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Rapid evolution of the cerebellum in humans and other great apes

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Running title: cerebellum evolution in apes

Summary

Humans' unique cognitive abilities are usually attributed to a greatly expanded neocortex, which has been described as "the crowning achievement of evolution and the biological substrate of human mental prowess" [1]. The human cerebellum, however contains four times more neurons than the neocortex [2], and is attracting increasing attention for its wide range of cognitive functions. Using a method for detecting evolutionary rate changes along the branches of phylogenetic trees, we show that the cerebellum underwent rapid size increase throughout the evolution of apes, including humans, expanding significantly faster than predicted by the change in neocortex size. As a result, humans and other apes deviate significantly from the general evolutionary trend for neocortex and cerebellum to change in tandem, having significantly larger cerebella relative to neocortex size than in other anthropoid primates. These results suggest that cerebellar specialization was a far more important component of human brain evolution than hitherto recognized, and that technical intelligence was likely to have been at least as important as social intelligence in human cognitive evolution. Given the role of the cerebellum in sensory-motor control and learning complex action sequences, cerebellar specialization is likely to have underpinned the evolution of humans' advanced technological capacities, which in turn may have been a pre-adaptation for language.

Highlights

- The cerebellum expanded rapidly in parallel lineages of apes, including humans
- The cerebellum increased in absolute size and relative to the neocortex
- This expansion began at the origin of apes but accelerated in the great ape clade
- Cerebellar expansion may have been critical for technological intelligence

Results and Discussion

We apply a method for estimating branch-specific evolutionary rates on a phylogeny [3] to comparative neuro-volumetric data (see Supplemental Information for data and sources), allowing us to detect shifts in the rates of evolutionary size change in individual brain structures. In line with previous studies indicating a strong general pattern of correlated evolution between cerebellum and neocortex [4-6], rates of size change in these two structures are significantly associated (β=0.94, t=35.95, p<0.0001), and both increased on phylogenetic branches within the ape clade (Figure 1 and ref [5]). However, our analysis reveals a striking deviation of apes from the otherwise tightly correlated evolution between the two structures, with ape branches showing a marked increase in the rate of cerebellar relative to neocortical expansion (Figure 2). Branches within the ape clade show a significantly faster rate of cerebellar relative to neocortical evolution than found on the rest of the tree (β_{ape}=1.12, t=5.61, p<0.0001), and this remains true even when comparing ape branches only to those other branches showing a relative increase (β_{ape}=1.29, t=7.33, p<0.0001). Rates of cerebellar relative to cortical evolution were up to 6 times faster on ape compared to non-ape branches (Table 1).

Increased relative cerebellar rates are apparent on the ancestral ape branch (Figure 2 and Table 1), suggesting that the initial impetus may have been the demands of below-branch locomotion and arboreal route-planning in large-bodied primates, just as predicted by one theory of ape cognitive evolution [7]. Although Povinelli & Cant [8] argued that this adaptive shift occurred after the split between lesser and

great ape lineages, fossil evidence suggests that it predated the split [8], potentially providing the initial impetus for cerebellar expansion, with gibbons (*Hylobates)* then showing a distinct adaptive shift into a smaller-bodied true brachiation niche. It was during the radiation of the great ape clade, however, that cerebellar expansion became notably rapid. Whilst there was a slight but significant (1.5-fold) increase in the relative rate along the branches leading to all apes, the average relative rate increase along branches within the great ape clade was 3.2-fold, including a 3.6-fold increase on the branch leading to *Homo* (Figure 2 and Table 1).

If the acceleration we observe in cerebellar relative to neocortical rates across ape lineages reflects directional selection for enlargement, cerebellum size should be significantly larger relative to neocortex size in apes than in non-apes (a "grade shift") [9,10]. Indeed, in our combined data set, ape cerebella are significantly larger than predicted from the scaling relationship with neocortex size (Figure 3; phylogenetic ANCOVA with log cerebellum volume as dependent variable, log neocortex as covariate, apes versus non-apes,; λ=0.63, $t_{2,34}$=3.08 , p=0.004). This result is strengthened slightly by controlling for body mass by including it as an additional covariate in the model (ANCOVA $t_{3,33}$=3.46, p=0.001; λ=0.46; effect of body mass, $t_{3,33}$=1.92, p=0.06). The grade shift is also apparent in the individual volumetric data sets making up our combined data (Supplemental Figure 1A-F). Moreover, the same pattern is evident in further data sets on cerebellar mass (Supplemental Figure 1G), cerebellar granule cell layer volume (Supplemental Figure 1H), and - when an outlier with high leverage on the regression slope is excluded - in numbers of cerebellar neurons (Supplemental Figure 1I). Considering

data on cerebellar to cortical neuron number, humans (the only ape for which such data are available for both structures) fall above the regression line for non-apes (Supplemental Figure 2).

Two of the studies providing volumetric data noted a difference between apes and other primate species, but obtained ambiguous results for humans, with humans appearing to have a relatively small cerebellum [9] or lateral cerebellum [10] relative to the size of the rest of the brain. In contrast, our increased sample size, together with the use of phylogenetic methods for estimating evolutionary rates and allometric slopes, suggest that human cerebellar expansion represents the extreme – in terms of extension along the same allometric trajectory - of the trend for cerebellar specialization shown in apes generally. Although it has been claimed that the human brain conforms to a general linear scaling law for numbers of cerebellar to neocortical neurons in all non-human primates, dictating that the ratio between these neuron numbers is approximately constant across species [2,11], the ratio of 4.2 cerebellar to each cortical neuron in humans contrasts with ratios of 1.2-3.2 in other (non-ape) anthropoids [2].

Our analyses indicate relative cerebellar expansion in apes and provide compelling evidence for a significant shift away from the otherwise tight evolutionary coupling between neocortex and cerebellum [4-6). It is well known that neocortex volume scales with positive allometry relative to the volume of other brain structures, such that large-bodied and large-brained species tend to have a disproportionately large neocortex [12], perhaps encouraging the traditional view that cortical expansion is

the most important feature of mammalian brain evolution. This scaling effect is due primarily to disproportionate expansion of cortical white matter, and secondarily to increases in size of neurons and fibres within grey matter, both associated with the need to maintain functional equivalence in connectivity and long-distance neural conduction in larger nervous systems [6, 13,14]. In the cerebellum, white matter increases less rapidly with overall volume than in the neocortex, whilst neuron number increases more rapidly [6, 11]. Higher ratios of neocortical to subcortical volumes are therefore expected in larger species, such as great apes compared to non-apes, whilst ratios between numbers of neurons remains approximately constant [11]. In a reversal of this general scaling effect, however, the apes in our combined sample have a significantly larger ratio of cerebellum to neocortex volume than do non-apes (PGLS on logged ratios, controlling for body size, $t_{2,34}$=2.28, p=0.029). Thus, for example, chimpanzees (*Pan troglodytes*) have a neocortex 230% larger than the neocortex of baboons (*Papio*) but a cerebellum that is 300% larger, while humans have a neocortex 818% larger than the baboon's but a cerebellum that is 940% larger. These proportional differences are indicative of the extent to which ape brains diverged from those of non-apes as they are counter to the strong general scaling effect in mammalian brains. Using phylogenetic prediction (see Experimental Procedures) we estimate that the human cerebellum (at 139,316 mm^2) is 31% larger than it would be based on the scaling of these structures in non-apes (predicted value = 106,198 mm^2). Extrapolating from human cerebellar neuron densities [2], this is equivalent to adding approximately 16 billion extra cerebellar neurons relative to the allometric expectation for a non-ape brain of

human size. Bearing in mind that this figure is the same as the total number of neurons in the human neocortex [2], these extra cerebellar neurons are likely to be of considerable biological significance.

Our results thus repudiate the widespread assumption that the human brain is distinguished primarily by relative expansion of the neocortex, and indicate that commonly used comparative measures such as overall brain size, neocortex size or ratio and number of neocortical neurons fail to capture important aspects of brain evolution. An expanded neocortex has generally been considered to be the substrate of higher cognition [1] and has been linked in particular to the evolution of social intelligence [15]. Human evolution was, however, characterized by increasing technological complexity as well as social complexity. The cerebellum is particularly likely to have played a role in the former, through its involvement in learning of sensory-motor skills, imitation and the production of complex sequences of behaviors such as those involved in making and using tools [16-20].

Although the cerebellum and neocortex tended to evolve together [4-6], reflecting their major anatomical and functional connections [21], our results suggest that natural selection acted disproportionately on the cerebellar components of cortico-cerebellar mechanisms during the evolution of hominoids, including humans. Recent evidence for relative cerebellar expansion in some other large-brained mammalian lineages, notably elephants and cetaceans [22] raises the possibility of evolutionary convergence, but more detailed work is needed to determine the extent of these parallels. In apes, the specific nature of the neuro-cognitive

enhancement may at a more detailed anatomical level be related to a unique feature of the hominoid cerebellum: a pattern of elaborate folding and increased surface area of the dentate nucleus, associated with a finer topographic mapping of the connections between the cerebellar cortex and the dentate nucleus [23]. Sultan et al [23] propose that this cerebellar specialization supports the computations necessary for longer and more complex sequences of motor acts. This idea is clearly congruent with both an initial locomotor impetus for cerebellar evolution at the origin of apes, and its further elaboration in the context of extractive foraging and tool use in great apes. In particular, it has been suggested that the capacity to flexibly construct and imitate hierarchically nested action sequences underlies specialized extractive foraging skills and tool use, and that such capacities are enhanced in great apes [24-27]. In turn, enhancement of these capacities is consistent with evidence for cerebellar contributions to planning and comprehension of complex sequences [18,23], and may have laid the foundations for syntactical aspects of language [28-31].

The confluence between different lines of evidence, namely the cognitive neuroscience of cerebellar function and its role in complex sequence production and comprehension, including language [18, 29-30], observations of technical intelligence and tool use in hominins and other great apes [24-28], the comparative anatomy of cerebellar fine structure [10,23], and our documentation of rapid cerebellar expansion, thus suggests that the current almost exclusive emphasis on the forebrain as the locus of advanced cognitive functions may be exaggerated, and points to a key role for the cerebellum in human cognitive evolution.

Experimental procedures

Data and Phylogeny

Data on cerebellum and neocortex volumes (mm^3) in anthropoid primates were collated from six primary sources. Mean species values were log-transformed prior to analysis. In addition, we obtained one data set on neocortical and cerebellar mass (g) one on volume of the cerebellar granule cell layer (μm3), and one on neuron numbers. These data and associated references are presented in Supplemental Table 1 and Supplemental Figure 1. For phylogenetic analyses (see below), we used the 10k Trees consensus primate phylogeny with GenBank species names [32]. The tree was pruned according to the species in our data set.

Phylogenetic and Statistical Methods

To determine the branch-wise rates of evolution separately for the cerebellum and neocortex, we used the Bayesian reversible-jump variable-rates model of trait evolution [33]. This model allows us to trace the evolutionary history of shifts in the rate and timing of evolution without specifying in advance where these events are located. To examine the cerebellar rate relative to neocortical, we apply the variable rates model in a phylogenetic regression framework, where log cerebellum volume is the dependent variable and log neocortex volume is the independent variable. This allows us to estimate the rate of cerebellum evolution while accounting for the neocortex. For each analysis, over the course of one billion of iterations after convergence, sampling every 100,000 to ensure each subsequent sample is independent, we record for each branch in the tree what its mean rate is. These mean rates are then be used to scale the branches of

phylogenetic tree to produce a scaled tree that better represent the evolution of the morphological trait of interest (the scaled branches are plotted in figure to along with the untransformed branches in time). We repeated each of our analyses multiple times to ensure convergence was achieved.

We reconstructed the ancestral states for each node in our tree while accounting for the rate variation revealed by the variable rates model of trait evolution (shown in Figure 1). Accounting for rate variation along the branches of the trees allows us to detect trends in size that would be opaque to other methods. We us *BayesTraits* following the protocol outlined in Organ *et al* [34] to impute the ancestral sizes as this approach has been show to outperform other methods for reconstruction ancestral states for continuously varying data [35]. This two stage Bayesian reconstruction methods first identifies the best fitting phylogenetic evolutionary model to the species data, then uses this model to infer unknown ancestral states at specified internal nodes in the tree – we ran the MCMC chains to the same specifications as above and plot the means of the posterior distributions in Figure 1.

We used Phylogenetic Least Squares (PGLS) [36-38] implemented in the R-package 'Caper' (http://cran.r-project.org/web/packages/caper/vignettes/caper.pdf) to compute maximum likelihood (ML) parameter estimates for regressions and to test for significant differences between apes and other species while accounting for the shared ancestry implied by our phylogeny. In each regression the phylogenetic signal is estimated as the value of λ of the residuals, varying between 0 (where the data have no phylogenetic

structure) and 1 (where the best fit to the data is provided by a "Brownian Motion" model of trait evolution) [38], with variation at the tips proportional to the duration of common evolution [36-37]. The estimated ML value of λ is simultaneously estimated together with the other parameters in the model, thus controlling for phylogenetic signal in the data. Predicted values for an individual species based on the relationship between cerebellum and neocortex size can be tested using phylogenetic prediction, as outlined in Organ et al [34]

Author contributions

RB and CV contributed equally to this study.

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Figure legends

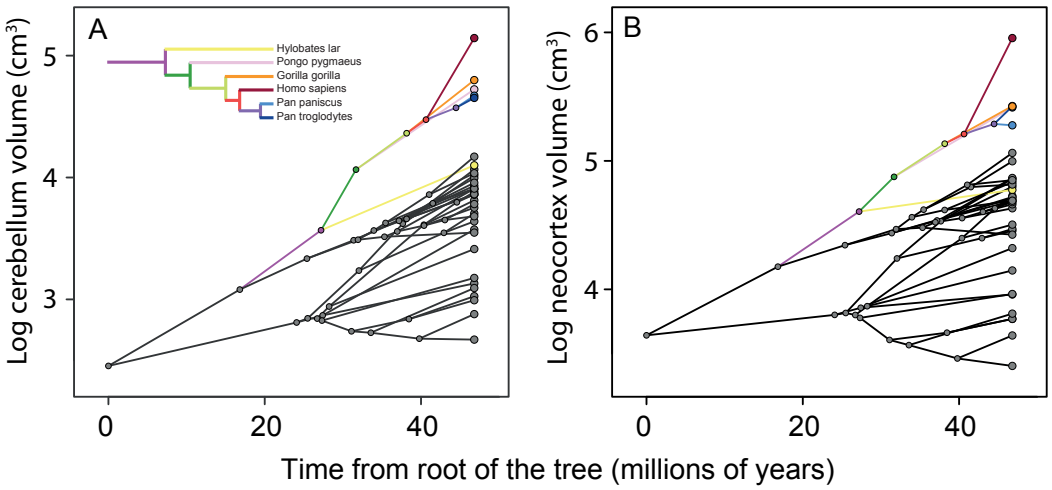
Figure 1. Ancestral reconstruction of changes in cerebellum (A) and neocortex (B) volume during anthropoid primate evolution taking account of rates of evolution (see Methods). Smaller points show reconstructed volumes and large points display the species data. The grey points are non-apes and colour coding of the ape points corresponds to the branches displayed in the inset tree. The points are connected to show the phylogenetic relationships.

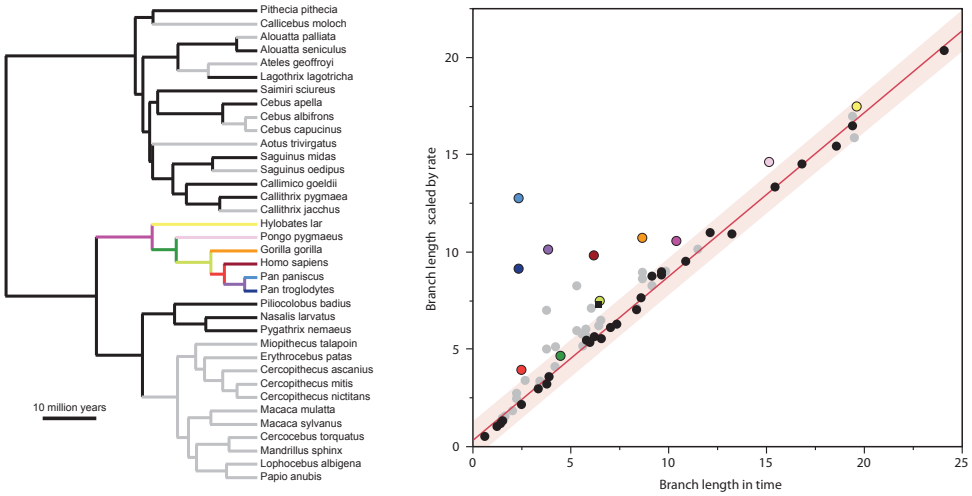
Figure 2. Relative rates of cerebellar evolution in anthropoid primates compared to time (see methods). A. The phylogeny shows the topology of the tree used for phylogenetic analyses, with each ape branch displayed in a different colour. 1b. The plot displays relative rates of cerebellar evolution (controlling for rates of neocortical evolution) on the y-axis as a function of branch lengths in time, on the x-axis. The colour coding of the points corresponds to the branches displayed in A. Black circles are non-ape branches on which relative cerebellum size increased, grey circles are non-ape branches on which relative cerebellum size decreased (thus grey circles falling above the prediction intervals represent non-ape branches with relatively rapid rates of relative cerebellar *decrease*). The regression line and shaded 95% prediction intervals are fitted to the non-ape branches showing increases in relative cerebellum volume. All ape branches showed an increase in relative cerebellum size. 9 out of the 11 ape branches fall outside prediction intervals and a phylogenetic ANCOVA demonstrates that apes had higher relative rates of change compared to all other anthropoid primates (see text).

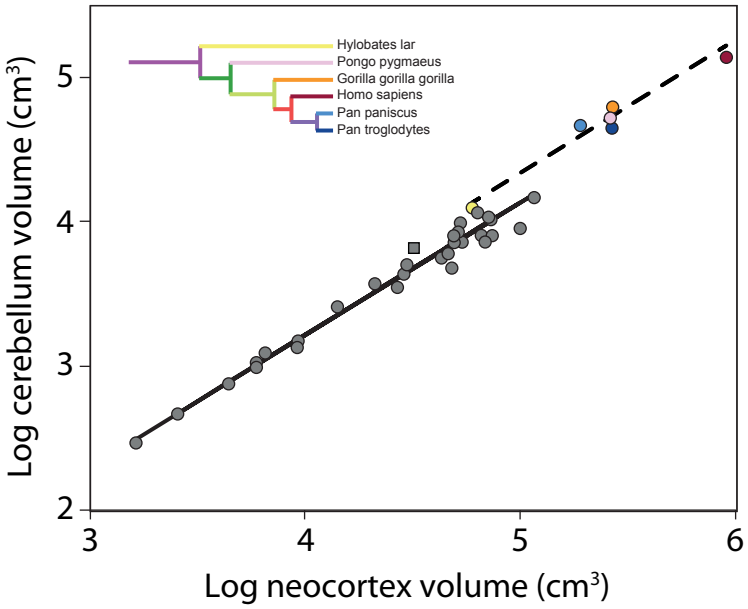
Figure 3. Log cerebellum volume relative to log neocortex volume size in apes (coloured points coded as implied by the terminal branches of the inset tree and dotted regression line) compared to other anthropoid primates (grey points and black regression line). A phylogenetic ANCOVA demonstrates that cerebellum volume is significantly larger relative to neocortex volume in apes (see text).

Table 1: Branchwise increases in relative rates of cerebellum evolution within the ape clade (see text for explanation)

Phylogenetic branch	**x-fold increase in rate of cerebellum evolution relative to rate of neocortex evolution**	
	Compared to other non-ape branches that show increases in size	Compared to all non-ape branches
Branch leading to *Homo*	3.55	3.14
Branch leading to *Pan troglodytes*	4.10	3.56
Branch leading to *Pan paniscus*	5.89	5.35
Branch leading to *Gorilla*	3.52	3.20
Branch leading to *Pongo*	1.53	1.44
Branch leading to *Hylobates*	1.18	1.25
Branch leading to *Pan paniscus* and *Pan troglodytes*	4.06	3.57
Branch leading to *Pan paniscus*, *Pan troglodytes* and *Homo*	1.12	0.58
Branch leading to *Gorilla*, *Pan paniscus*, *Pan troglodytes* and *Homo*	1.74	1.34
Branch leading to Great Apes	0.35	0.12
Branch leading to Apes	1.52	1.26


A
B
Hylobates lar
Pongo pygmaeus
Gorilla gorilla
Homo sapiens
Pan paniscus
Pan troglodytes
Log cerebellum volume (cm³)
Log neocortex volume (cm³)
Time from root of the tree (millions of years)
0
20
40
3
4
5
6


Pithecia pithecia
Callicebus moloch
Alouatta palliata
Alouatta seniculus
Ateles geoffroyi
Lagothrix lagotricha
Saimiri sciureus
Cebus apella
Cebus albifrons
Cebus capucinus
Aotus trivirgatus
Saguinus midas
Saguinus oedipus
Callimico goeldii
Callithrix pygmaea
Callithrix jacchus
Hylobates lar
Pongo pygmaeus
Gorilla gorilla
Homo sapiens
Pan paniscus
Pan troglodytes
Piliocolobus badius
Nasalis larvatus
Pygathrix nemaeus
Miopithecus talapoin
Erythrocebus patas
Cercopithecus ascanius
Cercopithecus mitis
Cercopithecus nictitans
Macaca mulatta
Macaca sylvanus
Cercocebus torquatus
Mandrillus sphinx
Lophocebus albigena
Papio anubis
10 million years
Branch length scaled by rate
Branch length in time
0
5
10
15
20
25


Hylobates lar
Pongo pygmaeus
Gorilla gorilla gorilla
Homo sapiens
Pan paniscus
Pan troglodytes
Log cerebellum volume (cm3)
Log neocortex volume (cm3)
2
3
4
5
3
4
5
6