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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies in Honor of Ralph L. Holloway

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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.
Upper left: A modern human brain.
Upper right: Ralph measuring landmarks on an endocast ca. 1976.
Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).
Lower left: Ralph with an endocast of the Flores “hobbit” cranium.

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CHAPTER 6

THE EVOLUTION OF THE PARIETAL CORTICAL AREAS IN THE HUMAN GENUS: BETWEEN STRUCTURE AND COGNITION

EMILIANO BRUNER

ABSTRACT

Recently, the renewed interest for concepts such as morphological integration, functional craniology, and the analysis of covariance patterns has spawned a change in paleoneurology that has to be interpreted as the study of the evolutionary variations in the relationships between brain and braincase. The parietal lobes have been hypothesised to have undergone important morphological changes in early hominid evolution. Nonetheless, the role of these areas within the evolution of the human genus has been rather neglected because of their alleged lack of association with "higher" cognitive functions. Some allometric constraints could have affected the changes in the parietal surfaces in non-modern humans. On the other hand, modern humans display a non-allometric change in the shape of these areas which are bulging at their midsagittal profile. Such changes raise questions on the relationship between structural rearrangements and cognitive adaptations. Focusing on the parietal surface, it seems that the upper lobule and the intraparietal sulcus might be directly involved in the evolution of the modern human brain morphology. This is particularly intriguing considering the many cortico-cortical reciprocal connections between these areas and the prefrontal ones. Most of all, they are directly involved in integrating inner and outer information to reproduce a subjective "virtual inner reality" necessary not only to organise movements, but also to make decisions, to perform thought experiments, and to handle the interaction between the self and such imagined space physically and conceptually. Whether or not the origin of the modern human lineage coincided with the origin of a modern human brain is still to be investigated.

FUNCTIONAL CRANIOLOGY AND ENDOCRANIAL MORPHOGENESIS

Morphogenesis is a complex process in which a poligenic and pleiotropic network linking genes and characters is expressed within a given functional and structural framework. Structure (both in terms of biomechanical and developmental constraints) and function generate the unique combination of forces and physical relationships in which a specific genetic background produces a given phenotype. Following the principles of functional craniology (Moss and Young, 1960), morphogenesis is the result of two components, namely growth (changes in size) and development (changes in shape). The correct balance between these two components leads to the normal phenotype, while an improper redirection of the growth forces leads to subpathological or pathological dysmorphologies associated with osteoblast/osteoclast induction or timing and rate of sutural activity (Moss, 1959). Neurocranial vault morphogenesis is mainly related to brain growth for the size changes and to the connective meningeal tensors for the shape variation. The principal connective tensors are the falx cerebri and the tentorium cerebelli, exerting forces on five main points: crista galli, small wings of the sphenoid, and petrous pyramids.

Of course, such simplification is useful to produce hypotheses to investigate these processes, but subtle variables can play an important role in the general structural management. For example, although brain growth and pressure are the principal forces leading to the modelling of the vault, strains are integrated by responses and inductions through the dura mater and the vascular system by mechanical transduction or by biochemical signalling (Henderson et al., 2004). Figure 1 synthesises the main components and relationships within the brain versus braincase matrix.

The embryological context is also rather heterogeneous, with some components originating from the mesoderm and others from the neural crests, some through direct ossification, others with cartilaginous precursors (Jiang et al., 2002; Morriss-Key & Wilkie, 2005). For example, both frontals and parietals are dermal bones, but the former is ectoderm-derived while the latter has mesodermic contributions. Such differences make morphogenesis a polyphasic process with many possible steps in which small changes could exert large phenotypic variations during evolution.

The reticulated system of forces, functions, constraints, and genes, underlying the actual morphological variability through ontogeny and phylogeny has convinced biologists to move from the study of single traits and isolated characters to the analysis of the patterns of covariance, i.e. *morphological integration* (Olson and Miller, 1958; Cheverud, 1996). Phenotype is hence interpreted not as a sum of features, but as a combination of relationships between features. This is clearly true for the human skull (Bookstein et al., 2003; Bruner, 2007) as well as for the relationship between the neurocranium and brain (Richtsmeier et al.; 2006; Bruner and Ripani, 2008).

Paleoneurology, as the study of the nervous system in extinct species (Holloway, 1978; Falk, 1987; Bruner, 2003a), deals exactly with this last issue: the interpretation of the endocranial morphology as the result of the integration between its structural (developmental, biomechanical) and functional (neural, cognitive) components.

NEUROCRANIAL SHAPE VARIATION AND PARIETAL LOBES

Despite the never-ending struggle on the lunate sulcus debate (see Holloway et al., 2003), we can currently state that if any differences between Australopithecinae and the other apes did occur, it was at the posterior parietal boundary. Holloway very early recognised that such differences, because associated with the visuo-spatial integration and recognition of the outer reality, could provide a relevant rearrangement of the ecological and social organisation of the early Hominids (see Holloway, 1995). And, through a pioneering stereoplotting surface analysis, the parietal areas were hypothesised to be a crucial source of morphological variation in both Hominoids and Hominids (Holloway, 1981).

The parietal lobes have been generally described as "associative cortex" by virtue of the many connections (neural and anatomical) with the other districts. Excluding the postcentral gyrus, mainly involved in the

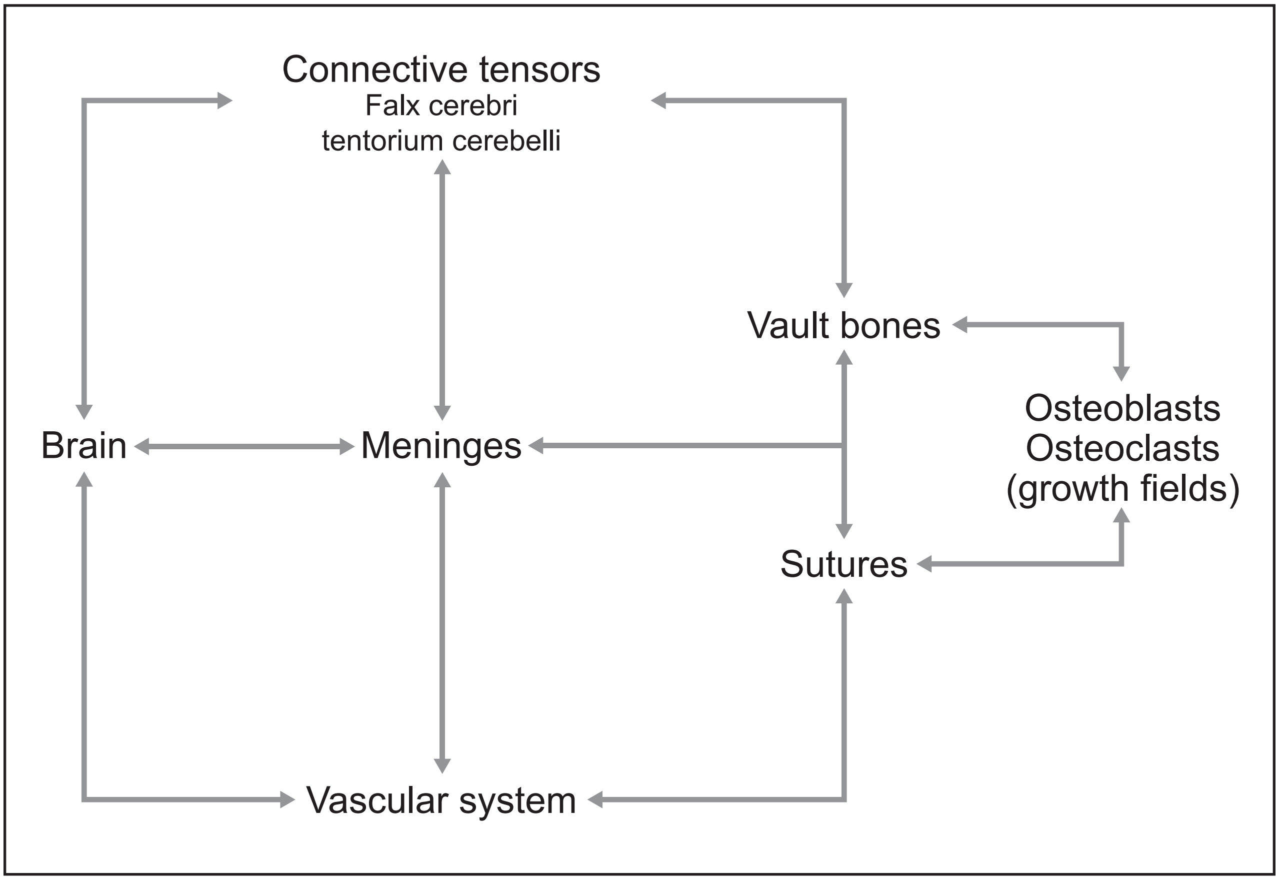

Figure 1. Paleoneurology deals with the morphogenetic relationship between neurocranium and brain, associated with functional and structural responses between hard and soft tissues resulting from the interaction between genetic programs (cellular differentiation and activation) and developmental forces (strains, biomechanics).

somato-sensorial system, the posterior parietal areas are basically divided into upper and lower parts, separated by the intraparietal sulcus (Eidelberg and Galaburda, 1984). The upper lobule almost gradually fades into the occipital one, both in terms of gross anatomy and cytoarchitecture. The lower lobule is part of the Wernicke area, including the over-studied angular and supramarginal gyri. The intraparietal sulcus is a rather peculiar structure, providing a large part of the parietal surface deepened into the cortical volumes, showing different cytoarchitectonic patterns, and supporting heterogeneous neural functions (e.g., Bisley and Goldberg, 2003; Choi et al., 2006). Its displays at least five different morphological patterns, showing generally (about 75% of the cases) a continuity with the postcentral sulcus (Ebeling and Steinmetz, 1995).

Considering the evolution of the human skull, its globularity has always been described as the main traits and trends associated with the encephalisation process (Lieberman et al., 2002). Actually, quantifying such variations and analysing the midsagittal cranial shape in the human genus, modern humans stand apart from the other taxa mostly by virtue of their fronto-parietal bulging (Bruner et al., 2004; Fig. 2).

Moving from the ectocranium to the endocranium, some evidence comes from simple traditional metrics. Using the main endocranial diameters (hemispheric length, frontal and maximum widths, and vault mid-height) to perform a factor analysis on a sample of 21 endocasts from the human genus (see Bruner et al., 2003 for details), the first vector is easily recognised as an allometric component, with all positive loadings, accounting for almost 90% of the total variation (Fig. 3). This is to be expected, considering the simple metrics involved and the large correlation between these diameters. It is nonetheless worth noting that the first factor is almost parallel to the hemispheric length vector. Therefore, we can assume that hemispheric length in humans is a good (and easy, and quick) proxy for encephalisation, or at least for cranial capacity. Hence, we can use these diameters both in a traditional approach as a size index, and in geometric superimpositions as a relevant baseline. Us-

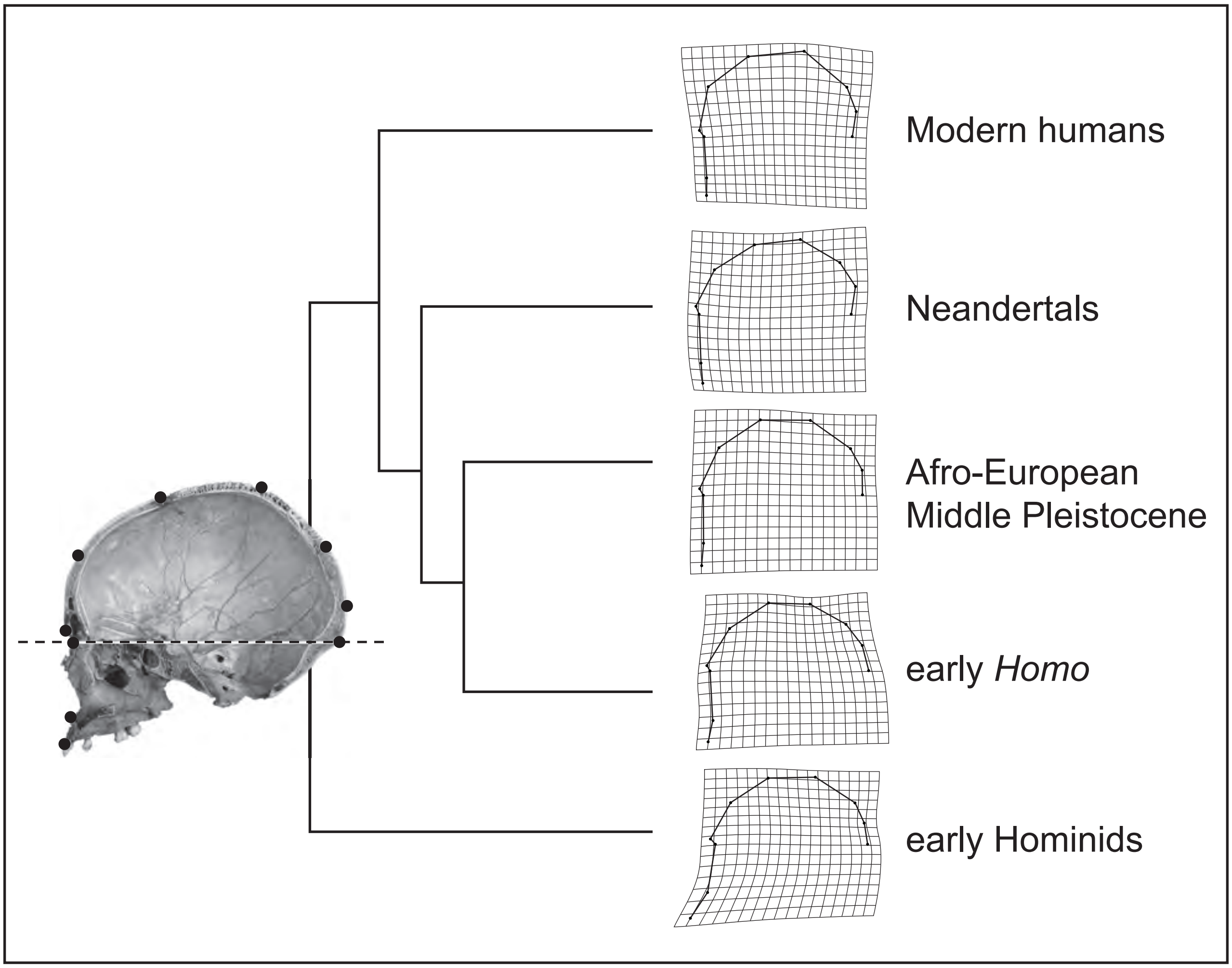

Figure 2. The ectocranial midsagittal profile largely characterises the major extinct human taxa. Apart from a general trend towards reduction of the facial block, Neandertals show a specific projection of the midface, while modern humans show a definite bulging of the parietal profile. Here, average midsagittal configurations from the main Hominid groups are compared using a nasion-inion baseline, and the thin-plate spline deformation grids. The degree of facial reduction and the parietal bulging set modern humans apart from the rest of the human morphotypes (after Bruner et al., 2004).

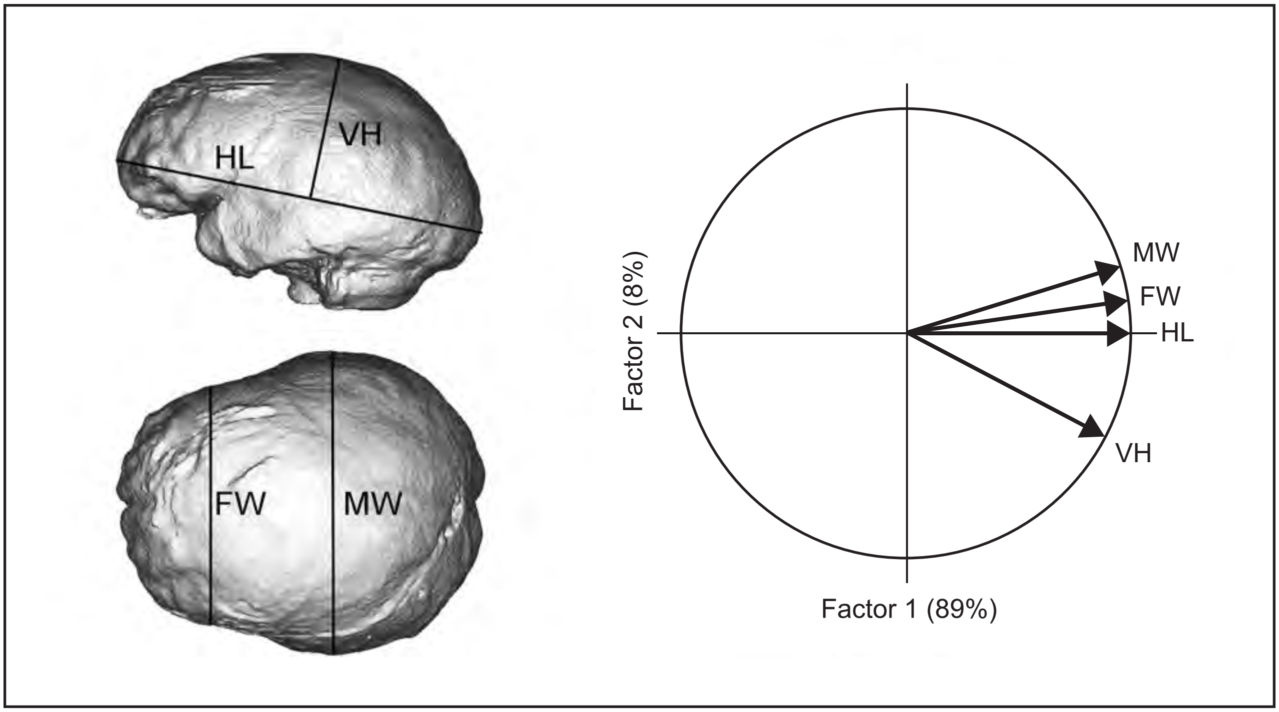

Figure 3. The main endocranial diameters can be used to perform a factor analysis in the human genus (see Bruner et al., 2003). HL: hemispheric length; VH: midvault height; MW: maximum endocranial width; FW: frontal width (at the Broca's cap). The first component is largely allometric, while the second is associated with inverse relation between height and width. Interestingly, the hemispheric length vector is parallel to the first component, i.e., among the main raw endocranial diameters the hemispheric length is a good linear proxy for brain size. The diameters are shown on the digital reconstruction of the endocast of Saccopastore 1 (Bruner and Manzi, 2008).

ing simple endocranial diameters like these, it has been described how modern humans display largest parietal length and height when compared with the *Homo* allometric trajectories (Bruner, 2004). Interestingly, encephalisation in the human genus is associated with a relative shortening of the parietal chord, with the exception of modern humans showing a discrete morphological change because of a definite enlargement of the parietal diameters (Bruner et al. 2003).

Similar results are supported and further detailed using geometrical endocranial models. Figure 4 shows the comparison between a mean modern human lateral endocranial configuration and the mean Neandertal figure, using the fronto-occipital baseline, visualised through thin-plate spline deformation grids (Bookstein, 1991), and mapping of the Euclidean distance differences on two representative specimens (Bruner, 2008a). The registration according to the same hemispheric length shows the main differences at the parietal outline, the deformation grids suggest that the main spatial changes are represented by the parietal bulging, and the Euclidean distance matrix evidences an absolute enlargement of the parieto-cerebellar diameters.

Using the Procrustes superimposition (i.e., translating, scaling, and rotating the geometric models to minimise the residual coordinate differences; Bookstein, 1991), a three dimensional comparison between average endocranial shapes in archaic humans, Neandertals, and *Homo sapiens*, shows very scanty differences between the formers, and a marked morphological change in the latter, associated with the parietal midsagittal enlargement (Bruner et al., 2003). Again, the same results were confirmed by a two-dimensional analysis of the lateral endocranial profile performed through multivariate statistics, mean shapes, and phenetic distances, suggesting a morphological gap between the modern and non-modern variations (Bruner, 2004).

These analyses were computed using homologous landmarks of the brain, which of course are difficult to recognise on the endocasts, requiring experience and a lot of caution. Nonetheless, the same results can be obtained using simple geometrical references not associated with given anatomical structures. Figure 5 shows a Procrustes comparison of the lateral profile between the Salé (archaic *Homo*, Africa, about 400 ka) and the Combe Capelle (modern human, Europe, about 25 ka) endocasts. The endocast from Salé was supposed to be a good example of basic *Homo* endocranial morphology because of the absence of specific derived traits, including the marked projection of the occipital lobes displayed by the Asian *Homo erectus* (Bruner, 2003b, 2004). Nonetheless, there is a certain disagreement on this point, and in other studies, this endocast has been hypothesised to be largely comparable with those from the Asian groups (Holloway et al., 2004). Unfortunately, the endocast shows damage exactly at the parieto-oc-

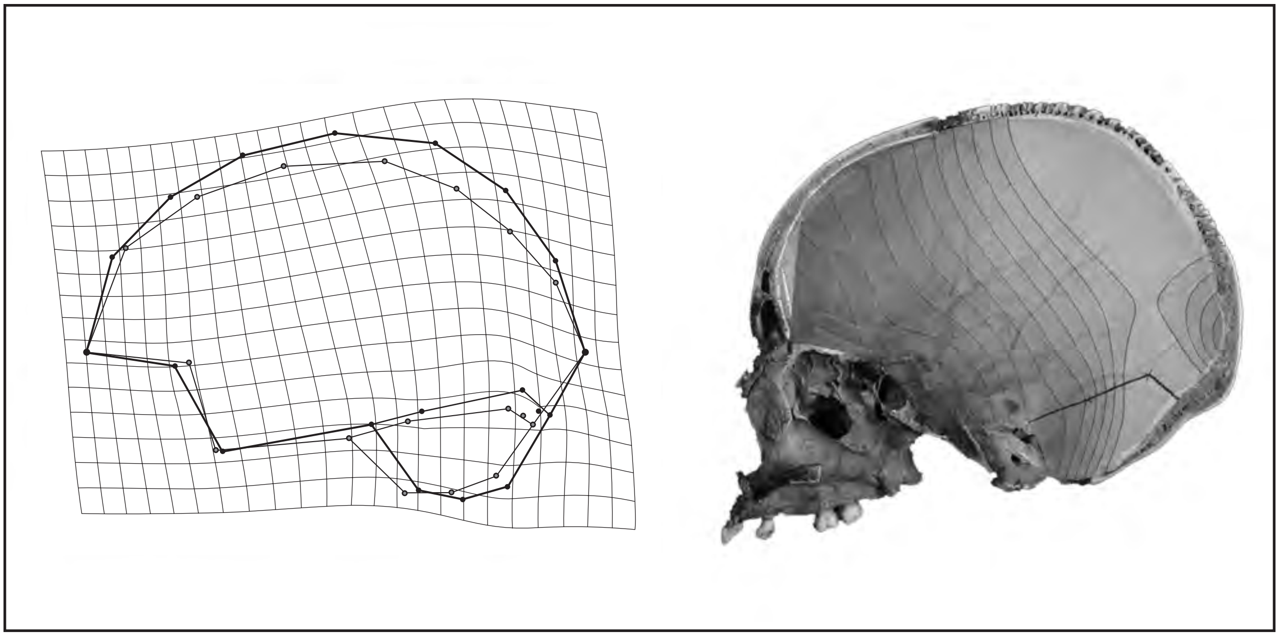

Figure 4. Geometric comparison of the lateral endocranial profile in modern humans (thick links) and Neandertals (thin links), through fronto-occipital superimposition and thin-plate spline deformation grids (left) and mapping of Euclidean distance matrix analysis (right)(see Bruner, 2008a for details). The baseline comparison is computed on mean shapes, while EDMA data are from two representative complete specimens: La Ferrassie 1 for Neandertals, and one Mesolithic Italian fossil for modern humans. The main differences can be clearly detected at the upper parietal areas, both in terms of shape (grid deformation and superimposed profile describing the parietal bulging) and form (EDMA map; dark grey: shorter diameters in the modern specimen; light grey: longer diameters in the modern specimen).

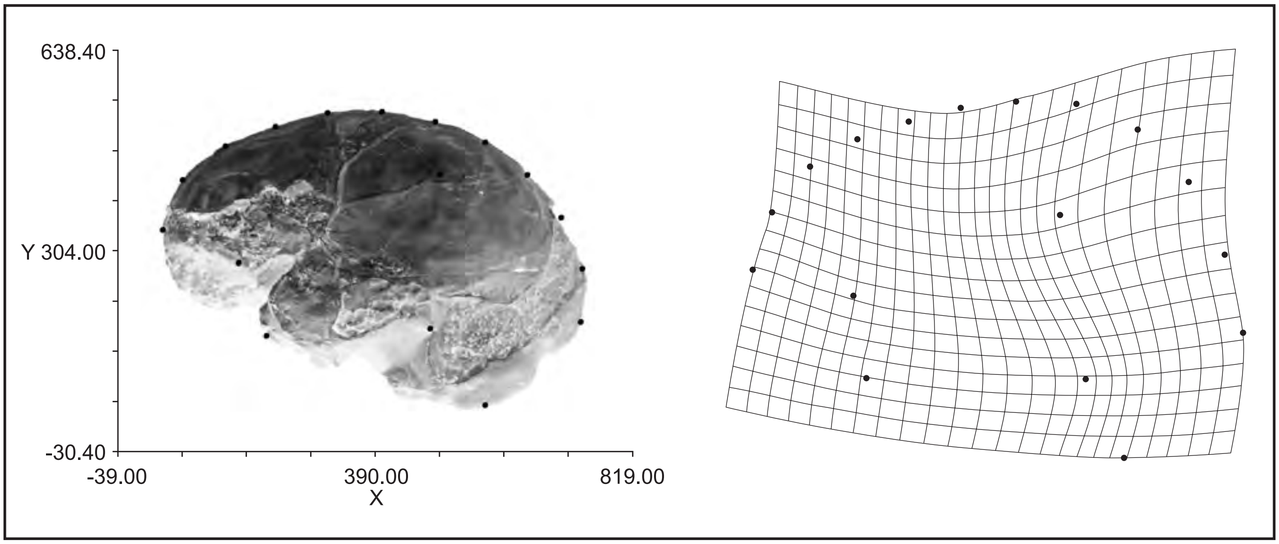

Figure 5. Using sliding landmarks to delineate the upper (fronto-occipital) endocranial profile by using a Procrustes superimposition and minimisation of the bending energy, the result is similar to the previous comparisons. The lateral endocranial configuration from the 400 ka Moroccan specimen from Salé (left) is superimposed onto the configuration of the 25 ka European specimen from Combe Capelle, showing again bulging of the upper parietal surface associated with convolution of the brain morphology. In this comparison it can be also recognised a certain lengthening of the temporal lobe. Although these areas have been hypothesised to have undergone a relative enlargement in modern humans, in this case it may be related just to a specimen-specific morphology, being not always detected in other similar comparisons between modern and non-modern endocasts. Superimposition and deformation grids are computed by using tpsSplin 1.20 (Rohlf, 2004). Both endocasts are from the University La Sapienza, Roma.

cipital boundary, hampering a robust assessment of the missed morphology. Furthermore, it must be always taken into account that paleoneurology necessarily relies on different endocranial collections, with comparisons made upon casts from different authors, different materials, and different historical periods. Interestingly this specimen also shows a certain lateral bulging of the parietal surfaces.

After lateral photography, the endocranial profile of the two specimens was modelled using some main anatomical references, and 10 sliding-landmarks between the frontal and the occipital poles (see Zelditch et al., 2004 for further details on the geometric morphometric tools). Again, after Procrustes superimposition and thin-plate spline interpolation the parietal bulging is easily recognised as the main morphological change of the endocranial geometry.

Sliding landmarks can be also used to perform a principal component analysis of the fronto-parieto-occipital profile, from the anterior insertion of the crista galli to the internal occipital protuberance (Fig. 6). The first component explains 55% of the total variance, being associated with parietal bulging and occipital flattening, characterising the modern human hemispheres. The second component separates Neandertals and archaic humans mainly because of the occipital projection of the latter.

Of course, because the brain versus neurocranium is a unique structural and functional system, changes in a given region could be associated with differences in other related districts. Accordingly, the bulging of the upper parietal areas described in modern humans can be the result of at least three different processes: 1) a change in the upper parietal neural mass; 2) a change in other neural areas influencing the position and topology of the upper parietal surface (e.g., the lower parietal structures); 3) a change of the skull organisation (e.g., the cranial base) involving rearrangement and redistribution of the endocranial volumes.

Some information to better evaluate this framework can be provided by comparing directly the parietal components by using again a landmark-based approach (Fig. 7). Superimposing the lateral parietal morphology from Salè and from a modern human endocast using the hemispheric length as a baseline, the lateral sulcus shows a similar position and orientation, and the lower parietal

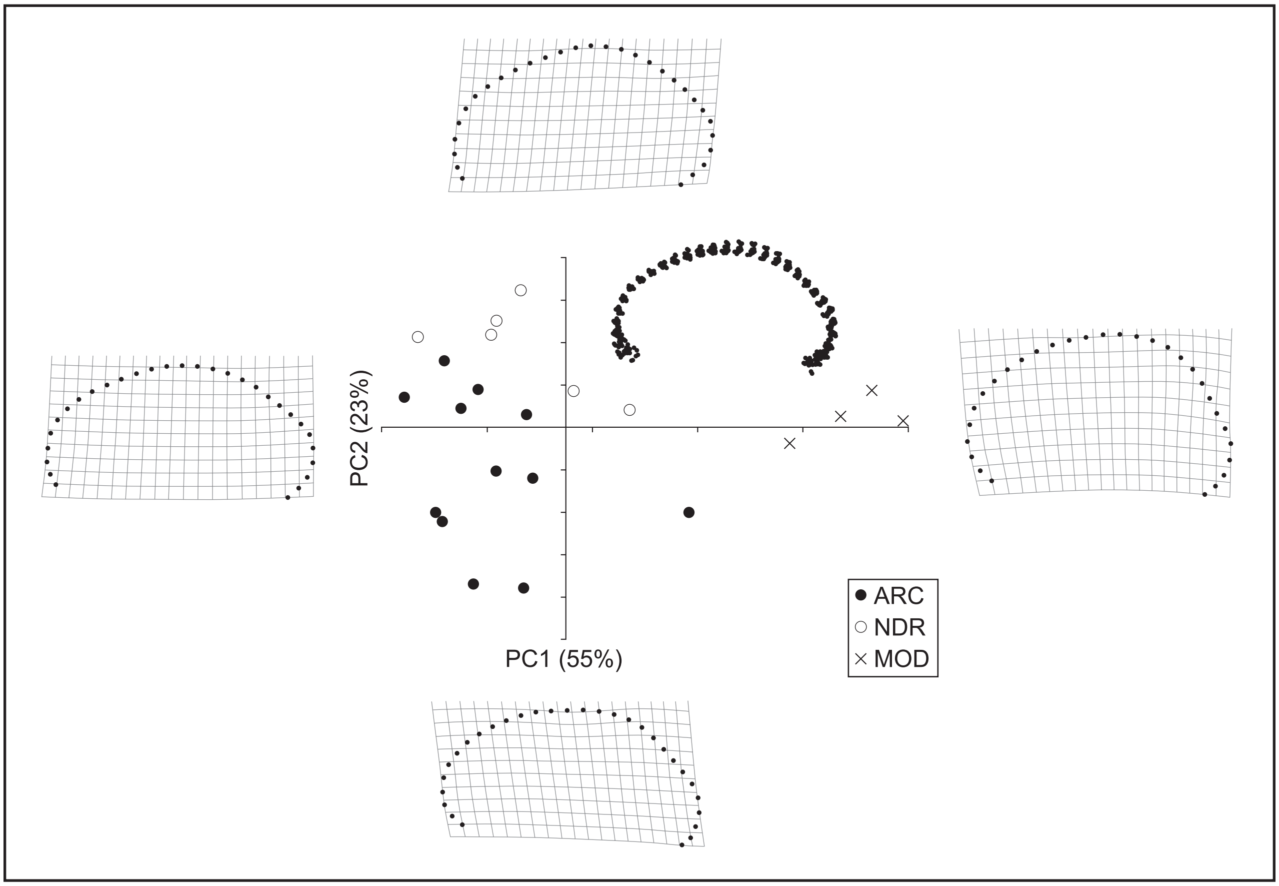

Figure 6. A Principal Component Analysis was performed using sliding landmarks and Procrustes registration to outline the fronto-parieto-occipital profile (from crista galli to internal occipital protuberance), by using tpsRelw 1.45 (Rohlf, 2007). The first component separates modern (MOD) from non-modern specimens because of the parietal bulging of the former. The second component separates (to a lesser degree) archaic humans (ARC) from Neandertals (NDR), because of the occipital projection of the former. ARC: Salé, Arago, Trinil 2, Zhoukoudien 3, Zhoukoudien 12, Sambungmacan 3; NDR: Saccopastore 1, Guattari, La Chapelle-aux-Saints; MOD: Combe Capelle, Vatte di Zambana (both hemispheres).

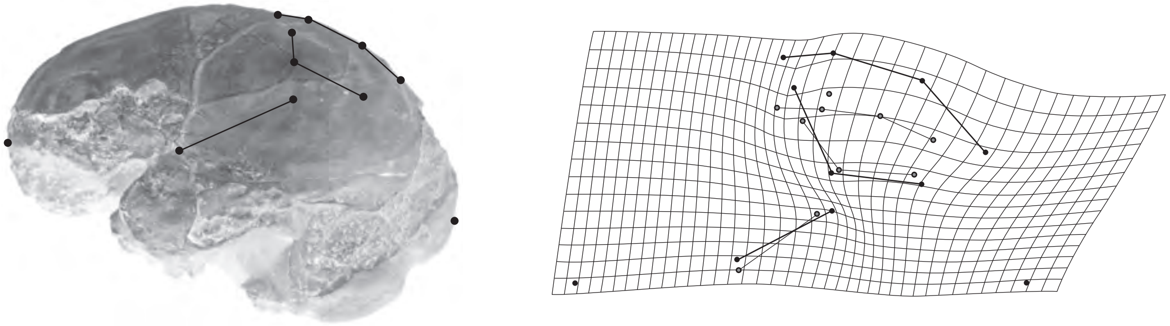

Figure 7. The parietal areas from Salé (Middle Pleistocene, North Africa) and Vatte di Zambana (Mesolithic, Italy) are compared through fronto-occipital registration and thin-plate spline deformation grids, by using Morpheus et al. (Slice, 2000). Apart from the frontal and occipital poles, the configuration includes the lower fronto-parietal boundary and the posterior edge of the lateral sulcus, the supramarginal and angular gyri, the anterior edge of the intraparietal groove, the anterior and posterior midsagittal boundaries of the parietal lobes, the midagittal projection of the postcentral sulcus, and the midpoint on the upper lobule midsagittal profile. Each configuration is the mean of five independent resampling procedures. According to the hemispheric length (wireframes) and minimum deformation (grids), the differences are clearly localised at the upper parietal volumes, enlarged in the modern specimen. The intra-parietal area seems to delineate the lower border of such expansion.

areas do not display relative enlargements. The thin-plate spline deformation grids (which are superimposition-independent and account for the minimum spatial deformation required for the geometrical fitting of the two systems of coordinates) further confirm this evidence. Once more, changes localised at the upper parietal lobule seem to be the more striking features of modern human endocranial morphology. The intra-parietal area seems to separate an area of relative expansion (upper lobule) from an area of relative compression (lower lobule), at least in lateral view.

A final indication comes from the endocranial traces of the middle meningeal vessels, as record of fossilised physiological and morphogenetic processes. The patterns of these vascular imprints show interesting differences within the human genus in its complexity, position, and general organisation (Grimaud-Hervé, 1997). Although the endocranial angiogenesis has an active role in neurocranial growth and development (Henderson et al., 2004), the vascular organisation is largely influenced by the neurocranial structural and functional environment (O'Laughlin, 1996). Using a fractal analysis, the degree of reticulation of the meningeal vessels has been demonstrated to be similar in Neandertals and archaic humans, but definitely higher in *Homo sapiens* (Bruner et al., 2005). The increasing reticulation of the middle meningeal vessels concerns the whole endocranial surface, mostly through its anterior branches, but it is particularly stressed at the parietal surface (e.g., Saban, 1982). The evolution and morphogenesis of these vessels has been largely ignored (Falk, 1993; Bruner and Sherkat, 2008). The more complex branching pattern and larger number of anastomoses detected in modern humans through endocranial imprints may be related to a more reticulated vascular system (associated with cognitive or metabolic functions), or to a larger number of traces left on the endocranial wall (associated with some structure/pressure differences). In both cases, they once more suggest that in modern humans some factors have induced changes in the brain versus braincase relationship at the parietal surfaces.

Of course, the fossil record is far from being a robust statistical sample, and there are some interesting exceptions. One of these is the European Middle Pleistocene parietal from Arago (Fig. 8a) showing no midsagittal bulging but a rather large parietal surface and branched vascular traces. Other reticulated middle meningeal traces can be described for the Neandertals from Biache-Saint-Vaast (Saban, 1979) and for some fragmented parietals from Krapina (Bruner et al., 2006).

The Evolution of the Parietal Areas in the Human Genus

According to the shape differences in the endocranial profile of the genus *Homo* and the patterns of morphological covariation associated with the human extinct variability, it has been hypothesised that some structural constraints could have characterised the evolution of the parietal areas (Bruner, 2004). Considering the non-modern variation, as the brain gets larger the longitudinal and vertical diameters of the parietal areas do not keep pace with the frontal and occipital changes. This negative allometry of the parietal profile leads to a morphological compression and flattening of the parietal areas along the encephalisation trajectories. Such relative

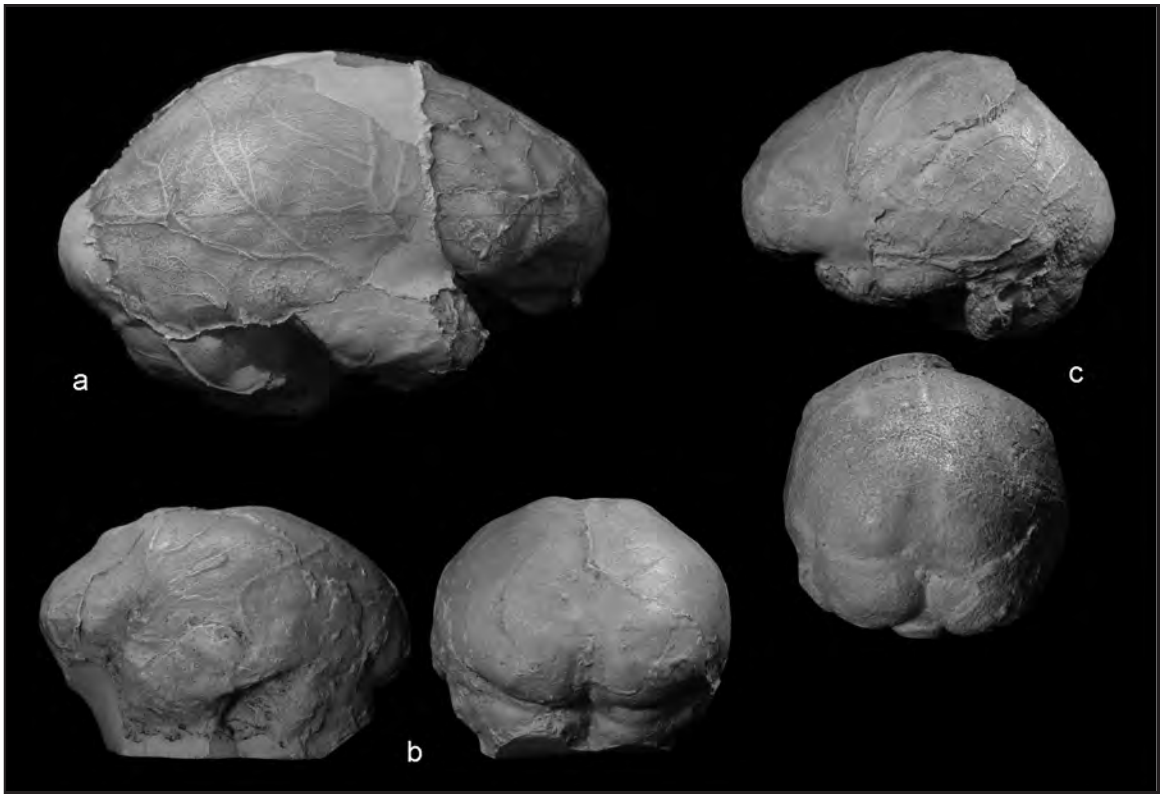

Figure 8. The reconstructed endocast from Arago at the Istituto Italiano di Paleontologia Umana, Roma (a). The parietal surface is rather large and bossed, with reticulated traces of the middle meningeal vessels. The endocast from Jebel Irhoud (b) and Skhul V (c) at the Institut de Paleontologie Humaine, Paris, in left and posterior views. The first shows a general archaic appearance, but with a certain lateral bulging of the upper parietal areas (most evident on the left side) as described for Neandertals. The second unfortunately is damaged at the anterior parietal boundaries, but the overall parietal morphology is closer to the modern human figure.

shortening and flattening of the upper parietal structures could have been induced by two factors, mostly based on the tight causal relationship between the brain and vault morphogenesis, in which the former largely determines the latter (Moss and Young, 1960; Enlow, 1990). Firstly, the position of the parietal areas between the frontal and occipital ones may suggest that, while the anterior and posterior volumes are able to arrange their topology according to the allometric changes of the hard (the cranial base) and soft (the subcortical structures) tissues, the interposed volumes are forced to vary accordingly. Secondly, being the vault shape largely associated with the strains of the meningeal tensions, it may be hypothesised that allometric and structural constraints may be related to the relationship between cortical volumes and the falx cerebri. For example, such a relationship can be easily influenced by a classical spatial interaction between structures growing at the power of three (the brain) and structures growing at the power of two (the falx).

Neandertals were the most encephalised non-modern human group, showing a sort of vault upward “bending” possibly related to this allometric pattern. Interestingly, Neandertals often display supernumerary ossicles at the parieto-occipital boundary, revealing a sort of “morphological instability” of those areas (Sergi, 1934, 1948). Such hypostotic traits, even when sub-pathological, suggest a lack of morphogenetic balance during ontogeny (Manzi et al., 1996), revealing some possible evolutionary limits, i.e we can assume that at the parieto-occipital boundary Neandertals could have been characterised by a loss of balance between size (growth) and shape (developments) changes during ontongeny. This is not particularly surprising, the basic organisation of their neurocranial system having evolved at the end of the Pliocene for brains of 600-700 cubic centimetres.

Considering this hypothesis about the non-modern endocranial variation of the human genus, the modern configuration can be interpreted in two ways. First, the parietal rearrangement in *Homo sapiens* could have been a structural solution to the allometric endocranial constraints. Of course, such a solution could have revealed some interesting cognitive involvements. Alternatively, the cognitive changes associated with the upper parietal areas could have been the selective force leading to the morphological changes, which secondarily could have led to the structural solution to trespass the allometric constraints.

The Neandertal lineage displayed a “Neandertal brain” from 100-120 ka, as suggested by the morphology of the Saccopastore (Bruner and Manzi, 2008) and possibly Krapina (Bruner et al., 2007) endocasts. Nonetheless, they reached a “classic” morphology around 50-60 ka.

However, the modern endocranial organisation is supposed to have evolved at least around 100 ka. The skull from Jebel Irhoud (Morocco, about 150 ka), although showing a plesiomorph neurocranial morphology, displays a modern-like overall profile (Bruner et al., 2004). The endocast (Fig. 8b - see Holloway, 1981) shows a non-modern morphology (Bruner et al., 2003). More interestingly, the parietal morphology displays a Neandertal-like lateral expansion leading to the *en bombe* profile in posterior view (Bruner, 2003b; but see Grimaud-Hervé, 2005). The endocast from Skhul V (Near East, around 120 ka), supposed to be a full anatomically modern human, shows the modern-like parietal bulging but not so stressed like in the Upper Pleistocene European fossil record. Unfortunately, some damage at the mid-parietal surface hampers a reliable assessment of the endocranial upper morphology (Fig. 8c).

The first modern humans shared the Mousterian lithic assemblage with the Neandertals. Also, the cognitive evidence of higher level processing capability ("enhanced working memory"; see Wynn and Coolidge, 2003, 2004, 2006; Coolidge and Wynn, 2005) are definitely recognisable much after the first appearance of the modern fossil record. All this incomplete evidence lead us to question whether or not the origin of the modern human lineage coincided with the origin of the modern human brain. This issue is particularly intriguing, and it will represent the most interesting topic in paleoneurology in the next years.

Of course, even if these morphological changes are actually related to the enlargement of the upper parietal cortical areas, the exact nature of such differences must be further investigated, being possibly related to an increased number of neurons, or increased number of connections, or even increased glial component (for example, to support metabolism). On the other hand, this anatomical change can be surely investigated in terms of functional craniology and morphological integration, including considerations on the overall cranial architecture. For example, the modern neurocranial globularity was hypothesised to be a consequence of changes at the temporal and frontal poles (Lieberman et al., 2002). Now, in the evolution of the human genus, the frontal lobes display only some allometric variations (Semendeferi et al., 1997: Rilling, 2006), mainly related to lateral enlargement (Bruner, 2004), and without any relevant changes of the midsagittal profile (Bookstein et al., 1999). Concerning the temporal lobes, although they could show some derived traits mostly related to the lateral morphology (Bastir et al., 2008), their changes are mostly associated with structural and functional constraints related to the biomechanical association of the middle fossa with the underlying mandibular structures (Bastir et al., 2004a, 2004b). Therefore, both the frontal and temporal areas seem hardly related to the neurocranial globularity described for the modern human populations. On the other hand, the parietal enlargement should be carefully considered when the general geometric convolution of the modern brain is acknowledged, associated with forward shifting of the cerebellar and temporal lobes, cranial base flexion, and closure of the interposed spaces (Sylvian valley at the lesser wings of the sphenoid and temporal valley at the petrous pyramids).

Interestingly, the occipital and parietal bones have been hypothesised to be part of a single integrated unit with modern humans and Neandertals being the extremes of a continuous structural trajectory, characterised respectively by bulging occipital and flat parietals, and bulging parietals and flat occipital (Gunz & Harvati, 2007). This information raises two relevant questions: 1) whether the modern human transition has been discrete or more gradual; 2) whether the modern human transition has been based on an actual morphological reorganisation or simply on the variation of pre-existing relationships. Of course, these questions can be only investigated after increasing the fossil record from North Africa, East Africa, and Levant, associated with the second half of the Middle Pleistocene.

Clearly, neontological studies are also needed to move further on these topics, being the current knowledge on the endocranial morphogenesis rather fragmented and heterogeneous.

A large amount of MRI brain studies suggest that the temporal lobes are the only areas in modern humans showing a definite exceeding volume when the allometric pattern of the non-human primates is taken into account (Rilling & Insel, 1999; Semendeferi & Damasio, 2000; Rilling & Seligman, 2002; Rilling, 2006). As already mentioned, a forward shifting of the anterior temporal areas in modern humans has been also described relatively to other extinct human species (Bastir et al., 2008). Unfortunately, mostly because of the blurred boundaries between the parietal and occipital lobes, no volumetric comparisons are currently available for the parietal areas alone. Clearly, it must be assessed whether or not the parietal volume in the modern human brain fits the expected allometric value for primates. I suspect that even these areas could show a positive departure from the allometric trajectory of the primates brain organisation, in its volumetric component or considering the surface/volume relationship.

Other information comes directly from the neurogenetic process of the modern cortical areas. During the brain ontogeny the upper parietal areas reach maturation very early compared with other structures (Gogtay et al., 2004). Considering the common statement that early maturing structures are the most primitive, or the upper parietal cortical areas are not so derived, or the statement is quite misleading! On the other hand, there is evidence that single gene changes can promote/demote the growth of large cortical surfaces (like in polymicrogyria; see Rakic, 2004), suggesting that discrete neural evolutionary steps are at least possible. Finally, there are very interesting approaches remarking the role of neurons as biomechanical tensors in shaping the brain morphology directing the growing forces during ontogeny (Van Es-

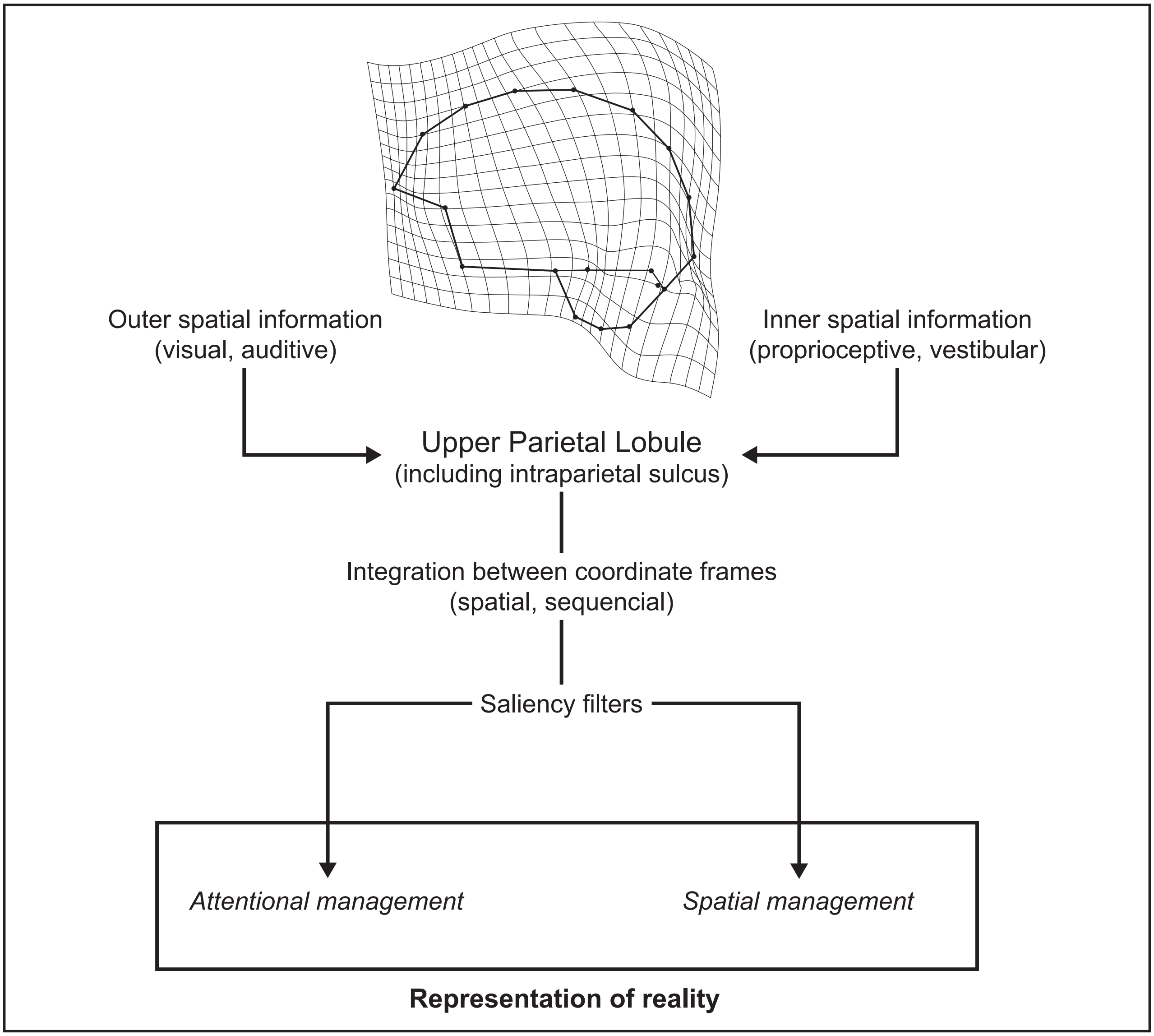

Figure 9. The upper parietal lobules (including the heterogeneous and specialised cortical surface deepened in the intraparietal sulcus) receive spatial information from the outer and inner environments, integrating the different coordinate frameworks in time and space, and producing a mental representation of both the self and the outer reality according to rules, priorities, and cues, associated with relevance, attention, and decision making processes. The upper parietal areas are the interface between mind and environment, reproducing and "handling" reality within a virtual and ordered frame.

sen, 1997; Hilgetag and Barbas, 2005; Toro and Burnod, 2005). In fact, neurons are not only part of the synaptical networks, but also physical anisotropic structures, with specific densities and strain distributions related to their biochemical composition. A change in the neural morphology or cellular organisation will influence the way size and shape changes can be directed throughout the anatomical components during the ontogenesis. Such structural frameworks linking geometry and morphogenesis are even more relevant in paleoneurology when considering that brain morphology also influences physiological variables like thermoregulation or connectivity. This last topic, being related to geometry (Sporns et al., 2002, 2004), should be further considered in paleoneurological studies. In fossils, soft tissues are gone, but the form of the endocranium still provides some information on their processes.

Naturally, the analysis of the parietal evolution has its neuropsychological and behavioural counterpart (Bruner, 2008b; Fig. 9). The studies on the parietal lobes have undergone a relevant development in the last decades (Mountcastle, 1995). The visuo-spatial integration processes associated with the upper parietal areas (including the deepened layers in the intraparietal sulcus) is aimed at receiving information from the inside (eyes, head, limbs) and outside (visual and acoustic stimuli) through different coordinate systems, generating one single coordinate frame able to represent the outer environment and the relationship between the environment and the self (Sakata et al., 1997; Wise et al., 1997). Such a representation is not "objective", being mediated by the personal experience which moulds saliency filters giving a different degree of relevance to different stimuli, and leading to important behavioural responses associated with decision-making and attention (Gootlieb et al., 1998; Rushworth et al., 2001; Andersen and Buneo, 2002; Wardak et al., 2005; Freedman and Assad, 2006). Finally, if the lower parietal areas are mostly linked with the temporal lobes and involved in speech functions, the upper parietal lobules are largely connected with the prefrontal dorsal districts interacting through re-entrant signalling (Battaglia-Mayer and Caminiti 2002; Battaglia-Mayer et al. 2006), opening to speculations on their reciprocal influence in functions associated with working memory and other high-order capabilities.

Most of the literature on the upper parietal areas focus on the intraparietal region as main centre of integration between the self and the outer environment, ranging from hand-eye coordination (that is, physical interaction) to "thought experiments" (that is, virtual interaction) (Andersen et al., 1997; Sakata et al., 1997; Rushworth et al., 2001; Andersen and Buneo, 2002; Bisley and Goldberg, 2003). The integration between self and non-self at the intraparietal sulcus directly leads to intention and goal organisation, including the interpetation of possible actions performed by other individuals (see Tunik et al., 2007 for a detailed review). The geometric comparisons preliminarily suggest that volumetric variation around the intraparietal area are compatible with the morphological differences observed between the modern and non-modern human endocasts. Although the intraparietal sulcus is hardly considered when dealing with the cortical surface, it represents a large volumetric percentage of the parietal cortex, being a rather deep structure, with a mean sulcal depth of 20 mm (Ebeling and Steinmetz, 1995). So, taking into account its functional role, its volumetric component, and the variation highlighted in the geometrical analyses, these areas should be carefully considered when dealing with the origin of the modern brain. It is worth also noting that the intraparietal sulcus is the main area of neural activation when a stone tool is produced (Stout and Chaminade, 2007), this process requiring a three dimensional virtual image of the raw object in mind, the future form visualised into it, shaping hands according to the outer reality, and a project.

In this regard, it must be once more stressed that also Neandertals showed a lateral widening of the upper parietal lobule (Bruner et al., 2003). This should be taken in mind when such a morphological change is associated with a technological one (Mousterian shared also with early modern humans), and a further difference is related to another cultural transition (Aurignacian associated with full modern humans). This leads to another very relevant question, of whether the "domed" appearance in rear view of the modern endocranium is derived from a "tent-like" morphology (maximum endocranial width at the upper temporal areas, like in *H. ergaster*/*erectus*, and maybe in *H. heidelbergensis* too) or from a "en-bombe" morphology (shared with Neandertals by means of a lateral widening of the upper parietal areas without any vertical and midsagittal enlargement).

Of course, one of the major cognitive proofs of some underlying neural evolution is art (Hodgson, 2006). Here, again we need to understand the spatial organisation of the outer reality, giving a differential importance to its components, to make a virtual projection of the outer scene, and to coordinate our hands and movements with our perceptions and with the relationship we have in mind to represent (i.e., a *simulation*). It is hence rather amazing that, since the early findings on the cave walls, such kinds of first evidence of the modern brain were called "parietal" art!

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REFERENCES

Andersen, R.A., Buneo, C.A., 2002. Intentional maps in posterior parietal cortex. Annual Review of Neuroscience 25, 189-220.

Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annual Review of Neuroscience 20, 303-330.

Bastir, M., Rosas, A., Kuroe, K., 2004a. Petrosal orientation and mandibular ramus breadth: evidence for an integrated petroso-mandibular developmental unit. American Journal of Physical Anthropology 123, 340-350.

Bastir, M., Rosas, A., O'Higgins, P., 2004b. Craniofacial levels and the morphological maturation of the human skull. Journal of Anatomy 209, 637-654.

Bastir, M., Rosas, A., Lieberman, D.E., O'Higgins, P., 2008. Middle cranial fossa anatomy and the origin of modern humans. Anatomical Record 291, 130-140.

Battaglia-Mayer, A., Caminiti, R., 2002. Optic ataxia as a result of the breakdown of the global tuning fields of parietal neurons. Brain 125, 225-237.

Battaglia-Mayer, A., Archambault, P.S., Caminiti, R., 2006. The cortical network for eye-hand coordination and its relevance to understanting motor disorders of parietal patients. Neuropsychologia 44, 2607-2620.

Bisley, J.W., Goldberg, M.E., 2003. Neuronal activity in the lateral intraparietal area and spatial attention. Science 299, 81-86.

Bookstein, F.L., 1991. Morphometric tools for landmark data. Cambridge: Cambridge University Press.

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., Marcus, L.F., 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. Anatomical Record 257, 217-224.

Bookstein, F.L., Gunz, P., Mitteroecker, P., Prossinger, H., Schaefer, K., Seidler, H., 2003. Cranial integration in *Homo*: singular warps analysis of the midsagittal plane in ontogeny and evolution. Journal of Human Evolution 44, 167-87.

Bruner, E., 2003a. Fossil traces of the human thought: paleoneurology and the evolution of the genus *Homo*. Riv Antropol 81, 29-56.

Bruner, E., 2003b. Computer tomography and paleoneurology: the Saccopastore Neandertals and brain evolution in the European Middle Pleistocene. Ph.D. Dissertation. University La Sapienza, Roma.

Bruner, E., 2004. Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. Journal of Human Evolution 47, 279-303.

Bruner, E., 2007. Cranial shape and size variation in human evolution: structural and functional perspectives. Child's Nervous System 23, 1357-1365.

Bruner, E., 2008a. Comparing endocranial form and shape differences in modern humans and Neandertal: a geometric approach. Paleoanthropology (in press).

Bruner, E., 2008b. Morphological differences in the parietal lobes within the human genus: a neurofunctional perspective. In: Coolodge, F., Wynn, T., (Eds.), Working Memory and the Evolution of Modern Thinking. International Symposium series. Berg Publishers (in press).

Bruner, E., Manzi, G., 2008. Paleoneurology of an "early" Neanderthal: endocranial size, shape, and features of Saccopastore 1. Journal of Human Evolution doi:10.1016/j.jhevol.2007.08.014.

Bruner, E., Ripani, M., 2008. A quantitative and descriptive approach to morphological variation of the endocranial base in Modern Humans. American Journal of Physical Anthropology doi: 10.1002/ajpa.20837.

Bruner, E., Sherkat, S., 2008. The middle meningeal artery: from clinics to fossils. Manuscript.

Bruner, E., Manzi, G., Arsuaga, J.L., 2003. Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineges. Proceedings of the National Academy of Sciences USA 100, 15335-15340.

Bruner, E., Saracino, B., Passarello, P., Ricci, F., Tafuri, M., Manzi, G., 2004. Midsagittal cranial shape variation in the genus *Homo* by geometric morphometrics. Collegium Antropologicum 28, 99-112.

Bruner, E., Mantini, S., Perna, A., Maffei, C., Manzi, G., 2005. Fractal dimension of the middle meningeal vessels: variation and evolution in *Homo erectus*, Neanderthals, and modern humans. European Journal of Morphology 42, 217-224.

Bruner, E., Manzi, G., Holloway, R., 2006. Krapina and Saccopastore: endocranial morphology in the pre-Würmian Europeans. Period Biolog 108, 433-441.

Cheverud, J.M., 1996. Developmental integration and the evolutino of pleiotropy. American Zoologist 36, 44-50.

Choi, H.J., Zilles, K., Mohlberg, H., Schleicher, A., Fink, G.R., Armstrong, E., Amunts, K., 2006. Cytoarchitectonic identification and probabilistic mapping of two distinct areas within the anterior ventral bank of the human intraparietal sulcus. Journal of Comparative Neurology 495, 53-69.

Coolidge, F., Wynn, T., 2005. Working memory, its executive functions, and the emergence of modern thinking. Cambridge Archaeological Journal 15, 5-26.

Ebeling, U., Steinmetz, H., 1995. Anatomy of the parietal lobe: mapping the individual pattern. Acta Neurochirurgica (Wien) 136, 8-11.

Eidelberg, D., Galaburda, A.M., 1984. Inferior parietal lobule. Archives of Neurology 41, 843-852.

Enlow, D.H., 1990. Facial Growth. Philadelphia: WB Saunders Company.

Falk, D., 1987. Hominid paleoneurology. Annual Review of Anthropology 16, 13-30.

Falk, D., 1993. Meningeal arterial pattern in great apes: implication for hominoid vascular evolution. American Journal of Physical Anthropology 92, 81-97.

Freedman, D.J., Assad, J.A., 2006. Experience-dependent representation of visual categories in parietal cortex. Nature 443, 85-88.

Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Nugent III, T.F., Herman, D.H., Clasen, L.S., Toga, A.W., Rapoport, J.L., Thompson, P.M., 2004. Dynamic mapping of human cortical development during childhood through early adulthood. Proceedings of the Nationall Academy of Sciences USA 101, 8174-8179.

Gottlieb, J.P., Kusunoki, M., Goldberg, M.E., 1998. The representation of visual salience in monkey parietal cortex. Nature 391, 481-484.

Grimaud-Hervè, D., 1997. L'évolution de l'enchéphale chez *Homo erectus* et *Homo sapiens*. Paris : CNRS Editions.

Grimaud-Hervé, D., 2005. Apports de quelques caractères morphologiques endocraniens dans la determination taxinomique des hominidés de Jebel Ihroud (Maroc). Anthropologie XLIII: 101-112.

Gunz, P., Harvati, K., 2007. The Neanderthal "chignon": variation, integration, and homology. Journal of Human Evolution 52, 262-274.

Henderson, J.H., Longaker, M.T., Carter, D.R., 2004. Sutural bone deposition rate and strain magnitude during cranial development. Bone 34, 271-80.

Hilgetag, C.C., Barbas, H., 2005. Developmental mechanics of the primate cerebral cortex. Anatomy and Embryology 210, 411-417

Hodgson, D., 2006. Understanding the origin of the paleoart: the neurovisual resonance theory and brain functioning. Paleoanthropology 2006, 54-67.

Holloway, R.L., 1978. The relevance of endocasts for studying primate brain evolution. In: Noback, C.R., (Ed.), Sensory Systems of Primates. New York: Plenum Press. pp. 181-200.

Holloway, R.L., 1981. Exploring the dorsal surface of hominoid brain endocasts by stereoplotter and discriminant analysis. Philisophical Transactions of the Royal Society of London - Series B 393, 155 -166.

Holloway, R.L., 1995. Toward a synthetic theory of human brain evolution. In: Changeaux, J.P., Chavaillon, J., (Eds.), Origins of the Human Brain. Oxford: Clarendon Press. pp. 42-54.

Holloway, R.L., Broadfield, D.C., Yuan, M.S., 2003. Morphology and histology of chimpanzee primary visual striate cortex indicate that brain reorganization predated brain expansion in early hominid evolution. Anatomical Record A 273, 594-602.

Holloway, R.L., Broadfield, D.C., Yuan, M.S., 2004. Brain endocasts: The paleoneurological evidence. The Human fossil record (Vol III). Hoboken, New Jersey: Wiley-Liss.

Jiang, X., Iseki, S., Maxson, R.E., Sucov, H.M., Morriss-Kay, G.M., 2002. Tissue origins and interactions in the mammalian skull vault. Develop. Biol. 241, 106-116.

Lieberman, D.E., McBratney, B.M., Krovitz, G., 2002. The evolution and development of cranial form in Homo sapiens. Proceedings of the Nationall Academy of Sciences USA 99, 1134-9.

Manzi, G., Vienna, A., Hauser, G., 1996. Developmental stress and cranial hypostosis by epigenetic trait occurrence and distribution: an exploratory study on the Italian Neandertals. Journal of Human Evolution 30, 511-527.

Morriss-Kay, G.M., Wilkie, A.O., 2005. Growth of the normal skull vault and its alteration in craniosynostosis: insights from human genetics and experimental studies. Journal of Anatomy 207, 637-53.

Moss, M.L., 1959. The pathogenesis of premature cranial synostosis in man. Acta Anatomica 37, 351-370.

Moss, M.L., Young, R.W., 1960. A functional approach to craniology. American Journal of Physical Anthropology 18, 281-292.

Mountcastle, V.B., 1995. The parietal system and some higher brain functions. Cerebral Cortex 5, 377-390.

O'Laughlin, V., 1996. Comparative endocranial vascular changes due to craniosynostosis and artificial cranial deformation. American Journal of Physical Anthropology 101, 369-385.

Olson, E.C., Miller, R.L., 1958. Morphological integration. University of Chicago Press, Chicago.

Rakic, P., 2004. Genetic control of cortical convolutions. Science 303, 1983-1984.

Richtsmeier, J.T., Aldridge, K., de Leon, V.B., Panchal, J., Kane, A.A., Marsh, J.L., Yan, P., Cole, T.M., 2006. Phenotypic integration of neurocranium and brain. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution) 306B, 360-378.

Rilling, J.K., 2006. Human and non-human primate brains: are they allometrically scaled versions of the same design? Evolutionary Anthropology 15, 65-67.

Rilling, J.K., Insel, T.R., 1999. The primate neocortex in comparative perspective using magnetic resonance imaging. Journal of Human Evolution 37, 191-223.

Rilling, J.K., Seligman, R.A., 2002. A quantitative morphometric comparative analysis of the primate temporal lobe. Journal of Human Evolution 42, 505-533.

Rohlf, F.J., 2004. tpsSplin 1.20. Ecology and Evolution, SUNY at Stony Brook, NY.

Rohlf, F.J., 2007. tpsRelw 1.45. Ecology and Evolution, SUNY at Stony Brook, NY.

Rushworth, M.F.S., Paus T., Sipila, P.K., 2001. Attentional system and organisation of the human parietal cortex. Journal of Neuroscience 21, 5262-5271.

Saban, R., 1979. Le systeme veineux méningé de l'homme fossile de Biache-Saint-Vaast Pas de Calais, d'apres le moulange endocranien. C R Acad Sci Paris D 289, 1129-1132.

Saban, R., 1982 Le systéme des veines méningées moyennes chez les hommes fossiles de Tchécoslovaquie, d'aprés le moulage endocranien. Anthropos 21, 281-295.

Sakata, H., Taira, M., Kusunoki, M., Murata, A., Tanaka, Y., 1997. The parietal association cortex in depth perception and visual control of hand action. Trends in Neurosciences 20, 350-357.

Semendeferi, K., Damasio, H., 2000. The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. Journal of Human Evolution 38, 317-332.

Semendeferi, K., Damasio, H., Frank, R., Van Hoesen, G.W., 1997. The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. Journal of Human Evolution 32, 375-388.

Sergi, S., 1934. Ossicini fontanellari della regione del lambda nel cranio di Saccopastore e nei crani neandertaliani. Riv Antropol 30, 101-112.

Sergi, S., 1948. L'uomo di Saccopastore. Paleontographia Italica XLII, 25-164.

Slice, D.E., 2000. *Morpheus et al*. Ecology and Evolution, SUNY at Stony Brook, NY.

Sporns, O., Tononi, G., Edelman, G.M., 2002. Theoretical neuroanatomy and the connectivity of the cerebral cortex. Behavioural Brain Research 135, 69-74.

Sporns, O., Chialvo, D.R., Kaiser, M., Hilgetag, C.C., 2004. Organization, development and function of complex brain networks. Trends in Cognitive Sciences 8, 418-425.

Stout, D., Chaminade, T., 2007. The evolutionary neuroscience of tool making. Neuropsychologia 45, 1091-100.

Toro, R., Burnod, Y., 2005. A morphogenetic model for the development of cortical convolutions. Cerebral Cortex 15, 1900-1913.

Tunik, E., Rice, N.J., Hamilton, A., Grafton, S.T., 2007. Beyond grasping: representation of action in human anterior intraparietal sulcus. Neuroimage 36, T77-T86.

Van Essen, D.C., 1997. A tension-based theory of morphogenesis and compact wiring in the central nervous system. Nature 385, 313-318.

Wardak, C., Ben Hamed, S., Duhamel, J.R., 2005. Parietal mechanism of selective attention in monkeys and humans. In: Dehaene, S., Duhamel, J.R., Hauser, M.D., Rizzolatti, G., (Eds.), From monkey brain to human brain. Cambridge: MIT Press. pp. 273-291.

Wise, S., Boussaoud, D., Johnson, P.B., Caminiti, R., 1997. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. Annual Review of Neuroscience 20, 25-42.

Wynn, T., Coolidge, F., 2003. The role of working memory in the evolution of managed foraging. Before Farming 2, 1-16.

Wynn, T., Coolidge, F., 2006. The effect of enhanced working memory on language. Journal of Human Evolution 50, 230-231.

Wynn, T., Coolidge, F.L., 2004. The expert Neandertal mind. Journal of Human Evolution 46, 467-487.

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