

Title

Morphological integration in the gorilla, chimpanzee and human neck

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Abstract

Objectives: Although integration studies are important to understanding the evolution of organisms' traits across phylogenies, vertebral integration in primates is still unexplored. Here we describe and quantify patterns of morphological integration and modularity in the subaxial cervical vertebrae (C3-C7) in extant hominines incorporating the potential influence of size.

Materials and methods: Three-dimensional landmarks were digitized on 546 subaxial cervical vertebrae from 141 adult individuals of *Gorilla gorilla*, *Pan troglodytes* and *Homo sapiens*. Integration and modularity, and the influence of size effects, were quantified using geometric morphometric approaches.

Results: All subaxial cervical vertebrae from the three species show a strong degree of integration. Gorillas show the highest degree of integration; conversely, humans have the lowest degree of integration. Analyses of allometric regression residuals show that size is an important factor promoting integration in gorillas, with lesser influence in chimpanzees and almost no effect in humans.

Discussion: Results point to a likely ancestral pattern of integration in non-human hominines, whereby the degree of integration decreases from cranial to caudal positions. Humans deviate from this pattern in the cranialmost (C3) and, to a lesser extent, in the caudalmost (C7) vertebrae, which are less integrated. These differences can be tentatively related to the emergence of bipedalism due to the presence of modern human-like C3 in australopiths, which still preserve a more chimpanzee-like C7.

1 INTRODUCTION

The morphology of the spine is directly related to, and has an influence on, both body posture and locomotion (Arlegi et al., 2017; Barrey, Jund, Nosedá & Roussouly, 2007; Boszczyk, Boszczyk, & Putz, 2001; Boulay et al., 2006; Gadow, 1933; Nalley & Grider-Potter, 2017; Pierce, Clack & Hutchinson, 2011; Russo & Williams, 2015). Extant hominines (*sensu* Wood & Richmond, 2000; i.e. *Homo*, *Pan* and *Gorilla* genera) display different body postures and a varied locomotor repertoire. While *Homo sapiens* is characterized by a bipedal mode of locomotion, *Gorilla gorilla* and *Pan troglodytes* display a knuckle-walking mode of locomotion. However, these two species have been modeled to differ in their engagement in bipedalism and vertical climbing (Manfreda et al., 2006), which is consistent with their different percentages of the use of vertical and overall climbing when all the activities are taken into account (Hunt, 1991; Tuttle & Watts, 1985). There is a link between between the spine and locomotion (Feipel, De Mesmaeker, Klein & Rooze, 2001; Zhao et al., 2008). An example of it can be found in the fact that the bent-hip-bent-knee gait of *Pan* and *Gorilla* is a direct consequence of an absence of lumbar spine mobility caused by a short post-transitional spine and the “entrapment” of the most caudal lumbar vertebra(e), and not a function of limitations imposed by hip or knee anatomy (Lovejoy & McCollum, 2010).

Morphological differences related to locomotion and posture are not only circumscribed to the lumbar spine (Lovejoy & McCollum, 2010), but are also present in the cervical region (Arlegi et al., 2017; Manfreda, Mitteroecker, Bookstein & Schaefer, 2006; Meyer, Williams, Schmid, Churchill & Berger, 2017; Nalley & Grider-Potter, 2015). The study of the cervical spine shows an advantage when compared to the lumbar spine: whereas the number of seven cervical vertebrae is remarkably constant in almost all species of mammals regardless of their neck length (Varela-Lasheras et al., 2011), the lumbar spine shows differences in the number of vertebrae even within the same genus (e.g., genus *Gorilla*; Pilbeam, 2004; Schultz & Straus, 1945; Williams, Middleton, Villamil & Shattuck, 2016). The

constant number of cervical vertebrae in mammals is controlled by Hox gene patterning during development, providing stability in the developing axial skeletal and nervous system (Galis, 1999). It has been hypothesized that this constancy in the number of cervical vertebrae may result from stabilizing selection and pleiotropic constraints resulting in an evolutionary conservation of body plans (Galis & Metz, 2007). This evolutionary stasis in the number of cervical vertebrae across mammals means that variation in the anatomy of the neck relies only on shape and size modification of those vertebrae rather than on variation in the number of vertebrae. This constraint in the number of vertebrae may favor a higher degree of integration in the cervical spine than in the thoracic and lumbar areas. These characteristics of the cervical spine make it suitable to explore its patterns of integration and modularity across species, which will be compared with the patterns of integration of the thoracic and lumbar spine in future studies.

The concept of merism makes reference to the repetition of segments in an organism, and the variation resulting in this seriation of elements is commonly known as metameric variation (Bateson, 1894; Hlusko, 2002). The vertebral column is one of the clearest examples of seriated structures in mammals and other vertebrates. Meristic elements play an important role in paleontological studies because they express variation that is not related to phylogeny (Bateson, 1894) and can shed light on differences related to developmental and functional factors. Specializations of teeth and digits are good examples that show how selection can modify anatomical structures that have a similar morphological origin and configuration (Gómez-Robles & Polly, 2012; Randau & Goswami, 2017a,b; Rolian, 2009). In the case of the vertebrae, anatomical variation originated during development is critically constrained by functional factors, limiting variation in vertebral morphology and avoiding strong changes in the global structure that could cause severe functional disruption (Riedl, 1975). Patterns of integration can evolve in response to natural selection (Grabowski, Polk & Roseman, 2011), so their study in seriated structures can shed light on both evolutionary differences between taxa and between

elements from the same structure.

Morphological integration and modularity (Olson & Miller, 1958) are related concepts associated with phenotypic covariation between traits of an organism, which may reflect a common influence from genetic, developmental and/or functional factors (Hlusko, 2004; Rolian & Willmore, 2009). Morphological integration occurs when traits covary to a strong degree due to common influences, which may result in long-term coevolution (Cheverud, 1996). Modularity favors a relative independence of traits that are part of different developmental or functional regions, which are termed modules. These modules can be defined as sets of traits that are more tightly integrated with one another than they are with traits in other modules, from which they evolve relatively independently. Modularity and integration strongly influence evolutionary change; the relative independence of the modules can lead to different evolutionary trajectories among body features and is linked with greater evolvability (Rolian & Willmore, 2009). On the other hand, integration, which describes high levels of interaction among traits, will constrain evolutionary change because changes in one trait will be associated with phenotypic changes in other correlated traits, restricting variation.

Integration and modularity studies are important to understanding how organisms' traits have evolved across phylogenies (Goswami, Smaers & Polly, 2014). Multiple studies have been carried out to analyze patterns of integration and modularity in cranial and postcranial features (Bastir, Rosas & Sheets, 2005; Gómez-Robles & Polly, 2012; Grabowski, Polk & Roseman, 2011; Polanski, 2011; Polanski & Franciscus, 2006; Williams, 2010). Integration in the context of meristic variation in hominins and other primates has been analyzed in the dental complex, digits and limbs (Gómez-Robles & Polly, 2012; Rolian, 2009; Rolian, Lieberman & Hallgrímsson, 2010; Young and Hallgrímsson, 2005). However, morphological integration in the vertebral column, until recently, has been unexplored in primates (Villamil, in press), although vertebral integration has been studied in detail in felids and

dogs (Arnold, Forterre, Lang & Fischer, 2016; Randau & Goswami, 2017a, b). Several studies have shown that size is an important factor of integration (Marroig, Shirai, Porto, de Oliveira & De Conto, 2009; Zelditch, 1988) and allometry generally influences patterns of shape variation in hominines (Shea, 1992). Thus, we have quantified integration and modularity in two important aspects of the subaxial cervical spine, the mid-sagittal morphology and facet size, shape and orientation, before and after accounting for the potential influence of size. We have focused on the five subaxial cervical vertebrae, from the third to the seventh, as they show a homologous morphological pattern, with a vertebral body and a neural arch. In this first study we did not include the first two vertebrae —atlas and axis— because they differ substantially in morphology and the identification of homologous landmarks that can be comparable with the other cervical vertebrae is particularly challenging.

2 MATERIALS AND METHODS

2.1 Data

The sample studied here comprises 141 male and female adult extant individuals from three extant hominine species: *Homo sapiens*, n = 54; *Pan troglodytes*, n = 58 and *Gorilla gorilla*, n = 29 (SOM Table S1). Only individuals with at least three complete subaxial cervical vertebrae were included. A table with the number of vertebrae per taxa and anatomical element included in the analyses is provided (SOM Table S2). Damaged vertebrae or pathological individuals were excluded.

A set of fifteen three-dimensional landmarks (L01-L15) on each subaxial cervical vertebra (C3-C7) was obtained using a Microscribe SX2: five on the mid-sagittal plane and five on each of the superior articular facets (Fig 1; SOM Table S3). To overcome the obstacle of bifurcated tips of the spinous processes present in some *H. sapiens* cervical vertebrae (mostly C3-C5), we filled the space with modeling clay. In the previous study (using the same landmarks and species) we demonstrated that the effect of measurement error was negligible (Arlegi et al., 2017). All geometric morphometric (GM)

analyses were performed in R 3.2.0 (R Core Team, 2015) using the package *geomorph* version 3.0.5.(Adams, Collyer, Kaliontzopoulou & Sherratt, 2017).

[Figure 1 here]

2.2 Statistical analyses

First, a Generalized Procrustes Analysis (GPA) (Rohlf & Slice, 1990) was performed for each vertebra and taxon to remove the information related to scale, position and orientation of specimens in the digitizing space.

Integration within cervical vertebrae and modularity

The amount of integration within each landmark dataset was quantified using the “globalIntegration” function from *geomorph* package (Adams & Otárola-Castillo, 2013). In this function, the degree of integration is quantified using the global integration coefficient (Bookstein, 2015). The function examines in a set of Procrustes coordinates the regression coefficient for log partial warp variance against log bending energy in the standard thin-plate spline setup. The values obtained with the regression slope were used to distinguish between three possible models: *a*, the self-similarity model where neither non-integration nor disintegration was detected (value of the regression slope = -1); *b*, the integration model (values < -1) and *c*, the disintegration model (values > -1).

Hypotheses of modularity were tested between three *a priori* proposed modules: vertebral body (L01-L03), spinous process (L04-L05) and the superior articular facets (L06-L15). Additionally, an alternative second hypothesis of modularity addressed the question of whether the vertebral body (L01-L03) and the neural arch (L04-L15) correspond to units with a low degree of covariation. Note that these analyses of modularity were performed with the caveat of an unequal number of landmarks on each module. For these analyses, we used the covariance ratio (CR), which calculates the degree of relative independence between modules by measuring the ratio of covariation between modules relative to the covariation within them (Adams, 2016). Significant CR values that are lower than 1 suggest that

there is a relative independence between the modules. We chose to use this approach rather than the broadly-used *RV*-coefficient (Escoufier, 1973) because it yields results that are unaffected by sample size or by the number of variables (Adams, 2016), which, as mentioned above, differ in our study. A test to estimate the degree of morphological integration among modules using partial least square correlation (PLScorr) coefficients (Adams & Collyer, 2016) was also performed. The function uses two-block partial least squares analysis (2B-PLS), which is based on a singular value decomposition of the between-block covariance matrix (Rohlf & Corti, 2000). Through this procedure, new pairs of axes are found that account for the maximum amount of covariance between the sets of variables. Because we used more than two sets of variables, the average pairwise PLS correlation was used as the test statistic (Adams & Collyer, 2016).

Covariance comparisons across cervical vertebrae

Integration across different vertebrae and differences in the degree of covariation displayed by diverse taxa were assessed using a partial least square (PLS) analysis. For both correlation analyses (i.e. integration among modules and integration across vertebrae) we used the PLScorr coefficient proposed by Adams & Collyer (2016).

Allometry

Allometry is the statistical association between size and shape (Mosimann, 1970). The effect of allometry was calculated using a multivariate regression analysis (Monteiro, 1999; Drake & Klingenberg, 2008) of Procrustes shape coordinates on the natural logarithm of centroid size (log-CS). Centroid size (CS), calculated as the square root of the summed squared distances of each landmark from the centroid of the landmark configuration, was used as an independent variable and the shape coordinates as dependent ones. The residuals obtained from this regression analyses were used to re-compute all the analyses explained previously after removing allometric effects.

[Table 1 here]

3 RESULTS

3.1 Integration and modularity within vertebrae

Global integration

All the subaxial cervical vertebrae from the three species are globally integrated (Fig 2; SOM Table S4). In general terms, gorillas tend to show the highest values of integration, followed by chimpanzees in the cranialmost (C3) and caudalmost (C7) subaxial cervical vertebrae, and by humans in the more “centrally” located vertebrae (C4-C6). The magnitude of integration decreases from the cranialmost vertebra (C3) to the caudalmost (C7) in gorillas and chimpanzees, with the C6 of gorillas departing from this trend. In humans, the degree of integration increases from C3 to C4, and then decreases caudally, also following the pattern observed in non-human hominines.

Allometry analyses (Table 1) reveal that the influence of size on shape is larger in gorillas than in chimpanzees and humans. In the three species the largest values are shown in the C3 and smallest in the C7. Humans and chimpanzees show similar percentages, although in some vertebrae (i.e. C6 and C7 in humans and C5 and C6 in chimpanzees) values are not significant. Global integration values are more similar across different taxa once size is removed. Removing the allometric component of variation mainly influences gorillas and, to a lesser degree, chimpanzees, and it has the strongest impact on the cranialmost (C3) and caudalmost (C6-C7) subaxial cervical vertebrae (Fig 2; SOM Table S4).

[Figure 2 here]

Modularity analysis

In the analysis of modularity among the three subsets of landmarks within each vertebra (SOM Table S5), only the C6 in gorillas yielded a significant CR value below 1.0 (which is the limit for modularized structures). These results are consistent with those obtained in the integration analysis among modules (PLScorr), which yield highly significant values in all cases, confirming the strong integration among the three proposed modules. Although gorillas show lower PLScorr values than chimpanzees and humans (especially in C3 and C6), differences in the strength of integration across

taxa are minor (SOM Table S5).

A second test of modularity was carried out to test whether a separation into two units, the vertebral body and the neural arch (comprising the spinous process and superior articular facets), shows significant modularity. The null hypothesis of no modular structure was rejected in all the subaxial cervical vertebrae of gorillas, in C4-C6 of chimpanzees, and only in the C6 of humans (SOM Table S6). From a biological point of view, the modularized nature of some of the hominine vertebrae when two modules (vertebral body and neural arch) are proposed seems to parallel ontogeny. The subaxial cervical vertebrae are formed by the fusion of three principal centers of ossification: one for the vertebral body and one for each half of neural arch (and the portion of the vertebral body to which the pedicles are attached) (Scheuer, Black & Christie, 2000).

In summary, the results of the global integration test (SOM Table S4 and Fig. 2) and the results obtained from testing the three-module hypothesis (SOM Table S5) reveal that subaxial cervical vertebrae are not internally subdivided into three different modules. However, the analysis of modularity for two anatomical modules revealed a different scenario where all the gorilla vertebrae were modularized, as well as C4-C6 of chimpanzees and the C6 of humans. The two- and three-module analyses based on allometry residuals reveal a reduction of the degree of modularity and its significance when removing size-related variation (SOM Tables S5 and S6).

3.2 Covariation across vertebrae

In all the taxa, the highest degree of covariation between vertebrae is shown by contiguous elements (Fig 3; SOM Table S7). With the exception of the C3, gorillas display the highest PLS_{corr} values, followed by chimpanzees. In humans, however, covariation values across non-adjacent vertebrae are not significant in most cases. Humans also show the most uniform values in all comparisons. As opposed to chimpanzees and humans, gorillas evince a pattern of covariation where the strength of covariance between pairs of subaxial cervical vertebrae increases from the cranial to the

caudal direction, showing the highest values of covariance between C6-C7, and the lowest between C3-C4 (Table S7). Removing size-related variation has a particularly strong effect on gorillas, and especially on their C3. After removing allometric effects, covariation values in gorillas look more homogenous and more similar to chimpanzees'. The general patterns of cross-vertebrae comparison, however, remain unchanged.

In summary, the three species show different patterns of covariation across vertebrae. Chimpanzees show high covariation across all cervical subaxial vertebrae. This pattern is also observed in gorillas with the exception of C3, which shows lower degrees of covariation when compared to the other vertebrae. In humans, only adjacent vertebrae tend to show significant covariation.

[Figure 3 here]

4 DISCUSSION

Previous studies have demonstrated that species with low degrees of integration show strong responses that are aligned with the direction of selection, whereas more integrated species show strong responses along the direction of size-related variation (Grabowski et al., 2011; Marroig et al., 2009; Porto, de Oliveira, Shirai, De Conto & Marroig, 2009). In fact, for the evolution of the hip bone, it has been suggested that the transition from nonhuman great ape-like morphology to that of humans would have been attained more easily with a modern human pattern of integration (Grabowski et al., 2011). Here, we have also observed these differences in the degree of integration between human and African great apes, with the lowest values shown by modern humans. Nevertheless, in this case it is difficult to ascertain whether lower integration also implies greater evolvability as in these previous studies. These differences highlight the importance of integration patterns in facilitating evolutionary transitions and have important implications for the emergence of bipedalism. In addition, we consider that the study of the patterns of integration in the subaxial cervical spine has some implications that can further our understanding of the evolutionary changes observed in the fossil record (see below).

4.1 Integration within vertebrae

A recently published study of vertebral integration in hominoids has shown, in concordance with our results, high integration in their neck, with the lowest values of integration in all the taxa in the seventh cervical vertebra (Villamil, in press). Another study of the subaxial cervical spine of dogs revealed a strong integration in the neck, and proposed that this could be the general pattern for all mammals (Arnold et al., 2016). Nevertheless, felidae display a moderate level of integration in the cervical region, and their pattern of integration, as in this study, is consistent with the hypothesis of developmental modularity non-central (Randau & Goswami, 2017a).

More specifically, in this study we have observed a similar pattern of cranio-caudal decrease in integration in gorillas and chimpanzees from C3 to C7. Humans follow this model from C4 to C7, but the third cervical vertebra shows lower values of integration than the central vertebrae (C4–C6), thus departing from the nonhuman pattern of integration. The strong integration of the third cervical vertebra in gorillas and chimpanzees may be related to the high variability of the mediolateral angle of the superior articular facets and/or the high variability in the length of the spinous processes (Arlegi et al., 2017). The two latter variables are both related to size, which is reflected in the decrease of the levels of integration when this factor is removed (Figure 2). Human C3s differ from the morphological pattern of African great apes because they are mediolaterally wider and have a more cranial orientation of the superior articular facets. These traits are correlated with bipedal locomotion, so they are thought to play a major functional role (Arlegi et al., 2017). We suggest that the caudally decreasing pattern of integration observed in nonhuman hominines could represent the ancestral pattern for the clade, and could be related to the functional role played by each vertebra in the cervical spine. In humans, the joints of the C3 and C7 with their adjacent vertebrae do not allow for a large degree of flexion/extension, lateral bending and axial rotation in the cervical spine (White & Panjabi, 1978). For these reasons, these vertebrae play a minor functional role in the movement of the neck. Conversely, C4 and C5, with the highest values of integration, are associated with the largest degree of range

motion.

The departure of the human C3 from the likely ancestral hominine pattern of integration could be related to its functional role regarding head posture in relation with the emergence of bipedalism. It has been proposed that differences in patterns of integration are concentrated in traits that are functionally involved in bipedalism (Grabowski et al., 2011). This suggests that natural selection changed patterns of integration by minimizing constraints and integration in traits associated with bipedalism, which would allow them to respond to further selective pressures in a relatively independent way. We hypothesize that the low level of integration in the human C3 may have facilitated the emergence of new phenotypes more adapted to bipedalism. This hypothesis is supported by the more modern human-like C3 observed in australopiths compared to gorillas and chimpanzees, which would be consistent with a breakdown of the ancestral hominine pattern of integration, similar to that suggested by Grabowski et al. (2011) in the coxal bone. However, australopiths like *A. sediba* still preserve a more chimpanzee like C7, and still retained a stiff, ape-like neck, essentially part of the shoulder complex (Arlegi et al., 2017; Meyer et al., 2017; Williams et al., 2013). Observations made on some early representatives of the genus *Homo*, such as those from Dmanisi (C3 D2674), are consistent with our hypothesis, showing a modern human-like reduced uncinat process that would have increased the range of movements (Meyer, 2005). Not only the C3, but also the C7 of humans displays much lower levels of integration than nonhuman hominines, which would be also a derived condition. The modern human-like C7 of KNM-WT 15000 (*Homo erectus*), suggests that the low degree of integration in the human C7 appeared in early *Homo*. This lower degree of integration could have favored the selection of morphological traits related to a more mobile neck associated with the emergence of endurance running (Bramble & Lieberman, 2004; Meyer, 2005). This evolutionary modification is related to changes in the vertebral body and in the orientation of the superior articular facets, which can be also related to differences in the head equilibrium and neck posture between australopiths and *Homo*

(Been et al., 2017).

4.2 Covariation across vertebrae

Regarding covariation across vertebrae, the highest levels of covariation are observed between adjacent vertebrae. These interactions are in general stronger in gorillas, whereas they are weaker in humans and have intermediate values in chimpanzees. These results are consistent with the principles of functional integration. Indeed, anatomical elements playing important functional roles and working in concert with other elements are expected to be highly integrated, since changes in one element without associated changes in the other elements of a system can compromise functionality (Riedl, 1975). According to our results, adjacent vertebrae are the only ones that show significant integration in humans, whereas non-adjacent vertebrae are not significantly integrated. This human-specific pattern can be tentatively related to the more vertical transmission of the weight of the head throughout the subaxial cervical spine that is typical of our species. Functional interaction among nonadjacent cervical vertebrae balancing the head may not be as strong as in the more pronograde African apes. In the case of gorillas, their more dorso-ventrally oriented upper articular facets likely result in a limitation of the movement between the subaxial cervical vertebrae, which would be paralleled by the limitation in the flexion-extension movement due to their long spinous processes (Arlegi et al., 2017). This difference may add to the allometric effect and increase the level of integration and stability of the gorilla neck. A more stable neck may be required by the large absolute mass of the gorilla cranium, whose movements will result in larger moments of inertia. This phenomenon, which is common in quadrupedal large-sized taxa, is observed because, whereas body mass increases in a volumetric ratio, the muscle force increases in a power of two. This results in an increase of the length of the spinous processes and requires an increase of the associated muscle masses to compensate the created disequilibrium (Slijper, 1946).

4.4 The influence of size

Allometry has been claimed to be an important factor of integration (Klingenberg, 2009; Mitteroecker & Bookstein, 2007; Zelditch, 1988). This is consistent with our results in chimpanzees and, especially, in gorillas, which show that the degree of integration decreases when the effect of allometry is removed. On the contrary, the effect of size as an integration factor in humans is negligible. In hominines, phenotypic variation in the direction of size mainly occurs in the spinous processes (Arlegi et al., 2017), so the longer spinous processes of gorillas and chimpanzees may play an important functional role promoting integration (Cheverud, 1996) in the cervical spine.

4.4 Evolutionary implications

Neck posture and subaxial cervical morphology are derived in *Homo sapiens* (Arlegi et al., 2017; Been et al., 2017; Meyer, 2005, 2016; Meyer et al., 2017), and so is bipedalism. In fact, the differences we have found in the patterns of integration in *Homo sapiens* with respect to chimpanzees and gorillas are in line with the patterns of variation observed in the limited cervical fossil record (see above).

However, whether neck morphology and posture of chimpanzees and gorillas are primitive or derived is currently unknown. Gorillas have been proposed to represent allometric variants from chimpanzees for certain cranial characteristics (e.g., cranial base; Martínez, 1995). However, in certain postcranial features, such as the ratio between femoral to humeral length (Holliday, 2012), chimpanzees and gorillas show different patterns. In fact, the allometric pattern of the subaxial cervical spine differs in chimpanzees and gorillas (Arlegi et al., 2017), which is consistent with the differences we have found in this study between these two taxa. These differences between Pan and Gorilla are also consistent with postural differences, including the inclination of the neck, which shows differences of about 25° between these taxa (Strait & Ross, 1999) and parallels other differences in knuckle-walking between these two genera (Kivell & Schmitt, 2009). The differences in both morphology and integration patterns of the subaxial cervical spine, which is a priori the most stable region of the vertebral column,

point to a complex evolutionary scenario where developmental constraints and functional demands interact in different ways.

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Figure legends

Figure 1. Landmarks used in this study. For landmark definitions see Table S3. The figure represents a seventh cervical vertebra (C7) in left lateral (top) and cranial (bottom) views.

Figure 2. Colored vertebrae representing the strength of integration within each subaxial cervical vertebra. Top: integration from raw data; bottom: integration as calculated from allometry residuals. All represented vertebrae are globally integrated (see the electronic supplementary material, Table S3). Red color represents strong integration and purple represents weaker integration. Gorillas display higher integration followed by chimpanzees and humans. A decreasing cranio-caudal pattern of integration can be observed, which is more evident when size is removed. Humans depart from this decreasing cranio-caudal pattern by showing lower integration values in the C3 than in more caudal elements. Results from residuals show lower values of integration in all subaxial cervical vertebrae in gorillas and chimpanzees, demonstrating that size has an important effect on integration in non-human hominines. In humans, results from residuals are very similar to those obtained from raw data, which means that size is not a factor of integration in this group. Different images are not to the same scale.

Figure 3. Contour line diagrams represent correlation fields (Kurtén, 1953) across subaxial cervical vertebrae (C3-C7) in hominines based on raw data (top) and on allometry residuals (bottom). The numerical values on which these figures are based are displayed in the electronic supplementary material, Table S7). Plots are symmetric such that redundant information is represented in the upper-right and lower-left half of each plot. Red color represents strong integration between vertebrae and purple represents weak integration. Gorillas show the highest integration across all cervical vertebrae, whereas humans show lower values and only adjacent vertebrae covary significantly. Size is not an important integration factor in humans and chimpanzees. In gorillas, however, removing size reduces the level of integration between non-adjacent elements increases