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Ontogenetic integration of the hominoid face

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Abstract

By investigating similarity in cranial covariation patterns, it is possible to locate underlying functional and developmental causes for the patterning, and to make inferences about the evolutionary forces that have acted to produce the patterns. Furthermore, establishing where these covariation patterns may diverge in ontogeny can offer insight into when selection may have acted on development. Here, covariation patterns are compared among adult and non-adult members of the African ape/human clade, in order to address three questions. First, are integration patterns constant among adult African apes and humans? Second, are they constant in non-adults – i.e. throughout ontogeny? Third, if they are not constant, when do they diverge? Measurements are obtained from 677 crania of adult and non-adult African apes and humans. In order to address the first two questions, correlation matrices and theoretical integration matrices are compared using matrix correlation methods. The third question is evaluated by comparing correlation and variance/covariance patterns, using matrix correlation and random skewers methods, respectively, between adjacent age categories within each species, and between equivalent age categories among the four species. Results show that the hominoids share a similar pattern of ontogenetic integration, suggesting that common developmental/functional integrative processes may play an important role in keeping covariance structure stable across this lineage. However, there are some important differences in the magnitude of integration and in phenotypic covariance structure among the species, which may provide some insight into how selection acted to differentiate humans from the great apes.

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Introduction

“In our view, a complete lack of integration (i.e., complete independence among traits)

requires the most complex developmental mechanism and should be rejected when simpler hypotheses suffice.” (Chernoff & Magwene, 1999).

Morphological integration is – most simply – the connectivity or relationships among parts. Olson and Miller (1958) developed this concept,

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hypothesizing that traits that interacted during development or function would tend to be inherited as complexes, thereby evolving together (Olson & Miller, 1958). Cheverud (1995, 1996) further expanded this notion, developing explicit quantitative theoretical models for measuring the relationships among morphological elements of the primate skull. This research, and work that followed, showed that similar patterns of cranial morphological integration occur in adults of both New and Old World monkeys (Cheverud, 1996; Ackermann & Cheverud, 2000; Marroig & Cheverud, 2001), and African apes and humans (Ackermann 2002, 2003a; González-José et al., 2004), raising the possibility that they occur across the anthropoid primates and even the entire Primate Order (Ackermann & Cheverud, 2004).

While much of the pioneering work on morphological integration in primates has been done by Cheverud and colleagues, there have been a number of other recent studies that have evaluated this topic in primates (Lieberman et al., 2000; Strait, 2001; Hallgrímsson et al., 2002; González-José et al., 2004), bolstering a growing appreciation for the *lack* of independence of morphological traits – i.e. for their interconnectedness – and for the importance of understanding the modular architecture of the primate skull. This appreciation has infiltrated into paleoanthropological studies as well, although as Strait (2001) points out, this rarely translates into direct hypothesis testing but instead takes the form of a more generalized acknowledgement that the evolution of trait complexes is an important concern (Skelton et al., 1986; Begun, 1992; Skelton & Mchenry, 1992; Strait et al., 1997; Strait & Grine, 1998; Asfaw et al., 1999; Lovejoy et al., 1999; McCollum, 1999).

But what *exactly* can morphological integration tell us about human evolution? Clearly, it can affect our methodological choices. For example, if groups of traits are integrated and thereby inherited as units, treating them as independent in cladistic studies of fossils could bias the analysis (Strait 2001). Similarly, if patterns of integration (and by extension variation) are not constant across primates, then models which use extant variation to assess fossil relationships might not be tenable (Ackermann, 2003b). But more importantly – and

more substantially – understanding trait relationships can help us get at deeper questions of evolutionary process. This is because morphological integration plays an important role in directing evolutionary change, by constraining or facilitating the evolution of complex phenotypes. Morphological integration also provides a conceptual framework for exploring hypotheses about modularity, because different elements of the phenotype can become independently integrated and thereby modularized, which can release constraints, allowing different parts to essentially evolve independently.

In theory, this means that by looking at changes in the pattern of integration through time in the hominoid lineage, we can say something about how selection was acting to produce evolutionary change in our recent primate ancestors. In practice, as small sample sizes limit the direct evaluation of morphological integration through time in fossil hominids, empirical approaches that interpret patterns of covariation and integration in extant populations in the context of their phylogenetic relationships are substituted. As mentioned above, this approach has been taken with some success in New World monkeys; while patterns of integration were generally similar among all these primates, where they diverged it was often possible to point to evolutionary reasons for their divergence (Ackermann & Cheverud, 2000; Marroig & Cheverud, 2001). For example, the divergence of the covariation pattern of night monkeys from other South American primates could be associated with changes in cranial functional relationships tied to the evolution of night vision in this taxon (a unique state among South American monkeys). Similarly, the lack of facial integration seen in the relatively monomorphic Callitrichids could result from a lack of selection for sexual dimorphism in the face (see Ackermann & Cheverud, 2004 for further discussion). Studies of African apes and humans have also supported the notion of similar integration patterns among primates, although again there seems to be some minor divergence which may occur along phylogenetic lines (Ackermann, 2002, 2003a).

What is not clear from this work is whether the similarities in patterns of integration seen in adult

primates arise through homologous ontogenetic pathways – i.e. if ontogenetic covariation patterns are themselves shared. It is also not clear whether it is possible to separate the processes that produce adult integration (and ultimately the patterns they produce) into those that are developmental versus functional in origin. Such knowledge is essential for interpreting the past. Homology plays an important role in deciphering evolutionary relationships from morphological patterns, and similarity in patterns of morphological integration that can be linked to developmental processes are arguably more likely to be homologous. Conversely, when similarity occurs in regions where morphological integration is functional in origin, such similarity is more likely to be homoplastic. Clearly, since modularization and integration result from the hierarchical structure of developmental processes (West-Eberhard, 2003), both functional and developmental integration are in some sense developmentally based. However, it may be possible to distinguish between them in some instances. For example, Zelditch and Carmichael (1989) concluded that early developmental integration constrained the covariance structure of rats, but later on functional integration seemed to take over, providing constraint, while developmental integration patterns became unstable; they suggested that this showed a pre-weaning repatterning of integration (Zelditch & Carmichael, 1989). By comparing patterns of integration across closely related species and among adjacent age categories we can gain insight into whether integration patterns of hominoids vary through evolutionary or ontogenetic time, whether these patterns are better explained by developmental versus functional processes, and by extension whether similarity seen among taxa is likely to be homologous or homoplastic.

This paper presents an analysis of morphological integration in the facial skeleton of humans, chimpanzees, bonobos and gorillas. In particular, this study will assess: (1) whether integration patterns are constant in adult African apes and humans, (2) whether they are constant in non-adults – i.e. throughout ontogeny, and (3) whether and when they diverge. By evaluating cranial integration in these living hominoid populations, we can gain a deeper understanding of the

evolution of the African ape/human clade – both in terms of the patterns we see in hominoid morphology, as well as the processes that may have produced those patterns. Because this analysis is grounded in phylogenetic context, it also extends our knowledge of the relationship between developmental and evolutionary change, and will clarify the role that our understanding of morphological integration plays in furthering our understanding and interpretation of the human fossil record.

Materials and methods

Skeletal sample

Measurements were obtained from 677 crania of adult and non-adult African apes and humans. The specimens were drawn from collections at the Cleveland Natural History Museum, the University of the Witwatersrand (Johannesburg, South Africa), the Musée Royal de Centrale Afrique (Tervuren, Belgium), and the National Museum of Natural History (Washington, DC). Crania with complete dental eruption and fused sphenoccipital synchondroses were considered adult. The non-adult samples were made up of individuals from four different ontogenetic stages: infant, juvenile, adolescent, and subadult – categories delineated by the eruption of the first, second, and third permanent molars, respectively. Dividing the young individuals into these categories is problematic for a number of reasons. Undoubtedly, the categories are not precisely homologous among species, as there is variation in eruption sequence among taxa (Godfrey et al., 2001) – in this case, apes and humans do not share the same dental eruption sequence. However, their molars do erupt in the same sequence, and bracket similar stages in their development. Generally the emergence of the first molar marks the end of infancy (and beginning of weaning), although in humans weaning typically occurs earlier (Smith, 1994), while the emergence of the third molar marks subadulthood – the onset of sexual maturation (Smith, 1991). Here, because apes undergo extreme form change in their faces between weaning and

subadulthood, I have also broken up the time between first and third molar emergence into two categories, juvenile and adolescent, delineated by the emergence of the second molar. It is important to note that at their boundaries these categories are somewhat arbitrary, as they by definition divide a continuum.

The *Homo sapiens* sample consists of 192 adult individuals (76 females, 116 males) and 68 non-adult individuals from Sub-Saharan Africa, housed in the Raymond Dart skeletal collection at the University of the Witwatersrand. All of the individuals are cadaver specimens collected in the last hundred years from known individuals. While this population does not strictly represent worldwide diversity, it has been chosen because of the excellent ontogenetic series, and because Sub-Saharan Africa is generally considered to be highly variable genetically (Lewontin, 1972; Barbujani et al., 1997), and therefore probably represents most of the diversity seen in *Homo sapiens*. The adult ape species samples are a subset of those described in Ackermann (2002), where the reader is referred for details (the slight reduction in sample size is due to an increase in variables in this analysis). The *Gorilla gorilla* sample is composed of 86 adult crania (32 females, 54 males) from subspecific groups *G. g. gorilla* ($n = 59$), *G. g. graueri* ($n = 11$) and *G. g. berengei* ($n = 16$) and 82 non-adult crania. The *Pan troglodytes* sample contains 51 adult crania (23 females, 28 males), from sub-specific groups consisting of 25 *P. t. troglodytes* and 26 *P. t. schweinfurthi*, and 94 non-adult crania. The *Pan paniscus* sample consists of 15 adult bonobo crania (6 females, 9 males) and 89 non-adult crania.

It is important to consider how differences in sample size and structure might bias the results of this analysis. Differences in patterns of sexual dimorphism among species are mitigated using a size-correction, described below. Differences in structure due to subspecific affiliation in the adult samples were considered in Ackermann (2002); of particular concern was the uneven subspecific distribution of the gorillas. It was concluded via analysis of heterogeneity (Hartley, 1950) that this would not unduly affect the analysis, as will be assumed here. Of more concern here are the small and uneven sample sizes in the ontogenetic

categories. In particular, when samples are very small, estimates of variation and covariation may be unreliable. Additionally, when the samples are less than the number of variables, as is the case for a number of the analyses, the matrices can be overdetermined. In order to deal with these issues, four approaches are taken (see below for further description): (1) to account for error due to small sample size, matrix repeatability is calculated and is used to correct the matrices where appropriate; (2) to correct those matrices that are overdetermined, the matrices are 'bent'; (3) to further assess the effects of small sample size estimates of true variance for each matrix are calculated and weighed against the results; (4) where appropriate (i.e. if very small sample sizes seem to be affecting the analysis), non-adult samples are pooled in additional analyses.

Data collection and analysis

Three-dimensional coordinates were recorded for 16 landmarks (Table 1, Fig. 1). Each specimen was digitized once, as measurement error has been shown to be negligible (Ackermann, 1998). A set of 22 linear measurements was calculated from the coordinate values (Table 2). These variables were chosen to cover the face without redundancy, and to closely mirror those presented in Cheverud (1996), Ackermann and Cheverud (2000), and Marroig and Cheverud (2001). All measurements were calculated on the left side of the face, and supplemented with data from the right side if data were missing. Phenotypic correlation and variance/covariance matrices (hereafter referred to as correlation and covariance matrices, respectively) were obtained for these 22 facial variables in the adult gorilla and chimpanzee samples, using the residual correlation matrix and residual covariance matrix from a MANOVA with the 22 traits as dependent variables and subspecific affiliation as the independent variable, thus pooling the correlations and covariances across subspecies. Because of non-existent subspecific composition in the adult humans and bonobos, and unknown subspecific affiliation of the juvenile samples, simple Pearson correlation and covariance matrices were calculated for these samples.

Table 1
Craniofacial landmarks recorded from hominoid crania using three-dimensional digitizer*

Landmark	Description	Position(s)
NA	Nasion	midline
NSL	Nasale	midline
ANS	Anterior nasal spine	midline
IS	Intradentale superior	midline
FMN	Frontal-maxillary-nasal suture	right, left
ZS	Zygomaxillare superior	right, left
ZI	Zygomaxillare inferior	right, left
FM	Fronto-malare	right, left
ZTS	Superior zygo-temporal suture	right, left
ZTI	Inferior zygo-temporal suture	right, left
MT	Maxillary tuberosity	right, left
PNS	Posterior nasal spine	midline
PT	Pterion	right, left

* Landmarks are also identified in Fig. 1. Adapted from Cheverud (1995) and Ackermann (2002).

Correlation or covariance matrices that were overdetermined (some eigenvalues of the correlation and covariance matrices were negative) are corrected by ‘bending’ the matrices (Hill & Thompson, 1978; Hayes & Hill, 1981). In colloquial terms, this essentially ‘squeezes’ the matrix slightly (i.e. increases the negative covariances while decreasing the positive ones) via multiplication by a constant that is less than one; the values in the matrix change slightly, but not the overall pattern of covariation. This is done by first determining the eigenvalues and eigenvectors of the selected correlation or covariance matrix, then multiplying the deviations of the eigenvalues from the mean eigenvalue (μ) by a constant (k ; this value is determined based on how much bending is actually needed), and adding the mean back to these values, to bring all of the resultant values above zero, as follows:

For each eigenvalue (X), a new eigenvalue (Y) is calculated:

$$Y = (X - \mu) \cdot k + \mu$$

These new eigenvalues form the diagonal of an eigenvalue matrix (E_{mx}), with zeros in the other positions. The bent correlation/covariance matrix (B_{mx}) is then calculated from the eigenvector matrix (V_{mx}) obtained from the original correlation/covariance matrix, and this same eigenvector

matrix, transposed (TV_{mx}), so that $B_{mx} = TV_{mx} \cdot E_{mx} \cdot V_{mx}$.

Differences in size can produce differences in levels and patterns of correlations among traits (Zelditch, 1988), and can confound comparisons of variance patterns, since traits with larger means typically have larger variances (Cheverud et al., 1989). Yet size is an important biological factor in growth studies, as measurements may be highly correlated due to increase in size during development. Therefore, the entire analysis described below is done twice. First, in order to compare variation and correlation across species that are absolutely different in size and have different levels of sexual dimorphism, as well as across ontogenetic samples which differ in size both between and within species, the data were adjusted to reduce the effects of size (Ackermann, 2002). This ratio-based size adjustment follows Darroch and Mosimann (1985), where each variable (Y) is divided by the geometric mean of all variables (GM) for that individual, creating a new scale-free shape variable (X), so that $X = Y/GM$ (Darroch & Mosimann, 1985; Jungers et al., 1995). This adjustment removes isometric size but not size-related (allometric) shape. In interpreting these results relative to previous studies, it is important to note that removing a general size factor should result in lower levels of correlation overall among all traits (Marroig et al., 2004). Second, the analysis is repeated using unscaled raw data. These results may be affected by differences in absolute size and sexual dimorphism both among species and across ontogenetic categories.

The analyses that follow compare: (1) the level and patterning of morphological integration in both adult and non-adult African apes and humans, (2) correlation and covariance structure across adjacent age categories within species, (3) correlation and covariance structure across species for each developmental category. The first comparison will be accomplished by calculating matrix correlations between sample correlation matrices and connectivity matrices designed *a priori* to test hypotheses of integration at each ontogenetic stage within each species. The second will be accomplished using matrix correlation and random-skewers analysis to compare correlation and

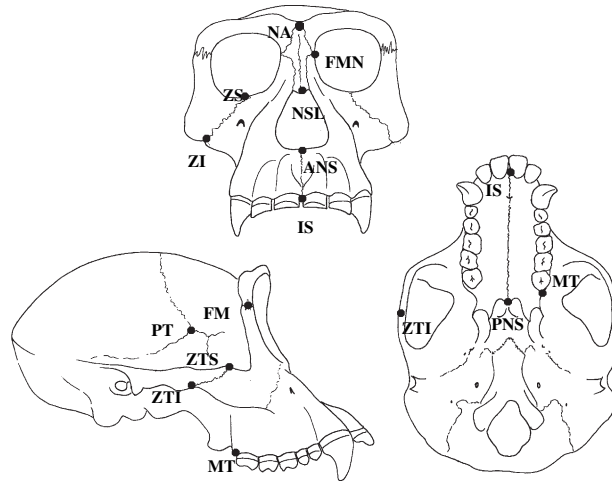


Fig. 1. Craniofacial landmarks recorded from hominoid crania using three-dimensional digitizer. Also see Table 1.

covariance matrices, respectively, in order to gain insight into when in ontogeny integration patterns might diverge within species. Similarly, the third

Table 2

Twenty-two linear skull measurements (distances between landmarks) and membership in the four developmental/functional groups*

Measurement	Developmental/Functional Group
NA-NSL	Nasal
NA-FM	Orbit
NA-PNS	Nasal
NSL-ANS	Nasal
NSL-ZS	Nasal
ANS-IS	Oral
ANS-ZS	Nasal
ANS-ZI	Oral, Nasal
IS-ZI	Oral
IS-MT	Oral
IS-PNS	Oral, Nasal
FMN-ZS	Orbit
ZS-ZI	Oral, Zygomatic
ZS-FM	Orbit
ZI-FM	Zygomatic
ZI-ZTI	Zygomatic
ZI-MT	Oral
FM-ZTS	Zygomatic
FM-MT	Zygomatic
ZTI-MT	Zygomatic
MT-PNS	Oral
FM-PT	Orbit

* See Table 1 and Fig. 1 for landmark definitions and their locations.

comparison will be made across species for each developmental category, using matrix correlation and random-skewers analysis to compare correlation and covariance matrices, respectively, in order to determine whether developmental stage versus species affiliation primarily drives similarity. Importantly, these analyses will also provide insight into morphological patterning, and will add to our understanding of variation in African ape and human crania.

Morphological integration

Elementwise matrix correlations (Sneath & Sokal, 1972) are calculated between the observed species' correlation matrices and designed morphological integration connectivity matrices, in order to test hypotheses of morphological integration – i.e. to quantify the connections or relationships among morphological elements. This analysis provides information on both the level of integration (magnitude of the matrix correlations) and on the pattern of integration (relative degree of integration among different regions). Following Cheverud (1995, 1996), Ackermann and Cheverud (2000), and Marroig and Cheverud (2001), connectivity matrices are designed to assess morphological integration within four distinct regions of the face (oral, nasal, zygomatic, orbit), and within the face as a whole (total morphological

integration). These connectivity matrices are constructed in the following manner: when two traits belong to the specified developmental/functional set, a value of one is entered in the integration connectivity matrix; otherwise a value of zero is entered. For the total integration matrix, a one is entered if traits belong to the same developmental/functional trait set; otherwise a zero is entered (Cheverud, 1995, 1996). Matrix correlations between the designed integration matrices and observed species' correlation matrices will fall between -1 and 1 , with the extremes indicating high negative and positive correlation, respectively. The overall mean for the observed species' correlation coefficients for traits with one (positive) or zero (negative) in each of the designed integration matrices is also calculated, in order to assess the degree to which shared developmental/functional regions influence the integration process (Marroig & Cheverud 2001).

Significance of these correlations is assessed using Mantel's test (Cheverud et al., 1989). For each comparison, the rows (and associated columns) of one matrix are randomly permuted and the matrix correlation is calculated between the unaltered matrix and the permuted matrix. This is repeated 10000 times, to produce a distribution of matrix correlations expected under the null hypothesis of no structural similarity between matrices. When the observed correlation is compared to this empirically derived distribution, the percent of permutation correlations greater than or equal to the observed correlation serves as an estimate of the probability of obtaining that observed correlation. Patterns are considered significantly similar when the observed matrix correlation exceeds 95% of the randomly generated correlations.

Where matrix correlation results are significant and differences between ontogenetic groups within each species are shown to be real (i.e. not an artifact of sample size as shown by the corrected matrices – see below), three-way Mantel tests (Cheverud & Dow, 1985; Smouse et al., 1986) are performed in order to test whether one correlation matrix fits the design matrix better than another. For example, if both adult and subadult human covariance matrices are highly integrated in the

zygomatic region, but to differing degrees, this test would tell us whether the difference between them is significant. To perform this test, matrices A and B are standardized so their elements have a mean of zero and a variance of one. Then the difference matrix obtained by subtracting one matrix from the other (A minus B) is correlated to the design matrix, as above; a significantly positive correlation indicates that matrix A fits the design matrix better than B, while a significantly negative correlation indicates the opposite.

Correlation and covariance patterns

To test whether correlation and covariance structure is similar across adjacent age categories within species, and across species for each developmental category, correlation and covariance matrices were compared using matrix correlations and random skewers methods, respectively. The matrix correlation method (and its significance test) is the same as described above, although here the results reflect the similarity in patterning between two samples, rather than fit of one sample to a design matrix. The random skewers method is a more appropriate test for evaluating covariance matrix similarity (Cheverud et al., 1983; Cheverud, 1996), and compares the evolutionary responses of each covariance matrix to random selection vectors (Ackermann, 2002, Marroig & Cheverud, 2001). To estimate similarity in two separate covariance matrices, a single random selection vector is generated from a uniform distribution of values between 0 and 1, and standardized to a vector length of one (sum of squared elements = 1). This vector is then multiplied by each of the two covariance matrices being compared, and the two resulting vectors (Δz_1 and Δz_2) are then correlated. This is repeated 1000 times, and the average of these repeats is the average expected evolutionary response to selection – a measure of covariance matrix similarity. These average vector correlations will fall between 0 and 1, with the extremes indicating inequality and equality in covariance structure, respectively. In order to compare similarity in correlation and covariance structure to ontogenetic patterns of shape variation, two principal components analyses are also

performed using the measurements shown in Table 2, extracting correlation and covariance matrices, respectively.

A resampling method of vector correlation is used to estimate the statistical significance of the random skewers results (Cheverud, 1996; Cheverud et al., 1983; Ackermann, 2002; see (Efron & Tibshirani, 1993), for overview of bootstrapping). For each species sample, a sample of size N is generated from the observations by randomly selecting N individuals with replacement from the original observations. The covariance matrices specified by the bootstrap samples are then calculated and compared to each other via the random skewers method (described above); this is repeated 1000 times. Ninety-five percent confidence limits are generated from the bootstrap distribution to determine significance.

Matrix repeatability and adjusted matrix correlations

Phenotypic correlation and covariance matrices are estimated with error (Cheverud, 1996). To estimate and account for the impact of sampling error in this analysis, matrix repeatability (t) is determined. These estimates of repeatability are then used to calculate a theoretical maximum ($r_{\max} = \sqrt{t_1 t_2}$) expected when comparing correlation or covariance matrices, in order to adjust the observed correlations so they represent actual matrix or vector correlations (Cheverud 1996; Ackermann & Cheverud, 2000). These repeatabilities are similarly used to adjust the matrix correlation levels for the tests of integration (for design matrices $t = 1$), in order to judge how these results are affected by sample size. They are also used to estimate the true variance (V_t) of each matrix, which is the repeatability (t) multiplied by the observed variance (V_{obs}) of each matrix, and allows us to determine whether lower fit to designed morphological integration matrices is due to lower matrix variance.

Adjusted matrix/vector correlations (r_{adj}) are calculated as the observed correlation (r_o) divided by the maximum matrix/vector correlation (r_{\max}) calculated for each pairwise comparison. Repeatabilities are determined by using a resampling

method of auto-correlation (Ackermann, 2002, Marroig & Cheverud, 2001). For the correlation matrices, for each population of size N , N samples are drawn from the population with replacement, and a correlation matrix calculated. This matrix is then correlated with the observed population correlation matrix using the matrix correlation method, described above. This process is repeated 1000 times, and the average correlation between the resampled matrices and the population matrix serves as an estimate of repeatability for each sample. For the covariance matrices, a similar process is used. A bootstrap sample of size N is generated from the observations by randomly selecting N individuals with replacement from the original species observations. The covariance matrix calculated from this sample is then correlated with the observed population covariance matrix using the random skewers method, as described in the previous section. This process is repeated 1000 times, and the average vector correlation between the resampled matrices and the population matrix serves as an estimate of repeatability for each sample (Cheverud, 1996).

Results

Phenotypic covariance and correlation matrices were calculated for each age group within each extant species, for both the scaled and unscaled data. These matrices are available from the author upon request. All of the sample matrices with sample sizes below 20 were found to be over-determined (i.e. some eigenvalues of the correlation and covariance matrices were negative), and were corrected by ‘bending’ the matrices (Hill & Thompson, 1978; Hayes & Hill, 1981). The matrices needed very little bending (i.e. their negative eigenvalues were very small), and therefore a constant of $k = 0.9999$ was used (see Methods).

Morphological integration

The morphological integration results are presented in Tables 3 and 4. The scaled and the

unscaled results of the tests for morphological integration are qualitatively similar, although there are some differences, particularly in the nasal region. For all scaled analyses, where regions are integrated, correlations among functionally and developmentally related traits across all species and age groups are consistently much larger than those among unrelated traits (an average of 0.09, compared with -0.06). Because of the size adjustment, it is hard to characterize this as a percentage increase as is done in Marroig and Cheverud (2001), but generally the correlation values found here are consistent with those for the size adjusted residual matrices presented in an analysis of *Pithecia* by Marroig et al. (2004), which in turn corresponded with non-adjusted matrix correlation values that were around 50% higher in integrated compared to non-integrated regions. This in turn corresponds with the results of the unscaled analyses seen here, where the average correlation among functionally or developmentally related traits is 0.51, compared with 0.36 among unrelated traits, indicating that correlations are 42% higher on average in integrated regions. The adjusted total morphological integration (Adj TMI) values are also presented in Tables 3 and 4, and show that while correcting for small sample size increases levels of integration slightly, it does not dramatically alter the relative patterning of this integration (i.e. whether one developmental stage is more or less integrated relative to another). Estimates of true variance for each matrix (V_t) are also presented, and indicate that there is not a clear relationship between low V_t and low integration values, again suggesting that sample size has not had undue influence on the results.

In order to evaluate whether differences in the levels of integration seen among the ontogenetic categories (discussed below) within each species are significant, a 3-way Mantel test was performed for all of the possible pairs that show significant integration within each species for each integration test (total, zygomatic, etc.). In summary, the results of these tests indicate that the threshold at which you start to see significant effects at the level of $p < 0.1$ is approximately 0.1 for unscaled data and 0.07 for scaled data. In other words, for any given pair of age groups within a species, the

difference between their correlation values must exceed 0.10 and 0.07 (for the unscaled and scaled analyses, respectively) in order for one sample to 'fit' the design matrix better than the other. In such instances the matrix with the higher correlation value represents the better fit.

Matrix correlations between observed correlation matrices and designed total integration connectivity matrices for the adults of all four species are positive and significant. Primary contributions to this pattern of adult total integration come from the oral and zygomatic regions, and to a lesser extent the nasal region (Tables 3 and 4). Subadults of all the species also show a similarly high level and pattern of total integration, as indicated by the high correlation values for the total integration matrix and by the similar relative contributions of oral/zygomatic/nasal integration to this pattern of total integration. After this, small differences begin to emerge among the species, and between the scaled and unscaled analyses, although the overall pattern is similar. In some of the species there is an age group where total integration breaks down (i.e. is relatively low or non-existent), however given that this frequently occurs in the groups with the lowest sample size, it may be unwise to place too much significance on it. On average total integration early on in ontogeny (infants/juveniles) across all species, though positive and significant, is somewhat less than in subadults and adults. The primary contribution to the pattern of total integration is also somewhat different in early versus late ontogeny. In the scaled analysis, ontogenetically early integration comes entirely from the oral region in humans, and from both the oral and to a lesser extent the zygomatic regions in the apes (see Tables 3 and 4), with the gorilla showing particularly strong integration in the zygomatic region. For the unscaled analysis, in addition to what is seen in the scaled analysis, there is a minor contribution from the nasal region in gorillas and humans, and once again gorillas show an unusually high level of zygomatic integration early in ontogeny. In contrast, integration in later ontogeny derives primarily from the oral and zygomatic regions across all groups for both scaled and unscaled analyses, while sporadic contributions

Table 3
Morphological integration for each hominoid species: Scaled data*

	N	Vt	Total MI	Adj TMI	p	Avg (+)	Avg (–)	Zyg MI	p	Avg (+)	Avg (–)	Orbit MI	p	Avg (+)	Avg (–)	Oral MI	p	Avg (+)	Avg (–)	Nasal MI	p	Avg (+)	Avg (–)
<i>H. sapiens</i>																							
adult	192	0.041	0.341	0.350	0.000	0.07	–0.08	0.215	0.003	0.13	–0.05	0.023	0.318	/	/	0.207	0.002	0.08	–0.05	0.109	0.039	0.04	–0.04
subadult	21	0.069	0.251	0.277	0.001	0.08	–0.08	0.148	0.022	0.13	–0.04	–0.048	0.900	/	/	0.133	0.035	0.07	–0.05	0.145	0.025	0.10	–0.04
adolescent	14	0.093	0.107	0.121	0.055	0.01	–0.07	0.068	0.112	/	/	–0.020	0.574	/	/	0.132	0.018	0.08	–0.06	–0.033	0.701	/	/
juvenile	10	0.139	0.036	0.040	0.248	/	/	0.041	0.206	/	/	0.004	0.365	/	/	–0.010	0.463	/	/	0.025	0.281	/	/
infant	23	0.060	0.186	0.214	0.006	0.04	–0.07	0.055	0.160	/	/	0.042	0.073	/	/	0.165	0.005	0.09	–0.06	0.030	0.243	/	/
<i>P. troglodytes</i>																							
adult	51	0.050	0.299	0.319	0.000	0.07	–0.09	0.145	0.016	0.09	–0.05	–0.051	0.791	/	/	0.250	0.001	0.12	–0.06	0.103	0.043	0.04	–0.05
subadult	24	0.074	0.251	0.274	0.001	0.05	–0.08	0.143	0.015	0.12	–0.05	0.030	0.293	/	/	0.078	0.077	0.02	–0.05	0.081	0.084	0.03	–0.05
adolescent	24	0.069	0.298	0.327	0.000	0.09	–0.10	0.124	0.026	0.28	–0.06	0.027	0.308	/	/	0.261	0.000	0.16	–0.07	0.061	0.127	/	/
juvenile	30	0.055	0.270	0.300	0.000	0.08	–0.08	0.139	0.023	0.11	–0.04	0.015	0.368	/	/	0.235	0.001	0.14	–0.05	0.051	0.194	/	/
infant	16	0.169	0.102	0.108	0.067	0.03	–0.07	0.025	0.243	/	/	–0.033	0.658	/	/	0.180	0.011	0.17	–0.07	–0.037	0.767	/	/
<i>P. paniscus</i>																							
adult	15	0.079	0.211	0.239	0.003	0.07	–0.08	0.208	0.003	0.22	–0.05	0.050	0.196	/	/	0.100	0.051	0.05	–0.05	0.017	0.335	/	/
subadult	15	0.109	0.247	0.271	0.001	0.11	–0.09	0.260	0.001	0.33	–0.06	–0.025	0.595	/	/	0.121	0.032	0.09	–0.05	0.031	0.251	/	/
adolescent	16	0.090	0.076	0.085	0.120	/	/	0.113	0.043	0.11	–0.05	0.003	0.399	/	/	–0.024	0.615	/	/	0.069	0.110	/	/
juvenile	39	0.065	0.148	0.158	0.019	0.03	–0.06	0.122	0.042	0.09	–0.04	–0.053	0.779	/	/	0.153	0.019	0.08	–0.05	–0.009	0.491	/	/
infant	19	0.085	0.176	0.193	0.009	0.05	–0.07	0.075	0.107	/	/	0.013	0.366	/	/	0.178	0.008	0.12	–0.06	0.003	0.410	/	/
<i>G. gorilla</i>																							
adult	86	0.057	0.220	0.228	0.002	0.04	–0.08	0.087	0.072	0.04	–0.05	–0.002	0.463	/	/	0.174	0.005	0.08	–0.06	0.076	0.097	0.02	–0.05
subadult	19	0.090	0.227	0.248	0.001	0.08	–0.09	0.263	0.000	0.29	–0.06	0.048	0.203	/	/	0.002	0.404	/	/	0.088	0.072	0.05	–0.05
adolescent	27	0.104	0.239	0.252	0.001	0.09	–0.09	0.246	0.002	0.08	–0.05	0.024	0.304	/	/	0.099	0.042	0.05	–0.05	0.036	0.212	/	/
juvenile	30	0.090	0.176	0.187	0.010	0.04	–0.08	0.140	0.022	0.13	–0.05	–0.001	0.456	/	/	0.126	0.024	0.07	–0.07	0.028	0.261	/	/
infant	6	0.201	0.117	0.135	0.051	0.06	–0.07	0.101	0.065	0.16	–0.05	0.068	0.143	/	/	–0.004	0.401	/	/	0.053	0.147	/	/
AVERAGE						0.06	–0.08			0.15	–0.05			/	/			0.09	–0.06			0.05	–0.05
<i>P. paniscus</i> adol/sa	31	0.045	0.199	0.215	0.004	0.05	–0.07	0.227	0.003	0.21	–0.05	0.014	0.351	/	/	0.059	0.129	/	/	0.041	0.209	/	/
<i>H. sapiens</i> juv/adol	24	0.077	0.123	0.135	0.042	0.03	–0.06	0.071	0.115	/	/	0.014	0.350	/	/	0.110	0.052	0.06	–0.04	–0.007	0.475	/	/

* Morphological integration (MI) is displayed as the matrix correlation between the correlation matrices for each sample and the morphological integration matrices. Observed matrix correlation coefficient (Total MI, Zyg MI, etc.), significance level (p), and average of correlation coefficients of traits included (Avg +) and not included (Avg –) in the effect tested are shown. In addition, adjusted total morphological integration (Adj TMI) and true variance of the correlation matrices (Vt) are presented, and demonstrate that small sample size has minimal consequences. Overall means of the average correlation coefficients (Avg +/-) are also shown at the bottom, along with the additional pooled bonobo and human analyses described in the text.

Table 4
Morphological integration for each hominoid species: Unscaled data*

	N	Vt	Total MI	Adj TMI	p	Avg (+)	Avg (–)	Zyg MI	p	Avg (+)	Avg (–)	Orbit MI	p	Avg (+)	Avg (–)	Oral MI	p	Avg (+)	Avg (–)	Nasal MI	p	Avg (+)	Avg (–)
<i>H. sapiens</i>																							
adult	192	0.032	0.281	0.288	0.000	0.38	0.26	0.199	0.031	0.44	0.29	–0.144	0.958	/	/	0.203	0.048	0.40	0.28	0.136	0.118	/	/
subadult	21	0.058	0.183	0.205	0.008	0.17	0.06	0.185	0.006	0.53	0.15	0.023	0.383	/	/	0.027	0.370	/	/	0.086	0.090	0.17	0.08
adolescent	14	0.057	0.075	0.084	0.173	/	/	–0.003	0.558	/	/	0.050	0.698	/	/	0.239	0.019	0.65	0.49	–0.121	0.435	/	/
juvenile	10	0.051	0.072	0.081	0.176	/	/	–0.049	0.676	/	/	–0.220	0.984	/	/	0.069	0.308	/	/	0.210	0.019	0.71	0.52
infant	23	0.021	0.123	0.136	0.056	0.67	0.63	–0.031	0.392	/	/	–0.103	0.869	/	/	0.152	0.125	/	/	0.056	0.150	/	/
<i>P. troglodytes</i>																							
adult	51	0.038	0.216	0.231	0.003	0.36	0.26	0.149	0.069	0.41	0.28	–0.133	0.945	/	/	0.245	0.020	0.43	0.27	0.022	0.401	/	/
subadult	24	0.036	0.178	0.196	0.011	0.50	0.42	0.155	0.042	0.56	0.43	–0.121	0.915	/	/	0.204	0.023	0.56	0.43	–0.007	0.543	/	/
adolescent	24	0.051	0.306	0.334	0.000	0.46	0.30	0.115	0.128	/	/	–0.227	0.990	/	/	0.343	0.001	0.57	0.31	0.133	0.122	/	/
juvenile	30	0.043	0.245	0.265	0.001	0.51	0.39	0.129	0.124	/	/	–0.103	0.852	/	/	0.256	0.017	0.58	0.40	0.052	0.347	/	/
infant	16	0.095	0.078	0.085	0.122	/	/	0.081	0.106	/	/	–0.062	0.844	/	/	0.075	0.111	/	/	0.003	0.448	/	/
<i>P. paniscus</i>																							
adult	15	0.058	0.190	0.219	0.007	0.34	0.23	0.199	0.013	0.47	0.25	–0.016	0.584	/	/	0.110	0.152	/	/	0.016	0.441	/	/
subadult	15	0.091	0.224	0.250	0.003	0.29	0.12	0.285	0.001	0.41	0.15	–0.087	0.878	/	/	0.151	0.057	0.31	0.15	–0.007	0.502	/	/
adolescent	16	0.075	0.170	0.189	0.017	0.36	0.25	0.142	0.091	0.47	0.34	–0.217	0.998	/	/	0.170	0.079	0.42	0.27	0.089	0.215	/	/
juvenile	39	0.078	0.135	0.140	0.045	0.48	0.39	0.169	0.060	0.60	0.40	–0.212	0.993	/	/	0.205	0.061	0.58	0.39	–0.028	0.558	/	/
infant	19	0.046	0.158	0.171	0.020	0.60	0.52	0.122	0.140	/	/	–0.254	0.997	/	/	0.288	0.012	0.72	0.52	–0.028	0.599	/	/
<i>G. gorilla</i>																							
adult	86	0.037	0.207	0.212	0.005	0.65	0.57	0.164	0.086	0.71	0.58	–0.277	0.998	/	/	0.210	0.073	0.76	0.58	0.118	0.218	/	/
subadult	19	0.095	0.186	0.199	0.010	0.36	0.23	0.277	0.002	0.62	0.25	–0.181	0.976	/	/	0.043	0.358	/	/	0.106	0.199	/	/
adolescent	27	0.049	0.182	0.197	0.011	0.45	0.36	0.141	0.059	0.51	0.38	–0.025	0.626	/	/	0.60	0.255	/	/	0.121	0.087	0.48	0.38
juvenile	30	0.047	0.134	0.142	0.042	0.56	0.49	0.196	0.027	0.68	0.50	–0.249	0.994	/	/	0.032	0.397	/	/	0.167	0.082	0.53	0.51
infant	6	0.081	0.138	0.158	0.032	0.66	0.56	0.157	0.061	0.78	0.58	–0.209	0.968	/	/	0.194	0.052	0.76	0.57	–0.016	0.594	/	/
AVERAGE						0.46	0.36			0.55	0.35			/	/			0.56	0.39			0.47	0.37
<i>P. paniscus</i> adol/sa	31	0.046	0.234	0.249	0.003	0.58	0.47	0.201	0.040	0.68	0.49	–0.232	0.997	/	/	0.268	0.021	0.67	0.48	0.040	0.372	/	/
<i>H. sapiens</i> juv/adol	24	0.031	0.095	0.103	0.123	/	/	–0.024	0.603	/	/	–0.158	0.915	/	/	0.202	0.704	0.73	0.61	0.039	0.398	/	/

*See Table 3 for description of the presented variables.

occur from the nasal region. In the scaled analysis, this nasal integration occurs only in late ontogeny in humans, chimpanzees and gorillas, while in the unscaled analysis it occurs in mid-ontogeny, only in humans and gorillas. Its pattern in both analyses differs from that seen in the oral regions, and in the unscaled analysis is complementary to the oral region (i.e. in groups with nasal integration there is no oral integration and vice versa). Importantly, although integration in adult humans tends to be quite strong where it is significant, below this ontogenetic level humans tend to be less integrated overall than their ape counterparts. Again, this difference seems to be primarily driven by ontogenetically early strong integration in the zygomatic and oral regions among the apes.

In two instances – for the human juveniles and adolescents, and the bonobo adolescents and subadults – the data were pooled to increase sample size and to make sure the results were not unduly affected by small samples due to poor matrix estimates. These results are also presented in [Tables 3 and 4](#), and while they do indicate a modest increase in integration in these pooled samples, this does not dramatically alter the results discussed above.

Correlation and covariance patterns

For these comparisons, although the results from the scaled and unscaled analyses were somewhat different quantitatively they were qualitatively similar, and therefore only the results from the scaled analyses will be presented here, as it is arguably the more appropriate choice when comparing matrix structure across differently sized species. Matrix repeatability for each correlation and covariance matrix is shown alongside comparisons in [Tables 5 and 6](#). For all the analyses, repeatabilities are fairly high, limiting somewhat the impact of estimation error on this analysis. [Table 5](#) presents the results of comparing adjacent developmental stages within species. Both matrix correlations (elementwise correlations between correlation matrices) and vector correlations (random skewers comparisons of covariance matrices) are consistently strong within each of the species,

suggesting a shared pattern of covariation among all ontogenetic stages within each species. Adjusted matrix correlations range from 0.36 to 0.77, with an average of 0.56, while adjusted vector correlations range from 0.45 to 0.83, with an average of 0.70. All correlations are highly repeatable (0.76 – 0.97) and significant (with the exception of the gorilla infant-juvenile covariance matrix comparison). Ignoring the infant gorilla sample ($N = 6$), the lowest adjusted matrix correlations occur at different places for each species: between infants and juveniles (humans), juveniles and adolescents (bonobos), adolescents and subadults (chimpanzee), or subadults and adults (gorilla). Difference in covariance structure is arguably a better indicator of divergent integration than difference in correlation structure ([Zelditch, 1988](#)). Where significant, the lowest adjusted vector correlations occur either between infant and juvenile (humans) or between adolescents and subadults (chimpanzees, bonobos, and gorillas), indicating dissimilarity of covariance matrix structure at this point. There is no clear phylogenetic patterning of the average results within each species. However, there does seem to be some difference between humans and the great apes, with the similarity among non-adult samples for humans being somewhat lower than what is seen for the other species.

The results of the comparisons between species at each developmental stage are shown in [Table 6](#). Although adjusted matrix correlations are strong and significant, on average they are lower than those seen for comparisons within species (average = 0.47), which is primarily driven by a range that is expanded on the lower end, ranging from 0.19 to 0.78. Similarly, adjusted vector correlations are on average lower than what was seen within species (average 0.64, range 0.38 – 0.87), and a number of them are not significant (i.e. the correlations are not significantly different from zero). Adjusted matrix and vector correlations among adults are strongest (0.61 and 0.78 on average), followed by subadults (0.54, 0.68), adolescents (0.43, 0.63), juveniles (0.42, 0.62), and infants (0.34, 0.50) – a clear ontogenetic trend. Another important result emerges when comparing correlations between humans and apes versus apes

Table 5
Matrix correlation and random skewers vector correlation between adjacent ontogenetic categories within species*

Stage 1	Stage 2	Correlation Matrices					Covariance Matrices				
		t1	t2	Maximum correlation	Observed correlation	Adjusted correlation	t1	t2	Maximum vector correlation	Observed vector correlation	Adjusted vector correlation
infant	juvenile	0.758	0.782	0.770	0.276	0.358	0.817	0.821	0.819	0.442	0.540
juvenile	adolescent	0.782	0.780	0.781	0.282	0.361	0.821	0.805	0.813	0.488	0.600
adolescent	subadult	0.780	0.821	0.800	0.297	0.371	0.805	0.880	0.842	0.504	0.599
subadult	adult	0.821	0.949	0.882	0.549	0.622	0.880	0.971	0.925	0.763	0.825
infant	juvenile	0.889	0.809	0.848	0.508	0.599	0.886	0.869	0.877	0.640	0.729
juvenile	adolescent	0.809	0.830	0.820	0.468	0.571	0.869	0.882	0.875	0.624	0.713
adolescent	subadult	0.830	0.838	0.834	0.415	0.498	0.882	0.876	0.879	0.624	0.710
subadult	adult	0.838	0.876	0.857	0.628	0.733	0.876	0.925	0.900	0.737	0.819
infant	juvenile	0.832	0.875	0.853	0.655	0.768	0.879	0.916	0.897	0.732	0.816
juvenile	adolescent	0.875	0.798	0.835	0.377	0.451	0.916	0.844	0.879	0.560	0.637
adolescent	subadult	0.798	0.828	0.813	0.377	0.464	0.844	0.841	0.842	0.530	0.629
subadult	adult	0.828	0.780	0.803	0.514	0.640	0.841	0.845	0.843	0.677	0.803
infant	juvenile	0.748	0.885	0.814	0.341	0.419	0.775	0.906	0.838	<i>0.376</i>	<i>0.449</i>
juvenile	adolescent	0.885	0.890	0.887	0.668	0.753	0.906	0.912	0.909	0.746	0.821
adolescent	subadult	0.890	0.840	0.865	0.576	0.666	0.912	0.861	0.886	0.690	0.779
subadult	adult	0.840	0.930	0.884	0.584	0.661	0.861	0.959	0.909	0.718	0.790
Total					0.470	0.558				0.616	0.704
<i>H. sapiens</i>					0.351	0.428				0.549	0.641
<i>P. troglodytes</i>					0.505	0.600				0.656	0.743
<i>P. paniscus</i>					0.481	0.581				0.625	0.721
<i>G. gorilla</i>					0.542	0.625				0.633	0.709

* Repeatabilities for ontogenetic stage 1 (t1) and 2 (t2) are presented. The maximum possible correlation ($\sqrt{t1t2}$) is shown for each pair compared. Observed and adjusted matrix correlations and random skewers vector correlations are also presented. All matrix correlation comparisons were significant at $P < 0.001$ in 10,000 permutations. All vector correlations between the non-adult human samples are significant at $P < 0.10$, while all other vector correlations are significant at $P < 0.05$, with the exception of that between the infant and juvenile gorilla (shown italicized), which is not significant. The overall average of all observed and adjusted comparisons, as well as the averages for each species, is presented at the bottom.

and apes at each non-adult stage. For adults, the strongest similarity in correlation and covariance structure is between humans and chimpanzees. However, below this level this is not always the case, and the apes seem to share strong similarity (to the exclusion of humans) at the subadult and juvenile stages. The average adjusted vector correlations among human-ape comparisons versus ape-ape comparisons are, respectively: infants (0.54, 0.45); juveniles (0.55, 0.70); adolescents (0.67, 0.59); subadults (0.63, 0.74); adults (0.78, 0.77). The average matrix correlations among human-apes versus ape-ape comparisons are: infants (0.42, 0.25); juveniles (0.28, 0.55); adolescents (0.49,

0.38); subadults (0.45, 0.62); adults (0.66, 0.57). At each non-adult age category where the matrix and vector correlations between humans and apes are stronger than between apes and humans, this phenomenon is driven primarily by an unusually strong correlation between the human and either the bonobo or the chimpanzee.

Principal components analyses were performed in order to compare similarity in correlation and covariance structure to ontogenetic patterns of shape variation. Plots of the first two principal components (with both scaled and unscaled data) are shown in Fig. 2. Only plots of the first two PCs are presented, as they represent most of the

Table 6

Matrix correlation and random skewers vector correlation between homologous ontogenetic categories among species*

Developmental stage	Species 1	Species 2	Correlation Matrices					Covariance Matrices				
			t1	t2	Maximum correlation	Observed correlation	Adjusted correlation	t1	t2	Maximum vector correlation	Observed vector correlation	Adjusted vector correlation
Infant	<i>H. sapiens</i>	<i>P. troglodytes</i>	0.758	0.889	0.821	0.229	0.279	0.817	0.886	0.851	0.406	0.477
	<i>H. sapiens</i>	<i>P. paniscus</i>	0.758	0.832	0.794	0.511	0.643	0.817	0.879	0.847	0.619	0.730
	<i>H. sapiens</i>	<i>G. gorilla</i>	0.758	0.748	0.753	0.255	0.339	0.817	0.775	0.796	0.331	0.416
	<i>P. troglodytes</i>	<i>P. paniscus</i>	0.889	0.832	0.860	0.172	0.200	0.886	0.879	0.882	0.367	0.416
	<i>P. troglodytes</i>	<i>G. gorilla</i>	0.889	0.748	0.816	0.296	0.363	0.886	0.775	0.829	0.457	0.552
	<i>P. paniscus</i>	<i>G. gorilla</i>	0.832	0.748	0.789	0.150	0.191	0.879	0.775	0.825	0.316	0.383
Juvenile	<i>H. sapiens</i>	<i>P. troglodytes</i>	0.792	0.809	0.801	0.207	0.259	0.821	0.869	0.845	0.442	0.523
	<i>H. sapiens</i>	<i>P. paniscus</i>	0.792	0.875	0.832	0.290	0.348	0.821	0.916	0.867	0.487	0.562
	<i>H. sapiens</i>	<i>G. gorilla</i>	0.792	0.885	0.837	0.200	0.239	0.821	0.906	0.863	0.449	0.521
	<i>P. troglodytes</i>	<i>P. paniscus</i>	0.809	0.875	0.841	0.448	0.533	0.869	0.916	0.892	0.635	0.712
	<i>P. troglodytes</i>	<i>G. gorilla</i>	0.809	0.885	0.846	0.465	0.549	0.869	0.906	0.887	0.618	0.696
	<i>P. paniscus</i>	<i>G. gorilla</i>	0.875	0.885	0.880	0.494	0.561	0.916	0.906	0.911	0.638	0.700
Adolescent	<i>H. sapiens</i>	<i>P. troglodytes</i>	0.780	0.830	0.805	0.543	0.675	0.805	0.882	0.843	0.605	0.718
	<i>H. sapiens</i>	<i>P. paniscus</i>	0.780	0.798	0.789	0.361	0.458	0.805	0.844	0.824	0.601	0.729
	<i>H. sapiens</i>	<i>G. gorilla</i>	0.780	0.896	0.836	0.278	0.333	0.805	0.912	0.857	0.490	0.572
	<i>P. troglodytes</i>	<i>P. paniscus</i>	0.830	0.798	0.814	0.326	0.401	0.882	0.844	0.863	0.546	0.633
	<i>P. troglodytes</i>	<i>G. gorilla</i>	0.830	0.896	0.862	0.369	0.428	0.882	0.912	0.897	0.550	0.613
	<i>P. paniscus</i>	<i>G. gorilla</i>	0.798	0.896	0.846	0.263	0.310	0.844	0.912	0.877	0.455	0.518
Subadult	<i>H. sapiens</i>	<i>P. troglodytes</i>	0.821	0.838	0.829	0.340	0.410	0.880	0.876	0.878	0.537	0.612
	<i>H. sapiens</i>	<i>P. paniscus</i>	0.821	0.828	0.824	0.373	0.452	0.880	0.841	0.860	0.532	0.618
	<i>H. sapiens</i>	<i>G. gorilla</i>	0.821	0.840	0.830	0.415	0.500	0.880	0.861	0.870	0.567	0.651
	<i>P. troglodytes</i>	<i>P. paniscus</i>	0.838	0.828	0.833	0.596	0.715	0.876	0.841	0.858	0.658	0.767
	<i>P. troglodytes</i>	<i>G. gorilla</i>	0.838	0.840	0.839	0.507	0.604	0.876	0.861	0.868	0.629	0.724
	<i>P. paniscus</i>	<i>G. gorilla</i>	0.828	0.840	0.834	0.458	0.550	0.841	0.861	0.851	0.613	0.720
Adult	<i>H. sapiens</i>	<i>P. troglodytes</i>	0.949	0.876	0.912	0.712	0.781	0.971	0.925	0.948	0.822	0.867
	<i>H. sapiens</i>	<i>P. paniscus</i>	0.949	0.780	0.860	0.495	0.575	0.971	0.845	0.906	0.660	0.728
	<i>H. sapiens</i>	<i>G. gorilla</i>	0.949	0.930	0.939	0.577	0.614	0.971	0.959	0.965	0.724	0.750
	<i>P. troglodytes</i>	<i>P. paniscus</i>	0.876	0.780	0.827	0.482	0.583	0.925	0.845	0.884	0.710	0.802
	<i>P. troglodytes</i>	<i>G. gorilla</i>	0.876	0.930	0.903	0.514	0.569	0.925	0.959	0.942	0.721	0.765
	<i>P. paniscus</i>	<i>G. gorilla</i>	0.780	0.930	0.852	0.468	0.550	0.845	0.959	0.900	0.675	0.750

Average	Total	0.393	0.467	0.562	0.641
Infants	0.269	0.336	0.416	0.496	
Juveniles	0.351	0.415	0.545	0.619	
Adolescents	0.357	0.434	0.541	0.631	
Subadults	0.448	0.539	0.589	0.682	
Adults	0.541	0.612	0.719	0.777	

* Repeatabilities for species 1 (t1) and 2 (t2) at each developmental stage are presented. The maximum possible correlation ($\sqrt{t1t2}$) is shown for each pair compared. Observed and adjusted matrix correlations and random skewers vector correlations are also presented. All matrix correlation comparisons were significant at $P < 0.025$ in 10,000 permutations. All vector correlation comparisons that are significantly different from zero at $P < 0.05$ are shown italicized. The overall average of all observed and adjusted comparisons, as well as the averages for each developmental stage, is presented at the bottom.

variation, particularly in the unscaled analysis (90% and 94% for the correlation and covariance analyses, respectively); certainly other patterns may exist in higher PCs which are not discussed here. Plots from these analyses are displayed in two ways: first with the group means of the factor scores shown as squares, which clearly reflects the distinct morphological trajectory of each species, and second with all of the individuals plotted, which also allows for comparisons of the shape variation through time among the species. Note that in both analyses the humans lie distant from the apes, although in the analysis based on correlation structure the general direction of their ontogenetic pathway is similar (see Ackermann & Krovitz, 2002), while in that based on covariance structure more divergence is apparent between the apes and humans.

Discussion

Four main conclusions can be drawn from this study; each will be expanded on below. First, the overall level and patterning of morphological integration across adult apes and humans is remarkably similar, though not identical. Second, all of the species show a similar pattern of integration during ontogeny, with ontogenetically early and late total integration powered by different underlying factors, although there may be some interspecific differences in the level of ontogenetic integration. Third, patterns of covariation are more similar among ontogenetic stages from any given species than among species at any given point in ontogeny. Fourth, while similarity in covariance structure among the species during adulthood may be loosely tied to phylogeny, similarity during ontogeny is not.

All adult hominoids fit a model of total integration, with the primary contributions to this coming from the oral and zygomatic regions, and to a lesser extent the nasal region, indicating a strong connectivity among those skeletal elements that are associated most closely with mastication. This differs slightly from what was seen in a preliminary analysis of morphological integration in adult gorillas, chimpanzees, and

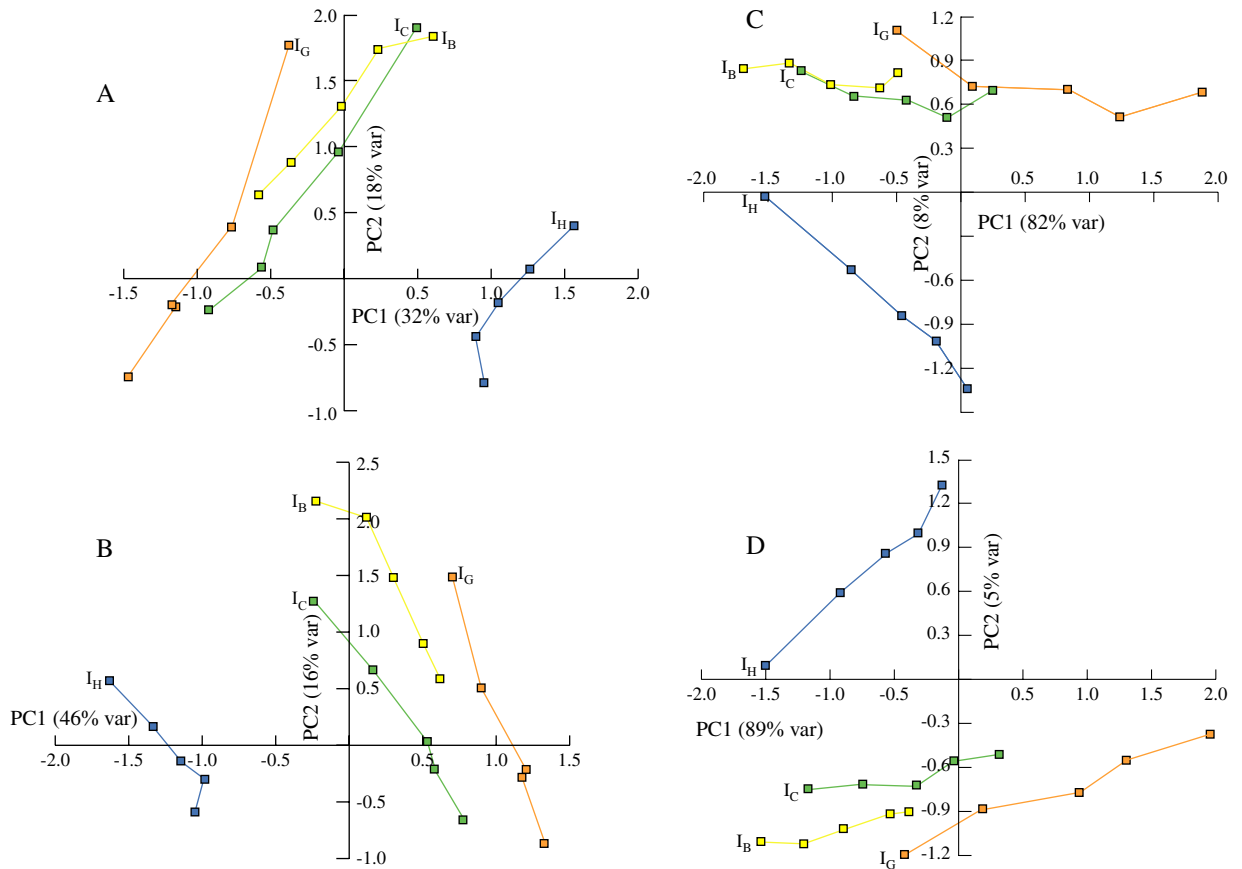


Fig. 2. Plot of factor loadings from principal components analyses. Plots A through D show the mean form for each species and age category, calculated as the average factor score for the group, with lines drawn showing the ontogenetic trajectories of each species as follows: humans (blue), chimpanzees (green), bonobos (yellow), gorillas (orange). Analyses are based on: (A) analysis of correlation using scaled data, (B) analysis of covariance using scaled data, (C) analysis of correlation using unscaled data, (D) analysis of covariance using unscaled data. The squares representing infant stages are labeled I_H , I_C , I_B , and I_G (for humans, chimpanzees, bonobos, and gorillas, respectively), with subsequent ontogenetic stages (juvenile, adolescent, subadult, adult) represented by adjacent squares as you move along the trajectory. Plots E through H show the same analyses, but with individuals plotted rather than means, in order to illustrate inter-population variation as well as to show how adjusting for scale affects the data by removing isometric size. In addition to the above color coding, triangles are shown pointing down (humans), up (chimps), right (bonobos) and left (gorillas).

humans, where the chimpanzees were not significantly integrated in the zygomatic region, albeit just barely so (Ackermann, 2003a), and the nasal integration was not significant. This is probably due to an increase in and slight change of variables used in this analysis. More importantly, the results vary somewhat from what has been seen in analyses of other adult primate skulls. Studies of both Old and New World monkeys (Cheverud, 1982, 1989, 1995, 1996; Ackermann & Cheverud, 2000; Marroig & Cheverud, 2001; Marroig et al.,

2004) show that the oral region alone is the primary facial contributor to total integration, although there are sporadic contributions from other regions. This suggests that while there is much similarity in the pattern of total morphological integration across Anthropoid primates, there are also some important differences in the African great apes and humans which could be linked to specific functional and developmental differences, and tied to evolutionary change. In particular, because zygomatic integration is not

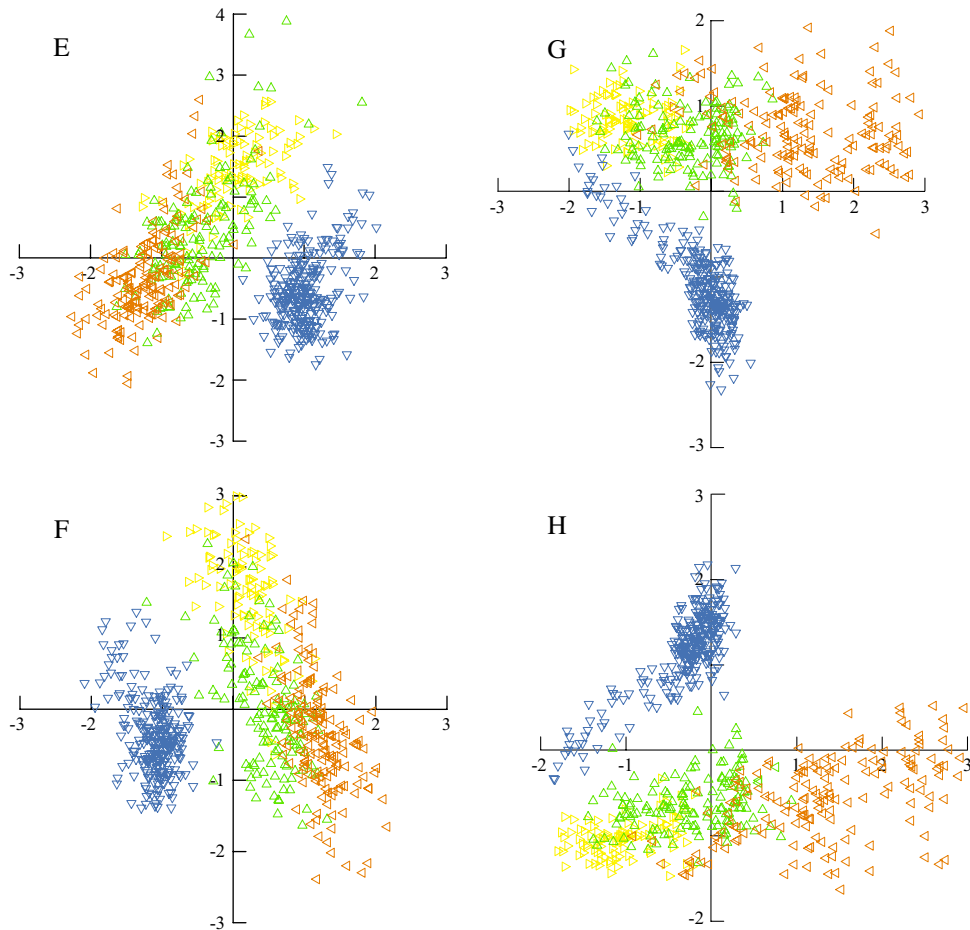


Fig. 2. (continued).

generally seen in the rest of the Anthropoid primates, it may have evolved in the ape lineage, sometime after the divergence of apes and monkeys. This shift could be associated with functional change such as a shift in diet, or alternatively with selection in this lineage for large body size — apes and humans are the largest primates, which affects overall muscular and associated craniofacial changes. This second possibility is particularly compelling as allometry has been shown to affect the patterning of craniofacial variation in the human lineage (Rosas & Bastir, 2004).

Although the pattern of integration in sub-adulthood generally conforms to what is seen in adulthood across all of the hominoid species, there are important differences between the integration

patterns seen in adulthood/subadulthood and those seen earlier in ontogeny. Early ontogeny across all species is marked by strong integration in the oral region, and although the average correlations across integrated variables when testing for oral integration tend to be quite high in the infants, they are also frequently high at other ontogenetic stages, including adulthood, indicating that oral integration remains strong throughout life. In contrast, the timing of the onset of zygomatic integration differs among the species. In humans, early ontogeny shows no contribution of zygomatic integration to the pattern of total integration — this only appears in later ontogeny. In bonobos and chimpanzees zygomatic integration appears during the juvenile/adolescent periods

and becomes stronger in subadulthood/adulthood. Gorillas show a similar pattern to the other apes, although zygomatic integration begins in infancy, gaining some strength later in development. Rather than supporting a pre-weaning/post-weaning shift in the patterning of integration (*sensu* Zelditch, 1988; Zelditch & Carmichael, 1989) the overall pattern seen here indicates that the oral region may remain highly integrated throughout life, and that other types of integration - especially zygomatic integration - accumulate following infancy. Nasal integration also makes sporadic contributions to the pattern of overall integration, sometimes occurring in late or mid-ontogeny. Interestingly, its pattern in these analyses differs from that seen in the oral regions, and in the unscaled analysis is complementary to the oral region (i.e. in groups with nasal integration there is no oral integration and vice versa), which may indicate that these regions vary independently and are therefore independently modularized. This could be explained by differences in the coordination of these regions in early development, as the nasal and oral regions arise via distinct morphogenetic pathways, with the latter a derivative of the first pharyngeal arch.

Although the overall pattern and magnitude of integration is similar across the species, there are also some important differences among the species which tend to distinguish humans from the great apes. As mentioned above, one of these differences concerns the onset of zygomatic integration. The relatively early integration seen in the zygomatic region in apes could be tied to changes in form related to early and sustained growth in all of the apes, but especially in the gorilla, whose rate of absolute growth is approximately twice that of the chimpanzee (Fleagle, 1999). Another important difference occurs among the adults, where the highest overall magnitude of integration is seen in humans followed by the chimpanzees, followed by the other two species. As it has been proposed that correlating selection - a form of stabilizing selection - will favor functionally or developmentally well-integrated phenotypes (Sokal, 1978; Cheverud, 1982; Lande & Arnold, 1983; Cheverud, 1984), these values might indicate some constraint in the human lineage evolutionarily.

However, although integration in adult humans tends to be quite strong where it is significant, below this ontogenetic level humans tend to be less integrated overall than their ape counterparts. Again, this difference is in contrast to the ontogenetically early, strong integration in the zygomatic and oral regions among the apes. This could indicate that early developmental stages in humans are more morphologically flexible, and therefore less constrained (Klingenberg, 1998) than their ape counterparts.

The amount and timing (evolutionarily) of divergence in covariation patterns during morphological diversification is important for answering evolutionary questions (Roff, 1996). Similarly, the time (developmentally) at which selection acts on the correlations between patterns of integration at each ontogenetic stage may influence how selection acts on the phenotype as a whole (Lande, 1982; Cheverud et al., 1983). The results of the comparisons of correlation and especially covariance structure between adjacent ontogenetic stages within species, and between comparable ontogenetic stages among species, offer additional insight into how and where covariation patterns might diverge. The within species comparisons indicate slightly different things for the different species. All of the apes show a shift in covariance/correlation structure late in ontogeny, around the time of the onset of sexual maturation or soon thereafter, as indicated by low correlations between adjacent age categories. Humans also show a shift in structure, although here it is represented by a change from relatively low correlations between ontogenetic stages throughout early ontogeny to high correlations between subadults and adults. Like in the apes, this indicates a shift around the time of the onset of sexual maturity. But the low correlations throughout early human ontogeny illustrate a different pattern from what is seen in the apes. This corroborates the results of the integration analysis, and again may point towards flexibility in covariation patterning early in human ontogeny. Yet the within species comparisons also show that while differences exist among adjacent age categories within each species, they are still similar overall, especially when compared to differences between species at each developmental stage. This

strengthens recent arguments that even at ontogenetically early ages, hominoid species have developed their own unique morphological patterning (Richtsmeier & Walker, 1993; Ponce de León & Zollikofer, 2001; Ackermann & Krovitz, 2002; Viðarsdóttir et al., 2002; Mitteroecker et al., 2004).

When comparing across species, matrix and vector correlations among adults are strongest, decreasing as ontogenetically younger stages are considered. So in other words, adults of different species have covariance patterns which are more similar to each other than adolescents, which are more similar than infants. This pattern may be tied to the pattern of increased total integration seen in subadults and adults, which would support the above proposal that the similarity in correlation and covariance structure seen in adults is best explained by integration due to shared adult function or hormonally driven changes in form. Muscles of mastication grow throughout later ontogeny under the influence of the growth hormone, and facial features affected by this growth – such as those around the oral cavity and zygomatic regions – might become integrated as a result (see Marroig & Cheverud, 2001). It is also possible that designed integration matrices, which are drawn from studies of completed growth in primates (i.e. adults), do not “fit” earlier ontogenetic stages well. In this case, as new integrating factors arise later in ontogeny, they may actually be improving fit to the expectations of the adult model and increasing the similarity across species; this does not necessarily mean that there are not other patterns of integration in earlier ontogeny, just that they are not being tested for.

Alternatively, the greater variation seen among the hominoids early in ontogeny could be another piece of evidence for morphological lability in early developmental stages across the lineage, and especially so within humans (see above). This possibility is particularly interesting when considered against ontogenetic trajectories of shape variation, as shown in the results of the principal components analysis, which clearly differentiate humans from the apes throughout ontogeny (see Fig. 2). There is a growing body of work that

shows that many of the differences in primate craniofacial form are set early in ontogeny, and that following this ontogenetic trajectories are often both parallel (Ponce de León & Zollikofer, 2001; Ackermann & Krovitz, 2002) and somewhat divergent (O’Higgins et al., 2001; Viðarsdóttir et al., 2002). Taken together, these studies suggest that craniofacial growth is a highly conserved process which works largely on differences which are already present ontogenetically early, although in some cases differences in postnatal growth may act to further enhance or to modify form causing inter-population divergence in adult form. The information gained here is slightly different, and shows that ontogenetic integration is both parallel (i.e. generally similar across species) and in some respects convergent (i.e. covariance becomes increasingly similar through ontogeny), and increases in magnitude in all of the species through time. Like some studies of ontogenetic shape variation (O’Higgins et al., 2001; Viðarsdóttir et al., 2002) this suggests plasticity in early postnatal growth and development, but it also suggests that this plasticity is lost throughout postnatal growth, as the phenotype becomes increasingly integrated and constrained.

Do the similarities in covariance structure among the species correlate with what we know about their phylogenetic or morphological relationships? Correlations between the adult humans and chimpanzees are greater than those between any other adult pairing. Although this is consistent with molecular data suggesting that humans are more closely related to chimpanzees than either is to gorillas (Ruvolo, 1997), the pattern breaks down after this comparison. Matrix and vector correlations among the apes during two developmental stages (juvenile and subadulthood) are higher than those between the humans and apes, while the opposite is true in infancy and adolescence. This suggests that during ontogeny similarity in covariance pattern does not split clearly along phylogenetic lines. However, at certain stages in development there is some increased similarity among apes to the exclusion of humans, and this together with the differences seen in the pattern and strength of integration between humans and apes may indicate some split along morphological lines,

indicating different underlying functional or developmental causes in these groups for at least some of the differences seen here.

This leaves one important question. What evolutionary processes best explain the similarities and differences in integration patterns seen among the hominoids throughout development and into adulthood? Similarity in covariance structure across populations can occur via stabilizing selection acting through common developmental systems – this may account for shared covariance structure even when means are divergent (Marroig & Cheverud, 2001). Alternatively, divergence in covariance structure can result from directional selection acting either indirectly, to change group means and as a result variances and covariances, or directly, to select for new developmental or functional integration patterns (Marroig and Cheverud, 2001). The pattern seen here is complex. There is a common pattern of ontogenetic integration across the groups, which suggests a similar pattern of development or function during development. This is consistent with what is seen in other primates, and is probably the result of stabilizing selection acting to constrain some core aspects of development. The high level of integration within and similarity seen among adult apes and humans could also be explained by stabilizing selection acting on a common developmental system to coordinate and constrain growth, and associated changes in body size and musculature. In these respects the overall pattern of covariance should be considered homologous among these species. Yet despite these similarities, differences exist between the groups at each ontogenetic stage, suggesting that there are some important differences in covariance structure during development, especially between the apes and humans. At least some of these differences could result from directional or diversifying selection for differing body sizes and associated shape changes, especially in the gorilla. It may also be that directional selection has acted on the human lineage to directly change developmental integration patterns, perhaps allowing for more early developmental plasticity in this lineage, following the divergence of human ancestors from chimpanzee ancestors. This is consistent with

arguments that underlying developmental differences may explain much of the evolutionary diversification in the hominin lineage (Richtsmeier & Walker, 1993; Krovitz, 2000; Ponce de León & Zollikofer, 2001), and may also lend support to studies that indicate different underlying patterns of developmental integration in robust australopithecines (McCollum et al., 1993; McCollum, 1999). Alternatively, Marroig and Cheverud (2001) find that diet is more strongly correlated with correlation and covariance matrix similarity than is phylogenetic distance, and it is also possible that some of the similarity seen among the apes during ontogeny reflects shared function rather than development, especially since integration is most apparent in regions that relate to mastication. If so, this would caution that some of the similarity in variation patterning that we see among hominoids and their ancestors may also be the result of shared function, and thereby potentially homoplastic in nature. It could also be that the divergence in covariation patterning is a result of directional selection acting on the human masticatory system early in ontogeny, perhaps tied to the divergent diet of *Homo* and the spread of tool-use around 2.5 million years ago. Recent evidence of a gene mutation affecting masticatory muscle size and composition early on in the *Homo* lineage supports this idea (Stedman et al., 2004); undoubtedly such a mutation would have affected the development and ultimate function of the human masticatory complex, although the evolutionary implications of this are not entirely clear. What is clear is that teasing apart these issues is a topic that requires much future study.

Conclusions

To date, studies of primate cranial integration have shown that patterns of integration are shared across adult primates (Cheverud, 1996; Ackermann & Cheverud, 2000; Marroig & Cheverud, 2001; Ackermann, 2002, 2003; González-José et al., 2004). This study adds to that body of work, indicating that while patterns of integration are not identical, they are similar among adult African apes and humans. The shared patterning extends back in

ontogenetic time, with each species showing contributions to total integration from the oral region, as well as from the zygomatic and to a lesser extent the nasal regions. The general pattern of increased integration through development may reflect the onset of ontogenetically late changes in integration patterning among hominoids, perhaps powered by shared adult function or hormonally-driven changes in body size and musculature.

However, despite these similarities, there are some important differences among the hominoids, and especially between humans and the other apes. In particular, the lower overall integration within and lack of covariance structure similarity among adjacent ontogenetic stages in early human ontogeny differs from what we see in the other apes. It is not entirely clear why this might be so, although it indicates that selection was working in this lineage – either on humans or the apes – to distinguish them not only in morphology, but in variation patterning. The fact that humans are most similar to chimpanzees in covariance structure during adulthood emphasizes that our understanding of adult variation – and particularly its link to evolutionary change – remains incomplete without a deeper understanding of variation throughout ontogeny.

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