



HAL
open science

Asymmetry of the midfacial skeleton of eastern lowland gorillas (*Gorilla beringei graueri*) and potential association with frontal lobe asymmetries

Yann Heuzé, Antoine Balzeau

► **To cite this version:**

Yann Heuzé, Antoine Balzeau. Asymmetry of the midfacial skeleton of eastern lowland gorillas (*Gorilla beringei graueri*) and potential association with frontal lobe asymmetries. *Journal of Human Evolution*, 2014, 74, pp.123-129. 10.1016/j.jhevol.2014.03.005 . hal-02322764

HAL Id: hal-02322764

<https://hal.science/hal-02322764v1>

Submitted on 7 Feb 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Published in final edited form as:

J Hum Evol. 2014 September ; 0: 123–129. doi:10.1016/j.jhevol.2014.03.005.

Asymmetry of the midfacial skeleton of eastern lowland gorillas (*Gorilla beringei graueri*) and potential association with frontal lobe asymmetries

Yann Heuzé^a and Antoine Balzeau^b

^aDepartment of Anthropology, The Pennsylvania State University, University Park, PA, USA

^bÉquipe de Paléontologie Humaine, UMR 7194 du CNRS, Département de Préhistoire du Muséum national d'Histoire naturelle, Paris, France

Keywords

Hominoid; Directional asymmetry; Brain and face co-variation; Petalia

Introduction

In 1973, Groves and Humphrey reported facial asymmetry in eastern gorillas and suggested that it may be indicative of asymmetrical brain function. Being cautious, the authors favored the explanation that facial asymmetry was likely due to asymmetrical chewing behavior rather than anatomical asymmetry of the cerebral hemispheres. The nature of the association between lateralized functions (e.g., handedness, mastication) and brain asymmetries in hominoids represents an active field of research. There has been both support (Hoogmartens and Caubergh, 1987; Nisan et al., 2004) and lack of support (Martinez-Gomis et al., 2009) for an association between chewing side preference and handedness in humans. In gorillas, contradictory results can be found on the question of handedness, varying from no handedness (Harrison and Nystrom, 2010) to equal proportion of right and left (Fagot and Vauclair, 1988; Byrne and Byrne, 1991; Parnell, 2001; Lambert, 2012) to true handedness (Meguerditchian et al., 2010). Cerebral anatomical asymmetries, and particularly fronto-occipital petalia, have been found to be related to handedness in modern humans (LeMay, 1976, 1977; Galaburda et al., 1978; LeMay and Kido, 1978; LeMay et al., 1982; Kertesz et al., 1986, 1990; but see Chiu and Damasio, 1980), and more generally to specific aspects of human cognition (Hecaen and Albert, 1978; Nass and Gazzaniga, 1987; Bryden, 1988; Gazzaniga, 1995a, b; Harrington, 1995). The existence of asymmetrical patterns for the frontal and occipital petalias in great apes, including *Gorilla beringei graueri*, have recently been reported (Balzeau and Gilissen, 2010; Balzeau et al., 2012). However, the potential association between facial and cerebral anatomical asymmetries in great apes and its

© 2014 Elsevier Ltd. All rights reserved.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

functional and evolutionary implications remain unclear. Moreover, the original paper of Groves and Humphrey (1973) has been over-interpreted, as several authors refer to it as a claim of cerebellar asymmetry in gorillas (e.g., Balonov et al., 1984; Hopkins and Marino, 2000; Holloway et al., 2004). Here, we propose to quantify facial asymmetry in adult eastern lowland gorillas (*Gorilla beringei graueri*), determine whether or not directional asymmetry (DA) is present in our sample, and subsequently investigate the potential relationship between facial and frontal lobe asymmetries using data previously published by Balzeau and Gilissen (2010).

Materials and methods

Image data and landmarks

Facial skeletal form was quantified in three dimensions by recording the 3D coordinates of 18 landmarks on computed tomography (CT) images of the cranium in 32 adult specimens (18 females and 14 males) from the primate collection of the Royal Museum for Central Africa, Tervuren, Belgium (Fig. 1, Table 1). The difficulty of measuring landmarks with small intra-observer error on the upper-face, coupled with the absence of mandibular data for several specimens, led us to focus on the mid-face. The landmark coordinates were used (i) to compute the Procrustes superimposition of all specimens (Rohlf and Slice, 1990; Dryden and Mardia, 1998) and subsequently perform Procrustes analysis of variance (ANOVA) (Klingenberg and McIntyre, 1998), and (ii) to measure and analyze linear distances using Euclidean distance matrix analysis (EDMA) (Lele and Richtsmeier, 2001). All specimens were measured twice by the same observer (YH) to test for intra-observer error, which can generate bias when quantifying asymmetry. Intra-observer error was assessed by Procrustes ANOVA (see Singh et al., 2012 for a recent application).

Frontal lobe asymmetry is quantified in three dimensions by recording 3D coordinates of the two landmarks corresponding to the most protruding areas of the right and left frontal lobes on the reconstructed endocranial surface (Fig. 1, Table 1). The complete methodology is detailed in Balzeau and Gilissen (2010) and Balzeau et al. (2012), and the results on *Gorilla beringei graueri* are published in Balzeau and Gilissen (2010) using the same specimens as those used in the present study. The term 'petalia' originally refers to the protrusion of one hemisphere beyond the other (Hadziselimovic and Cus, 1966) and is utilized here in this sense. An external and independent reference is defined based on anatomical points on the skull (i.e., glabella, inion, and basion). In order to precisely describe the pattern of variation in frontal lobe petalia, the antero-posterior, vertical and lateral components are dissociated. The two landmarks measured on the frontal lobes are orthogonally projected on the line (L1) through glabella and inion. The distance between the projected images of the points corresponds to the antero-posterior component of frontal petalia. Similarly, the frontal lobe landmarks are projected on the line through basion and perpendicular to L1, and on the plane defined by glabella, inion and basion, defining the vertical and lateral components of frontal lobe petalia, respectively.

Procrustes ANOVA

Procrustes ANOVA is a method outlined by Klingenberg and McIntyre (1998) that combines quantification of individual variation and asymmetry by ANOVA (Palmer and Strobeck, 1986) with the analysis of shape, represented as configurations of landmarks (Bookstein, 1991). Procrustes ANOVA allows quantification of the different components of asymmetry and tests them statistically. The method involves a four-step procedure: quantification of within-individual shape variation in the dataset (Individual); calculation of the effects of directional asymmetry (Side); accounting for fluctuating asymmetry (Individual \times Side); and quantification of variation among repeat measurements, which is the residual and a value for measurement error in the dataset (Table 2). Here, the level of measurement error relative to the level of fluctuating asymmetry was negligible as indicated by the mean square values, implying that the present data are suitable to study asymmetry.

Euclidean distance matrix analysis

Euclidean distance matrix analysis (Lele and Richtsmeier, 2001) represents an alternative way to measure DA based on linear measurements. The full method is outlined in Richtsmeier et al. (2005). For each individual, a form matrix is computed, consisting of all unique interlandmark distances. The linear distances that occur bilaterally are paired, one from the left side (L) and the other from the right (R). For each individual, the asymmetry of all distance pairs is defined as (R-L). The sign of the (R-L) subtraction defines which side is the largest for each measurement. The mean of the sample, (R-L), measures DA for each measurement. Significance of DA for each measurement is determined by obtaining confidence intervals using bootstrapping ($n = 10,000$; alpha level = 0.05). If zero (the expected value of (R-L) in absence of DA) is not included in the confidence interval, then there is significant DA for this measurement.

Qualitative assessment of asymmetry

Regardless of whether the sample displays significant DA, it is possible to determine, specimen by specimen, how each landmark deviates from the corresponding landmark of an artificially symmetric configuration. The symmetric configuration is obtained by reflecting and re-labeling all paired landmarks and subsequently by superimposing the original and reflected configurations in a generalized Procrustes fit (Rohlf and Slice, 1990; Dryden and Mardia, 1998). The landmark deviations of the original configuration from the symmetric consensus of the original and mirror image represent the asymmetric component of shape variation (Klingenberg et al., 2002). The sign of the x, y, z coordinates of the individual asymmetric component of shape variation determines how the landmarks of the original configuration deviate from the symmetric consensus. To determine if the specimen displays a larger right side of the face (> 0) or a larger left side (< 0), the number of landmarks that deviated on the right side is subtracted by the number of landmarks that deviated on the left side. The corresponding subtractions were also done for the vertical and antero-posterior dimensions for each landmark for all specimens to determine which side of the face was more superiorly projected and which side was more anteriorly projected. Analysis of the asymmetric component of shape variation was performed with MorphoJ (Klingenberg, 2011).

We also examined, specimen by specimen, the landmark deviations of the original configuration from the symmetric consensus of the original and mirror image (i.e., asymmetric component) for the upper part and lower part of the mid-face as defined in Table 1. For the lateral dimension, the number of landmarks that deviate from the symmetric consensus of the original and mirror image on the right side are subtracted by the number of landmarks that deviate from the symmetric consensus of the original and mirror image on the left side. The resulting variable is obtained for the upper part and lower part of the mid-face. The relationship between the two variables is analyzed by linear regression. The same analysis is performed for the vertical and antero-posterior dimensions.

In order to assess the potential association between midfacial and frontal lobe asymmetries, we used the directions of individual asymmetries of the frontal lobes published by Balzeau and Gilissen (2010), identifying which one of the left or right frontal lobe is the most anteriorly, superiorly and laterally projected.

Results

Directional asymmetry of the mid-face of *Gorilla beringei graueri*

Based on the Procrustes ANOVA results, combined males and females did not display significant DA for the mid-face (Table 2). However, when analyzed separately, males displayed significant DA for the mid-face ($p = 0.0401$) contrary to females. Analyzed separately, neither the upper mid-face nor the lower mid-face displayed significant DA (Table 2).

When males and females were combined, the EDMA results showed only two distances out of 49 with significant DA (Fig. 2). Analyzed separately, males and females displayed five and 10 distances, respectively, associated with significant DA (Fig. 2).

The asymmetric relationship between the upper and lower mid-face of *Gorilla beringei graueri*

Analysis of the landmark deviations of the original configuration from the symmetric consensus of the original and mirror image for the upper and lower mid-face revealed a tendency for *Gorilla beringei graueri* to display either a larger right upper mid-face associated with a larger left lower mid-face or vice versa ($R^2 = 0.5121$, $p = 0.00001$; Fig. 3). This morphological pattern was not reflected for the antero-posterior or vertical dimensions ($R^2 = 0.1518$, $p = 0.0540$ and $R^2 = 0.0197$, $p = 0.4438$, respectively). The EDMA results showed that females displayed a larger left upper mid-face associated with a larger right lower mid-face, while the opposite was seen in males (Fig. 2).

Relationship between midfacial and frontal lobe asymmetries

Using the Balzeau and Gilissen (2010) results that confirmed the existence of an asymmetrical pattern for frontal petalia in *Gorilla beringei graueri*, we investigated specimen by specimen the potential association between midfacial and frontal lobe asymmetries. A majority of specimens displayed an association between frontal petalia and midfacial asymmetries for the lateral dimension, with the same side of the frontal pole and

mid-face being larger than the other side (59% of ipsilateral asymmetries (13/22); Fig. 4). A majority of specimens displayed the same side of the frontal pole and mid-face as being more superiorly projected than the other side (62% of ipsilateral asymmetries (19/31); Fig. 4). Finally, a majority of specimens displayed an association between frontal lobe and midfacial asymmetries for the antero-posterior dimension, with the same side of the frontal pole and mid-face being more anteriorly projected than the other side (58% of ipsilateral asymmetries (18/31); Fig. 4). When analyzed separately, males and females displayed a majority of ipsilateral asymmetries for the vertical and antero-posterior dimensions, while only males displayed a majority of ipsilateral asymmetries for the lateral dimension (Fig. 4).

Discussion and conclusion

To our knowledge, these results represent the first attempt to characterize and quantify brain and facial anatomical asymmetries in *Gorilla beringei graueri* and, more generally, in any primate species. Our results showed either a lack of DA or rather small DA of the mid-face of *Gorilla beringei graueri* depending on the method used (i.e., Procrustes ANOVA or EDMA). When analyzed separately, males displayed some level of DA of the mid-face with both methods, while females showed DA only with EDMA. Surprisingly, the direction of asymmetries of the upper part and lower part of the mid-face among females was the opposite of males as revealed by EDMA. This explains why DA was stronger when sexes were analyzed separately than when combined. We interpret our results as an indication that EDMA is more sensitive and appropriate when measuring DA than Procrustes ANOVA; the main reason being most likely related to the Procrustes superimposition itself, which distributes potentially very small and localized asymmetries to other landmarks.

Procrustes ANOVA results are contradictory to those published by Groves and Humphrey (1973) who reported DA of the face of *Gorilla beringei graueri*, while EDMA results tend to support their findings (though only two measurements out of 49 displayed significant DA). However, their measurement accounted for a larger portion of the face including the mandible and it is possible that if we had analyzed the entire face, we might have recorded stronger DA with the two methods. Additionally, the quantification of facial DA by Groves and Humphrey (1973) was based on a single bilateral linear measurement accounting for 'skull length' from the anterior-most point of the temporal fossa to the most inferior point of the mandible in the midline (i.e., gnathion), two landmarks that can be challenging to measure in gorillas.

Though based on a relatively small sample size, our results highlight the potential association between the direction of the anatomical asymmetries of the facial skeleton and frontal lobe at the individual level. We have seen that whatever the dimension considered, approximately 60% of the specimens displayed ipsilateral anatomical asymmetries. One possible interpretation of this result resides in the co-variation of the brain and face that can be traced back as far as early embryological development (Marcucio et al., 2011). The association between the direction of the midfacial and frontal lobe asymmetries at the individual level would have to be studied in a larger sample to corroborate our findings. Further work is expected concerning the co-variation of brain and face and their anatomical

asymmetries in adults, and the relationship between these features and lateralized functions such as handedness and mastication.

Acknowledgments

We thank Emmanuel Gilissen from the Royal Museum for Central Africa (Tervuren, Belgium) for giving us access to the primate skeletal collection and imaging datasets in his care. We are also grateful to Nandini Singh, Joan T. Richtsmeier, and Tim M. Ryan for their input on previous versions of the manuscript. We thank the two reviewers and the Associate Editor for their constructive comments that helped to enhance the overall quality of this manuscript. This research was partially funded by NIH/NIDCR R01DE018500 and R01DE016886; and the EU FP6 'Paul Broca II – The evolution of cerebral asymmetry in *Homo sapiens*' project.

References

- Balonov LY, Deglin VL, Kaufman DA, Nikolaenko NN. Functional asymmetry of the animal brain. *Neurosci. Behav. Physiol.* 1984; 14:427–434. [PubMed: 6435010]
- Balzeau A, Gilissen E. Endocranial shape asymmetries in *Pan paniscus*, *Pan troglodytes* and *Gorilla gorilla* assessed via skull based landmark analysis. *J. Hum. Evol.* 2010; 59:54–69. [PubMed: 20537369]
- Balzeau A, Gilissen E, Grimaud-Hervé D. Shared pattern of endocranial shape asymmetries among great apes, anatomically modern humans, and fossil hominins. *PLoS One.* 2012; 7:e29581. [PubMed: 22242147]
- Bookstein, FL. *Morphometric tools for landmark data: geometry and biology.* Cambridge University Press; Cambridge: 1991.
- Bryden, M. Cerebral specialization: clinical and experimental assessment.. In: Boller, F.; Grafman, J., editors. *Handbook of Neuropsychology, Volume 1.* Elsevier Science Publishers; New York: 1988. p. 143-159.
- Byrne RW, Byrne JM. Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. berengei*). *Cortex.* 1991; 27:521–546. [PubMed: 1782788]
- Chiu HC, Damasio AR. Human cerebral asymmetries evaluated by computed tomography. *J. Neurol. Neurosurg. Psychiatry.* 1980; 43:873–878. [PubMed: 7441265]
- Dryden, IL.; Mardia, KV. *Statistical Shape Analysis.* Wiley; Chichester: 1998.
- Fagot J, Vauclair J. Handedness and bimanual coordination in the lowland gorilla. *Brain Behav. Evol.* 1988; 32:89–95. [PubMed: 3179697]
- Galaburda AM, LeMay M, Kemper TL, Geschwind N. Right-left asymmetries in the brain. *Science.* 1978; 199:852–856. [PubMed: 341314]
- Gazzaniga MS. On neural circuits and cognition. *Neural Comput.* 1995a; 7:1–12. [PubMed: 8936056]
- Gazzaniga MS. Principles of human brain organization derived from split-brain studies. *Neuron.* 1995b; 14:217–228. [PubMed: 7857634]
- Groves CP, Humphrey NK. Letter: Asymmetry in gorilla skulls: evidence of lateralized brain function? *Nature.* 1973; 244:53–54. [PubMed: 4582492]
- Hadziselimovic H, Cus M. The appearance of internal structures of the brain in relation to configuration of the human skull. *Acta Anat.* 1966; 63:289–299. [PubMed: 5918440]
- Harrington, A. Unfinished business: Models of laterality in the nineteenth century.. In: Davidson, R.; Hugdahl, K., editors. *Brain Asymmetry.* The MIT Press; Cambridge: 1995. p. 3-27.
- Harrison RM, Nystrom P. Handedness in captive gorillas (*Gorilla gorilla*). *Primates.* 2010; 51:251–261. [PubMed: 20224914]
- Hecaen, H.; Albert, M. *Human neuropsychology.* John Wiley & Sons; New York: 1978.
- Holloway, RL.; Broadfield, DC.; Yuan, MS. *The Human Fossil Record: Brain Endocasts: The Paleoneurological Evidence.* John Wiley & Sons; New York: 2004.
- Hoogmartens MJ, Caubergh MA. Chewing side preference in man correlated with handedness, footedness, eyedness and earedness. *Electromyogr. Clin. Neurophysiol.* 1987; 27:293–300. [PubMed: 3665815]

- Hopkins WD, Marino L. Asymmetries in cerebral width in nonhuman primate brains as revealed by magnetic resonance imaging (MRI). *Neuropsychologia*. 2000; 38:493–499. [PubMed: 10683399]
- Kertesz A, Black SE, Polk M, Howell J. Cerebral asymmetries on magnetic resonance imaging. *Cortex*. 1986; 22:117–127. [PubMed: 3709188]
- Kertesz A, Polk M, Black SE, Howell J. Sex, handedness, and the morphometry of cerebral asymmetries on magnetic resonance imaging. *Brain Res*. 1990; 530:40–48. [PubMed: 2271951]
- Klingenberg CP. MorphoJ: an integrated software package for geometric morphometrics. *Mol. Ecol. Resour.* 2011; 11:353–357. [PubMed: 21429143]
- Klingenberg CP, McIntyre GS. Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution*. 1998; 52:1363–1375.
- Klingenberg CP, Barluenga M, Meyer A. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution*. 2002; 56:1909–1920. [PubMed: 12449478]
- Lambert M. Brief communication: Hand preference for bimanual and unimanual feeding in captive gorillas: extension in a second colony of apes. *Am. J. Phys. Anthropol.* 2012; 148:641–647. [PubMed: 22639326]
- Lele, SR.; Richtsmeier, JT. *An Invariant Approach to Statistical Analysis of Shapes*. First edition.. Chapman and Hall/CRC; Boca Raton: 2001.
- LeMay M. Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. *Ann. N. Y. Acad. Sci.* 1976; 280:349–366. [PubMed: 827951]
- LeMay M. Asymmetries of the skull and handedness. *Phrenology revisited. J. Neurol. Sci.* 1977; 32:243–253. [PubMed: 874523]
- LeMay M, Kido DK. Asymmetries of the cerebral hemispheres on computed tomograms. *J. Comput. Assist. Tomogr.* 1978; 2:471–476. [PubMed: 708500]
- LeMay, M.; Billig, M.; Geschwind, N. Asymmetries of the brains and skulls of nonhuman primates.. In: Falk, D.; Armstrong, E., editors. *Primate Brain Evolution. Methods and Concepts*. Plenum Press; New York: 1982. p. 263-277.
- Marcucio RS, Young NM, Hu D, Hallgrímsson B. Mechanisms that underlie covariation of the brain and face. *Genesis*. 2011; 49:177–189. [PubMed: 21381182]
- Martinez-Gomis J, Lujan-Climent M, Palau S, Bizar J, Salsench J, Peraire M. Relationship between chewing side preference and handedness and lateral asymmetry of peripheral factors. *Arch. Oral Biol.* 2009; 54:101–107. [PubMed: 18947820]
- Meguerditchian A, Calcutt SE, Lonsdorf EV, Ross SR, Hopkins WD. Brief communication: Captive gorillas are right-handed for bimanual feeding. *Am. J. Phys. Anthropol.* 2010; 141:638–645. [PubMed: 20033918]
- Nass, R.; Gazzaniga, M. Cerebral lateralization and specialization in human central nervous system.. In: Plum, F., editor. *Handbook of Physiology, the Nervous System, Volume 5. An American Physiological Society Book*; Bethesda: 1987. p. 701-761.
- Nissan J, Gross MD, Shifman A, Tzadok L, Assif D. Chewing side preference as a type of hemispheric laterality. *J. Oral Rehabil.* 2004; 31:412–416. [PubMed: 15140165]
- Parnell RJ. Hand preference for food processing in wild western lowland gorillas (*Gorilla gorilla gorilla*). *J. Comp. Psychol.* 2001; 115:365–375. [PubMed: 11824899]
- Palmer AR, Strobeck C. Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* 1986; 17:391–421.
- Richtsmeier, JT.; Cole, TM.; Lele, SR. An invariant approach to the study of fluctuating asymmetry: Developmental instability in a mouse model for Down Syndrome.. In: Slice, DE., editor. *Modern Morphometrics in Physical Anthropology*. Kluwer Academic/Plenum Publishers; New York: 2005. p. 187-212.
- Rohlf FJ, Slice D. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* 1990; 39:40–59.
- Singh N, Harvati K, Hublin JJ, Klingenberg CP. Morphological evolution through integration: a quantitative study of cranial integration in *Homo*, *Pan*, *Gorilla* and *Pongo*. *J. Hum. Evol.* 2012; 63:155–164. [PubMed: 22178399]

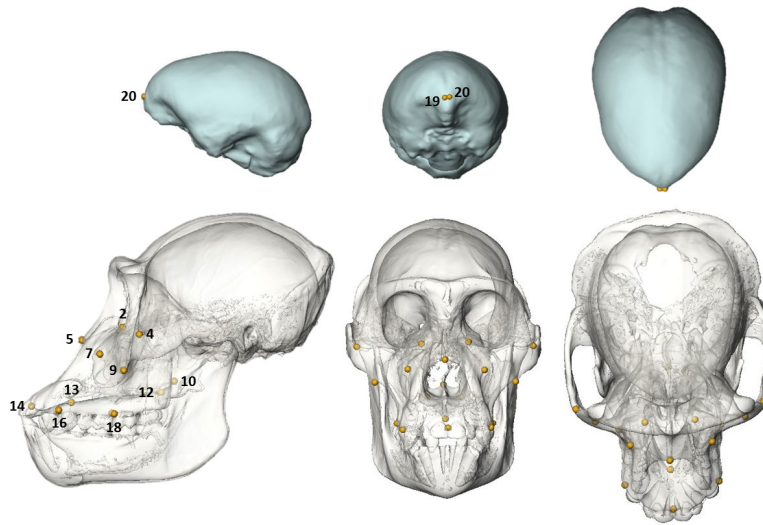


Figure 1. Three-dimensional landmarks recorded on the skull and endocranial surface of adult *Gorilla beringei graueri*. See Table 1 for the definition of the landmarks.

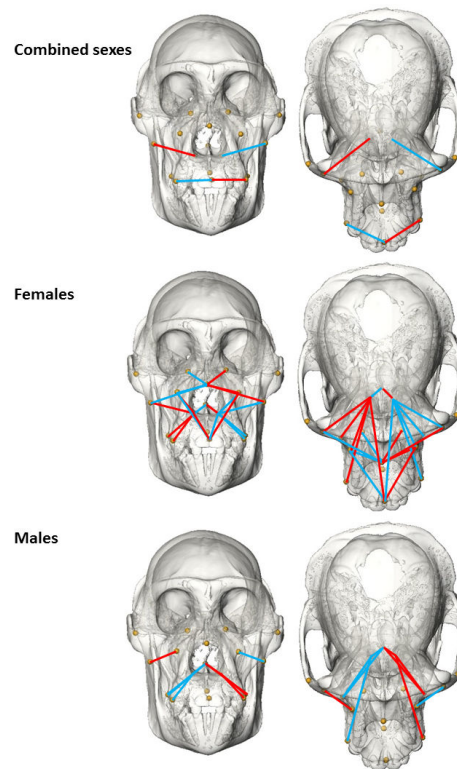


Figure 2. Directional asymmetry of the mid-face of *Gorilla beringei graueri* as measured using EDMA. The anterior and superior views are represented for combined sexes, females, and males. Distances significantly larger on one side are in red, the corresponding distances shorter on the other side are in blue. See Table 1 and Figure 1 for the definition of the landmarks. Females display 10 linear measurements associated with significant DA and males display five linear measurements.

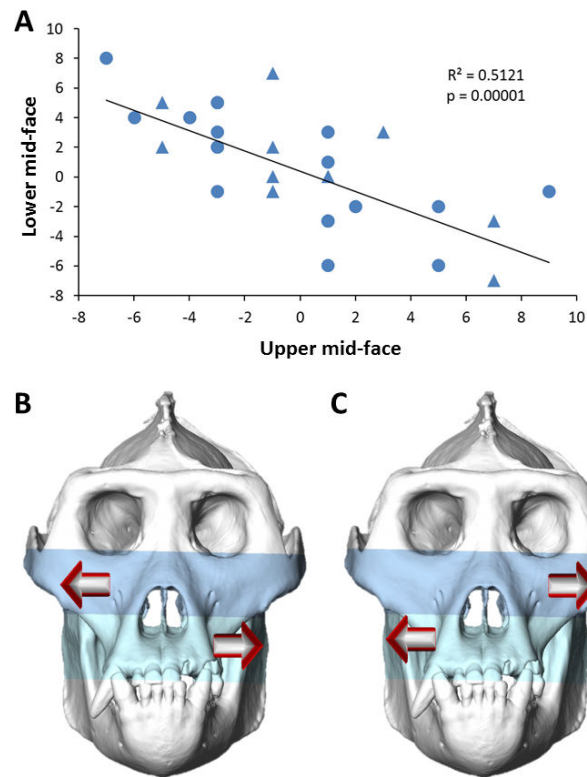


Figure 3.

The asymmetric relationship between the upper and lower mid-face of *Gorilla beringei graueri*. (A) Correlation between the direction of upper and lower midfacial asymmetries. Females and males are represented by circles and triangles, respectively. Positive x and y values indicate a larger right side for the upper and lower mid-face, respectively. Note that several specimens have the same coordinates. (B) Association between a larger right side of the upper mid-face and a larger left side of the lower mid-face. (C) Association between a larger left side of the upper mid-face and a larger right side of the lower mid-face.

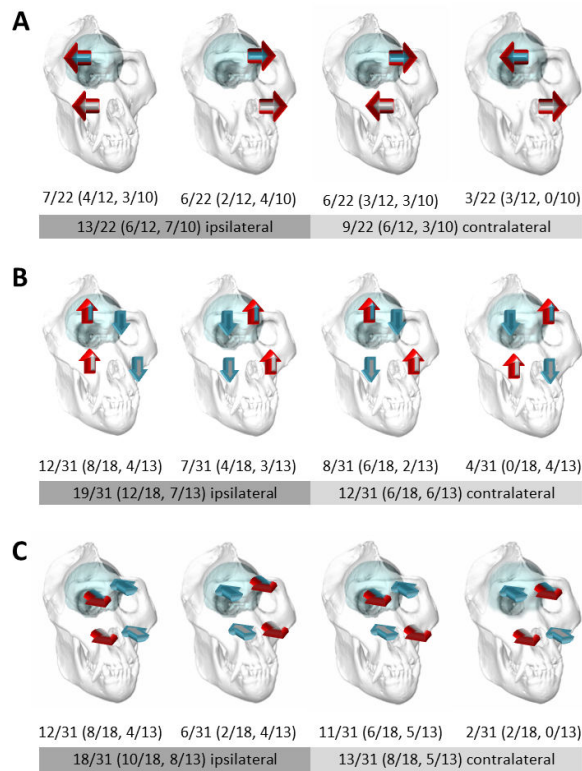


Figure 4.

Illustration of the relationship between frontal petalia and midfacial asymmetries in three dimensional space (A, lateral; B, vertical; C, antero-posterior). Arrows indicate the direction of the asymmetries (blue, cerebral asymmetries; grey, midfacial asymmetries). Proportions for each configuration are reported for combined sexes and between brackets for females and males (F, M). Because some specimens did not display midfacial asymmetries when measured qualitatively, the number of specimens studied in the present analysis is different from the number of specimens included in the original sample ($N = 32$).

Table 1

Landmark definition.

Landmark	Landmark definition	Anatomical region
1, 2	Dacryon (R, L)	Upper mid-face
3, 4	Anterior-most point on zygomatic branch (R, L)	Upper mid-face
5	Nasale	Upper mid-face
6, 7	Foramen infra-orbital, most superior (R, L)	Upper mid-face
8, 9	Anterior-most attachment of the masseter (R, L)	Upper mid-face
10	Posterior nasal spine	Lower mid-face
11, 12	Palatine canal (R, L)	Lower mid-face
13	Incisor canal	Lower mid-face
14	Prosthion	Lower mid-face
15, 16	Post-canine (R, L)	Lower mid-face
17, 18	Post-first molar (R, L)	Lower mid-face
19, 20	Most protruding areas of frontal lobe (R, L)	Frontal lobe

Table 2

Procrustes ANOVA tests.

	Effect	Sum of Squares	Mean Squares	df	F	<i>p</i>
Mid-face	Combined (N=32)					
	Individual	0.27965	0.000361	775	9.20	<0.0001
	Side (DA)	0.00105	0.000048	22	1.22	0.2211
	Individual*Side (FA)	0.02675	0.000039	682	22.79	<0.0001
	Residual (error)	0.00259	0.000002	1504		
	Females (N=18)					
	Individual	0.11376	0.000268	425	8.53	<0.0001
	Side (DA)	0.00083	0.000038	22	1.20	0.2457
	Individual*Side (FA)	0.01174	0.000031	374	18.66	<0.0001
	Residual (error)	0.00142	0.000002	846		
	Males (N=14)					
	Individual	0.09809	0.000302	325	6.33	<0.0001
	Side (DA)	0.00170	0.000077	22	1.63	0.0401
Individual*Side (FA)	0.01363	0.000048	286	26.99	<0.0001	
Residual (error)	0.00118	0.000002	658			
Upper Mid-face	Combined (N=32)					
	Individual	0.23708	0.000765	310	8.19	<0.0001
	Side (DA)	0.00079	0.000079	10	0.85	0.5795
	Individual*Side (FA)	0.02893	0.000093	310	21.02	<0.0001
	Residual (error)	0.00284	0.000004	640		
	Females (N=18)					
	Individual	0.10545	0.000620	170	8.68	<0.0001
	Side (DA)	0.00168	0.000117	10	1.63	0.1007
	Individual*Side (FA)	0.01215	0.000071	170	16.40	<0.0001
	Residual (error)	0.00157	0.000004	360		
	Males (N=14)					
	Individual	0.10883	0.000837	130	7.15	<0.0001
	Side (DA)	0.00126	0.000126	10	1.08	0.3848
Individual*Side (FA)	0.01521	0.000117	130	25.68	<0.0001	
Residual (error)	0.00128	0.000005	280			
Lower Mid-face	Combined (N=32)					
	Individual	0.18760	0.000550	341	8.08	<0.0001
	Side (DA)	0.00088	0.000098	9	1.44	0.1704
	Individual*Side (FA)	0.01900	0.000068	279	17.34	<0.0001
	Residual (error)	0.00251	0.000004	640		
	Females (N=18)					
	Individual	0.07685	0.000411	187	8.09	<0.0001
	Side (DA)	0.00088	0.000097	9	1.92	0.0530
	Individual*Side (FA)	0.00777	0.000051	153	13.70	<0.0001

Effect	Sum of Squares	Mean Squares	df	F	p
Residual (error)	0.00133	0.000004	360		
Males (N=14)					
Individual	0.05860	0.000410	143	4.86	<0.0001
Side (DA)	0.00143	0.000159	9	1.89	0.0606
Individual*Side (FA)	0.00986	0.000084	117	19.91	<0.0001
Residual (error)	0.00119	0.000004	280		

Individual effects represent overall variation in the dataset. 'Side' is the measure for directional asymmetry (DA). 'Individual*Side' is the measurement for fluctuating asymmetry (FA).

'Residual' is the measurement error calculated from the variation among repeat measurements.

'df' is degrees of freedom, 'F' F statistic, and 'p' p-value.