

Supplementary Materials for

Evolution of brain lateralization: A shared hominid pattern of endocranial asymmetry is much more variable in humans than in great apes

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Other Supplementary Material for this manuscript includes the following:

(available at advances.sciencemag.org/cgi/content/full/6/7/eaax9935/DC1)

Movie S1 (.mp4 format). Shared directional shape asymmetry.

Movie S2 (.mp4 format). Human-specific asymmetry patterns.

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FIGURES

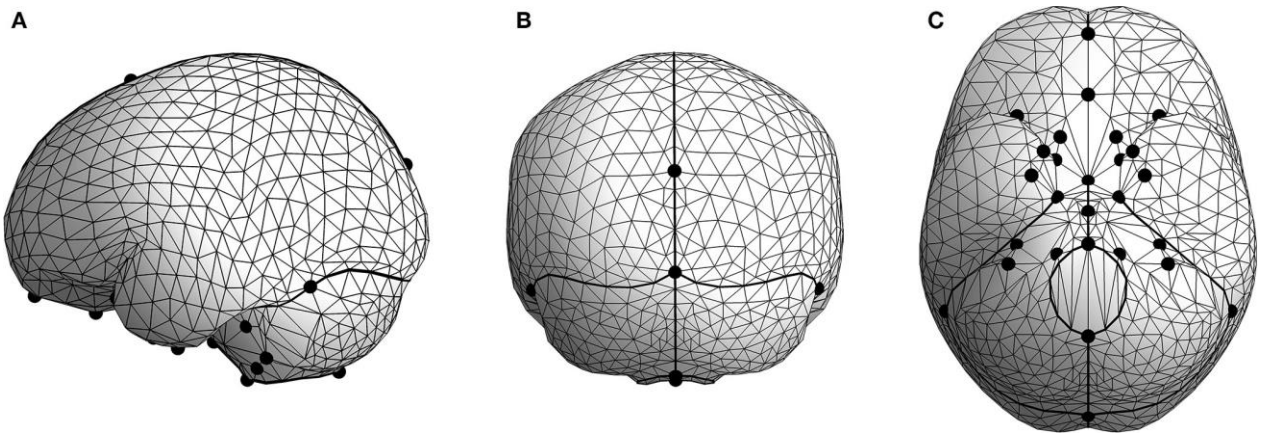


Fig. S1. Endocranial landmark set shown as triangulated surface mesh, including 29 landmarks (spheres), 110 semilandmarks along curves (black lines), and 796 surface semilandmarks (vertices of the mesh). **(A)** Left lateral, **(B)** occipital and **(C)** inferior view.

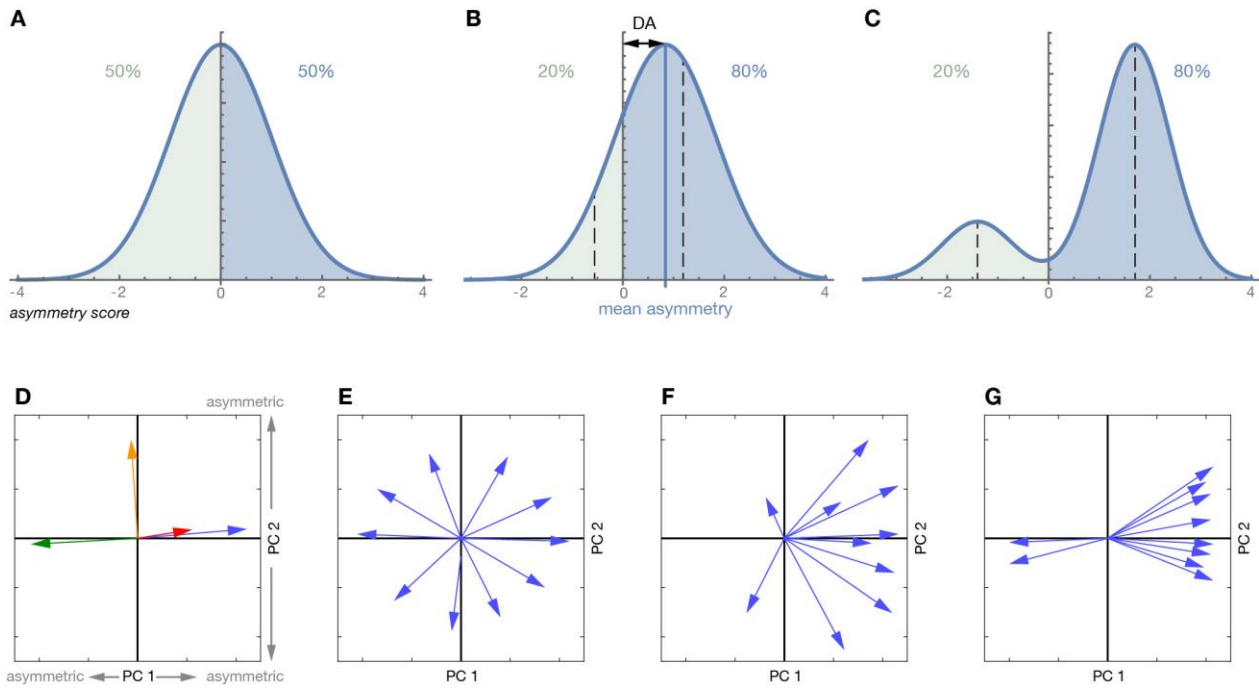


Fig. S2. Classic types of asymmetry and shape asymmetry. (A-C) illustrate the three classic types of asymmetry for a single trait. (A) The distribution of an asymmetry score (difference between left and right trait expression) is unimodal and symmetric, with a mean close to zero, implying that one half of the population shows the opposite asymmetry pattern than the other half (positive versus negative asymmetry scores; blue and green areas, respectively). The individual variation of asymmetry about the symmetric population mean is commonly referred to as “fluctuating asymmetry.” (B) Unimodal distribution of asymmetry scores with a mean deviating clearly from zero. Most individuals (80% in this illustration) have positive asymmetry scores (blue area); only few (20%) show a reversed asymmetry pattern (negative scores, green area). The deviation of the average asymmetry score from zero is referred to as “directional asymmetry.” Individual variation in asymmetry can thus be decomposed into a directional component and a fluctuating component (individual variation around the asymmetric population mean). Note that because of the mean shift, the average *magnitude* of asymmetry (average absolute asymmetry score) in individuals with negative scores is smaller than that in individuals with positive scores (0.56 versus 1.19, the dashed lines in panel B). (C) Asymmetry has a bimodal distribution, indicating that two subgroups differ in their (epi)genetic control of bilateral development, leading to opposite patterns of directional asymmetry. Note that the bimodal distribution leads to a higher average magnitude of asymmetry in individuals with negative scores (1.40, left dashed line) than in panel B). (D-G) illustrate how to interpret the adjusted PCA to investigate multivariate shape asymmetry (see Methods). (D) Each arrow represents the deviation from symmetry (the origin of the coordinate system) for one individual: the blue and red individuals have a similar spatial pattern but different magnitude of asymmetry; the green individual has the same spatial pattern as the blue and red individuals but reversed in direction; the orange individual shows a different spatial pattern of asymmetry than the other individuals. (E) A sample of individuals with large variation of asymmetry without any directionality (“fluctuating asymmetry”). (F) This sample shows a directionality of asymmetry; the average asymmetry pattern (“directional asymmetry”) closely aligns with PC 1. 80% of individuals share the same direction along PC 1, while

20% show the reversed pattern with a lower magnitude (compare to panel B). The asymmetry pattern captured by PC 2 is not directed (50% show positive scores, 50% show negative scores). (G) 80% of individuals share a similar asymmetry pattern captured by PC 1, while 20% show the reversed pattern with a comparable magnitude (bimodal distribution, compare to panel C).

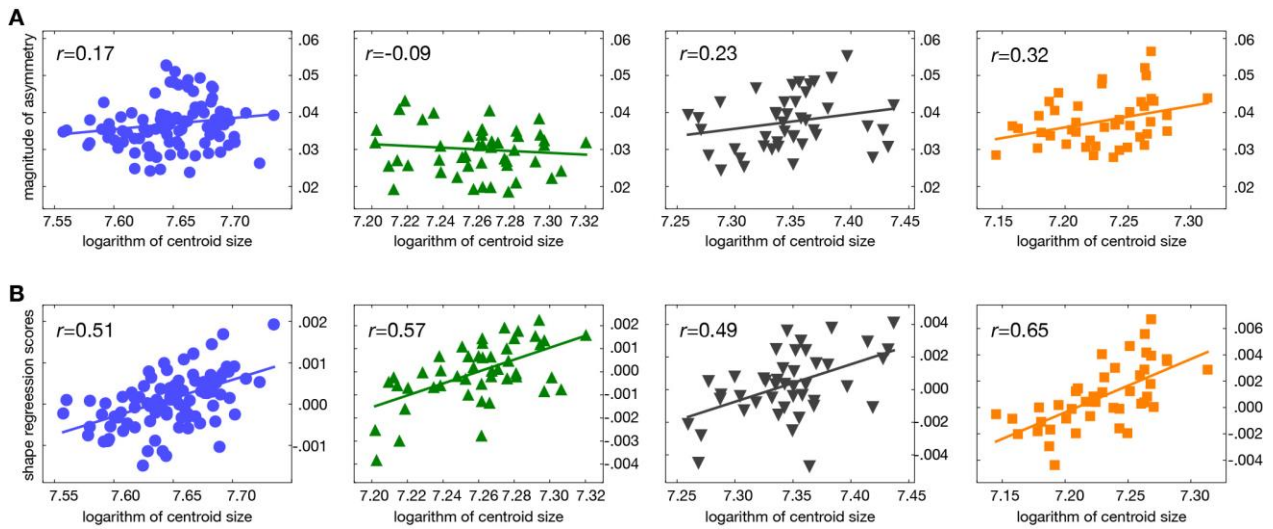


Fig. S3. Relationship of shape asymmetry and endocranial size. (A) Correlation (r) of the magnitude of total asymmetry and the logarithm of centroid size. (B) Correlation (r) of shape regression scores and the logarithm of centroid size. Humans ($n=95$) shown in blue (circles), chimpanzees ($n=47$) in green (up triangles), gorillas ($n=43$) in black (down triangles), and orangutans ($n=43$) in orange (squares).

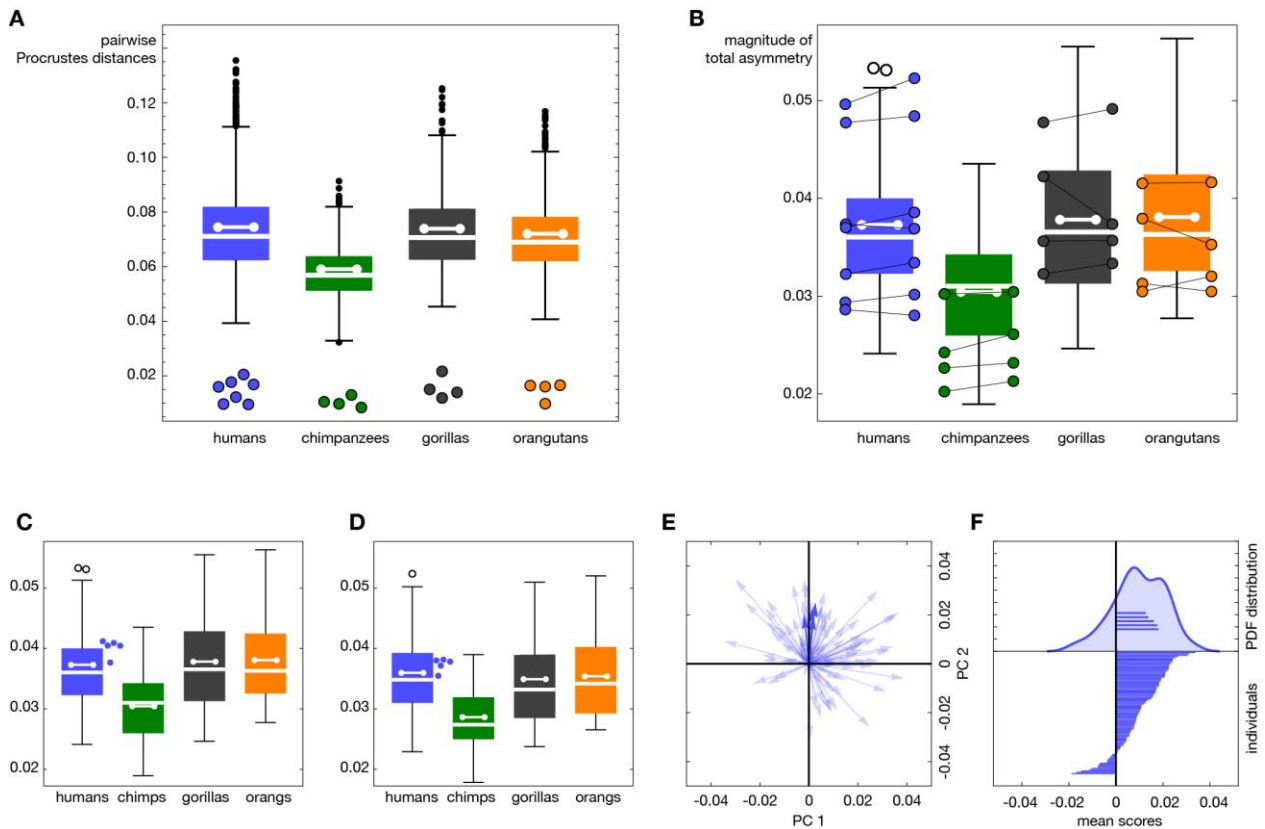


Fig. S4. Measurement error in repeated measurements analyses. (A, B) Analysis of two measurements for 19 individuals (seven humans and four individuals for each non-human taxon): (A) Measurement error (Procrustes distance between repeated measurements) compared to Box-Whisker plots of pairwise Procrustes distances between different individuals. (B) Magnitude of total asymmetry of the entire samples with magnitudes of asymmetry of pairs of repeated measurements. (C-F) Analysis of five measurements for one human individual (represented by five points, arrows, or lines, respectively): (C) Magnitude of total asymmetry. (D) Magnitude of fluctuating asymmetry. (E) Human taxon-specific principal component analysis of endocranial shape asymmetry. PC 1 versus PC 2. (F) Human taxon-specific mean asymmetry scores.

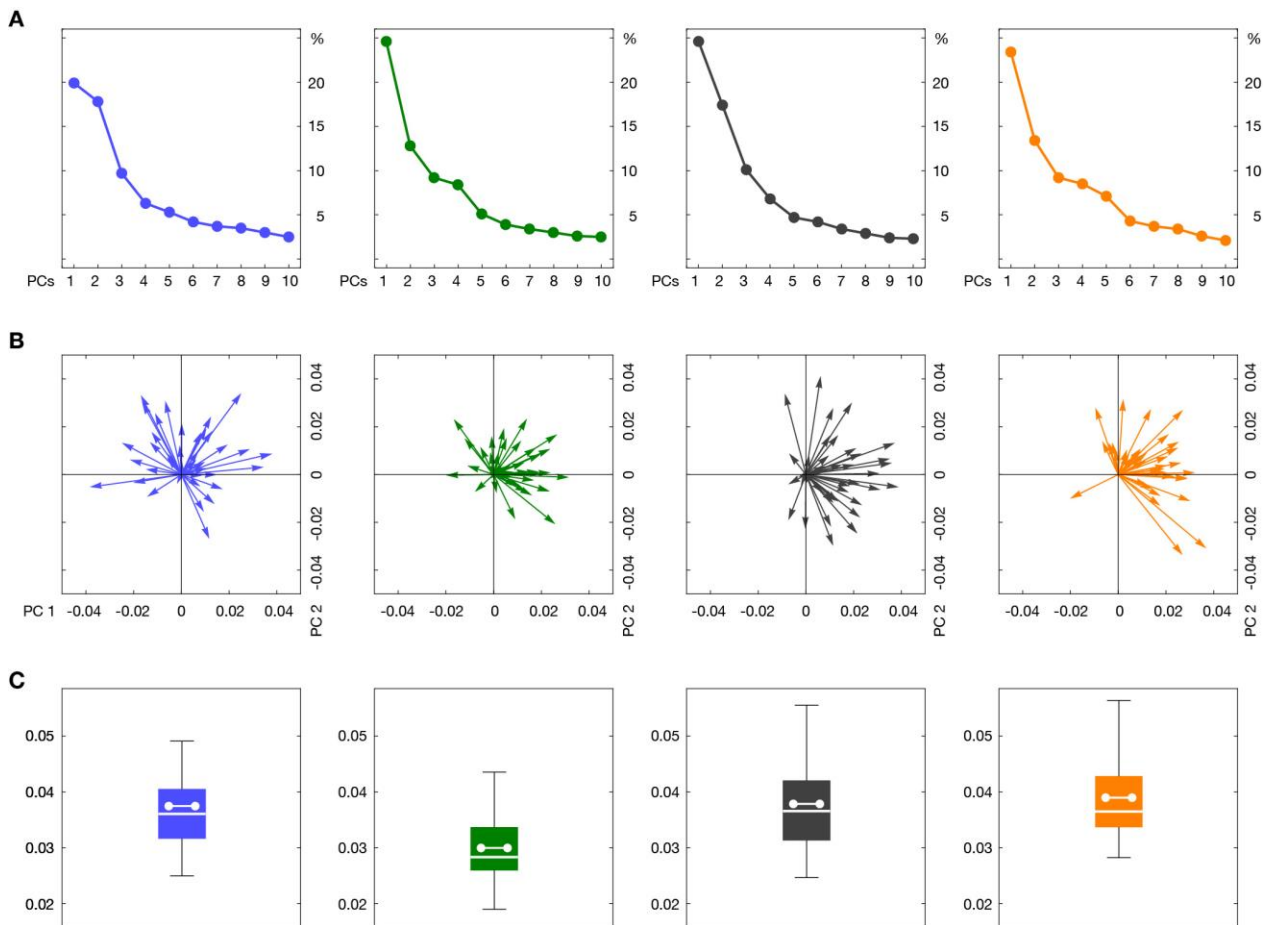


Fig. S5. Effects of sample size and composition. Analysis based on a random subsample of 39 humans (blue), a random subsample of 39 *Pan troglodytes* (green), a random subsample of 39 *G. gorilla* (black), and the subsample of 39 *Pongo pygmaeus* (orange). **(A)** Scree plots for taxon-specific principal component analyses of shape asymmetry display the portion of variance explained by PCs 1-10. **(B)** Taxon-specific principal component (PC) analyses of endocranial shape asymmetry. For each taxon, PC 1 versus PC 2 is shown. PC scores shown as arrows, representing deviations from symmetry (which corresponds to the origin of the coordinate system). **(C)** Magnitude of shape asymmetry (Box-Whisker plots by species). Whiskers show the range, box and white line the three quartiles, and the dumbbell represents the average.

TABLES

Table S1. Descriptive statistics of PCA for the first five principal components (PCs 1-5) of endocranial shape asymmetry (as presented in Fig. 2b), for the first five taxon-specific principal components (PCs 1-5) of endocranial shape asymmetry (as presented in Fig. 4c-e) as well as for the individual scores along the mean asymmetry vector (as presented in Fig. 4a): explained variance of total variance; directionality, i.e., frequencies of arrows with positive PC scores (pointing to the right when plotted on the x-axis), and frequencies of arrows with negative PC scores (pointing to the left), mean length of arrows (i.e., average magnitude of asymmetry) for individuals with positive and negative PC scores, respectively, as well as their ratio.

	explained variance	directionality		magnitude		+/- ratio
		positive	negative	positive	negative	
pooled sample						
PC 1	18.8%	174 (76.3%)	54 (23.7%)	0.0144	-0.0079	1.8
PC 2	13.8%	127 (55.7%)	101 (44.3%)	0.0118	-0.009	1.3
PC 3	8.5%	113 (49.6%)	115 (50.4%)	0.0089	-0.0084	1.1
PC 4	6.0%	106 (46.5%)	122 (53.5%)	0.0072	-0.0075	1.
PC 5	5.3%	122 (53.5%)	106 (46.5%)	0.0064	-0.007	0.9
humans						
mean asymmetry		79 (83.2%)	16 (16.8%)	0.0133	-0.0073	1.8
PC 1	18.8%	62 (65.3%)	33 (34.7%)	0.0141	-0.0108	1.3
PC 2	17.5%	71 (74.7%)	24 (25.3%)	0.0132	-0.0112	1.2
PC 3	9.2%	49 (51.6%)	46 (48.4%)	0.0096	-0.0089	1.1
PC 4	5.5%	51 (53.7%)	44 (46.3%)	0.0068	-0.0076	0.9
PC 5	4.7%	51 (53.7%)	44 (46.3%)	0.0067	-0.0064	1.1
chimpanzees						
mean asymmetry		41 (87.2%)	6 (12.8%)	0.0125	-0.0035	3.6
PC 1	21.8%	39 (83.%)	8 (17.%)	0.0127	-0.0084	1.5
PC 2	13.4%	26 (55.3%)	21 (44.7%)	0.0099	-0.0069	1.4
PC 3	11.5%	31 (66.%)	16 (34.%)	0.0092	-0.0063	1.5
PC 4	7.4%	24 (51.1%)	23 (48.9%)	0.0058	-0.0074	0.8
PC 5	4.8%	21 (44.7%)	26 (55.3%)	0.0059	-0.0046	1.3
gorillas						
mean asymmetry		39 (90.7%)	4 (9.3%)	0.0166	-0.0038	4.4
PC 1	24.3%	36 (83.7%)	7 (16.3%)	0.0172	-0.0072	2.4
PC 2	18.2%	25 (58.1%)	18 (41.9%)	0.0146	-0.0106	1.4
PC 3	9.8%	26 (60.5%)	17 (39.5%)	0.0108	-0.0068	1.6
PC 4	6.1%	17 (39.5%)	26 (60.5%)	0.0084	-0.0079	1.1
PC 5	5.0%	24 (55.8%)	19 (44.2%)	0.0067	-0.0074	0.9
orangutans						
mean asymmetry		39 (90.7%)	4 (9.3%)	0.0160	-0.0051	3.2

PC 1	22.0%	35 (81.4%)	8 (18.6%)	0.017	-0.0061	2.8
PC 2	14.4%	29 (67.4%)	14 (32.6%)	0.0116	-0.0103	1.1
PC 3	9.0%	20 (46.5%)	23 (53.5%)	0.0109	-0.0073	1.5
PC 4	8.3%	20 (46.5%)	23 (53.5%)	0.008	-0.0096	0.8
PC 5	6.6%	23 (53.5%)	20 (46.5%)	0.007	-0.0078	0.9

Table S2. Symmetric and asymmetric variance in units of squared Procrustes distance per taxon.

	humans	chimpanzees	gorillas	orangutans
total shape variance	0.0028	0.0017	0.0027	0.0026
symmetric shape variance	0.0025 (88.2%)	0.0015 (87.6%)	0.0024 (88.4%)	0.0023 (87.4%)
asymmetric shape variance	0.0003 (11.9%)	0.0002 (12.4%)	0.0003 (11.6%)	0.0003 (12.6%)

Table S3. Magnitudes of sample asymmetries decomposed into directional and fluctuating components with uncorrected p -values (F -test) for the directional asymmetry (DA) component.

	humans	chimpanzees	gorillas	orangutans
n	95	47	43	43
total variance	0.13337	0.04418	0.06251	0.06302
DA variance	0.00924 (6.9%)	0.00515 (11.7%)	0.00924 (14.8%)	0.00850 (13.5%)
FA variance	0.12413 (93.1%)	0.03903 (88.3%)	0.05327 (85.2%)	0.05456 (86.5%)
DA significance	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$

Table S4. Variance of shape asymmetry explained by log centroid size, with P values (permutation test) for the variance explained.

	expl. variance	p -value
pooled sample	3.3%	<0.01
humans	2.9%	0.12
chimpanzees	1.2%	0.57
gorillas	5.4%	0.14
orangutans	10.6%	0.03

Table S5. Descriptive statistics of absolute deviations from symmetry for all landmarks and semilandmarks by taxon. Maximal values are found in the occipital region in all of the taxa.

	mean	standard deviation	maximum
humans	1.14 mm	0.61 mm	5.76 mm
chimps	0.62 mm	0.35 mm	3.61 mm
gorillas	0.84 mm	0.48 mm	5.61 mm
orangutans	0.76 mm	0.42 mm	3.95 mm

MOVIES

Movie S1. Shared directional shape asymmetry pattern (PC 1 of endocranial shape asymmetry, as presented in Figure 3). The deformation from a symmetric endocranial shape represents the spatial pattern of shape asymmetry; orange surfaces have larger areas as compared to the other side, blue surfaces have smaller areas. The movie shows the deformation from a symmetric shape to the asymmetric shape in different views.

Movie S2. Human-specific asymmetry patterns: mean asymmetry pattern (i.e., directional asymmetry), and PC 1 and PC 2 of shape asymmetry, compared to the shared asymmetry pattern (PC 1 of pooled sample). The deformation from a symmetric endocranial shape represents the spatial pattern of shape asymmetry; orange surfaces have larger areas as compared to the other side, blue surfaces have smaller areas. The movie shows the deformation from a symmetric shape to the asymmetric shape in different views.

Movie S3. Chimpanzee-specific asymmetry patterns: mean asymmetry pattern (i.e., directional asymmetry), and PC 1 and PC 2 of shape asymmetry, compared to the shared asymmetry pattern (PC 1 of pooled sample). The deformation from a symmetric endocranial shape represents the spatial pattern of shape asymmetry; orange surfaces have larger areas as compared to the other side, blue surfaces have smaller areas. The movie shows the deformation from a symmetric shape to the asymmetric shape in different views.

Movie S4. Gorilla-specific asymmetry patterns: mean asymmetry pattern (i.e., directional asymmetry), and PC 1 and PC 2 of shape asymmetry, compared to the shared asymmetry pattern (PC 1 of pooled sample). The deformation from a symmetric endocranial shape represents the spatial pattern of shape asymmetry; orange surfaces have larger areas as compared to the other side, blue surfaces have smaller areas. The movie shows the deformation from a symmetric shape to the asymmetric shape in different views.

Movie S5. Orangutan-specific asymmetry patterns: mean asymmetry pattern (i.e., directional asymmetry), and PC 1 and PC 2 of shape asymmetry, compared to the shared asymmetry pattern (PC 1 of pooled sample). The deformation from a symmetric endocranial shape represents the spatial pattern of shape asymmetry; orange surfaces have larger areas as compared to the other side, blue surfaces have smaller areas. The movie shows the deformation from a symmetric shape to the asymmetric shape in different views.