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Brain organization of gorillas reflects species differences in ecology

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Abstract

Gorillas include separate eastern (*Gorilla beringei*) and western (*Gorilla gorilla*) African species that diverged from each other approximately 2 million years ago. Although anatomical, genetic, behavioral, and socioecological differences have been noted among gorilla populations, little is known about variation in their brain structure. This study examines neuroanatomical variation between gorilla species using structural neuroimaging. Postmortem magnetic resonance images were obtained of brains from 18 captive western lowland gorillas (*Gorilla gorilla gorilla*), 15 wild mountain gorillas (*Gorilla beringei beringei*), and 3 Grauer's gorillas (*Gorilla beringei graueri*) (both wild and captive). Stereologic methods were used to measure volumes of brain structures, including left and right frontal lobe gray and white matter, temporal lobe gray and white matter, parietal and occipital lobes gray and white matter, insular gray matter, hippocampus, striatum, thalamus, each hemisphere and the vermis of the cerebellum, and the external and extreme capsules together with the claustrum. Among the species differences, the volumes of the hippocampus and cerebellum were significantly larger in *G. gorilla* than *G. beringei*. These anatomical differences may relate to divergent ecological adaptations of the two species. Specifically, *G. gorilla* engage in more arboreal locomotion and thus may rely more on cerebellar circuits. In addition, they tend to eat more fruit and have larger home ranges and consequently might depend more on spatial mapping functions of the hippocampus.

Keywords

primate brain evolution; cerebellum; hippocampus

Gorillas are diverse and widespread African great apes that include two geographically distinct species: western gorillas (*Gorilla gorilla*) and eastern gorillas (*G. beringei*) (Groves, 2001; Grubb et al., 2003). The latter includes two subspecies, mountain gorillas (*G. beringei beringei*) and Grauer's gorillas (*G. beringei graueri*). The two gorilla species diverged approximately two million years ago (perhaps with subsequent gene flow between the western and eastern populations), based on analyses of mitochondrial and nuclear DNA (Jensen-Seaman et al., 2003; Scally et al., 2012); this genetic difference is similar in magnitude to that observed between chimpanzees and bonobos (Jensen-Seaman et al., 2003). Extensive anatomical, genetic, behavioral, and socioecological differences have been observed among gorillas throughout their distribution in Africa. Mountain gorillas are more likely than western lowland gorillas to have multi-male groups (Yamagiwa et al., 2001; Robbins, 2007). Mountain gorillas in the Virungas are almost entirely folivorous (Goldsmith, 2003; Tutin, 2003; Watts, 1996, 2003; Robbins, 2007), are much more terrestrial than other subspecies, and have smaller home ranges (Doran, 1996; Taylor, 1997; Doran and McNeilage, 2001; Caillaud et al., 2014). Mountain gorillas in Bwindi and Grauer's gorillas in high altitude habitats are also highly folivorous, but eat considerable fruit when it is available and show levels of frugivory and arboreal feeding intermediate between Virunga gorillas and western lowland gorillas, which are the most frugivorous of the taxa (Yamigawa et al., 1994; Robbins and McNeilage, 2003; Yamigawa et al., 2003). Virunga mountain gorillas have a faster life history in many respects than either western lowland or Grauer's gorillas, with earlier ages of first birth, earlier weaning, and higher fertility overall (Yamagiwa and Kahekwa, 2001; Robbins et al., 2004, 2009; Breuer et al., 2009), as well as remarkably fast development of adult brain size (McFarlin et al., 2013). Furthermore, morphological differences between western and eastern gorillas have been reported in the scapula (Schultz, 1934; Taylor, 1997), foot (Tocheri et al., 2011; Dunn et al., 2014), and dentition (Leigh et al., 2003).

The possibility that brain organization also differs between these gorilla species has not yet been fully addressed. Barks et al. (2014) reported a pattern of cortical folding prevalent in eastern gorillas but rare in western gorillas and other great apes, possibly related to a genetic bottleneck in the eastern populations. A preliminary study comparing neuroanatomical variation in a small sample of gorillas among other great apes (Sherwood et al., 2004) noted two differences between the gorilla species: mountain gorillas had a relatively larger striatum and relatively smaller cerebellum than western lowland gorillas. The present research analyzes data from a much larger sample of gorillas across a range of ages, providing a better representation of within-species variation. Although the brains of great ape species are in many ways quite similar overall in terms of the size of neural structures (Sherwood et al., 2004), differences among them can highlight the mosaic nature of brain evolution in which specializations occur in response to the sensorimotor and cognitive demands of local ecological conditions.

Methods

Sample

Postmortem magnetic resonance (MR) brain images were obtained from a total of 36 gorillas, including captive western lowland gorillas (*Gorilla gorilla gorilla*), wild mountain gorillas from the Virunga massif (*Gorilla beringei beringei*), and both wild and captive Grauer's gorillas (*Gorilla beringei graueri*) (Table 1). All animals included in this study died from non-neurological causes.

G. beringei beringei brains came from a wild population in the Volcanoes National Park in Rwanda, monitored daily by the Rwanda Development Board, the Dian Fossey Gorilla Fund International's Karisoke Research Center, and the Mountain Gorilla Veterinary Project. When deceased mountain gorilla remains were encountered during daily monitoring (typically within 24 hours of death), a postmortem necropsy examination was performed, which included collection of brain tissue whenever preservation conditions permitted. One *G. beringei beringei* brain in our sample is from a population in the Parc National des Virunga in the Democratic Republic of Congo (DRC). The two wild *G. beringei graueri* individuals in this sample are from DRC: one originated from the Mount Tshiaberimu population, and one is from an unknown population. Captive *G. gorilla* and *G. beringei graueri* brains were obtained from zoos in the United States and from the Yerkes National Primate Research Center. The research presented here is in accordance with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates and adhered to the legal requirements of Rwanda.

MR image acquisition

MR images of *G. beringei* brains were acquired on a Siemens 3 T Allegra (Siemens Medical System, Erlangen, Germany) running Syngo 2002B software. Coronal T1-weighted MR images were acquired through the entire brain with repetition time (TR) = 2500 ms and echo time (TE) = 4.4 ms with an echo-train of 1. Slices were obtained as 0.7-mm-thick contiguous sections with a matrix size of 256×256 and a field of view (FOV) of $18.0 \text{ cm} \times 18.0 \text{ cm}$, resulting in a final voxel size of 0.7 mm isotropic. For *G. gorilla* brains, either 4.7 or 7 T magnets were used and T2-weighted images were collected in the transverse plane using a gradient echo protocol (pulse repetition = 22.0 s, echo time = 78.0 ms, number of signals averaged = 8–12, and a 256×192 matrix reconstructed to 256×256), with a final voxel size of 0.7 mm isotropic. There was sufficient contrast in all images to clearly identify the boundaries of the anatomical structures measured.

Measurement of brain structure volumes

Analyses of brain structure volumes were performed on the complete sample of 36 gorillas, including *G. beringei beringei* (n = 15; five male, nine female, one unknown sex; age range 1.6–39 years including some adults of unknown age), *G. gorilla* (n = 18; nine male, nine female, age range 8–55 years), and *G. beringei graueri* (n = 3; including one captive male age 51, one wild juvenile male, and one wild juvenile female, exact ages unknown but younger than 6 years).

Using the Cavalieri point-counting method (Gundersen et al., 1988), we measured the volume (in cm^3) of the gray matter and white matter (separately) of regions listed in Table 2. MR images were initially viewed in all orthogonal planes and three-dimensional reconstructions were created using ITK-SNAP (Yushkevich et al., 2006; www.itksnap.org). Lines indicating the central sulcus, lateral sulcus, circular insular sulcus, amygdala-hippocampal transition, and parieto-occipital sulcus were drawn in three dimensions. A series of coronal images were then exported, and loaded into Image J (Schneider et al., 2012) for point-counting using custom macros. Systematic-random point sampling in all three dimensions was optimized to produce an average stereological coefficient of error (CE) of less than 5% (Gundersen and Jensen, 1987; see Table 2). Points for each region were superimposed over each image (Fig. 1), and a trained analyst manually identified which points fell within the region.

The recorded locations for all points/regions were subsequently reviewed and anatomy was corrected as necessary by three authors (SB, MC, CS; see Fig. 1). Volume of each region was calculated as the product of the number of points counted, the point area, and slice sample-spacing. A “cloud” of all points sampled in one mountain gorilla brain is presented in Figure 2, representing the complete volume of all structures measured. The cerebral lobar subdivisions were modified from Semendeferi and Damasio (2000) as follows. The central sulcus was designated as the posterior limit of the frontal lobe. The posterior limit of the temporal lobe was defined on the lateral surface of the brain as a straight line connecting the preoccipital notch and the posterior end of the sylvian fissure, and on the mesial surface as a line connecting the preoccipital notch and the caudal end of the hippocampal sulcus. The parietal and occipital lobes were combined into one region, demarcated anteriorly by the central sulcus and the posterior boundaries of the temporal lobe described above. Following Allen et al. (2008), the insula was defined laterally by the circular sulcus and mesially by a line linking the deepest extents of the two ends of that sulcus.

Statistical analyses

We used PAST (Paleontological Statistics) software, version 2.17c (Hammer et al., 2001) to perform principal component analyses (PCA) as an initial approach to explore the data. Two PCAs were performed: one including absolute values of measures, and a second including each measure's proportion of the total volume measured from the sum of all regions of interest. We examined proportional volume in order to account for variation in shrinkage across specimens resulting from fixation of postmortem tissue. In SPSS Statistics v. 21 (SPSS Statistics for Windows, Version 21.0., IBM, Armonk, NY), pairwise Mann-Whitney U tests, corrected for multiple comparisons (corrected $\alpha = 0.002$), were performed on all pairs of measures for which PCAs showed a significant separation between the *G. beringei* and *G. gorilla* populations. Interaction effects of sex and species were assessed with a two-way ANOVA.

Results

Total brain volume did not differ significantly between the two species, either within the entire sample or among adults only (Table 1). Because *G. beringei graueri* falls between *G.*

gorilla and *G. beringei beringei* in a number of socioecological factors, we examined brain volume data both with and without the three *G. beringei graueri* individuals. The mean brain volume of all *G. beringei* in this sample was 389.4 cm³ (standard deviation 49.09), and of all *G. gorilla* was 419.6 cm³ (SD 69.42) (Mann-Whitney U = 107, p = 0.085). The mean of all *G. beringei beringei* (i.e., exclusive of *G. beringei graueri*) was 384.2 cm³ (SD 50.52). Within adults of each species, there was no significant difference between male and female brain volumes. Mean brain volume of adult female *G. beringei* was 374.9 cm³ (SD 26.91) and of adult male *G. beringei* was 405.6 cm³ (SD 100.90) (Mann-Whitney U = 3, p = 0.7); mean brain volume of adult female *G. gorilla* was 409.8 cm³ (SD 60.72) and of adult male *G. gorilla* was 429.3 cm³ (SD 79.60) (Mann-Whitney U = 33, p = 0.815). Adult and juvenile/infant (i.e. younger than 6 years, following Robbins (2007)) *G. beringei* did not significantly differ in their brain volume (adult mean brain volume was 386.4 cm³, SD 63.04; juvenile/infant mean brain volume was 383.3 cm³, SD 40.91) (Mann-Whitney U = 30, p = 0.918; the *G. gorilla* sample did not contain any juvenile or infant specimens.)

In the PCA of brain structure volumes, the first 7 PCs explained 95% of the total variance (Fig. 3A). *G. beringei* and *G. gorilla* populations overlapped in their distributions on the first two PCs, but displayed greater separation on PC 3, which loads primarily on the bilateral cerebellar hemispheres, bilateral frontal gray matter, and bilateral parietal and occipital white matter (Fig. 3B, C). In the PCA of proportion of total brain structure volumes measured (i.e. each structure's ratio to total measurement), the first 3 PCs explained 91% of the total variance (Fig. 3D). *G. beringei* and *G. gorilla* populations showed the most separation on PC 2, which loads primarily on the cerebellum, bilateral frontal gray matter, and white and gray matter of the parietal and occipital lobes (Fig. 3E, F).

G. beringei graueri were not analyzed separately because of their small sample size (n = 3), but tended to cluster with *G. beringei beringei* in PCAs. The data from the single captive adult *G. beringei graueri* fell closer to the *G. gorilla* sample than the two wild juvenile subjects. The PCA results do not change significantly if *G. beringei graueri* subjects are removed from the analyses: in the PCA of absolute volumes, the first 7 PCs explain 96% of the total variance, and *G. gorilla* and *G. beringei beringei* again separate on PC 3, which loads primarily on the bilateral cerebellar hemispheres, bilateral frontal gray matter, and bilateral parietal and occipital white matter. In the PCA of proportional volumes, the first 3 PCs explained 91% of the total variance. *G. gorilla* and *G. beringei* again separated on PC 2, which loads on the cerebellum, bilateral frontal gray and white matter, and parietal and occipital gray and white matter.

Follow-up Mann-Whitney pairwise tests of absolute volumes showed significant differences between the two species, with larger volumes in *G. gorilla* than in *G. beringei* for the left hippocampus (U = 29, p < 0.000), right hippocampus (U = 43, p < 0.000), left cerebellar hemisphere (Mann-Whitney U = 63, p = 0.002), and vermis of the cerebellum (U = 26.5, p < 0.000) (Fig. 4A). Other differences were non-significant after correction for multiple comparisons. Pairwise tests of proportional volumes also showed a significantly larger volume of the left hippocampus in *G. gorilla* compared to *G. beringei* (U = 41, p < 0.000), and significantly larger volume of right frontal gray matter (U = 58.5, p = 0.001) and right striatum (U = 63.5, p = 0.002) in *G. beringei* compared to *G. gorilla* (Fig. 4B). No other

differences in proportional volumes were significant after correction for multiple comparisons. However, the cerebellar regions that were significantly different between the two species in comparisons of absolute volumes approached significance: the left cerebellar hemisphere (Mann-Whitney $U = 70.5$, $p = 0.003$) and cerebellar vermis (Mann-Whitney $U = 66$, $p = 0.003$) were both larger in *G. gorilla* than in *G. beringei*.

Because the *G. beringei* sample in this study contained a large number of juveniles and infants, we also analyzed these brain structure measurements with the sample restricted to only adults. This age-range restriction removes two out of three *G. beringei graueri* from the sample in the analyses that follow. Pairwise tests of absolute volumes in adults showed a significant difference (*G. gorilla* > *G. beringei*) in the cerebellar vermis (Mann-Whitney $U = 18$, $p = 0.001$) and left hippocampus ($U = 23$, $p = 0.001$) (Fig. 5A). Pairwise tests of proportional volumes in adults showed a significant difference in the right frontal white matter, with *G. beringei* larger than *G. gorilla* ($U = 23$, $p = 0.002$) (Fig. 5B).

Captive western lowland gorillas in this sample varied in their place of birth (either in the wild or in captivity) and in rearing condition (either parent-reared or hand-reared). A PCA of brain structure volumes did not reveal any separation among these groups, nor did follow-up Mann-Whitney pairwise tests.

Age- and sex-related variation in *Gorilla beringei*

Within *G. beringei* we compared brain structure volumes in adults versus juveniles/infants, defining “adult” as older than age 10 years ($n = 7$ adults, 9 juveniles/infants), the median age for first birth in mountain gorillas (Watts 1991). Note that our sample does not include any individuals between age 6 and 16, ensuring that all individuals described as adults are fully mature. No significant differences were observed in pairwise tests between these two age groups in either absolute or proportional volume of any brain structure after correction for multiple comparisons.

No significant differences in either absolute or proportional volume were observed in pairwise tests between males and females for any brain structure, nor were significant interaction effects of sex and species observed in a two-way ANOVA. Males and females did not separate in any PCA.

Discussion

We examined variation in brain structure volumes among gorillas using neuroimaging. Our results demonstrated that gorilla species differ in the size of particular regions, despite displaying similar overall brain size, suggesting that neuroanatomical specializations have been shaped by selection in response to species-typical ecological conditions. Notably, the hippocampus was both absolutely and proportionately larger in *G. gorilla* than in *G. beringei* in comparisons of the entire sample, and its absolute volume was significantly larger in adult *G. gorilla* than in adult *G. beringei* (when juveniles are removed from the sample, the difference in the left hippocampus in proportional volumes is present with a significance level of $p = 0.004$, equivalent to an uncorrected level of 0.15). Also, absolute volumes of cerebellar substructures were significantly larger in *G. gorilla* than in *G.*

beringei, for both the entire sample and for adults only. This difference also approaches conventional levels of statistical significance in a comparison of proportional volumes ($p < 0.1$ before correction for multiple comparisons; corrected $\alpha = 0.004$). In contrast, areas that have significantly larger proportional volumes in *G. beringei* than in *G. gorilla*—right frontal gray matter, right frontal white matter, and right striatum—were not significantly different in absolute volumes, with a lowest significance level of $p = 0.211$. In considering these results overall, we interpret the larger hippocampus and cerebellum in *G. gorilla* as the most robust findings in this study.

These anatomical differences may reflect divergent ecological adaptations between the two species. First, western lowland gorillas have a more frugivorous diet than mountain gorillas, which are almost entirely folivorous because of the lack of fruit trees in their high-altitude habitat, particularly in the Virunga Mountains from where the eastern gorillas in this sample originated (Tutin, 2003; Robbins, 2007), and they have larger home ranges (Doran, 1996; Caillaud et al., 2014). These two factors likely place an increased demand on spatial memory, which relies on the hippocampus (Eichenbaum et al., 1999; Burgess et al., 2002). Studies across multiple species indicate interplay between ecological conditions that require greater spatial memory and navigation skills and a relative increase in hippocampus size (e.g. Jacobs et al., 1990; Clayton and Krebs, 1995; Maguire, 2000). Exploiting fruit as a dietary source may place greater demands on spatial cognition than relying on non-reproductive plant parts, because the availability of fruit varies more and can be less predictable and less abundant. Thus, frugivores stand to benefit more from effective cognitive maps of tree locations and, in the case of plant species that reliably fruit at the same time each year, memory of seasonality. For example, Janmaat et al. (2013) describe a fruit-foraging strategy in which female chimpanzees in a lowland forest habitat similar to those used by *G. gorilla* inspected individual trees of synchronously fruiting species days before they produced ripe fruit as if in expectation of the fruit's appearance; this suggested that they were relying on such mental maps and memory.

The more dispersed nature of fruit patches has implications for home range size as well: *G. gorilla*'s travel range expands in conjunction with the abundance of fruit resources (Tutin, 2003; Masi et al., 2009). Yamagiwa and colleagues (Yamagiwa et al., 1994; Yamagiwa et al., 2003) have observed that *G. b. graueri* shows both a level of frugivory and a mean day journey length intermediate between that of *G. gorilla* and *G. b. beringei*. Notably, chimpanzees (*Pan troglodytes*) have the largest hippocampal volume relative to total brain size among the great apes, possibly reflecting their high dependence on fruit and correspondingly large home ranges (Sherwood et al., 2004; Stumpf, 2007). However, the relationship between fruit consumption and home range size, even in gorillas, is not always straightforward. For example, in reviewing data on the population of *G. b. beringei* in the Bwindi Impenetrable National Park, Uganda, which is considerably more frugivorous overall than the Virunga population and in which home range sizes are similar to those of *G. gorilla*, Robbins and McNeillage (2003) describe considerable variation in both fruit consumption and home range size, but found no significant correlation between these two variables. However, because the *G. b. beringei* brains in this study were obtained

exclusively from the Virunga population, data from this habitat are most relevant to the present analyses.

Second, *G. gorilla* tends to spend more time foraging in trees, incorporating more arboreality into their locomotor patterns than *G. b. beringei* (Doran, 1996; Taylor, 1997). Differences in arboreality between the two gorilla species largely relate to differences in habitat and diet: the high-altitude home ranges of mountain gorillas have few fruit trees and the majority of their food is terrestrial herbaceous vegetation. Comparable data for degree of arboreality in *G. b. graueri* are not available, although Yamagiwa et al. (1994) observed both climbing of trees to obtain ripe fruit and eating of ripe fruit from the ground by gorillas in the lowland sector of Kahuzi-Biega National Park (where all the gorillas belonged to a single population). *G. b. graueri*'s positional behavior, like its diet, probably varies with altitude-related ecological variation, with gorillas in lower-altitude habitats more like *G. gorilla* and those in montane forest more like *G. beringei*.

The cerebellum is known to control complex aspects of locomotion, including planning of sequential behaviors like those employed in moving through trees. Great apes as a group have larger cerebelli relative to total brain size than do other primates (MacLeod et al., 2003). Further, a large cerebellum relative to total brain size in *G. gorilla*—more so than in other great apes—has also been noted in previous studies (Stephan et al., 1981; Rilling and Insel, 1998; Semendeferi and Damasio, 2000), including specifically in comparison to *G. beringei* (Sherwood et al., 2004). The enlarged cerebellum of *G. gorilla* might relate to the greater degree of arboreal locomotion employed than in *G. beringei*. Matano and Hirasaki (1997), for example, noted increased development of the size of cerebellar nuclei in arboreal quadrupedal primates relative to terrestrial primates, suggesting that these structures play a role in the navigation of a three-dimensional arboreal space. Gorillas' large body size may have also played a role in the development of their large cerebellum relative to other ape taxa. Povinelli and Cant (1995) proposed that large-bodied hominoids' navigation through complex substrates—particularly trees—was a significant selective pressure in their cognitive development.

All specimens of *G. gorilla* in this study were obtained from individuals raised in captivity, whereas all but one *G. beringei* specimen were from wild animals. Therefore, we must acknowledge the possibility that what we have identified as species-level differences may be attributed, at least in part, to differences in rearing conditions. However, research showing developmental effects on the volume of specific brain regions in other animals provides reason to think that if anything, captivity would decrease any differences among the gorilla taxa in our sample in terms of brain structures involved in locomotion and spatial memory, including the cerebellum and hippocampus. For example, impoverished housing or rearing conditions can lead to diminished cognitive function associated with neurochemical changes in rodents (Robbins et al., 1996; Würbel, 2001), and specific decreases in hippocampal volume have been documented in birds kept in captivity with lesser spatial cognitive demands than wild counterparts (Day et al., 2008). Conversely, both environmental enrichment and experience can produce increases in brain weight and in brain structure volumes, as well as changes to synapses, cortical thickness, and neurotransmitter receptors (Rosenzweig and Bennett, 1996; van Praag et al., 2000). Human neuroimaging studies have

demonstrated an increase in cerebellar volume (but not total brain size) in skilled musicians relative to controls (Gaser and Schlaug, 2003; Hutchinson, 2003), and an increase in subregions of the vermis of the cerebellum in basketball players relative to controls (Park et al., 2009). A well-known study (Maguire, 2000) showed a redistribution of gray matter in the hippocampus of experienced London taxi drivers (i.e., an increase in posterior hippocampal volume and decrease in anterior volume), associated with significant demands on spatial memory and navigation. While the neuroanatomical differences described within single species in these studies are qualitatively similar to those described here between species, they are generally smaller. The results of the present study suggest that ecological selective pressures that typify the habitats of wild *G. gorilla* appear to be reflected in the brains of captive animals, despite developing in a more limited environment.

Chimpanzees and bonobos are also congeners within the African great apes and diverged approximately 2 million years ago. Neuroanatomical differences between these two species, on a scale comparable to that reported here, have also been described, based entirely on samples from captive individuals. Hopkins and colleagues (2009) reported larger cerebellum, hippocampus, and putamen in chimpanzees compared to bonobos assessed via MR images, and a greater degree in asymmetry of the striatum and cortical motor hand area in bonobos. Schenker et al. (2005), also using MRI data, showed that the dorsal frontal lobe of chimpanzees is proportionally larger than that of bonobos, relative to the rest of the frontal lobe. Finally, Rilling et al. (2011) described neuroanatomical differences between these two species using voxel-based morphometry and diffusion tensor imaging in areas related to social behavior. Specifically, bonobos had more gray matter than chimpanzees in right anterior amygdala, right dorsal amygdala, and hypothalamus, and a larger pathway between the amygdala and the ventral anterior cingulate cortex.

The current study contributes to our understanding of diversity among gorillas by exploring neuroanatomical variation. *G. gorilla* and *G. beringei* are distinct in terms of behavior, morphology, and ecology (Doran and McNeillage, 2001; Leigh et al., 2003; Robbins, 2007). Our present data show that species-level variation also exists in the brain structure of gorillas.

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Figure 1.

Example of measures of brain structure volume using stereology. Four coronal sections from a mountain gorilla brain are shown, anterior to posterior (see inset for level of each section). Structures shown, section 1: frontal gray (light yellow) and white matter (dark yellow). Section 2: parietal and occipital gray (light green) and white matter (dark green), temporal gray (light blue) and white matter (dark blue), hippocampus (tan). Section 3: parietal and occipital gray (light green) and white matter (dark green), thalamus (medium blue), insula gray (pink), external capsule/claustum/extreme capsule (purple), striatum (orange), amygdala (red), temporal gray (light blue) and white matter (dark blue). Section 4: parietal and occipital gray (light green) and white matter (dark green), cerebellar vermis (dark yellow) and hemispheres (light yellow).

Figure 2.

3-D “cloud” of all points measured in one mountain gorilla brain, representing the complete volume of all structures measured. “Claustrum area” refers to the region encompassing external capsule, claustrum, and extreme capsule.

Absolute volume

Proportional volume

Figure 3.

PCA results. Blue circles represent *G. gorilla*; red squares represent *G. b. beringei*; red triangles represent *G. b. graueri*. A. Variance explained by each principal component (PC) for absolute volume of brain structures. B. PCA plot for absolute volumes, PCs 1 and 2. C. PCA plot for absolute volumes, PCs 3 and 4. D. Variance explained by each PC for proportional volume of brain structures. E. PCA plot for proportional volumes, PCs 1 and 2. F. PCA plot for proportional volumes, PCs 3 and 4.

Absolute volumes, all subjects

Proportional volumes, all subjects

Figure 4.

Comparison of mean brain structure volumes in eastern (*G.b.b.*, gray) and western gorillas (*G.g.g.*, black), all subjects, assessed by Mann-Whitney pairwise tests. Error bars indicate +1 SD. Asterisks denote significant differences after correction for multiple comparisons, $p < 0.05$ (corrected $\alpha = 0.002$). Bullets denote significant differences after correction for multiple comparisons, $p < 0.10$ (corrected $\alpha = 0.004$). “Clastrum area” refers to the region encompassing external capsule, claustrum, and extreme capsule. A. Absolute volume (cm³). B. Proportional volume.

Absolute volumes, adults only

Proportional volumes, adults only

Figure 5.

Comparison of mean brain structure volumes in eastern (*G. b. b.*, gray) and western gorillas (*G. g. g.*, black), adult subjects, assessed by Mann-Whitney pairwise tests. Error bars indicate +1 SD. Asterisks denote significant differences after correction for multiple comparisons (corrected $\alpha = 0.002$). “Claustrum area” refers to the region encompassing external capsule, claustrum, and extreme capsule. A. Absolute volume (cm³). B. Proportional volume.

Table 1

Individual data

Subject	Sex	Age (years)	Rearing history	Brain volume (cm ³)
Mountain gorillas (<i>Gorilla beringei beringei</i>)				
0003	male	1.6	wild	445.6
0012	male	adult	wild	488.9
0005	male	5.5	wild	411.7
0045	female	adult	wild	369.4
0046	female	33	wild	398.1
0002	female	1.3	wild	326.0
0006	female	1.5	wild	360.5
0029	male	adult	wild	293.4*
0030	female	39	wild	406.0
0035	female	16	wild	358.9
0032	male	31.5	wild	434.6
0033	female	adult	wild	359.8
0034	female	2.5	wild	336.4
0004	unknown	unknown	wild	363.5
0007	female	2.8	wild	410.3
Grauer's gorillas (<i>Gorilla beringei graueri</i>)				
9907	male	51	captive	442.7
0049	female	juvenile	wild	372.4
0028	male	juvenile	wild	430.7
Western lowland gorillas (<i>Gorilla gorilla gorilla</i>)				
0224	female	43	captive	380.5
0897	male	21	captive	435.2
0653	male	27	captive	488.3
0506	male	31	captive	449.2
0015	female	50	captive	490.2
0393	female	44	captive	339.0
0062	female	55	captive	461.5
1108	male	8	captive	540.4
0820	female	13	captive	417.2
0783	male	25	captive	459.4
0444	male	34	captive	433.4
0713	female	44	captive	380.7
0191	female	41	captive	401.8
0232	male	31	captive	346.4
0072	male	49	captive	445.7
0234	female	48	captive	490.7

Subject	Sex	Age (years)	Rearing history	Brain volume (cm ³)
0172	female	49	captive	326.2
0115	male	42	captive	564.3

* Cerebellum is missing

Table 2

Stereological sampling of brains.

Region	Hemisphere	Average number points counted	CE
Frontal Gray	L	191.1	0.026
	R	192.1	0.031
Frontal White	L	124.6	0.034
	R	130.4	0.028
Temporal Gray	L	141.3	0.037
	R	149.5	0.036
Temporal White	L	77.6	0.052
	R	86.5	0.054
Parietal&Occipital Gray	L	531.5	0.021
	R	528.6	0.017
Parietal&Occipital White	L	375.4	0.026
	R	357.8	0.027
Insula	L	205.5	0.018
	R	206.1	0.021
External capsule/ claustrum/extreme capsule	L	195.0	0.020
	R	193.6	0.021
Cerebellar Hemisphere	L	220.9	0.029
	R	207.1	0.026
Cerebellar Vermis	bilateral	197.6	0.041
Amygdala	L	140.3	0.033
	R	135.8	0.027
Hippocampus	L	229.4	0.013
	R	230.9	0.014
Striatum	L	179.2	0.017
	R	181.8	0.014
Thalamus	bilateral	237.1	0.013