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A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya

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ABSTRACT

The globular braincase of modern humans is distinct from all fossil human species, including our closest extinct relatives, the Neandertals. Such adult shape differences must ultimately be rooted in different developmental patterns, but it is unclear at which point during ontogeny these group characteristics emerge.

Here we compared internal shape changes of the braincase from birth to adulthood in Neandertals ($N = 10$), modern humans ($N = 62$), and chimpanzees ($N = 62$). Incomplete fossil specimens, including the two Neandertal newborns from Le Moustier 2 and Mezmaiskaya, were reconstructed using reference-based estimation methods. We used 3D geometric morphometrics to statistically compare shapes of virtual endocasts extracted from computed-tomographic scans. Throughout the analysis, we kept track of possible uncertainties due to the missing data values and small fossil sample sizes.

We find that some aspects of endocranial development are shared by the three species. However, in the first year of life, modern humans depart from this presumably ancestral pattern of development. Newborn Neandertals and newborn modern humans have elongated braincases, and similar endocranial volumes. During a 'globularization-phase' modern human endocasts change to the globular shape that is characteristic for *Homo sapiens*. This phase of early development is unique to modern humans, and absent from chimpanzees and Neandertals.

Our results support the notion that Neandertals and modern humans reach comparable adult brain sizes via different developmental pathways. The differences between these two human groups are most prominent directly after birth, a critical phase for cognitive development.

Introduction

Imprints of the brain and its surrounding structures in the bone, so called 'endocasts', make it possible to study evolutionary changes of brain size and shape (Falk, 1980; Conroy et al., 1998; Holloway et al., 2004). Endocranial shape and size changes during individual ontogeny (Neubauer et al., 2009, in press) provide important clues about differences in the patterns of brain development between species (Neubauer et al., 2010). Based on detailed measurements of endocranial shape changes from birth to adulthood, we have recently shown that the chimpanzee and modern human endocranial trajectories are remarkably similar after the eruption of the deciduous dentition (Neubauer et al., 2010). However, directly after birth, modern human endocasts change from an elongated to a more globular shape, during a 'globularization-phase' that does not exist in chimpanzees (Fig. 1). This species difference in the ontogenetic shape trajectories coincides with the timing of major species differences in the pattern of brain growth. The neonatal brain weight of modern humans is more than twice that of chimpanzees (DeSilva and Lesnik, 2006, 2008), and the velocity of brain growth in the first years of life is higher in humans than in chimpanzees (Leigh, 2004). Longitudinal magnetic resonance imaging (MRI) studies have shown that brain volume doubles within the first year of life in modern humans (Gilmore et al., 2007; Knickmeyer et al., 2008). During this period, the parietal and occipital areas 'bulge' and the cranial base flexes in modern humans (Gunz et al., 2010; Neubauer et al., 2010). Interestingly, these shape changes seem to mirror the adult shape differences between modern humans and Neandertals (Lieberman et al., 2002, 2004; Harvati,

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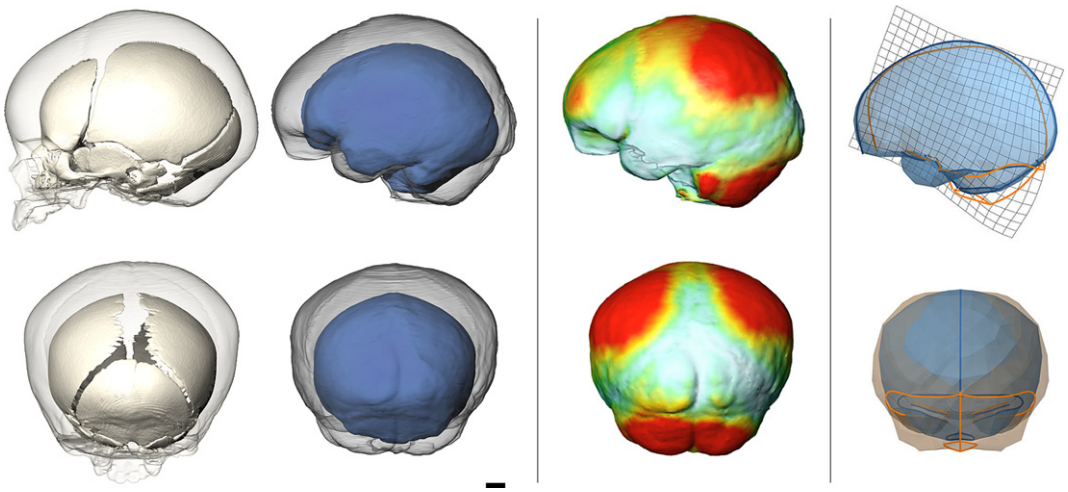

Figure 1. Modern human 'globularization-phase'. Left: A modern human neonate (white: bone; blue: virtual endocast) and a one-year old *Homo sapiens* infant (semitransparent surfaces) in lateral and posterior view. Scale bar is 10 mm. Middle: Shape differences after Procrustes registration of the two endocasts from the left panel: a relative expansion of the parietal area and the cerebellum. Colour gradient (from blue to red) codes the vector length between surface-vertices. Right: Thin-plate spline deformation between the mean shapes of age group 1 (blue) and age group 2 (orange). Note that while the heat map in the middle panel is sensitive to the Procrustes superimposition, the thin-plate spline deformation grid is not affected by this potential bias. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2003, 2009; Harvati et al., 2004, 2007; Gunz and Harvati, 2007; Pearson, 2008; Gunz et al., 2009a; Neubauer et al., 2010; Stansfield and Gunz, 2011). We therefore tested whether we could find evidence for a 'globularization-phase' in Neandertals (Gunz et al., 2010). The contrast between modern human and Neandertal endocranial development corroborated the notion, originally put forward by Bruner and colleagues (Bruner et al., 2003; Bruner, 2004, 2007, 2010), that modern humans and Neandertals reached similar endocranial capacities through different developmental pathways (Fig. 2).

However, the analysis of Gunz et al. (2010) was limited by the fact that it relied on a single Neandertal neonate, which did not preserve all of the relevant morphology. The main aim of this paper therefore is to reassess our previous findings on endocranial development in Neandertals (Gunz et al., 2010), using a new virtual reconstruction of the Neandertal newborn from Mezmaiskaya (Golovanova et al., 1999, 2010; Pinhasi et al., 2011). Including the Mezmaiskaya newborn will allow a critical reevaluation of our previous analysis (Gunz et al., 2010), as this specimen preserves a complete and undistorted right parietal bone, whereas this region is only partially preserved in Le Moustier 2 (Maureille, 2002a, b). Our second aim is to extend the comparative sample of Gunz et al. (2010) to include a cross-sectional series of chimpanzees. By establishing which aspects of endocranial development from birth to adulthood are shared among modern humans, Neandertals and chimpanzees, and which are species-specific, we explore the evolutionary changes within the hominin lineage. As every reconstruction of incomplete fossil material is based on implicit and explicit prior assumptions that will affect the final reconstruction, we compute developmental simulations (McNulty et al., 2006; Gunz et al., 2010; Neubauer et al., 2010) that do not rely on subadult fossils, in order to assess the validity of our findings. Finally, we discuss potential inferences about Neandertal cognition and behaviour by briefly reviewing evidence from clinical studies that support a link between alterations of early brain development and cognition.

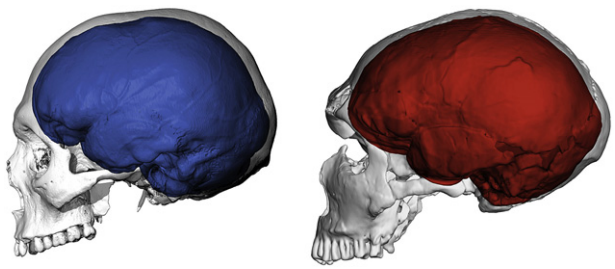

Figure 2. CT scans of a modern human and a Neandertal adult (La Ferrassie 1). Neandertals have elongated braincases and endocasts when compared with modern human adults. Neandertal faces are larger and more projecting than in *Homo sapiens*.

Hypotheses and predictions

We hypothesize that the pattern of endocranial development in the first year of life is unique to *Homo sapiens*, and absent in fossil human species. We therefore test whether we can find evidence for a 'globularization-phase' in the ontogenetic trajectory of our closest relatives, the Neandertals. While the fossil record of Neandertal crania is the richest of all extinct hominin species and comprises all stages of development from birth to adulthood, the sample size of nearly complete subadult fossil crania is still too small to provide a reliable estimate of the average Neandertal endocranial developmental trajectory. We therefore use the contrast between the trajectories of chimpanzees and modern humans (Neubauer et al., 2010) to formulate concrete models about Neandertal development and assess virtual reconstructions of six subadult Neandertals of different ages in light of these predictions.

Hypothesis A

The endocranial developmental patterns of Neandertals and modern humans are the same after birth. This model implies that all species differences are already established at the time of birth, and that the braincase of Neandertal neonates looks substantially different from modern human newborns. If true, we would find evidence for a 'globularization-phase' in Neandertals, specifically between the two Neandertal neonates Mezmaiskaya (Golovanova et al., 1999) and Le Moustier 2 (Maureille, 2002a, b) and the infant specimen from Pech de l'Azé (Patte, 1957; Ferembach et al., 1970).

Hypothesis B1

Neandertals follow a modern human pattern in later ontogeny (from the eruption of the deciduous dentition onwards), but do not have a 'globularization-phase' after birth.

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Hypothesis B2

The pattern of shape changes throughout development is similar between Neandertals and chimpanzees.

Note that hypothesis B1 and hypothesis B2 are not mutually exclusive, given the similarity of the modern human and chimpanzee growth trajectories after the eruption of the deciduous dentition (Neubauer et al., 2010).

Material and methods

Sample

Our cross-sectional ontogenetic samples comprise crania of 62 modern humans and 62 chimpanzees, ranging from neonates to adults (Table 1). The human sample comprises specimens from the Medicine Faculty of Strasbourg, the University of Vienna, the University of Leipzig, and the University of Freiburg. The chimpanzee sample is from collections of the Max Planck Institute for Evolutionary Anthropology, the Muséum National d'Histoire Naturelle Paris, and the Naturkundemuseum Berlin (cf. Neubauer et al., 2010 for additional details about the sample). The extant samples include many individuals of known age and sex (Strasbourg human ontogenetic series (Coqueugniot et al., 2004; Coqueugniot and Hublin, in press) as well as the human subadults from the University of Vienna, and the chimpanzees from the Taï Forest collection (Boesch and Boesch-Achermann, 2000; Neubauer et al., in press)), but this information was not available for all individuals. The specimens were therefore grouped in dental age groups (1–6) according to maxillary dental eruption patterns (Table 1). The fossil sample comprises ten subadult and adult Neandertals and two other adult archaic *Homo* (Table 2). All crania were scanned using computed-tomography (CT).

Virtual reconstructions

As the reconstruction protocol for Le Moustier 2 is described in the supplemental material for Gunz et al. (2010, 2011), the following description will focus on the virtual reconstruction of Mezmaiskaya. Using the software Avizo (Visualization Sciences Group), we isolated the individual fragments of the Mezmaiskaya cranium via segmentation of the CT scan (Fig. 3). Subsequently, the digital fragments were assembled based on anatomical criteria (Zollikofer et al., 1995, 1998, 2005; Ponce de León and Zollikofer, 1999; Zollikofer, 2002; Gunz, 2005; Ponce de León et al., 2008; Gunz et al., 2009b; Grine et al., 2010; Weber and Bookstein, 2011). Anatomical parts that were only missing on one side were mirror-imaged in Avizo (Figs. 3–5). The distorted left parietal fragments (red in Fig. 3) were not used; instead we used a mirror-image of the right parietal. Our reconstruction of the Mezmaiskaya neonate was based on the following prior assumptions (Gunz et al., 2009b; Grine et al., 2010): (A) We assumed that the pattern of suture spacing was similar in Neandertal and modern human newborns. Following Ponce de León et al. (2008), we estimated the spacing of interosseous sutures in the two Neandertal newborns from modern human perinatal wet specimens (Fig. 4). (B) Our computer algorithm for missing-data estimation was based on the assumption that the large-scale patterns of morphological integration among cranial parts are similar between modern humans and Neandertals. (C) The cranial fragments of the Mezmaiskaya newborn are exceptionally well preserved. We could not detect evidence for plastic deformation, except for the left parietal fragments which were not used here (see also: Ponce de León et al., 2008). We therefore assumed that there was negligible plastic deformation in the cranial fragments.

Missing parts were estimated using geometric morphometric methods, following the thin-plate spline reconstruction protocol described by Gunz et al. (2009b). Landmarks and semilandmarks (see below) were measured on the fossil surfaces completed by mirror-imaging, as well as on complete reference crania. The missing points in the fossil specimens were estimated based on the thin-plate spline interpolation computed from the subset of landmarks and semilandmarks available in the respective incomplete fossil. Semilandmarks were constrained to slide along their respective curves and surfaces, and missing points (landmarks as well as semilandmarks) were free to move without constraints, so as to minimize the thin-plate spline bending energy (Gunz et al., 2005). In the same computational step, we created virtual endocasts (see below) for Mezmaiskaya and Le Moustier 2 using the thin-plate spline interpolation to warp the respective endocasts from the complete reference specimens.

Given that the choice of the reference specimen affects the estimation, we used multiple reference specimens to create a distribution of reconstructions for each incomplete fossil (Gunz

Table 2
Fossil human sample.

Label	Specimen	Group	References
Subadults			
LeM2	Le Moustier 2	Neandertal	Maureille, 2002a, b
Mez	Mezmaiskaya	Neandertal	Golovanova et al., 1999; Ponce de León et al., 2008
Pech	Pech de l'Azé	Neandertal	Patte, 1957; Ferembach et al., 1970
R	Roc de Marsal	Neandertal	Bordes and Lafille, 1962; Madre-Dupouy, 1992
E	Engis 2	Neandertal	Schmerling, 1833; Fraipont, 1936
M1	Le Moustier 1	Neandertal	Klaatsch, 1909; Ullrich, 2005
Adults			
Fe	La Ferrassie 1	Neandertal	Heim, 1974
Ch	La Chapelle	Neandertal	Boule, 1911
Gu	Guattari	Neandertal	Sergi and Ascenzi, 1974
Gi	Gibraltar 1	Neandertal	Busk, 1864
Kb	Kabwe	Archaic *Homo*	Woodward, 1921
Pe	Petralona	Archaic *Homo*	Stringer et al., 1979

Table 1
Modern human and chimpanzee sample.

Age group	Dentition	*Homo sapiens*				*Pan troglodytes*			
		All	Male	Female	Indet	All	Male	Female	Indet
1	No teeth erupted	**6**	4	2	–	**7**	3	–	4
2	Incomplete deciduous dentition	**7**	2	5	–	**5**	2	2	1
3	Complete deciduous dentition	**19**	11	8	–	**7**	2	–	5
4	M1 erupted	**6**	1	1	4	**12**	4	5	3
5	M2 erupted	–	–	–	–	**7**	1	5	1
6	M3 erupted	**24**	13	11	–	**24**	6	6	12
Total		**62**	31	27	4	**62**	18	18	26

Homo sapiens: Collections from the Medicine Faculty of Strasbourg, University of Vienna, University of Leipzig, University of Freiburg; *Pan troglodytes*: Max Planck Institute for Evolutionary Anthropology, Museum National d'Histoire Naturelle Paris, and Naturkundemuseum Berlin.

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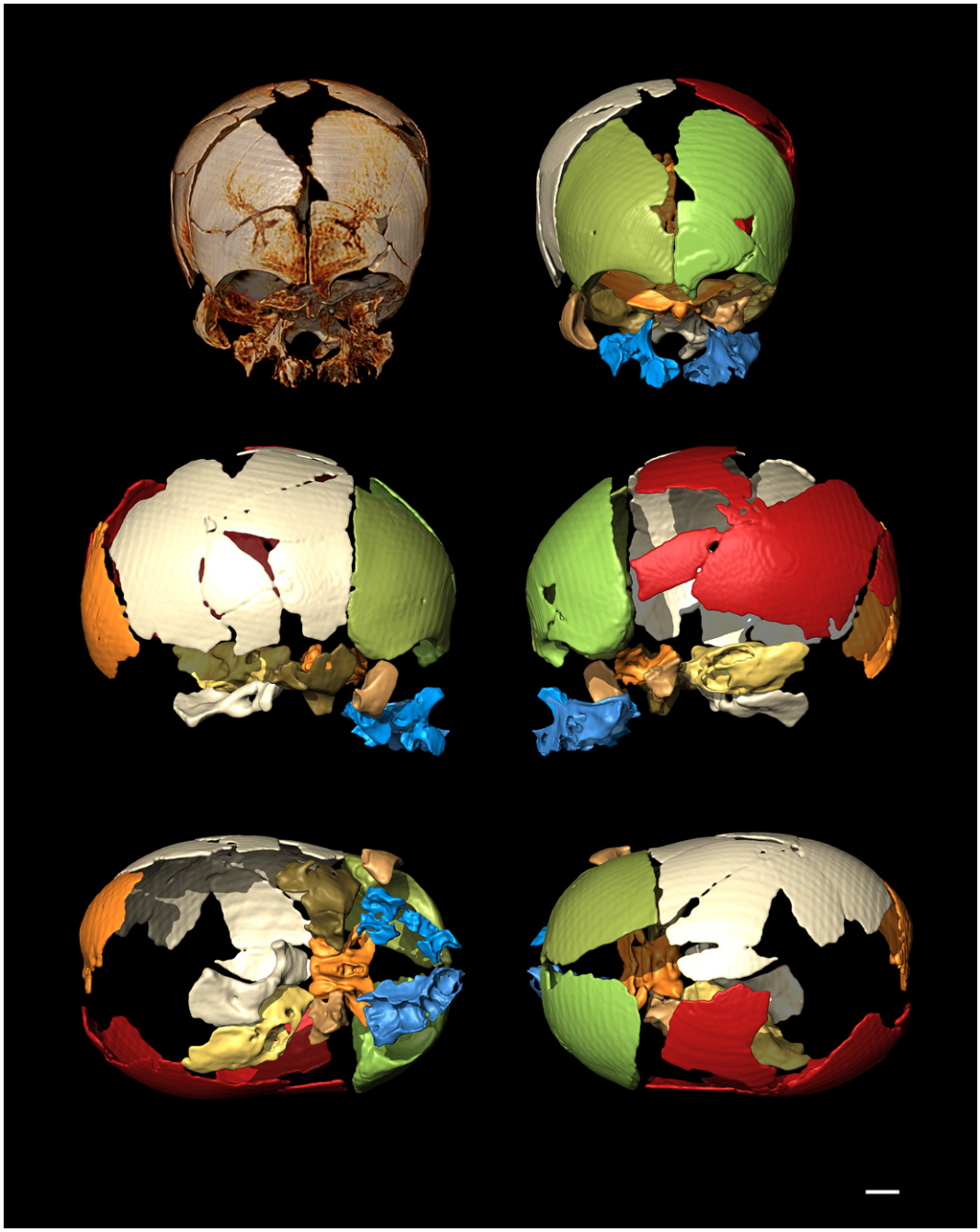

Figure 3. Segmentation of the CT scan of Mezmaiskaya. Individual bone fragments were isolated from the CT scan of the original specimen and then realigned on the computer. The distorted left parietal fragments (red) were not used. Instead we used a mirror-image of the right parietal. See also Fig. 5. Scale bar is 10 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2009b, 2010; Grine et al., 2010). Each cranium in our sample was used to estimate missing data for each incomplete fossil. The resulting reconstruction distributions therefore represent conservative estimates of the uncertainty that stems from the choice of the reference specimen.

Endocasts and measurement protocol

We created virtual endocasts for each individual using semi-automated segmentation of the endocranial cavity from CT scans of the original specimens (Neubauer et al., 2004, 2009, 2010). The endocasts of Le Moustier 2 and Mezmaiskaya were created by thin-plate spline warping during the missing-data estimation, as described above.

We measured 29 anatomical landmarks on each specimen (Table 3), as well as semilandmarks on curves and surfaces following the protocol established by Neubauer et al. (2009). Points along curves were measured on the surface of the bone in Avizo and then later resampled to equal point count in Mathematica (Wolfram Research). The sphenoid curve separates the anterior and the middle cranial fossa and the petrous curve delineates the middle from the posterior cranial fossa. The transverse sinus curve forms the boundary between the posterior cranial fossa and the vault. Two additional curves on the cranial base capture the shape

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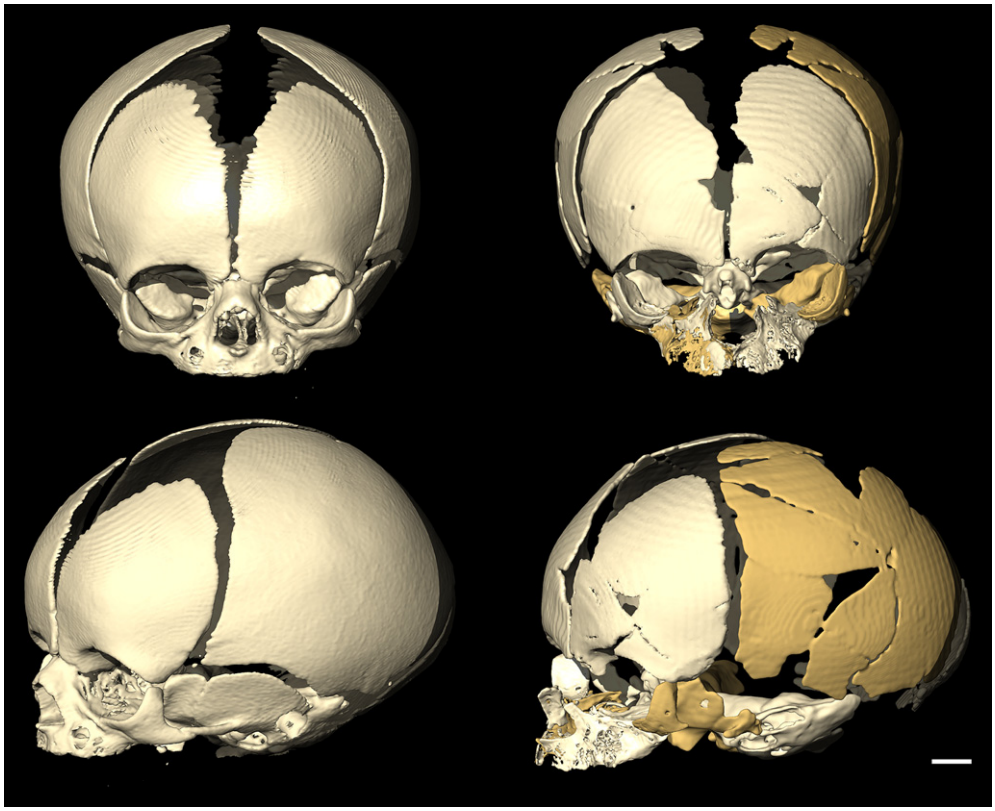

Figure 4. A modern human neonate and a virtual reconstruction of Mezmaiskaya. Parts obtained via mirror-imaging are plotted in a darker shade. The face of the Neandertal neonate (right) is larger and more projecting than in the modern human (left). Scale bar is 10 mm.

of the foramen magnum as well as basicranial angulation. To distribute the same number of surface semilandmarks on all specimens, we first measured a mesh of semilandmarks on the cerebral and cerebellar surfaces of a template specimen. We then used a thin-plate spline interpolation based on the anatomical landmarks and the curve-semilandmarks to warp this template mesh onto each specimen. Finally, we projected these warped meshes onto the surfaces of the respective endocasts (Neubauer et al., 2009; Gunz et al., 2009b), by selecting the closest triangle vertex on the endocranial surface. All specimens were measured by one observer (SN). Intra-observer error, as assessed from analyses of repeated measurements, was small and did not affect specimen affinity (Neubauer et al., 2009).

Statistical analysis

Given that many fossil specimens were reconstructed using mirror-imaging, we first symmetrized all data using reflected relabelling (Mardia et al., 2000), so as to remove the signal of brain laterality from all specimens. The symmetrized coordinates were then converted to shape variables using Procrustes superimposition (Rohlf and Slice, 1990), in order to standardize

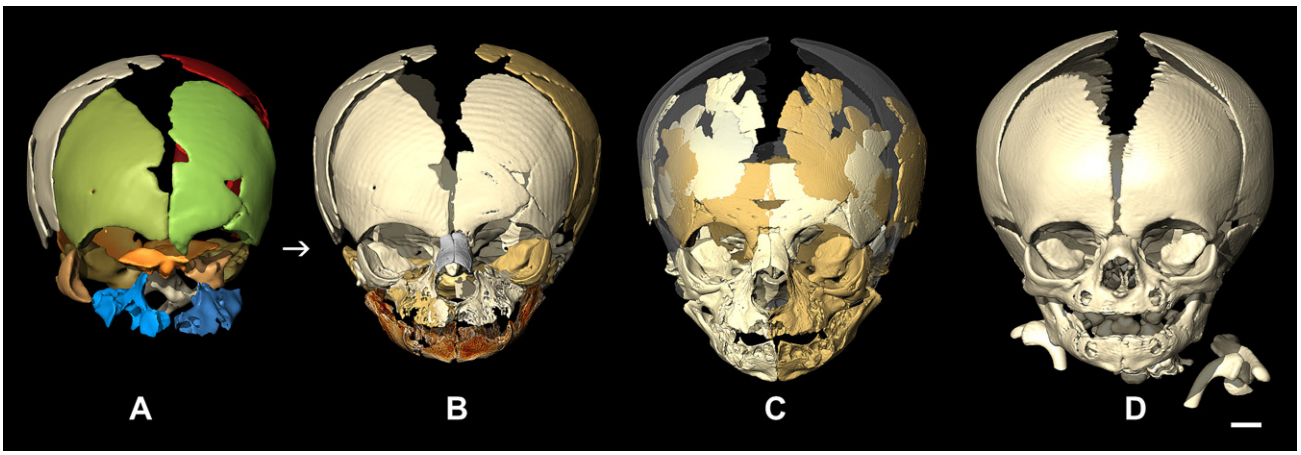

Figure 5. Virtual reconstructions of Mezmaiskaya, Le Moustier 2 and a modern human neonate. Segmentation of the original CT scan of Mezmaiskaya before (A) and after reconstruction (B). The two nasal bones (grey) are from Le Moustier 2. C: Virtual reconstruction of Le Moustier 2. Parts obtained via mirror-imaging are plotted in a darker shade; semitransparent surfaces were estimated based on complete reference crania. D: Modern human neonate. Scale bar is 10 mm.

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Table 3
Landmark definitions.

Endocranial landmarks	
M	anterior sphenoid spine
M	foramen caecum
M	endobregma
M	endolambda
M	internal occipital protuberance
M	opisthion
M	basion
M	endosphenobasion
M	dorsum sellae
B	anterior clinoid process
B	optic canal
B	superior orbital fissure
B	foramen rotundum
B	foramen ovale
B	petrous apex
B	internal accustic meatus
B	maximum curvature point between transverse and petrous curve
B	foramen jugulare
B	hypoglossic canal

M – midsagittal landmarks, B – bilateral landmarks measured on the left and right side.

position, orientation, and scale. Semilandmarks were allowed to slide along the curves and surfaces so as to minimize the bending energy between each specimen and the Procrustes average shape (Bookstein, 1997; Mitteroecker and Gunz, 2009). Because semilandmarks are analyzed as if they are homologous points, the curves and surfaces on which they are measured are required to be homologous (Bookstein, 1997; Gunz et al., 2005, 2009b).

Principal component analysis (PCA) of the Procrustes shape variables was used as an ordination technique to visualize the large-scale trends of shape changes during ontogeny. The principal component axes were computed using the extant specimens and the average of each fossil reconstruction distribution. All fossil reconstructions were then projected into this principal component space. All trajectories, developmental simulations (see below), and visualizations were computed using all dimensions of Procrustes shape space. We estimated the species developmental trajectories as the shape changes between consecutive mean shapes of dental age groups. The trajectories plotted in the principal component score plots are BsplineCurves, using the mean age group scores as control points. The multiple lines in Fig. 7 are based on bootstrap estimates of the group means. Ideally, such developmental trajectories would be computed based on longitudinal data, but such growth series that include perinatal humans and chimpanzees are not available. In Neubauer et al. (2010), we could show that the average trajectories of our cross-sectional samples represent reasonable estimates of the individual ontogenetic trajectories.

Developmental simulations

'Backward' simulations We computed developmental simulations (Gunz et al., 2010; Neubauer et al., 2010) using the respective developmental trajectories of modern humans (hypothesis A) and chimpanzees (hypothesis B2) to predict 'backwards' from the mean endocranial shape of adult Neandertals. We also predicted the endocranial shape of a hypothetical Neandertal baby based on the modern human pattern, without the 'globularization-phase' (hypothesis B1) by leaving the endocranial shape changes that occur in modern humans between birth and dental stage 2 (incomplete deciduous dentition) out entirely. These simulations were computed in Mathematica by translating the respective average developmental trajectories of chimpanzees and humans to the adult Neandertal mean, taking into account the variability of the extant species and the uncertainty of the mean differences between adults via bootstrapping. We then assessed whether the reconstructions of the six subadult fossils plot within the variation along the simulated trajectories.

'Forward' simulations We also computed developmental simulations that did not rely on subadult Neandertals (Gunz et al., 2010). We simulated the growth of modern human newborns without the 'globularization-phase', and along the chimpanzee trajectory. For the first simulation, we translated the average human developmental trajectory between age groups 2 and 6 to every modern human neonate, thus leaving out the shape changes associated with the 'globularization-phase'. For the second simulation, we used the average developmental trajectory of chimpanzees (age groups 1–6). We then assessed how closely these simulated adults fell to actual Neandertal adults.

If Neandertals and modern humans had similar endocranial shapes around the time of birth, and Neandertals lack a postnatal 'globularization-phase' but developed like modern humans between age groups 2 and 6, then these simulated adults are expected to plot close to the adult Neandertal variation. We have shown previously that the average species trajectories between age groups 2 and 6 are so similar between modern humans and chimpanzees that they are interchangeable (Neubauer et al., 2010). The second simulation, using the chimpanzee trajectory on modern human neonates, is therefore only subtly different from the first simulation; the main difference pertains to the 'amount' of shape change (for more details see Neubauer et al., 2010).

Results

Morphology of newborns

The faces of Neandertal newborns are larger and more projecting than in modern human neonates of comparable endocranial volume (Fig. 5). The width of the piriform aperture, the length of

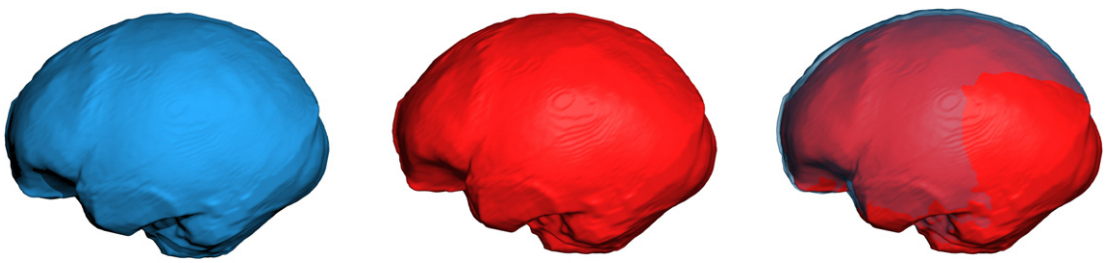

Figure 6. Endocasts of a modern human neonate and Mezmaiskaya. The endocranial shapes and volumes are very similar around the time of birth (blue: modern human neonate; red: Mezmaiskaya). The third image shows the two endocasts superimposed; the modern human endocasts drawn as a semitransparent surface. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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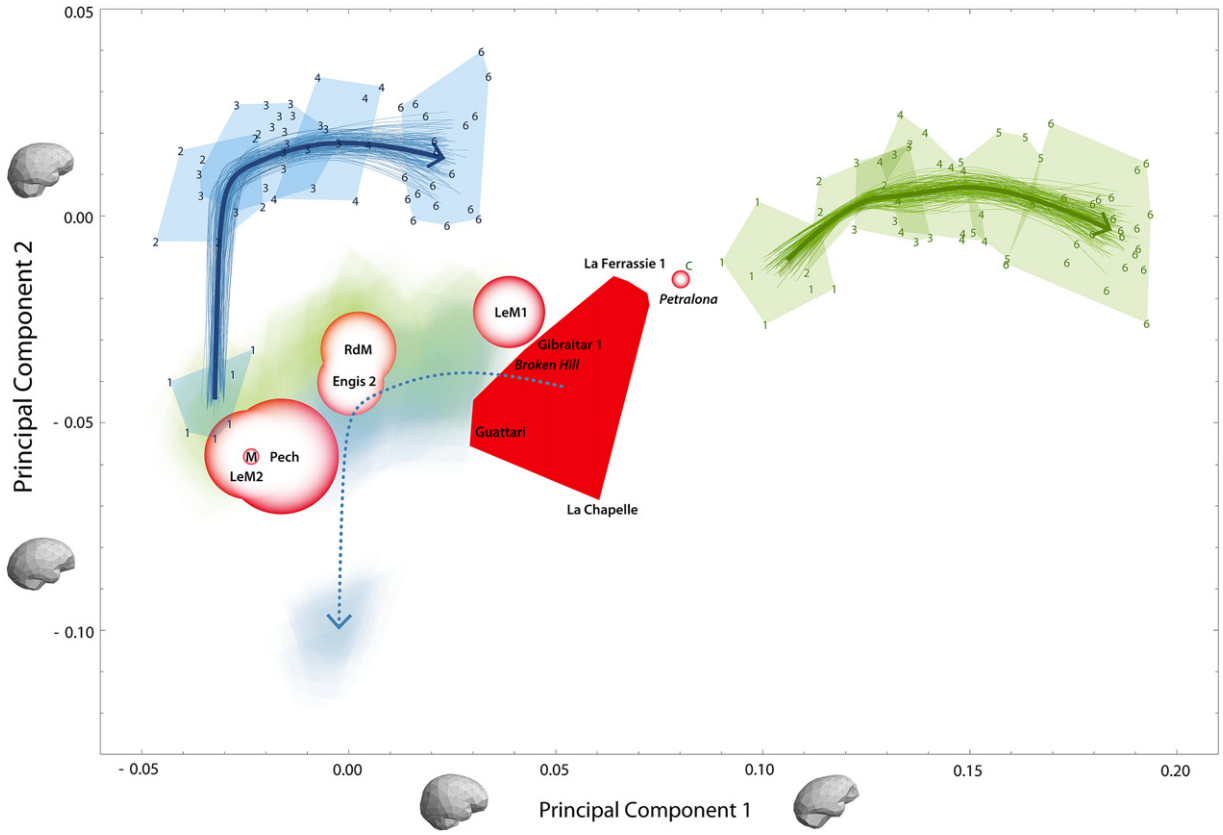

Figure 7. Principal component analysis in shape space. PC 1 and PC 2 together explain approx. 71% of the sample variance; the associated shape differences are plotted as surface deformations of the mean shape 2 s.d. in either direction. Specimen labels and convex hulls for modern humans (blue) and chimpanzees (green) are based on dental age groups. The convex hull for Neandertals (red) is based on adults only. The multiple reconstructions of each subadult fossil specimen fall within the respective semitransparent disks. These reconstruction distributions represent the estimation uncertainty. Note that the reconstruction distributions for the three youngest Neandertals, Mezmaiskaya, Le Moustier 2, and Pech de L'Azé overlap. No matter how we reconstruct these fossils, they plot close to modern human neonates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the nasal bones (only preserved in Le Moustier 2), and the shape of the orbit, clearly distinguish the Neandertal neonates Le Moustier 2 and Mezmaiskaya from the modern human newborns in our sample.

Around the time of birth, modern humans and Neandertals have very similar endocranial shapes. Our estimates for the endocranial capacity of Mezmaiskaya range from 414 to 423 cm^3 (Mean: 417.7 cm^3, SD = 1.86 cm^3). The endocranial capacities of different reconstructions of Le Moustier 2 range between 408 and 428 cm^3 (Gunz et al., 2010). When the virtual endocasts of a modern human and Mezmaiskaya are superimposed, the shape differences are only subtle (Fig. 6). Our reconstruction of Mezmaiskaya's braincase is slightly more elongated than that of a modern human newborn, with flatter parietal bones and a slightly flatter occipital. Only fragments of the parietal bones are preserved in Le Moustier 2. However, their shape, together with the morphology of the frontal bones and the occipital bone, suggest that the braincase shape of Le Moustier 2 was similar to Mezmaiskaya's (Fig. 5; see also Figures in Gunz et al., 2010).

Endocranial development

The Neandertal adults, as well as the two archaic *Homo* specimens, are well separated from the extant groups in Procrustes shape space (Figs. 6 and 7). The endocranial shape changes between age groups 2 and 6 are shared among modern humans, Neandertals, and chimpanzees (Fig. 7). Modern human, Neandertal and chimpanzee endocasts widen at the temporal lobes, as the temporal poles rotate medially. The cribriform plate rotates upwards, and the clivus extends inferiorly. The posterior cranial fossa moves inferiorly and its relative size increases. When the principal component (PC) axes are computed without chimpanzees (Fig. 8), they differ only subtly from the PC axes of the full sample shown in Fig. 7. In both cases, the reconstruction distributions for the three youngest Neandertals (Mezmaiskaya (age group 1), Le Moustier 2 (age group 1), and Pech de L'Azé (age group 3)) overlap in these dimensions of shape space. This means that no matter how we reconstruct these fossils, they fall close to modern human neonates.

In the 'backward' simulation (Figs. 7 and 8), all subadult Neandertals fall within the ranges predicted based on the bootstrapped extant developmental models (semitransparent green and blue convex hulls). While the chimpanzee and human model predictions overlap along the 'shared' part of the trajectory between dental age groups 2 and 6, the predictions about the endocranial shape of a Neandertal neonate differ substantially between hypotheses A and B1, and slightly between B1 and B2.

All of our reconstructions of Le Moustier 2 and Mezmaiskaya fall within the predictions of hypothesis B1 and B2. No reconstruction of these two Neandertal newborns plots within, or even close to the prediction of hypothesis A (Fig. 8). When we visualize the predicted endocranial shape of hypothesis A via TPS warping of a modern human newborn (inset in Fig. 8), we can see that if Neandertals had a postnatal 'globularization phase' just like modern humans, the braincase of a Neandertal newborn would have to be extremely

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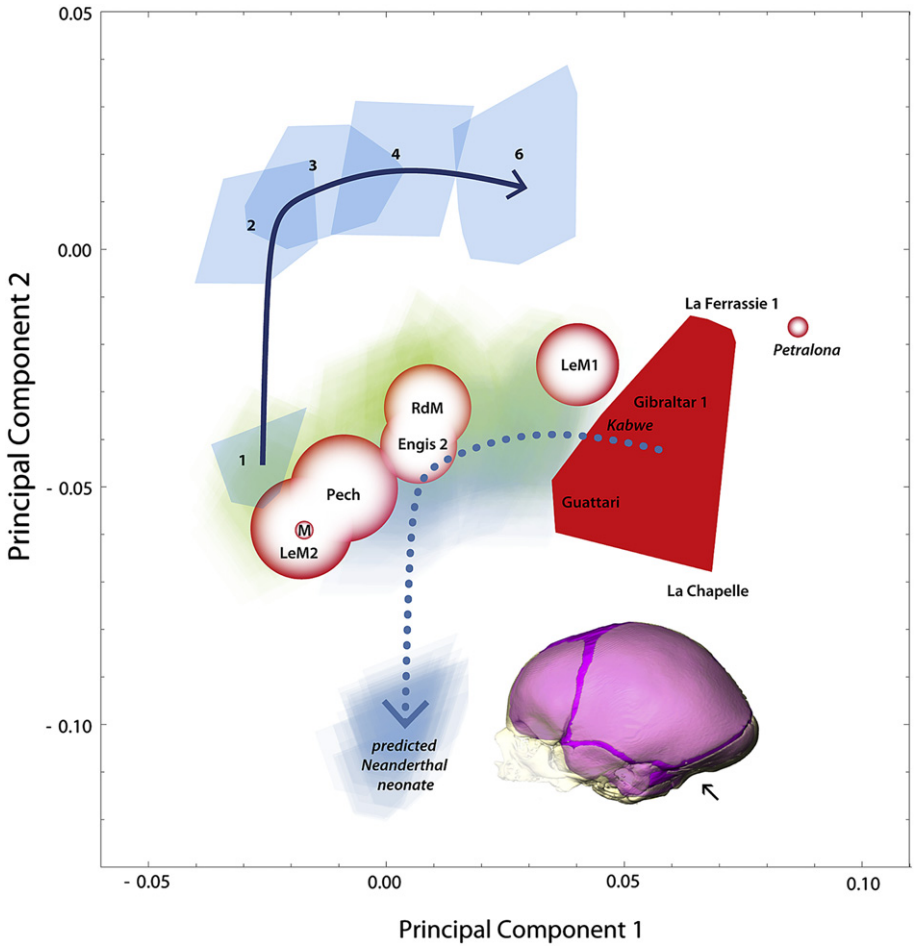

Figure 8. Principal component analysis of human specimens. The dotted blue arrow shows the 'backward simulation' based on the modern human average trajectory. If the Neandertal and modern human developmental pattern were the same (hypothesis A), then reconstructions of the Neandertal neonates Le Moustier 2 and Mezmaiskaya would be expected to fall within the predicted convex hulls. However, none of the reconstructions plot within or close to this prediction. This predicted endocranial shape (purple endocast) of a Neandertal newborn is much more elongated than the endocasts of Le Moustier 2 and Mezmaiskaya. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

elongated with a poorly developed cerebellum. The predicted endocranial shape of a Neandertal newborn of hypothesis A is much more elongated than the actual endocasts of Le Moustier 2 and Mezmaiskaya.

In the 'forward' simulations shown in Fig. 9, which were based on modern human neonates, the simulated adults bear a striking resemblance to the average Neandertal shape (Fig. 9A). In principal component space, the simulated adults fall close to actual endocasts of Neandertal adults (Fig. 9B and C). The predicted adult shapes, however, have a slightly more pronounced parietal than the actual Neandertal mean and are also slightly rounder in the occipital area (Fig. 9A).

Discussion

Our reconstructions of two Neandertal neonates (Fig. 5) support the notion that many Neandertal characteristics of the facial skeleton are already established at the time of birth (Tillier, 1996; Ponce de León and Zollikofer, 2001; Ponce de León, 2002; Maureille, 2002a, b; Nicholson and Harvati, 2006; Bastir et al., 2007; Ponce de León et al., 2008; Zollikofer and Ponce de León, 2010). Our estimates of the endocranial volume for Mezmaiskaya, ranging between 414 and 423 cm^3, are slightly smaller than the estimates reported by Ponce de León et al. (2008). These authors reported a range of 422 cm^3–436 cm^3 for comparable virtual reconstructions of Mezmaiskaya. Given the uncertainty about the suture spacing in this perinatal specimen, this close correspondence of these independent virtual reconstructions is quite remarkable. Hüppi et al. (1998) report brain volumes at birth based on in-vivo MRI ranging between 380 and 420 cm^3 in recent modern humans. Both EV ranges for Mezmaiskaya (the EV at birth of this perinatal specimen was extrapolated to be around 400 cm^3 by Ponce de León et al., 2008 based on the assumption that it was two weeks old at the time of death), as well as our estimates for Le Moustier 2 (408–428 cm^3, cf. Gunz et al., 2010), are therefore consistent with the notion that brain size at birth was comparable in Neandertals and modern humans (Ponce de León et al., 2008; Weaver and Hublin, 2009; however see also Coqueugniot & Hublin, in press).

Shape differences between the braincases of modern human neonates and the two Neandertal neonates from Mezmaiskaya and Le Moustier 2 are only subtle. The pronounced endocranial differences between adult modern humans and Neandertals (Bruner et al., 2003; Bruner, 2004; Bastir et al., 2011; Fig. 2) therefore develop after birth. We have previously shown that a 'globularization-phase' (Fig. 1) directly after birth distinguishes modern humans from chimpanzees (Neubauer et al., 2010). The statistical analyses presented here show that this phase is also absent from Neandertals.

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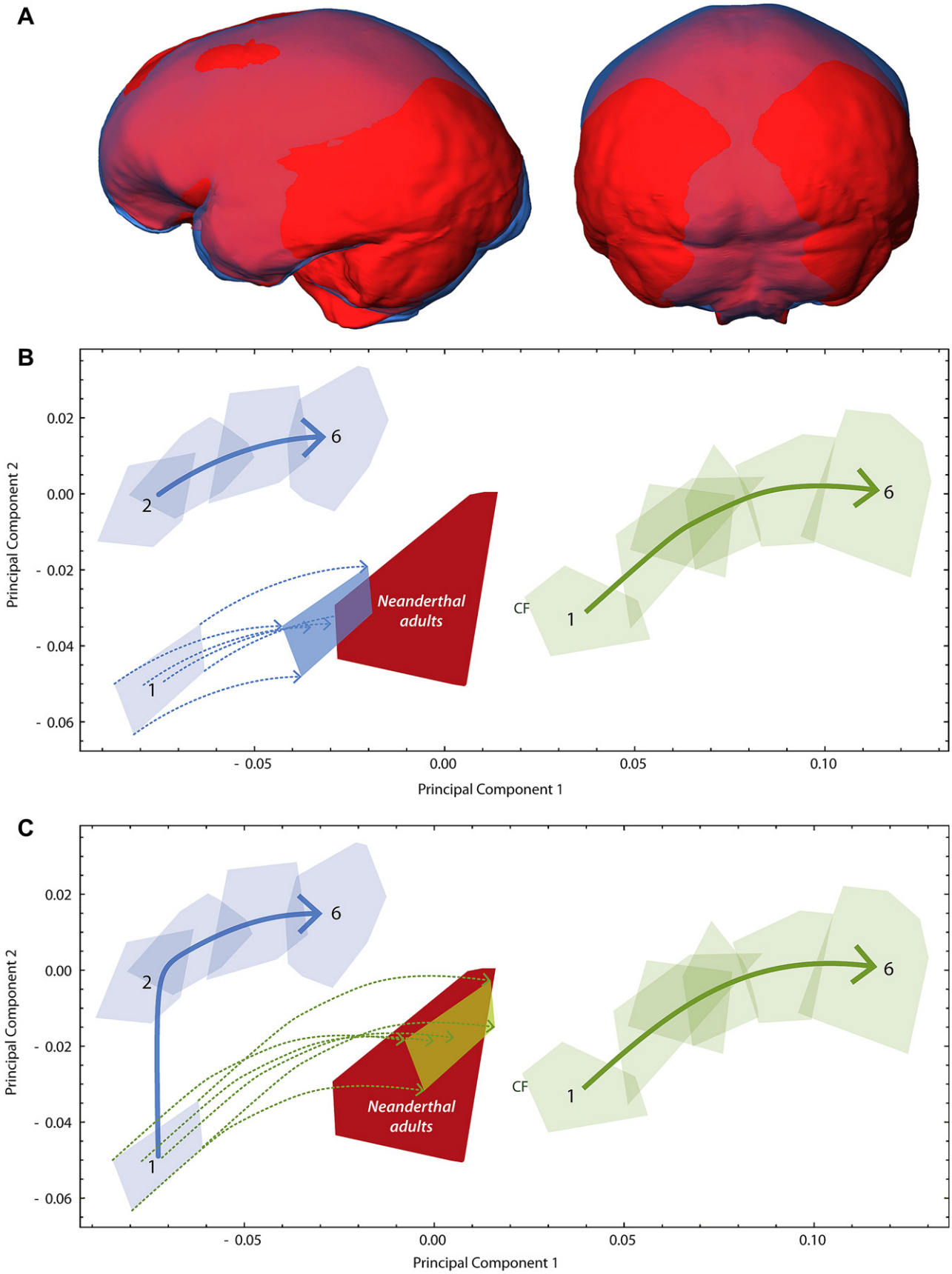

Figure 9. Forward Simulations of hypothesis B1 (upper and middle panel) and B2 (lower panel). (A) Simulating how the endocasts of human neonates would look if they grew up without a 'globularization phase'. The mean shape of the simulated adults (blue) looks almost exactly like the actual Neandertal mean shape (red). (B) In the PCA space of Fig. 7 these simulated adults plot close to actual Neandertal adults. (C) Simulating how the endocasts of human neonates would look if they grew up along the developmental trajectory of chimpanzees. Likewise, these simulated adults fall near to actual Neandertal adults in PC space. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Between dental ages 1 and 2, the endocast changes from an elongated to a more globular shape in *H. sapiens*. By contrast, the shape differences between the two Neandertal newborns Le Moustier 2 and Mezmaiskaya (age group 1) and Pech de L'Azé (age group 3) are so small that their reconstruction distributions overlap in Figs. 6 and 7.

Our 'backward' simulations demonstrate that if Neandertals had a 'globularization-phase', then their crania would have to be extremely elongated at the time of birth (Fig. 8). This prediction, however, is not consistent with the preserved morphology of Mezmaiskaya (Fig. 5) and Le Moustier 2 (Gunz et al., 2010, 2011).

We used 'forward simulations' based on modern human neonates to test our hypothesis, independent of the estimation uncertainty that is inherent to reconstructing incomplete fossils. If the brain of a modern human baby would grow up without a 'globularization phase', or along the developmental trajectory of a chimpanzee, then its endocast would look almost exactly like a Neandertal (Fig. 9). These 'forward simulations' make the idealized assumption that Neandertal neonates look exactly like modern human neonates. The difference between the actual adult Neandertal mean and the predicted mean shape (Fig. 9) implies that some Neandertal characteristics are already established at the time of birth. Consequently, to support our hypothesis that Neandertals did not have a 'globularization-phase' the endocast of a Neandertal neonate would have to be slightly more elongated than that of a modern human newborn, with flatter parietal bones and a slightly flatter occipital. Both predictions are consistent with the morphology of the Neandertal neonates, Le Moustier 2 and Mezmaiskaya.

Collectively, these results conclusively demonstrate that the postnatal developmental trajectories of the endocranium differ among modern humans, Neandertals, and chimpanzees.

We interpret those aspects of endocranial shape change that are shared among modern humans, Neandertals, and chimpanzees (dental age groups 2–6) as conserved. They likely represent a generalized developmental pattern in apes and hominins (Leigh, 2004). Analyzing Neandertal endocasts in this comparative framework suggests that they achieved endocranial volumes comparable with modern humans following this presumably ancestral pattern of development. Our results therefore provide an ontogenetic dimension to the adult endocranial shape differences between modern and archaic humans described by Bruner and colleagues (Bruner et al., 2003; Bruner, 2004, 2007, 2010).

What underlies endocranial shape?

Early ontogenetic shape changes of the endocranium are influenced by two factors: the volume expansion of the brain, its surrounding tissues and the cerebrospinal fluid on one hand, and sutural growth of the neurocranial bones on the other hand. During the first years of life, the cranial bones are thin and the cranial sutures are still open to accommodate the rapidly expanding brain (Moss and Young, 1960; Enlow, 1968; Enlow and Hans, 1996). Evidence from patients with craniosynostosis shows that if cranial sutures close before brain growth is complete, then the cranium yields to the pressure by growing at those sutures that are still open as well as via compensatory appositional growth of other parts of the skull, resulting in deformed braincases (Morriss-Kay and Wilkie, 2005; Richtsmeier et al., 2006; Richtsmeier and Deleon, 2009; Heuzé et al., 2010). It follows that the growth rate and timing of brain development and the timing of suture closure affect endocranial shape. Recent evidence from the Neandertal genome project suggests that genes involved in cognitive development as well as genes that have been linked to bone growth show evidence for a selective sweep in modern humans (Burbano et al., 2010; Green et al., 2010). It is therefore possible that both major factors affecting braincase shape—mode and timing of brain development and timing of sutural growth—distinguish modern humans from Neandertals.

While during early postnatal development the brain is the main factor that drives the shape changes of the braincase (Moss and Young, 1960; Enlow, 1968; Enlow and Hans, 1996), not all of the shape changes along the developmental trajectory are tied exclusively to brain development. The cranial base has its own developmental trajectory (Jeffery, 2003, 2005; Jeffery and Spoor, 2004), and its shape changes after the cessation of brain growth are largely driven by the continued development of the face (Sperber, 1989; Bookstein et al., 2003; Bastir and Rosas, 2006, 2009; Bastir, 2008; Rosas et al., 2008; Neubauer et al., 2009, 2010; Bastir et al., 2010). Maureille and Bar (1999) suggested that the premaxillary suture could have had a slower synostosis in Neandertals, which could indicate an extended period of facial growth in Neandertals. The endocranial shape changes along the 'shared' part of the developmental trajectory are most prominent in the cranial base. The upward rotation of the cribriform plate and the extension of the clivus, are consistent with the increase in facial size, height and projection during ontogeny. However, it is unlikely that facial development alone could explain the shape changes of the parietal and occipital bones during modern human ontogeny. The documented shape changes of the occipital bone are most likely related to the rapid growth of the cerebellum. Longitudinal MRI data show a 240% increase in the size of the cerebellum in the first year of life (Knickmeyer et al., 2008). We therefore suggest that the endocranial 'globularization-phase' reflects a uniquely modern human pattern of early brain development (Neubauer et al., 2009; Gunz et al., 2010), which involves the cerebellum as well as parts of the cerebral cortex.

Relationship between cognition and development

Discussions about the cognitive abilities of fossil hominins often focus on material culture and endocranial volumes. However, these proxies are not sufficient to resolve the ongoing debate about potential cognitive differences between modern humans and Neandertals, as the interpretation of the archaeological evidence remains controversial (Chase and Dibble, 1987; Klein, 2000; McBrearty and Brooks, 2000; d'Errico, 2003; Golovanova et al., 2010), and the brain size ranges of Neandertals and modern humans overlap (Ruff et al., 1997). Moreover, there is a long-standing debate as to the relationship of brain size and measures of cognitive performance among living modern humans. Multiple lines of evidence suggest that the internal organization of the brain is more important for cognitive abilities than its absolute size is (Schoenemann et al., 2000; Schmithorst et al., 2005; Shaw et al., 2006; Luders et al., 2009; van Leeuwen et al., 2009).

It has been posited that the globular brain shape of modern humans might have a positive effect on the wiring efficiency of the brain's neural network (Hofman, 1989; Chklovskii and Stevens, 2000; Chklovskii et al., 2002), and Li et al. (2009) have shown that the efficiency the brain's structural organization may be an important biological basis for intelligence. Bruner et al. (2011) recently studied the correlation between the overall shape of the brain's midsagittal profile and several psychological measures. These authors found only limited correlation between the overall brain geometry and mental speed among modern individuals, with only 2–3% of the variance of some cognitive measures explained by the midline shape of the brain. The large-scale properties of the brain's network topology sensu Li et al. (2009) aside, it therefore seems that the overall shape of the braincase per se does not have much significance for brain function.

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From the parameters that can readily be gleaned from endocasts, neither brain size nor overall brain shape seems to play a key role for cognitive abilities among living people. While the developmental process underlying the modern 'globularization-phase' is currently unknown, the fact that it occurs during the first year of life might provide an important clue regarding its potential impact on cognition. Clinical studies have demonstrated that the tempo and mode of brain development affect the pattern of neural wiring, and thereby behaviour and cognition. A well-documented example for the severe effects of alterations of early brain development is autism, where an accelerated rate of brain growth in the first years of life has been linked to local over-connectivity and fewer large-scale, long-distance connections between brain regions that are far apart (Courchesne et al., 2003, 2005). It has been suggested that this early overgrowth prevents the formation of neural circuitry essential for initiation, perception, and interpretation of socio-emotional and communicative functions (Herschkowitz, 2000; Gale et al., 2004), as well as higher order cognitive, memory and attention functions (Courchesne et al., 2007).

While ontogenetic changes of shape and ontogenetic changes of endocranial size can be separated algebraically during the Procrustes superimposition, they are tightly related. The schematic in Fig. 10 illustrates that the tempo and mode of brain development not only affect the brain's internal organization but endocranial shape as well. It matters for the shape of the braincase, which parts of the brain grow when, and at which rate. Brain-shape changes during early ontogeny therefore reflect the developmental speed and timing of the underlying neural circuitry.

The brains of humans are not simply allometrically scaled compared with non-human primates (Preuss and Coleman, 2002; Rilling, 2006; Kaas, 2008). All great apes and humans have a large frontal lobe and frontal cortex (Semendeferi and Damasio, 2000; Semendeferi et al., 2002) and some have suggested that the pre-frontal cortex in particular is disproportionally enlarged in modern humans compared with non-human primates (e.g., Schoenemann et al., 2005; Rilling, 2006; Schoenemann, 2006). An increase of white matter volume seems to be the most important factor distinguishing modern humans from their ape cousins (Semendeferi et al., 1997; Schoenemann et al., 2005). Comparisons with non-human primates, especially the intensively studied macaque monkey, also reveal regional species differences in the pattern of cortical maturation (Hill et al., 2010). It has recently been shown that both humans and chimpanzees differ from macaques in the delayed development of white matter volume, especially in the pre-frontal portion of the brain (Sakai et al., 2011). Compared with macaques, the brains of humans and chimpanzees are therefore less mature at the time of birth. It has been suggested that the protracted period of development in certain areas of the human brain increases the influence of postnatal experience on these regions (Johnson, 2001; Coqueugniot et al., 2004; Hill et al., 2010; Sakai et al., 2011). Sakai et al. (2011) could also show a dramatic increase of pre-frontal white matter volume during human infancy, which was not observed in chimpanzees.

Around the time of birth the neural circuitry is sparse in humans (Huttenlocher, 2002) and the subsequent emergence of functional capacity depends on the creation and refinement of synapses, neuronal growth and differentiation, as well as myelination (Quartz and Sejnowski, 1997; Karmiloff-Smith, 1998; Courchesne and Pierce, 2005; Knickmeyer et al., 2008; Sherwood et al., 2008; Rakic, 2009). The brain's internal organization depends on precisely timed sequences of synaptogenesis and the subsequent selection and elimination of connections, but it is not intrinsically predetermined (Changeux and Danchin, 1976). During early development, synaptic connections are over-produced to about two times the adult number and are subsequently pruned (Rakic et al., 1986; Petanjek et al., 2011). In modern humans, major internal brain reorganizations have been documented until adolescence (Giedd et al., 1999; Sowell et al., 2004; Paus, 2005; Toga et al., 2006; Schumann et al., 2010) and beyond (Dosenbach et al., 2010). To a large extent the wiring of the human brain is therefore established after birth, under the strong influence of environmental stimuli and experiences (Als et al., 2004; Coqueugniot et al., 2004).

While inferences about the cognitive abilities of extinct humans must necessarily remain tentative, our findings draw attention to a potentially informative developmental difference between modern humans and their closest fossil relatives during a critical time for cognitive development. Studies of brain growth (Ponce de León et al., 2008) and dental development suggest that some aspects of Neandertal development occurred at a faster rate than in modern humans (Smith et al., 2007a,b, 2010), although overlap exists (Guatelli-Steinberg et al., 2005; Macchiarelli et al., 2006; Bayle et al., 2009). We therefore consider it likely that the

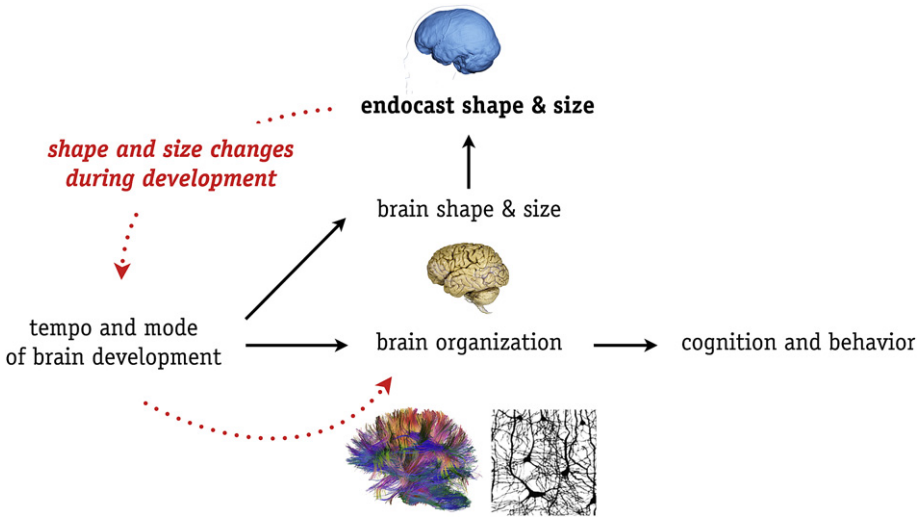

Figure 10. Clinical studies have demonstrated that the tempo and mode of brain development affect the pattern of neural wiring, and thereby behaviour and cognition. Tempo and mode of brain development also affect brain shape and size. Brain-shape changes during development reflect the developmental speed and timing of the underlying brain circuitry. In this schematic, the macroscopic and microscopic levels of brain organization are illustrated by an in-vivo image of the brain's white-matter structural connectivity (using diffusion tensor imaging data; colours reflect the main fibre orientations), and a histological section of pyramidal neurons.

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developmental processes that underlie the modern human 'globularization phase' reflect species differences in either localized or overall brain growth rates and timing. Either the cerebellum (Dobbing and Sands, 1973; Weaver, 2005; Volpe, 2009) and the parietal lobe grow at different rates and times in modern humans and Neandertals, or the presence or absence of a 'globularization phase' reflects differences in overall developmental speed and timing that affect the entire brain. With regards to the developmental differences between Neandertals and modern humans, we therefore suggest that not the shape changes associated with the 'globularization phase' per se, but the underlying species differences in postnatal brain growth rates and timing are likely to affect the layout of the synaptic connections and thereby behaviour and cognition.

Conclusions

We document a uniquely modern human pattern of endocranial development that separates us from our closest living and fossil relatives, the chimpanzees and Neandertals. Analyzing ten adult and subadult Neandertals in a comparative ontogenetic framework of recent *H. sapiens* and *Pan troglodytes*, we show that many aspects of the endocranial developmental patterns are shared by the three groups. However, in the first year of life, modern humans depart from this presumably ancestral pattern. The distinct globular shape of the braincase of adult *H. sapiens* is largely the result of a 'globularization phase' in the first year of life, which is not present in chimpanzees and Neandertals. All of our adult and subadult fossil reconstructions support the same conclusion, even in light of the estimation uncertainties. Developmental simulations that do not rely on subadult Neandertals also confirm that the endocasts of modern humans and Neandertals developed differently after birth. Modern humans and Neandertals therefore reach similar adult endocranial capacity through different postnatal ontogenetic pathways. The differences between these two human groups are most prominent directly after birth, a critical phase for cognitive development.

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Appendix. Supplementary material

Supplementary data related to this article can be found online at, doi:10.1016/j.jhevol.2011.11.013.

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