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From Smart Apes to Human Brain Boxes. A Uniquely Derived Brain Shape in Late Hominins Clade

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Modern humans have larger and more globular brains when compared to other primates. Such anatomical features are further reflected in the possession of a moderately asymmetrical brain with the two hemispheres apparently rotated counterclockwise and slid anteroposteriorly on one another, in what is traditionally described as the Yakovlevian torque. Developmental disturbance in human brain asymmetry, or lack thereof, has been linked to several cognitive disorders including schizophrenia and depression. More importantly, the presence of the Yakovlevian torque is often advocated as the exterior manifestation of our unparalleled cognitive abilities. Consequently, studies of brain size and asymmetry in our own lineage indirectly address the question of what, and when, made us humans, trying to trace the emergence of brain asymmetry and expansion of cortical areas back in our *Homo* antecedents. Here, we tackle this same issue by studying the evolution of human brain size, shape, and asymmetry on a phylogenetic tree including 19 apes and *Homo* species, inclusive of our fellow ancestors. We found that a significant positive shift in the rate of brain shape evolution pertains to the clade including modern humans, Neanderthals, and *Homo heidelbergensis*. Although the Yakovlevian torque is well evident in these species and levels of brain asymmetry are correlated to changes in brain shape, further early *Homo* species possess the torque. Even though a strong allometric component is present in hominoid brain shape variability, this component seems unrelated to asymmetry and to the rate shift we recorded. These results suggest that changes in brain size and asymmetry were not the sole factors behind the fast evolution of brain shape in the most recent *Homo* species. The emergence of handedness and early manifestations of cultural modernity in the archeological record nicely coincide with the same three species sharing the largest and most rapidly evolving brains among all hominoids.

Keywords: endocast, brain volume, asymmetry, primates, human evolution, *Homo neanderthalensis*, *Homo heidelbergensis*

INTRODUCTION

The evolution of the human brain is one of the most intensely investigated topics in anthropology. Most studies on the subject matter focus on the achievement of our outstanding brain size (Rilling, 2006); fewer more focus on brain shape, which is intrinsically hard to study given it takes producing skull endocasts of our ancestors that come short in numbers and are not always easily accessible (Holloway, 2018). Recent developments in virtual anthropology (Weber, 2014) are now making fossil human endocasts a less rare commodity (Bruner et al., 2018), so that we are gaining scientific knowledge on our brain evolution at an unprecedented rate (Falk et al., 2000; Zollikofer and De León, 2013). Paralleling such increasing availability of brain endocasts, phylogenetic comparative methods offer ever better opportunities to study the rate and direction of phenotypic evolution, allowing the inclusion of fossil forms in studies of trait evolution. This is a key addition as the inclusion of fossils to extant-species phylogenies provides better understanding of the tempo and mode of evolution (Slater et al., 2012; Puttick, 2016; Schnitzler et al., 2017).

Recent studies on endocranial volume (i.e., the best proxy for brain size) in hominins invariably point to the presence of phenotypic leaps coinciding with the appearance of *Homo* (Du et al., 2018), although several lines of evidence indicate that not all *Homo* species belong to this "unusually big-brained" class of species, the latter being restricted to *Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo sapiens* (Ruff et al., 1997; Rightmire, 2004; Profico et al., 2017; Diniz-Filho et al., 2019). These studies point to a non-gradual process of brain increase along the hominin lineage, probably prompted by the causal association between speciation and brain size (Du et al., 2018; Melchionna et al., 2019; Rocatti and Perez, 2019; Sansalone et al., 2020). These recent findings are slowly superseding earlier reports describing a pattern of gradual brain size increase in hominins (e.g., Lee and Wolpoff, 2016).

Our understanding of the evolution of brain shape in the human lineage might be experiencing a reverse trend. Despite logical enthusiasm around early findings illustrating an exquisitely human brain shape and level of brain asymmetry (Holloway, 1981; Holloway and De La Coste-Lareymondie, 1982), it has been later noted that the typical brain shape in *H. sapiens*, which is characterized by a strong left-occipital right-frontal asymmetry known as the Yakovlevian torque (Toga and Thompson, 2003) or occipital bending (LeMay, 1976; Holloway and De La Coste-Lareymondie, 1982; Chance and Crow, 2007; Balzeau et al., 2013), is present to a degree in both fossil human species and great apes (Gannon et al., 1998; Balzeau and Gilissen, 2010; Frayer et al., 2016; Neubauer et al., 2020). This casts doubt on the link between brain asymmetry and properly human cognitive abilities and still suggests that the evolution of human brain shape is best viewed as a gradual process toward exaggerated asymmetry and large size (Balzeau and Gilissen, 2010; Corballis, 2010; Gomez-Robles et al., 2013; Neubauer et al., 2018). However, the observation by Xiang et al. (2019) that torque magnitude is independent of brain size variation within *H. sapiens* and repeated findings that brain asymmetry is more variable in humans than in apes (Balzeau et al., 2012a; Neubauer et al., 2020) challenge this view and point to either a punctuational evolutionary event (Crow, 1993; Hou et al., 2019; Xiang et al., 2019) or a shift in the rate of evolution adding variability in humans (Balzeau et al., 2012a; Neubauer et al., 2020).

Here, we used 3D geometric morphometrics to study brain size and shape evolution in Hominoidea using 123 cranial endocasts belonging to 19 different extant and fossil species, including *Australopithecus africanus*, *Homo ergaster*, *Homo erectus*, *H. heidelbergensis*, and *H. neanderthalensis*. We built a phylogenetic tree for the species in the study sample and applied a phylogenetic comparative method especially thought to work with phylogenetic hypotheses including paleontological data. We computed the rate of brain shape evolution and searched for possible rate shifts, and how they correlate to levels of brain asymmetry. We eventually tested whether there is a significant allometric component in brain shape variation.

MATERIALS AND METHODS

Endocasts, Volumes, and Landmark Configuration

We included 123 skull digital models of both extinct and extant species in the analysis. The fossil specimens are Sts 5 (*A. africanus*); KNM-ER 3733 and KNM-ER 3883 (*H. ergaster*); Ngandong 7, Ngandong 12, Sambungmacan 3, Zhoukoudian DI, and Zhoukoudian LIII (*H. erectus*); Kabwe 1, Petralona, and Atapuerca 4 (*H. heidelbergensis*); Saccopastore 1, La Chapelle-aux-Saints, and La Quina 5 (*H. neanderthalensis*); and Abri Pataud, Chancelade 1, Cro-Magnon 1, Mladeè 1, and Skhul V (anatomically modern humans). We also included endocasts of 10 modern *H. sapiens*, 10 *Pan troglodytes*, 10 *Gorilla beringei*, 10 *Gorilla gorilla*, six *Pongo abelii*, eight *Hylobates agilis*, nine *Hydrophis klossi*, 10 *Hylobates lar*, 10 *Hylobates muelleri*, four *Hoolock hoolock*, five *Hylobates pileatus*, eight *Symphalangus syndactylus*, two *Nomascus concolor*, and two *Nomascus leucogenys*. To produce the digital endocasts, we used the CT scans of crania belonging to living species from the Smithsonian Institute and the Digital Morphology Museum, Kupri[1], repositories. We first reconstructed the cranial surfaces by using the software Amira® (version 5.4.5, Visualization Sciences Group, ©2013[2]). Endocasts were obtained within the R software environment by using the *endomaker* function (Profico et al., 2020). The function works by reproducing the inner surface of the cranial cavity. It is based on an automatic reconstruction procedure named AST-3D (Profico et al., 2018). The procedure consists in reproducing the inner surface starting from multiple points of view (POVs) manually placed inside the cavity. The advantage of *endomaker* is that it performs the AST-3D algorithm automatically on brain case, without placing POVs. The function further computes the endocranial volume (i.e., the actual volume of the digital endocast) calling the *volendo* function of the

[1]http://dmm.pri.kyoto-u.ac.jp/dmm/WebGallery/index.html
[2]https://www.fei.com/software/amira-for-life-sciences/

Arothron R package. *volendo* calculates the 3D space occupied by the digital endocast discretized into voxels, identifying the voxels inside the mesh as those included within a concave-hull containing the mesh of the endocast and then computing the sum of inner voxels.

We extracted the cranial endocasts of Sts 5, Petralona, Saccopastore 1, Ngandong 7, Ngandong 12, KNM-ER-3733, and KNM-ER-3883 by using the Arothron R package (**Figure 1**). The other hominin fossil specimens are either manually segmented 3D models or laser-scanned physical casts (details are reported in **Supplementary Table S1**).

To register endocast shapes, we manually collected from each specimen 16 landmarks by using Amira (**Supplementary Table S2**). Then, 1000 bilateral semilandmarks (500 on each side) were automatically placed and slid in the R software environment by using the Morpho R package (Schlager, 2017) (**Figure 2**).

Some fossil specimens may suffer distortion by the taphonomic process, including missing portions. We did not include deformed specimens as they miss the relevant phenotypic information. However, in order to maximize sample size, we applied shape mirroring some specimens but nonetheless excluded them from the analysis of brain asymmetry as the mirroring erases such information. In particular, Kabwe I, La Quina 5, and KNM-ER 3883 are incomplete. In Kabwe I, small portions of the right occipital and parietal lobe are missing. A portion of the left cerebellum is missing in KNM-ER 3883. La Quina 5 lacks the entire base and a portion of the left frontoparietal lobe. Whenever we were not able to sample specific landmarks due to missing parts, the configurations were fixed by using the Morpho function *fixLMmirror*, estimating missing landmarks from their bilateral counterparts. This procedure is based on the reflecting and relabeling technique (Gunz et al., 2009). More specifically, the landmark configuration is mirrored, left and right landmarks are relabeled, and the missing data are imputed by deforming the mirrored version to the original one (Schlager, 2017). The same procedure was applied on the semilandmark sets after the sliding step. As this technique involves mirroring, the hominin specimens Kabwe I, La Quina 5, and KNM-ER 3883 were excluded from the asymmetry analysis.

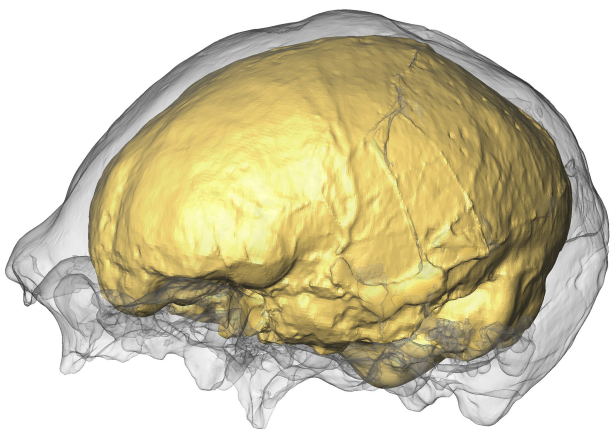

FIGURE 1 | Ngandong 7 skull (gray) and its endocast produced with the function *endomaker*.

Procrustes Analysis and RRphylo

We computed the mean landmark configuration per species. To this aim, we first performed a preliminary alignment of the specimens via Generalized Procrustes Analysis (GPA) (Gower, 1975) using the function *procGPA* in Morpho (Schlager, 2017). Subsequently, we computed the mean shape configuration per species.

To analyze the differences in brain shape among different species, we performed a Procrustes superimposition and a principal component analysis (PCA) on the vectorized landmark sets through the Morpho function *procSym*. This function returns both aligned coordinates and scores from the PCA.

In order to analyze the rate of brain shape evolution, we computed the phylogenetic tree for the species under analysis by using the phylogenetic hypotheses implemented in Meloro et al. (2015) and Melchionna et al. (2019). To search for evolutionary shifts in brain shape, we applied the *RRphylo* function in the R package RRphylo (Raia et al., 2020). The function relies on ridge regression to compute phenotypic evolutionary rates for each branch of the phylogeny and to estimate ancestral phenotypes with either univariate or multivariate data (Castiglione et al., 2018). In the present framework, we used all the principal component (PC) scores retrieved from the PCA pooled by species as phenotypic data, along with the Hominidae tree including the 19 analyzed species as the phylogeny (see **Supplementary Material**). Individual clades within the phylogeny were tested for the presence of rate shifts in brain shape evolution by applying the function *search.shift*. This function locates nodes subtending to clades possessing significantly higher/lower absolute phenotypic rate values by using a two-tailed permutation test (Castiglione et al., 2018). Since brain shape variations might possess a strong allometric component (Aristide et al., 2016), and brain asymmetry (see below) might represent an important source of brain shape variation, we performed the analysis by using once the endocranial volume and once the mean asymmetry per species as predictors. This is currently implemented in the multiple regression version of *RRphylo* (Melchionna et al., 2019; Serio et al., 2019). The analysis without endocranial volume taken as a prediction (pure shape) is presented as part of the **Supplementary Material**.

We analyzed the evolution of brain size using the mean endocranial volume per species as the phenotype and scanned the phylogeny and data seeking after significant shifts in the endocranial volume. The same procedure was applied to brain asymmetry. Eventually, to assess the presence of allometry in the brain shape data, we regressed brain shape against the mean endocranial volumes by means of generalized phylogenetic least squares regression (multivariate PGLS). We applied two different PGLS models. The first implements classic PGLS by using the *procD.gls* function in geomorph (Adams et al., 2019). The second rescales the tree branch lengths according to the multivariate rate variation across the tree branches as calculated by *RRphylo* before running *procD.gls*. These implementations are available in the function *PGLS_fossil* in the RRphylo package.

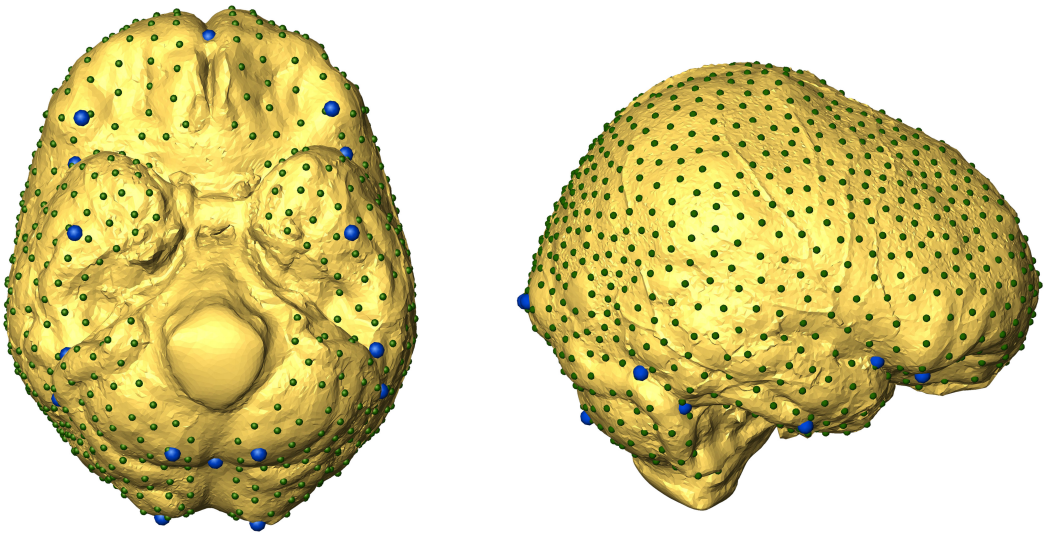

FIGURE 2 | Landmark configurations used in the present work. Fixed landmarks (in blue) were manually defined. Semilandmarks are shown smaller and in dark green.

Measuring Asymmetry in Cranial Endocasts

Bilateral endocast asymmetry was assessed by comparing the brain morphology on the right and left sides. We used the same landmark and semilandmark configurations shown in Section "Endocasts, Volumes, and Landmarks Configuration." In order to record differences in shape between the two halves of the endocast, we defined a set of 1000 semilandmarks, sampling 500 homologous points on each side. We built a symmetric reference for semilandmark placing and sliding procedures. In this way, the slid semilandmarks can be used as a proxy to calculate the difference in shape between right and left sides in all the specimens composing the sample.

After the sliding procedure, we applied the following procedure to each bilateral semilandmark configuration:

i. Calculation of the rotation matrix to mirror, scale, and align (ordinary Procrustes analysis step) the left side into the right side and *vice versa* following Klingenberg et al. (2002) (**Figure 3**);
ii. Definition of a matrix of differences between the symmetric semilandmark configuration and the original one;
iii. Definition of a matrix of difference between right and mirrored left sides and *vice versa*.

At the end of this process, we obtained two suitable matrices to analyze the asymmetry of the cranial endocasts. We explored the relation between asymmetry and shape by applying a partial least squares (PLS). We defined as first block the endocast shape and as second block the matrix of asymmetry calculated on each specimen. The endocast shape consists in the semilandmark configurations after the GPA analysis (scaling included). We perform also a PLS on a less dense semilandmark configuration (50 semilandmarks on each side).

RESULTS

The PCA results are shown in **Figure 4** (PC1 vs PC2). On the PC1 (which explains 35.93% of the total variance), the overall shape goes from flattened endocasts (PC1 positive values) to more globular shapes with a rounded and expanded frontoparietal region. The occipital lobes become markedly asymmetric at PC1 negative values. Along the PC1, there is a separation between the most recent species of *Homo* (*H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*) and the other hominids. Positive values of PC2 correspond to a brain shape that narrows in the temporal area (which is typical of the *Australopithecus* brain morphology), whereas at negative values of the PC2, the brain endocast flattens dorsoventrally.

Brain volume (per unit mass) shows a negative rate shift coinciding with the genus *Hylobates* ($p_{\text{two-tailed}} < 0.001$; **Supplementary Figure S1**). Interestingly, brain shape asymmetry shows a positive rate shift regarding the species of the genus *Homo* ($p_{\text{two-tailed}} = 0.979$; **Figure 5**, right). When the average brain volume is considered as a predictor in *RRphylo*, there is a positive and significant rate shift in brain shape evolution for the clade including *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* ($p_{\text{two-tailed}} = 0.999$; **Figure 5**, left) and a negative and significant rate shift for the Hylobatidae clade ($p_{\text{two-tailed}} < 0.001$; **Figure 5**, left). When brain asymmetry is considered as a predictor in *RRphylo*, the results do not change; there is a positive and significant rate shift in brain shape evolution for the clade including *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* ($p_{\text{two-tailed}} = 0.999$) and a negative and significant rate shift for the Hylobatidae clade

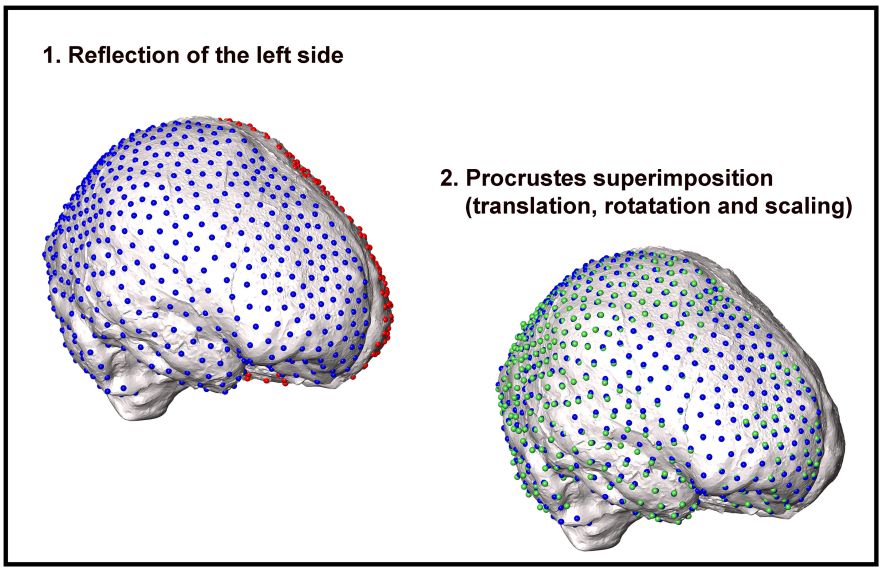

FIGURE 3 | Workflow illustrating the procedure to compute bilateral asymmetry in cranial endocasts. First, the semilandmark configuration of one side (red spheres on the left side) is reflected on the other hemisphere (green spheres). Second, the mirrored semilandmark configuration is scaled to the centroid size of the right side (blue spheres). Third, the configurations are superimposed and rotated around the common centroid to achieve the best fit between the corresponding semilandmarks. For graphical purposes, the procedure is shown on one side only.

($p_{\text{two-tailed}} < 0.001$). Eventually, the same two rate shifts still apply when shape is analyzed on its own, ignoring the allometric component.

We found a positive allometric scaling between the brain shape and the endocast volume, either using the Brownian motion ($p = 0.001$) or allowing the evolutionary rates to change across the tree with *RRphylo* ($p = 0.001$).

The PLS performed between endocast shape and asymmetry highlights a significant correlation between the two blocks. The correlation coefficient related to the first axis is equal to 0.56, and the *p*-value is equal to 0.010 as assessed by a permutation test ($N = 1000$). The correlation coefficient of the second axis is equal to 0.45, and the *p*-value is equal to 0.001 (see **Supplementary Figure S2**). On the first PLS axis, *Homo erectus* and Middle to Late Pleistocene humans (i.e., *H. neanderthalensis*, *H. heidelbergensis*, and *H. sapiens*) are located at negative values of both axes (shape and asymmetry, **Figure 6**). The Hylobatidae are found at positive values of blocks 1 and 2. The first axis of covariation (PLS1, block 1) explains 14.23% of the total variance of the endocast shape. The shape variations related to the genus *Homo* show as in this group of species that the left hemisphere is larger (see **Figure 6** and **Supplementary Figure S3**) with an expansion of the right parietal lobe.

On the second axis of the PLS (see **Supplementary Figure S2**), the morphology associated at positive values highlights the right hemisphere extending anteriorly, according to the classical Yakovlevian torque pattern. At negative values of both axes, the endocast morphology shows a distortion along the midsagittal profile with a greater asymmetry in the superior parietal region and in the anterior portion of the frontal lobe. By reducing the number of semilandmarks on each hemisphere from 500 to 50, we observe the same pattern of shape variations in the PLS analysis (see **Supplementary Figures S6, S7**).

DISCUSSION

Humans are often noted for their exceptional brain size and extremely developed cognitive abilities. It has long been noted that our brain is strongly asymmetric, with evident differences between the left and right sides (Leuret and Gratiolet, 1839). The left cerebral hemisphere often extends posteriorly beyond the right, and the latter extends beyond the left frontally, originating the so-called *petalia* (Galaburda et al., 1978; Toga and Thompson, 2003; Balzeau and Gilissen, 2010). This asymmetric structure is often described as the Yakovlevian torque (Yakovlev and Rakic, 1966). The torque is more than a mere distortion of the bilateral symmetry of the brain. Several studies have indicated that a significant relationship exists between brain asymmetry and the lateralization of cognitive functions such as handedness and linguistic processing. In modern humans, the right frontal (RF) protrusion and left occipital (LO) protrusion are statistically correlated with right-handedness in 85–90% of individuals (Cashmore et al., 2008; Häberling and Corballis, 2016), whereas the reverse pattern is associated to some degree with left-handedness and ambidexterity (Cashmore et al., 2008; Grimaud-Herve and Lordkipanidze, 2010). Lateralization is further observed in hemispheric language dominance. Approximately 95% of right-handed individuals have left-hemispheric dominance for language (Rasmussen and Milner, 1977; Pujol et al., 1999; Szaflarski et al., 2002). A strong variation in the degree of Yakovlevian torque is associated with several functional disorders

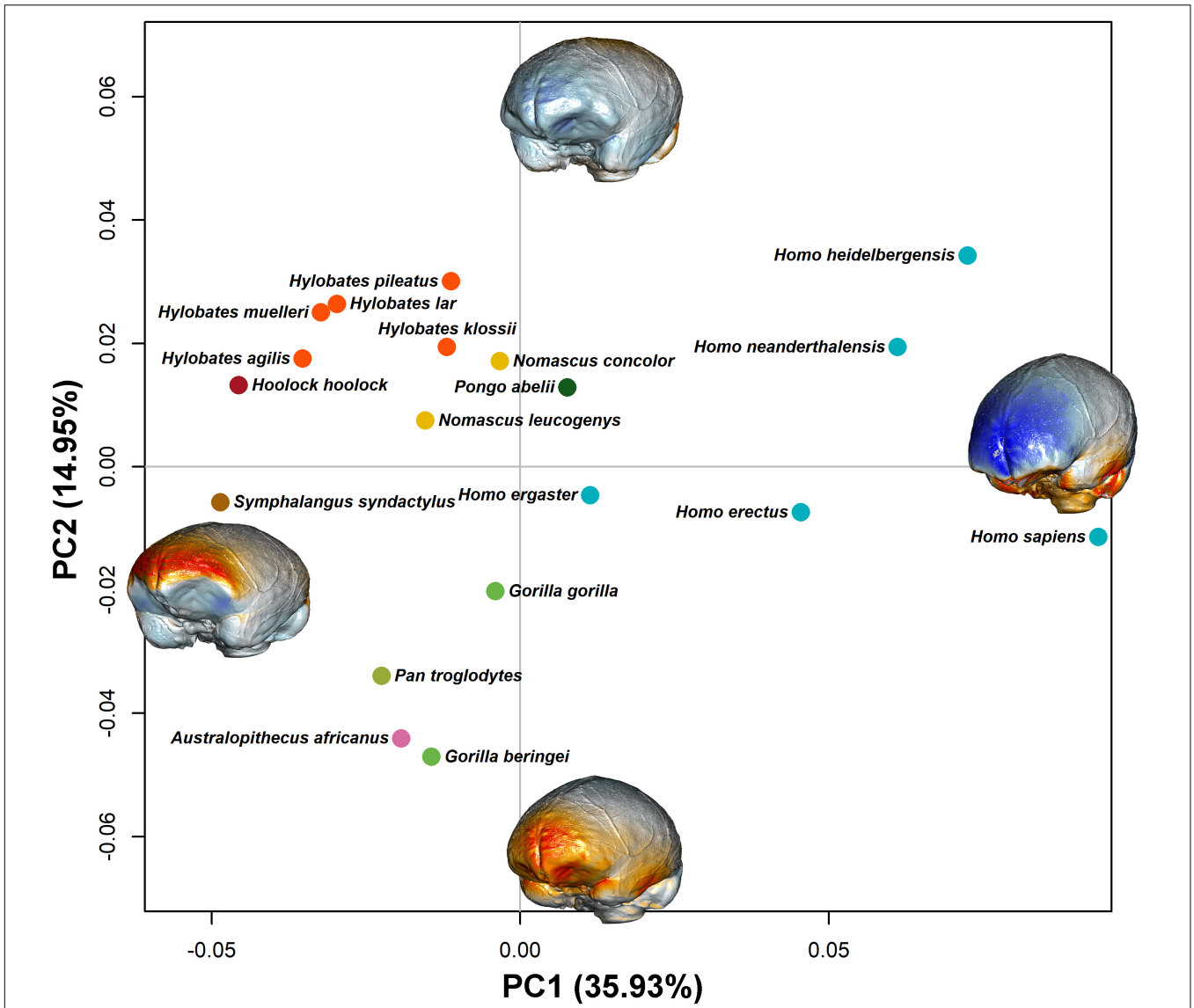

FIGURE 4 | PC1 and PC2 scores are shown. Species represents the mean shape configuration between samples after alignment. They are colored by genus. The endocasts represent the shape at the extreme of the PC axis (endocasts are not in scale). Blue tones represent expansion from the consensus shape, and orange/red tones represent contraction. The two PCs explain, respectively, 35.93 and 14.95% of the total variation.

like depression and schizophrenia (Mackay et al., 2010; Maller et al., 2015; Liu et al., 2016). In schizophrenia, in particular, cerebral asymmetry is reduced, and language processing is less lateralized than in non-schizophrenic subjects (Sommer et al., 2001). This evidence testifies to the intimate connection between the pattern of structural brain asymmetry and lateralization in the development of higher cognitive abilities (Walker, 1980; Gevins et al., 1983; Lefebvre et al., 2004).

Brains of non-human anthropoids are also functionally lateralized to a degree (Holloway, 1981; Cantalupo and Hopkins, 2001; Wu et al., 2006; Falk, 2007; Hofman and Falk, 2012; Gomez-Robles et al., 2013; Hopkins et al., 2015; Poza-Rey et al., 2017). Hylobatids possibly show higher frequency of left- than right-handers (Morino et al., 2017). The great apes present specific patterns of hemispheric asymmetry, which is less frequent than in humans and rarely involves both the frontal and the occipital lobes. Some scholars (Prieur et al., 2016, 2019; Marie et al., 2018) noted the presence of a low-frequency right-handedness bias in bimanual tasks in chimpanzees and gorillas (Hopkins et al., 2019). Although several studies (McGrew and Marchant, 2001; Mosquera et al., 2007; Harrison and Nystrom, 2008) indicate that great apes do not display any hand preference at the population level (Fitch and Braccini, 2013; Uomini, 2015), some groups can have a majority of left-handers (Cashmore et al., 2008; Uomini, 2009; Chapelain et al., 2011), chimpanzee groups were reported to be predominantly right-handed (Hopkins et al., 2004), and even in monkeys, handedness is related to hemispheric specialization (Margiotoudi et al., 2019).

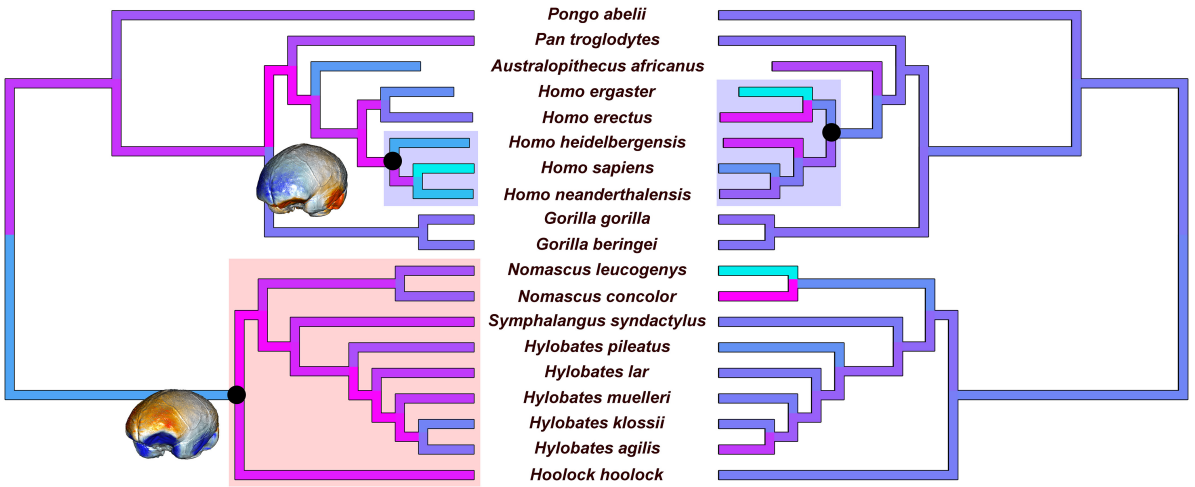

FIGURE 5 | Results of the evolutionary rate analysis of brain shape when mean volume per species is used as a predictor (left). The reconstruction of the endocast shape of the common ancestors is provided (endocasts are not in scale) for the tree root and for the common ancestor of modern *Homo* species. Results of the rate analysis of the average asymmetry values are shown on the right side. Evolutionary rates are scaled for the branches of the tree from higher (cyan) to lower (magenta) values. Clades that show significantly higher and lower rates are highlighted with blue and red rectangles, respectively.

With so much emphasis on brain asymmetry and its relationship to cognition, it is unsurprising that profound effort has been devoted to studying fossil endocasts so as to reveal the evolution of brain asymmetry in hominids and non-human apes. Different studies now point in the direction that a clearly asymmetrical brain pertains to modern human species, whereas the status of australopiths and early *Homo* is much less obvious (Tobias, 1987; Rightmire, 2004; Wu et al., 2006). Brain asymmetry is documented in Paleolithic *H. sapiens*, in *H. neanderthalensis* (albeit the endocast of La Chapelle-aux-Saints has a reversed RO/LF petalia pattern), and in Middle Pleistocene *H. heidelbergensis* (Holloway et al., 2004). A reversed RO/LF petalia pattern has been described in *Homo floresiensis* (Falk et al., 2005) as well in KNM-ER 1813, in some specimens of *H. erectus* from Asia (Sangiran 2, Sangiran 10, Sangiran 17, and Ckn.L.2) and in D2280 from Dmanisi, while D2282 is described as possessing an RF/LO pattern (Grimaud-Herve and Lordkipanidze, 2010) like four of the five endocasts of *H. erectus* from Ngandong (Poza-Rey et al., 2017). A human-like pattern is also described in *Homo rudolfensis* KNM-ER 1470 (Holloway, 1983) and *H. ergaster* KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000 (Holloway et al., 2004). Small RF/LO petalias have been described for *A. africanus*, *Paranthropus boisei*, and *Paranthropus aethiopicus* (Holloway et al., 2004), while the *Homo habilis* specimens from Olduvai usually lack RF/LO petalias (Tobias, 1987; Holloway et al., 2004, but see Frayer et al., 2016). Despite this wealth of data apparently suggesting a continuous development of brain asymmetry throughout human evolution, the precise quantification of the magnitude of the asymmetry and its evolutionary significance in terms of cognitive abilities remain elusive (Balzeau et al., 2020). Furthermore, given the 3D geometric complexity of the torque, its recognition on endocranial casts by using traditional linear measurements as in these studies is often prone to a consistent degree of uncertainty. Our analysis based on 3D geometric morphometrics overcomes this limitation and offers the first integrated glimpse on the rates of evolutionary change of brain shape in the different branches of the Hominoidea. Although the allometric component of brain shape change is strong, the pattern is not linear. Rates of the shape change are distinctly lower for Hylobatidae and distinctly higher for the clade including *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. The early *Homo* (*H. erectus* + *H. ergaster*) and *Australopithecus*, conversely, are in line with the apes (**Figures 4**, **6**), although early *Homo* show the same level of asymmetry as later species in the genus, resulting in a significant rate shift in the asymmetry level coinciding with the genus (**Figure 5**, right). This means that the relative expansion of brain size in Middle to Late Pleistocene *Homo* is accompanied by a major reorganization in the brain morphology that goes beyond sheer allometric effects and asymmetry and possibly keeps changing in *H. sapiens* (Bastir et al., 2008; Neubauer et al., 2018; Weaver and Gunz, 2018; Gunz et al., 2019) and *H. neanderthalensis* (Balzeau et al., 2012b; Mounier et al., 2016).

The pattern of low evolutionary rates in hylobatids is consistent with their evolutionary history and ecologies. The origin of Hylobatidae is placed at 21.8 Ma, and the radiation of the clade occurred between 6.4 and 8.0 Ma (Israfil et al., 2011). Israfil et al. (2011) suggest that such rapid radiation could be paired with biogeographic factors as the population dispersal and variations in the density of the forestal habitat (vicariant speciation). The low degree of body size differentiation and relatively minor ecological diversity when compared to great apes might be responsible for the apparently slow rate of brain shape evolution in this group.

Along the human lineage, the shifts in evolutionary rate in brain size evolution (Du et al., 2018; Diniz-Filho et al., 2019) and increased rates of brain shape evolution (this study) coincide, thus suggesting that brain evolution followed a distinctive path

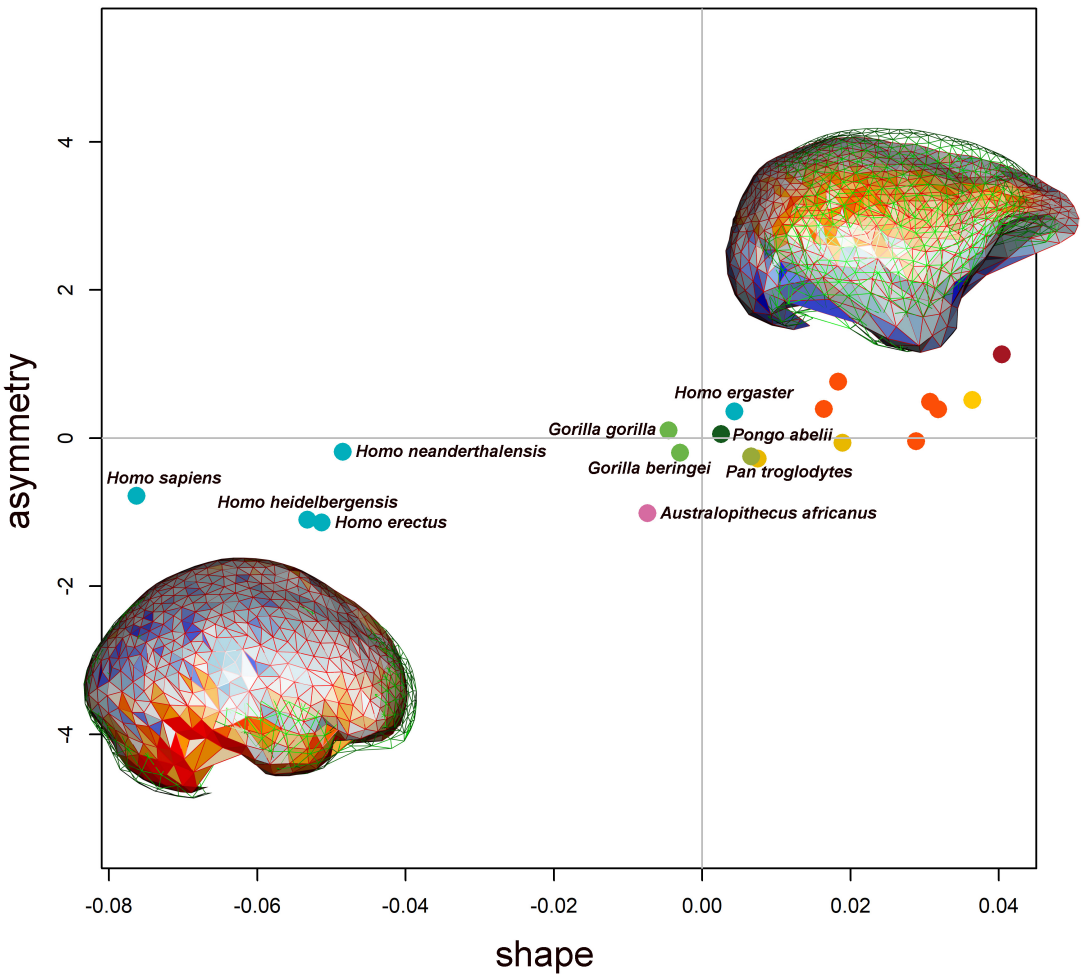

FIGURE 6 | Biplot showing the first axis of the PLS. On the *x*-axis is the endocast shape, and on the *y*-axis is the endocast asymmetry. The species are reported with the same dot colors reported in **Figure 4**. The shape variations related to both shape and asymmetry are reported at the extreme of the *x*- and *y*-axes. The displacement between the right (wireframe in red) and left (wireframe in green) sides is shown overlapped to the colored mesh, indicating the local deformation. Warm and cold colors indicate, respectively, which regions are more contracted and expanded in the right side compared with the left one.

joining *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. This is entirely consistent with the archeological record of human behavior. Numerous studies on the anterior dentition in *H. heidelbergensis*, Neanderthals, and Paleolithic modern humans show a predominant right-hand frequency (> 90%), similar to the pattern for living humans attributed to right-handers (de Castro et al., 1988; Lozano et al., 2009; Frayer et al., 2012; Poza-Rey et al., 2017). Studies of experimental production of lithic stone tools demonstrate that brain lateralization is involved in the production of late Acheulean tools or when participants watch Acheulean tool production, but not when participants make or watch others making Oldowan tools (Stout, 2011; Stout and Khreisheh, 2015). Uomini and Meyer (2013) suggested that the same areas for stone tool manufacture, of the Acheulean in particular, are lateralized and located on the left side in brain areas also involved in language processing and social learning.

It is intriguing that the birth of symbolic culture, marked by the use of pigments and personal ornamentation, traces back to the Middle Stone Age with Acheulean tradition at some 300 ka and is itself consistent with human fossil specimens belonging to the species *H. heidelbergensis* (Henshilwood et al., 2002; d'Errico, 2003; d'Errico and Henshilwood, 2007; Manzi, 2016) and *H. neanderthalensis* (Zilhão et al., 2010). It must be noted, though, that the indication for symbolic culture in species other than *H. sapiens* is controversial to say the least (Mcbrearty and Brooks, 2000; White et al., 2019).

Here, we demonstrate that the pace of brain shape evolution shifted since the appearance of the common ancestor to *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. Although these species share a large brain, levels of brain asymmetry were comparatively large in earlier *Homo* species, and allometric effects cannot entirely account for the shift toward the faster rate of brain shape evolution in the Middle to Late human species. Remarkably, the rate shift coincides with archeological evidence for the emergence of symbolic culture.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

PR, MM, and AP conceived the study. MM, AP, SC, and CS performed the analyses. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2020.00273/full#supplementary-material

This file includes:

The phylogenetic tree used in the analyses in Newick format.

FIGURE S1 | Results of the evolutionary rate analysis on the average volumes.

FIGURE S2 | Biplot showing the second axis of the PLS.

FIGURE S3 | Variation in centroid size between right and left hemisphere within the genus *Homo*.

FIGURE S4 | Variation in centroid size between right and left hemisphere in great apes (*Homo* excluded) plus *Australopithecus africanus*.

FIGURE S5 | Variation in centroid size between right and left hemisphere in lesser apes.

FIGURE S6 | Biplot showing the first axis of the PLS using a subset of 100 semilandmarks (50 on each side).

FIGURE S7 | Biplot showing the second axis of the PLS using a subset of 100 semilandmarks (50 on each side).

TABLE S1 | List of materials used in this study.

TABLE S2 | Definition of landmarks acquired on each endocast.

DATA.rda: an RData file containing the phylogenetic tree, the landmark and semilandmark sets used in the analyses of the endocast shape (123 specimens), the semilandmark sets used in the asymmetry analyses (120 specimens), the vector of the corresponding ECV values and a mesh containing the triangulated semilandmark configuration.

script.R: The annotated script used to replicate the analyses reported in this study. The supplementary material is available on Melchionna et al. (2020). From smart apes to human brain boxes. A uniquely derived brain shape in late hominins clade: supplementary material. *Zenodo*: doi: 10.5281/zenodo.3931032.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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