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Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration

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ABSTRACT

This paper aims at quantifying ontogenetic differences between bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) endocrania, using dental development as a timeline. We utilize a methodology based on smooth and invertible deformations combined with a metric of "currents" that defines a distance between endocranial surfaces and does not rely on correspondence between landmarks. This allows us to perform a temporal surface regression that estimates typical endocranial ontogenetic trajectories separately for bonobos and chimpanzees. We highlight non-linear patterns of endocranial ontogenetic change and significant differences between species at local anatomical levels rather than considering the endocranium as a uniform entity. A spatiotemporal registration permits the quantification of inter-species differences decomposed into a *morphological deformation* (accounting for size and shape differences independently of age) and a *time warp* (accounting for changes in the dynamics of development). Our statistical simulations suggest that patterns of endocranial volume (EV) increase may differ significantly between bonobos and chimpanzees, with an earlier phase of a relatively rapid increase (preferentially at some endocranial subdivisions) in the former and a much later phase of relatively rapid increase in the latter. As a consequence, the chimpanzee endocranium appears to reach its adult size later. Moreover, the time warp indicates that juvenile bonobos develop much slower than juvenile chimpanzees, suggesting that inter-specific ontogenetic shifts do not only concern EV increase, but also the rate of shape changes over time. Our method provides, for the first time, a quantitative estimation of inter-specific ontogenetic shifts that appear to differentiate non-linearly.

Introduction

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), two species of the genus *Pan*, are the closest relatives to humans. However, the comparative anatomy of bonobos has received less attention than that of chimpanzees, despite its emphasis in Kinzey's (1984) influential chapter (see also Shea et al., 1993; Braga, 1995a, 1998; Uchida, 1996; Braga and Boesch, 1997). The habitats of chimpanzees are ecologically more diverse than those of bonobos, and the latter seems to show less intraspecific variability in morphology (Shea et al., 1993; Braga, 1995b; Uchida, 1996) and DNA (Morin et al., 1994; Gonder et al., 1997, 2011; Kaessmann et al., 1999; Deinard and Kidd, 2000; Fischer et al., 2011). Genetic comparisons estimate that bonobo and chimpanzee lineages diverged approximately between 2 Ma (Horai et al., 1992) and 0.9 Ma (Won and Hey, 2005), even if both species, and chimpanzee subspecies, may have an intermixed genetic relationship (Kaessmann et al., 1999). This finding has important implications for hypotheses on behavior, phylogeography, ontogeny, and the evolution of both species. Variation in some morphological features correlates more closely with genetic data than others. For example, traditional craniometric data do not distinguish chimpanzee subspecies as clearly as discrete cranial (Braga, 1995b) and dental (Uchida, 1992) features. Questions of how different chimpanzees and bonobos are from one another are central to the understanding of evolutionary trends that may have caused the divergence between the two species of *Pan*.

Ontogeny of body size and sexual dimorphism

Bonobos were originally called pygmy chimpanzees. However, the use of large samples of individuals demonstrated that bonobos

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were not smaller in body weight than some populations of the eastern subspecies of chimpanzee (*Pan troglodytes schweinfurthi*) as most measurements overlapped (Jungers and Susman, 1984; Morbeck and Zilhman, 1989). Body growth (i.e., changes in body size over ontogeny) is probably retarded in the infant bonobo and closely corresponds to delays in motor and social development during its first years of postnatal life (Kuroda, 1989). Bonobos are also characterized by a longer dependency of the offspring on the mother (de Waal and Lanting, 1997), an earlier onset of menarche (Thompson-Handler, 1990), higher reproductive output in its natural habitat, better infant survival rates, and shorter inter-birth intervals (De Lathouwers and Van Elsacker, 2005). This creates a complex interplay between behavioral and reproductive traits, which are uncommon in other ape species. The two species of *Pan* show limited sexual dimorphism in overall body size. Leigh and Shea (1995) investigated possible differences in the ontogeny of adult body size dimorphism between chimpanzees and bonobos (among other species of apes) and concluded that bonobos become dimorphic primarily through sex differences in growth duration (bimaturism), while the moderate dimorphism observed in chimpanzees is the outcome of differences in growth rates. They suggested that the difference in sexual dimorphism was linked to differences in social systems. Data from captive animals and from field studies both suggest that, unlike chimpanzee society, bonobo society is female-dominated (Kano, 1992). Of particular interest is the understanding of hormonal regulation of body size. Among apes, body size is significantly positively correlated with the levels of two hormones (insulin-like growth factor, IGF, and growth hormone binding protein, GHBP) (Bernstein, 2010). Bernstein (2010: Figures 2 and 3) noted important differences in these hormone levels between bonobos and chimpanzees, and in their degrees of sexual dimorphism (sample sizes not specified). If these differences are confirmed by further studies, it would be interesting to investigate more precisely how these hormones regulate differential body size growth between the two *Pan* species.

Shea (1983a,b) suggested that inter-specific differences may be consequences of differential extension or truncation of a common ontogenetic trajectory (ontogenetic scaling). Later on, Leigh and Shea (1995) suggested that the extension of female growth in chimpanzees limited sexual dimorphism within this species, while truncated female growth in bonobos enhanced dimorphism. Subsequent comparative studies between the two species of *Pan* have focused mainly on analytical aspects of ontogenies—on comparisons between allometric ontogenetic trajectories (size-related shape changes) and heterochronies (real temporal differences in development), and on the possible correspondence between them (McKinney and McNamara, 1991; Godfrey and Sutherland, 1995). This was done to investigate whether or not size-related changes (allometric) during ontogeny were independent of those between shape and ontogeny.

The importance of endocranial ontogeny

The study of brain growth and development is essential to the investigation of diversity in *Pan* in terms of behavior and life-history parameters (Leigh, 2004; De Lathouwers and Van Elsacker, 2005; Kennedy, 2005), even if differences in ecological conditions may also play a significant role. However, because of allometric differences in brain size between primate species (Martin, 1983; Harvey et al., 1985; Leigh, 2004; Vinicius, 2005), and in the context of differential body size growth between bonobos and chimpanzees, the endocranium certainly requires more attention in order to understand how different these two species may be. The surface of the endocranium provides a replica of the inner cranial vault, or neurocranium, and therefore has often played an important role in analyses of brain evolution in fossil hominins (Holloway et al., 2005). The endocranium is sufficiently accurate and reliable as approximation of brain size and shape in ontogenetic studies, as discussed in Tobias (1994). The reasons are: (1) the percentage of the capacity occupied by the brain is inversely correlated with age up to adulthood (Tobias, 1994), and (2) sexual differentiation in absolute endocranial capacity and shape is not marked until after the emergence of the first permanent molar in chimpanzees (Zuckerman, 1928). So far, comparative data are typically derived from only a few crania and ontogenetic studies focus exclusively on mean values. Therefore, there are potential problems in studies that do not take into account variability within samples and species. In this study, we propose to address these issues in order to investigate possible differences in endocranial ontogenetic patterns between the two species of *Pan*.

The study of potential ontogenetic differences between chimpanzee and bonobo endocrania is not only a matter of size change (growth) but also implies shape change (development). In the past decade, studies have focused on differences in ontogenies of size (growth) or shape (development) (Williams et al., 2002; Mitteroecker et al., 2004, 2005; Lieberman et al., 2007). Williams et al. (2002) observed that the neurocranium, which embeds the brain, usually grows faster and reaches larger adult sizes in chimpanzees than in bonobos, with postnatal ontogeny contributing to differences between species at adulthood. Interestingly, in regard to ontogenetic shape changes across the postnatal life span, changes tended to be greater in the face than in the neurocranium. In terms of inter-species ontogenetic shape differences in timing and putative heterochronic interpretations, Williams et al. (2002) noticed that the infant bonobo cranial vault more resembled the shape of the infant chimpanzee than that of the adult bonobo. Likewise, allometric growth explains an important part of the morphological differences between the two species rather than a simple and overall ontogenetic dissociation between size and shape only. However, the size and shape of the outer neurocranium was captured using only four linear measurements (Williams et al., 2002). In contrast, Lieberman et al. (2007) viewed the bonobo skull as paedomorphic. However, using a larger set of neurocranial landmarks and semi-landmarks, Mitteroecker et al. (2004, 2005) falsified the hypothesis of pure heterochrony to explain morphological differences between bonobo and chimpanzee outer neurocrania. Even if their results were still considered within a heterochronic context, they argued that the developmental trajectories of the two related species did not lie along the same path; instead, dissociation of size changes against shape changes occurred during ontogeny. Even if these studies demonstrated important trends during the ontogeny of *Pan* species, they did not investigate the possible role of ontogenetic divergences at inner neurocranial (endocranial) local levels. In other words, the neurocranium has been considered a global entity represented by configurations of landmarks rather than an association of modules represented by *continuous* surfaces. It follows that these previous studies have not developed methods to adequately contribute to discussions on one of the most important biological principles of brain organization, evolution, and development: modularity (Redies and Puelles, 2001). Indeed, it is now well established that primate brains evolved through dissociations between modules of gene co-expression networks that correspond to the major anatomical subdivisions of the brain (Oldham et al., 2006).

Aims of this study

In this study, we aim to investigate non-linear, anisotropic inter-species and ontogenetic endocranial changes at local anatomical levels. We focus on two contrasting processes. First, we calibrate

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the ontogeny of each species in order to provide a synthetic representation of their modes as continuous surface changes over time, called an "ontogenetic trajectory." Second, we compare the ontogenetic trajectories of the two species to highlight both the morphological differences at each age and differences in development rate.

The description and interpretation of these two processes will be based on original statistical estimations computed from a set of virtual endocasts. Note that we do not assume any ancestral relationship between chimpanzees and bonobos because they likely represent two derived species, evidenced by their divergence from a common ancestor and the *Pan*-hominin dichotomy (Wood and Harrison, 2011). Therefore, we do not consider our data in a heterochronic framework.

A methodology based on deformations

In his seminal work, the zoologist D'Arcy Thompson (Thompson, 1917) emphasized the importance of mechanical and physical forces to explain the form of living organisms. Recently, his hypothesis has been demonstrated experimentally (Hamant et al., 2008; Mulder, 2008). Ontogeny is not only driven by the genetic program of individuals, but also by results from equilibrium between anatomical structures and their environment. From the point of view of continuum mechanics, the balance between the internal constraints of a biological tissue and the external forces exerted on to it, results in the deformation of this biological material. In the absence of tearing, and without the appearance of new structures, this deformation is mathematically modeled as a "diffeomorphism": a one-to-one deformation of the 3D space that is smooth, invertible, and with a smooth inverse. D'Arcy Thompson observed that differences in shape between species can be well explained by such deformations, which in turn, are indicative of the effects of the physical forces that led to these differences (Thompson, 1917). This has several important consequences. First, even if the ontogeny and the evolution of an organism are two very different processes, they can be modeled with the same mathematical tool, the diffeomorphisms, as an estimation of deformation. Second, analysis of biological shapes should not be contingent on the positions of points sparsely distributed on their contours. A powerful alternative is to rely on the deformation of the underlying continuous 3D space, which maps one shape onto another shape. In this paper, we will take this alternative approach, which might give a more efficient characterization of shape differences from a statistical point of view because the number of degrees of freedom of a smooth map between surfaces is independent of (and in practice often much smaller than) the number of sample points on the shapes. Third, the comparison between biological shapes should be made at a certain scale. It is clear, even in D'Arcy Thompson's work, that one should not look for an *exact point-to-point* correspondence between shapes, since the reproducible effects across individuals and species occur at a certain scale—the differences at smaller scales being characteristic of a single individual. When working with virtual data, small-scale differences could also result from noise introduced during the imaging process and during image segmentation.

Based on these considerations, the present study relies on fitting deformation-based models to data. We will utilize the work of Miller et al. (1993), Trouvé (1998), and Grenander and Miller (1998), which give the mathematical, statistical, and algorithmic foundations of the seminal vision of D'Arcy Thompson. More precisely, we will use one of the latest developments of this research (Durrleman, 2010), which introduced statistical models for the analysis of longitudinal and time-series shape data via the introduction of spatiotemporal deformations.

Methodological contributions in light of Geometric Morphometrics

A typical method for comparing fossil data is Geometric Morphometrics (GM) (Bookstein, 1991; Dryden and Mardia, 1998). Although our method relies on an initial Procrustes alignment of unscaled-shapes, it differs in two ways from GM. Firstly, the Procrustes alignment and the measure of shape differences are not based on prior definition of homologous points but on correspondences between continuous surfaces. Secondly, the statistics are not based on the positions of individual points but on deformations, which establish mappings between unscaled surfaces. Although GM has often considered itself in opposition to deformation-based morphometry (see Bookstein, 1996; Mitteroecker and Gunz, 2009), we will see that GM is essentially a linearization of deformation-based models.

From landmarks to currents Geometric Morphometrics is based on the correspondence among homologous points across samples. Originally, these landmarks corresponded to anatomical points whose definition allows one to identify them uniquely in all samples. However, for shapes like the endocast, such landmarks are rare. Summarizing a complex 3D surface into a sparse set of landmarks is not sufficient to describe surface changes accurately across time or across species. This makes the use of GM on these data particularly challenging. To overcome this limitation, the notion of pseudo-landmarks, which are defined by relative locations, has been introduced. Because this set of points is still often too sparse, one defines semi-landmarks, which aim at covering the surface in between the previous landmarks with a more dense set of points (Bookstein, 1991; Dryden and Mardia, 1998). However, the assumption that pseudo- or semi-landmarks are homologous across samples does not account for the fact that their positions depend on the procedure used to find them. Efforts have been made to make these procedures reproducible and therefore limit variations due to user choice. From this perspective, the "currents" can be considered the next generation of morphometric tools, in that they address both the problem of selecting relevant points on the surface and the problem of finding correspondences between these point sets (Glaunès, 2005; Vaillant and Glaunès, 2005). The metric of currents takes all data points into account (without selecting any of them) and does not assume a point-to-point correspondence between samples. This enables the direct comparison of surfaces, even if they have a different number of sample points. Moreover, this metric takes into account the local orientation of a surface (i.e., its normals). This extra feature strengthens the measure of shape dissimilarities. The metric does not only measure how distant two surfaces are, but also how their respective local orientations differ.

From point displacements to dense and smooth deformations Fundamental to GM is the analysis of the residual positions of the landmarks after a Procrustes alignment of the point sets. To analyze these residuals, one often computes a Principal Components Analysis (PCA) on the point positions and the principal components (PCs) are used as descriptors of the shape variability. The ontogeny of a structure is characterized by the difference in landmark positions at different observation time-points. In any case, the results are expressed in terms of a displacement of the landmark points along a fixed direction (the one given by the PC, for instance). Such an approach makes sense from a statistical point of view, though it raises the issue of compatibility between the landmarks' *displacement* and the global *deformation* of underlying biological tissue. The landmark set is discrete whereas the tissue is continuous: this approach lacks an interpolation scheme, which explains how the landmark displacements can be seen as a discretization of a continuous deformation of the

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underlying tissue. To address this issue, one calls upon thin-plate splines as an interpolation function (Bookstein, 1989). However, these functions do not preserve the topological properties of the tissue. In particular, there is no guarantee that the proposed transformation does not imply a tearing of the biological tissue. Deformation-based models address this issue by adding the constraint that ensures the motion of the points will be compatible with a smooth and invertible deformation of the tissue. Even if the deformation is estimated from a discrete set of points, it guarantees that the deformation applied to a continuous surface will not involve tearing, shearing, important folding, or other unrealistic shape changes.

This constraint for consistency in the comparison of the configuration of point sets has an important consequence: the points very rarely follow a *straight* line, as in PCA, from their initial position on the source surface to their final position on the target surface. On the contrary, the motions of points induced by a smooth deformation of the underlying tissue are often *curved*. In this sense, the deformation process is *non-linear*.[1] This is particularly evident in the case of large displacements: if one goes too far in the direction of the PC, then some points move away from others, which clearly becomes incompatible with a smooth deformation of the tissue. Thin-plate splines are invertible only in case of "small deformations" (e.g., if the magnitude of the displacement and the Jacobian of the splines transformation is small). To build large diffeomorphic deformations, one concatenates infinitesimal splines transformations, which yield a globally smooth and invertible deformation between any configurations of point sets (cf. Trouvé, 1998). This construction shows that the thin-plate splines used in GM are nothing but the linearization of a smooth deformation—thin-plate splines are used as speed vectors (tangent to the point trajectories) instead of displacement vectors. Therefore, if important shape changes are involved, either during ontogeny or during evolution, and if one wants to avoid unrealistic tearing or folding of the shape, then a generalization of the thin-plate splines must be used, like the diffeomorphic deformations that are used in this study.

The problem with generalizations is that the models become so flexible that they can accommodate any surface changes. When deformations perfectly align two surfaces, they are likely to capture features that are specific to individuals and not indicative of a general trend in the population. To avoid so-called statistical overfits, we introduce a regularity constraint and intrinsic smoothness scales in our deformation-based models.

Characterization of ontogeny as a continuous process The difference between approaches based on linear displacements and those based on non-linear deformations is well illustrated in the case of analyses of development (shape changes in time inferred from time series data). In Neubauer et al. (2010), for instance, a shape change is described as the succession of landmark displacements between consecutive observations. In the absence of intermediate observations, landmarks are supposed to move along straight lines. As a consequence, the motion of the points follows broken lines. This is a linear interpolation scheme. By contrast, in deformation-based models, one supposes that the shape smoothly develops in time between the observations. The interpolation satisfies a minimum energy principle (like a mechanical system of self-interacting particles). The constraint of smoothness implies that the point trajectories are curved. This model mimics the true (though unknown) motion of the developing shape, in the sense that it guarantees the preservation of the topology of the tissues even in the presence of a large deformation between consecutive observations.

With an observation of the shape at a finer and finer resolution (in the limit, continuously in time), the linear interpolation of Neubauer et al. (2010) would converge to a diffeomorphic deformation—the broken lines would converge to smooth curves and the displacement during smaller and smaller time intervals would converge to the instantaneous speed of the points. With only a small number of consecutive observations, our interpolation scheme deviates less from the true solution, in that it maintains the smoothness of the shape development.

Linearity and non-linearity in models of developmental shifts In this study, we are interested in the differences in the timing of the modes of growth between species. The single tool available in the framework of GM for measuring relations between time and shape changes is statistical regression: regression between shape variables and a temporal marker like age or size (in the context of allometry). To the very best of our knowledge, only linear regressions have been considered so far in the context of fossil data analysis (e.g., Ponce de León and Zollikofer, 2001; Williams et al., 2002; Lieberman et al., 2007; Harvati, 2009; Neubauer et al., 2009, 2010; Mounier et al., 2011), although non-linear regressions could have been investigated as well. As a consequence, a classification of different configurations has emerged in heterochronic studies, assuming a linear relationship between shape variables and time (or size) (e.g., Alberch et al., 1979; Alba, 2002; Mitteroecker et al., 2004, 2005; Lieberman et al., 2007). Our comparative study between the two species of *Pan* is not made in this heterochronic context—we do not assume that one extant species (either *P. paniscus* or *P. troglodytes*) results from developmental changes that occurred over evolutionary time from the other species. Whether in a heterochronic framework or not, the assumption of a linear relationship between modes of growth is probably too simple, as would be the hypothesis that shapes differ only by isometric or affine transformations across species. We consider that differences in linear configurations are valid only *locally*, at a specific age, or during a small period of time. Indeed, the relative difference in growth pace between species has no reason to remain constant over time. One species may be advanced at infancy and delayed at adulthood. The succession of different linear configurations may lead to non-linear relationships between the paces of ontogenetic modes. This is exactly what models the "time warp" in our approach: a smooth, monotonic 1D function that maps the developmental stages of one species to those of another. The constraint of monotonic correspondences between the modes of growth guarantees the same ordering of the events, and therefore avoids time reversal. If the estimation of this time warp shows a linear pattern (i.e., its graph is a straight line) over a large period of time, this would result from data analysis and not from a prior assumption.

Analyses of residuals versus analyses of deformations From a more general perspective, GM can be seen as a particular instantiation of Kendall's (1984) shape space theory, mathematically modeled as quotient spaces: one considers the residual positions of the co-aligned points using a certain group of deformations, such as rigid-body, linear, or affine transformations. By contrast, the proposed methodology derives from Grenander (1993), which does not focus on the residual positions of the surfaces after registration, but on the deformations that align the surfaces. The statistical object of interest becomes the deformation itself instead of the residual positions after deformation. This requires using deformations with more degrees of freedom than linear transformations, like general diffeomorphisms, in order to capture most of the differences between the surfaces. The metric

[1] To avoid confusion, note that the non-linearity concerns here the time variable (i.e. the trajectory of the points). Both the splines and the diffeomorphic deformations are non-linear in the space variable.

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of currents, which plays the role of the sum of squared differences between landmark positions in GM, is not used to derive statistics on the shapes, but to drive the estimation of an optimal non-linear deformation that maps one shape onto another. Note that very recent works are tentative approaches to conciliate both Kendall's and Grenander's visions of shape statistics that take into account both the information given by the deformations and the one given by the dissimilarity metric, as in Trouvé and Younes (2005), Allassonnière et al. (2007), and Durrleman et al. (2009a).

Size and shape In GM, size is the scaling component of the initial linear alignment and shape is the residual to be analyzed. Such a distinction could also be made in the proposed framework—one pragmatic solution could have been to scale the specimen beforehand. More intrinsically, one could have decomposed the estimated deformations into a scaling and a volume-preserving deformation. However, in this study, we choose not to make such a distinction and to consider the surface deformation as a whole, as an estimation of the joint changes both in size and in shape. This inherently takes into account correlations between size changes and shape changes.

Summary of our approach

Surface regression for the estimation of species-specific ontogenetic trajectories For the proposed approach, we model the ontogenesis of a given species as the smooth deformation of a reference infant anatomy. This deformation shows how the reference anatomy continuously deforms across different developmental stages, and is therefore called an "ontogenetic trajectory." Mathematically speaking, the anatomy at each age t (S_t) can be derived from the anatomy at a reference age t_0, (S_{t0}) via a diffeomorphic deformation: $S_t = \chi_t(S_{t0})$. The time-varying 3D deformations χ_t characterizes the ontogenesis of each species. The movie of the moving S_t is the ontogenetic trajectory (see Supplemental Online Materials [SOM]).

Spatiotemporal registration between ontogenetic trajectories We model ontogenetic differences between species in two ways. First, differences can be due to a global change in shape. This models a factor, which affects the whole ontogeny in a similar manner, independent of a specific age. Second, we model the differences at any given age in which the ontogeny of a given species may be delayed or advanced compared to another species. This joint modeling assumes that the two species share the same modes up to an age-independent morphological deformation and an alteration of their timing. This excludes, for instance, the appearance of new modes of growth at a specific developmental stage of one species, which have not been observed in the other species. Mathematically speaking, shape differences are modeled by an age-independent 3D-deformation $\phi(x)$, which is called a "morphological deformation." The difference in the tempo is modeled by a 1D function $\Psi(t)$, which is called a "time warp." This function maps the ontogenetic stages of one species to the ontogenetic stages of the other species. We suppose this function to be a smooth increasing function of the time, meaning that the sequence of the developmental stages of the different species occur in the *same order*, even if their paces differ. The combination of the two deformations (ϕ,Ψ) is called a spatiotemporal deformation. Given B(t) as the bonobo ontogenetic trajectory, and C(t) as the chimpanzee ontogenetic trajectory, we postulate that the bonobo trajectory B(t) is equal to a regular spatiotemporal deformation of the chimpanzee trajectory: $\phi(C(\Psi(t)))$, up to a residual error. The residual error accounts for noise in the data, non-reproducible small-scale variations, and, more generally, for everything in the data that the model cannot explain. The estimation of this model leads to the best possible fit of the model to the data, namely the one that minimizes the residual error up to a regularity constraint. The norm of the residuals gives an estimate of the "goodness of fit."

In this framework, we analyze the differences between ontogenetic trajectories without assuming any ancestral relationship between the two species, outside any heterochronic framework. Mitteroecker et al. (2004, 2005) distinguished species with different ontogenetic trajectories (in shape or size) from those that share the same ontogeny (superimposition of every mode of growth), but with a different timing. The latter "ontogenetically scaled" species falls into the framework of heterochrony. In our modeling, we do not focus only on these two extreme cases, as the differences between ontogenies may combine both effects: size + shape changes, which make the modes different, and differences in timing. Indeed, using the same sample, Lieberman et al. (2007: 647) noticed that the first principal component of shape variation coincides between bonobos and chimpanzees up to a different timing, whereas the other principal components are different, thus concluding "not all aspects of shape differences (…) can be attributed to heterochronic transformation and (…) additional developmental differences must also have occurred during their evolution." Our model aims at precisely measuring such complex differences by decomposing them into morphological and temporal components. The role of the morphological deformation ϕ is to map the modes of ontogeny of one species to those of the other. This could be referred to as "ontogenetic scaling" (Mitteroecker et al., 2005), although this terminology can be confusing, since our deformation is non-linear and our modeling is not limited to allometry. The time-warp Ψ measures the different timing between the "ontogenetically aligned" growth trajectories.

Assuming that differences in shape and timing may co-exist raises an important methodological issue: if one species is delayed with respect to another, then analyses of shape differences between the species should not use data from both species at the *same* age, but at the ages that correspond to the same degree of development. Otherwise, shape differences will be confounded by differences in ontogenetic pace. As a consequence, the two components of the spatiotemporal deformations are estimated *simultaneously*: the analysis of ontogenetic differences takes into account current estimations of temporal delays that are assessed once the unscaled shape differences have been discarded (or "ontogenetically scaled") by the morphological deformation.

As a generalization of GM approaches, we propose to use the metric of "currents" to measure inter-surface differences (Glaunès, 2005; Vaillant and Glaunès, 2005). This metric does not select any particular point on the surfaces and does not assume any kind of correspondence between points. It considers all pairs of points, whose weights depend on their relative distance. This metric also has the advantage of taking the local orientation of the shapes (i.e., normals) into account: one does not only measure how distant two surfaces are, but also how the orientations of their tangent planes differ (i.e., the metric is sensitive to the curvature of the surfaces). In this way, one does not discard any information about the surfaces. Moreover, this metric does not depend on how the surfaces are sampled, in the sense that the computed metric is a controlled approximation of the metric between the two underlying continuous surfaces. We refer the reader to Durrleman et al. (2009b) and Durrleman (2010) for more computational details and a more exhaustive explanation about the estimation of these deformation-based models using the metric of "currents." For examples on the use of such methods in the context of biomedical imaging, we refer the reader to Qiu et al. (2007), Durrleman et al. (2008), Auzias et al. (2008), and Tilotta et al. (2010).

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Materials and methods

Data

We used a set of endocrania reconstructed from the dry skulls of 59 chimpanzees and 60 bonobos (housed in the Musée de l'Afrique Centrale, Tervuren, Belgium). Most, if not all, of the bonobo skulls sampled in GM studies (Mitteroecker et al., 2004, 2005; Lieberman et al., 2007) come from this collection. It represents the best available source of data for anatomical comparisons between bonobos and chimpanzees and has been widely used for this purpose. These skulls represent pooled-sex (with approximately equal numbers of males and females) and cross-sectional samples of mostly wild-shot animals (some specimens may have been captive for some period). They have been scanned using a Siemens Somatom Esprit Spiral CT, with slice thickness between 0.33 mm and 0.50 mm. The segmentation of the endocrania using itkSNAP (Yushkevich et al., 2006) leads to surface meshes that have been rigidly co-registered using GMMREG (Jian and Vemuri, 2005): shapes are "superimposed" using only translation and rotation but not scaling. The technique developed in Jian and Vemuri (2005) achieves this optimal alignment even in the absence of point correspondences between surfaces.

A proxy for age

Aspects of ontogenetic changes have often been investigated by using size as a proxy for age, when this later chronological age data were not available. However, because size cannot be considered as uniformly increasing with age independently of the species considered, a substitution of size for age might be problematic (McKinney, 1988; Godfrey and Sutherland, 1995). Moreover, such an approach confounds shape changes, which does not imply a change in volume. At the same time, tooth calcification is critically integrated into the life cycle in living mammals and represents an important maker of maturity on both extant and fossil primate species. For example, it has been demonstrated that the age of emergence of the permanent mandibular first molar is correlated with markers of prenatal, infantile, juvenile, and adult periods, as well as with brain weight for 21 primate species (Smith, 1991). In particular, it is well established that, in extant primate species, M1 emergence occurs near the time of the cessation of neural growth. Therefore, in this study, since the developmental sequence of permanent teeth is considered as essentially identical in bonobos and chimpanzees (Kinzey, 1984), we assume that tooth calcification stages provide a useful interface for the comparison of ontogenetic patterns between the two species of *Pan*. The ontogenetic trajectories are estimated as regressions between the unscaled shapes and the dental developmental stages. Delays between two ontogenetic trajectories are defined with respect to these dental stages.

The degree of development of the permanent tooth germs is assessed using CTs in order to classify each skull into one of the following six dental stages (Shea, 1989) (Table 1): "infant" (<1 year of age) with incomplete deciduous dentition; "stage 2 infant" (1–3 years of age) with complete deciduous dentition but with no permanent teeth emerged; "young juvenile" (3–6 years of age) with the second permanent molar not yet emerged; "old juvenile" (6–11 years of age) with the third permanent molar not yet emerged; "sub-adult" with a complete permanent dentition but unfused spheno-occipital synchondrosis; and "adult" with a fused spheno-occipital synchondrosis. To refine the classification, some skulls have been associated with the intermediate class of "stage 2 infant/young juvenile."

For the application of our methodology and without loss of generality, we suppose that each "dental stage" lasts the same amount of time, namely five time-points. Different durations would only scale the rate of shape/size changes over time and therefore would not change the speed of development of one species relative to the other. Therefore, postnatal time interval is divided into 30 time-steps and the endocrania are associated to the time-point $t_i = 5$, 10, 15, 20, 25, or 30, according to their dental age. The "stage 2 infant/young juvenile" stage has been associated to time-point 13. We do not make any assumptions on the relationship between the estimated dental stage and the real age of the individuals. Chronological data from living free animals represent the ideal data to compare the rates of growth and development between chimpanzees and bonobos. In the absence of these data, we use dental eruption markers only to help us to define life stages and the transitions between them. The dental eruption markers used in the present study may not occur at the same chronological ages in living free chimpanzees and bonobos. Ideally, this crucial matter needs to be investigated in future histological analyses of large samples of wild-born specimens.

Table 1
Number of individuals within each age group used in this study.

	Bonobos	Chimpanzees
Infant	4	2
Stage 2 infant	8	6
Stage 2 infant/young juvenile	3	4
Young juvenile	11	10
Old juvenile	7	13
Sub-adult	9	10
Adult	18	14
Total	60	59

Estimation of the deformation-based models

As already outlined, the estimation of deformation-based models relies on the metric of "currents" to measure the dissimilarity between endocrania. This metric depends on a parameter λ_W, to determine the typical spatial scale at which differences are taken into account. The effect of the parameter on the metric is not unlike smoothing the surfaces with a Gaussian kernel of standard deviation λ_W (although, to be more precise, this Gaussian smoothing is done on the test space of the vector fields, which is used to probe the surfaces and not the surfaces themselves [Durrleman, 2010]). This parameter is introduced so that the metric is made insensitive to small-scale surface variations, which may likely be due to shape variations that are specific to individuals and not reproducible across individuals. It also accounts for segmentation errors or inherent differences that may occur when using different segmentation methods. Considering the typical size of the endocrania (diameters between 60 mm and 70 mm), and surface enlargement due to growth, we set this parameter to $\lambda_W = 10$ mm.

Our model introduces two 3D deformations, $\chi(x)$ and $\phi(x)$, which are diffeomorphisms of the underlying 3D space, and one 1D-deformation, $\Psi(t)$. The hypotheses about the smoothness and monotonic property of the time-warp $\Psi(t)$ make this function a diffeomorphism of the time interval of interest. Each of the introduced deformations has an intrinsic scale that controls its regularity. This scale is denoted λ_χ; λ_ϕ for each 3D-deformation is a length, which determines the typical scale at which we consider different modules to deform independently. The scale of the 1D-deformation $\Psi(t)$ is denoted λ_Ψ. It is a time-length that determines how fast a temporal shift between the tempos of the modes of growth may occur. Note that none of these parameters are hard thresholds, but are indicative of the bandwidth of a Gaussian kernel.

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Estimation of ontogenetic trajectories The estimation of an ontogenetic trajectory for each species is stated as a surface regression problem, which minimizes a least-squares criterion up to a regularity constraint. This leads to the estimation of two ontogenetic trajectories of the form $B(t) = \chi^b_t(B_0)$ and $C(t) = \chi^c_t(C_0)$, where $\chi^b_t(x)$ and $\chi^c_t(x)$ are two continuously time-varying deformations, and B_0 and C_0 are the smallest endocrania within the bonobo and the chimpanzee samples, respectively. The origin of the time interval has been set to the time-point $t_0 = 1$. For this estimation, the intrinsic rigidity parameter of the deformations has been set to $\lambda_\chi = 20$ mm, considering the ontogenetic rate of the endocasts. The trade-off between the regularity of the deformations and the fidelity-to-data has been set to $\gamma_\chi = 10^{-3}$ mm^2 (unit of time).

Estimation of the spatiotemporal deformation The estimation of the spatiotemporal deformation (the combination of the 3D morphological deformation ϕ and the time-warp Ψ, which maps the chimpanzee ontogenetic trajectory to the bonobo one) is stated as the minimization of the discrepancy between the deformed chimpanzee ontogenetic trajectory $\phi(C(\Psi(t)))$ and the bonobo ontogenetic trajectory, up to a regularity constraint. For this estimation, both ontogenetic trajectories have been sampled at every two time-points. In order not to rely on the small number of infant data, we remove from the two ontogenetic trajectories the part corresponding to infancy between time-points 1 and 10. As a consequence, we detect differences in ontogenetic modes *from stage 2 infancy only*. To set the parameters of the spatiotemporal deformations estimation, we perform an exhaustive search of the best parameters within a reasonable range. The best parameters set is the one for which the residual errors were the smallest, meaning that it achieves the best possible alignment between the two species' trajectories. This results in the intrinsic regularity parameter of the morphological deformation $\lambda_\phi = 10$ mm, the regularity parameter of the time-warp $\lambda_\Psi = 1$ unit of time, the trade-off between the fidelity-to-data and the morphological deformation $\gamma_\phi = 10^{-5}$ mm^2, the trade-off between the fidelity-to-data and the time-warp $\gamma_\Psi = 10^{-5}$ mm^4/(unit of time), and the relative importance of the morphological deformation with respect to the time-warp $\sigma_\phi/\sigma_\Psi = 8$.

Estimation of confidence intervals with bootstrap

We estimate confidence intervals for the endocranial volume changes (growth) given by the ontogenetic trajectory and for the estimated time warp, which measures the possible ontogenetic shifts between the two species. We rely on a bootstrap procedure: within the age group of each species, we randomly resample with replacement a new set of specimens with the same original sample size. From these new samples, we estimate a new bonobo and chimpanzee ontogenetic trajectory and a new spatiotemporal registration between them (discarding the part of the trajectory corresponding to infancy between time-points 1 and 10). This procedure is repeated 100 times. For each time-point, we discard the five largest values and the five smallest values to give an estimate of the 90% confidence interval.

Robustness of the results with respect to dental age estimation

Because different individuals within the same dental age group may correspond to different developmental stages, our classification into a few developmental stages and age groups may confound differences in temporal development. To assess this possible confounding effect, we simulate a *continuous* dental age estimate within each age group by randomly shifting every dental age along the time axis. This is done by adding a zero-mean Gaussian variable with a standard deviation of one time-point to the dental age of each sample. This means that in 50% of the cases the dental ages have been shifted by $+1$ or -1 time-points, in 10% of the cases they have been shifted by more than one time-point, and in 40% of the cases they have not moved. We recall that the duration of every dental age group was of five time-points in the original experiments, meaning that in 10% of the cases, the age estimate was shifted at or beyond the boundaries of its group. Given these new age estimates, we compute two new ontogenetic trajectories and then the spatiotemporal deformations between the part of the trajectories between stage 2 infancy and adulthood. We repeat this procedure 100 times. We define a 90% variability interval by discarding the five largest and five smallest values of any scalar measurements taken out of these simulations.

Robustness of the results with respect to parameter values

We assess the effect of the parameter values on the estimation of the spatiotemporal deformations between the two ontogenetic trajectories. We recall that the chosen values of the parameters achieve the best possible alignment between the trajectories. We duplicate this spatiotemporal registration for the parameters σ_ϕ varying between 17 and 90, σ_ϕ varying between 2 and 15 (for the ratio σ_ϕ/σ_ϕ varying between 7 and 9), and λ_Ψ varying between 0.5 and 2 time-points. These parameters mostly affect the balance between the morphological deformation and the time warp. We notice that the variations of the estimated deformations due to these parameter changes are much smaller than the variations due to the bootstrap sampling and to shifts in age estimates (results not shown).

Results

Local changes in endocranial ontogeny

For each species considered separately, we performed temporal regressions of endocrania with respect to successive dental developmental stages as proxies of postnatal somatic growth. This leads to a trajectory of local endocranial expansions within each species (Figs. 1 and 2; SOM Movies 1–4). In these two trajectories, both shape and size differences are expressed jointly. Moreover, local endocranial ontogenetic changes can be visualized with expanding (size increase and shape changes) areas in red or yellow (Figs. 1 and 2). A closer look at the two species-specific trajectories reveals that, in both cases, the various endocranial subdivisions change in different amounts, directions, and periods. The consequence of this differential expansion of the various subdivisions is a reshaping of the endocranium during ontogeny. In other words, endocranial changes in size and shape do not correspond to a simple global scaling; they involve non-linear and anisotropic effects (Figs. 1 and 2). Notably, in both species, the endocranium expands and reshapes only locally with different patterns between chimpanzees and bonobos.

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Common features shared by the chimpanzee and bonobo trajectories For both species, the most salient change is an elongation along the posterior–anterior axis associated with a limited elongation along the superior–inferior axis (Figs. 1 and 2; SOM Movies 1–4). As a consequence, in both species, the geometry of the endocranium becomes more and more ellipsoidal, and less and less rounded.

Differences in trajectories between chimpanzees and bonobos The two ontogenetic trajectories differ notably at the stages of "infant"

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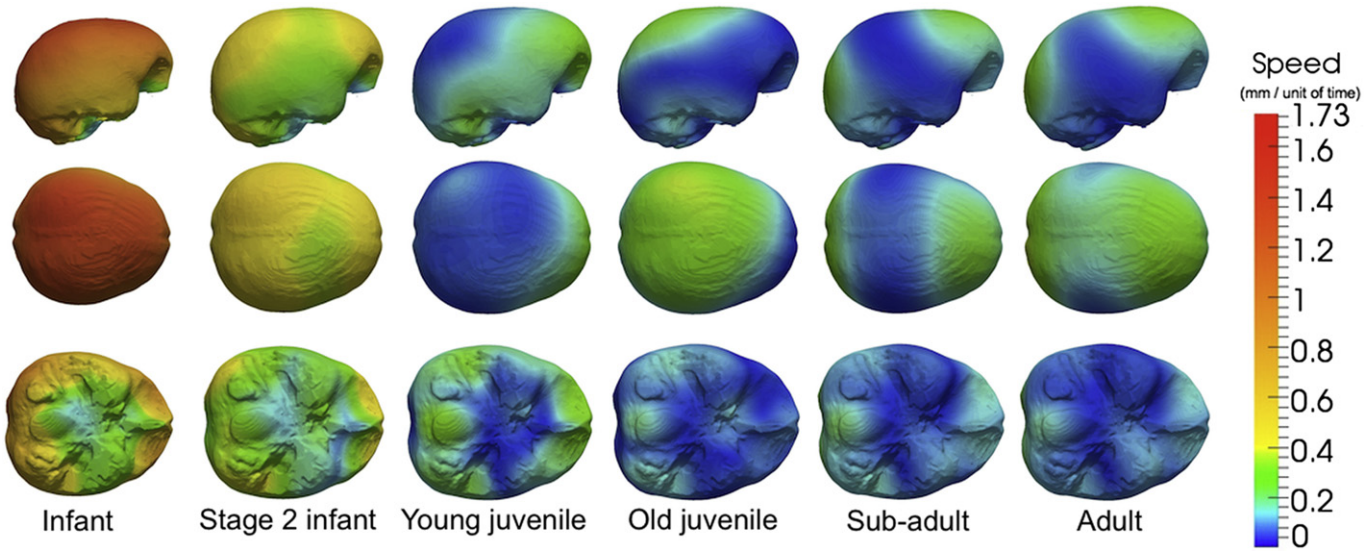

Figure 1. Six frames of the continuous ontogenetic trajectory estimated from the bonobo data. Colors indicate the instantaneous speed of the surface deformation. Best seen as a movie (SOM Movies 1 and 2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and "stage 2 infant" (Figs. 1 and 2). This difference may be partly due to the relatively small number in the "infant" sample. The chimpanzee endocranium shows the strongest anisotropy at all stages (Fig. 2). This anisotropy increases during postnatal growth and is more pronounced starting in the "old juvenile" stage. By comparison, the bonobo endocranium also shows an increasing anisotropic pattern in the anteroposterior direction, but this pattern seems to be more pronounced only from the "sub-adult" stage. The subsequent spatiotemporal registration will, more precisely, measure the consequences of this increasing anisotropic pattern in terms of inter-species differences.

In bonobos, well before the emergence of the first permanent molars, when the adult brain size is not yet reached, the endocranium expands notably in the frontal lobe and occipital lobes and in the superior part of the parietal lobe (Fig. 1; SOM Movies 1 and 2). Around these expanding zones, the remaining and much larger part of the endocast almost does not change. This mean pattern of endocranial shape expansion in the "stage 2 infant" bonobos moves the frontal and occipital poles apart. As a result, the frontal lobe moves upward, forward, and outward, resulting in an orbital divergence and an increase of the root of the inter-orbital segment. At the same time, the whole inferior aspect of the endocast remains unchanged. This causes a bending of the endocast, which may result in a small flexure of the cranial base and gives the endocasts a bulbous aspect.

In chimpanzees, we observe a very different pattern of endocranial expansion, with more local changes at each dental developmental stage (Fig. 2; SOM Movies 3 and 4). Expansions in the cerebellar area are notable in the "stage 2 infant" and "young juvenile" samples. An expansion of the frontal lobe is clearly visible in the "old juvenile" sample (associated with an expansion of the upper part of the parietal lobe) and to a smaller extent in the "adult" sample. However, this frontal expansion is topographically more limited than the one observed in bonobos at a much younger dental

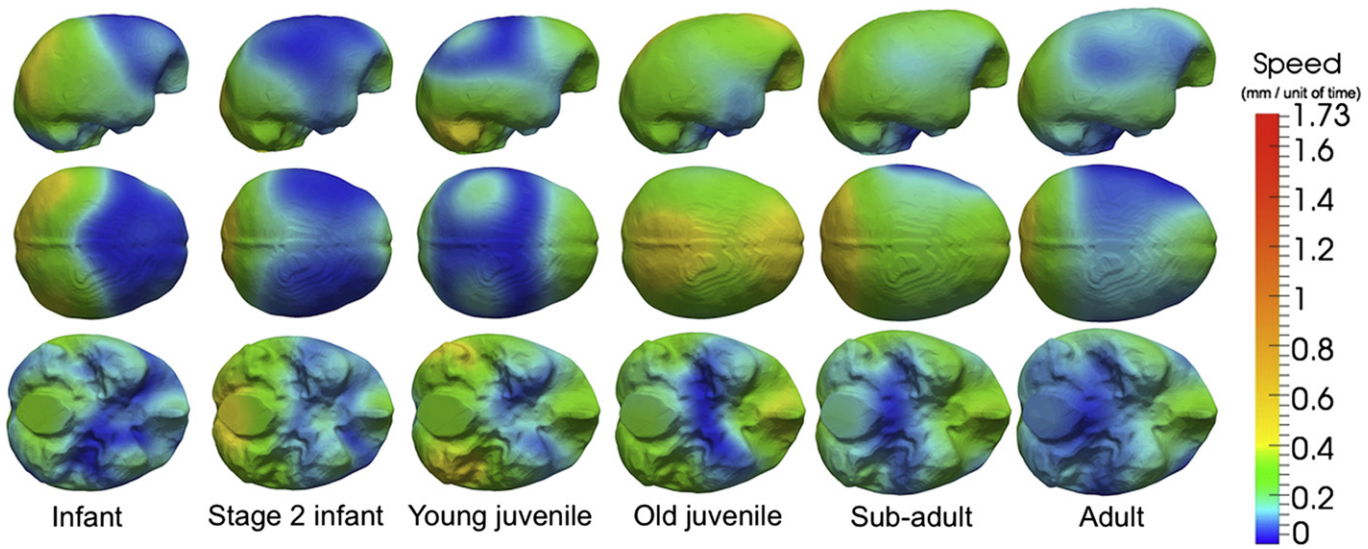

Figure 2. Six frames of the continuous ontogenetic trajectory estimated from the chimpanzee data. Colors indicate the instantaneous speed of the surface deformation. Best seen as a movie (SOM Movies 3 and 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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stage. The occipital lobe expands slightly backward and outward in the "infant" and more notably backward in the "sub-adult" samples.

Endocranial volume increase estimated from ontogenetic trajectories

We now focus on the endocranial volume (EV) increase, a measure that we derive from the previously estimated trajectories of endocranial expansion. Note here that the EV extracted from the surface regression (Fig. 3; computed from the ontogenetic trajectories shown in Figs. 1 and 2) is considered one feature of interest among others. In other words, an increasing EV is more likely due to a local expansion rather than to a more global and isotropic phenomenon. A simple visual inspection of the EV growth curves in bonobos and chimpanzees reveals two odd results (Fig. 3). The first intriguing result is an important difference during early postnatal development. The bonobo curve shows a significant EV increase across dental stages until the "young juvenile" stage. During the same period, the chimpanzee curve shows a slight decrease in EV. However, we consider this result cautiously because of the relatively small number of samples in this age group—it is likely due to a sampling bias that the two chimpanzee infant endocrania sampled here show larger values than the ones placed in the "stage 2 infant" category. More infant chimpanzee data are needed to clarify this issue. The second intriguing result is the apparent decrease of the bonobo EV at the "sub-adult" stage. However, when we compare the volume distribution of original samples corresponding to the "old juvenile" and "sub-adult" stages, the Mann–Whitney U test indicates a p-value of 0.47. Therefore, the medians of the two distributions are not proved to be statistically different. The test run for every pair of consecutive distributions shows a significant increase of EV on the following three occasions: (i) between "infant" and "stage 2 infant" for the bonobos (p-value: 9×10^{-3}); (ii) between "stage 2 infant" and "young juvenile" for the chimpanzees (p-value: 0.07); (iii) and between "old juvenile" and "sub-adult" for the chimpanzees (p-value: 0.02).

The bootstrap procedure indicates that the EV measured from the ontogenetic trajectories is significantly different between bonobos and chimpanzees at the "sub-adult" and "adult" stages only (p-value <0.1) (Fig. 4a). By contrast, the confidence intervals at the categories of "stage 2 infant," "young juvenile," and "old juvenile" all overlap (Fig. 4a) and therefore fail to show any significant difference in EV increase between the two species. Interestingly, these results are corroborated by the analysis of the distribution of the volume of the original data: the medians of the EV distributions of each species within each age group are statistically different in only two occasions: at the "sub-adult" stage (Mann–Whitney U p-value: 0.043) and at the "adult" stage (Mann–Whitney U p-value: 0.0025). For each bootstrap simulation, we measured the EV increase at each dental stage with respect to the volume achieved at the "adult" stage. From a statistical point of view, bonobo endocrania achieve their adult size before the chimpanzees (Fig. 4b). Bonobo juvenile endocranial volume reaches 90–100% of its adult size, whereas the chimpanzee juvenile endocranial volume reaches only 80–90% of its adult size. The bootstrap indicates that this difference is significant with a p-value smaller than 0.1 (Fig. 4b).

We also investigated the impact of the uncertainty in the dental stage estimates on our results, and we observe that this uncertainty does not call our results into question (Fig. 4c and d). Indeed, the 90% variability interval induced by randomly shifting the dental age estimates along the time axis is generally smaller than the 90% confidence interval of the bootstrap. This indicates that grouping the samples into 6 classes does not produce important variations of our results. A more precise estimation of the age of the individuals should not lead to different conclusions. Nevertheless, we notice that the most important differences between the variability and bootstrap intervals occur for the bonobos at the "sub-adult" stage (Fig. 4), which is also the age at which both intervals are at their largest. This suggests that the "sub-adult" developmental stage might not be relevant to EV increase. For instance, larger endocrania associated with the "sub-adult" dental stage might correspond to the "adult" EV.

To briefly summarize these results, we should say that even if the small amount of available specimens and the cross-sectional nature of our sample represents a limitation for the interpretation of our results, our statistical simulations suggest that the pattern of EV increase may differ significantly between bonobos and chimpanzees—bonobos experience an earlier phase of a relatively rapid increase (preferentially at some endocranial subdivisions), while chimpanzees experience a much later phase of relatively rapid increase. As a consequence, the chimpanzee endocranium appears to reach its adult size later than the bonobo.

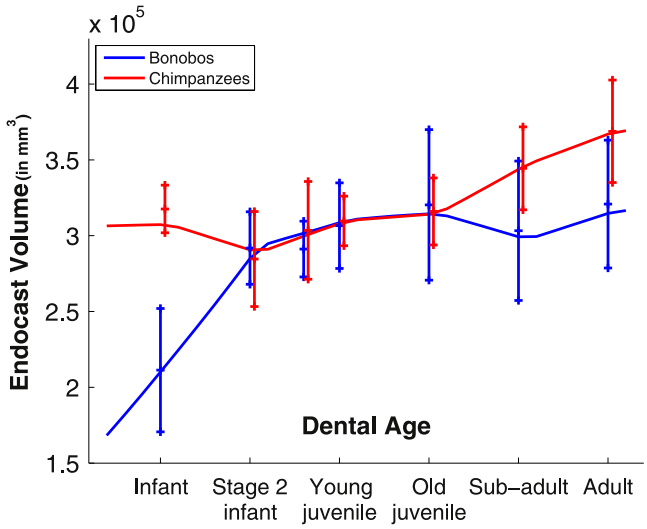

Figure 3. Temporal changes in endocranial volume. The continuous change in volume is measured from the estimated ontogenetic scenarios (Figs. 2 and 3). Mean and standard deviation of the endocranial volume of the original data is superimposed.

Spatiotemporal registration of the two trajectories of endocranial expansion

As a result of the aforementioned sampling bias, the spatiotemporal registration of the two trajectories of endocranial expansion is done from the "stage 2 infant" category (i.e., from time-point $t = 10$) onwards. Therefore, the postnatal period between "infant" and "stage 2 infant" has not been taken into account. The spatiotemporal deformation of the bonobo trajectory to the chimpanzee one is decomposed into a morphological (shape and size) deformation (Fig. 5; SOM Movie 5) and a time warp (Fig. 6).

SOM associated with this article can be found in the online version at doi:10.1016/j.jhevol.2011.10.004.

Morphological deformation The morphological deformation is shown using the chimpanzee data at each dental stage as a reference (Fig. 5; SOM Movie 5). Independent of dental development, the bonobo endocrania are more globular than the chimpanzee ones. At the "stage 2 infant," "old juvenile," and (to a lesser extent) "adult" stages, we observe almost the same pattern of inter-species shape differences. This pattern is due to an anteroposterior contraction in bonobo endocrania associated with a lateral expansion of its temporal and frontal lobes and an

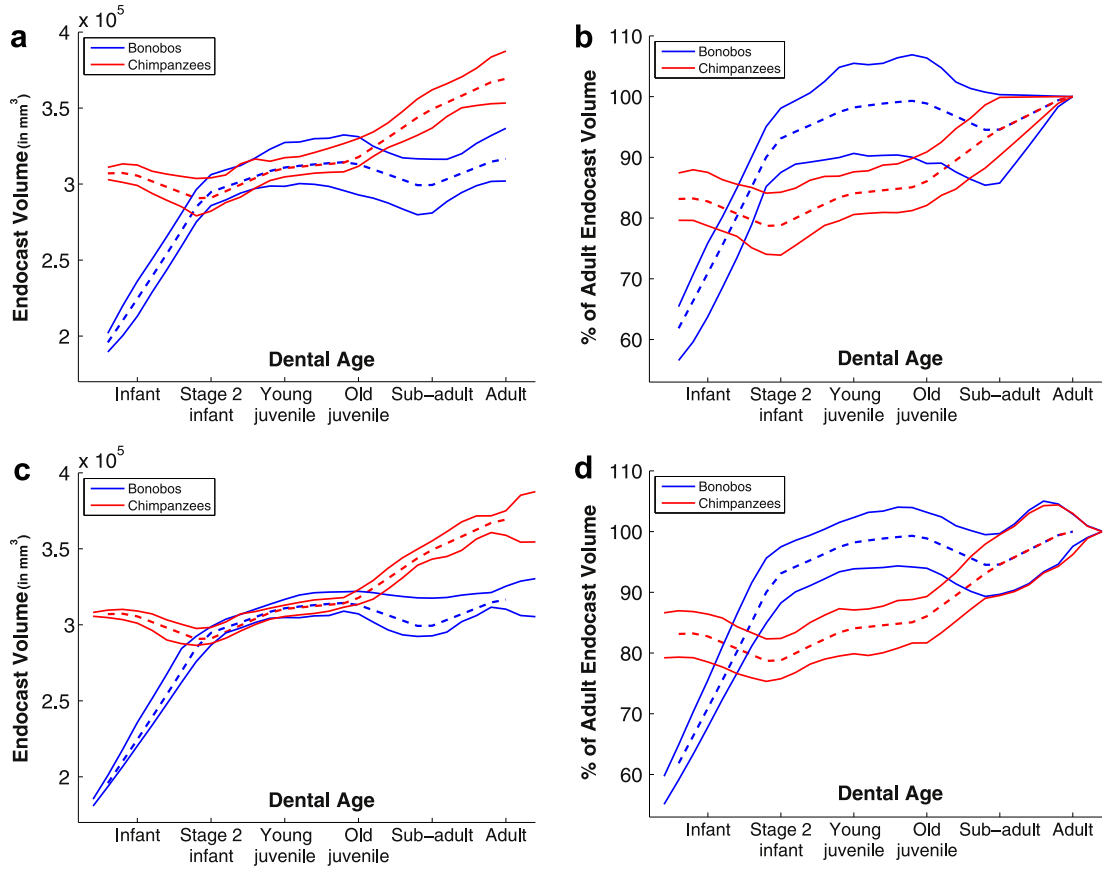

Figure 4. Temporal changes in endocranial volume (dashed line) with superimposition of the 90% confidence interval estimated by the bootstrap simulations (a) and the 90% variability interval due to random shifts of the dental age estimates along the time axis (c) (limits of the intervals are given by the solid lines). Volume growth rate expressed in percentage of adult size (dashed line) with superimposition of the confidence interval (b) and variability interval (d) (limits of the intervals are given by the solid lines).

upward expansion of the parieto-occipital boundary. On average, the bonobo endocranium is, at all dental stages, more rounded and less elongated than that of the chimpanzee.

Time warp The graph of the estimated time warp (Fig. 6) allows us to investigate the different pace of the total non-linear and anisotropic shape expansions calculated between bonobos and chimpanzees, once the ontogenetic trajectories have been "normalized" using the morphological deformation. The time warp measures the different timing in shape changes between the normalized ontogenetic trajectories. Note that the morphological

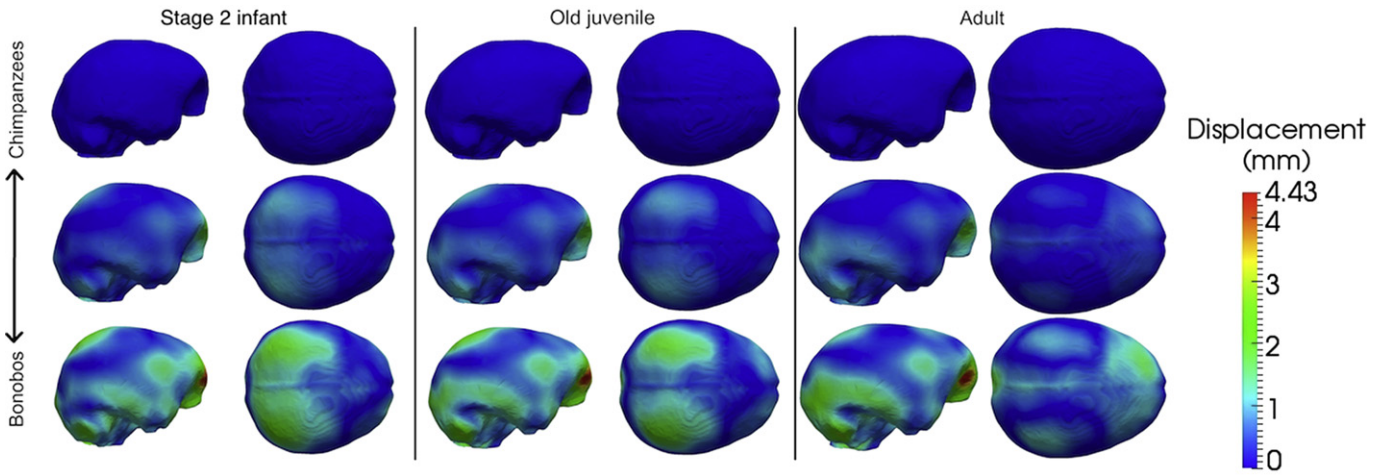

Figure 5. Effects of the morphological deformation on the chimpanzee ontogenetic trajectory, shown at three different dental ages. For each stage t_i, we show the chimpanzee trajectory $C(t_i)$ (top row), its morphological deformation $\phi(C(t_i))$ (bottom row), and an intermediate point along this deformation (middle row). Colors indicate cumulative displacement during deformation. Note that the deformed ontogenetic trajectory does not match the bonobo ontogenetic trajectory at the same dental age, but at the dental age given by the correspondence established by the time warp (see Fig. 7). Best seen as a movie (SOM Movie 5). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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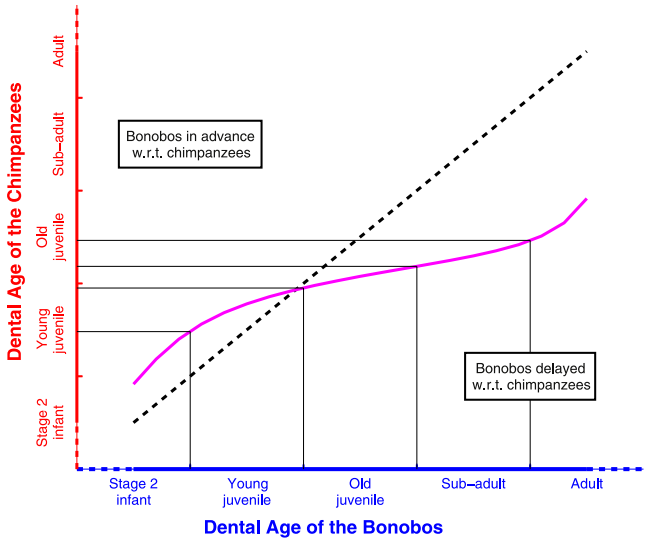

Figure 6. Estimated time warp (solid pink line), which maps the developmental stages of the chimpanzee ontogenetic trajectory to the bonobo ontogenetic trajectory (w.r.t. = "with respect to"). The dashed black line corresponds to the non-dynamical change axis ($x = y$ axis.). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

deformation accounts for the averaged differences in terms of EV observed in Figs. 3 and 4.

The dashed black line (Fig. 6) corresponds to the non-dynamical change axis ($x = y$), meaning an identical timing of the normalized trajectories. The time warp shown as the solid line (Fig. 6) puts into correspondence the developmental stages of the two species. When the time warp is above the dashed line ($\Psi(t) > 1$), this implies that the total expansion changes recorded in bonobos are advanced in comparison to those of chimpanzees and vice versa.

The time warp shows that bonobos are advanced relative to chimpanzees during the "stage 2 infant" and "young juvenile" stages. Then, we observe an important speed reduction between the "old-juvenile" and "sub-adult" stages in bonobos relative to chimpanzees. The almost constant slope of the curve during this latter period of time indicates that the bonobo development speed is 0.25 times that of the chimpanzee. Eventually, during sub-adulthood, the bonobo delay seems to be reduced. The bootstrap simulations give more statistical insights into these findings (Fig. 7). It appears that the advanced development of the "stage 2 infant" bonobos may not be significant. Testing that the time warp at stage 2 infancy (time-point 10) is above the non-dynamical change axis ($x = y$ line) returns a p-value of 0.12 (i.e., it occurs in 88 out of 100 experiments), which is below the usual threshold to decide statistical significance. Therefore, more data and possibly other methods should be called upon to confirm or reject the observed trend. The bootstrap simulations also allow us to give an uncertainty interval for the reduced development speed of the bonobos at juvenility: in 90% of the cases, the slope of the time warp at juvenility (slope between time-points 18 and 22) falls into the interval [0.136, 0.347], meaning a speed reduction of a factor 0.24 ± 0.1. Eventually, the reduction of the developmental delay of the bonobo at adulthood is significant. In all cases, the difference between the delays at the "adult" (time-point 30) and late "sub-adult" (time-point 27) dental stages is negative in all experiments, showing an acceleration of the bonobo ontogenetic trajectory with p-value smaller than 0.01.

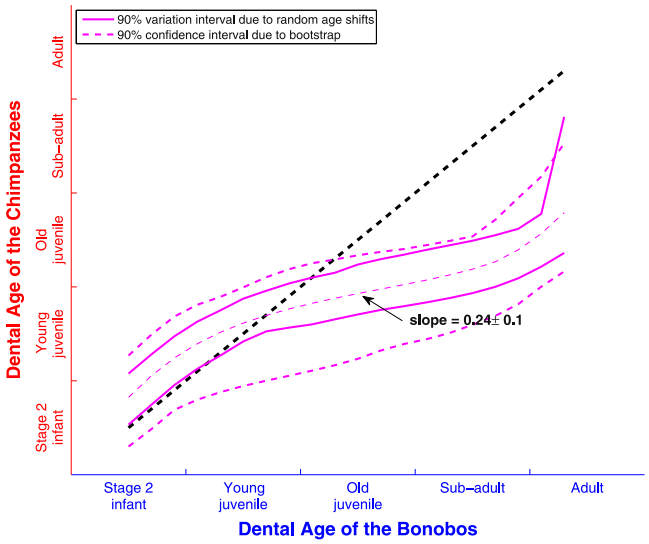

Figure 7. Estimated time warp with superimposition of the 90% confidence interval estimated by the bootstrap simulations and the 90% variability interval due to random age shifts. The dashed black line corresponds to the non-dynamical change axis ($x = y$ axis).

Our time warp results are robust to a random change in the dental stage estimates. Indeed, the 90% variability interval is much narrower than the 90% confidence interval estimated by the bootstrap simulations. In particular, for all 100 simulations, the time warp is above the non-dynamical axis at the "stage 2 infant" category. This suggests that this result, even if not proven to be statistically significant (see bootstrap interval), is not a consequence of the particular way we define our age groups at "stage 2 infant" and "young juvenile." On the contrary, this result suggests that the endocrania can rarely be misclassified at these ages and that the dental age may be a good proxy to assess endocranial early postnatal ontogeny in these species. This is not surprising considering the dramatic changes one observes from stage 2 infancy to juvenility, as compared from juvenility to adulthood.

Last but not least, this time warp shows that the shift in endocranial development between both species is detected not only in the size variable (cf. changes in endocranial volume in Fig. 4) but also in the rate of shape + size changes over time (cf. time warp in Fig. 6).

We recall that the morphological deformation and the time warp have been estimated *jointly*. This means that morphological differences have been detected by comparing endocranial surfaces at developmental stages that have been put into correspondence by the time warp (e.g., sub-adult bonobos with juvenile chimpanzees), and not within the same age group. Conversely, the time warp is estimated by comparing the rate of shape change in the two ontogenetic trajectories, once they have been "normalized" by the morphological deformation. The resulting decomposition into a temporal part and a spatial part explains most of the differences between the two ontogenetic trajectories.

Discussion

Comparative studies that reported on postnatal changes in brain shape and size between chimpanzees and bonobos are still incomplete. Our methodology enabled detection, measurement, and comparison of patterns of change in size and shape in a set of time-indexed endocrania that are not considered uniform entities with the use of semi-landmarks. This study of endocranial data relied on a methodology based on deformations for the analysis of time series surface data. This kind of approach is relatively unusual in the fields of evolutionary anthropology, primatology, and

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paleontology, in which analyses based on GM play a tremendous role. Our method is complementary to GM, in that it gives different insights into the data and reveals different patterns. On the one hand, GM is a relatively simple to use, robust, and well-understood method. But it is based on a model with simple assumptions, which therefore limits the possible patterns that can be revealed by analysis. At the core of GM are two questionable foundations: (1) the definition of homologous points across surfaces, whereas the number of such anatomical landmarks is very small on endocrania, and (2) the assumption that the differences in the positions of these homologous points are always due to Gaussian variations of point sets, regardless of what causes the differences: growth, inter-individual, or inter-species variations. The deformation-based methodology that underlies this study aims at mitigating the consequences of these two potential limitations. The counterpart is a more complex method, both from a theoretical and algorithmic point of view, and one that depends on more parameters. This may make the approach more difficult to apprehend. However, we hope that this study will convince the reader that this complexity is worth the potential of the approach. Note that other alternatives are also available, based on the map of closed surfaces to the sphere (e.g., Specht et al., 2007).

Postnatal endocranial trajectories: similarities and differences between bonobos and chimpanzees

Previous results for the neurocranium It is important, when comparing ontogenies, to first decide if and when they diverge, and, second, to measure differences as precisely as possible. It is also important to accurately define and compare non-monotonic trajectories that differ by a non-uniform rate change. We believe that our comparison of the bonobo and chimpanzee trajectories of regional endocranial expansion, and the subsequent spatiotemporal registration, addresses these issues in a methodologically appropriate way. Several studies have compared ontogenetic changes within *Pan* species. These studies investigated inter-species differences at comparable "ages" within a multivariate neurocranial shape space (e.g., Williams et al., 2002; Mitteroecker et al., 2005; Lieberman et al., 2007). However, there remain few size/shape comparisons between the bonobo and chimpanzee neurocranium. Shea et al.'s (1993) analysis still stands as the most complete analysis of craniometric variation within all the subspecies and species of *Pan*. These authors concluded that much of the morphometric cranial differentiation between bonobos and chimpanzees disappeared after allometric size correction. Also using cranial variation and a large sample, Braga (1995a,b, 1998) and Braga and Boesch (1997) concluded that non-metric variants indicated not only a significant difference between chimpanzees and bonobos, but also an important difference between the western chimpanzee subspecies (*Pan troglodytes verus*) and the other two subspecies of chimpanzees. Importantly, these non-metric variants indicated differences in cranial ossification, innervations, and vascularization. Williams et al. (2002) noted that the features reported in the bonobo as "paedomorphic" were slight and largely expressed in the outer neurocranium (adult bonobos being more similar to sub-adult chimpanzees, and bonobo adults differing from chimpanzee adults almost entirely on the basis of their relatively shorter neurocrania) rather than in the face (including the mandible). Williams et al. (2002) and Mitteroecker et al. (2004, 2005) argued that most of the observed shape differences between bonobo and chimpanzee neurocrania were due to divergent developmental trajectories (at least for principal component 3; craniofacial shape changes being stronger in *Pan* than in *Homo*). In their analysis of a more limited set (in comparison to Mitteroecker et al. [2004, 2005]) of outer and inner neurocranial landmarks, Lieberman et al. (2007: 656), using only principal component 1 with a variance of 56.7%, argued that adult bonobos showed the same values as young chimpanzees, with "more flexed cranial bases, with more globular braincases, more anteriorly positioned foramina magna, and relatively shorter anterior cranial bases."

Differences from previous results Our results demonstrate that the relationships of size/shape versus dental stage are not the same between the two species of *Pan* (Figs. 3 and 4). The non-linearity of the time warp allowed us to detect not only the expected developmental delay in bonobos, but also the more subtle effects and unexpected results. Bonobo ontogeny seems to be advanced at the "stage 2 infant" and "young juvenile" dental stages. It appears subsequently delayed, but this delay is reduced at adulthood. Our time warp results confirm that the ratio between the rates of shape change in these two species does not necessarily remain constant during ontogeny. Therefore, inter-species comparisons solely based on the analysis of regression slopes between principal components and age may not be sufficient to capture differences in growth or developmental patterns. Even within a heterochronic framework, these results suggest that the pace of endocranial shape changes, and their differences between bonobos and chimpanzees, cannot be reduced to a black-and-white decision between paedomorphosis and peramorphosis. Moreover, our method provides a quantitative estimate of developmental delays. It appears that the bonobo rate of ontogenetic change is much lower than that of the chimpanzee between the "old juvenile" and "sub-adult" stages. Our "four times" lower rate for the bonobo is given as an overall indication. It does not aim at providing a precise measure of differences in rates of shape change since we dealt only with cross-sectional data. Besides this most salient effect, our method also retrieved non-linear deviations: the bonobo advance at the "stage 2 infant" dental stage and their delay at the "adult" stage, although only the latter rate change has been shown to be statistically significant. Such second order non-linear effects cannot be detected by the intrinsically linear treatment proposed in Lieberman et al. (2007), in which the detected developmental delays are necessarily constant over time. By contrast, our methodology allowed an almost 1D function as a profile for the time warp. The two conditions are that the 1D profile has to be monotonic to avoid time reversal, and that it has bounded variations to avoid unrealistic discontinuities or accelerations that are too fast. The possible time warps therefore contain, but are not limited to, linear, polynomial, exponential, or spline curves, as proposed in Neubauer et al. (2009). Quantitative differences between our results and those from Lieberman et al. (2007) may also result from the fact that we explicitly introduced a time warp, so that we compared the shape of the endocrania that corresponded to the same developmental stage (once developmental delays had been taken into account). Lieberman et al. (2007) compared endocrania that corresponded to the same dental age. Such comparisons may be "blurred" by the fact that endocrania of the same age may correspond to a different stage of development.

Local changes may reveal the modular nature of inter-species differences In their comparison of gene co-expression networks in human and chimpanzee brains, Oldham et al. (2006) observed that inter-species module conservation may be greater in the primary sensory cortex than in regions considered representative of the association cortex. In this modular context, it will be important to compare chimpanzee and bonobo endocrania for different anatomical subdivisions of the brain. The ontogenetic delay was assessed by considering the whole endocranium. Considering brain modularity in our modeling could help in the future to distinguish different growth speeds for different

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endocranial parts, and therefore refine our understanding of the differences between postnatal trajectories. Measures of morphological differences based on non-linear 3D deformations already allow us to detect anisotropic variations (Figs. 1, 2, and 5) that cannot be seen by analysis of simple geometrical features like volume. An important finding of our study is that the inner neurocranium cannot be considered as a uniformly changing structure during ontogeny. Instead, it is clear that local ontogenetic expansions occur differently between the two species of *Pan* and that they have not been reported so far. For example, in bonobos and chimpanzees, we observe notable expansions of the areas corresponding to the frontal lobes of the cerebrum. These expansions may relate to a rotation of the orbits toward the midline, and into a binocular position. However, these frontal expansions occur not only at two very different periods of bonobo and chimpanzee postnatal ontogeny (Fig. 1), but also in association with changes involving other endocranial regions. A more precise analysis of these distinct associations of expansions will be necessary to assess possible implications in terms of modularity.

Evolutionary perspectives

Evolutionary change can occur through multiple mechanisms. Heterochrony can be one of these mechanisms even if, as already discussed, we consider this possibility as doubtful for methodological reasons. We also argue that inferring evolutionary mechanisms from extant species is highly problematic, as chimpanzees and bonobos may have evolved considerably since their descent from an unknown common ancestor that lived approximately between 2 Ma and 1 Ma. Nevertheless, the shape changes described here need to be related to particular evolutionary processes. Body growth is considered to be delayed in the infant bonobo. Two- to three-year-old bonobos and chimpanzees in their natural habitat weigh 2.3 (Kuroda, 1989) and 4–5 (Uehara and Nishida, 1987) times, respectively, more than neonate bonobos and chimpanzees. This delay in body growth in bonobos closely corresponds to the delay in motor and social development during the first years of its postnatal life (Kuroda, 1989; Kano, 1992; de Waal and Lanting, 1997). It may also explain our results. Does the bonobo delay in body growth indicate a delay in brain growth? Behavior at birth is primarily a function of brain size relative to body weight and brain size relative to that in the adult (Portmann, 1941; Martin, 1983). In humans, neonatal brain weight expressed as a percentage of final brain size varies from 25% to 30% (Martin, 1983; Vinicius, 2005; Kennedy, 2005). This human pattern of brain growth is responsible for the degree of motor helplessness seen in human neonates and infants, and is also associated with important social, reproductive, metabolic, and life history traits (Martin, 1983; Allman et al., 1993; Bogin, 1997; Leonard et al., 2003; Leigh, 2004). Chimpanzee neonatal brain weight reaches between 30% and 45% of final adult size (Martin, 1983), whereas the neonatal brain to body weight ratio reaches between 7.3% and 8.2% (Schultz, 1940; Portmann, 1941; Keeling and Riddle, 1975; Herndon et al., 1999) and then decreases rapidly (Herndon et al., 1999). However, data on brain growth in bonobos are inadequate.

It is known that bonobos adopt characteristic social behaviors and parental strategies to increase reproductive success in natural habitats and to promote infant weaning (De Lathouwers and Van Elsacker, 2005). Childhood is considered as a feeding and reproductive adaptation to free the mother from the demands of nursing and the inhibition of ovulation related to continuous nursing (Leigh, 2004; Kennedy, 2005). Our results tend to underscore important differences between bonobos and chimpanzees in terms of postnatal changes in endocranial size and shape. These differences seem to be consistent with the aforementioned behavioral and life history differences between chimpanzees and bonobos. Indeed, while chimpanzee endocranial expansions remain significant at the “old juvenile” and “sub-adult” stages (Fig. 5; see the frontal area and the parieto-occipital boundary), bonobos show a very different pattern of shape change in which the major expansions occur before the emergence of the first permanent molar. This result may indicate an association between an early weaning in bonobos and an earlier cessation of its brain expansion. The evolutionary processes responsible for this earlier cessation are difficult to determine.

Possible confounding factors: sampling, dental growth, sexual dimorphism, and captivity

Sampling Our sample of CT-scanned crania is modest in size and represents cross-sectional data of mainly wild animals. Nevertheless, our sample represents the largest data set investigated so far in comparison with studies based on landmarking methods. Previous results were based on fewer variables (Williams et al., 2002) or fewer juvenile specimen samples (Mitteroecker et al., 2004, 2005; Lieberman et al., 2007). For example, we acknowledge that our “infant” and “stage 2 infant” dental stages are represented only by 12 bonobos and 8 chimpanzees, and that our “juvenile” stage is represented by 21 bonobos and 33 chimpanzees. However, Mitteroecker et al.’s (2004, 2005) results were based on 12 juvenile bonobos and 8 juvenile chimpanzees, and, in our study, earlier postnatal stages are better sampled and topographical coverage of the neurocranium is complete. The previous study conducted by Lieberman et al. (2007) included only 30 chimpanzees and 19 bonobos (compared to 59 chimpanzees and 60 bonobos in our study).

Dental growth Our comparison of chimpanzee and bonobo postnatal endocranial changes is based on mandibular dental eruption as a marker of growth. This situation is not ideal. From the study of dental emergence in 5 captive bonobos of known chronological age, Bolter and Zihlman (2011) concluded that *P. paniscus* dental timing and sequences show differences from that of *P. troglodytes*. If these results are confirmed by further studies on larger samples and wild animals, differences in dental growth between chimpanzees and bonobos may represent an additional confounding factor in our study. Interestingly, Bolter and Zihlman (2011) noted distinctions in dental emergence specifically and mainly for the upper lateral incisors and canines, as well as for the upper and lower third molars. Using large samples of mostly wild-born animals, differences in facial growth and incisive suture closure were observed between chimpanzees and bonobos (Braga, 1998). Braga (1998) concluded that such differences may be associated with differences in upper incisor eruption. Indeed, the growth of the upper permanent incisors and canines may be influenced by the ossification of the embedding and developmentally associated premaxillary and maxillary bones. More studies are needed to clarify this potential association using precise markers of the continuous process of dental growth (not only emergence). If real, this association may obscure ontogenetic comparisons between chimpanzee and bonobo endocrania solely based mandibular dental developmental stages. However, as noted by Bolter and Zihlman (2011) in their preliminary of study, to the contrary of their upper counterparts, anterior lower teeth do not seem to evince significant differences in emergence between bonobos and chimpanzees.

Sexual dimorphism Using longitudinal data, Leigh and Shea (1995) investigated the ontogeny of body size dimorphism in both species

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of *Pan* represented by captive animals. They observed that, in both species, males and females shared a common ontogenetic trajectory until about 5 years of age. Therefore, sexual dimorphism is likely not a confounding factor responsible for the differences in endocranial size and shape change that we report between our categories of "infant," "stage 2 infant," and "young juvenile" bonobos and chimpanzees. Herndon et al. (1999) performed the most complete ($N = 275$) postmortem examination of chimpanzees from a single colony to evaluate the effects of development, sex, and aging on fresh brain weights throughout the life span (no data being available for bonobos). They observed that the chimpanzee brain reaches its adult size by the 7th year of life. After the effect of sex had been statistically removed, they observed a slight (p-value $= 0.07$) age-related loss of brain weight in chimpanzees (of 0.9 g/year), which is also shown in comparative studies of human postmortem material. In addition, Herndon et al. (1999) reported that the mean brain weight of male chimpanzees was 100% of the mean brain weight of females: a sex difference close to the 111% reported for humans (e.g., Peters et al., 1998). If this degree of sexual dimorphism also applies to bonobos, and if the sex ratio represented at the various dental developmental stages is not constant, this may well explain why we observed a decrease in bonobo endocranial volume at sub-adulthood.

Captivity The use of data from captive animals is not ideal. All the specimens included in our sample were located according to their precise geographic origin and are wild (Braga, 1995b), even though a few of them may have been captive during some periods of their lives. This may confound some of our results, since it has been argued that wild chimpanzees mature more slowly, but in the same sequence as captive animals (Zihlman et al., 2004). However, Zihlman et al.'s (2004) study on wild chimpanzees was largely based on *Pan troglodytes verus*. The captive chimpanzees (from LEMSIP and YERKES), for which almost all aging data come, were very likely not of the same subspecies. Therefore, a possible confounding factor in Zihlman et al.'s (2004) interpretation of captive versus wild differences is that the animals considered in each of these samples were probably from different chimpanzees subspecies for which morphological and genetic differences are important (Morin et al., 1994; Braga, 1995a, 1998; Uchida, 1996; Braga and Boesch, 1997; Deinard and Kidd, 2000; Gonder et al., 2011).

Summary and conclusions

Our analysis of endocranial postnatal changes in chimpanzees and bonobos revealed important non-linear and anisotropic effects. Therefore, inter-specific comparisons solely based on the analysis of regression slopes between principal components and age may not be sufficient to capture differences in growth or in developmental patterns at local endocranial levels. In bonobos, well before the emergence of the first permanent molars when the adult brain size is not yet reached, we observed a strong anisotropic pattern of endocranial expansion that caused a bending of endocranial shape due to local expansions to the frontal pole, the occipital lobe, and the superior part of the parietal lobe. This pattern is very different in chimpanzees, in which endocranial expansions remained significant at the "old juvenile" and "sub-adult" dental stages. The patterns of endocranial expansion also differed between chimpanzees and bonobos in terms of size, with a phase of relatively rapid increase in EV that occurs later in chimpanzees than in bonobos. Our time warp results showed that this delay in development still holds when measuring the rate of shape change during ontogeny: the speed of development is about four times less in bonobos relative to chimpanzees at juvenility. It also showed that the correspondence between the rates of ontogenetic change is not necessarily constant between species. Indeed, the developmental delay at the "juvenile" stage is reduced at the "adult" stage. An unexpected trend of a developmental advance in the bonobos at late infancy relative to the chimpanzees has been also highlighted. However, more data and more investigations should be called upon to confirm this hypothesis.

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