Ontogenetic Study of the Skull in Modern Humans and the Common Chimpanzees: Neotenic Hypothesis Reconsidered With a Tridimensional Procrustes Analysis

Xavier Penin,[1] Christine Berge,[2] and Michel Baylac[3]

[1]*Dépt. Orthodontie, Faculté de Chirurgie Dentaire, Université Paris V, Montrouge 92120, France*
[2]*U.M.R. 85 70, CNRS, Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris 75005, France*
[3]*Groupe de Travail Morphométrie and ESA 8043, CNRS, Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, Paris 75005, France*

KEY WORDS Procrustes superimposition; *Pan troglodytes*; *Homo sapiens*; heterochrony; allometry

ABSTRACT Heterochronic studies compare ontogenetic trajectories of an organ in different species: here, the skulls of common chimpanzees and modern humans. A growth trajectory requires three parameters: size, shape, and ontogenetic age. One of the great advantages of the Procrustes method is the precise definition of size and shape for whole organs such as the skull. The estimated ontogenetic age (dental stages) is added to the plot to give a graphical representation to compare growth trajectories.

We used the skulls of 41 *Homo sapiens* and 50 *Pan troglodytes* at various stages of growth. The Procrustes superimposition of all specimens was completed by statistical procedures (principal component analysis, multivariate regression, and discriminant function) to calculate separately size-related shape changes (allometry common to chimpanzees and humans), and interspecific shape differences (discriminant function).

The results confirm the neotenic theory of the human skull (sensu Gould [1977] Ontogeny and Phylogeny, Cambridge: Harvard University Press; Alberch et al. [1979] Paleobiology *5:*296–317), but modify it slightly. Human growth is clearly retarded in terms of both the magnitude of changes (size-shape covariation) and shape alone (size-shape dissociation) with respect to the chimpanzees. At the end of growth, the adult skull in humans reaches an allometric shape (size-related shape) which is equivalent to that of juvenile chimpanzees with no permanent teeth, and a size which is equivalent to that of adult chimpanzees. Our results show that human neoteny involves not only shape retardation (paedomorphosis), but also changes in relative growth velocity. Before the eruption of the first molar, human growth is accelerated, and then strongly decelerated, relative to the growth of the chimpanzee as a reference. This entails a complex process, which explains why these species reach the same overall (i.e., brain + face) size in adult stage. The neotenic traits seem to concern primarily the function of encephalization, but less so other parts of the skull. Our results, based on the discriminant function, reveal that additional structural traits (corresponding to the non-allometric part of the shape which is specific to humans) are rather situated in the other part of the skull. They mainly concern the equilibrium of the head related to bipedalism, and the respiratory and masticatory functions. Thus, the reduced prognathism, the flexed cranial base (forward position of the foramen magnum which is brought closer to the palate), the reduced anterior portion of the face, the reduced glabella, and the prominent nose mainly correspond to functional innovations which have nothing to do with a neotenic process in human evolution. The statistical analysis used here gives us the possibility to point out that some traits, which have been classically described as paedomorphic because they superficially resemble juvenile traits, are in reality independent of growth. Am J Phys Anthropol 118:50–62, 2002.

Recent decades have seen much discussion of heterochronic hypotheses in human evolution. Originally, Bolk (1926) and contemporaries such as Schultz (1927) based the neotenic theory on a resemblance in skull shape between a juvenile chimpanzee and an adult human. Fifty years later, Gould (1977) provided support for the heterochronic theory, using a schematic representation of human neoteny ("clock model"), described as a "qualitative account of human neoteny" in his Figure 40 ("maturation is retarded, size increases, and shape remains in the realm of juvenile ancestors", p. 260). Our study sets out to reconsider the heterochronic hypotheses quantitatively, on the basis of ontogenetic changes in the skull morphology of chimpanzees and hu-

Grant sponsor: French MESR.

*Correspondence to: Christine Berge, U.M.R. 85 70, CNRS, Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, 55 rue Buffon, Paris 75005, France. E-mail: berge@mnhn.fr

Received 3 April 2000; accepted 26 October 2001.

Published online in Wiley InterScience (www.interscience.wiley.com).
DOI 10.1002/ajpa.10044

mans, using the Procrustes superimposition method (Gower, 1975; Rohlf and Slice, 1990; Goodall, 1991, 1995; Dryden and Mardia, 1998).

ALLOMETRY IN HETEROCHRONY

Gould (1977) and Alberch et al. (1979) defined heterochrony (the parallel of ontogeny and phylogeny) as the comparison of ontogenetic trajectories between two species representing ancestors and descendants. The basic idea of Gould (1977) was to represent the ontogenetic trajectories as changes in three "potentially" independent "vectors:" size, shape, and ontogenetic age (p. 246). In Gould (1977), heterochrony is represented in a clock model in which the three vectors move at their own rates. In Alberch et al. (1979), heterochrony is represented in a three-dimensional Cartesian space. However, as noticed by Gould (1977), the most important difficulty lies in the choice of methods capable of calculating size and shape independently. Gould (1977) gives some examples of clock models where size is a linear dimension (body length), and shape a ratio (index of proportion).

Ontogenetic changes in size and shape refer to allometry. Classical allometry, as defined by Huxley (1932) and Teissier (1948), is the comparison of two body dimensions which does not aim at dissociating size and shape. Therefore, the allometric relation cannot be straightforwardly applied to heterochronic studies. At the beginning of his chapter giving the method for building clock models, Gould (1977) specifies, "The standard techniques of allometry do not provide an optimal metric for heterochrony because they subtly reinforce a prejudice directed against the dissociability upon which heterochrony depends" (p. 246). For a similar reason, Godfrey and Sutherland (1996) criticized examples of heterochrony constructed from classical allometries. The same problem is not met here, because size and shape are calculated as independent vectors with the Procrustes method, using the precise mathematical definition given by the shape theory (Kendall, 1984, 1989; Bookstein, 1991). Allometry becomes the relation between size and shape, where size and shape are calculated independently. In other words, allometry may be defined as the covariation between size and shape (Gould, 1966; Mosimann, 1970; Bookstein, 1989, 1991).

THE "COMMON ALLOMETRY" OF THE SKULL AND ITS BIOLOGICAL SIGNIFICANCE

In Shea (1989) and Alberch (1990), heterochronies are described as perturbations of a "common pattern of growth allometry," either in growth duration (prolonged or truncated growth) or in growth speed (retarded or accelerated growth). The multivariate approach to allometry allows us to obtain the ontogenetic shape changes which are shared by humans and chimpanzees. This fundamental concept of heterochrony (perturbations of a common growth pattern) disappears when inadequate metric methods are used (see Klingenberg, 1998). The common growth pattern of the skull makes reference to similarities in craniofacial development in mammals, and more particularly in apes and humans (Enlow, 1968; Enlow and Hunter, 1970; Bromage, 1992).

Homology is the key to biometrically comparing related forms in terms of transformation (Thompson, 1917; Bookstein, 1991). However, as explained by O'Higgins (2000), the definition of homology depends entirely on biological rather than mathematical or geometric criteria. In morphometric studies of growth, geometric similarities are generally supposed to be the expression of biological homology. For example, Delattre and Fénart (1960) demonstrated that the skulls of chimpanzees and humans grow similarly down and forward relative to the horizontal vestibular axis.

Despite this common growth pattern, ontogenetic trajectories in chimpanzees and humans differ, if various cranial dimensions are considered separately (Heintz, 1964, 1966; Petit-Maire, 1972). In great apes, the face grows much longer than the vault, whereas the face and the vault grow together with the same rate of growth in modern humans (Petit-Maire, 1972). Dean and Wood (1984), who compared the growth of the cranial base in humans and chimpanzees, expressed the same opinion when they asserted that evolutionary changes in rate of growth and duration lead to important differences in adults. Thus, they concluded that heterochronic changes are insufficient to account for the morphological differences between humans and great apes, and that it would be an oversimplification to regard the morphology of the cranial base in humans as a simple neotenic feature. Lieberman (2000) goes further and suggests that craniofacial structures are not homologous in apes and humans in terms of growth processes, and consequently hardly comparable. Indeed, in Lieberman and McCarthy (1999), it is demonstrated that the cranial base in humans flexes rapidly after birth prior to complete brain expansion, whereas it extends after the brain has completed its growth in nonhuman primates.

Nonetheless, we may object here that homology is not a priori knowledge. In this study, we calculate the part of the ontogenetic shape change which is common to chimpanzees and humans. Even though some other developmental events may interact in the growth pattern leading to nonhomologous morphological traits in humans and chimpanzees, we hypothesize that if there is a common growth allometry, it may correspond to similar rules of construction, and consequently to homology in terms of developmental constraints (e.g., Alberch, 1990; Wagner, 1994).

CONTROVERSIAL OPINIONS ABOUT NEOTENY

Human neoteny is classically described as a "retardation" in shape generally associated with an increase in the duration of growth (Gould, 1977; see

also McKinney and McNamara, 1991). The increase in duration of growth has been reported for all human dental stages by comparison with African apes and fossil hominids (e.g., Dean and Wood, 1984; Smith; 1986; Bromage, 1987, 1992; Ramirez Rozzi, 1993, 1998; Smith et al., 1995; Anemone et al., 1996). Postcranial data, such as for pelvic and femoral morphology, are also consistent with a longer growth period in *Homo* than in *Australopithecus*, although a "retarded" shape on the postcranium has not been demonstrated; indeed, rather the contrary (Berge, 1993, 1995a,b, 1998; Tardieu, 1997, 1998).

Although graphical methods illustrating the shape retardation of the human skull have been debated at length, numerical data establishing such a retardation remain questionable. There is widespread agreement that the changes in skull shape in humans should be expressed in terms of changes in growth allometry (using a set of bivariate plots) from an ape-like ancestral pattern to a human descendant pattern (McKinney and McNamara, 1991; Shea, 1989). However, the way in which differences in the slopes of the allometric regression lines should be interpreted is a matter of debate (e.g., Shea, 1989, 1992; Shea et al., 1990; McKinney and McNamara, 1991; Godfrey and Sutherland, 1995, 1996; Godfrey et al., 1998). As explained above, many divergent opinions in the field of heterochrony arise from the use of inadequate methods to quantify size and shape as potentially independent vectors. Despite confusion regarding methodology, it is clear that the notion of size-shape association or dissociation is particularly useful to interpret allometric heterochronies (Shea, 1989). For example, Shea (1989, 1992) explained that a simple extension (or truncation) of the ancestral pattern of growth allometry without changes in size-shape covariation must be distinguished from a size-shape dissociation corresponding to a more fundamental alteration in growth pattern.

THE PROBLEM UNDER INVESTIGATION HERE

Graphical representations of both growth allometry and heterochrony are obtained with the Procrustes method, to which is added the scaling of ages given with the dental stage of the specimens. The dental stages are used here as an intrinsic measure of time which reflects a developmental process within the organism. The choice between an intrinsic or extrinsic measure of time (true time) in heterochronic studies is debatable (Klingenberg, 1998). However, in the present study, the use of dental age cannot bias conclusions about the temporal retardation of the growth of the human skull in comparison with chimpanzees. We know that dental stages are retarded in humans as compared with chimpanzees (e.g., Dean and Wood, 1984; Smith et al., 1994). Thus, if a human retardation is revealed from dental stages, it will only be emphasized with the use of real ages. Another advantage of the Procrustes method is that it makes it possible to clearly dissociate ontogenetic allometric differences from taxonomic nonallometric differences. Graphical and statistical results are used to study shape traits that are progressively modified with growth, separately from the specific shape traits that discriminate humans from chimpanzees, regardless of growth. To clarify the neotenic hypothesis, we added a clock model built from our data, to be compared with classical clock models proposed in Gould (1977) and Shea (1989).

MATERIALS AND METHODS

We used 91 skulls from extant hominoids: 41 *Homo sapiens* (18 adults, 23 juveniles), and 50 *Pan troglodytes* (17 adults, 33 juveniles). The specimens were classified into four stages of growth, based on the eruption status of permanent molars. In stage 0, there is no permanent molar erupted; in stage 1, the first permanent molar is erupted; in stage 2, the second permanent molar is also erupted; and in stage 3, all the permanent molars are erupted. The human sample comprised 8 specimens of stage 0; 8 of stage 1; 7 of stage 2; and 18 of stage 3. The chimpanzee sample comprised 9 specimens of stage 0; 12 of stage 1; 12 of stage 2; and 17 of stage 3.

The human specimens were obtained from the collection of the Royal College of Surgeons of London (UK), and the chimpanzee specimens from the Powell-Cotton Museum at Birchington (UK).

Landmarks and Procrustes superimposition

Twenty-nine skull landmarks (Fig. 1, Table 1) were digitized using a 3 Draw Space Digitizer© (Polhemus, Inc.). To define homologous landmarks, we have to specify their level of homology. Bookstein (1991) illustrated several kinds of homology relations that require additional information for resolution of morphological correspondence. Homology type 1 concerns discrete juxtapositions of tissues (this category includes points in space at which three structures meet, such as cranial sutures). Homology type 2 concerns maxima of curvatures of morphogenetic processes (e.g., the protruding glabella). Homology type 3 concerns constructed landmarks (e.g., endpoints of diameters, centroids, intersections of interlandmark segments). In our study, 16 landmarks are type I according to the homology of Bookstein (1991) (i.e., located at the discrete juxtaposition of 2 or 3 bones), and 11 landmarks are type II (i.e., tips of extrusions). The pterion may be regarded as intermediate between types I and II because it may have various shapes. Landmarks are type I for X-shaped pterions, and type II for H-shaped pterions. Twelve landmarks are located in the sagittal plane, and 17 on the right side of the skull. The 91 sets of landmarks (corresponding to the 91 specimens) were scaled, translated, and rotated for superimposition (Rohlf and Slice, 1990). The three-dimensional (3D) superimposition can be viewed in the three planes of the skull: sagittal,

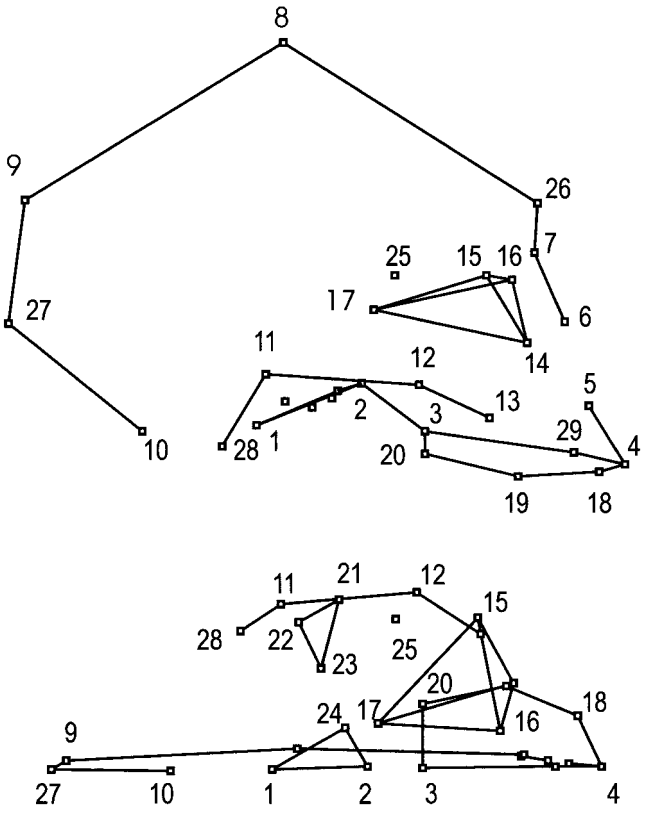

Fig. 1. The 29 landmarks are plotted on the consensus (mean shape of the 91 specimens). Top: Sagittal view. Bottom: Inferior view. The face of the skull is turned to the right. For definition of landmarks, see Table 1. Links are drawn to make anatomical structures clearer. Landmarks 7-26-8-9-27-10: Outline of cranial vault. Landmarks 14-16-15-17: Orbital cavity. Landmarks 3-29-4-18-19-20: palate. Landmarks 21-22-23: Glenoid fossa. Landmarks 28-11-12-13: Mastoid and zygomatic arch. Landmarks 1-2-24: Sphenoid clivus. The foramen magnum is located between landmarks 1–10, and the nasal aperture between landmarks 5–6.

TABLE 1. Landmarks

No.	Anthropological landmarks and definitions	Type
1	Basion[1]	II
2	Hormion[1]	I
3	Staphilion[1]	I
4	Prosthion[1]	I
5	Nasospinale[1]	I
6	Superior border of nasal aperture (sagittal plane)	I
7	Nasion[1]	I
8	Bregma[1]	I
9	Lambda[1]	I
10	Opisthion[1]	I
11	Porion[1]	II
12	Zygion[1]	II
13	Zygomallare[1]	I
14	Orbitale[1]	I
15	Fronto-malar suture (orbit margin)	I
16	Dacryon[1]	I
17	Optic foramen	II
18	Premaxillary suture, between I^2 and C (external edge of alveolar process)	I
19	External edge of alveolar process between P^2 and M^1	II
20	Maxillary tuberosity (dorsal extremity of the alveolar process)	II
21	Lateral condylion[1]	II
22	Postglenoid process of mandibular fossa	II
23	Medial condylion[1]	II
24	Foramen lacerum medium (sphenoid body-pterygoid ala)	I
25	Pterion[1]	I or II
26	Glabella[1]	II
27	Inion[1]	II
28	Extremity of mastoid process	II
29	Anterior palatine canal	I

[1] Classical anatomical landmarks defined in Aiello and Dean (1990, p. 50–53). Types I and II homology are defined in Bookstein (1991), and in present text. Landmarks are situated either in the sagittal plane or in the right side of the skull.

horizontal, and frontal. Figure 1 shows the landmarks projected onto the sagittal and horizontal planes only, because changes in the frontal plane can be deduced from these planes. To identify shape changes in precise anatomical regions, a wire frame was drawn between landmarks corresponding to the various structures (see legend, Fig. 1).

The variable used for size normalization was centroid size, calculated for each specimen as the square root of the sum of the squared deviations of landmarks from the centroid (Gower, 1975). The superimposition algorithm used was the generalized least square (GLS), which translates and rotates normalized figures to minimize the squared differences between all landmarks (Rohlf and Slice, 1990; Goodall, 1991). The superimposition computes a mean shape of the specimens, referred to as the "consensus." The shapes of individual specimens are then defined as Procrustes residuals, that is to say, as deviations of landmarks from the consensus. A single superimposition of all specimens (humans and chimpanzees) was done.

Statistical models for biological covariance

The principal components of shape (PCS) were calculated from a principal component analysis of the variance-covariance matrix of the Procrustes residuals. Projection of the Procrustes residuals onto PCS gives PCS scores. The next step was the statistical procedure, using the shape space defined by all the PCS in the following calculations:

1) The "common allometric shape vector" was used to identify ontogenetic allometries. The meaning of the term allometry, as used here, differs from the classical meaning given by Huxley (1924). In classical allometry, the variables do not distinguish form, size, and shape. The Procrustes method allows size differences to be eliminated by size normalization, and therefore it allows us to obtain shape variables. The size variables become "external" data, which may be used to calculate allometry as shape changes associated with size changes. Therefore, allometry becomes the study of the covariance between size and shape (Mosimann, 1970; O'Higgins, 2000). Allometry is calculated using a regression in which the independent variable is the size, and the dependent variables are the PCS scores. A regression where many dependent variables are used instead of a

single one is a multivariate regression. The basic principles of multivariate regression are given in Kraznowski (1988), and have been widely applied to geometric morphometry (Walker, 1993; Loy et al., 1996; Penin and Baylac, 1995, 1999; Penin, 1997; Baylac and Penin, 1998). We calculated the allometry common to humans and chimpanzees using the mean variance-covariance matrix of the two species, as suggested in Burnaby (1966) for a sample corresponding to more than one taxon.

In the multivariate regression we must solve the following equation where y^i_j is the score of the ith specimen in the jth principal components of shape (PCS), x^i the size of the ith specimen (centroid size), and b_j the unknown.

$$\begin{pmatrix} y^1_1 & y^1_2 & \dots & y^1_j \\ y^2_1 & y^2_2 & \dots & y^2_j \\ \dots & \dots & \dots & \dots \\ y^i_1 & \dots & \dots & y^i_j \end{pmatrix} = \begin{pmatrix} x_1 \\ x_2 \\ \dots \\ x_j \end{pmatrix} \times (b_1 b_2 \dots b_j)$$

The solution to this equation gives the b coefficients used to calculate the linear combination of PCS giving the "common allometric shape vector," V, as follows:

$$V = (b_1 \times PCS_1 + b_2 \times PCS_2 + \dots + b_j \times PCS_j)$$

2) The discriminant function was used to identify taxonomic differences between chimpanzees and humans. Computation of the discriminant function is similar to multivariate regression, in which the x variable is a dummy variable which characterizes the group (e.g., 0 for chimpanzees and 1 for humans). The discriminant function and the multivariate regression are used to build graphs of shape changes associated with either growth allometries or taxonomic differences.

Graphical results

The shape differences are studied with two different sorts of graphs. 1) Scatter plots give the position of the specimens either in the shape space (PCS, common allometric (shape) vector, discriminant vector), or in function of their size. 2) "Sketches" show shape changes associated with PCS (not given here), common allometric vector, and discriminant vector. These "sketches" represent simultaneously extreme shape differences (e.g., juveniles vs. adults, and humans vs. chimpanzees).

Statistical tests

Allometry was tested using the coefficient of determination (R^2) of a multiple regression, as suggested by Mosimann (1970) and Bookstein (1991). R^2 was also used for the discriminant function. The parametric F value was calculated from the R^2 of the pooled mean covariance matrix. For calculation, we did not use the total number of PCS. Instead, we used the significant PCS, in this case PCS1, PCS2, and PCS3, according to the results of statistical tests. We also used two nonparametric tests: one for allometry based on a resampled R^2 (Good, 1997), and one for discrimination based on cross-validation.

Superimpositions, graphs, and statistical tests were carried out with APS software, version 2.30 (Penin, 2000).

RESULTS

The consensus of all specimens, as calculated by the Procrustes superimposition, is given in Figure 1.

PCS analysis

In Figure 2, the individuals are projected onto the plane of the first two principal components of shape (PCS1 and PCS2). These two components represent 77% and 8%, respectively, of total shape variance. At this stage of the analysis, the PCS are only used to show how the variance is partitioned and not to visualize shape differences, which are better viewed using the statistical models (common allometric vector, and discriminant vector). One may notice that since no biological model is used to generate these components, there is no special reason to suppose that PCS could be *directly* related to a biological source of variation (Marcus, 1990). This graph gives the respective magnitude of shape changes in humans and chimpanzees. The individuals fall into two parallel clouds, clearly separated by the origin (consensus localization). The chimpanzees are on the left and the humans on the right. Each cloud is obliquely oriented in PCS1 and PCS2, with a gradient scaling from the earliest stage of growth (stage 0) to the adult stage (stage 3). Two important features should be noted. Firstly, the chimpanzee cloud is more extended than the human cloud, showing that changes in shape are globally more important in chimpanzees than in humans. Secondly, the groups of specimens corresponding to the various stages of growth (stages 0–3) have similar lengths and are regularly spaced in chimpanzees but not in humans. The magnitude of shape changes varies in humans according to the period of growth.

Allometry

In Figure 3, the x-coordinates are the centroid sizes and the y-coordinates the common allometric vector (see Materials and Methods). The graph allows us to visualize the magnitude of size-related shape changes which are common to humans and apes ("common allometry") relatively to their size (centroid sizes). We analyze size-shape differences between and within the different stages of growth given by dental stages in the two species. The two clouds corresponding to the two genera are clearly separated and have parallel directions, as a result of the allometric patterns being similar in chimpanzees and humans in terms of size-shape association. However, they differ considerably in the following traits. Firstly, the overall size of the skulls (centroid sizes, x-axis) is very different in humans and chim-

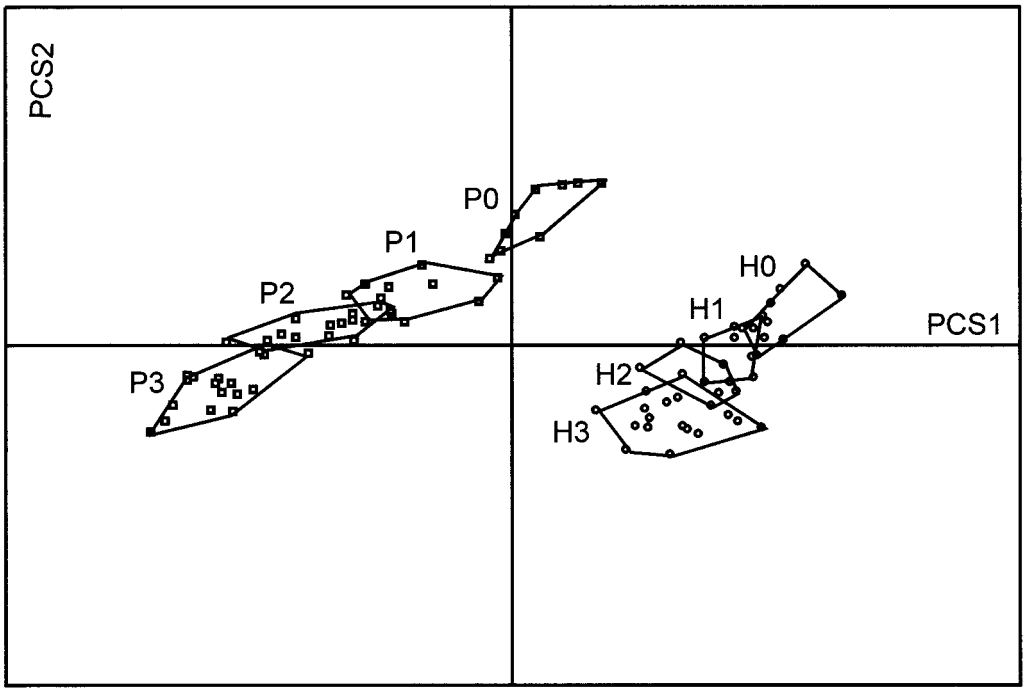

Fig. 2. The 91 specimens projected onto the plane of the first two principal components of shape PCS1 (77% of variance) and PCS 2 (8% of variance). Stages of growth: 0 (no permanent molar); 1 (first permanent molar); 2 (second permanent molar); and 3 (third permanent molar). H0–H3: *Homo sapiens*. P0–P3: *Pan troglodytes*. The human cloud is less extended than the chimpanzee cloud, showing that changes in shape are globally less important in humans than in chimpanzees.

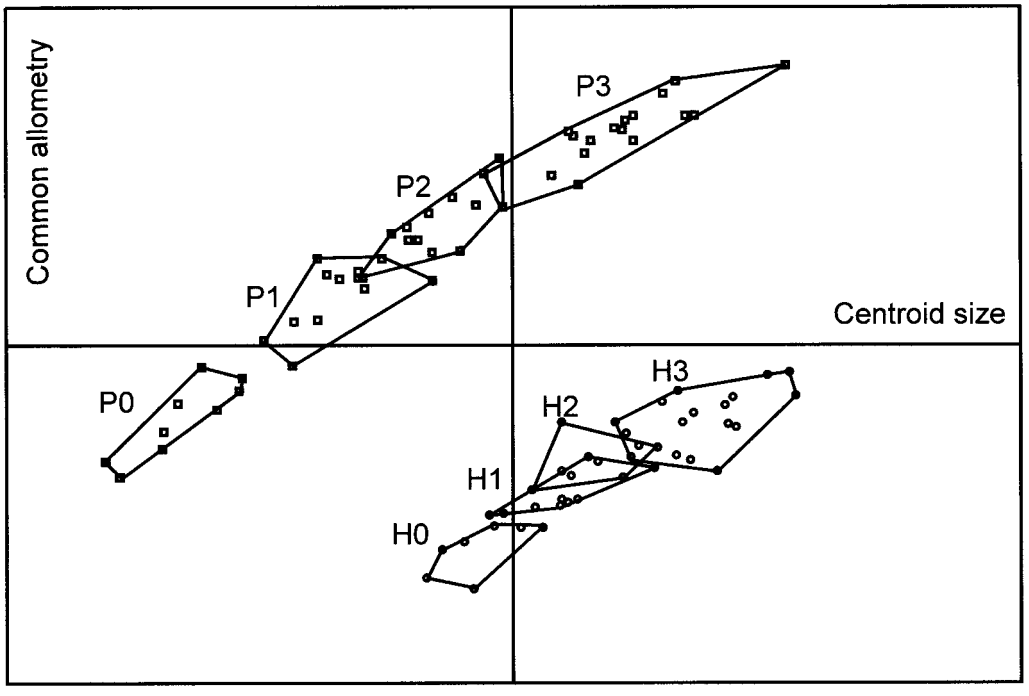

Fig. 3. Allometric changes in humans and chimpanzees. Stages of growth: 0 (no permanent molar); 1 (first permanent molar); 2 (second permanent molar); and 3 (third permanent molar). H0–H3: *Homo sapiens*; P0–P3: *Pan troglodytes*. Common allometry: common shape allometric vector. In terms of common allometry, adult humans do not exceed the shape of very young chimpanzees (P0 in y-axis), whereas the size of the skull (centroid size) becomes equivalent to that of adult chimpanzees (P3 in x-axis).

panzees at the beginning of growth. Very young chimpanzees without permanent teeth (stage 0) have much smaller skulls than humans at a similar stage of growth, whereas there is very little difference in size between the skulls of adult humans and chimpanzees. Secondly, the chimpanzee cloud is

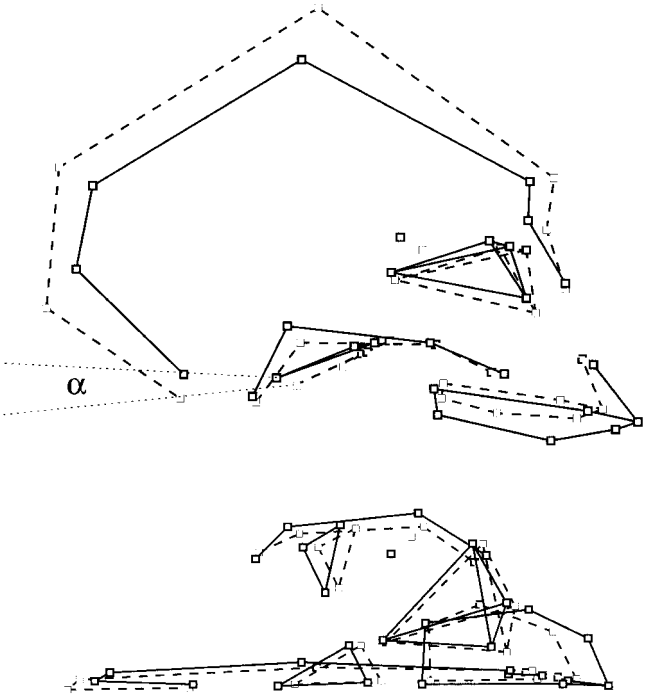

Fig. 4. Common allometry in humans and chimpanzees. The two designs represent size-related shape changes in a chimpanzee-human consensus. Dashed lines, juvenile specimens (no permanent molar); solid lines, adult specimens; dotted lines, plane of the foramen magnum (landmarks 1–10). Top: Sagittal view. Bottom: Inferior view. Faces of skulls are turned to right. The most important change in shape during growth concerns the relative volume of the neurocranium, which becomes proportionally smaller relative to the face. The plane of the foramen magnum becomes less obliquely oriented. Angle α measures the part of the change in the orientation of the foramen magnum related to the common allometry.

twice as long as the human cloud. Thus the two allometric patterns differ in terms of magnitude. The allometric ontogenetic changes are much more important in chimpanzees than in humans. The size-related shape changes common to both chimpanzees and humans are the variations in y-coordinates on either side of the consensus (coordinates 0, 0).

The common allometric vector (y-coordinates in Fig. 3) may be visualized in a "sketch" representing the shape differences between the two stages of growth. In Figure 4, shape changes are described for the chimpanzee-human consensus. The magnitude and location of shape changes are given by the "deformation" of the configuration of landmarks as a whole, from stage 0 to stage 3. However, we describe different regions of this configuration. We observe that the most important change in shape during growth concerns the relative volume of the neurocranium that becomes proportionally smaller relative to the face. The sagittal view of the skull shows that the neurocranial vault becomes proportionally lower and shorter (landmarks 7–10). In contrast, the volume of the face increases proportionally downward, forward, and backward. Other changes in shape are particularly noticeable at the base of the skull. The foramen magnum (landmarks 1–10), inion (landmark 27), cranial base (landmarks 21–24), and porion (landmark 11) are relatively higher. The mastoid (landmark 28) remains unchanged. The plane of the foramen magnum (landmarks 1–10) is slightly modified with growth and becomes less obliquely oriented, from upward and forward to downward and backward. Similarly, the body of the sphenoid (landmarks 1–2) also becomes less inclined. In the face, the largest change observed concerns the alveolar portion of the face, which becomes relatively longer and higher (landmarks 4, 18, 19, and 29). The rest of the face changes less with growth, apart from a slight upward movement of the portion of the face corresponding to the orbital cavity and the pterion (landmarks 14–17 and 25). The inferior view of the skull also indicates that the face widens at the zygomatic arch, with a backward relative movement of the whole cranial base (landmarks 1, 2, and 24) and of the temporomandibular joint (TMJ; landmarks 21–23), whereas the palate becomes longer in its anterior part, as explained above.

To reinforce the notion of common allometry, we calculate the percentage of shape changes which is related to the common allometry in each species. We found that the common allometry is nearly equal to the first component of each within-species PCA. In chimpanzees, the common allometry corresponds to 71% of the total shape changes (PCS1 = 72%), whereas in humans, the common allometry corresponds to 29% of the total shape changes (PCS1 = 31%).

Discrimination

The discriminant function was used to try to find the shape differences that best separate these two genera. Shape differences between humans and chimpanzees, which are independent of growth, may be visualized in a "sketch" representing the human consensus and the chimpanzee one when superimposed. As previously explained in the sketch of the common allometry, the magnitude and location of discriminant shape are given by the "deformation" of the configuration of landmarks as a whole (from the chimpanzee configuration to the human one), although we describe different regions of this configuration. Figure 5 shows differences in shape regardless of growth stages between chimpanzees (dotted lines) and humans (solid lines). The discriminant traits are described at first in the sagittal view, and then in the inferior view. Firstly, there is little difference between chimpanzees and humans in the vault, apart from the glabella (landmark 26), which is lower, and bregma (landmark 8), which is higher in humans than in chimpanzees. Secondly, there was extensive movement of landmarks in the lower part of the skull for humans, relative to chimpanzees. Two regions, the foramen magnum (landmarks 1–10) and the mastoid process (landmark 28), were shifted much further downward and forward in humans than in chimpanzees. The discriminant traits

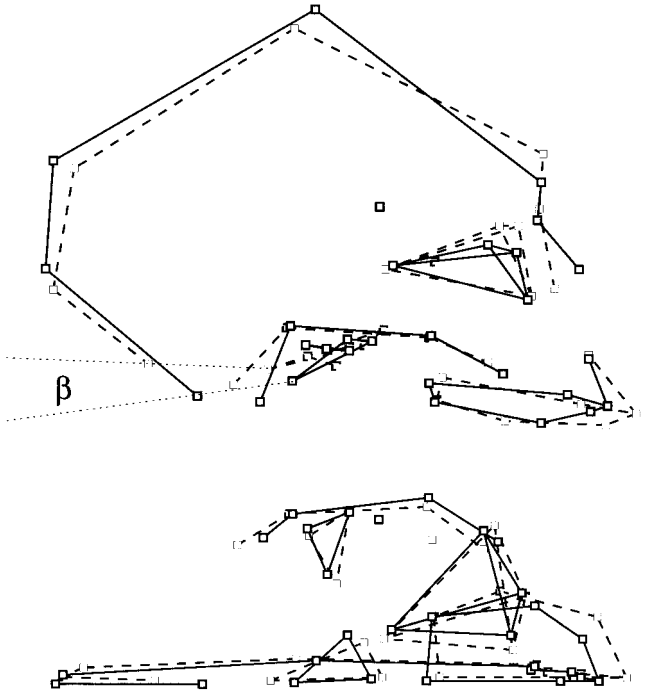

Fig. 5. Discriminant shape changes. Dashed lines, chimpanzees (all ontogenetic stages confounded); solid lines, humans (all ontogenetic stages confounded); dotted lines, plane of the foramen magnum (landmarks 1–10). Top: Sagittal view. Bottom: Inferior view. Faces of skulls are turned to right. The shape traits that discriminate humans from chimpanzees involve remodeling of the shape of the skull and face, which is clearly different from ontogenetic changes given in Figure 4. Angle β measures the part of the change in the orientation of the foramen magnum unrelated to the common allometry, which discriminates humans from chimpanzees independent of growth.

shown in Figure 5 are very different from the ontogenetic changes shown in Figure 4. The shape traits that discriminate humans from chimpanzees involve complete remodeling of the shape of the skull and face, whereas ontogenetic shape changes concern mainly the overall proportions of the neurocranium and the face. This reshaping in humans leads to an apparently similar orientation of the foramen magnum and sphenoid body to that found early in ontogeny (Fig. 4). In humans, the foramen magnum and the sphenoid body are slightly more inclined, from upward and forward to downward and backward, than in chimpanzees. Again, this apparent likeness between early ontogenetic traits and discriminant traits in humans corresponds to very different movements of landmarks. In human children, the cranial base is lower than in adults (Fig. 4), whereas the cranial base is located further forward in humans than in chimpanzees (Fig. 5). The discriminant traits of the face mainly concern the region of the nose and the alveolar region with the palate (Fig. 5). In humans, the nasal bones are very prominent, and the anterior part of the palate (landmark 4) is much further back than in chimpanzees. The orbital cavities slightly differ in shape because the orbit margin (landmark 15) and the dacryon (landmark 16) are situated relatively lower in humans than in chimpanzees. The axial view of the skulls shows other traits that discriminate humans from chimpanzees, such as the broadness of the face at the zygomatic arches and orbits, the very short anterior part of the palate, and the forward situation of the foramen magnum in humans.

Allometry versus discrimination

We calculated the angle between the common allometric vector and the discriminant vector. The two vectors were almost orthogonal (angular value, 90.11°) in the shape space. This geometrical orthogonality of the two vectors shows that the variables represented by those vectors are statistically independent. Thus, ontogenetic shape changes were independent of the traits discriminating between humans and chimpanzees. Figure 6 emphasizes the differences between humans and chimpanzees by comparing specific shape traits (discrimination) with allometric traits (common allometry). The two clouds corresponding to humans and chimpanzees are perpendicular to the discriminant vector (y-axis) and parallel to the common allometric vector (x-axis). The chimpanzee cloud is twice as elongated as the human cloud, indicating that during growth and particularly during stages 1 and 2 (first and second permanent molars), shape changes are greater in chimpanzees than in humans. The human cloud is laterally displaced along the x-axis relative to the chimpanzee cloud. Thus, the very young chimpanzees (stage 0) have x-coordinates similar to adolescent and adult humans (stages 2 and 3), but very different y-coordinates (discrimination). This indicates why very young chimpanzees show some similarity to adult humans in terms of shape, but differ greatly in terms of discriminant traits.

Statistical tests for common allometry and discrimination

The F test for common allometry was highly significant. We obtained the following values for the first three PCS, accounting for 86.18% of total variability: $R^2 = 0.923337$, $F = 349.281056$ with 3 and 87 degrees of freedom (DF), $P < 10^{-6}$. The F test for the discriminant function was also highly significant: $R^2 = 0.981369$, $F = 1527.566907$ with 3 and 87 DF, $P < 10^{-6}$ for three PCS.

The nonparametric tests were also highly significant. For the common allometry, the probability of obtaining a permutated R^2 value greater than the initial value was lower than 10^{-3}. Cross-validations for the discriminant function showed no misclassification.

Two statistical tests were carried out to compare the variances for size and shape between *Homo* and *Pan*. Bartlett's test of variance homogeneity showed that the variances for both size and shape were significantly larger in chimpanzees than in humans. The variance for size in chimpanzees was three

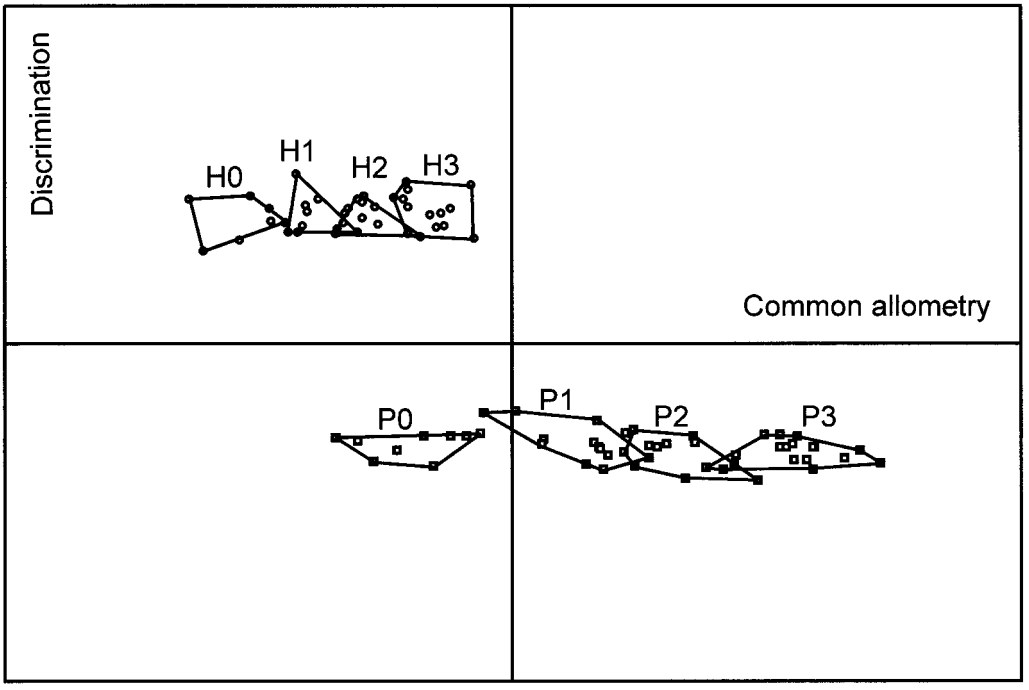

Fig. 6. Allometry vs. discriminant shape changes. Stages of growth: 0 (no permanent molar); 1 (first permanent molar); 2 (second permanent molar); and 3 (third permanent molar). H0–H3: *Homo sapiens*. P0–P3: *Pan troglodytes*. Common allometry: common shape allometric vector. Discrimination: discriminant vector; see Materials and Methods. Two clouds corresponding to humans and chimpanzees are perpendicular to the discriminant vector (y-axis) and parallel to the common allometric vector (x-axis), showing independence of the two processes.

times that in humans: 15.62 and 5.09, respectively ($F = 3.06$ with 49 and 40 DF, $P < 10^{-3}$). The variance for shape allometry in chimpanzees was four times that in humans (0.0065 and 0.0016, respectively; $F = 4.03$ with 49 and 40 DF, $P < 10^{-4}$).

DISCUSSION

The value of comparative ontogenetic study for the investigation of evolutionary processes such as human neoteny has been recognized for many years. The results of our study support the hypothesis of a neotenic human skull proposed by Gould (1977) (i.e., "retardation" in shape, increase in size, and increase in duration of growth), but modify it slightly. Gould (1977) believed that the human neoteny was "a general, temporal retardation of development" (p. 365). Thus, an increase in size signified for Gould (1977) an increase in brain size as a consequence of a larger body size ("the human brain is paedomorphic because it has increased by prolonging to later times and larger body size," p. 365). In our results, at the adult stage the human skull is not different in size from that of the chimpanzee because size is the multivariate size of the skull which includes the face and the neurocranium. However, if we consider not the final step of ontogenetic processes (adults), but earlier stages of growth (before the second permanent molar), humans reach a larger size of skull as compared with the chimpanzees, as in the theory of Gould (1977). The reason is in the growth of the face, which is accelerated relative to that of the neurocranium at the end of growth. As previously suggested by Dean and Wood (1984) and Shea (1989), this is more an issue of changes in growth rates and timing than real neoteny. If morphology is analyzed in terms of size and shape, human neoteny appears to be even more complicated than was thought at first. One of the most important findings of this study concerns the shape traits of the skull that are classically described as neotenic in humans. The apparent likeness in the shape of the skull in adult humans and juvenile chimpanzees may be partially masked by specific human traits, which superficially resemble juvenile traits but which are, in reality, independent of growth.

Human skull neoteny as overall or partial retardation

We used the Procrustes superimposition to calculate and describe the general growth trend, common to chimpanzees and humans (Figs. 3, 4). The parallelism between the within-species growth trajectories (as in Fig. 3) showed that chimpanzees and humans have homologous ontogenetic shape changes. This result is in accordance with those of Delattre and Fénart (1960), who used the vestibular axis to compare ontogenetic shape changes in the skulls of humans and chimpanzees. However, such similarity in growth pattern is not true in terms of magnitude. The allometric change in human growth decreases in magnitude in reference to that of chimpanzees (Fig. 3). The statistical tests comparing

variances for size and shape separately showed that the overall magnitude of size-shape variations in human growth appears to be truncated, being less extended than that of chimpanzees. At the end of growth, the human skull is globally retarded compared to the size and shape it would have if it grew like the skull of the chimpanzee. Such a heterochronic process concerning the magnitude of size-shape changes in the common growth pattern may be described as a rate hypomorphosis, because it refers to a problem of growth velocity, i.e., an overall retardation of the pattern of allometry according to Shea (1989). However, the process is not so simple.

We may first state that such retardation in terms of velocity within the allometric pattern is true, even though the real ages of specimens were used instead of dental stages. The retardation of the pattern of allometry will be more marked with real ages owing to the retardation of dental stages in humans as compared with chimpanzees (Dean and Wood, 1984; Smith, 1986; Bromage, 1987, 1992; Smith et al., 1995; Anemone et al., 1996). For example, at the end of growth, the human skull reaches the morphology of the skull of a chimpanzee of 4 years of age only in terms of allometrical changes. Secondly, our results cannot coincide with schematic representations of heterochrony, such as clock models (Gould, 1977; Shea, 1989), which give a single comparison between adult stages. For example, the graph of Figure 3 also shows that human skull growth involves variations in relative growth velocity, whereas the skull of the chimpanzee grows very regularly.

To characterize the irregularity in human skull growth in greater detail, we considered variations in size and shape separately, in reference to the growth of the chimpanzee skull. Actually, another type of heterochronic change has to be considered, size-shape dissociation, when the two species are compared at similar stages of growth. This feature is revealed in Figure 3 with the lateral transposition between the two ontegenetic trajectories (from dental stage 0 to adult stage). This means that in terms of shape alone, the human skull is retarded as compared with that of the chimpanzee. Differences in the shape of the skull are visible at every stage of growth. Although there were no neonates in our sample, we may assert that very young chimpanzees have much more mature skulls in terms of shape than very young humans, and this is true through to adulthood. However, this is untrue in terms of size (Fig. 3).

The youngest humans, around 2 years of age in this study, are displaced relative to the youngest chimpanzees of similar age, or similar growth stage, with a much larger skull. Qualitatively, human neonates have a huge cranial cavity and brain relative to ape neonates (C.B., unpublished observations). Differences in overall size of the skull persist during infancy. Many authors, such as Schultz (1927) and Dean and Wood (1984), noticed some accelerative processes in the size of the skull at the beginning of growth in humans. Shea (1989) reminds us that, as Weidenreich stated (1941), "in humans, we do extend in time the early period of rapid prenatal and early postnatal brain growth " (p. 82). In this study, we found that human skull growth is strongly accelerated in terms of size during infancy, whereas it is strongly decelerated later during the juvenile and adolescent periods of growth (Fig. 3). However, as the human skull is larger at birth and at the beginning of growth than the skull of the chimpanzee, it reaches the same size at the end of growth.

One of the main questions arising relative to human neoteny concerns the increase in overall size that is supposed to be the consequence of a retarded and prolonged growth. As previously discussed by Berge (1998), the size of the postcranium must be considered separately from the size of the skull in studies of heterochronies, because the cranium and postcranium have a different velocity and duration of growth (e.g., see comparison of growth curves in Bogin, 1999). These results show that the human skull is retarded in terms of magnitude of growth (intraspecific size-shape covariation), as well as in terms of shape, but not so much in terms of size (interspecific size-shape dissociation).

To conclude about neoteny, we interpret our results as follows. If we consider the chimpanzees as representing the ancestral pattern of allometrical growth for apes and hominids, then humans, who share the same allometrical pattern in terms of morphological changes but not in terms of magnitude, are "retarded." We interpret our results as a combination of two heterochronic processes: a rate hypomorphosis (i.e., retardation in terms of magnitude of allometrical changes), and a shape retardation (i.e., retardation in terms of shape changes resulting from a size-shape dissociation). The two processes refer to different paedomorphoses described by Shea (1989; clock models A and C, p. 72). However, our results also include a change in growth velocity and duration, since the dental stages of human growth are retarded and the period of growth prolonged in reference to chimpanzees. The retarded adult stage in humans is not taken into account in the clock models representing either the rate of hypomorphosis or neoteny in Shea (1989). Only the representation given by Gould (1977) for human neoteny is relatively close to our results (Fig. 7). They support the hypothesis by Gould (1977) of paedomorphosis via size-shape dissociation, including changes in ontogenetic age. Neoteny sensu Gould (1977) is paedomorphosis (juvenile shape) through slow development. Shea (1989) predicts other possibilities for paedomorphosis with the use of classical allometrical methods (comparison of allometrical slopes). However, application of classical bivariate allometry to heterochrony is questionable (discussed above). Our purpose here is not to discuss the validity of such heterochronic models, but rather to underline the necessity of having valid data in terms of potentially independent size and shape.

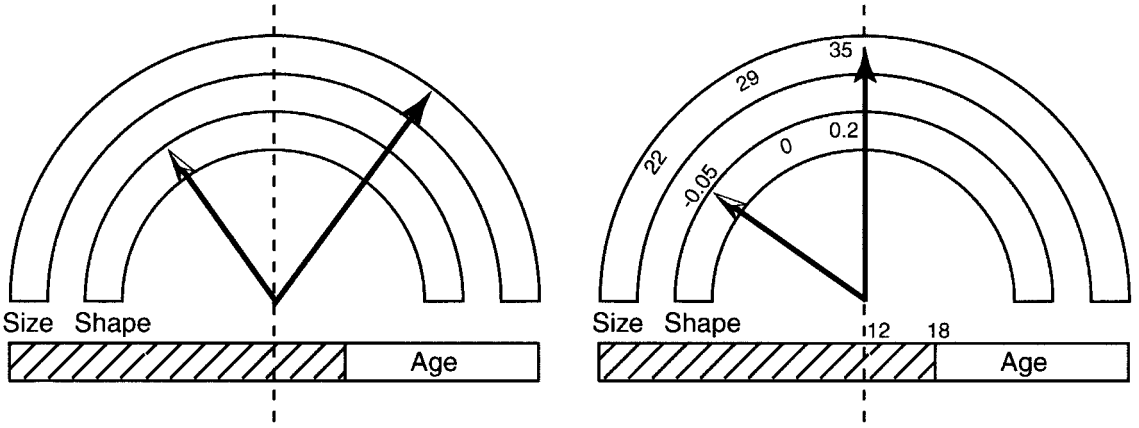

Fig. 7. Clock models for human neoteny. In each clock, the "ancestral" condition (adult chimpanzees) corresponds to the vertical line. The "descendant" condition (adult humans) corresponds to the displacement of the three independent vectors: size, shape, and age. Left: Qualitative account of human neoteny in Gould (1977). Right: Quantitative account of human neoteny from our data (adult coordinates in Fig. 3). "Size" is the centroid size; "shape" is the common allometry ("common shape allometric vector;" see Materials and Methods). Calibration of size and shape is given by units on x-axis and y-axis in Figure 3 (numbers not represented in Fig. 3). "Age" is age of maturity in terms of dental stages: around 12 years for chimpanzees, and 18 years for humans (Dean and Wood, 1984; Smith, 1986; Smith et al., 1994, 1995).

Neotenic versus discriminant traits in the human skull

Human neoteny makes reference to the paedomorphic traits described by Bolk (1926) and contemporaries, and reviewed in Gould (1977). In modern language, the neotenic traits of the human skull have been described as follows: 1) the cranial vault is high, broad, and globular, with no supraorbital torus; 2) the face is short (orthognathism); and 3) the cranial base is flexed and the foramen magnum has a forward position. However, Shea (1989) supposes that many traits generally cited as neotenic are arguably paedomorphic. He considers that a relatively larger brain may be attributed to neoteny. Dean and Wood (1984) also consider that the morphology of the cranial base in humans is not simply paedomorphic but is probably partly related to basic differences between great apes and humans. One of the main difficulties in identifying neotenic traits in the morphology of the human skull lies in the fact that many traits that discriminate humans from apes, regardless of growth, resemble paedomorphic traits. Thus, one of the most important results in this analysis is the finding that the vector of common allometry (size-related shape changes in ontogenetic allometry in humans and chimpanzees), and the discriminant vector (between chimpanzees and humans, regardless of growth stage), are orthogonal. This means that neotenic and discriminant traits are independent, although qualitatively they may be superficially confused. Therefore, if we consider the neotenic traits cited above, we can identify which traits of the skull may really be regarded as being retarded in growth, and which traits are specific to humans, by comparing Figures 4 and 5:

1) As previously suggested by Shea (1989), we can say that the very large cerebral volume in humans may be largely but not entirely regarded as neotenic. Part of the increase in cerebral volume (high bregma) is not neotenic. However, other traits which concern the precise shape of the cranial vault, such as the smoothed glabella and high lambda, are not due to retarded growth, but rather to specific new traits in humans that are independent of growth.
2) Cerebral volume may also have an influence on the shape of the cranial base (Ross and Ravosa, 1993), and the flexed cranial base has been described as a neotenic trait in humans. In this study, only a very small part of this trait appeared to be the consequence of retarded shape. The preservation of the juvenile shape of the whole cranial cavity leads to a slightly more oblique position of the foramen magnum and of the sphenoid body in adult humans than in adult chimpanzees. The foramen magnum and the sphenoid are slightly more inclined from upward and forward to downward and backward. However, the flexed cranial base in adult humans is mainly the consequence of additional traits which are independent of growth. The foramen magnum and the sphenoid have an oblique position in humans, because the foramen magnum is strongly displaced to a more forward position (Fig. 5). This new structural trait artificially amplifies the apparent juvenilization of the human skull.
3) The shape of the face in adult humans is neotenic only in its overall size, which is very small relative to cerebral volume. The retarded growth does partly reduce prognathism. However, human orthognathism is only partly neotenic, and is more the consequence of additional structural traits arising early in growth. Humans have a much shorter anterior portion of the face (the portion of

the alveolar arch, anterior to the molars) than do chimpanzees (Fig. 5). Other additional traits, such as the prominent nasal bone and the high situation of the orbits, are also part of the reshaping of the human face (Fig. 5).

Evolution and adaptation

As regards functional adaptation, it is clear that both during growth and by additional traits, the three main modifications of the shape of the skull in humans (cerebralization, orthognathism, and flexed cranial base) are linked. For example, the equilibrium of the head in the sagittal plane requires the ponderal moment of the face to be counterbalanced by the moment of the nuchal muscles (Kummer, 1959). A reduced prognathism consequently leads to a severe reshaping of the occipital area, via the reduction of the muscular and ponderal moments. Thus, a short and flexed cranial base is inevitably linked with orthognathism. Similarly, the flexed cranial base is also linked to an increase in cerebral volume via encephalization (Ross and Ravosa, 1993).

As regards evolutionary processes, this study indicates that the shape of the skull in adult humans results from both alterations in growth (heterochronic processes) and additional traits appearing very early in human growth as innovations. The shape of the human skull results to a greater extent from a retarded growth both in terms of magnitude (size-shape covariation) and in terms of shape (size-shape dissociation) in reference to chimpanzees. The evolution of the human skull via neotenic processes mainly concerns the increase in cerebral volume and, consequently, the process of encephalization. However, it seems that additional structural traits that have appeared in human evolution, such as a flexed cranial base, a reduced anterior portion of the face, a prominent nose, and a smoothed glabella, are more related to masticatory, respiratory, and locomotor functions. The flexed cranial base, for example, is directly linked with permanent bipedalism, via the vertical equilibrium of the head. One point that must be stressed is that all the bipedal traits studied, whether in the skull (basicranium) or postcranium (pelvis and femur, see above), do not result from neotenic processes but rather from additional structural traits. Indeed, as demonstrated by Lieberman and McCarthy (1999) for the cranial base in humans, structural traits appear very early, either during fetal life or at the very beginning of childhood (before 2 years of age, not only for the cranial base but also for the pelvis), whereas allometric changes are regulated during all of growth. In biological terms, it does not means that the human brain results from a simple change in growth allometry via regulator genes. Actually, it suggests that genetic determinants, which are not only structural genes leading to the formation of additional morphological traits, but also regulator genes, may interact strongly in the process of encephalization.

ACKNOWLEDGMENTS

We thank Mr. D. Howell of the Powell-Cotton Museum of Birchington and Dr. C. Grigson of the Museum of Anatomy of the Royal College of Surgeons of England for allowing us to study their material. This study is a contribution of the “Groupe de Travail, Morphométrie et Analyse de Forme” of the Muséum National d’Histoire Naturelle (Paris), which is funded by a Contrat Pluriformations from the French MESR. This paper is dedicated to F.J. Rohlf on the occasion of his sixty-fifth birthday.

LITERATURE CITED

Aiello L, Dean C. 1990. An introduction to human evolutionary anatomy. London, San Diego, New York, Boston, Sydney, Tokyo, and Toronto: Academic Press, Harcourt Brace and Co.

Alberch P. 1990. Natural selection and developmental constraints: external versus internal determinants of order in nature. In: De Rousseau CJ, editor. Primate life history and evolution. New York: Wiley-Liss. p 15–35.

Alberch P, Gould SJ, Oster GF, Wake DB. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

Anemone RL, Mooney MP, Siegel MI. 1996. Longitudinal study of dental development in chimpanzees of known chronological age: implications for understanding the age at death of Plio-Pleistocene Hominids. Am J Phys Anthropol 99:119–133.

Baylac M, Penin X. 1998. Wing static allometry in *Drosophila simulans* males (Diptera, Drosophilidae) and its relationships with developmental compartments. Acta Zool 44:97–112.

Berge C. 1993. L’évolution de la hanche et du pelvis des hominidés: bipédie, parturition, croissance, allométrie. Paris: Cahiers de Paléoanthropologie, CNRS Éditions.

Berge C. 1995a. La croissance du pelvis de l’homme comparée à celle des pongidés africains: implications dans l’évolution de la bipédie. Anthropol Préhist 106:45–56.

Berge C. 1995b. The pelvic growth in extant and extinct hominids: implications for the evolution of body proportions and body size in humans. Anthropologie 33:47–56.

Berge C. 1998. Heterochronic processes in human evolution. An ontogenic analysis of the hominid pelvis. Am J Phys Anthropol 105:441–459.

Bogin B. 1999. Patterns of human growth. 2nd ed. Cambridge: Cambridge University Press.

Bolk L. 1926. On the problem of anthropogenesis. Proc Sect Sci Kongr Akad Wetens (Amsterdam) 29:465–475.

Bookstein FL. 1989. Size and shape: a comment on semantics. Syst Zool 38:173–180.

Bookstein FL. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge: Cambridge University Press.

Bromage TG. 1987. The biological and chronological maturation of early hominids. J Hum Evol 16:257–272.

Bromage TG. 1992. The ontogeny of *Pan troglodytes* craniofacial architectural relationships and implications for early hominids. J Hum Evol 23:235–251.

Burnaby TP. 1966. Growth invariant discriminant functions and generalized distances. Biometrics 22:96–110.

Dean MC, Wood BA. 1984. Phylogeny, neoteny and growth of the cranial base in hominoids. Folia Primatol (Basel) 43:157–180.

Delattre A, Fénart R. 1960. L’hominisation du crâne étudiée par la méthode vestibulaire. Paris: CNRS Éditions.

Dryden IL, Mardia KV. 1998. Statistical shape analysis. Wiley series in probability and statistics. Chichester, Weinheim, Brisbane, Singapore, Toronto: John Wiley & Sons, Inc.

Enlow DH. 1968. The human face: an account of the postnatal growth and development of the craniofacial skeleton. New York: Harper and Row.

Enlow DH, Hunter WS. 1970. The growth of the face in relation to the cranial base. Eur Orthod Soc Congr Rep 44:321–335.

Godfrey LR, Sutherland MR. 1995. What’s growth got to do with it? Process and product in the evolution of ontogeny. J Hum Evol 29:405–431.

Godfrey LR, Sutherland MR. 1996. Paradox of peramorphic paedomorphosis: heterochrony and human evolution. Am J Phys Anthropol 99:17–42.
Godfrey LR, King SJ, Sutherland MR. 1998. Heterochronic approaches to the study of locomotion. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. Primate locomotion, recent advances. New York and London: Plenum Press. p 277–307.
Good P. 1997. Permutation tests: a practical guide to resampling methods for testing hypotheses. Springer series in statistics. New York: Springer-Verlag.
Goodall C. 1991. Procrustes methods in the statistical analysis of shape. J R Stat Soc 53:285–339.
Goodall C. 1995. Procrustes methods in the statistical analysis of shape revisited. In: Mardia KV, Gill CA, editors. Current issues in statistical shape analysis. Leeds: Leeds University Press. p 18–33.
Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. Biol Rev 41:587–640.
Gould SJ. 1977. Ontogeny and phylogeny. Cambridge, MA: Harvard University Press.
Gower JC. 1975. Generalized Procrustes analysis. Psychometrica 40:33–51.
Heintz N. 1964. Aspects infantiles tardifs de la croissance du crâne humain. C R Acad Sci groupe 2 259:2297–2299.
Heintz N. 1966. Le crâne des anthropomorphes, croissance relative, variabilité, évolution. Musée Royal Afrique Centrale, Tervuren, Belgique. Ann Sci Zool 6:1–122.
Huxley JS. 1924. Constant differential growth-ratios and their significance. Nature 114:895–896.
Huxley JS. 1932. Problems of relative growth. London: Methuen.
Kendall DG. 1984. Shape manifolds, Procrustean metrics and complex projective spaces. Bull Lond Math Soc 16:81–121.
Kendall DG. 1989. A survey of the statistical theory of shape (with discussion). Stat Sci 4:87–120.
Klingerberg CP. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol Rev 73:79–123.
Kraznowski WJ. 1988. Principles of multivariate analysis. Oxford: Clarendon Press.
Kummer B. 1959. Bauprinzipien des Säugerskeletes. Stuttgart: Georg Thieme Verlag.
Lieberman DE. 2000. Ontogeny, homology, and phylogeny in the hominid craniofacial skeleton: the problem of the browridge. In: O'Higgins P, Cohn M, editors. Development, growth and evolution. Implications for the study of the hominid skeleton. London: Linnean Society of London, Academic Press. p 85–122.
Liebermann DE, McCarthy RC. 1999. The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions. J Hum Evol 36:487–517.
Loy A, Cataudella S, Corti M. 1996. Shape changes during the growth of the sea bass, *Dicentrarchus labrax* (Teleostea, Perciformes), in relation to different rearing conditions: an application of thin plate spline regression analysis. In: Marcus LF, Corti M, Loy A, Naylor G, Slice DE, editors. Advances in morphometrics. NATO-ASI series, volume 284. New York and London: Plenum Press. p 399–406.
Marcus LF. 1990. Traditional morphometrics. In: Rohlf FJ, Bookstein FL, editors. Proceedings of the Michigan Morphometrics Workshop. Special publication number 2. Ann Arbor: University of Michigan Museum of Zoology. p 77–122.
McKinney ML, McNamara KJ. 1991. Heterochrony: the evolution of ontogeny. New York: Plenum Press.
Mosimann JE. 1970. Size allometry: size and shape variables with characterization of the lognormal and generalized gamma distributions. J Am Stat Assoc 65:930–945.
O'Higgins P. 2000. Quantitative approaches to the study of craniofacial growth and evolution: advances in morphometric techniques. In: O'Higgins P, Cohn M, editors. Development, growth and evolution. Implications for the study of the hominid skeleton. London: Linnean Society of London, Academic Press. p 163–185.
Penin X. 1997. Modélisation tridimensionnelle des variations morphologiques du complexe crânio-facial des hominoidea. Thèse d'Université Paris 6.
Penin X. 2000. APS. A Procrustes software. Freeware: http://www.cpod.com/monoweb/aps.
Penin X, Baylac M. 1995. Analysis of the skull shape changes in apes using 3D Procrustes superimposition. In: Mardia KV, Gill CA, editors. Current issues in statistical shape analysis. Leeds: Leeds University Press. p 208–210.
Penin X, Baylac M. 1999. Comparaison tridimensionnelle des crânes de *Pan* et *Pongo* par superposition procruste. C R Acad Sci [III] 322:1099–1104.
Petit-Maire N. 1972. Evolution trends and comparative ontogenesis in primate cranium. J Hum Evol 1:17–22.
Ramirez Rozzi FV. 1993. Aspects de la chronologie du développement dentaire des hominidés plio-pléistocènes de l'Omo. C R Acad Sci [IIA] 316:1155–1162.
Ramirez Rozzi FV. 1998. Enamel structure and development, and its application in hominid evolution and taxonomy. J Hum Evol (special issue) 35:327–330.
Rohlf F, Slice D. 1990. Extensions of the Procrustes methods for the optimal superposition of landmarks. Syst Zool 39:40–59.
Ross CF, Ravosa MJ. 1993. Basicranial flexion, relative brain size, and facial kyphosis in nonhuman primates. Am J Phys Anthropol 91:305–324.
Schultz AH. 1927. Studies of the growth of gorilla and other higher primates with special reference to a fetus of gorilla, preserved in the Carnegie Museum. Mem Carnegie Mus 11:1–88.
Shea BT. 1989. Heterochrony in human evolution. The case of neoteny reconsidered. Yrbk Phys Anthropol 32:69–101.
Shea BT. 1992. A developmental perspective on size change and allometry in evolution. Evol Anthropol 1:125–134.
Shea BT, Hammer RE, Brinster RL, Ravosa MJ. 1990. Relative growth of the skull and postcranium in giant transgenic mice. Genet Res Camb 56:21–34.
Smith BH. 1986. Dental development in *Australopithecus* and early *Homo*. Nature 323:327–330.
Smith BH, Crummet TL, Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yrbk Phys Anthropol 37:177–231.
Smith RJ, Gannon PJ, Smith RL. 1995. Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. J Hum Evol 29:155–168.
Tardieu C. 1997. Femur ontogeny in humans and great apes: heterochronic implications for hominid evolution. C R Acad Sci [III] 325:899–904.
Tardieu C. 1998. Short adolescence in early hominids: infantile and adolescent growth of the human femur. Am J Phys Anthropol 107:163–178.
Teissier G. 1948. La relation d'allométrie, sa signification statistique et biologique. Biometrics 4:14–53.
Thompson DW. 1917. On growth and form. Cambridge: Cambridge University Press.
Wagner GP. 1994. Homology and the mechanisms of development. In: Hall BK, editor. Homology, the hierarchical basis of comparative biology. San Diego, New York, and London: Academic Press. p 243–299.
Walker JA. 1993. Ontogenic allometry of threespine stickleback body form using landmark based morphometrics. In: Marcus LF, Bello E, Garcia-Valdecasas, editors. Contribution to morphometrics. Monografias del Museo Nacional de Ciencias Naturales 8. Madrid: Museo Nacional de Ciencias Naturales. p 193–214.
Weidenreich F. 1941. The brain and its role in the phylogenetic transformation of the human skull. Trans Am Philos Soc NS 31:321–442.