Annals of Anatomy xxx (2014) xxx–xxx

Contents lists available at ScienceDirect

Annals of Anatomy

journal homepage: www.elsevier.de/aanat

Research article

Developmental covariation of human vault and base throughout postnatal ontogeny

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ARTICLE INFO

Article history:
Received 27 February 2014
Received in revised form
30 September 2014
Accepted 2 October 2014
Available online xxx

Keywords:
Morphological integration
Neurocranial growth
Partial least squares
Modularity
Allometry
Geometric morphometrics

ABSTRACT

In the present study, we analyzed postnatal ontogenetic integration among morphological traits of the human neurocranium. Particularly, the covariation between the vault and the base during postnatal life was assessed. Since the association between these regions may depend on the generalized change produced by allometry, we tested its effect on their covariation. On a sample of adults and subadults ranging from 0 to 31 years, 3D coordinates of neurocranial landmarks and semilandmarks were digitized and geometric morphometric technics were applied. Main aspects of shape variation were examined using Principal Components analysis. Covariation between the vault and the base was examined by Partial Least Squares analysis. According to our results, the vault and the base covary strongly during postnatal ontogeny and their relation depends largely on allometry. Two size variables were studied: centroid size, which was obtained from the recorded morphometric points, and endocranial volume, taken as an estimation of brain size. Although growing brain was found to be a developmental process that contributes to covariation among neurocranial traits, there would be other factors that exert their influence during ontogeny. These results lead to reconsider cranial morphological evolution taking into account the developmental constraints given by ontogenetic patterns of integration and reinforcing the idea that in human evolution a suite of relevant characters may be fuelled by few developmental processes.

1. Introduction

Phenotypic variation is generated by several developmental processes where genetic and environmental factors intervene. As a result of these ontogenetic dynamics, a structure of association among morphological traits emerges (Mitteroecker and Bookstein, 2007; Jamniczky et al., 2010). This tendency to produce coordinated variation among different traits is known as morphological integration (Olson and Miller, 1958; Hallgrímsson et al., 2009). In the context of modern morphometrics, morphological integration is expressed by covariances of landmarks that describe anatomical structures (Klingenberg, 2009; Goswami and Polly, 2010).

One of the developmental processes that lead to coordinated variation of different traits is generalized increase of size. Those anatomical features simultaneously affected by size change would vary in a coordinated fashion to some extent. Allometry represents all size-related shape changes, which usually affect several parts of an anatomical region or even an entire organism (Chernoff and Magwene, 1999; Klingenberg, 2013). Ontogenetic allometry, in particular, deals with variation of traits associated with size change along ontogeny. Systemic and local processes could be related to allometric change during postnatal life. For example, growth hormone (GH) in mammals induces changes in most organs and structures, including the skull (Gonzalez et al., 2013). Locally, a growing organ, such as the brain, can produce size expansion and promote changes in different cranial regions, through mechanical interactions (Hallgrímsson and Hall, 2011).

The most accepted division of the mammalian skull distinguishes the face from the neurocranium (Cheverud, 1982, 2007; Enlow and Hans, 1998; Sardi and Ramírez Rozzi, 2005; Sardi et al., 2007). Furthermore, the neurocranium includes the vault

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http://dx.doi.org/10.1016/j.aanat.2014.10.002
0940-9602/

Table 1
Sample constitution.

Age group	Females	Males	Total
Infant-child	7	12	19
Juvenile	11	16	27
Adolescent	15	12	27
Adult	51	15	66
Total	82	53	139

and the base (Sperber, 2001; Lieberman, 2011). Various lines of evidence indicate that the brain and the meninges influence both neurocranial regions and constitute their main driving force of growth (Moss and Young, 1960; Bradley et al., 1996; Opperman, 2000; Richtsmeier et al., 2006). However, the vault and the base develop through different processes. The bones of the vault ossify intramembranously and grow by bone deposition in the margins of the sutures, whereas the base forms endochondrally and its anteroposterior elongation is produced by intrinsic factors acting in three synchondroses (Sperber, 2001; Morriss-Kay and Wilkie, 2005). Additionally, the base relates to facial structures and the vertebral column (Lieberman et al., 2000a).

While interactions between the neurocranium and the face have been assessed in several studies (Bastir and Rosas, 2006; Mitteroecker and Bookstein, 2008; Gkantidis and Halazonetis, 2011; Martínez-Abadías et al., 2011), covariation between the human vault and base has been less explored from a developmental perspective. Among the few antecedents, Bookstein et al. (2003) observed general coordinated shape change between sagittal traits of the vault and the base during ontogeny.

The main aim of the present study was to analyze postnatal ontogenetic integration among morphological traits of the human neurocranium. In particular, we evaluated the covariation between the vault and the base during postnatal life and assessed the effect of allometry in this pattern of association.

Main evolutionary trends of morphological change are usually the result of modifications in the developmental processes that generate variation in correlated phenotypic characteristics (Raff, 1996; Lieberman et al., 2002). Since brain growth is thought to be a key developmental process leading to coordinated variation between different anatomical regions in the neurocranium, results of this study may provide insights into some important processes for human evolution. If traits of the vault and the base are integrated during ontogeny, single evolutionary changes in one region would result in global morphological modifications. In this context, changes in human neurocranial morphology may not be the consequence of isolated responses to diverse selective pressures but few developmental shifts would affect the direction or magnitude of variation upon related structures (Martínez-Abadías et al., 2012).

2. Materials and methods

2.1. Sample and data collection

In this study, we used head computed tomography (CT) images of 139 individuals from a dataset constructed at Fundación para la Lucha contra las Enfermedades Neurológicas de la Infancia (Buenos Aires, Argentina). The sample includes nonpathological humans from 0 to 31 years old of both sexes (Table 1). They were scanned with a General Electric Light Speed RT16 and, for each individual, 275 axial CT images with a resolution of 512×512 pixels and a voxel size equal to $0.449 \times 0.\ 449 \times 0.625$ mm, were produced. A trial version of Avizo 6.0 software (Visualization Science Group) was used to handle CT images. From CT slices, a reconstruction in three dimensions (3D) was created using a chosen density threshold that corresponds to the Hounsfield unit scale (Spoor et al., 2000).

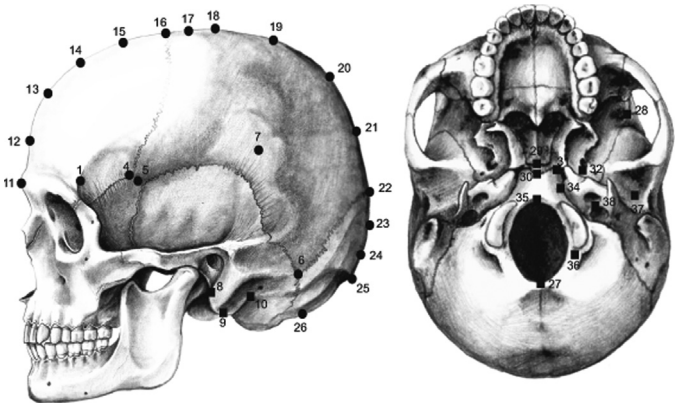

Fig. 1. Location of landmarks and semilandmarks. Circles represent vault points and squares represent base points. Detailed definitions of each point are provided in Table 2 as well as information about the neurocranial region to which they belong.

A threshold of 1150 Hounsfield units was empirically selected to show the maximum amount of bony tissue.

In order to provide a clear visualization of ontogenetic change in figures and descriptions, individuals were distinguished into the following age groups: infant-child (0–6 years), juvenile (7–12 years), adolescent (13–17 years) and adult (18–31 years), following Smith (1994).

On each individual, twenty-seven landmarks and 10 semilandmarks in 3D were digitized on the ectocranial surface (Table 2, Fig. 1). While landmarks are defined as discrete anatomical *loci* that can be recognized as the same *loci* in all the individuals of the sample (Zelditch et al., 2004), semilandmarks are frequently used to describe structures such as curves or surfaces, where landmarks are rare. In this study, a number of evenly-spaced semilandmarks were placed between specific landmarks to depict the sagittal contour of the neurocranium. As these contours have to be homologous among individuals, semilandmarks were resampled along the outline curve using a linear interpolation between the original curve points (Reddy et al., 2004).

Additionally, an estimation of the endocranial volume (EV) was obtained by semiautomatic segmentation of the endocranium. As an accepted indicator of brain size, EV provides a way to access to information about general size of this neural organ when soft tissues are not available (Conroy et al., 2000; Bienvenu et al., 2011).

To eliminate variation due to measurement error, an intra-observer error analysis was carried out by the author who collected the data (J.B.A.) prior to definite digitization. On a sample of 15 CTs, consisting of individuals of different ages, landmarks and semilandmarks were digitized three times and measurement error was estimated by means of different methodological approaches (Barbeito-Andrés et al., 2012). Following Corner et al. (1992), dispersion resulting of the placement of coordinates in repeated events of measure was assessed. Principal Component analysis (PCA) was carried out on the Procrustes coordinates obtained after Generalized Procrustes analysis (GPA) (see below for explanations about PCA and GPA). In a graphical representation, the position of each individual along the PCA axes that explain near 80% of variation were visualized taking into account that if repeated measures on the same individual are similar, they must occupy similar positions (O'Higgins and Jones, 1998). A complete description and discussion of the results of these analyses were presented elsewhere (Barbeito-Andrés et al., 2012). By means of this evaluation, problematic morphometric points were identified and their definitions were revised.

Intra-observer error analysis was repeated until the error was not significant ($p < 0.01$) according to an Analysis of the Variance for Repeated Measures and an Intraclass Correlation Coefficient.

Please cite this article in press as: Barbeito-Andrés, J., et al., Developmental covariation of human vault and base throughout postnatal ontogeny. Ann. Anatomy (2014), http://dx.doi.org/10.1016/j.aanat.2014.10.002