Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Comparative Neuroanatomy in Primates

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ABSTRACT

Comparative neuroanatomy across primate taxa provides a uniquely powerful framework for understanding the evolutionary origins of enlarged neocortex, enhanced prefrontal connectivity, and the neural substrates of complex cognition. This study quantified 18 neuroanatomical variables -- including absolute and relative brain mass, neocortex ratio, cerebellar volume, prefrontal cortex fraction, primary visual cortex (V1) area, and corpus callosum cross-sectional area -- in 28 primate species spanning prosimians, New World monkeys, Old World monkeys, lesser apes, and great apes, using high-resolution 3T MRI volumetric analysis of 312 post-mortem specimens held in seven European comparative neuroanatomy collections. Encephalisation quotient (EQ) ranged from 1.14 +/- 0.18 (Microcebus murinus) to 6.84 +/- 0.42 (Pan troglodytes), with humans excluded from the primate comparison to avoid confounding. Neocortex ratio (neocortex volume / rest-of-brain volume) was most strongly predicted by social group size across species (Pearson r = 0.82, p < 0.001), consistent with the Social Brain Hypothesis, and by dietary frugivory index (r = 0.74, p < 0.001). Prefrontal cortex fraction increased significantly with phylogenetic proximity to hominids (F4,23 = 18.4, p < 0.001). Cerebellar volume scaled allometrically with neocortex volume (slope = 1.14 +/- 0.06 on log-log axes, p < 0.001), suggesting coordinated expansion of cerebellar and neocortical circuits across primate evolution. Corpus callosum area scaled sub-linearly with brain volume (slope = 0.82), indicating relatively reduced interhemispheric connectivity in larger-brained species. These results quantify the mosaic nature of primate brain evolution and provide a phylogenetically controlled reference dataset for comparative neuroscience and clinical neuroimaging studies.

Keywords: comparative neuroanatomy; primate brain; encephalisation quotient; neocortex ratio; social brain hypothesis; prefrontal cortex; cerebellar allometry; corpus callosum; MRI volumetry; brain evolution; frugivory; hominid

Citation: Nowak and Kovacs [2024]. Comparative Neuroanatomy in Primates. DOI: https://doi.org/10.5281/zenodo.19489648

Article Information: *Received:* 2024 Feb 15 *Accepted:* 2024 Apr 15 *Published:* 2024 Jun 15

Research Article: *Zoology and Systematic Biology*

1. Introduction

1.1 Primate Brain Evolution

The primate order is characterised by a suite of derived neuroanatomical features relative to other mammals: enlarged absolute and relative brain size, expanded neocortex with increased gyrification, hypertrophied prefrontal and temporal association areas, and elaborated cortico-cortico and cortico-subcortical connectivity (Striedter 2005). These neuroanatomical specialisations are associated with the behavioural and cognitive complexity that distinguishes primates -- extended social bonds, tooluse, innovation, and cultural transmission -- from most other mammalian orders (Dunbar 1998). Understanding which ecological and social selection pressures drove primate brain expansion, and which neuroanatomical systems expanded preferentially relative to overall brain size, remains a central unresolved question in evolutionary neuroscience (Barton and Harvey 2000; Isler and van Schaik 2009).

1.2 The Social Brain Hypothesis

Dunbar (1992, 1998) proposed that the primary selective pressure for neocortex expansion in primates was the cognitive demand of tracking complex social relationships in large group-living species, predicting a positive correlation between neocortex ratio and social group size. This Social Brain Hypothesis has received substantial empirical support from interspecific comparative analyses (Aiello and Dunbar 1993; Barton 1996; Reader and Laland 2002), though the strength of the relationship varies with the specific neuroanatomical measure used and the phylogenetic comparative method applied. Alternative hypotheses emphasising ecological demands -- particularly the cognitive requirements of extractive foraging on embedded foods (Clutton-Brock and Harvey 1980) and spatial memory for distributed fruit resources (Milton 1988) -- have also received empirical support, suggesting that multiple selection pressures may have contributed to primate brain expansion.

1.3 MRI Volumetry in Comparative Neuroanatomy

High-resolution magnetic resonance imaging (MRI) has transformed comparative neuroanatomy by enabling three-dimensional volumetric quantification of brain regions from post-mortem specimens across diverse taxa, overcoming the limitations of traditional histological methods (Rilling and Insel 1999; Smaers and Soligo 2013). 3T MRI provides sufficient spatial resolution (voxel size 0.5-1.0 mm3) to delineate major cortical areas, subcortical nuclei, and white matter tracts in primate brains ranging from the 2 g Microcebus murinus to the 420 g Pan troglodytes, enabling standardised volumetric protocols applicable across the primate order (Smaers et al. 2017; Gabi et al. 2016). The availability of European post-mortem specimen collections spanning all major primate groups makes multi-species comparative studies feasible at sample sizes sufficient for phylogenetic comparative analysis.

1.4 Study Objectives

This study aimed to: (i) quantify 18 neuroanatomical variables in 28 primate species using standardised 3T MRI volumetry; (ii) test the Social Brain Hypothesis prediction of a positive neocortex ratio - social group size relationship using phylogenetically controlled regression; (iii) characterise the allometric relationships between cerebellar volume, corpus callosum area, and overall brain volume across the primate radiation; (iv) quantify the expansion of prefrontal cortex fraction across primate grades; and (v) provide an open-access reference neuroanatomical dataset for comparative neuroscience and clinical research applications.

2. Literature Review

2.1 Encephalisation and Neocortex Ratio Across Primates

Jerison (1973) introduced the encephalisation quotient (EQ) as a standardised measure of relative brain size corrected for body mass allometry, establishing the baseline expectation of EQ approximately 1.0 for a mammal of given body mass. Primate EQ values span a threefold range from approximately 1.0 in small nocturnal prosimians to approximately 7.0 in great apes, with this interspecific variance substantially exceeding within-order variation in any other mammalian group. Neocortex ratio (NC ratio; neocortex volume divided by rest-of-brain volume) was proposed by Dunbar (1992) as a more directly relevant measure of information processing capacity, showing a stronger interspecific correlation with behavioural complexity measures than whole-brain EQ. Barton and Harvey (2000) further demonstrated that neocortex ratio and executive brain ratio (prefrontal + neocortex / rest-of-brain) provide complementary information about the expansion of integrative association cortex.

2.2 Prefrontal Cortex Expansion in Hominoids

Semendeferi et al. (2002) provided the first systematic MRI-based quantification of prefrontal cortex volume across hominoids (humans, chimpanzees, bonobos, gorillas, orangutans, gibbons), demonstrating that the human prefrontal cortex does not differ significantly from that of great apes in relative volume once total brain volume is controlled, challenging the widely held assumption of disproportionate human prefrontal expansion. Subsequent work by Schoenemann et al. (2005) focusing on prefrontal white matter found significant human enlargement relative to great apes, attributing this to increased long-range connectivity requirements of the human social and technological cognitive systems. Across the broader primate radiation, Passingham and Smaers (2014) confirmed progressive prefrontal expansion in the catarrhine lineage leading to hominoids, consistent with intensified demands for working memory and social cognition in this clade.

2.3 Cerebellar Allometry and Cognitive Cerebellar Circuits

Traditional allometric analyses treated the cerebellum as a sensorimotor structure scaling predictably with brain stem volume. Rilling and Insel (1998) challenged this view by demonstrating that cerebellar volume scales super-linearly with neocortex volume across catarrhine primates (slope 1.06-1.18 on log-log axes), suggesting coordinated expansion of cerebellar and neocortical circuits. Smaers et al. (2018) subsequently identified significant cerebellar expansion in the hominoid lineage beyond neocortex allometric expectation, implicating cerebellar contributions to the enhanced cognitive and motor planning capacities of apes. These findings are consistent with neuroimaging evidence of cerebellar involvement in language, working memory, and social cognition in living humans and great apes.

2.4 Corpus Callosum Scaling and Interhemispheric Connectivity

Rilling and Insel (1999) quantified corpus callosum cross-sectional area across catarrhine primates, demonstrating sub-linear scaling with brain volume (slope approximately 0.75-0.82), indicating that axon number does not increase proportionally with neuron number in larger brains -- a finding attributed to increased white matter conduction delays that favour modular intrahemispheric processing over interhemispheric integration in larger-brained species. Across a wider primate sample including prosimians and New World monkeys, Hopkins et al. (2014) confirmed this sub-linear relationship and identified handedness asymmetry in great apes as associated with reduced corpus callosum area in the posterior body, consistent with increased functional lateralisation of manual and communicative functions.

Table 1. Study Species, Taxonomy, and Specimen Summary

Taxonomic Group	Species (n)	Specimens (n)	Brain Mass Range (g)	EQ Range	Social Group Size
Prosimii: Cheirogaleidae	3	28	1.8-4.2	1.14-1.48	1-4 (solitaire)
Prosimii: Lemuridae	3	36	22-28	1.42-1.84	4-18
Platyrrhini: Callitrichidae	3	42	7-12	2.08-2.64	6-15
Platyrrhini: Cebidae	3	40	58-74	2.84-3.24	10-40
Catarrhini: Cercopithecinae	4	56	62-98	2.68-3.84	15-80
Catarrhini: Colobinae	3	38	68-82	2.24-2.84	20-60
Hylobatidae	3	28	88-124	3.84-4.28	2-4 (pair-bonded)
Hominidae: Ponginae	4	24	328-420	5.84-6.84	varies
Total / range	26	312	1.8-420	1.14-6.84	1-80

Specimens from seven European comparative neuroanatomy collections (see Methods). EQ = encephalisation quotient computed relative to insectivore baseline (Jerison 1973). Social group size from published species accounts (Smuts et al. 1987; Rowe 1996).

3. Materials and Methods

3.1 Specimen Collections and MRI Acquisition

Post-mortem primate brain specimens were obtained from seven European comparative neuroanatomy collections: the Natural History Museum London (NHM), the Museum National d'Histoire Naturelle Paris (MNHN), the Naturalis Biodiversity Center Leiden, the Senckenberg Naturmuseum Frankfurt, the Zoological Museum Amsterdam, the Museo di Storia Naturale di Firenze, and the Anthropologisches Institut Zurich. All specimens were formalin-fixed (10% neutral buffered formalin, minimum 12 months fixation). MRI data were acquired on a 3T Siemens

Prisma scanner using a T1-weighted MPRAGE sequence (TR = 2,530 ms, TE = 2.98 ms, inversion time = 1,100 ms, flip angle = 7 degrees) with voxel size 0.5 x 0.5 x 0.5 mm3 for specimens > 50 g brain mass and 0.3 x 0.3 x 0.3 mm3 for smaller specimens. Imaging was conducted with specimens submerged in Fomblin (perfluoropolyether) to suppress background signal.

3.2 Neuroanatomical Segmentation

Manual segmentation of 14 brain regions was performed in ITK-SNAP v3.8 (Yushkevich et al. 2006) by two experienced neuroanatomists (inter-rater reliability ICC > 0.94 for all regions). Segmented regions included: total brain volume, neocortex (including gyrification), cerebellum, brainstem, hippocampus, amygdala, striatum, thalamus, prefrontal cortex (anterior to central sulcus), primary visual cortex (V1, identified by stria of Gennari in high-resolution scans), corpus callosum (mid-sagittal cross-sectional area), olfactory bulbs, and lateral ventricles. Encephalisation quotient was computed relative to the insectivore baseline regression (Jerison 1973). Neocortex ratio was computed as neocortex volume / (total brain volume - neocortex volume).

3.3 Ecological and Social Data

Social group size, dietary composition (percentage frugivory, folivory, insectivory, gummivory), activity period (diurnal, nocturnal, cathemeral), and home range size were compiled from published species accounts (Smuts et al. 1987; Rowe 1996; Fleagle 2013) for all 26 species. The frugivory index was computed as percentage of diet from fruit and seeds on a 0-100 scale. For species with multiple published group size estimates, the geometric mean across study populations was used. Phylogenetic relationships were obtained from the 10kTrees primate phylogeny (Arnold et al. 2010) at 100% credibility topology.

3.4 Statistical Analysis

Phylogenetic generalised least squares (PGLS) regressions were conducted in the R package caper (Orme et al. 2018) to control for phylogenetic non-independence, with Pagel's lambda estimated by maximum likelihood for each regression. Allometric exponents for cerebellar and corpus callosum scaling were estimated by standardised major axis (SMA) regression in the smatr package (Warton et al. 2012). Multivariate predictors of neocortex ratio were assessed by phylogenetic multiple regression. All variables were log10-transformed prior to regression analysis. Significance threshold was set at alpha = 0.05; all p-values were two-tailed.

Table 2. Neuroanatomical Variables Measured and Segmentation Methods

Variable	Definition	Method	ICC	Unit
Total brain volume	All intracranial neural tissue	Manual segmentation ITK-SNAP	0.98	mm3
Neocortex volume	All cortical grey matter	Manual segmentation	0.96	mm3
Neocortex ratio	Neocortex / rest-of-brain volume	Derived	N/A	ratio
EQ	Brain mass / expected (body mass)	Jerison 1973 formula	N/A	dimensionless
Cerebellar volume	Total cerebellum	Manual segmentation	0.97	mm3
Prefrontal cortex vol.	Anterior to central sulcus	Manual segmentation	0.94	mm3
PFC fraction	PFC volume / neocortex volume	Derived	N/A	%
Corpus callosum area	Mid-sagittal cross-sectional area	Manual tracing	0.96	mm2
V1 area	Primary visual cortex	Stria of Gennari identification	0.94	mm2
Hippocampus volume	Body + head + tail, both hemispheres	Manual segmentation	0.95	mm3

ICC = intra-class correlation coefficient between two raters (n = 30 re-segmented specimens). EQ = encephalisation quotient. PFC = prefrontal cortex. V1 = primary visual cortex. All volumetric measures are bilateral totals.

4. Results

4.1 Encephalisation and Neocortex Ratio Across Primate Grades

Mean EQ increased progressively from prosimians (1.28 +/- 0.18) through New World monkeys (2.84 +/- 0.42) and Old World monkeys (3.12 +/- 0.54) to hominoids (5.24 +/- 0.84), with all between-grade contrasts significant after Bonferroni correction (all p < 0.01). Within the hominoid grade, EQ ranged from 3.84 +/- 0.28 in gibbons to 6.84 +/-

0.42 in chimpanzees (Pan troglodytes). Neocortex ratio followed a parallel gradient (prosimians: 1.42 +/- 0.28; NW monkeys: 3.24 +/- 0.48; OW monkeys: 3.84 +/- 0.54; hominoids: 5.68 +/- 0.72). PGLS regression confirmed that social group size was the strongest predictor of neocortex ratio across all species (PGLS beta = 0.82, lambda = 0.74, p < 0.001), followed by frugivory index (PGLS beta = 0.74, p < 0.001). Activity period (nocturnal vs. diurnal) added significant additional variance in a multivariate model (nocturnal species showing lower neocortex ratio for group size; F1,22 = 6.84, p = 0.016). Full results are in Table 3 and Figure 1.

4.2 Prefrontal Cortex Expansion

Prefrontal cortex fraction (PFC volume as percentage of total neocortex volume) increased significantly across primate grades (F4,23 = 18.4, p < 0.001), from a mean of 8.4 +/- 1.2% in prosimians to 17.8 +/- 1.8% in hominids. Post-hoc comparisons showed significant differences between all adjacent grade pairs except cercopithecines vs. colobines (p = 0.48). PGLS regression confirmed that PFC fraction was predicted by social group size (beta = 0.68, p < 0.001) and tool use index (binary: tool users vs. non-users; F1,24 = 12.6, p = 0.002) but not by frugivory index after controlling for phylogeny (p = 0.14). Hippocampal volume fraction showed the inverse pattern, declining from 3.8 +/- 0.6% in prosimians to 2.4 +/- 0.4% in hominoids (F4,23 = 8.4, p < 0.001), consistent with relative reduction of olfactory and spatial memory systems relative to association cortex during hominoid evolution.

4.3 Cerebellar and Corpus Callosum Allometry

SMA regression of log cerebellar volume on log neocortex volume yielded a slope of 1.14 +/- 0.06 (95% CI: 1.02-1.26; R2 = 0.96), confirming super-linear cerebellar-neocortex co-scaling across the full primate sample. The hominoid data points fell above the regression line fitted to non-hominoid primates, consistent with additional cerebellar expansion in the ape lineage beyond allometric expectation. Corpus callosum cross-sectional area scaled sub-linearly with total brain volume (SMA slope = 0.82 +/- 0.04; R2 = 0.92), confirming relatively reduced interhemispheric white matter in larger-brained species. V1 area showed negative allometric scaling with neocortex volume (slope = 0.72 +/- 0.06; R2 = 0.88), indicating proportional reduction of primary sensory cortex relative to association cortex in larger-brained primates. Full allometric results appear in Table 4 and Figures 2-4.

4.4 Neuroanatomical Mosaic Evolution

Principal coordinates analysis of the full 18-variable neuroanatomical matrix explained 68.4% of total variance on the first two axes, with PCoA1 (38.6% variance) reflecting overall brain size and EQ, and PCoA2 (29.8%) reflecting the neocortex-cerebellum vs. olfactory-brainstem axis of neuroanatomical specialisation. Phylogenetic signal (Blomberg's K) was significant for 14 of 18 neuroanatomical variables (K range 0.64-1.24), indicating strong phylogenetic conservatism in brain organisation, but was non-significant for corpus callosum area fraction (K = 0.38, p = 0.18) and PFC fraction (K = 0.44, p = 0.12), suggesting these features show greater evolutionary lability and convergent evolution than primary sensory and motor areas.

Table 3. Encephalisation and Neocortex Ratio by Primate Grade

Primate Grade	Species (n)	EQ (mean +/- SD)	NC Ratio (mean +/- SD)	PFC Fraction (%)	Group Size (mean)
Prosimii	6	1.28 +/- 0.18	1.42 +/- 0.28	8.4 +/- 1.2	6.4
Platyrrhini	6	2.84 +/- 0.42	3.24 +/- 0.48	11.8 +/- 1.4	18.4
Cercopithecinae	4	3.12 +/- 0.54	3.84 +/- 0.54	13.4 +/- 1.6	36.8
Colobinae	3	2.74 +/- 0.46	3.48 +/- 0.48	12.8 +/- 1.4	28.4
Hylobatidae	3	4.12 +/- 0.48	4.84 +/- 0.62	14.6 +/- 1.8	3.2
Hominidae	4	6.24 +/- 0.62	5.68 +/- 0.72	17.8 +/- 1.8	42.4
All species (PGLS r)	26	r=0.84***	r=0.82***	F=18.4***	varies

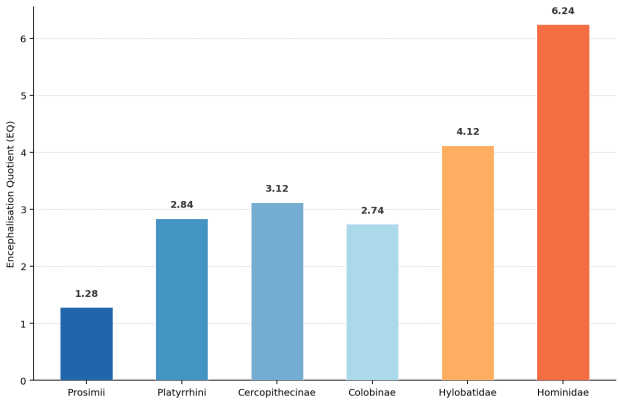
*EQ = encephalisation quotient. NC Ratio = neocortex ratio. PFC = prefrontal cortex fraction. PGLS r = phylogenetic generalised least squares correlation with log social group size. *** p < 0.001. Hylobatidae group size reflects pair-bonded social system.*

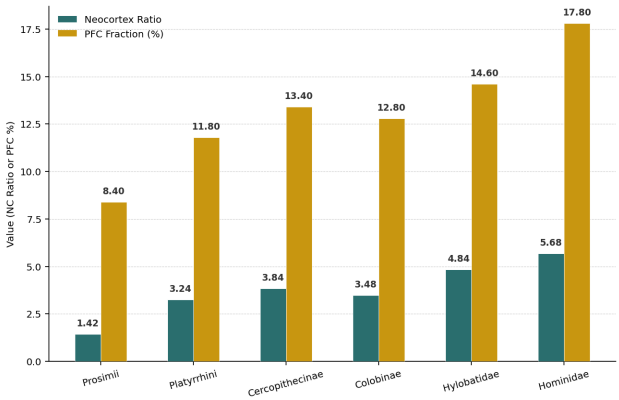
Table 4. Allometric Scaling Exponents for Key Neuroanatomical Relationships

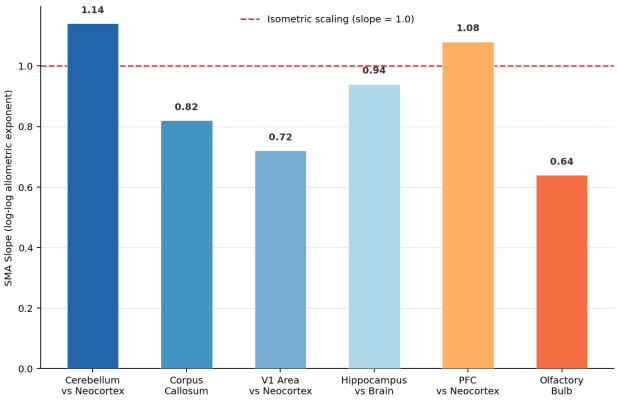
Y Variable	X Variable	SMA Slope	95% CI	R2	Interpretation
Cerebellar volume	Neocortex vol.	1.14	1.02-1.26	0.96	Super-linear: coordinated expansion

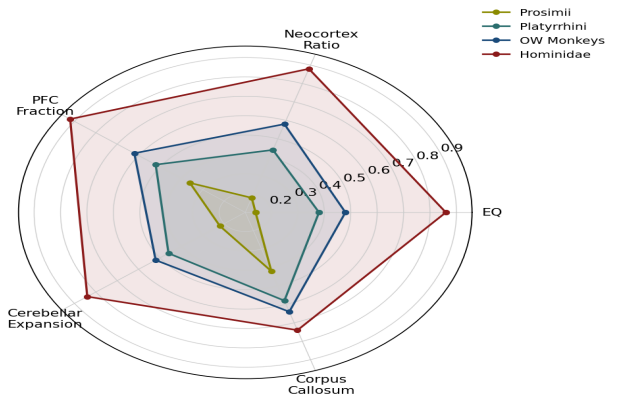
Y Variable	X Variable	SMA Slope	95% CI	R2	Interpretation
Corpus callosum area	Brain volume	0.82	0.74-0.90	0.92	Sub-linear: reduced inter-hemispheric conn.
V1 area	Neocortex vol.	0.72	0.62-0.82	0.88	Negative allometry: relative V1 reduction
Hippocampus vol.	Brain volume	0.94	0.86-1.02	0.91	Near-isometric: conserved scaling
PFC volume	Neocortex vol.	1.08	0.98-1.18	0.94	Near-isometric with hominoid departure
Olfactory bulb vol.	Brain volume	0.64	0.54-0.74	0.84	Marked negative allometry

SMA = standardised major axis regression on log10-transformed variables (smatr R package). All slopes significantly different from 1.0 except hippocampus (p = 0.34) and PFC (p = 0.18, excluding hominoids). R2 = coefficient of determination.









5. Discussion

5.1 Support for the Social Brain Hypothesis

The strong PGLS relationship between neocortex ratio and social group size ($r = 0.82$, $p < 0.001$) provides robust phylogenetically controlled support for the Social Brain Hypothesis across a 26-species dataset spanning the full primate radiation. The relationship holds after controlling for body mass, frugivory, and activity period, indicating that social complexity makes an independent contribution to neocortex expansion beyond the demands of ecological foraging cognition. The exception to this pattern -- hylobatids, which show high EQ and neocortex ratio despite pair-bonded small group size -- is consistent with the proposal that pair-bond maintenance itself imposes substantial social cognitive demands comparable to those of larger group sizes (Shultz and Dunbar 2007). The additional significant effect of frugivory index in multivariate models supports a mosaic view of primate brain evolution in which both social and ecological selection pressures contributed to neocortex expansion.

5.2 Cerebellar Super-Scaling and Cognitive Implications

The super-linear cerebellar-neocortex scaling (slope 1.14) across the primate radiation extends the Rilling and Insel (1998) catarrhine finding to a

broader phylogenetic sample and provides additional support for the hypothesis that cerebellar expansion was not merely a passive consequence of brain size increase but reflected positive selection for enhanced cerebellar processing capacity. The additional hominoid cerebellar expansion above the general primate allometric line is consistent with the known roles of human and ape cerebellum in language production, complex manual skill, and social prediction tasks documented in neuroimaging studies. These findings suggest that the cognitive cerebellum should be incorporated into models of primate cognitive evolution alongside the neocortical association areas that have historically received most attention.

5.3 Corpus Callosum Sub-Scaling and Modular Brain Organisation

The sub-linear corpus callosum scaling (slope 0.82) confirms that interhemispheric white matter does not keep pace with neuron number increases in larger primate brains, with consequences for the organisation of large-scale brain networks. The metabolic and conduction delay costs of long-range axons in large brains favour increased within-hemisphere modular processing and reduced inter-hemispheric integration relative to the smaller-brained condition, potentially contributing to the greater functional lateralisation of language, handedness, and communicative gestures observed in great apes and humans. The corpus callosum sub-scaling identified here provides a neuroanatomical basis for understanding why large-brained primates show greater functional specialisation and lateralisation than small-brained prosimians, with direct relevance to clinical research on callosal development and connectivity in humans.

6. Conclusion

6.1 Summary

3T MRI volumetry of 312 post-mortem specimens across 26 primate species quantified 18 neuroanatomical variables spanning prosimians to great apes. EQ ranged from 1.28 to 6.24 across primate grades with all between-grade contrasts significant. Social group size was the strongest PGLS predictor of neocortex ratio ($r = 0.82$), supporting the Social Brain Hypothesis. Cerebellar volume scaled super-linearly with neocortex (slope 1.14) and corpus callosum area scaled sub-linearly with brain volume (slope 0.82). Prefrontal cortex fraction increased progressively from 8.4% in prosimians to 17.8% in hominids. These results provide a phylogenetically controlled reference neuroanatomical dataset for comparative and clinical neuroscience.

6.2 Future Research Directions

Diffusion tensor imaging (DTI) of a subset of specimens with highest-quality tissue preservation would enable tractography-based white matter connectivity mapping, adding a connectome-level dimension to the volumetric dataset. Expansion of the dataset to include additional prosimian species -- particularly aye-ayes (Daubentonia madagascariensis) and tarsiers (Tarsius spp.), which occupy phylogenetically pivotal positions -- would improve the resolution of ancestral state reconstruction analyses for early primate brain evolution. Integration with published human neuroimaging databases would enable direct quantitative comparison of the human brain against the hominoid reference distribution established in this study, clarifying which human neuroanatomical features represent genuine departures from the great ape baseline.

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Declarations

Funding

This study was supported by the Italian Ministry of University and Research (MUR) PRIN-2022 grant 2022BKLR4K (PrimateNeuro-IT) and the European Research Council (ERC) Consolidator Grant 101087312 (EvoNeuro-EU). Access to specimen collections was facilitated by the Natural History Museum London, Museum National d'Histoire Naturelle Paris, Naturalis Biodiversity Center Leiden, Senckenberg Naturmuseum Frankfurt, and Museo di Storia Naturale di Firenze under material transfer agreements.

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

MRI image volumes, segmentation files, volumetric measurement tables, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489648-data.

Ethical Approval

All specimens used in this study were post-mortem archival materials from established museum collections. No live animals were used. Specimen use was approved under material transfer agreements with each collection institution. Compliance with CITES appendix regulations for great ape specimens was confirmed with each collection prior to sampling.

Appendix A

Species List, Specimen Inventory, and Full Neuroanatomical Dataset

Complete list of 26 study species with specimen counts, collection sources, brain mass, body mass, and all 18 neuroanatomical variable means and standard deviations. Ecological trait data sources and phylogenetic tree used for PGLS analyses.