

Comparing Endocranial Form and Shape Differences in Modern Humans and Neandertals: a Geometric Approach

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ABSTRACT

Paleoneurology is based on the analysis of the traces left by the brain cortical structures on the endocranial surface of fossil specimens. Although such information is indirect and fragmentary, it may provide useful insights on human brain evolution. Computed tomography and shape analysis deeply improve the toolkit available for paleoneurological studies. Shape analysis and multivariate approaches suggest that modern humans have undergone a specific evolution of the parietal areas. In this paper the endocranial lateral profiles of two complete specimens (one modern human and one Neandertal) are compared using both form and shape information by means of geometric comparison and coordinate-based maps, integrating superimpositions and Euclidean distance matrix analysis. Using both superimposed (shape) and non-transformed (form) data, the modern endocast is characterized by a midsagittal enlargement of the parietal and occipito-cerebellar areas, associated with antero-posterior shortening of the fronto-temporal profile. Differences can be quantified and synthesized using simple geometric tools. Modern brain morphology may be the result of both neural changes and structural constraints, in which modularity and integration make the endocranial geometry sensitive to the cranial base dynamics, facial changes, tissue strains, and metabolic/physiological adjustments. Although paleoanthropology often deals with fragments or single specimens, the use of geometrical modelling is a useful and simple tool to standardize, quantify, and describe morphological differences.

INTRODUCTION

The morphogenesis of the neurocranium is the result of a genetic program and the structural interaction between bone and soft tissues. The vault changes in size mostly in response to brain pressure and growth, while changing in shape under the constraints of connective tensors like the *falx cerebri* and the *tentorium cerebelli* (Moss and Young 1960). In contrast, the inferior surfaces of the endocranium display a more complex developmental basis, interacting with the cranial base dynamics and morphogenesis of the face (Lieberman et al. 2000; McCarthy 2001; Ross et al. 2004). The brain's cortical structures contact the endocranial wall through the layers of the dura mater, leaving their imprints on the bone surface. This relationship provides the basic framework of paleoneurology, aimed at characterizing brain morphology in fossil species (Bruner 2003; Falk 1987; Holloway 1978).

Of course, the absence of evidence is not always evidence of absence. Namely, the presence of a trace on the endocranial surface reveals the past existence of a structure, but the absence of imprints cannot prove the absence of the structure itself. Traces of tissue are preserved depending upon the pressure on the endocranial table and the thickness of the dura layers (see Kimbel 1984; Peña-Melian 2000). Small structures can leave large traces, and conversely large structures can leave no imprints at all, depending upon species-specific, as well as individual and local, anatomical conditions. Furthermore, the relationship between cortical morphology and neural districts is difficult to assess, as described for important functional areas

such as Broca's cap (Amunts et al. 1999). Nevertheless, fossil endocranial casts serve as the basis for paleoneurology, providing the only direct information for investigating variation in the brain morphology of extinct humans. Thus, endocasts must inevitably be a significant part of any study of brain evolution.

The applications of shape analysis (Richtsmeier et al. 1992; Rohlf and Marcus 1993; Slice 2004; Zelditch et al. 2004) and computed tomography (Zollikofer et al. 1998; Zollikofer and Ponce de León 2005) to the study of endocasts deeply improved and enlarged the available paleoneurological data. Using the tools of digital morphology, the brain in modern *Homo sapiens* has been hypothesized to show discrete differences in its organisation and structure when compared with non-modern human groups (Bruner et al. 2003). In particular, the parietal areas in modern humans display a definite enlargement, through widening of the superior surfaces and lengthening of the upper profile. The changes in the parietal areas can be related to both neurofunctional and structural processes. In terms of cognition, the upper parietal cortex is associated with visuo-spatial integration. In terms of structure, it has been hypothesized that human encephalisation may be characterized by allometric constraints at the parieto-occipital boundaries (Bruner 2004a). Similar differences between modern and non-modern neurocranial shapes also have been described, taking into account the ectocranial midsagittal profile (Bruner et al. 2004). Although the endocranial morphology of the earliest modern human groups is not completely known, the separation between modern and non-modern

variations seems discrete, suggesting a certain degree of discontinuity within the anatomical organization.

Particular attention must be paid to the comparison between Neandertals and modern humans. These two human morphs have been hypothesized to represent two distinct evolutionary pathways evolving more or less independently, regardless of any hypothetical interbreeding potentialities (e.g., Tattersall and Schwartz 2006). They share similar cranial capacity and overall brain dimensions (Holloway 1981; Holloway et al. 2004), but also differ in some cerebral traits (Bruner et al. 2003; Grimaud-Hervé 1997); as well as neurocranial architecture (Ponce de Leon and Zollikofer 2001). Therefore, this comparison is useful to investigate two different human brain models scaled at the same cerebral mass.

This consideration is relevant because a large percentage of endocranial variation within the human genus is allometric, namely associated with size-dependent relationships of structural and functional networks. The encephalisation process has been hypothesized to be largely associated with an allometric component involving widening of the frontal lobes, vertical stretching of the endocranial structure, and compression of the upper parietal surface (Bruner 2004a). Because Neandertals and modern humans share the same cranial capacity, specific departures from the *Homo* allometric trajectory may be identified, which can be interpreted as adaptations (the criterion of subtraction, *sensu* Gould 1966). Such discrete differences between Neandertals and modern humans have been described using geometric superimposition approaches. These iterative procedures standardize different geometric configurations to make the objects comparable in terms of fixed morphological axes or multivariate statistics (Bookstein et al. 1991; Zelditch et al. 2004). Here I rely upon an absolute geometric comparison of the endocranial profiles, independent of any kind of normalization, in order to display the actual differences between the modern and Neandertal morphotypes. This is a particularly useful approach for verifying and describing the differences at the parietal profile, as it integrates and compares the information available using superimposition techniques and relative geometric comparisons.

MATERIALS AND METHODS

SAMPLE AND CONFIGURATION

Generally, a geometrical “form” may be thought of as the result of size and shape components, where the size is related to the actual dimensions of the object, and the shape is related to its spatial properties, regardless of position, orientation, or scale (see Richtsmeier et al. 2002). That is, form and shape can be considered as different morphological concepts, providing different but complementary information. This is particularly useful when the importance of allometry and heterochrony are taken into account within evolutionary scenarios (e.g., Gould 1966; Klingenberg 1998; Shea 1992). This operational separation between variation

in dimensions and variation in spatial relationships is crucial to studying encephalisation, a process related to relative increases in cranial capacity.

Although many Neandertal endocasts are now available (Holloway et al. 2004), they are rarely completely preserved, hampering geometrical modelling of the whole endocranial form. In this paper the lateral endocranial morphology in Neandertals and modern humans will be compared through geometric superimposition of averaged configurations using six and eight specimens respectively (Table 1). In this sample, many specimens are incomplete, and the mean figures were calculated using the available landmarks. To gain a better understanding of the complete form and its integration, two *complete* endocasts were subsequently selected as representative for modern humans and Neandertal brain morphology, in order to provide a raw geometrical comparison of the lateral brain profiles. The use of sufficiently preserved endocasts is strictly necessary, if the actual position of the different components are to be considered along the endocranial outline in terms of absolute geometry (i.e., form). Using the superimposed and raw geometrical models and accounting for the discrete morphological gap between these two human groups (Bruner 2004a), this approach allows verification of the raw endocranial differences, testing also for the inevitable bias introduced by the superimposition procedures. The lateral view is the most suitable projection for describing the actual differences at the parietal midsagittal profile, which are

TABLE 1. COMPARATIVE SAMPLE

GROUPS	REPOSITORY
Neandertals	
Saccopastore 1	LSR
Feldhofer	LSR
La Ferrassie	IPH
La Chapelle aux Saints	ISIPU
Guattari 1	ISIPU
Teshik-Task	IPH
Modern humans	
Combe Capelle	LSR
Vatte di Zambana	ISIPU
Vestonice 2	IPH
Predmost 9	IPH
Predmost 3	IPH
Predmost 4	IPH
Predmost 10	IPH
Modern endocast	IPH

LSR: University La Sapienza, Roma

ISIPU: Istituto Italiano di Paleontologia Umana, Roma

IPH: Institut de Paleontologie Humaine, Paris

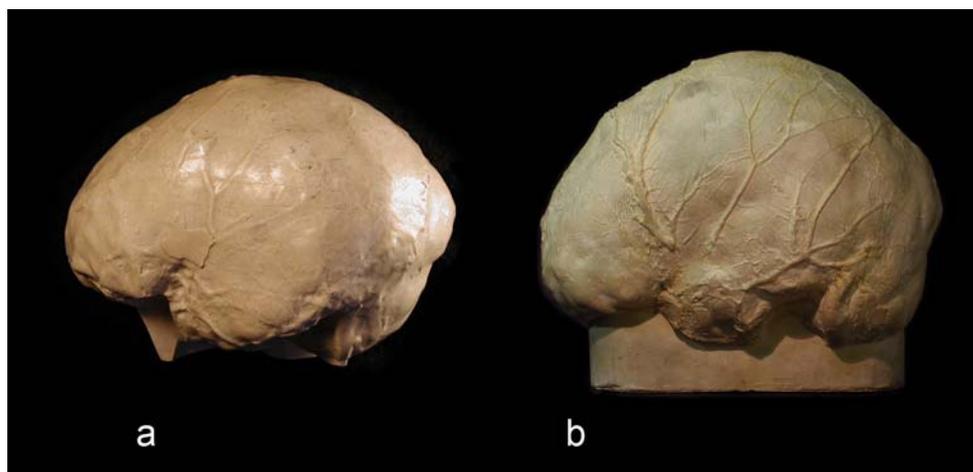


Figure 1. The endocranial cast of La Ferrassie 1, a Neandertal specimen dated to 60–70 ka (a), and the endocranial cast of Vatte di Zambana, anatomically modern human dated to 8 ka (b). The two endocranial casts are preserved at the Institut de Paleontologie Humaine of Paris, and at the Istituto Italiano di Paleontologia Umana of Roma, respectively. Photos are not to scale.

hypothesized to have undergone interesting changes in the evolution of modern humans.

The most complete and representative specimens within the available sample are the endocranial casts from La Ferrassie and Vatte di Zambana. The Neandertal skull *La Ferrassie 1* was found in 1909 in France, dated to no more than 70,000 years before present, with a cranial capacity of 1640cc, and generally regarded as a classic western European Neandertal (see Schwartz and Tattersall 2002). The endocranial cast is preserved at the Institut de Paléontologie Humaine (Paris). The skull from Vatte di Zambana was recovered in North Italy in 1967–1968, dated to 8,000 years before present, with a cranial capacity of 1480cc, and represents an anatomically modern human (Corrain et al. 1976; Newell et al. 1979). The endocranial cast is preserved at the Istituto Italiano di Paleontologia Umana (Roma). The endocranial casts of the two specimens are shown in Figure 1.

Nineteen two-dimensional landmarks were sampled on the left endocranial side of each endocranial cast, using a dioptrigraph (Figure 2), and reported as Cartesian coordinates using TPSDIG 1.20 (Rohlf 1998). Landmarks sampled on endocranial casts rarely represent well-defined homologous points because of the smooth and irregular morphology of the cortical surface. In the present configuration, the frontal, occipital, and temporal poles are the most projecting points of the respective lobes. The Rolandic scissure is tentatively localized using the other available sulci (precentral, postcentral, interparietal, 3rd frontal). Three anterior (A1–A3) and posterior (P1–P3) points are localized on the endocranial vault profile as projections at quarters of the fronto-rolandic and occipito-rolandic chords. P1 and P2 are supposed to be localized at the parietal areas. The internal occipital protuberance is taken at the deepest point between the occipital and cerebellar lobes. The cerebellar outline is defined according to its anterior-most and posterior-most lateral profile, with three projections at quarters of this chord. The lower boundary between the temporal and occipital area have been tentatively localized using the lower tem-

poral circumvolutions and traces of the temporo-occipital notch. The posterior edge of the temporal valley (between the cerebellar and temporal lobes) is localized about across the diameter of the relative transverse-sigmoid vessel. The Broca's cap is defined as the most lateral projecting point at the base of the third frontal circumvolution.

SUPERIMPOSITIONS

The specimens used to compare the modern and Neandertal means and the single configurations from La Ferrassie and Vatte di Zambana were superimposed using both a Procrustes procedure and a fronto-occipital baseline (Bookstein 1991). The Procrustes procedure minimizes the shape differences—the configurations are scaled to unit centroid size, translated to a common centroid, and rotated to minimize the least squares residuals between corresponding landmarks. The baseline registration superimposes the configuration according to a specific diameter, in general representing some relevant functional or structural axis.

The differences between shapes also are visualized using the thin-plate spline function and deformation grids, to show the actual spatial changes (Bookstein 1991). Deformation grids were initially proposed by D'Arcy Thompson in 1917 (see Thompson 1942), and reintroduced in morphometrics during the 1980s (Bookstein 1989; Marcus et al. 1996). The thin-plate spline interpolating function compares geometries according to the minimum energy required to bend a hypothetical surface transforming one shape into another. The interpolating function (and the spatial deformation of the grids) is not dependent upon superimposition procedures, being related only with the landmark spatial distribution of two comparable configurations. The energy required to bend the grids (or *bending energy*, a mathematical value related to the model of an infinite and infinitely thin plate) is proportional to the intensity of localized deformations, and it can be used to quantify differences which are independent upon simple “stretching” and “shearing” of the geometry. Thus, the bending en-

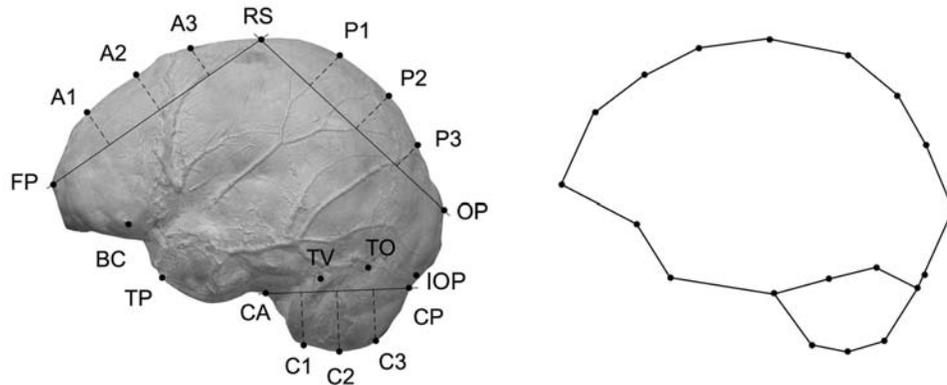


Figure 2. The configuration used in the present analysis (left) and the relative wireframe (right) are based on 19 two-dimensional landmarks sampled in lateral view on the endocranial casts (endocranial casts): FP: frontal pole; A1–A3: orthogonal projections at 25%, 50%, and 75% of the chord between the frontal pole and the Rolandic scissure; RS: Rolandic scissure; P1–P3: orthogonal projections at 25%, 50%, and 75% of the chord between the Rolandic scissure and the occipital pole; OP: occipital pole; IOP: internal occipital protuberance; TO: temporo-occipital lower boundary; TV: temporal valley; CA: cerebellum, anterior edge; PC: cerebellum, posterior edge; C1–C3: orthogonal projections at 25%, 50%, and 75% of the chord between the anterior and posterior cerebellar edges; TP: temporal pole; BC: Broca's cap.

ergy quantifies the degree of localized changes in the spatial deformation. Grids and bending energy are generally used to generate shape variables available to multivariate statistics and to visualize shape changes along multivariate vectors (see Zelditch et al. 2004 for further details). However, this is also a useful tool for providing simple pairwise comparisons between specimens or means, allowing for computation of the interpolated deformation in the surface between the landmarks, which is not included in the geometrical model (Bruner 2006). If the landmarks used are representative of the whole morphology (that is, if there are no peculiar differences in features not included in the models), grids represent the most complete visualisation tool to synthesize the whole pattern of morphological differences.

The geometrical model used here also includes landmarks localized onto profiles and obtained by orthogonal projection from chords based on other points. These landmarks are called *semi-landmarks*, because of their dependence upon other landmarks and consequently reduced degrees of freedom (Gunz et al. 2004). In general, semi-landmarks are more useful when their position can shift along the profile according to a given criterion of optimization, like the minimization of the bending energy or of the Procrustes distances (*sliding landmarks*; Zelditch et al. 2004). Nevertheless, this approach is more robust in a multivariate context, when the outline is characterized by a large number of points or when the profile undergoes large flexions (Perez et al., 2006). Therefore, the sliding approach was not used here and semi-landmarks were considered as ordinary landmarks. The pairwise superimpositions between the two specimens were performed to provide a size-adjusted comparison between the two endocranial profiles, and to produce outputs comparable with the published analyses.

Superimpositions and visualisations were computed using MORPHEUS ET AL. (Slice 2000).

EUCLIDEAN DISTANCE MATRIX ANALYSIS

Superimposition procedures are very effective to perform standardized comparisons and generate shape variables available to multivariate ordination procedures. However, each form adjustment (attempting to isolate the shape component) requires *a priori* assumptions and subjective choices that may confound the results or introduce noise in the database. The main debate concerns the actual differences between form and shape, and the question of whether there can be a formal separation between these two components (Richtsmeier et al. 2002; Rohlf 2003).

Euclidean Distance Matrix Analysis is a coordinate-free method independent upon the position of the specimens in space. Each form, whether of a single specimen or of a mean figure, is represented by a matrix showing all the distances between each pair of landmarks. Forms are then compared by producing a Form Difference Matrix in which each interlandmark value is represented by the ratio between the interlandmark distance of the first form and the interlandmark distance of the second (Richtsmeier et al. 1992). The relationship between each pair of landmarks is expressed as the percentage difference between the two compared forms. The Form Difference Matrix can be explored using univariate, bivariate, and multivariate statistics. A ratio of one means there are no actual differences for a given interlandmark distance. A ratio other than one quantifies the percentage difference between the two chords. Similar ratios throughout the matrix suggest isometry, whereas different ratios reflect changes in form. The mean or median value of all the interlandmark differences

represents the average difference in size between the two forms, and the distribution of all the values is a function of the variation in form. This distribution can be useful to localize the most relevant changes (Cole and Richtsmeier, 1998). The diameters primarily influencing the form differences can be reported directly on images, wireframes, and thin-plate spline deformation grids (e.g., Lieberman et al. 2002), and the average differences at each landmark can be mapped to provide a synthetic view of the spatial differences (Bruner et al. 2005a). In the latter approach, the variation at each landmark can be represented by the average of all the ratios associated with all the distances from the landmarks to the other points, indicating whether the landmark is more or less “shifted away” from the rest of the configuration. This method is generally appropriate when landmarks are organized along a closed profile, as in the present case-study. Accordingly, the landmarks are shown as generally approaching or moving away from the rest of the outline, and this difference can be quantified in terms of percentage of change. These average values can be mapped on two dimensions using functions aimed at describing the changes from one point to another, interpolating the variations along the surface.

Using this approach, the differences between the Euclidean distance matrix from the endocranial configurations of La Ferrassie 1 and Vatte di Zambana were mapped using both a precise (function inverse to the power of two) and a non-precise (radial basis function through multiquadric interpolation; Carlson and Foley 1991) approach. Precise functions are forced to exactly pass through the value at each point, while non-precise functions are smoothed, and do not necessarily pass through each value. This second approach produces surfaces representing a general trend of the interpolation, and is more appropriate when data are scarce, scattered, or heterogeneously distributed. EDMA was performed using WinEDMA (Cole 2002). Maps were computed using SURFER 7.0 (Golden Software, Inc).

RESULTS

SUPERIMPOSITIONS

Figure 3 shows the superimposed configurations by using baseline registration, Procrustes analysis, and thin-plate spline deformation grids. Compared with the mean Neandertal endocranial profile according to the same hemispher-

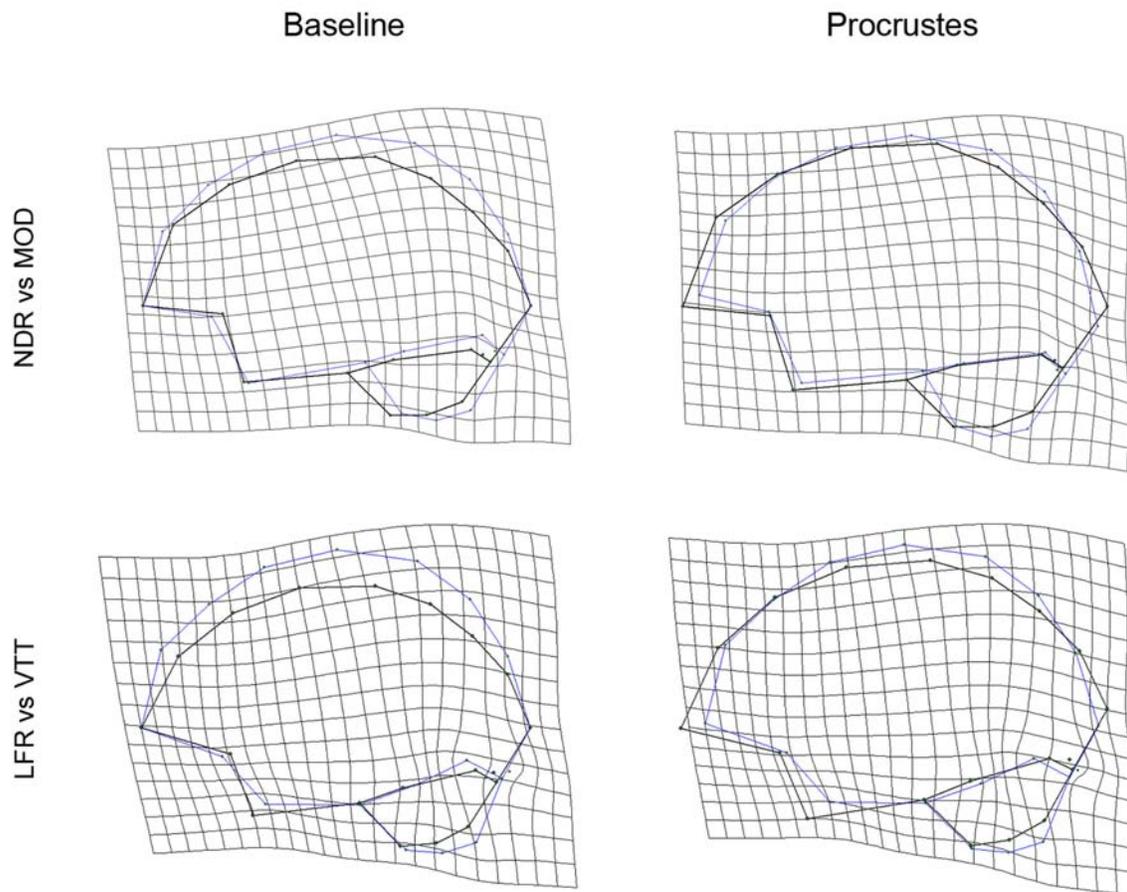


Figure 3. The mean Neandertal (black links) and modern (blue links) configurations (top), and the La Ferrassie (black links) and Vatte di Zambana (blue links) configurations (bottom) are compared by using a fronto-occipital baseline (left) and the Procrustes superimposition (right). The first approach compares the profile according to the same hemispheric length, the second through minimizing the residuals at each landmark. Deformation grids are based on the thin-plate spline interpolating function, and are not dependent upon the registration procedure.

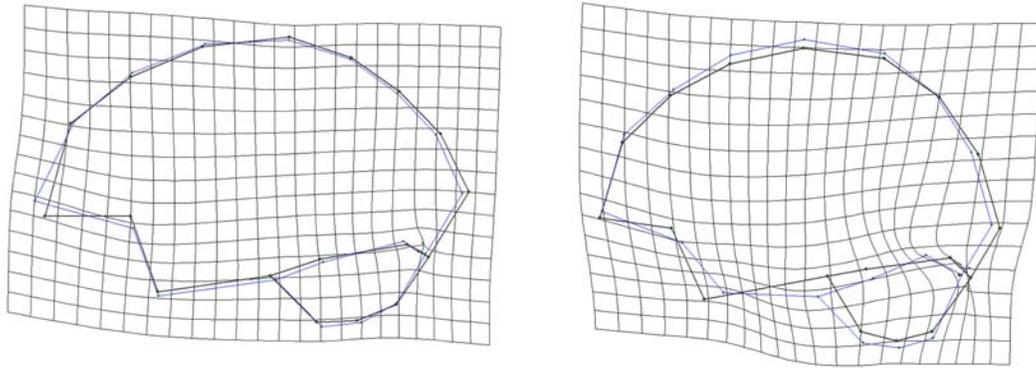


Figure 4. The endocranial shape from La Ferrassie is compared with the Neandertal mean (left), and the endocranial shape from Vatte di Zambana is compared with the modern mean, through Procrustes superimposition (mean shapes in black, individual endocranials in blue). The endocranial shape from La Ferrassie is very close to the Neandertal average, while the endocranial shape from Vatte di Zambana shows more individual traits when compared with the modern group mean profile.

ic length, the mean modern endocranial shape displays the bulging of the upper outline, more evident at the parietal area. The cerebellum profile is more posterior, and enlarged backward. Minimizing the shape differences by using the Procrustes superimposition, the relative vault enlargement is definitely distributed at the parietal profile, while the frontal and temporal areas display a relative reduction and antero-posterior shortening. The occipital profile is flattened, and the posterior cerebellar surface is relatively enlarged. The thin-plate spline grids stress the dilation at the parietal and cerebellar areas and the compression at the temporal pole.

The comparison between Vatte di Zambana (anatomically modern human) and La Ferrassie 1 (Neandertal) showed that the ratio between the centroid size of the modern specimen and that of the Neandertal is 1.03, indicating that the former is 3% larger than the latter. Relative to the fronto-occipital axis, the modern endocranial shape shows a relevant vertical enlargement of the fronto-parietal outline, more marked at the parietal area. The temporal pole is shorter, and the cerebellar profile undergoes a vertical posterior stretching. Using the Procrustes superimposition, the endocranial shape of the modern specimen is relatively shorter, and the vertical brain enlargement is particularly loaded behind the Rolandic area. The deformation grids computed by the thin-plate spline interpolating function suggest bulging of the posterior volumes (parietal, occipital, and cerebellar areas), flexion of the frontal surface, and compression at the temporal pole. The geometrical expansion is particularly evident at the upper parietal outline, and the anteriorward rotation of the cerebellar poles stresses the convolution (globularisation) of the whole endocranial structure.

Considering the pairwise comparison between means and the comparison between the two representative individuals, only minor differences can be detected. In particular, the pattern observed between the two different groups

is slightly magnified in the comparison of the two complete endocranials. If we compare the two complete specimens with their respective group means using the Procrustes superimposition (and excluding them from the computation of the reference), it is possible to describe their individual features, providing general information on how representative they are (Figure 4). The endocranial shape from La Ferrassie is very close to the Neandertal mean, showing just a vertical flexion of the frontal pole. The endocranial shape from Vatte di Zambana diverges more from the modern average, showing (apart from a slightly more bulging upper profile) shorter temporal lobes and a larger cerebellar profile.

EUCLIDEAN DISTANCE MATRIX ANALYSIS

A Form Difference Matrix was computed comparing Vatte di Zambana (numerator) and La Ferrassie 1 (denominator). The overall grand mean (\pm standard deviation) is 1.05 ± 0.15 , indicating that the modern configuration is on average 5% larger than the Neandertal one. For each landmark, the distribution of the differences between the two specimens was computed using both parametric and non-parametric estimators. The points showing a larger median ratio (that is, points included in diameters generally longer in the modern endocranial shape) are those landmarks approaching the parietal surface (P1, P2), the internal occipital protuberance (IOP), and the postero-inferior cerebellar landmark (C3). Conversely, the frontal pole and the temporal pole show the smallest values, thus they are closer to the rest of the profile when compared with the Neandertal figure (Figure 5). The higher median values are displayed by the parietal points (with diameters 14% and 12% longer respectively in the modern endocranials) and by the area of the Rolandic scissure (13%). These landmarks can be evidenced directly on the thin-plate spline deformation grid, synthesizing the form (EDMA) and shape (TPS) information (Figure 6a). An-

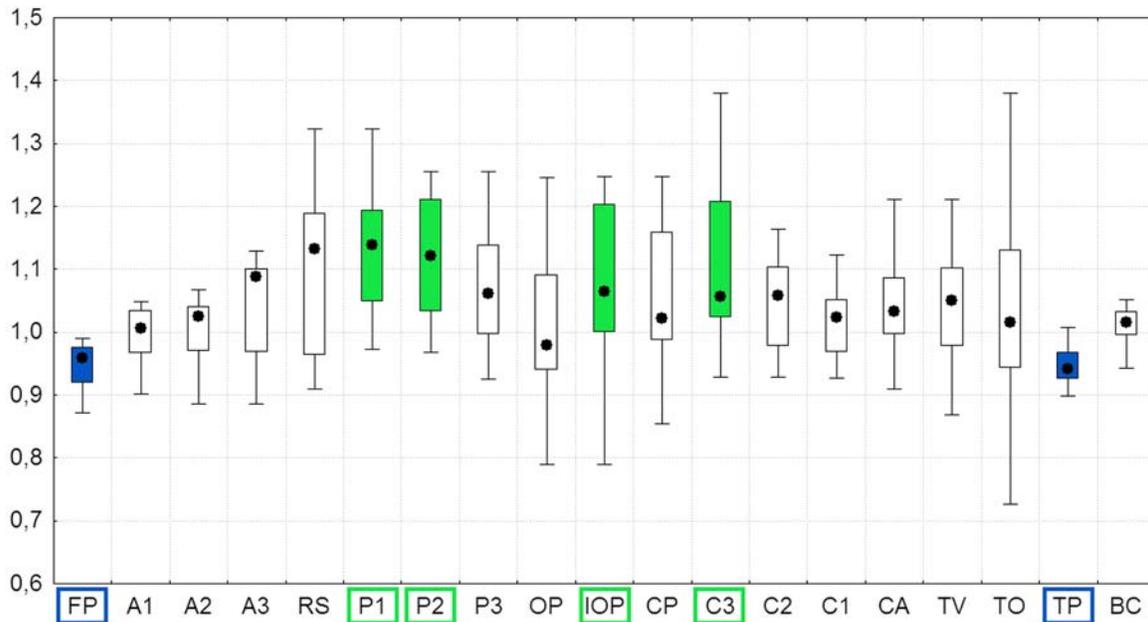


Figure 5. Median, quartiles, and range (outliers excluded), for each landmark according to the actual increase/decrease of the ratio between modern and Neandertal configuration for all the interlandmark distances. A median value of one means no change in average (the point shows the same mean distance from all the others in the two specimens). A different median value means that the point is more (>1) or less (<1) far from all the other points in the modern specimen than in the Neandertal one. Increasing range means that the points are closer to some areas but farther from others in the modern configuration. The landmarks showing the interquartile distribution higher (in green) and lower (in blue) than the value for isometry (ratio =1) are evidenced. These are the points that most of the others move away from or conversely approach the profile, respectively, when the modern form is compared with the Neandertal one.

other visualisation approach can associate the deformation grid with those diameters displaying larger/smaller values in the inter-landmark distances comparison (Figure 6b). In the modern endocranial casts the main actual differences are associated with antero-posterior shortening of the lower hemispheric diameters (temporo-occipital) and the upper frontal surfaces, and vertical lengthening of the posterior volumes (parieto-cerebellar).

Finally, the mean values at each landmark can be mapped by using both precise (Figure 7a) and non-precise (Figure 7b) approaches, as described above. These functions take into account the mean values at each point using a chromatic scale to mark areas of average longer/shorter diameters, then using these values to interpolate the differences along the surface of the geometrical model. This approach is able to synthesize the information of the Form Difference Map, showing the enlargement of the parietal and cerebellar outline (by an average of 8% in the modern specimen), and the antero-posterior gradient of compression at the frontal and temporal poles (by an average of 11% in the modern specimen).

DISCUSSION

THE COMPARISON OF THE ENDOCRANIAL LATERAL PROFILE

Human paleoneurology is based largely on fragmented information, due to the paucity of the fossil record and

scarce statistical power, the deformation of fossil remains because of their taphonomic history, and the difficulties in reconstructing accurate endocranial casts. Furthermore, as Weidenreich pointed out at the beginning of the first paleoneurological inferences (1948), this morphological information may be scarcely useful to support cognitive and neural hypotheses. However, the anatomy of the endocranium in extinct species is the only direct evidence of brain evolution, and indirect evidence of physiological processes like those involved in the vascular system and metabolism. Taking into account the endocranial differences already described between modern humans and Neandertals using geometric morphometrics and superimpositions (Bruner 2004a; Bruner et al. 2003) this paper aims to compare two complete specimens by applying a coordinate-free method accounting for the overall form component.

Different registration procedures (baseline and Procrustes) standardize the geometry according to a given criterion, which must be properly evaluated in terms of biological meaning. The baseline procedure compares two forms relative to a functional or structural axis. In the present case-study, the fronto-occipital baseline represents the major hemispheric axis, accounting for the neurocranial length and antero-posterior brain development. In contrast, the Procrustes registration minimizes the residuals between the two shapes, distributing the differences through all the landmarks. This approach may produce misleading results if differences are actually localized only onto specific points (the so-called “Pinocchio effect;” see von Cramon-Taub-

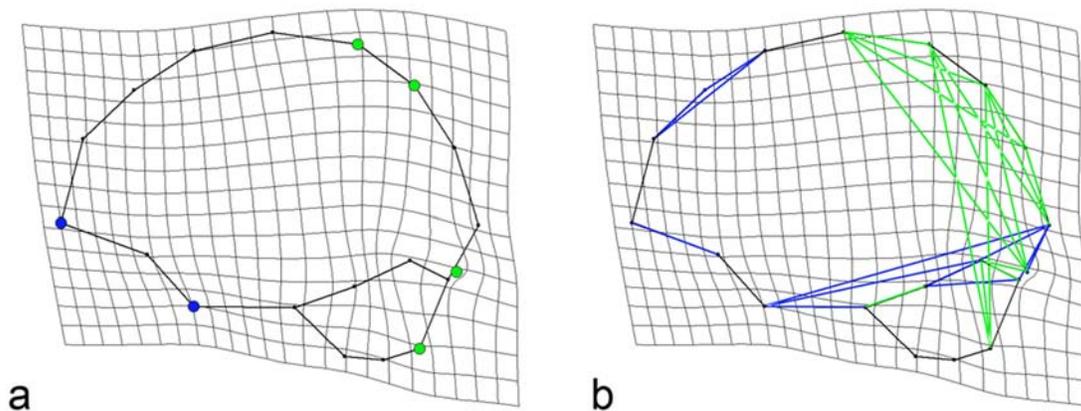


Figure 6. The landmarks evidenced in Figure 5 (blue: approaching the profile; green: shifting from the profile when the modern specimen is compared with the Neandertal figure) are reported on the thin-plate spline pairwise comparison from the modern to the Neandertal specimen (a), together with the interlandmark distances greater than (green) or smaller than (blue) one standard deviation from the mean difference. Accordingly, green diameters mean “lengthening;” blue diameters mean “shortening.”

adell et al. 2007; Zelditch et al. 2004), but it is nevertheless a useful way to decompose the overall variation according to a common assumption. Generally, the application of different superimposition procedures is useful to perform surveys on single specimens or on geometrical models to be further used in multivariate statistics (Bruner 2006).

The present comparison of the Neandertal and modern endocranial profiles using averaged data and superimposition procedures reinforces already described differences in the proportion and relative position between these two human groups, with modern humans displaying the bulging of the parietal profile and a geometrical compression between the anterior and middle cranial fossae.

The analysis of two complete endocasts (La Ferrassie and Vatte di Zambana) further allows for comparison of the size-adjusted geometry with the actual endocranial form. Size differences between the two specimens are smaller using the centroid size (3%) than using the mean interlandmarks distances (5%). Both metrics are size indices, and

should be not confused with the cranial capacity or with other volumetric variables. The higher mean size of the modern configuration compared to the Neandertal representative is not in contrast to the larger cranial capacity of the latter. This is because the Neandertal endocrania generally are more enlarged laterally and more platycephalic. In contrast, the “size” of the lateral profile is larger in modern humans because of the vertical development of their neurocranium.

In these pairwise comparisons, the superimposition approach once more indicates that the shape differences between the modern and the Neandertal specimens are related to the bulging of the parietal and posterior cerebellar areas in the former, associated with the antero-posterior compression of the prefrontal and temporal volumes. The Neandertal endocast (La Ferrassie 1) is representative of the mean Neandertal configuration. The modern specimen (Vatte di Zambana) shows more individual differences in traits when compared with the modern average, related to

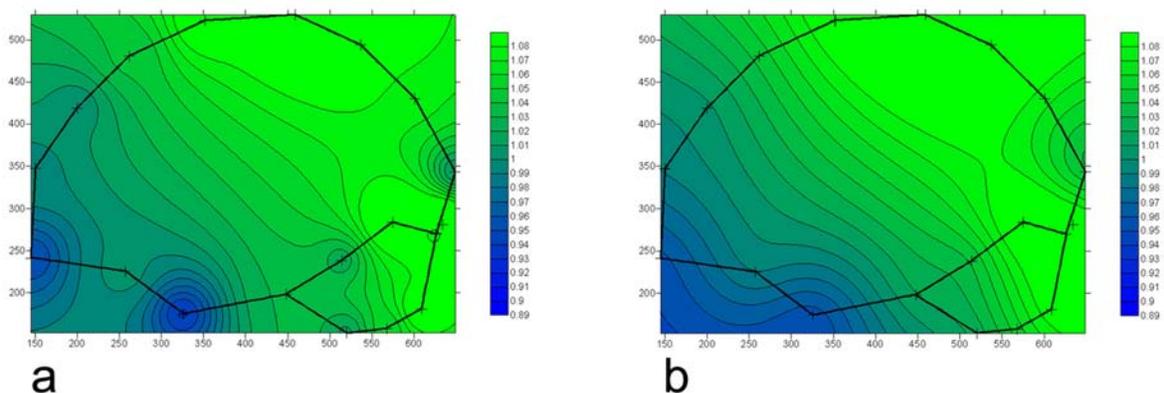


Figure 7. The average values from each landmark are mapped on the wireframe, filling the inter-landmarks space with a precise (a) and a non-precise (b) interpolating function. Green means average lengthening in the modern specimen, blue means average shortening in the modern specimen (scales are shown in terms of ratio; 1 = no changes).

shorter temporals and larger cerebellar profiles. Nonetheless, these individual features are similar to those described in the comparison between the two different groups, just slightly magnified. That is, for these characters, this specimen can be defined as “hyper-modern.” The upper profile, although more bulging than the average modern shape, is still very similar to the mean reference. This consideration suggests that the comparison between the individual endocasts is sufficiently representative of the comparison between group means, although the pattern expressed in the temporo-cerebellar areas may be exaggerated. These two endocasts have been selected because they are well-preserved. It is also important to note that the differences evidenced by the superimposition procedures are the same as those already described using three- and two-dimensional multivariate approaches on larger samples using less complete configurations (Bruner 2004a; Bruner et al. 2003). Thus, all the major differences described in the Neandertal versus modern human shape comparison, including bulging of the parietal outline, increase of the cerebellar height, and antero-posterior shortening of the anterior poles, can be confirmed using these two complete specimens.

As mentioned before, the superimposition procedures show relative changes, and the expansion of a given area may be the result of its enlargement, or conversely, the reduction of the surrounding structures. In this study, nevertheless, the parietal changes, the shortening of the prefrontal and temporal areas, and the general convolution of the endocranial volume were all shown in the Euclidean Distance Matrix Analysis. This latter approach is based on the direct comparison of the raw diameters, reflecting the actual form differences between configurations. So, what has been described in terms of shape differences can also be seen in form variation. The parietal outline enlarges not only relatively to the overall brain shape, but also in terms of absolute metrics. Accordingly, the parietal bulging is not a relative consequence of variation exerted on other endocranial regions, but is a true anatomical change in the underlying cortical structures. At the same time, the prefrontal and temporal compressions are related to antero-posterior shortening of the endocranial base. The concordance between the size and form approaches prevents bias that could be associated with the assumptions following from the shape composition from one side, or the more limited resolution of the interlandmark analysis from the other. Together, they concur to synthesize the global changes between the two geometric models, and thereby reciprocally support the final interpretation.

STRUCTURE AND FUNCTION IN HUMAN BRAIN EVOLUTION

The neurocranium and the brain represent a functional morphogenetic and evolutionary unit, and the endocranial bones match the shape and the traits of the cortical structures (Bruner 2007; Richtsmeier et al. 2006). The geometrical information synthesized in the present paper can be useful in developing a hypothetical basic framework to delineate

major trends in the evolution of the modern brain morphology (Figure 8).

The anterior cranial fossa can be used as a proxy to understand the morphology of the prefrontal cortical areas, and the middle cranial fossa includes parts of the temporal lobes. When compared with Neandertals, modern humans display a “geometrical compression” at the anterior and middle cranial fossae, undergoing both a relative and absolute shortening. The structures included between these endocranial volumes (cranial base and upper face) must undergo a similar pattern, and it is plausible that the biomechanical and functional constraints of these areas are responsible for the final fronto-temporal brain morphology, more than actual neural rearrangements. Concerning the prefrontal areas, their midsagittal profile has not changed remarkably in the last 500,000 years, when compared with the large variation of the ectocranial counterpart (frontal squama, browridge; Bookstein et al. 1999). Undoubtedly many phylogenetic differences involve their spatial relationship with underlying facial structures, more than the evolution of the prefrontal neural functions (Bruner and Manzi 2005; Bruner 2007). These differences may have been related also to the large variation of the frontal sinuses described in the extinct human taxa (Prossinger et al. 2003; Seidler et al. 1997), whose role still is largely debated and ignored. Primarily due to the structural continuity with relevant functional regions like the browridge, the orbits, and the ethmoid complex, the cranial functional matrix may have strongly constrained the vertical development of the prefrontal areas that underwent mostly a latero-lateral enlargement during human evolution (Bruner 2004a). Regarding the middle fossa, it has been largely shown that their morphology definitely is influenced by the mandibular system (Bastir et al. 2004; Bastir and Rosas 2005). This relationship strongly limits the anatomical evolutionary plasticity of the temporal lobes.

Taking into account the larger independence of cranial base morphogenesis from brain growth and development (Enlow 1990), and the multifactorial network involved in its structural and functional dynamics (Lieberman et al. 2000; McCarthy 2001; Strait 2001), the antero-posterior morphological flattening of the prefrontal and temporal areas described in this comparison should be related to physical rearrangements of the skull architecture (hard tissues) more than to actual and direct changes of the neural cortical surfaces (soft tissues). That is, it is likely that the brain’s cortical changes in these areas reflect passive morphological adjustments to the structural and functional network of the surrounding elements (including also constraints exerted by the non-cortical brain structures; Strait 1999).

In contrast, the development of the parietal areas may be regarded as an evolutionary, species-specific change of anatomically modern humans, in which the parietal cortical pressure induces neurocranial changes (Moss and Young 1960) as shown endocranially (Bruner 2004a) or on the ectocranial outline (Bruner et al. 2004). That is, changes at the upper endocranial volumes are more probably the result of cortical evolution (soft tissue) and consequent neurocranial

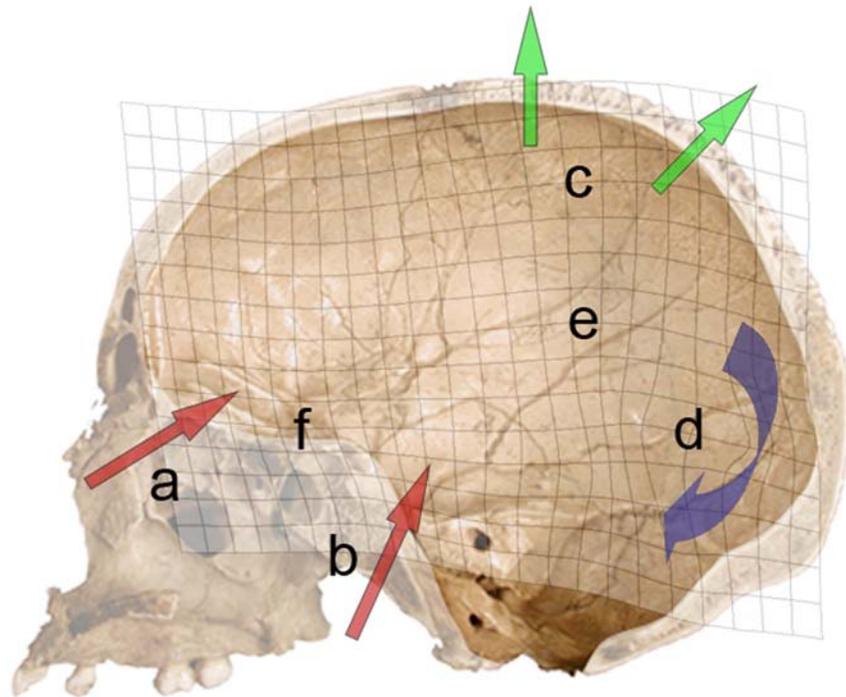


Figure 8. The shape and form differences of the modern human endocranium compared with the extinct human groups can be used to suggest some general structural hypotheses. The compression and shortening at the anterior and middle fossae can be related to structural constraints associated with the morphogenesis of the facial components (a) and to the evolutionary dynamics of the mandible and cranial base (b). In contrast, the enlargement of the parietal areas (c) can represent a definite morphological adaptation (forced by selection for physical arrangements or cognitive functions), perhaps inducing the convolution of the brain architecture (leading to globularity, d) and changes in the pattern of imprints of the middle meningeal vessels (e). Apart from these major changes detectable from the lateral endocranial profile, both Neandertals and modern humans display a definite widening of the frontal lobes (f).

adjustment (hard tissues). This is particularly interesting when the role of single genes is demonstrated to potentially affect the complexity of large cortical surfaces (Rakic 2004). It is also worth noting that Neandertals, showing a general flattening at the parietal outline when compared with small-brained human species, display supernumerary ossicles at the occipito-parietal boundary suggesting possible morphogenetic constraints leading to loss of balance during growth and development (Bruner 2004a).

Considering ectocranial morphology, it has been hypothesized that the differences at the parietal and occipital bones between modern humans and Neandertals may be the result of a shared structural pattern, with a continuum from bulging parietals and flat occipital in the former to the opposite figure in the latter (Gunz and Harvati 2006). This is particularly intriguing, taking into account the possible interplay between the evolution of the brain and braincase (Richtsmeier et al. 2006). Evolutionary inferences deal with the ranges and patterns of variation and covariation, within and between taxa. Even if phylogenetic independence is an historical product that is not necessarily associated with morphological evidence or potential to interbreed (Bruner 2004b), the comparison of such parameters is necessary to provide support for the phylogenetic hypotheses. The continuity of variation between these two morphological

extremes raises the question of whether or not the parietal morphology in *Homo sapiens* evolved in a discrete way, and if it can be regarded as a true evolutionary novelty. That is, are the differences between Neandertals and modern humans the result of a shared model of variation? If some discontinuity in the general structure is evidenced, the endocranial geometry in *Homo sapiens* must be regarded as a proper and “revolutionary” adaptation, whether or not it evolved at the beginning of the modern human lineage or later. Otherwise, if discrete structural and functional changes in the organization levels are not supported, there will be evidence that relevant evolutionary changes can take place using unexpressed potentiality of pre-existing morphological relationships. These issues can only be resolved with the study of a much larger sample, and the development of a robust model for brain versus braincase dynamics.

SOME FINAL REMARKS ON FUNCTIONAL CRANIOLOGY

Once differences and relationships within the neurocranial system are localized using geometrical modelling, the network of causes and consequences must be investigated in terms of structural and functional integration. For instance, the parietal changes can be interpreted as cognitive adapta-

tions inducing architectural changes, or conversely as structural neural rearrangements providing new cognitive functions. To understand the intimate connection between the structural and functional roles of neurons, it is necessary to consider that the physical organization of the cerebral units also can be interpreted in terms of internal tissue and cytoarchitectonic forces (Hilgetag and Barbas 2005; Toro and Burnod 2005; Van Essen 1997), or as the vector resolution of cortical versus non-cortical morphogenesis (Strait 1999). In such a structural network, inferences about cognitive changes must be absolutely integrated in a way that acknowledges the influence of these variations on the organization of the brain itself. That is, the hypotheses about endocranial evolution and morphogenesis must necessarily take into account the modularity and the connectivity within the neural system (Klingenberg 2002; Richtsmeier et al. 2006; Sporns et al. 2004).

Apart from the endocranial neural components, other structural and functional information also may be rescued from the vascular system, in the form of traces left on the endocranial surface. The meningeal vessels display a marked morphogenetic plasticity, influenced by the neurocranial variables (O'Laughlin 1996). At the same time, vessels and nerves largely share a physiological and molecular environment (Eichmann et al. 2005). Except for the differences described in the neurocranial geometry, modern humans also display a unique pattern of middle meningeal vessels (Bruner et al. 2005b). These vascular traces are more reticulated, mostly at the parietal surface. This can be related to an increased complexity of the vascular network, or to an increase in the traces left by the soft tissues because of changes in the physical environment (i.e., pressures on the endocranial table exerted by the meningeal layers). In either case, some structural/functional changes at the parietal areas can be detected in the modern endocast also by using the meningeal imprints as "fossilized physiological processes," and further information on the neurocranial dynamics and evolution will be available by improving our knowledge on this topic.

Future efforts could be devoted profitably to a better representation of endocranial morphology. Conventional homologous landmarks are not easily localized on the smooth geometrical surface of the endocast, this process requires personal experience and a certain amount of extrapolation. Results must be confirmed by independent studies but, most of all, a large improvement will undoubtedly result from the application of surface analysis on specific anatomical areas (Gunz et al. 2004). Apart from the paleoneurological implications discussed, this paper also aims to show some simple tools of geometrical modelling in paleoanthropology. Techniques such as geometric morphometrics and EDMA are generally used to analyze patterns of covariance within morphological systems, generating multivariate spaces available to statistics, ordination of data, and inferential analyses. Of course, this is the principal target of these computational approaches, representing the most important advance in morphometrics. But simpler approaches such as the application of different superimpo-

sition procedures, and the direct comparison of means or specimens, should not always be regarded as simply preliminary to the successive multivariate steps. Superimpositions and pairwise comparisons also can be quick and easy tools to explore the geometrical properties of morphological systems, which of course need to be further considered within the more general framework of the covariance patterns. If this can be generally true for any morphological survey, it is probably more important in paleoanthropology, where the paucity and fragmentary nature of the fossil specimens often hamper robust statistical approaches. Although the information on single fossils is limited when a more general framework (i.e., multivariate statistics) is not available, such information should not be discarded. In this framework, geometrical models, superimposition procedures, and mapping of functions are tools available to describe the morphological properties of fossil remains in a more objective and analytical way than mere visual inspection and description of differences.

SUMMARY

The shape comparison of the endocast from extinct and modern humans suggested that the latter evolved a peculiar morphology of the parietal outline, associated with a process of cerebral convolution leading to their neurocranial globularity. Because shape is just a conceptual component of the overall form, in this paper two complete endocranial casts from one modern and one Neandertal specimen are compared without size-adjustments or registration procedures. The two specimens are sufficiently representative of their respective group morphology, with the modern one being even more "modernized" than the group average figure for some basicranial traits. The Euclidean distance matrix analysis confirms a definite enlargement of the parietal lateral outline in the modern endocast, and a certain flattening and reduction of the frontal and temporal districts. While the former process can be hypothesized to be a direct evolutionary change, the latter can be better interpreted as the result of structural constraints associated with the splanchnocranial and basicranial dynamics. Paleoneurology deals with very scarce information, biased by the small number of complete or well preserved fossil endocasts, the currently very limited knowledge of the endocranial morphogenetic relationship, and the imperfect relationship between morphological variation and neural/cognitive functions. Nonetheless, the application of simple geometrical approaches and visualization tools allows one to go a bit further with respect to vague and subjective descriptions.

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REFERENCES

- Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H.B.M., and Zilles, K. 1999. Broca's region revisited: cytoarchitecture and intersubject variability. *Journal of Comparative Neurology* 412, 319–341.
- Bookstein, F.L. 1989. Principal warps: thin-plate spline and the decomposition of deformations. *I.E.E.E. Transaction on Pattern Analysis and Machine Intelligence* 11, 567–585.
- Bookstein, F.L. 1991. *Morphometric tools for landmark data*. Cambridge University Press, Cambridge.
- Bookstein, F., Schafer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., Weber, G.W., Arsuaga, J.L., Slice, D.E., Rohlf, F.J., Recheis, W., Mariam, A.J., and Marcus, L.F. 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. *Anatomical Record The New Anatomist* 257, 217–224.
- Bastir, M. and Rosas, A. 2005. Hierarchical nature of morphological integration and modularity in the human posterior face. *American Journal of Physical Anthropology* 128, 26–34.
- Bastir, M. and Rosas, A. 2006. Correlated variation between the lateral basicranium and the face: a geometric morphometric study in different human groups. *Arc. Oral Biol.* 51, 814–824.
- Bastir, M., Rosas, A., and Kuroe, K. 2004. Petrosal orientation and mandibular ramus breadth: evidence for an integrated petroso-mandibular developmental unit. *American Journal of Physical Anthropology* 123, 340–350.
- Bruner, E. 2003. Fossil traces of the human thought: paleoneurology and the evolution of the genus *Homo*. *Riv. Antropol.* 81, 29–56.
- Bruner, E. 2004a. Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. *Journal of Human Evolution* 47, 279–303.
- Bruner, E. 2004b. Evolution, actuality and species concept: a need for a paleontological tool. *Human Evolution* 19, 93–112.
- Bruner, E. 2006. From Verheyen to Bookstein: history of colobids and superimpositions. *Journal of Anthropological Sciences* 84, 147–160.
- Bruner, E. 2007. Cranial shape and size variation in human evolution: structural and functional perspectives. *Child's Nervous System* 23, 1357–1365.
- Bruner, E. and Manzi, G. 2005. CT-based description and phyletic evaluation of the archaic human calvarium from Ceprano, Italy. *Anatomical Record* 285A, 643–658.
- Bruner, E., Manzi, G., and Arsuaga, J.L. 2003. Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineages. *Proceedings of the National Academy of Sciences USA* 100, 15335–15340.
- Bruner, E., Saracino, B., Passarello, P., Ricci, F., Tafuri, M., and Manzi, G. 2004. Midsagittal cranial shape variation in the genus *Homo* by geometric morphometrics. *Collegium Antropologicum* 28, 99–112.
- Bruner, E., Costantini, D., Fanfani, A., and dell'Omo, G. 2005a. Morphological variation and sexual dimorphism of the cephalic scales in *Lacerta bilineata*. *Acta Zoologica* 86, 245–254.
- Bruner, E., Mantini, S., Perna, A., Maffei, C., and Manzi, G. 2005b. Fractal dimension of the middle meningeal vessels: variation and evolution in *Homo erectus*, Neanderthals, and modern humans. *European Journal of Morphology* 42, 217–224.
- Carlson, R.E. and Foley, T.A. 1991. The parameter R2 in multiquadric interpolation. *Comp. Math. Applic.* 21, 29–42.
- Cole, T.M., III 2002. *WinEDMA: Software for Euclidean Distance Matrix Analysis, Version 1.0.1 beta*, University of Missouri, Kansas City School of Medicine, Kansas City.
- Cole, T. M., III and Richtsmeier, J. T. 1998. A simple method for visualization of influential landmarks when using Euclidean Distance Matrix Analysis. *American Journal of Physical Anthropology* 107, 273–283.
- Corrain, C., Graziati, G., and Leonardi, P. 1976. La sepoltura epipaleolitica nel riparo di Vatte di Zambana (Trento). *Preistoria Alpina* 12, 175–212.
- Enlow, D.H. 1990. *Facial Growth*. WB Saunders Company, Philadelphia.
- Falk, D. 1987. Hominid paleoneurology. *Annual Review of Anthropology* 16, 13–30.
- Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Review* 41, 587–640.
- Grimaud-Hervé, D. 1997. *L'évolution de l'enchéphale chez Homo erectus et Homo sapiens*. CNRS Editions, Paris.
- Gunz, P. and Harvati, K. 2007. The Neanderthal "chignon": variation, integration, and homology. *Journal of Human Evolution* 52, 262–274.
- Gunz, P., Mitteroecker, P., and Bookstein, F.L. 2004. Semi-landmarks in three dimensions. In (D.E. Slice, ed.) *Modern morphometrics in physical anthropology*, pp 73–98. Kluwer Academic – Plenum Publishers: New York.
- Eichmann, A., Le Noble, F., Autiero, M., and Carmeliet, P. 2005. Guidance of vascular and neural network formation. *Current Opinion in Neurobiology* 15, 108–115.
- Hilgetag, C.C. and Barbas, H. 2005. Developmental mechanics of the primate cerebral cortex. *Anatomy and Embryology* 210, 411–417.
- Holloway, R.L. 1978. The relevance of endocasts for studying primate brain evolution. In (C.R. Noback, ed.), *Sensory Systems of Primates*, pp. 181–200. Plenum Press, New York.
- Holloway, R.L. 1981. Volumetric and asymmetry determinations on recent hominid endocasts: Spy I and Spy II, Djebel Ihroud I, and the Salé *Homo erectus* specimen. With some notes on Neandertal brain size. *American Journal of Physical Anthropology* 55, 385–393.
- Holloway, R.L., Broadfield, D.C., and Yuan, M.S. 2004. Brain endocasts: The paleoneurological evidence. *The*

- Human fossil record (Vol III)*. Wiley-Liss, Hoboken, New Jersey.
- Kimbel, W.H. 1984. Variation in the pattern of cranial venous sinuses and hominid phylogeny. *American Journal of Physical Anthropology* 63, 243–263.
- Klingenberg, C.P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews of the Cambridge Philosophical Society* 73, 79–123.
- Klingenberg, C.P. 2002. Morphometrics and the role of the phenotype in studies of the evolution of developmental mechanisms. *Gene* 287, 3–10.
- Lieberman, D.E., Ross, C.F., and Ravosa, M.J. 2000. The primate cranial base: ontogeny, function, and integration. *Yearbook of Physical Anthropology* 43, 117–169.
- Lieberman, D.E., McBratney, B.M., and Krovitz, G. 2002. The evolution and development of cranial form in *Homo sapiens*. *Proceedings of the National Academy of Sciences USA* 99, 1134–9.
- Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P., and Slice, D.E. 1996. *Advances in morphometrics*. Plenum Press, New York.
- McCarthy, R.C. 2001. Anthropoid cranial base architecture and scaling relationships. *Journal of Human Evolution* 40, 41–66.
- Moss, M.L. and Young, R.W. 1960. A functional approach to craniology. *American Journal of Physical Anthropology* 18, 281–292.
- Newell, R.R., Constandse-Westermann, T.S., and Meiklejohn, C. 1979. The skeletal remains of mesolithic man in western Europe: an evaluative catalogue. *Journal of Human Evolution* 8.
- O’Laughlin, V. 1996. Comparative endocranial vascular changes due to cranosynostosis and artificial cranial deformation. *American Journal of Physical Anthropology* 101, 369–385.
- Peña-Melian, A. 2000. Development of human brain. *Human Evolution* 15, 99–112.
- Perez, S.I., Bernal, V., and Gonzalez, P.N. 2006. Differences between sliding semi-landmark method in geometric morphometrics, with an application to human craniofacial and dental variation. *Journal of Anatomy* 208, 769–784.
- Ponce de León, M.S. and Zollikofer, C.P.E. 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature* 412, 534–538.
- Prossinger, H., Seidler, H., Wicke, L., Weaver, D., Recheis, W., Stringer, C., and Muller, G.B. 2003. Electronic removal of encrustation inside the Steinheim cranium reveals paranasal sinus features and deformations, and provides a revised endocranial volume estimate. *Anatomical Record The New Anatomist* 273B, 132–142.
- Rakic, P. 2004. Genetic control of cortical convolutions. *Science* 303, 1983–1984.
- Richtsmeier, J.T., Cheverud, J.M., and Lele, S. 1992. Advances in anthropological morphometrics. *Annual Review of Anthropology* 21, 283–305.
- Richtsmeier, J.T., DeLeon, V.B., and Lele, S.R. 2002. The promise of geometric morphometrics. *Yearbook of Physical Anthropology* 45, 63–91.
- Richtsmeier, J.T., Aldridge, K., de Leon, V.B., Panchal, J., Kane, A.A., Marsh, J.L., Yan, P., and Cole, T.M. 2006. Phenotypic integration of neurocranium and brain. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution* 306B, 360–378.
- Rohlf, F.J. 1998. *tpsDig 1.2*. Ecology and Evolution, SUNY at Stony Brook, NY.
- Rohlf, F.J. 2003. Bias and error in estimates of mean shape in geometric morphometrics. *Journal of Human Evolution* 44, 665–683.
- Rohlf, F.J. and Marcus, L.F. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8, 129–132.
- Ross, C., Henneberg, M., Ravosa, M.J., and Richard, S. 2004. Curvilinear geometric and phylogenetic modeling of basicranial flexion: is it adaptive is it constrained? *Journal of Human Evolution* 46, 185–213.
- Schwartz, J.H. and Tattersall, I. 2002. *The Human Fossil Record*. Volume One. Wiley-Liss, New York.
- Seidler, H., Falk, D., Stringer, C., Wilfing, H., Muller, G.B., Zur Nedden, D., Weber, G.W., Reicheis, W., and Arsuaga, J.L. 1997. A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: implications for future studies of Middle Pleistocene hominid evolution. *Journal of Human Evolution* 33, 691–703.
- Shea, B.T. 1992. Developmental perspective on size change and allometry in evolution. *Evolutionary Anthropology* 1, 125–134.
- Slice, D.E. 2000. *Morpheus et al.* Ecology and Evolution, SUNY at Stony Brook, NY.
- Slice, D.E. 2004. *Modern morphometrics in physical anthropology*. Kluwer Academic – Plenum Publishers, New York.
- Sporns, O., Chialvo, D.R., Kaiser, M., and Hilgetag, C.C. 2004. Organization, development and function of complex brain networks. *Trends in Cognitive Neurosciences* 8, 418–425.
- Strait, D.S. 1999. The scaling of basicranial flexion and length. *Journal of Human Evolution* 37, 701–719.
- Strait, D.S. 2001. Integration, phylogeny, and the hominid cranial base. *American Journal of Physical Anthropology* 114, 273–297.
- Tattersall, I. and Schwartz, J.H. 2006. The distinctiveness and systematic context of *Homo neanderthalensis*. In (K. Harvati, K. and T. Harrison, eds.) *Neanderthals revisited: new approaches and perspectives*, pp. 9–22. Springer, New York.
- Toro, R. and Burnod, Y. 2005. A morphogenetic model for the development of cortical convolutions. *Cerebral Cortex* 15, 1900–1913.
- Van Essen, D.C. 1997. A tension-based theory of morphogenesis and compact wiring in the central nervous system. *Nature* 385, 313–318.
- Von Cramon-Taubadell, N., Frazier, B.C., and Mirazon-Lahr, M. 2007. The problem of assessing landmark error in geometric morphometrics: theory, methods, and modifications. *American Journal of Physical Anthropology*

134, 24–35.

Weidenreich, F. 1948. The human brain in the light of its phylogenetic development. *Scientific Monthly* 67, 103–109.

Zelditch, M.L., Swidersky, D.L., Sheets, H.D., and Fink, W.L. 2004. *Geometric morphometrics for biologists*. Elsevier, San Diego.

Zollikofer, C.P.E., and Ponce de León, M.S. 2005. *Virtual reconstruction: a primer in computer-assisted paleontology and biomedicine*. Wiley-Liss, New York.

Zollikofer, C.P.E., Ponce de León, M.S., and Martin, R.D. 1998. Computer assisted paleoanthropology. *Evolutionary Anthropology* 6, 41–54.