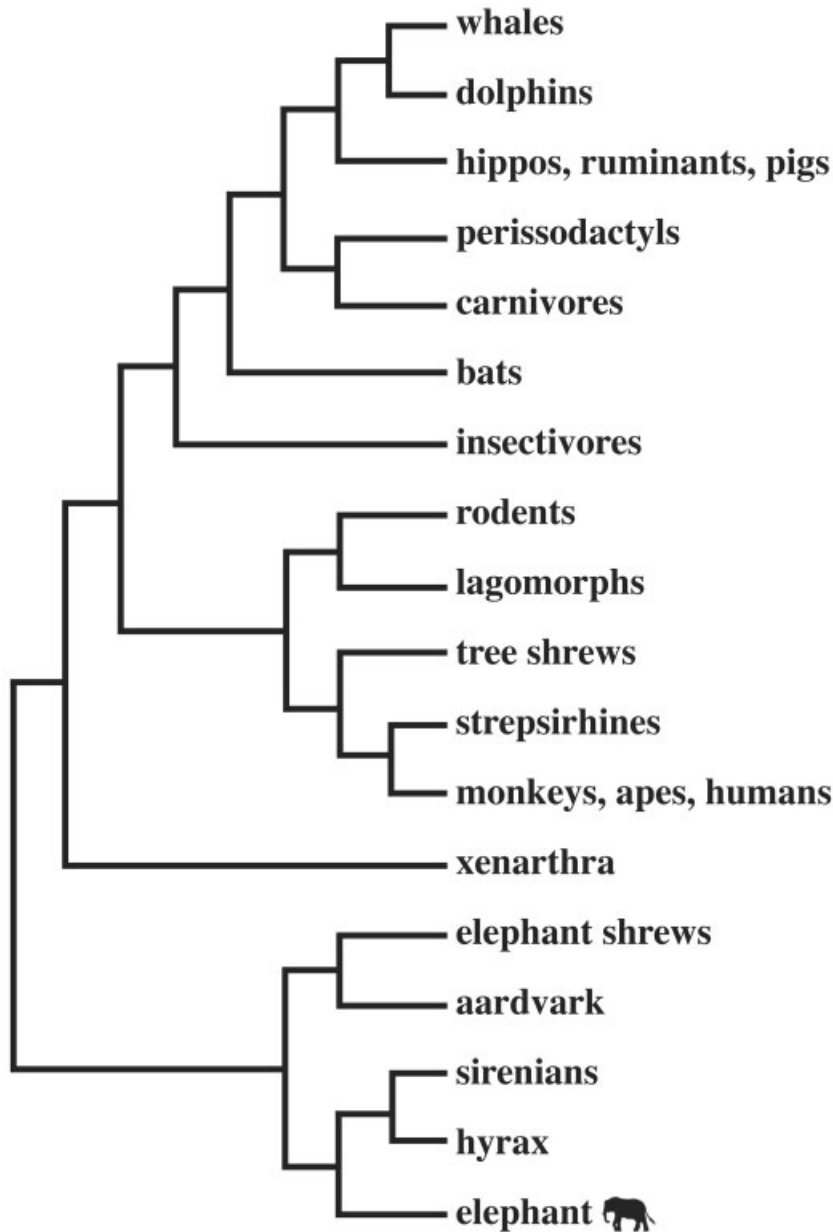


Fig. 1. Cladogram of the living placental mammals. Adapted from Murphy et al. (2001). The elephant is most closely related to the hyrax and the sirenians (manatees, dugongs, and sea cows). It is distant from the other large-brained mammals, the cetaceans and anthropoid primates, and is not closely related to either the perissodactyls (horses, rhinos, and tapirs) or the cetartiodactyls (pigs, ruminants, hippos, and cetaceans).

elephant, the first such society revealed in a nonhuman animal (Wittemyer et al., 2005). However, in a review of the available literature on the elephant nervous system, Cozzi et al. (2001) found that elephant brain size and architecture information has mostly been taken from only a few original investigations, some dating from as far back as the 19th century. Much literature is characterized by general statements such as that the cerebral cortex was “highly convoluted” and the gray matter was “thick,” although Haug (1970) made quantitative as well as qualitative measurements.

In this article, we present new elephant brain data. Through the use of magnetic resonance imaging (MRI) on a postmortem brain, we were able to produce a series of “slices” in which detailed brain structures may be seen, as

well as to make quantitative measurements of the volume of the whole brain and the neocortical and cerebellar gray and white matter, without the distortion introduced by physically sectioning the brain.

MATERIALS AND METHODS

Specimen

The specimen is the brain of an adult female wild-caught African elephant, *Loxodonta africana*, presumed to be in the mid-20, loaned by Dr. Rasmussen, from the Dr. Adams Collection. This individual was euthanized as a result of foot problems. The brain was perfusion-fixed with a neutral formalin solution and kept in the same fixative.

Magnetic Resonance Imaging

Images were acquired with a 3 T Siemens Trio MRI scanner at the Moore Brain Imaging Center at Caltech. Axial scans were acquired with a Time to Repetition (TR) of 20 and a Time to Echo (TE) of 36. Images are 1.3 mm thick with a matrix size of 256×256 and in-plane resolution of 32×32 cm, yielding a voxel size of $1.25 \times 1.25 \times 1.3$ mm. Parasagittal scans were acquired with a TR of 2,000 and a TE of 3. Images are 1.0 mm thick with a matrix size of 224×320 and in-plane resolution of 21×30 cm, yielding a voxel size of $0.94 \times 0.94 \times 1.0$ mm. Coronal slices were generated by 2D multiplanar reconstruction using OsiriX, a freeware open-source program written by Dr. Antoine Rosset (Rosset et al., 2004).

Volume Measurements and Scaling Exponents

MRI data were loaded into the Amira software package (Mercury Computer Systems, Berlin, Germany) and were segmented by slice using a combination of semiautomated and manual image segmentation tools. Amira was then used to generate a three-dimensional reconstruction of the brain using a polygonal surface model and to calculate the volumes enclosed by the different brain regions. We tested Amira using a variety of simple shapes of known volume constructed from image slices of comparable resolution to our MR images and determined that, even using entirely automated image segmentation, volume estimates were correct to within approximately 2%.

Cortical gray/white scaling exponents were calculated from a data set taken from Table 1 of Bush and Allman (2003) with the addition of our elephant data. Although the Bush and Allman (2003) data were calculated using celloidin-embedded brain sections, they were corrected for shrinkage using photographs of the fixed brain before sectioning. Thus, it should be approximately comparable to our elephant brain data. To calculate the exponents, the natural logarithm of the white matter volume (cerebellar or neocortical) was plotted against the natural logarithm of the gray matter volume for each species. The slope was determined by a reduced major axis fit (Sokal and Rohlf, 1981) performed by the program RMA (Andrew J. Bohonak, San Diego State University, <http://www.bio.sdsu.edu/pub/andy/RMA.html>). Ninety-five percent confidence intervals were calculated according to standard methods (Sokal and Rohlf, 1981) by the same program.

RESULTS

Elephant Brain Morphology

Figure 2 is a three-dimensional reconstruction of the whole elephant brain. Compared to a human or great ape brain, the elephant brain is expanded laterally, with very large, distinct temporal lobes. The telencephalon is similar in shape to those of the minke (*Balaenoptera acutorostrata*) (Igarashi and Kamiya, 1972) and humpback (*Megaptera novaeangliae*) (Cozzi et al., 2001) whales, but is less compressed in the rostrocaudal axis than in the Delphinidae (Igarashi and Kamiya, 1972; Marino et al., 2004). The large cerebellum is located posterior to and on a level with the rest of the brain, as in other quadrupeds (Igarashi and Kamiya, 1972).

Figures 3–6 are a selected series of anatomically labeled originally acquired axial scans. Each slice is 1.3 mm thick. Note that the right side of the image corresponds to the right side of the brain. Figures 7 and 8 are a selected series of originally acquired parasagittal sections, starting near the midline and proceeding laterally through the left side of the brain.

Figures 9 and 10 show coronal slices generated using 2D multiplanar reconstruction. Figure 9 (right) gives a good view of the extremely wide internal capsule, which carries the descending motor fibers. In Figure 10 (left), one can see the large cerebral peduncles.

Corpus callosum. When seen in cross-section near the midline, the elephant brain appears to have an unusually large corpus callosum with respect to the size of the cerebral hemispheres when compared to humans or cetaceans. Figure 11 shows a comparison between parasagittal sections near the midline in the elephant and human, with the area of the corpus callosum highlighted in red. However, because the brains of primates, cetaceans, and elephants have different physiological constraints on shape, the cross-sectional area of the forebrain near the midline may not offer an accurate measure of the relative sizes of forebrain and corpus callosum.

Previous investigators (Nieto et al., 1976; Tarpley and Ridgway, 1994) found that in cetaceans the corpus callosum is reduced in size with respect to whole brain mass in comparison with other mammals. Because the corpus callosum is the main fiber pathway connecting the gray matter of the two cerebral hemispheres, we wished to quantify the more specific relationship between corpus callosum area and neocortical gray matter volume.

The results of this comparison can be seen in Table 1. The elephant actually has slightly more neocortical gray matter volume per unit area of the corpus callosum than does the human. Presumably, the elephant brain is somewhat flattened vertically but expanded horizontally compared to the human to give a similar overall ratio. Both the elephant and the human have a far lower ratio of neocortex to corpus callosum than do the three species of Delphinidae. This is in agreement with the earlier findings by Tarpley and Ridgway (1994) and Nieto et al. (1976) for cetaceans and humans and implies that in this respect the elephant brain is more similar in organization to the brains of large primates than to those of cetaceans.

Hippocampus. Figures 4, 10, and 12 show the hippocampus, which is unusually large and surprisingly convoluted. This is in contrast to both the human and the cetaceans in general, in which the hippocampus is small (Morgane et al., 1980; Marino et al., 2003, 2004). It also agrees with calculations made from the publication of Haug (1970) that the hippocampus of the African elephant is about 0.7% of the central structures of the brain, comparable to 0.5% for humans and contrasting with 0.1% in Risso dolphins (*Grampus griseus*) and 0.05% in the bottlenose dolphin, *Tursiops truncatus* (Haug, 1970). It is also interesting that the hippocampus extends dorsally in the elephant (Fig. 10, left), whereas in cetaceans and anthropoid primates the hippocampus is found exclusively in a ventral position.

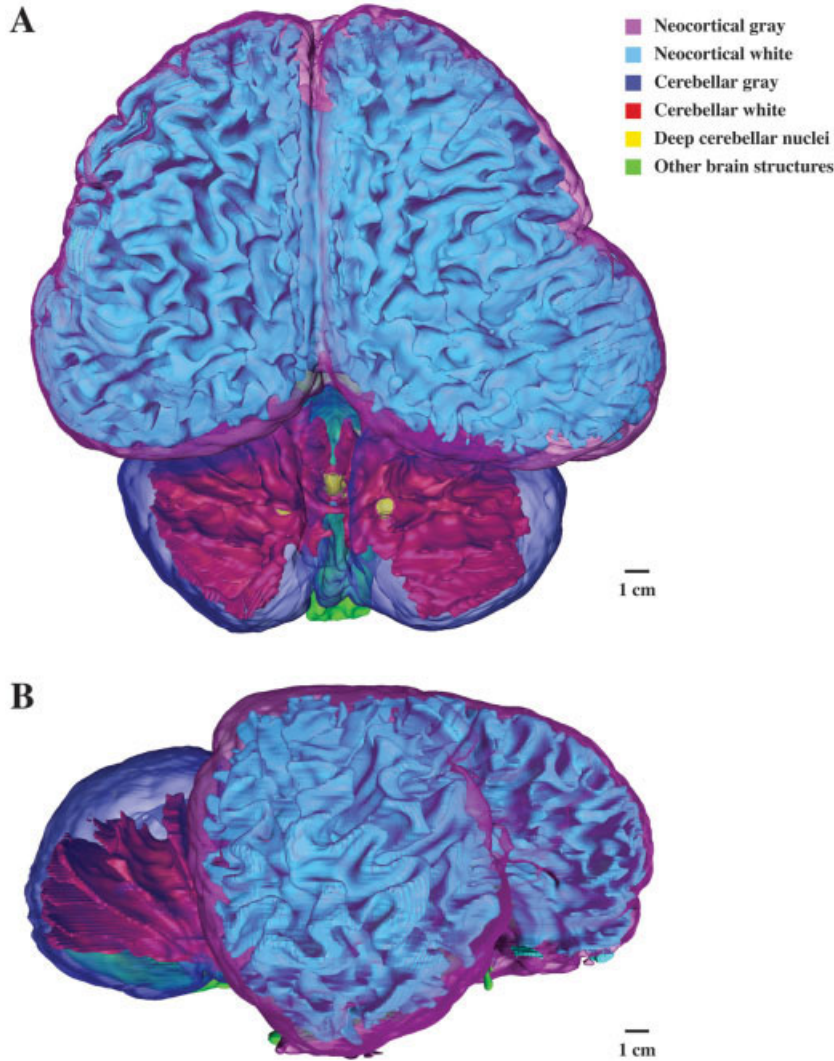


Fig. 2. A three-dimensional reconstruction of the elephant brain shown (A) in horizontal view, looking down on the brain from above, and (B) in sagittal view, looking at the brain from the right side. The brain has been segmented into neocortical gray matter, neocortical white matter, cerebellar gray matter, cerebellar white matter, deep cerebellar nuclei, and other structures. The neocortical and cerebellar gray matter are rendered translucent in order to reveal the structures below.

Some neuroanatomical features of large brains may be influenced by scaling factors. Thus, it is interesting to examine the elephant's smaller-brained relatives. Figure 12 is a comparison of the size and location of the hippocampus in the elephant (Fig. 12A) and two of its closest relatives, the rock hyrax *Procavia capensis* (Fig. 12B) and the Florida manatee *Trichechus manatus latirostris* (Fig. 12C). The rock hyrax has a very large hippocampus relative to its brain size. The hippocampus is not extremely convoluted, but it extends quite far in the lateral direction. In contrast, the Florida manatee has a very small hippocampus.

Cerebellar and Neocortical White/Gray Ratios

The ratio of the volume of neocortical white matter to that of neocortical gray matter in the mammalian brain has been found by many investigators to increase disproportionately with increasing brain size (Frahm et al., 1982; Allman, 1998; Rilling and Insel, 1999; Zhang and Sejnowski, 2000; Bush and Allman, 2003). That is, a larger brain has more white matter per unit gray

matter than does a smaller brain. This is also true of the ratio of cerebellar white matter to cerebellar gray matter, although with a shallower slope. Zhang and Sejnowski (2000) measured the neocortical white/gray matter ratio slope using a data set including the elephant [elephant data obtained from Hofman (1988)]. We wished to confirm these findings using volumes obtained from MR images, as well as to expand them to an examination of the cerebellar white/gray matter ratio. This ratio has been generally less studied and, as far as we can determine, has never been computed for an elephant brain.

To calculate brain volumes from our MRI data, we segmented each brain slice into regions of neocortical gray matter, neocortical white matter, cerebellar gray matter, cerebellar white matter, and cerebellar deep nuclei. The three-dimensional reconstruction shown in Figure 2 demonstrates the segmentation, with the cortical gray matter rendered translucent so that the white matter within is visible. Our volume measurements based on this reconstruction are presented in Table 2.

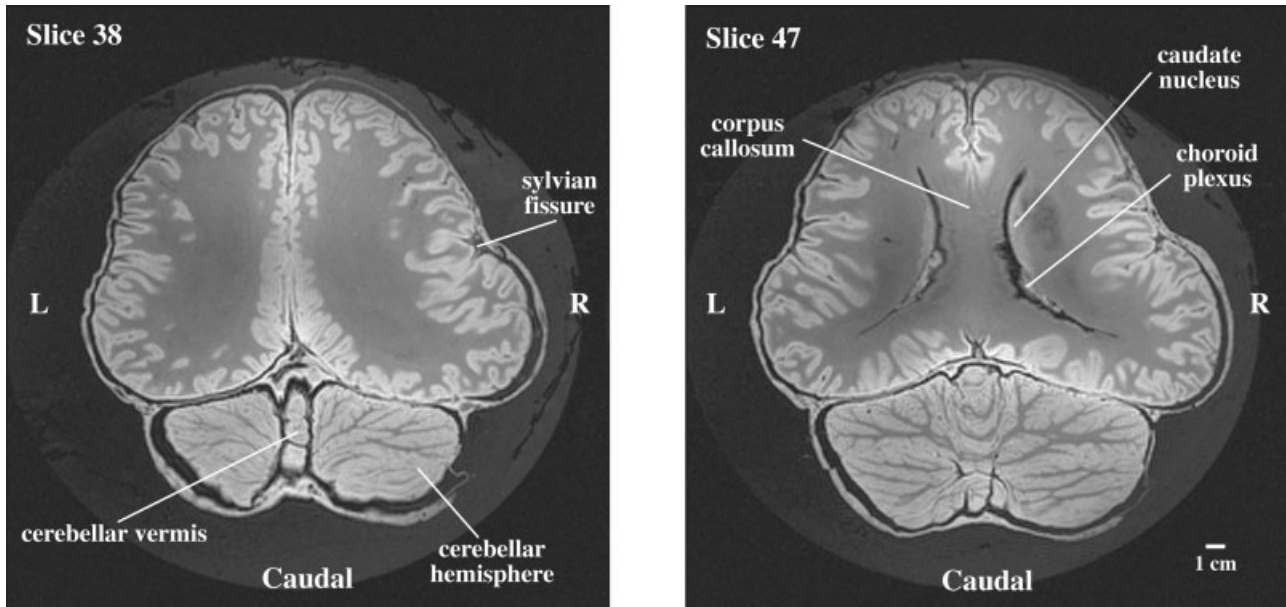


Fig. 3. Figures 3–6 are a dorsal-to-ventral sequence of anatomically labeled 1.3 mm thick axial scans of the elephant brain. Slices were chosen to best present brain structures of interest. Left is slice 38; right is slice 47.

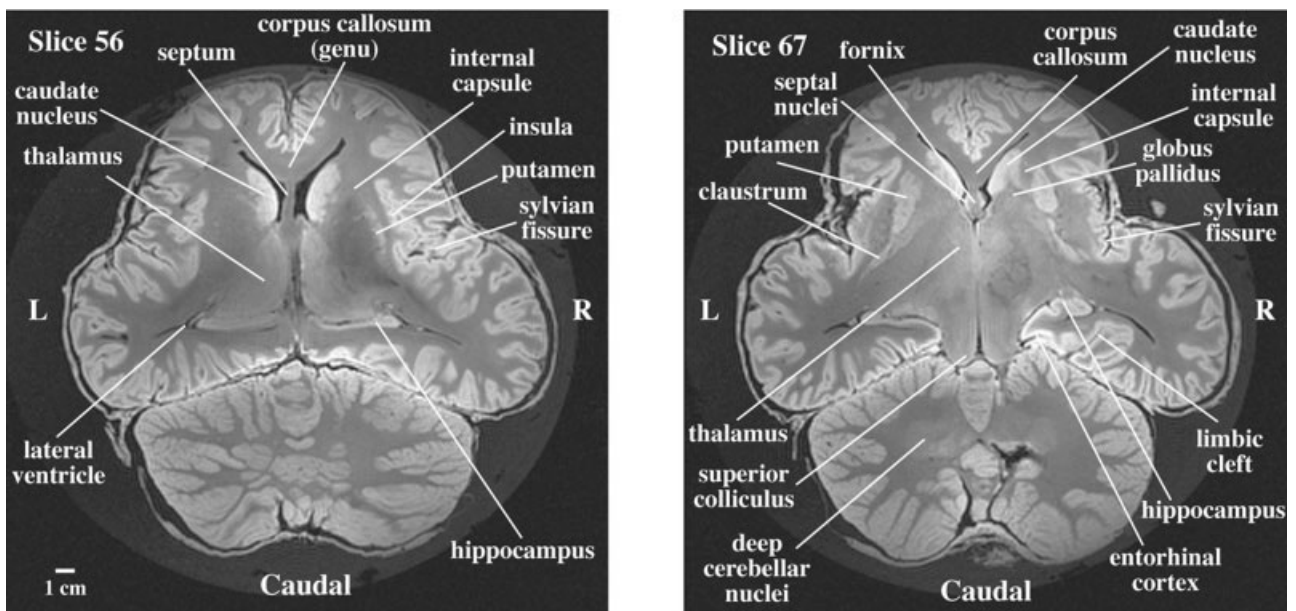


Fig. 4. Left, slice 56; right, slice 67.

Figure 13A shows the relationship between the natural logarithms of neocortical white and gray matter for a data set including a variety of primates, carnivores, and other mammals (Bush and Allman, 2003; Table 1), as well as the elephant. The slope of the reduced major axis fit is 1.265, with a 95% confidence interval from 1.220 to 1.310. This is consistent with Zhang and Sejnowski's (2000) least-squares slope of 1.23 for a somewhat different sample of mammals.

Figure 13B shows the relationship between cerebellar white and gray matter. The slope of the reduced major axis fit is 1.100, with a 95% confidence interval from 1.060 to 1.141. Note that, as found by Bush and Allman (2003) for this data set without the elephant, the confidence intervals for the neocortex and cerebellum do not overlap. This difference between the white matter/gray matter scaling exponents for neocortex and cerebellum suggests either differences in connectivity or differences

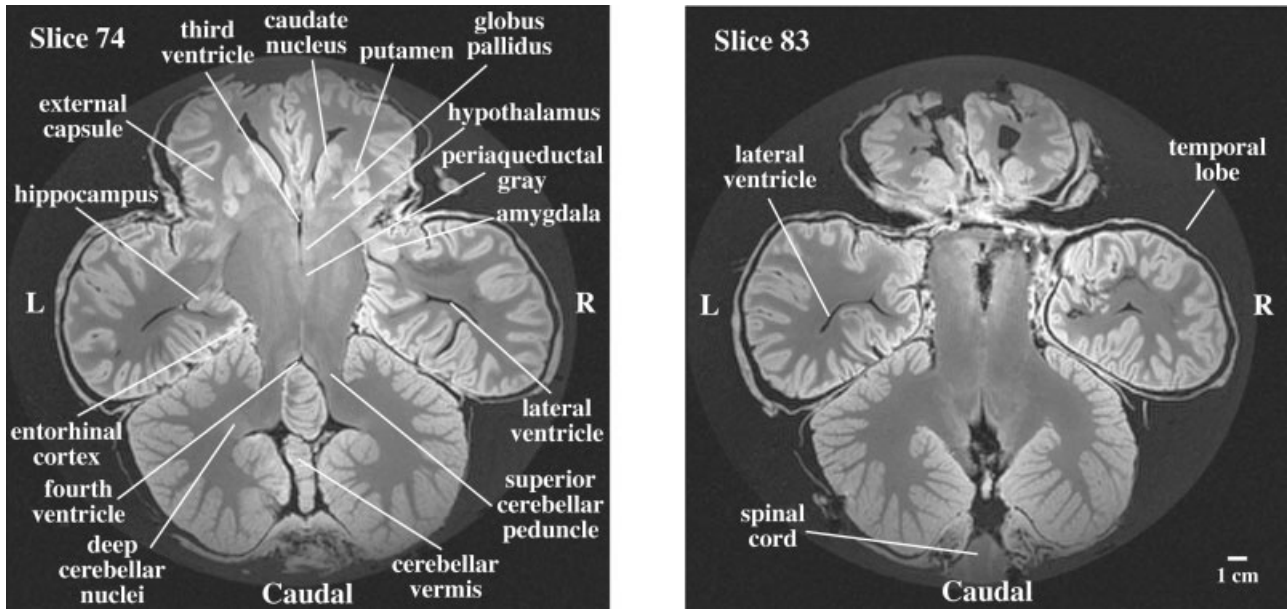


Fig. 5. Left, slice 74; right, slice 83.

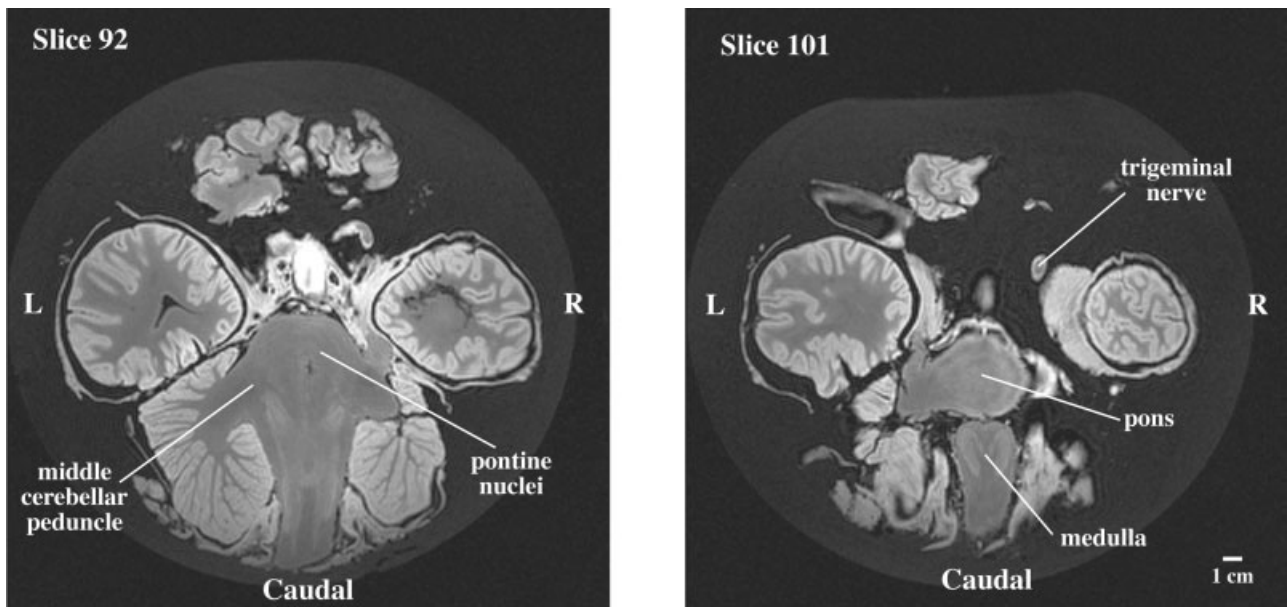


Fig. 6. Left, slice 92; right, slice 101.

in the scaling of axon diameter (Bush and Allman, 2003).

Because the elephant brain is significantly larger than any other brain in our data set, it is possible that it could unduly bias the fit. To examine this possibility, we performed reduced major axis fits on the data set with and without the elephant. The results are presented in Table 3. In both cases, the presence of the elephant did have a small effect on the slope, but the changes were well within the 95% confidence interval

for the fit. The result that the cerebellum and neocortex fits have 95% confidence intervals that are completely nonoverlapping was also not affected by the presence or absence of the elephant.

DISCUSSION

Our MRI-based investigation has allowed us to visualize and quantify the internal and external structures of the elephant brain simultaneously in multiple planes.

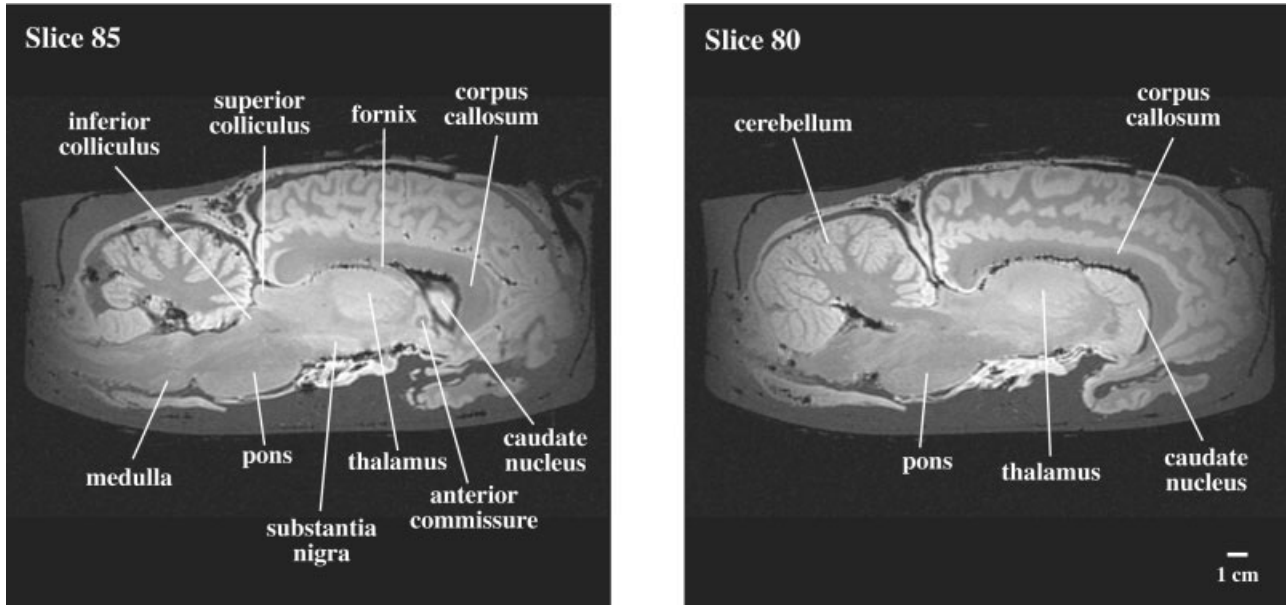


Fig. 7. Figures 7 and 8 are a medial-to-lateral sequence of anatomically labeled 1 mm thick parasagittal scans of the left hemisphere of the elephant brain. Slices were chosen to best present brain structures of interest. Left is slice 85; right is slice 80.

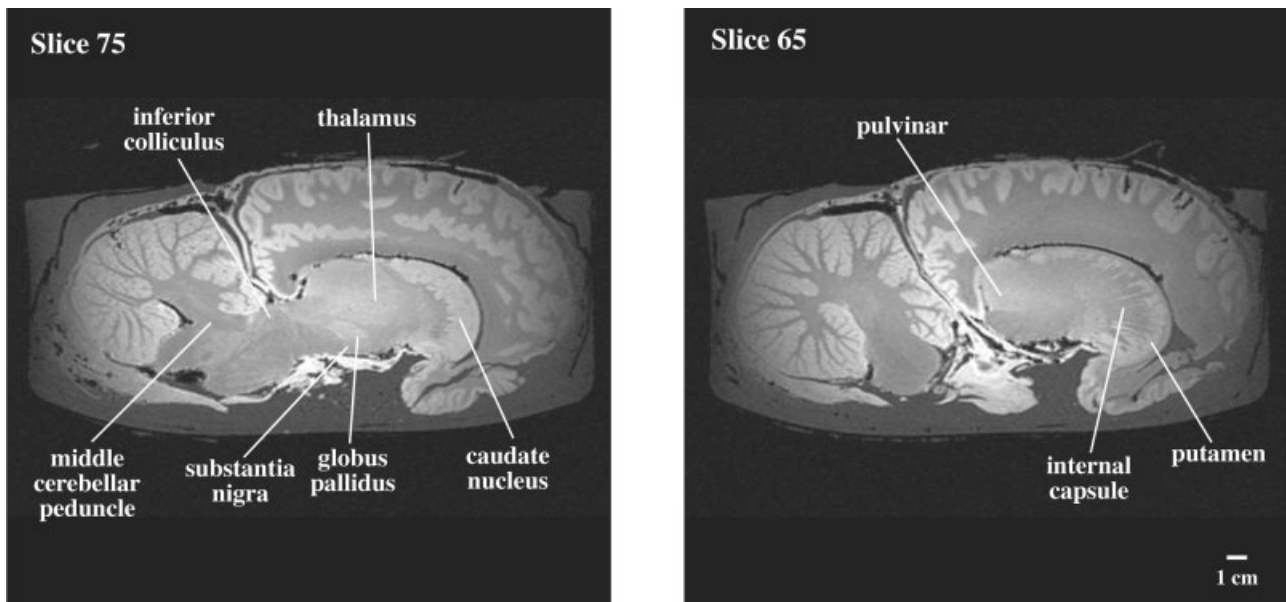


Fig. 8. Left, slice 75; right, slice 65.

This investigation has revealed both similarities and differences between the elephant brain and the large brains of primates and cetaceans.

Many investigators (Frahm et al., 1982; Allman, 1998; Rilling and Insel, 1999; Zhang and Sejnowski, 2000; Bush and Allman, 2003) have found that in mammals, neocortical white matter increases disproportionately with brain size. This is also true, with a lower

scaling exponent, for cerebellar white matter (Bush and Allman, 2003). Our results from the elephant brain for both neocortical and cerebellar white matter-to-gray matter ratio are in keeping with expected values for a brain of this size. That this very large brain follows the same scaling relationship as found in other mammals reaffirms the validity of the divergent scaling principles for neocortex and cerebellum.

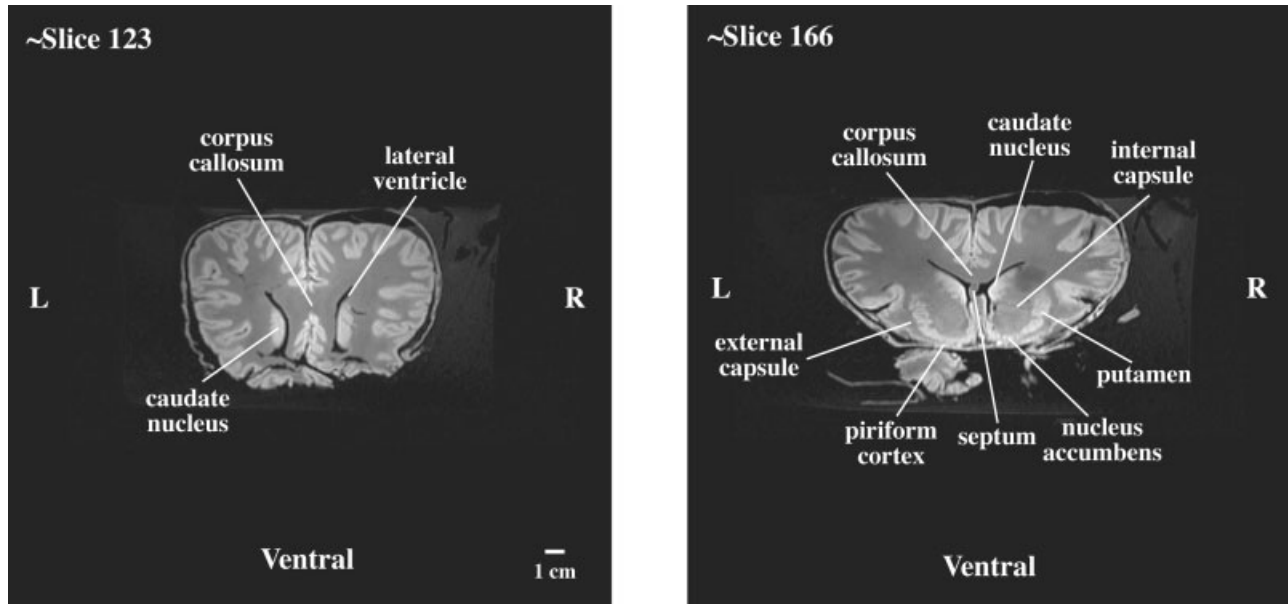


Fig. 9. Figures 9 and 10 are a rostral-to-caudal sequence of coronal slices of the elephant brain generated using two-dimensional multiplanar reconstruction on the series of axial scans used to create Figures 3–6. Virtual slices are approximately 1.25 mm thick. Left is virtual slice 123; right is virtual slice 166. Note that the right side of the image corresponds to the right side of the brain.

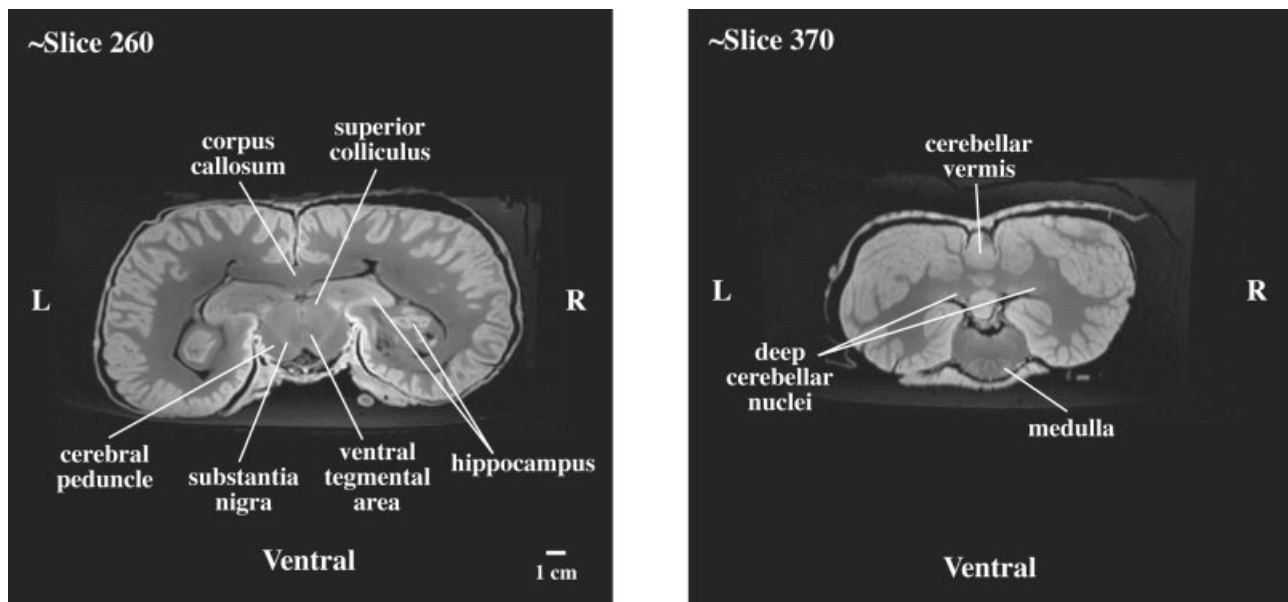


Fig. 10. Left, virtual slice 260; right, virtual slice 370.

Although the elephant and human brains have notably different shapes, they have a very similar ratio of neocortical gray matter to corpus callosum cross-sectional area. In contrast, the cetacean brains have only half as much corpus callosum area per unit volume of neocortical gray matter. This supports the idea that the

apparent poverty of interhemispheric connections in Cetacea reflects the results of an independent process of encephalization after the phylogenetic separation between cetaceans and terrestrial mammals (Tarpley and Ridgway, 1994). Further support for this theory can be found in the fact that the ruminants, the closest

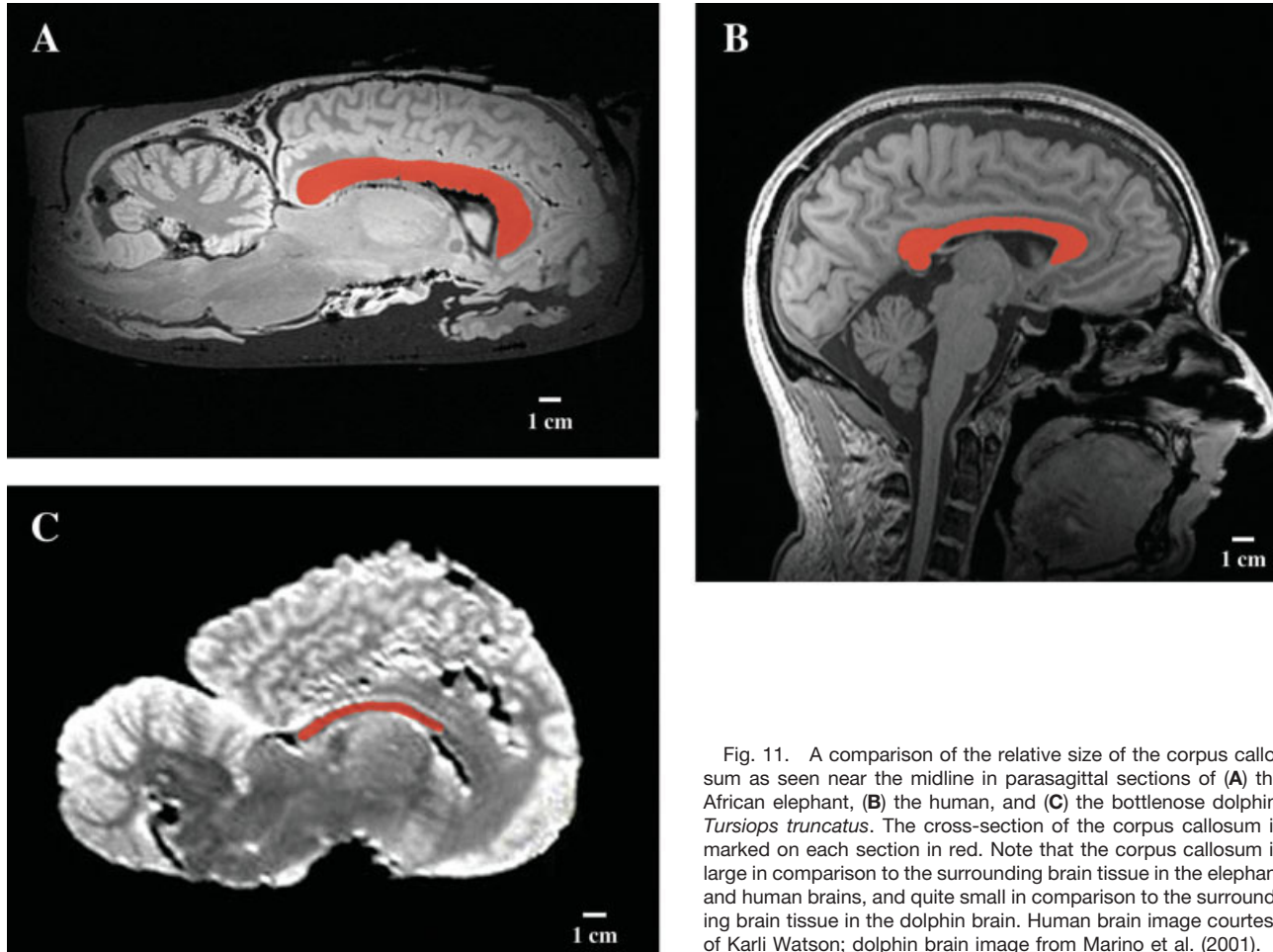


Fig. 11. A comparison of the relative size of the corpus callosum as seen near the midline in parasagittal sections of (A) the African elephant, (B) the human, and (C) the bottlenose dolphin, *Tursiops truncatus*. The cross-section of the corpus callosum is marked on each section in red. Note that the corpus callosum is large in comparison to the surrounding brain tissue in the elephant and human brains, and quite small in comparison to the surrounding brain tissue in the dolphin brain. Human brain image courtesy of Karli Watson; dolphin brain image from Marino et al. (2001).

terrestrial relatives to the cetaceans, appear similar to other terrestrial mammals rather than to cetaceans. Nieto et al. (1976), in a plot of brain weight vs. corpus callosum area, found that two ruminants (a deer and an antelope) fell close to the line for all mammals, while a spotted dolphin (*Stenella attenuata*) was an extreme outlier.

TABLE 1. Gray matter volume vs. cross-sectional area of corpus callosum (CC)

Species	CC area (cm ²)	Neocortical gray vol. (cm ³)	Neocortical gray vol./CC area
<i>Loxodonta africana</i>	12.8	1,378.7	108
<i>Homo sapiens</i>	5.99 ^a	583.0 ^b	97.3
<i>Tursiops truncatus</i>	2.56 ^c	463 ^d	181
<i>Grampus griseus</i>	2.91 ^c	624 ^d	214
<i>Globicephala macrorhynchus</i>	4.1 ^c	1,177 ^d	287

^aLacerda et al., 2005.

^bRilling and Insel, 1999.

^cTarpley and Ridgway, 1994.

^dHofman, 1988.

The elephant hippocampus is large and convoluted compared to that of either the human or the various cetaceans that have been studied (Morgane et al., 1980; Marino et al., 2003, 2004). In our earlier study of primate brain structure volumes (Allman et al., 1993), we found that the size of the hippocampus in primates is variable and poorly correlated with lifespan and the sizes of other brain structures. This suggests that the genetic regulation of hippocampal neuron number or volume may be to some extent decoupled from the regulation of other brain structures. In fact, an important signaling center has been identified at the “cortical hem” adjacent to the hippocampal primordium in the developing mammalian telencephalon. This site is rich in BMP and WNT proteins, which regulate regional growth and are required for normal development of the hippocampus (Lee et al., 2000; Shimogori et al., 2004). Examples of the long-term chemical and social memory of elephants abound in the popular and scientific literature alike; the matriarch, entrusted with the survival of her multigenerational family group, remembers geographical information such as the location of seasonal water sources (Payne, 2003) and social information such as the calls of familiar elephant groups (McComb et al., 2001). Remarkably, as documented with separated

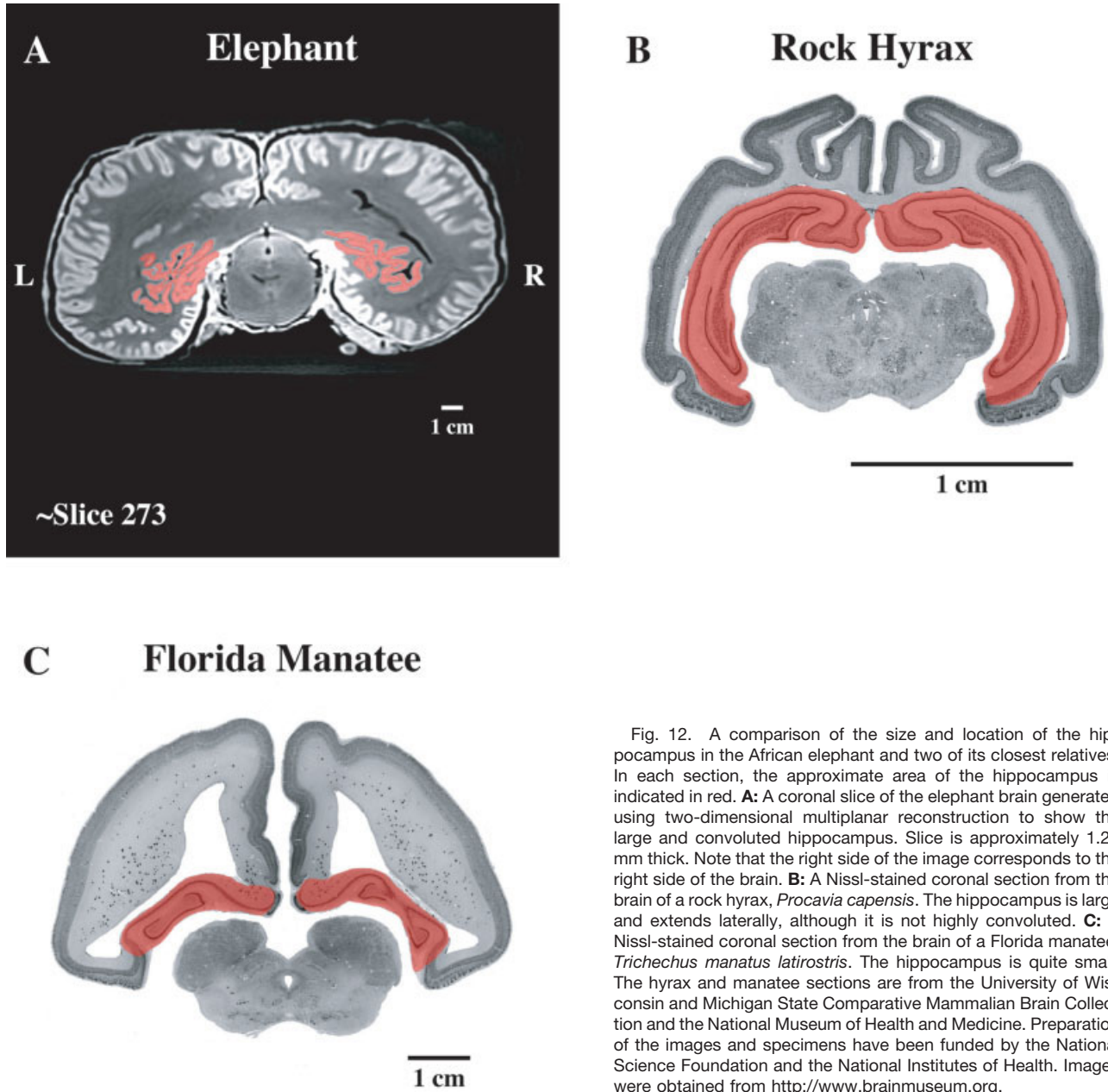


Fig. 12. A comparison of the size and location of the hippocampus in the African elephant and two of its closest relatives. In each section, the approximate area of the hippocampus is indicated in red. **A:** A coronal slice of the elephant brain generated using two-dimensional multiplanar reconstruction to show the large and convoluted hippocampus. Slice is approximately 1.25 mm thick. Note that the right side of the image corresponds to the right side of the brain. **B:** A Nissl-stained coronal section from the brain of a rock hyrax, *Procavia capensis*. The hippocampus is large and extends laterally, although it is not highly convoluted. **C:** A Nissl-stained coronal section from the brain of a Florida manatee, *Trichechus manatus latirostris*. The hippocampus is quite small. The hyrax and manatee sections are from the University of Wisconsin and Michigan State Comparative Mammalian Brain Collection and the National Museum of Health and Medicine. Preparation of the images and specimens have been funded by the National Science Foundation and the National Institutes of Health. Images were obtained from <http://www.brainmuseum.org>.

progeny, offspring retain a “chemical memory” of their maternal urine over several decades (Rasmussen and Krishnamurthy, 2000). It is tempting to posit a relationship between the elephant’s long memory and large hippocampus, but further study is required to make such a connection.

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TABLE 2. Elephant brain volume measurements

Structure	Volume (cm ³)
Whole brain	3,886.7
Neocortical gray	1,378.7
Neocortical white	1,081.4
Cerebellar gray	720.3
Cerebellar white	202.7
Other cerebellar structures	23.6

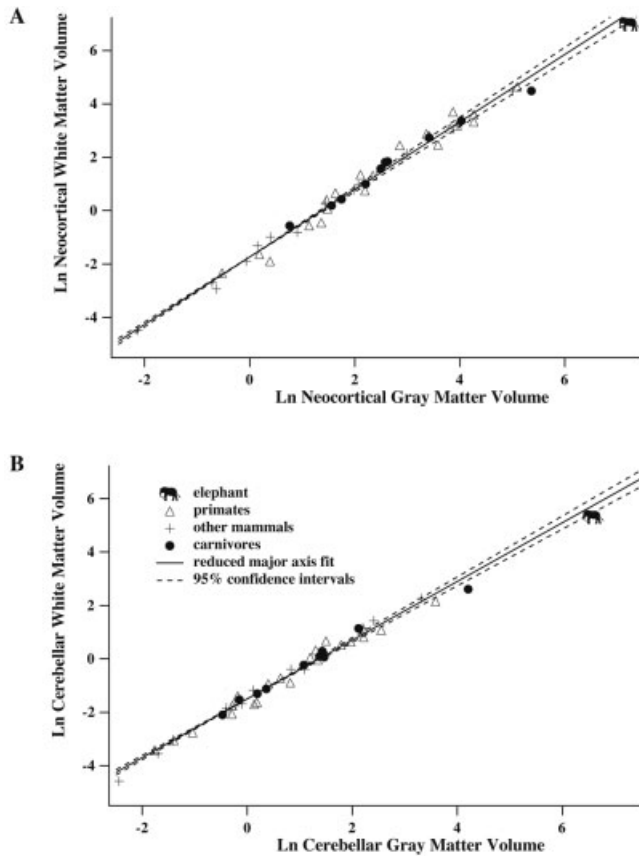


Fig. 13. Plots of the natural logarithm of white matter volume vs. the natural logarithm of gray matter volume for a sample of terrestrial mammals (Bush and Allman, 2003), including the African elephant. **A:** Neocortex. The slope of the reduced major axis fit is 1.265, with a 95% confidence interval from 1.220 to 1.310. **B:** Cerebellum. The slope of the reduced major axis fit is 1.100, with a 95% confidence interval from 1.060 to 1.141.

TABLE 3. White matter vs. gray matter volume reduced major axis fits for a group of mammals with and without the elephant. Data from Bush and Allman (2003)

	Slope	95% confidence interval	R ²	N
<i>With elephant</i>				
Neocortex	1.265	1.220–1.310	0.987	46
Cerebellum	1.100	1.060–1.141	0.985	46
<i>Without elephant</i>				
Neocortex	1.281	1.233–1.329	0.985	45
Cerebellum	1.126	1.081–1.172	0.983	45

LITERATURE CITED

Allman J, McLaughlin T, Hakeem A. 1993. Brain structures and life-span in primate species. *Proc Natl Acad Sci USA* 90:118–122.
 Allman J. 1998. *Evolving brains*. New York: W.H. Freeman.
 Bush EC, Allman JM. 2003. The scaling of white matter to gray matter in cerebellum and neocortex. *Brain Behav Evol* 61:1–5.
 Cozzi B, Spagnoli S, Bruno L. 2001. An overview of the central nervous system of the elephant through a critical appraisal of the literature published in the XIX and XX centuries. *Brain Res Bull* 54:219–227.
 Eggert LS, Rasner CA, Woodruff DS. 2002. The evolution and phylogeography of the African elephant inferred from mitochondrial

DNA sequence and nuclear microsatellite markers. *Proc R Soc Lond* 269:1993–2006.
 Frahm HD, Stephan H, Stephan M. 1982. Comparison of brain structure volumes in Insectivora and Primates: I, neocortex. *J Hirnforsch* 23:375–389.
 Haug H. 1970. *Die Makroskopische Aufbau des GroBhirns: qualitative und quantitative Untersuchungen an den Gehirnen des Menschen, der Delphinoidea und des Elefanten*. Berlin: Springer-Verlag.
 Hofman MA. 1988. Size and shape of the cerebral cortex in mammals: II, the cortical volume. *Brain Behav Evol* 32:17–26.
 Igarashi S, Kamiya T. 1972. *Atlas of the vertebrate brain*. Tokyo: University Park Press.
 Lacerda ALT, Brambilla P, Sassi RB, Nicoletti MA, Mallinger AG, Frank E, Kupfer DJ, Kashavan MS, Soares JC. 2005. Anatomical MRI study of corpus callosum in unipolar depression. *J Psychiatr Res* 39:347–354.
 Lee SM, Tole S, Grove E, McMahon AP. 2000. A local Wnt-3a signal is required for development of the mammalian hippocampus. *Development* 127:457–467.
 Marino L, Sudheimer KD, Murphy TL, Davis KK, Pabst DA, McLellan WA, Rilling JK, Johnson JI. 2001. Anatomy and three-dimensional reconstructions of the brain of a bottlenose dolphin (*Tursiops truncatus*) from magnetic resonance images. *Anat Rec* 264:397–414.
 Marino L, Sudheimer K, Sarko D, Sirpenski G, Johnson JI. 2003. Neuroanatomy of the harbor porpoise (*Phocoena phocoena*) from magnetic resonance images. *J Morphol* 257:308–347.
 Marino L, Sherwood CC, Delman BN, Tang CY, Naidich TP, Hof PR. 2004. Neuroanatomy of the killer whale (*Orcinus orca*) from magnetic resonance images. *Anat Rec* 281A:1256–1263.
 McComb K, Moss C, Durant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292:491–494.
 Morgane PJ, Jacobs MS, McFarland WL. 1980. The anatomy of the brain of the bottlenose dolphin (*Tursiops truncatus*): surface configurations of the telencephalon of the bottlenose dolphin with comparative anatomical observations in four other cetacean species. *Brain Res Bull* 5(Suppl 3):1–107.
 Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling E, Ryder OA, Stanhope MJ, de Jong WW, Springer MS. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294:2348–2351.
 Nieto A, Nieto D, Pacheco P. 1976. Possible phylogenetical significance of the corpus callosum with special reference to the dolphin brain (*Stenella graffmani*). *Acta Anat* 94:397–402.
 Payne K. 2003. Sources of social complexity in the three elephant species. In: de Waal FBM, Tyack PL, editors. *Animal social complexity*. Cambridge, MA: Harvard University Press. p 57–85.
 Rasmussen LEL, Krishnamurthy V. 2000. How chemical signals integrate Asian elephant society: the known and the unknown. *Zoo Biol* 19:405–423.
 Rilling JK, Insel TR. 1999. The primate neocortex in comparative perspective using magnetic resonance imaging. *J Hum Evol* 37:191–223.
 Rosset A, Spadola L, Ratib O. 2004. OsiriX: an open-source software for navigating in multidimensional DICOM images. *J Digit Imaging* 17:205–216.
 Shimogori T, Banuchi V, Ng HY, Strauss JB, Grove EA. 2004. Embryonic signaling centers expressing BMP, WNT and FGF proteins interact to pattern the cerebral cortex. *Development* 131:5639–5647.
 Sokal RR, Rohlf FJ. 1981. *Biometry*, 2nd ed. New York: W.H. Freeman.
 Sukumar R. 2003. *The living elephants*. New York: Oxford University Press.
 Tarpley RJ, Ridgway SH. 1994. Corpus callosum size in delphinid cetaceans. *Brain Behav Evol* 44:156–165.
 Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multi-tiered social structures. *Anim Behav* (in press).
 Zhang K, Sejnowski TJ. 2000. A universal scaling law between gray matter and white matter of cerebral cortex. *Proc Natl Acad Sci USA* 97:5621–5626.